

**Functional trait-based  
approaches to disentangle the  
complex mechanisms  
underlying plant diversity  
organization**

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KEITA NISHIZAWA

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# **Functional trait-based approaches to disentangle the complex mechanisms underlying plant diversity organization**

## **Abstract**

“How the plant communities are assembled.” This has been the central theme of community ecology for more than a century and is essential to understand biodiversity. The interactions of a variety of ecological and non-ecological processes contribute to multi-plant species assemblages (community) at the local scale. To understand the enigma of biodiversity, disentangling the factors shaping the local scale plant assemblages (community) is essential. In chapter 1, I have discussed how functional traits help explain existing diversity patterns (environment, space, and time) generated through mutually correlating processes (abiotic, biotic, disturbance, dispersal, and stochastic).

Even though the processes are the same, the importance is highly variable among regions. In chapter 2, I have tried to assess how herbivory (disturbance) and nutrient cycling affect plant diversity in extremely nutrient-limited high-Arctic wetlands. Here, wetland sites, where geese have been almost absent for at least 50 years (Pond Inlet), were compared to nearby sites, where geese are abundant but have been excluded experimentally by cages and where the ground has been experimentally fertilized for over 16 years (Bylot Island). From the community composition and weighted mean functional trait values, I could disentangle the direct disturbance and indirect fertilization effects. Long-term goose disappearance likely alters the competitive relationships between three dominant plant species. Taken together, the direct effects of goose herbivory on vegetation are more profound than their indirect effects, through an alternation of nutrient cycling in nutrient-limited Arctic wetlands.

Spatial factors are also important for plant distribution and diversity patterns. Even if the given environmental conditions are suitable for

certain species, they cannot establish in place when they cannot disperse. In chapter 3, by using dispersal related functional traits, I have tried to detect how dispersal processes influence plant community structure. The study site, patchy tundra vegetation, is suitable for testing the importance of dispersal processes. Here, I researched 433 vegetation patches (separate from each other) in a patchy tundra vegetation in northern Canada at three spatial scales (150 m, 2 km, and 10 km). The results showed that dispersal abilities were related to existing plant patterns. This could be because harsh arctic environmental conditions strictly sort the species, and its importance becomes much higher.

The third study site is the Shiretoko National Park cool-temperate forest. This site has a high abundance of deer. Contrary to high arctic areas, these temperate forests are characterized by substantial water, nutrients, and growing seasons. In Chapter 4, I assessed the effects of over- and no-grazing on the mechanisms of plant community assembly. By comparing the control with enclosure plots, vegetation coverage was found to be considerably lower, while species richness and diversity were higher in the plot with herbivory. Functional traits associated with competitive ability (leaf area and chlorophyll content) were significantly higher in the enclosure plot. The results emphasized that, although over-abundance of deer is of concern, without-deer had negative effects on plant diversity through competitive dominance.

Temporal factors are also important for plant distribution and diversity patterns. Temporal dynamics of a community are usually related to disturbance processes. However, they are not well synthesized since the effect of disturbance is depends on the types of disturbance, the strength and length. In chapter 5, by focusing on the different two types of disturbance “press” and “pulse”, I addressed how these types of the different affects the community dynamics. Here, I used six years of understory vegetation dynamics data under press (deer herbivory) and pulse (rodent outbreak herbivory) disturbance at the Shiretoko. The results showed that deer and rodent herbivory had opposite effects on plant community dynamics. The effects of press disturbance on existing community patterns (i.e., community weighted mean) were considerably higher. By assessing the temporal dynamics at plot scale (IWM, DWM), we could detect the opposite effects of existing patterns generated by stable conditions (no and press disturbance).

Ecologists are eagerly seeking general theories, but these do not necessarily solve every ecological issue. A lot of unique systems in nature and complex ecological systems remain unknown. To understand the diversity

formation and maintenance mechanisms in focal systems, we need to carefully gather information to deal with each ecological issue. In chapter 6, I outlined some of the results presented in former chapters, and discussed how functional traits contribute to disentangle the focal community assembly processes in three existing diversity generating patterns. In addition, I propose the use of functional traits in future studies.

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## **Author List**

Lucas Deschamps, Vincent Maire, Joël Bêty, Esther Lévesque, Ryo Kitagawa, Shota Masumoto, Isabelle Gosselin, Amélie Morneault, Line Rochefort, Gilles Gauthier, Yukiko Tanabe, Masaki Uchida and Akira S Mori contributed to chapter 2, Ryo Kitagawa, Shota Masumoto, Masaki Uchida, Marc W. Cadotte, Akira S. Mori contributed to chapter 3, Shinichi Tatsumi, Ryo Kitagawa, Akira S. Mori contributed to Chapter 4 and Akira S. Mori contributed to Chapter 5.

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# 1

## General Introduction

### 1.1 Introduction

“How the plant communities are assembled.” This has been the central theme of community ecology for more than a century and is essential to understand biodiversity. Ecologists have recently started paying greater attention to biodiversity issues (Millennium Ecosystem Assessment, 2005; Cardinale et al. 2012). Knowing what mechanisms generate and maintain biodiversity is important to solve fundamental questions of nature, and to formulate conservation strategies.

It is a general principle in ecology that two species competing for the same resource cannot coexist; this is known as competitive exclusion (Gause, 1934). Plants are known to require almost the same resources, such as water, light, and inorganic nutrients. However, there is a surprisingly high diversity of plant species, with approximately 400,000 species worldwide (Christenhusz and Byng, 2016). What generates such high diversity? Many plant species coexist, with no prevailing single competitor even in small spatial scales, which is close enough to enable interaction. A variety of ecological and non-ecological processes, and interactive effects contribute to multi-plant species assemblages (community) at the local scale. To understand the enigma of biodiversity, disentangling the factors shaping local scale plant assemblages (community) is essential.

Ecologists have tried to explain plant community differences by the heterogeneity of environmental conditions from the view of the diversified forms of plants, called niche partitioning (Hutchinson, 1957; Adler et al., 2013).

Although almost all plant species use similar resources, their preferences and performances are divided along the multi-dimensional axes. There are numerous variations in habitat conditions in nature. The combinations of various factors include temperature, humidity, nutrients, disturbances, and multi-trophic interactions. The differences in preferred environment between species (niche difference) are thought to contribute to preventing competitive exclusion and maintaining diversity (Chesson, 2000; Adler et al., 2007).

In addition, spatial differences are also important factors in generating and maintaining local plant diversity. Plants are organisms that cannot move after establishment; even if the habitat conditions are suitable for certain species, they cannot establish there without dispersal. The order of arrival, which is related to demographic stochasticity, is also important for plant establishment (Fukami et al., 2005). In practice, it is known that similarity in community compositions decreases with increasing spatial distance (Tobler, 1970; Okimura et al., 2016). Thus, the differences in location (spatial separation) are also important in generating and maintaining plant diversity.

Considering temporal differences offers us another diversity generating mechanism at the same places (Adler et al., 2006). Environmental conditions change over time. This kind of environmental heterogeneity contributes to plant diversity through temporal niche partitioning (Beisner, 2001; Lundholm and Larson, 2003). The differences in life history between plant species also contribute to temporal coexistence. Known as competition-colonization tradeoff, species with weak competitive ability are excluded by superior competitive species, but since they have high colonization (dispersal) ability, they can establish in advance when competitive superior species dies (Platt, 1975; Cadotte et al., 2006). These temporal fluctuations in a community are also important for plant diversity.

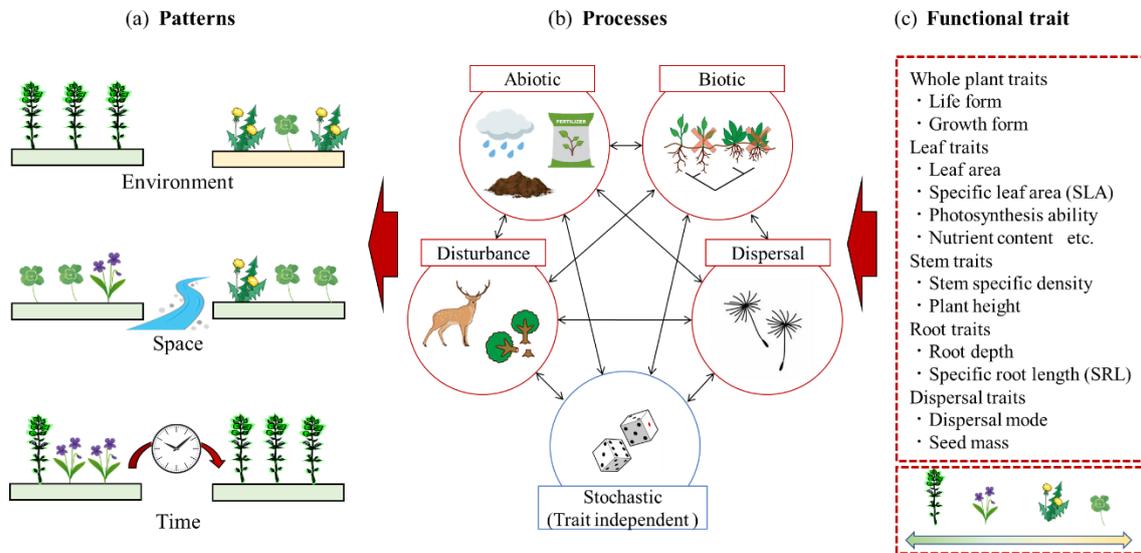


Fig. 1.1

The differences in community compositions that contribute to maintaining biodiversity are classified into three patterns—environmental, spatial, and temporal differences. To understand the mechanisms that generate such community differences, we need to consider the processes that contribute to generate these patterns, which include abiotic, biotic, disturbance, dispersal, and stochastic processes. Functional traits are important to understand what processes contribute to the community patterns. Abiotic, biotic, disturbance, and dispersal processes are related to functional traits. Simply considering these factors are not enough. All processes are mutually influencing, and combinations of these factors contribute to preventing the domination of certain species and maintaining plant diversity.

The mechanisms contributing to the maintenance of plant diversity are theoretically divided into three patterns (Fig1.1-a), differences in site conditions (environmental differences), location (spatial differences), and time (temporal differences). These existing patterns of community differences are the results of various ecological processes that influence plant community compositions (Fig. 1.1-b). This includes abiotic (differences in temperature, nutrients, and water), biotic (competition and facilitation), disturbance, dispersal (Crawley, 1997; Gurevitch, 2006), and stochastic processes (Simberloff, 1979; Chase & Leibold, 2003). These all processes are mutually influential, and combinations of these factors contribute to existing plant diversity. Furthermore, the relative

importance of these processes can vary between regions and study scales. For example, the importance of abiotic processes could be higher in temperate than in tropical regions (Myers et al., 2013). If there are influential herbivores, the plant community largely reflects the effect of herbivory (Côté et al., 2004). The spatial scales of the studies also change the relative importance of ecological processes. It is known that as spatial scale increases, dispersal processes become more important (Chase et al., 2014). To understand what promotes the existing plant diversity patterns, we need to carefully consider what processes are important in target regions and scales.

To detect the dominating processes, comparing the community with target processes is an effective method. Traditionally, ecologists have sought the dominant processes from the comparison of species richness and taxonomic structure of communities (Fig. 1.2). Although we can detect the changes in community structure only from taxonomic information, mechanistic information is limited. In recent years, the adaptation of functional trait-based approach is prevailing rapidly (Fig. 1.3). Functional traits are ecological features of the species; these are defined as morphological, physiological, or phenological measurable features in plants that can potentially affect individual performance, organism fitness, and life history strategy (Violle et al., 2007; Cadotte et al., 2011). These traits provide information such as the strength of competition under certain environmental conditions (Cadotte and Tucker, 2017), the species response to disturbances (Mouillot et al., 2013), and dispersal ability (Vittoz & Engler, 2007). By considering some differences in community patterns and functional trait (Fig. 1.3), we could acquire the mechanistic links between underlying processes and plant biodiversity (McGill et al., 2006; Westoby & Wright, 2006).

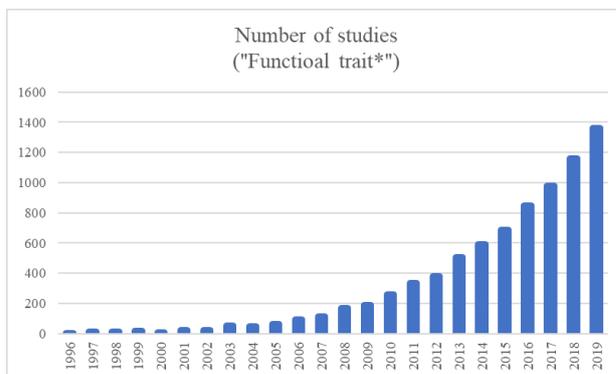


Fig. 1.2  
The number of studies searched by "Functional trait" at Web of Science in 2020/07/13. This indicates that studies of community assembly using functional traits has been rapidly increasing in the last ten years.

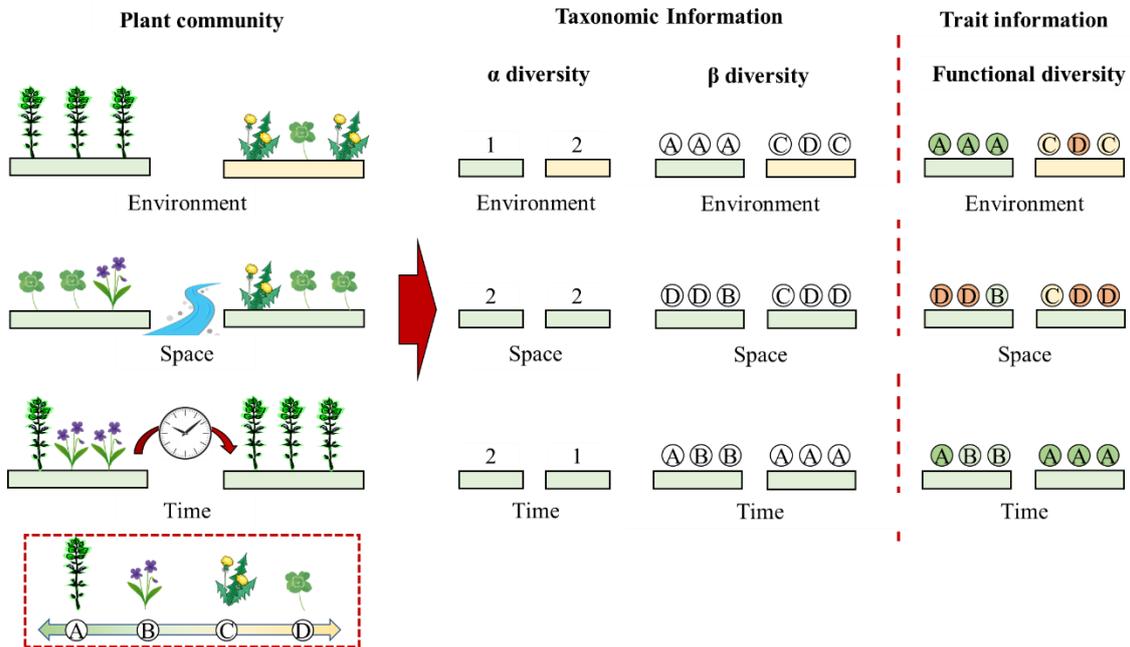


Fig. 1.3

Comparison of plant communities to distinguish factors that contribute in community differences. (a) is the comparison of environmentally different communities; (b) is comparison of spatially different but environmentally same communities; and (c) is the comparison of same communities observed in different times. Although methods using only species identities include  $\alpha$  diversity (species richness) and  $\beta$  diversity (species dissimilarity) can detect the community differences between conditions (environment, space, and time), considering species traits could give some mechanistic interpretation.

There is a need to assess the underlying processes carefully to understand the existing patterns of plant community and diversity by considering some site-specific differences. Ecological information greatly helps how the diversity were generated through mutually correlating processes. In this study, I introduced some of my empirical studies that address the mechanisms of diversity patterns from functional trait information.

I have focused on the diversity patterns generated by environmental differences in chapters 2 and 4, spatial differences in chapter 3, and temporal differences in chapter 5.

In Chapter 2, at extremely low-productivity high Arctic regions, I assessed the effects of long-term herbivory (disturbance) on plant communities

via changes in abiotic conditions (nutrient conditions), and the relationship of competition from the existing plant functional trait patterns. In Chapter 4, I assessed how the existence of disturbance influences plant diversity through competition and stochastic processes from functional dispersion patterns. In Chapter 3, I assessed how spatially separated patchy vegetations in sub-Arctic regions are generated. To test this, I adopted the traits related to dispersal ability. In Chapter 5, temporal diversity generating patterns were tested from the 6-year community dynamics patterns derived from 2 different types of disturbances—press and pulse. To address the mechanisms of temporal patterns, I assessed the temporal changes in community weighted mean trait values of plants through disturbances. Finally, in Chapter 6, I outlined how functional traits contribute to disentangle the focal community assembly processes in each of the three existing diversity generating patterns—differences in environment, space, and time. In addition, I propose the use of functional traits in future studies.

# 2

## **Long-term consequences of geese exclusion on nutrient cycling and plant community in the High-Arctic**

### **1. Introduction**

In recent years, behavior and distribution of herbivores have substantially changed in response to anthropogenic drivers such as global warming and land-use changes. As herbivores can profoundly affect their environment (Côté et al., 2004) it is becoming increasingly apparent that recent changes in their behavior and distribution might modify ecosystems (Noy-Meir, 1975; Mayer and Rietkerk, 2004; Beisner et al., 2003; Van der Wal, 2006). In the Arctic, because of the low primary productivity and the relatively short food chains (Ims and Fuglei, 2005), it is particularly concerned about the long-term influence of herbivores on terrestrial ecosystems (Kaarlejärvi et al., 2015). Although changes in herbivore activity in these high-latitude ecosystems can be often considerable (Barrio et al., 2016), there is still a knowledge gap to be filled.

Specifically, goose abundance has increased worldwide (Fox and Madsen, 2017) in response to changes in, for example, intensified agricultural practices and warming climate (Gauthier et al., 2005; Kéry et al., 2006; Fox and Abraham, 2017). The profound effects of geese on high-latitude ecosystems have been frequently reported (Gauthier et al., 1995; 2004; 2006; Ganter et al., 1996; Jefferies et al., 2004; Abraham et al., 2005; Alisauskas et al., 2006; Jasmin et al. 2008). Geese migrate to the region in summer to nest and rear young in graminoid-dominated nesting sites in mesic habitats surrounding ponds and

lakes (Gauthier et al., 1995; Jantunen et al., 2015). In these sites, nesting density can be often high (Reed et al., 2002), substantially altering plant community composition. In an extreme case, vegetation-free ecosystem states could emerge (Ganter et al., 1996; Zacheis et al., 2001; Jefferies and Rockwell, 2002; Jefferies et al., 2006; Peterson et al., 2013; 2014).

Not only do geese defoliate vegetation directly, but their feces can indirectly influence plant communities by changing nutrient cycling and plant-soil interactions (Bazely and Jefferies, 1985; Gauthier et al., 1996; Bardgett and Wardle, 2003). As a positive effect by geese, habitat enrichment via fecal material, rich in soluble nutrients include N and P, on nutrient cycles is well known (Ruess et al., 1989; Jefferies et al., 1994; Gauthier et al., 1996). Geese feces contains approximately 2 % Nitrogen (N) and 0.1 % Phosphorous (P) in the dry weight (Pouliot et al., 2009; Dessborn et al., 2016). In the Arctic, slow nutrient mineralization rates render soils low in nutrients, so that the effects of nutrient enrichment by geese can be pronounced (Jonasson et al., 1999; Sorensen et al., 2008). In contrast to these possible positive influences of geese on the environment, their overabundance could have negative consequences. There is a rich body of evidence showing that vertebrate herbivores, including mammals and birds, could reduce photosynthetic activity and litter supply of plants through grazing and browsing. These top-down effects have cascading effects on carbon and nutrient cycling by reducing supply of organic carbon to the soil and by decreasing abundance and activity of soil decomposers (Holt, 1997; Johnson and Matchett, 2001; Sankaran and Augustine, 2004). Especially in the nutrient-limited Arctic systems, such effects of abundant herbivores such as geese should be considerable.

While goose populations have been increasing globally, their local disappearance is also reported, especially near human settlements (Gagnon et al., 2009). Given adverse impacts of decrease or disappearance of herbivores on plant diversity and ecosystem functioning reported for different herbivore species (Nishizawa et al., 2016; Stokely and Betts, 2019), understanding the consequences of goose absence is as important as is appreciating the effects of their overabundance. This is especially true in the Arctic tundra, because of low nutrient availability to plants. Although several studies have simulated herbivore removal by establishing small-scale experimental exclosures, results are variable because of relatively short experimental duration. A serious knowledge gap exists for long-term effects of herbivore absence on nutrient cycling and resultantly

plant community composition in the Arctic.

In this study, I examine the long-term impacts of geese on tundra ecosystems by contrasting plant communities and nutrients at sites where geese are abundant with those where they have been largely absent for at least 50 years. I further compare these sites with others where geese are abundant, but their effect on plant communities and nutrient cycles has been experimentally manipulated through the use of exclusion cages, and the soil has been experimentally fertilized for over 16 years. Together, these experiments offer an opportunity to improve our understanding of how geese influence plant communities and alter wetland nutrient conditions. Through comparing sites where geese have been virtually absent for at least 50 years with those where they were experimentally excluded by cages, I also might validate the effects at different time scales.

To more accurately assess possible processes behind plant community change, I analyze plant functional traits—that is, measurable features of plants that potentially affect individual performance or organism fitness (Cadotte et al., 2011). These traits provide information regarding the species response to the disturbance (Mouillot et al., 2013) and the strength of competition at certain environmental conditions (Cadotte and Tucker., 2017). Responses of community-level plant traits (e.g., specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), N/C content or plant height) weighted by their relative abundances (CWM) reveal the effects of environmental change on plant communities (Garnier et al., 2004; Quétier et al., 2007; Li et al., 2017). By analyzing inorganic nutrient concentrations and plant functional traits among treatments, I infer the effects of long-term absence of geese on plant communities, changes in nutrient cycles, and the mechanisms possibly responsible for these changes.

## 2. Materials and methods

### *Study site*

Our two study sites were located on two islands in the North Baffin Region, Nunavut, Canada. For site selection, I referred to goose distribution map in Reed et al. (2002) and Gagnon et al. (2009) (Fig. 2.1). The first site was on the southern plain of Bylot Island (73°08'N, 80°03'W), and the second at Pond Inlet (72°39'N,

78°03'W) on Baffin Island (Fig. 2.1). Bylot Island is the main breeding site of the Greater Snow Goose (*Anser caerulescens atlanticus*) and supports > 15–20 thousand goose pairs annually (Reed et al., 2002; Gauthier et al., 2013). High density nesting of geese during summer results in intense herbivory, as a consequence of which vegetation, especially in wetlands, decreases. Up to 60% of the annual production of graminoids is consumed by geese in these wetland habitats (Gauthier et al., 1995; Massé et al., 2001; Valéry et al., 2010). Many long-term experiments since the 1980s have assessed the effects of high goose density on ecosystems in the southern plain (Gauthier et al., 2004; Marchand-Roy, 2009; Pouliot et al., 2009).

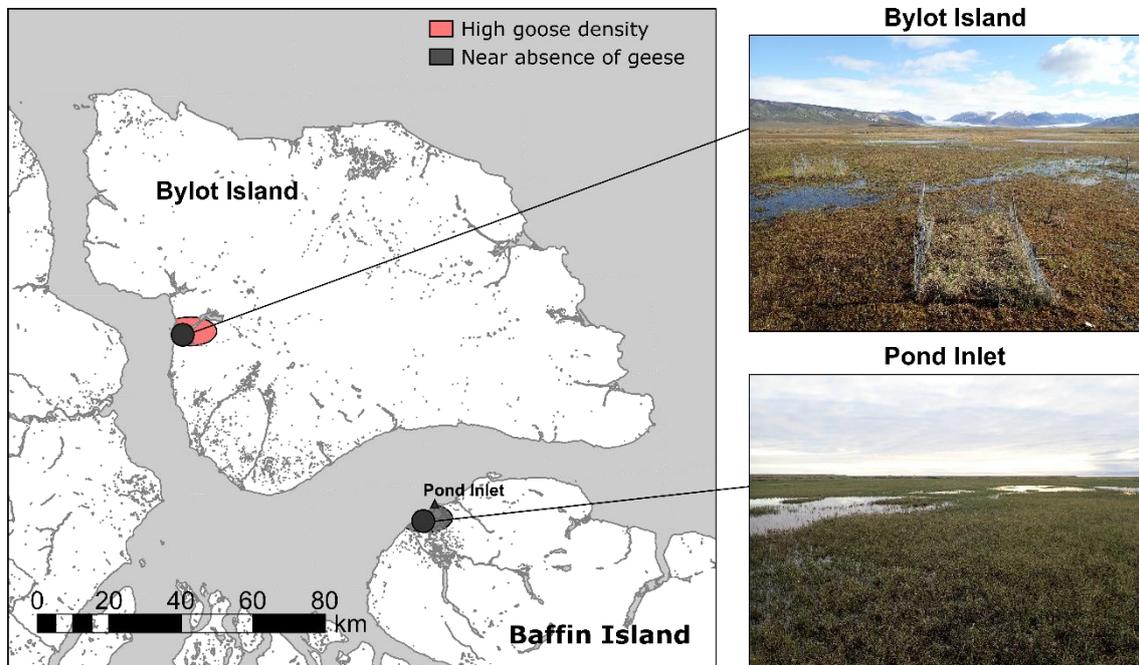


Fig. 2.1

Study sites, Bylot and Baffin islands. Relative abundance and distribution of greater snow geese (*Chen caerulescens atlantica*) around study sites from Reed et al. (2002) and Gagnon et al. (2009). Above right, Bylot Island (with 2 × 1 m goose exclusion fences); above left, Pond Inlet: graminoid-dominated wet meadows surrounding ponds.

Pond Inlet (Inuit name: Mittimatalik) is a small village in northern Baffin Island with a 1600-strong population, about 92% of which are Inuit (Qikiqtani Inuit Association, 2014). Archaeological evidence indicates nomadic Inuit have lived in this area for almost 4000 years (Mary-Rousselière, 1985), but in the

decade following establishment of a federal school in 1959, many Inuit families settled here in a permanent community. Following establishment of an airstrip in 1973–1974, the community developed rapidly (Qikiqtani Inuit Association, 2014). While goose nesting sites existed around Pond Inlet before the community development, density was likely extremely low because, during the first half of the 20<sup>th</sup> century, the total size of the greater snow goose population ranged from 0.5 to 3% of its size over the past 20 years (Gauthier et al., 2005). Since the establishment of the community, goose abundance around it has decreased considerably to a near absence (Gagnon et al., 2009). Consequently, for at least 50 years, geese have been unintentionally excluded from this site.

Dominant plant species at goose-nesting sites around these regions include *Dupontia fisheri*, *Eriophorum scheuchzeri*, and *Carex aquatilis* (Gauthier et al., 1995; 2013; Jasmin et al., 2008; Pouliot et al., 2009). Each site is also covered by a thick layer of brown mosses, dominated by the genus *Drepanocladus* (Pouliot et al., 2009). The greater snow goose is the most influential herbivore and other herbivores include brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings.

While Bylot and Pond Inlet sites are about 100 km apart, their climate is similar: the mean summer (June–August) temperature and precipitation at Bylot Island (southern plain) are 4.5°C and 27.6 mm, while those at Baffin Island (Pond Inlet) are 4.7°C and 26.8 mm, respectively (Duclos et al., 2006). These sites are also similar in geological age, being Mesozoic- and Tertiary-age sedimentary bedrock (Jackson et al., 1978; Miall et al., 1980).

### *Experimental design*

Seven study sites were established at both Bylot Island and Pond Inlet. Exclusion cages were established at 3 of the 7 Bylot Island sites (2 exclusion treatments × 3 sites), whereas the 4 remaining sites had combinations of five levels of fertilization and goose exclusion treatment, providing 10 treatment per study site (5 fertilization treatments × 2 exclusion treatments × 4 sites). Fertilization treatments were established in 2 × 2 m squares, with half (2 × 1 m) exposed to goose herbivory and half enclosed within a 50 cm high chicken-wire fence. Although this mesh size did not prevent lemming movement, the effects of lemming herbivory on vegetation are likely to be limited here (Gauthier et al. 2004). Each square was located at least 5 m from the next to prevent cross-

treatment contamination. To avoid the edge effects, I set 80 × 80 cm vegetation survey plots in the central portion of the enclosure at each square.

The five fertilization treatments at Bylot Island comprised: low N ( $N_L = 1 \text{ g m}^{-2}$ ), high N ( $N_H = 5 \text{ g m}^{-2}$ ), high P ( $P_H = 3 \text{ g m}^{-2}$ ), and high N and P ( $N_{HP} = 5 \text{ g m}^{-2}$  of N +  $1 \text{ g m}^{-2}$  of P), and control ( $C_0$ ) that received no fertilizer. These amounts exceed the amount of nutrients added to this ecosystem by goose droppings, which are around  $0.6 \text{ g m}^{-2}$  of N and  $0.03 \text{ g m}^{-2}$  of P in areas of high goose use (Pouliot et al., 2009). However, Pineau (1999) had shown that graminoid plants did not respond to the addition of  $1 \text{ g m}^{-2}$  g of N. Since I wished to detect the potential change at the community level induced by goose feces in a context of increasing populations, I added higher level of nutrient than those encountered at current population level.

Fertilizers were applied in a single dose in late June; N was applied as ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ), and P as superphosphate phosphoric acid ( $\text{H}_3\text{PO}_4$ ). While N was dissolved in 2L of water before application, P was scattered uniformly over the moss surface before watering (2L by experimental unit). For consistency, control treatments also received 2L water. Water was obtained from an open source near experimental sites (Pouliot et al., 2009). Exclusion cage and fertilization experiments at Bylot Island have been performed from 2002 to 2018.

Seven study sites were established near Pond Inlet in wetlands similar to those encountered on Bylot Island (Fig. 2.1, photos). According to local knowledge, these areas were reported to be used as nesting sites by geese in the past but geese were rarely encountered in those areas nowadays (Gagnon et al., 2009; G. Gauthier pers. obs.). To minimize human effects, each wetland site was located at least 5 km from the village, and was separated by at least 500 m. Three replicate 80 × 80 cm vegetation survey plots were established at each site.

### *Field data collection*

As a plant community data, number of tillers of vascular plants were measured from four randomly selected subplots (10 × 10 cm) within each 80 × 80 cm vegetation survey plot, and pooled. I also measured the aboveground biomass (g) per plot. Above-ground parts included green leaves and white parts of the tiller above the last leafing node.

The water table lies at or above the surface through most of the plant growing season. Graminoid plants grow in soils formed by mosses (e.g. Madsen

and Mortensen, 1987; Gauthier et al., 2006). As vascular plants mainly absorb nutrients from water around bryophytes, I measured  $\text{PO}_4^{2-}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and dissolved organic carbon concentrations (DOC) in wetland water; water samples were collected from the water table and immediately frozen until analysis. After thawing, water samples were filtered through 0.2  $\mu\text{m}$  membrane filter (DISMIC-25CS, Advantec, Japan);  $\text{PO}_4^-$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  concentrations were determined colorimetrically using a TRACCS-800 Autoanalyzer (Technico, Japan; Tanabe et al., 2010). DOC was measured with a Sievers 5310 C TOC Analyzer (GE Analytical Instrument, USA) in a two-stage process commonly referred to as T-IC; IC (inorganic carbon) was oxidized by sample acidification (pH2) and TC (total carbon) by ultraviolet lamp. DOC was calculated by subtracting sample IC from TC. Measurements of DOC were replicated three times; mean values are used in analysis.

Six plant functional traits were measured: leaf dry matter content (LDMC,  $\text{mm}^2 \text{g}^{-1}$ ), specific leaf area (SLA,  $\text{mm}^2 \text{g}^{-1}$ ), plant height (Height, cm), leaf nitrogen content (N,  $\text{mg g}^{-1}$ ), leaf carbon content (C,  $\text{mg g}^{-1}$ ), and leaf N C ratio (C/N). Fresh leaves were immediately scanned and weighed, then dried for 72 hours at  $70^\circ\text{C}$  to obtain leaf dry weight. LA was calculated from leaf scan data using Image-J (Rasband, 1997–2008). SLA and LDMC were calculated using LA and leaf weight data (SLA = LA/dry weight; LDMC = dry weight/fresh weight). Leaf N and C were measured by NC analyzer (Sumigraph NCH-22F, Sumika Chemical Analysis Service, Japan). Plant height was measured from the ground to the highest photosynthetic structure.

All data and samples were collected during the biomass peak in this region, between mid-July and early August 2018. Time and logistical constraints (e.g., helicopter schedules changing with weather) precluded sampling environmental data at 1 of 3 fertilization sites, and plant community data at 5 of 8 low N ( $\text{N}_L$ ) plots (2 control and 1 exclosure) on Bylot Island.

### *Data analysis*

The relative abundance of plant species per study plot, which I use to describe community composition, was determined from stem numbers. Environmental and trait data were log-transformed to follow a normal distribution.

To detect changes in community composition, principal component analysis (PCA) was performed on plant community composition data (relative

abundance). To evaluate communities by plant features, I calculate community-weighted mean (CWM) trait values for each plot—the mean trait value of all species in a community weighted by their relative abundance (Garnier et al., 2004). Trait data used for CWM were used for all sites and treatments to accommodate intraspecific variability.

Two types of multiple regression analysis were performed. First, to detect treatment effect (Goose exclusion and Fertilization (addition of P and N)) on wetland water quality, I constructed linear models. Response variables included any of four indices of wetland water quality ( $\text{PO}_4^{2-}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and DOC); treatments (Goose exclusion, and addition of P ( $\text{g m}^{-2}$ ), and N ( $\text{g m}^{-2}$ )) were used as explanatory variables. Second, to detect effects of environmental change on plant communities, generalized linear models were constructed. Response variables were any of eight indices represented by the species or trait composition in communities (PC1, PC2 and 6 of CWM (Leaf N, C, C/N ratio, LDMC, SLA, plant height)). Treatments (Goose exclusion (number of years), and addition of N and P) and wetland water quality ( $\text{PO}_4^{2-}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and DOC (dissolved organic carbon) concentrations) were taken as multiple experimental variables after standardization. The variable of goose exclusion was treated as categorical variables here (Control, Exclosure, Near absence) due to the uncertainty of geese exclusion duration in Pond Inlet (50 years in minimum). Values for N and P were quantity of fertilizer (e.g., for P:  $C_0 = 0$ ,  $P = 1$ , and  $P_H = 3$ ). For both models, I assumed a gaussian distribution for response variables to fit linear regressions. The model with lowest Akaike information criterion (AIC) was identified as the best model. All statistical tests were performed in R version 3.5.2 (<http://www.R-project.org>; R Development Core Team).

## 2.3 Results

I report 29 plant species (Table S2.1) from our study sites, for which mean species richness per plot was 4.4 (mean alpha diversity = 3.7 (Pond Inlet) and 4.8 (Bylot Island)). The three dominant species, *D. fisheri*, *E. scheuchzeri* and *C. aquatilis* were present in most plots. Other highly abundant species were the *Hierochloa pauciflora*, *Poa arctica*, and *Stellaria longipes*, which were especially abundant at plots with a high fertilization level (Table S2.1).

PC1 explained 44.8% and PC2 26.8% (71.6 % in total) of the variance in community structure. Factor loadings of each species onto the principal

components were given in Table S2.2. I infer that PC1 reflects the duration of goose exclusion (Fig. 2.2 (a)) and PC2 reflects fertilization treatment intensity (Fig. 2.2B). Results indicate that both long-term goose exclusion and nutrient addition have had considerable effects on plant community composition. As the duration of goose exclusion increased, *C. aquatilis* and *E. scheuchzeri* increased in dominance, and *D. fisheri* decreased. As the quantity of fertilizer increased, *H. pauciflora* and *P. arctica* increased their abundances.

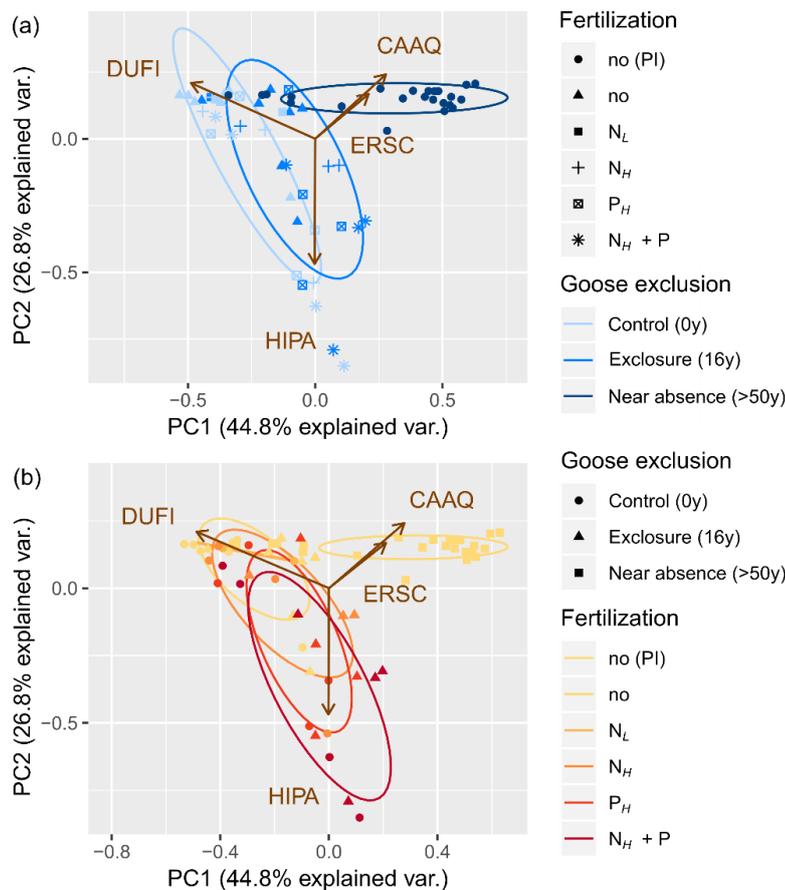


Fig. 2.2

Principal component analysis (PCA) of plant communities. Colored ellipses in A and B represent 68% ( $1\sigma$ ) confidence intervals for each treatment, goose exclusion (Control (0 years) on Bylot, Exclosure (16 years) on Bylot, or Near absence (> 50 years) on Pond Inlet) and fertilization (no (PI) (Pond Inlet), no, N<sub>L</sub>, N<sub>H</sub>, P<sub>H</sub>, N<sub>H</sub> + P), respectively. Solid lines show the direction and loadings of four dominant species (CAAQ = *Carex aquatilis*, DUFU = *Dupontia fisheri*, ERSC = *Eriophorum scheuchzeri*, HIPA = *Hierochloe pauciflora*). Each point represents vegetation survey plot (n = 60, 40 in Bylot Island and 21 in Pond Inlet).

The duration of goose exclusion considerably increased  $\text{PO}_4^{2-}$ , while P ( $\text{H}_3\text{PO}_4$ ) addition contributed to increased  $\text{PO}_4^{2-}$ , and addition of N ( $\text{NH}_4\text{NO}_3$ ) contributed to increased  $\text{NH}_4^+$  but the effects on  $\text{NO}_3^-$  was limited here (Table 2.1). DOC was conspicuously affected by P and N additions.

Table 2.1.

Best linear models. Response variables include wetland water quality ( $\text{PO}_4^{2-}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and DOC (dissolved organic carbon) concentrations); explanatory variables include treatment data (goose exclusion (dummy variables; Exclosure (16 years) and Near absence (> 50 years)), and N and P addition). The values in the rows of explanatory variables represent the multiple regression coefficients for selected explanatory variables (with 95% confidence interval).

	<b>Response variables:</b>			
	$\text{PO}_4^{2-}$	$\text{NO}_3^-$	$\text{NH}_4^+$	DOC
<b>Exclosure (16y)</b>	<b>0.84</b>	<b>0.29</b>		<b>0.14</b>
	(0.23, 1.46)	(-0.50, 1.09)		(-0.56, 0.85)
<b>Near absence (&gt;50y)</b>	<b>1.53</b>	<b>-0.49</b>		<b>0.65</b>
	(0.98, 2.07)	(-1.14, 0.16)		(-0.01, 1.32)
<b>N addition</b>			<b>0.23</b>	<b>0.3</b>
			(0.08, 0.39)	(0.14, 0.46)
<b>P addition</b>	<b>1.74</b>		<b>0.72</b>	<b>0.77</b>
	(1.10, 2.38)		(-0.001, 1.44)	(0.02, 1.52)
<b>Intercept</b>	<b>-1.22</b>	<b>0.23</b>	<b>-0.23</b>	<b>-0.64</b>
	(-1.67, -0.77)	(-0.29, 0.75)	(-0.52, 0.05)	(-1.20, -0.07)
<b>AIC Best model</b>	<b>95.85</b>	<b>116.95</b>	<b>108.01</b>	<b>108.15</b>
<b>AIC Null model</b>	<b>121.52</b>	<b>119.37</b>	<b>120.99</b>	<b>119.56</b>

Plant community composition indices were explained by treatments and water quality (Table 2.2). PC1 was mainly explained by the goose exclusion, while PC2 was mainly explained by the amount of P and N added to a treatment. Results are consistent with the trend seen in Fig. 2.2. Both fertilization (N and P) increased species richness. Plant biomass and CWM of plant height showed a similar pattern with PC1, with the duration of goose exclusion related to increased plant biomass accumulation (Table 2.2). Results of CWM of leaf C and N content and C/N ratio responded well to all treatments (include Exclosure and addition of N and P). More carbon rich and nutrient poor plant species, and increased C/N ratios correlated with increased duration of goose exclusion. Although addition

of P decreased plants high in N and C, the C/N ratio increased significantly and LMA was increased. These results indicate addition of P increased species with high C/N ratio and with thick tissues. Conversely, addition of N increased plant N content and decreased C/N ratio, indicating nutrient-rich species increased in abundance. The effects of wetland water quality on plant community indices were rarely detected.

Table 2.2.

Best generalized linear models. Response variables include PC1, PC2, Species richness (Sp rich), Biomass, and CWM of six traits (leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), mass per area (LMA), and dry matter (LDMC) contents, and plant height (Height)). Explanatory variables in treatments include goose exclusion (dummy variables; Exclosure (16 years) and Near absence (> 50 years), and addition of N and P; wetland water quality data include PO<sub>4</sub><sup>2-</sup>, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> and DOC (dissolved organic carbon) concentrations. The values in the rows of explanatory variables represent the multiple regression coefficients for selected explanatory variables (with 95% confidence interval).

	Response variables:									
	PC1 Gaussian	PC2 Gaussian	Sp rich Poisson	Biomass Gaussian	N Gaussian	C Gaussian	C/N Gaussian	LMA Gaussian	LDMC Gaussian	Height Gaussian
Exclosure (16y)	0.08 (-0.14, 0.30)			0.21 (-0.14, 0.55)	-0.47 (-0.84, -0.09)	-0.18 (-0.54, 0.18)	0.54 (0.10, 0.97)		0.73 (-0.07, 1.52)	1 (0.42, 1.58)
Near absence (>50y)	0.47 (0.28, 0.66)			1.96 (1.67, 2.24)	-0.99 (-1.36, -0.63)	0.83 (0.49, 1.17)	1.4 (0.99, 1.82)		0.002 (-0.70, 0.71)	1.72 (1.25, 2.20)
N addition		-0.050 (-0.08, -0.02)	0.080 (0.003, 0.15)		0.260 (0.18, 0.34)	0.060 (-0.02, 0.14)	-0.200 (-0.29, -0.10)			
P addition		-0.12 (-0.16, -0.07)	0.15 (0.01, 0.29)		-0.48 (-0.64, -0.32)	-0.61 (-0.77, -0.46)	0.57 (0.38, 0.75)	0.32 (0.01, 0.63)		
PO <sub>4</sub> <sup>2-</sup>	0.11 (0.03, 0.19)								0.59 (0.23, 0.96)	
DOC		-0.06 (-0.11, -0.002)		-0.14 (-0.27, -0.02)					-0.54 (-0.88, -0.20)	
NH <sub>4</sub> <sup>+</sup>										
NO <sub>3</sub> <sup>-</sup>										
Intercept	-0.220 (-0.36, -0.07)	0.130 (0.08, 0.18)	1.370 (1.20, 1.55)	-0.750 (-0.98, -0.52)	0.370 (0.06, 0.68)	0.050 (-0.25, 0.35)	-0.650 (-1.01, -0.29)	-0.340 (-0.63, -0.04)	-0.160 (-0.71, 0.38)	-0.95 (-1.33, -0.57)
AIC Best model	6.21	-39.28	162.41	48.41	55	51.26	67.38	115.31	111.33	90.47
AIC Null model	37.28	-4.08	166.82	125.58	111.34	115.08	119.29	117.48	124.25	121.4

## 2.4. Discussion

In arctic wetlands, geese have been considered to profoundly affect nutrient cycling through intense herbivory and fecal input (Gauthier et al., 2004; Van der Wal, 2006; Hillebrand et al., 2007). I compare sites with and without geese to those in which geese have been excluded but soils have been experimentally fertilized, to assess the long-term effects of geese on arctic wetland ecosystems.

### *Change in nutrient conditions*

Non-exclusion sites with geese lacked high nutrient concentrations, indicating fertilization through goose feces was limited. These results were consistent with previous studies. At moss dominated mesic sites in the Arctic, it is known that geese feces easily release nutrients which leach quickly into water that can be absorbed by thick moss cover (Kotanen et al., 2002; Pouliot et al., 2009). Conversely, sites at which geese were absent had high concentrations of  $\text{PO}_4^{2-}$ . Since  $\text{PO}_4^{2-}$  input is mainly from herbivore feces and plant litter decomposition, increased  $\text{PO}_4^{2-}$  in this habitat is most likely the result of increased plant decomposition. I infer from Sorensen et al. (2008) that accumulated leaf litter and increased biomass in areas where geese are absent facilitates decomposition, improving plant-soil interactions.

The effect of fertilization on wetland water conditions was straightforward. Addition of P increased  $\text{PO}_4^{2-}$ , and addition of N significantly increased  $\text{NH}_4^+$ . Although the effects of fertilization are on water quality thought to be limited because of thick moss cover and the flow of wetland water (Pouliot et al., 2009), long-term N and P addition has changed water quality. Conversely, addition of N did not change  $\text{NO}_3^-$  concentration, possibly because  $\text{NO}_3^-$  has chemical characteristics conducive to denitrification and leaching (Borman and Likens, 1979; Lin et al., 2001). In aquatic and terrestrial systems, studies reported that fertilization often increases DOC (Gale et al., 2003) as also found in our N and P addition treatments, likely resulting from microbial responses to carbon and nutrient availability (Findlay, 2003). As a consequence, I found some plant species atypical in wetlands at the fertilized plots.

### *Change in plant community*

PCA showed differences in plant communities among sites (Fig. 2.2, Table 2.2). The abundance of three dominant plant species (*D. fisheri*, *C. aquatilis* and *E. scheuchzeri*) varied between treatments (Fig. 2.2 (a)). Control sites were characterized by high abundance of *D. fisheri*, a small-sized pioneer plant highly abundant in young wetlands (Billings and Peterson, 1980), but as the duration of goose exclusion increased, *E. scheuchzeri* and *C. aquatilis* increased in abundance. Both *E. scheuchzeri* and *C. aquatilis* are larger, and dominate in undisturbed wetlands, with *C. aquatilis* a particularly strong competitor that can

outcompete other species, including *E. scheuchzeri* in older arctic wetlands (Billings and Peterson, 1980). In sum, our results suggest the substantial impacts of geese absence/presence on vegetation. However, careful interpretations are in due here, because edaphic conditions and geomorphological processes – other major determinants of structure and composition of tundra vegetation – are not necessarily equivalent between Bylot Island and Baffin Island (Ellis and Rochefort; 2004; Fortier et al., 2006). Given similarity in plant community composition between wetlands in the experimental exclosure sites and older wetlands with prolonged release from goose herbivory (Billings and Peterson, 1980).

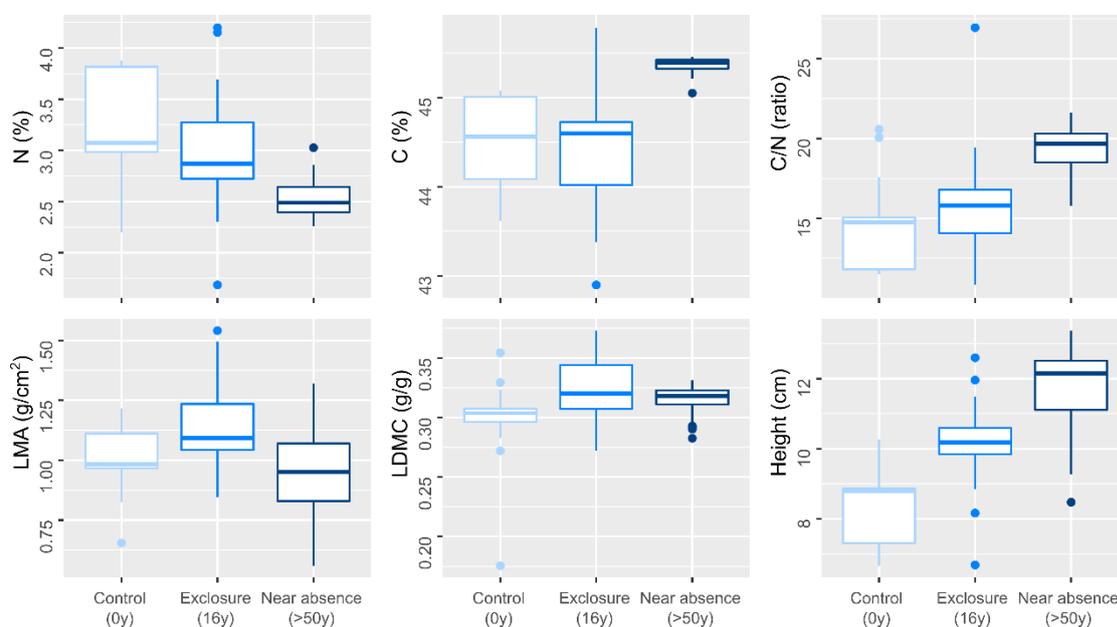


Fig. 2.3.

Boxplots showing median (central lines), 25 and 75% quartile ranges around the median (box width). Comparison of CWM of six plant traits (leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), mass per area (LMA), and dry matter (LDMC) contents, and plant height (Height)) in treatments where geese have been excluded for 0 years (Control (0 years on Bylot)), 16 years (Exclosure (16 years) on Bylot), and Near absence (> 50 years) on Pond Inlet. These boxplots contain all data include fertilized and unfertilized plots.

Community weighted means (CWM) of functional traits support these interpretations. Dominant plant species at sites where geese are absent had high

plant height and high C/N ratios (Fig. 2.3, Table 2.2). Linear relationships between traits and duration of goose exclusion indicate the existence of competitive relationships between plant species through the community assembly process. Height is a fundamental characteristic of plants and is associated with their competitive ability to intercept light. In general, competition for light intensifies as aboveground biomass or plant stature increases (Hautier et al., 2009). Here, with prolonged absence from goose herbivory, plant biomass increased (Table 2.2) and competition between plants intensified. In Arctic wetlands, almost all plants are summer green perennial herbs where plant height depends largely on accumulation of carbohydrates in rhizomes stored from previous years. Geese prefer graminoid rhizomes (Giroux and Bedard, 1987; Gauthier et al., 1995), and their grazing reduces carbohydrates (Beaulieu et al., 1996). Thus, the compound effects of competition and disadvantages of grazing contributed to a gradual change in plant community height.

The C/N ratio reflects plant growth strategies (Wright et al., 2004; Freschet et al., 2010). Generally, species with high N and low C/N ratio are described as having a resource acquisitive strategy, using a high amount of resources to rapidly acquire C. This strategy may benefit plants under high-resource conditions; however, due to excess respiratory costs, it is likely disadvantageous for plants under low-resource conditions. Species with low N and high C/N ratios are described as having a resource conservative strategy, which is advantageous to plant species in low-resource conditions (Reich, 2014). Here, plant species with conservative strategy were more abundant in sites where geese were absent, where low temperatures of Arctic limit the bioavailability of nutrients to plants (Shaver and Chapin, 1995).

Long-term fertilization substantially changed plant community composition in our study, in a different way to that of long-term goose exclusion. Important species contributing to changes in community composition were *H. pauciflora* and *P. arctica*. Although these species do not commonly occur in wetland habitats, they tend to dominate drier habitats (Duclos et al., 2006). These recruitments of non-wetland species could contribute higher species richness at both N and P addition sites (Table 2.2). The difference between plant communities in control treatments (C<sub>0</sub>) and N<sub>H</sub> + P addition treatments was greatest, followed by P, N<sub>H</sub> and N<sub>L</sub> treatments (Fig. 2.2 (b)).

While the effect of adding P and N was compounded in PCA results, CWM trait values revealed contrasting patterns between addition of these two fertilizers

(Table 2.2, Fig. 2.4). Addition of N increased species typical of resource acquisitive taxa (high N content and low C/N ratios). Here, the increase in non-graminoid species such as *S. longipes* might contribute to this trend. This indicates that addition of N released plants from nutrient limitations, enabling resource acquisitive strategy species to increase their abundance. Conversely, addition of P increased low N, C content and high C/N ratios species (Table 2.2, Fig. 2.4). LMA was also positively selected in our model, indicating that addition of P was advantageous for resource conservative species with thicker leaf tissues, perhaps reflected by the increased number of species in the family Poaceae, such as *H. pauciflora* and *P. arctica*. Despite the  $N_H + P$  addition treatment being most dissimilar to all other communities in PCA (Fig. 2.2), the CWM of N and C/N ratio in this treatment was half that of the  $N_H$  and P addition (Fig. 2.4) treatments. Thus, I speculate that these plots contain features of both N and P addition plots (Poaceae and non-graminoid species). The greater contribution of treatments (goose exclusion and fertilization) to plant community composition than nutrient conditions could be because nutrients were immediately absorbed by plants and mosses after treatment.

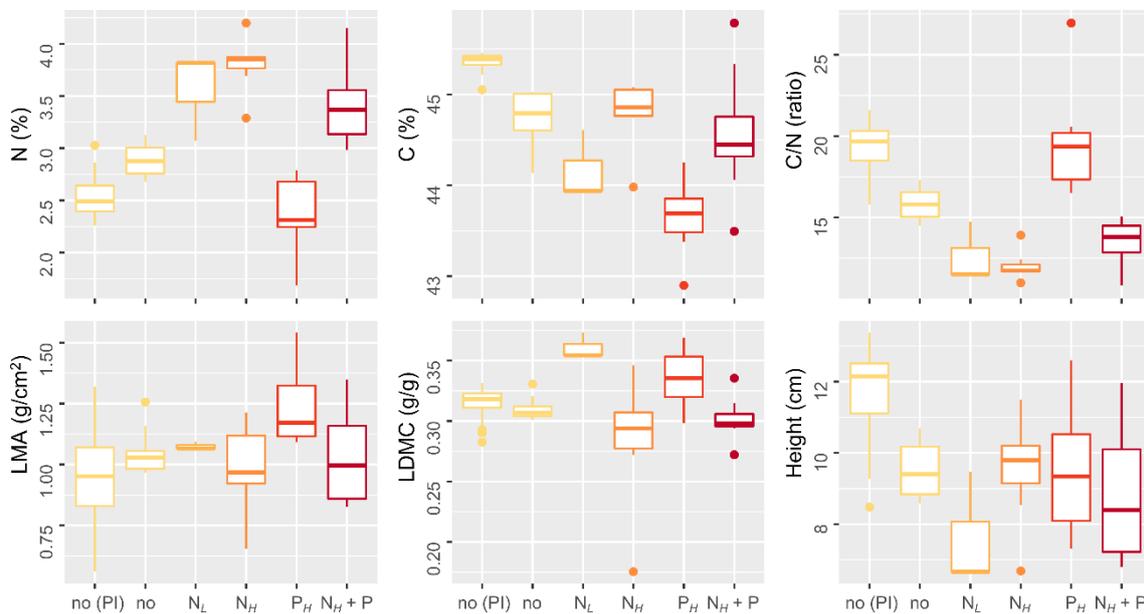


Fig. 2.4

Boxplots showing median (central lines), 25 and 75% quartile ranges around the median (box width). Comparison of CWM of six plant traits (Leaf nitrogen (N), carbon (C), carbon/nitrogen ratio (C/N), mass per area (LMA), and dry matter

(LDMC) contents, and plant height (Height)) among six fertilization treatments, Pond Inlet (no (PI)) and five treatments at Bylot Island (Co, N<sub>L</sub>, N<sub>H</sub>, P<sub>H</sub>, N<sub>H</sub> + P). These boxplots contain all data include geese excluded and control plots.

### *Conclusion*

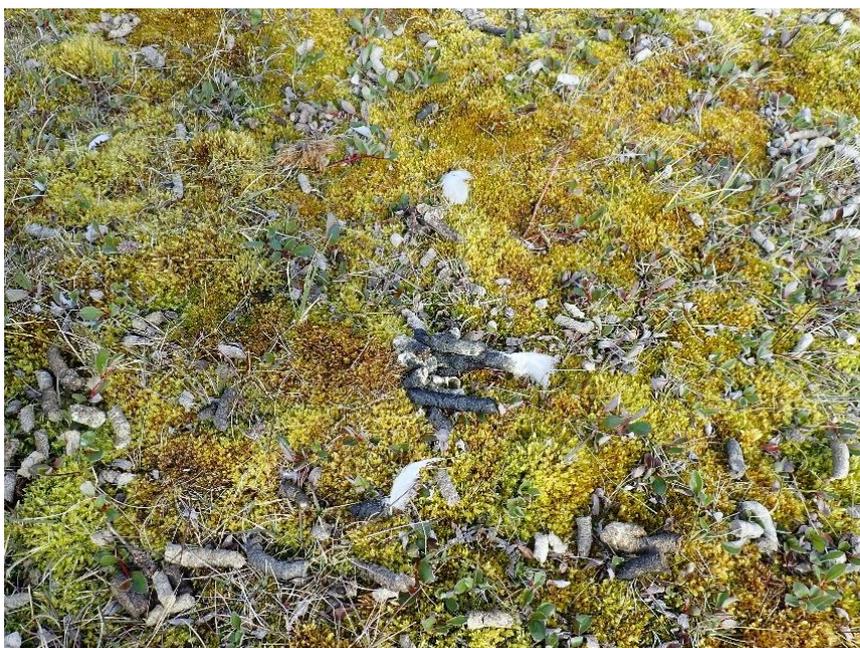
Our study was based on a unique opportunity that compared plant communities between Pond Inlet and Bylot Island to assess the long-term effects of geese on Arctic vegetation. Long-term goose exclusion would change plant community composition by altering competitive relationships between dominant plant species. Interestingly, fertilization experiments released plant species from the nutrient limitation and converted Arctic wetland habitats to a possible alternative state. Even after 50 years of goose disappearance, changes in plant community structure were incomparable to those I reported for fertilization treatments. While I found PO<sub>4</sub><sup>2-</sup> improvement at both exclusion and P-addition sites, results of plant community composition and traits were dissimilar between the sites. This finding indicates that the direct effects by goose herbivory on vegetation are more profound than their indirect effects through alternation of nutrient cycling even in nutrient-limited wetlands in Arctic.

To date, substantial number of exclusion experiments exist to evaluate the impacts of herbivory on vegetation; inferences gained from these studies are still limited, especially in a longer time horizon. By combining planned and unplanned goose exclusion, I have challenged this issue. I consider that nutrient condition and plant community composition in the sites, where are free from geese for more than a half century, could imply possible conditions in the future in our experimental enclosure sites, if the impacts of abundant geese are assumed to continue. Avian and mammal herbivores are often an ecosystem engineer, and thus the consequences of their population changes are far from negligible. Although challenging, I emphasize the need of studies that can quantify the long-term impacts of these engineers on composition, structure and functions of ecological systems.

## Appendix 2.1

Photos of goose feces on a xeric ridge near the study wetlands. Goose feces often last for >1 yr when deposited on xeric ridges along wetlands. There were abundant faces around the study sites in Bylot Island. In contrast, feces were very few in Pond Inlet and rarely found near the study sites in Pond Inlet.

### Bylot Island



### Pond Inlet



Table S2.2.

Heat map of the relative abundance of each plant species per plot.

Area	Site	Fertilization	Geese	DUFI	CAAQ	ERSC	HIPA	POAR	STLO	ERAN	FEBR	CAPR	PEAL	SAHI	SAFO	PLSA	Poaceae_sp1	EQAR	SAHE	SARI	Poaceae_sp2	SAAR	BIVI	ARUL	ARLA	Poaceae_sp3	Dicots	SARE	REHY	LYAN	VAUL	LUCO		
Pond Inlet	PA1	-	Disapper	0.87	0.13																													
Pond Inlet	PA2	-	Disapper	0.55	0.16	0.29																												
Pond Inlet	PA3	-	Disapper	0.64	0.18	0.18																												
Pond Inlet	PA4	-	Disapper	0.75	0.2								0.05																					
Pond Inlet	PA5	-	Disapper	0.19	0.34	0.46							0.01																					
Pond Inlet	PB1	-	Disapper	0.13	0.66	0.18															0.04													
Pond Inlet	PB2	-	Disapper	0.03	0.82	0.15																												
Pond Inlet	PB3	-	Disapper	0.01	0.46	0.41							0.06		0.05																			
Pond Inlet	PC1	-	Disapper	0.05	0.25	0.71																												
Pond Inlet	PC2	-	Disapper	0.04	0.44	0.52																												
Pond Inlet	PC3	-	Disapper	0.11	0.58	0.32																												
Pond Inlet	PD1	-	Disapper	0.09	0.46	0.4							0.06																					
Pond Inlet	PD2	-	Disapper	0.12	0.42	0.44							0.01																					
Pond Inlet	PD3	-	Disapper	0.29	0.6	0.1							0.02																					
Pond Inlet	PE1	-	Disapper	0.65	0.16	0.19																												
Pond Inlet	PE2	-	Disapper	0.38	0.62																													
Pond Inlet	PE3	-	Disapper	0.53	0.17	0.22		0.01					0.06																					
Pond Inlet	PF1	-	Disapper	0.24	0.71								0.01								0.04													
Pond Inlet	PF2	-	Disapper	0.1	0.59	0.32																												
Pond Inlet	PF3	-	Disapper	0.18	0.6	0.2							0.02																					
Pond Inlet	PG1	-	Disapper	0.36	0.22	0.32				0.1																								
Pond Inlet	PG2	-	Disapper	0.12	0.23	0.28				0.32											0.05													
Pond Inlet	PG3	-	Disapper	0.33	0.08	0.29	0.19			0.11																								
Bylot	R33	Co	Exclosure	0.46	0.07	0.09	0.16		0.07	0.14												0.01								0.01				
Bylot	R33	Co	Control	0.89		0.11																												
Bylot	R35	Co	Exclosure	0.54	0.19	0.2	0.05																	0.01										
Bylot	R35	Co	Control	0.77	0.13	0.1																												
Bylot	R36	Co	Exclosure	0.63	0.18	0.08				0.08		0.02															0.01							
Bylot	R36	Co	Control	0.75	0.05	0.11										0.08																		
Bylot	ROC3	Co	Exclosure	0.35		0.11	0.36			0.15		0.02																						
Bylot	ROC3	Co	Control	0.43	0.11	0.07	0.32			0.07																								
Bylot	ROC6	Co	Exclosure	0.83		0.13			0.02			0.02																						
Bylot	ROC6	Co	Control	0.91		0.09																												
Bylot	ROC7	Co	Exclosure	0.5	0.13	0.32	0.03	0.01																										
Bylot	ROC7	Co	Control	0.84		0.09						0.02	0.05																					
Bylot	ROC8	Co	Exclosure	0.64	0.33	0.03																												
Bylot	ROC8	Co	Control	0.77	0.21	0.02																												
Bylot	ROC7	NL	Control	0.56	0.12	0.26	0.04			0.01													0.01											
Bylot	ROC8	NL	Exclosure	0.81		0.19																												
Bylot	ROC8	NL	Control	0.78	0.09	0.07				0.02													0.02											0.01
Bylot	ROC3	NH	Exclosure	0.6	0.08	0.2	0.11																											
Bylot	ROC3	NH	Control	0.61	0.02	0.04			0.1	0.07					0.15	0.01																		
Bylot	ROC6	NH	Exclosure	0.78		0.04				0.1		0.08				0																		
Bylot	ROC6	NH	Control	0.27	0.01	0.08	0.62						0.01																					
Bylot	ROC7	NH	Control	0.18	0.04	0.14			0.57				0.07																					
Bylot	ROC8	NH	Exclosure	0.81		0.19																												
Bylot	ROC8	NH	Control	0.31	0.05		0.63			0.01																								
Bylot	ROC3	P	Exclosure	0.34	0.05		0.6			0.01																								
Bylot	ROC3	P	Control	0.11		0.01	0.2			0.01	0.66		0																					
Bylot	ROC6	P	Exclosure	0.74		0.03	0.08	0.08		0.07			0.01																					
Bylot	ROC6	P	Control	0.35	0.05	0.08	0.21	0.18	0.13																									
Bylot	ROC7	P	Exclosure	0.28	0.01	0.1	0.33	0.23	0.02							0.03																		
Bylot	ROC7	P	Control	0.58	0.36	0.06																												
Bylot	ROC8	P	Exclosure	0.71	0.22	0.01							0.06																					
Bylot	ROC8	P	Control	0.14	0.01		0.85																			0.01								
Bylot	ROC3	NH+P	Exclosure	0.22	0		0.66		0.1			0.01	0																					0.01
Bylot	ROC3	NH+P	Control		0.01	0.73	0.26																											
Bylot	ROC6	NH+P	Exclosure	0.63		0.02	0.03		0.11	0.01		0.12										0.07												0.01
Bylot	ROC6	NH+P	Control	0.07	0	0.07	0.12	0.71	0.02						0																			
Bylot	ROC7	NH+P	Exclosure	0.08		0	0.89	0.02					0																					
Bylot	ROC7	NH+P	Control	0.37	0.01			0.13	0.49																									
Bylot	ROC8	NH+P	Exclosure	0.73	0.05			0.09	0.03			0.1																						
Bylot	ROC8	NH+P	Control	0.02	0.2	0.71							0.03								0.01		0.02							0.01	0.01			

Table S2.3.

Factor loadings of each species onto the PC1, PC2, PC3, PC4 in PCA analysis.

	Principal component loadings			
	PC1	PC2	PC3	PC4
<i>Arctagrostis latifolia</i>	0.00	0.00	0.00	0.00
<i>Bistorta vivipara</i>	0.00	0.00	0.00	0.00
<i>Carex aquatilis</i>	0.16	0.11	<b>-0.09</b>	-0.06
<i>Cardamine pratensis</i>	-0.01	0.00	0.00	0.00
Unknown	0.00	0.00	0.00	0.00
<i>Dupontia fisheri</i>	<b>-0.27</b>	0.09	-0.03	0.01
<i>Equisetum arvense</i>	0.00	0.00	0.00	0.00
<i>Eriophorum angustifolium</i>	0.00	0.00	0.00	0.01
<i>Eriophorum scheuchzeri</i>	0.12	0.07	0.04	<b>0.11</b>
<i>Festuca brachyphylla</i>	0.00	-0.01	0.00	0.00
Poaceae_sp3	0.00	0.00	0.00	0.00
<i>Hierochloe pauciflora</i>	0.00	<b>-0.20</b>	-0.07	0.03
<i>Luzula confusa</i>	0.00	0.00	0.00	0.00
<i>Lycopodium annotium</i>	0.00	0.00	0.00	0.00
<i>Pedicularis albolabiata</i>	0.00	0.00	0.00	0.00
<i>Pleuropogon sabinei</i>	0.00	0.00	0.00	0.00
Poaceae_sp1	0.00	0.00	0.00	0.00
Poaceae_sp2	0.00	0.00	0.00	0.00
<i>Poa arctica</i>	0.01	-0.04	0.09	-0.07
<i>Ranunculus hyperboreus</i>	0.00	0.00	0.00	0.00
<i>Salix arctica</i>	0.00	0.00	0.00	0.00
<i>Saxifraga foliolosa</i>	0.00	0.00	0.00	0.00
<i>Salix herbacea</i>	0.00	0.00	0.00	0.00
<i>Saxifraga hirculus</i>	0.00	0.00	0.00	0.00
<i>Salix reticulata</i>	0.00	0.00	0.00	0.00
<i>Salix richardsonii</i>	0.00	0.00	0.00	0.00
<i>Stellaria longipes</i>	0.00	-0.02	0.05	-0.04
<i>Vaccinium uliginosum</i>	0.00	0.00	0.00	0.00
Unknown_1	0.00	0.00	0.00	0.00
% of variance	0.45	0.27	0.11	0.09
Cumulative %	0.45	0.72	0.82	0.91

# 3

## **Determinants of species distribution in a spatially separated patchy tundra meta-community**

### 3.1 Introduction

How are local communities assembled and diversity maintained? This is a central thesis in the field of community ecology. There are two main ideas that state that a community is determined by species characteristics, called the niche-based assembly process, and another that states that a community is determined indifferent to species characteristics, called the neutral assembly process. The niche-based process is generally linked to environmental similarities. If the community compositions are explained by environmental conditions, I can assume that species-sorting by environment is an important assembly process (Pitman et al., 2001; Tuomisto et al., 2003; John et al., 2007; Kraft et al., 2008). The neutral process is generally linked to dispersal limitations (arising from demographic stochasticity). The range a species can disperse is limited, and the possibility of dispersal is related to the distance and abundance of the seed source. Here, even assuming that species are ecologically neutral, community and diversity patterns are explained by the spatial arrangement due to dispersal limitations (Hurtt and Pacala, 1995; Hubbell et al., 1999; Condit et al., 2002).

From the accumulation of these studies, general patterns are found in community assembly processes under different environmental conditions. Generally, the importance of species niches is stronger in harsh environmental conditions (Mori et al., 2013). In the study presented by Myers et al. (2013), it is

shown that assembly processes may change along a latitudinal gradient. In temperate forests, community composition is mainly explained by environmental conditions, which implies that niche differences between species are important. However, in tropical forests, community compositions were mainly explained by dispersal limitation, which indicates that the process is indifferent to species characteristics (neutral assembly process). These results indicate that the relative importance of the assembly process changes through environmental gradients (including a latitudinal gradient). However, because of interest in high diversity regions, knowledge of extremely harsh environments, such as the Arctic tundra, is scarce.

Variation-partitioning analyses of community composition across environmental and spatial gradients provide insights into the mechanisms underlying community assembly (e.g., Gilbert and Lechowicz, 2004; Cottenie, 2005; Legendre et al., 2009). If beta-diversity is strongly correlated with environmental variation, processes associated with “species-sorting” (e.g. environmental filtering) models of meta-community structure (e.g. Chase and Leibold, 2003) are likely operating, whereas if beta-diversity is strongly correlated with spatial variation, processes associated with ‘dispersal-assembly’ models (Hubbell, 2001) are likely playing a stronger role. The proportion of variation in beta-diversity that is unexplained by environment and space—representing the ‘error’ term—may be influenced by local stochasticity due to ecological drift (Legendre et al., 2009), regional sampling effects (Chase & Myers, 2011) or unmeasured environmental and spatial variables (Borcard et al., 2004).

This method is an effective tool to test the hypothesis that meta-community structures are determined by niche (environmental affinity) or trait-neutral processes (dispersal limitation) (Legendre et al., 2005; Legendre et al., 2008). However, simply interpreting this result is insufficient in understanding the importance of species characteristics during community assembly processes. Here, spatially explained community structure is interpreted as the result of demographic stochasticity; each species is closely distributed because of the dispersal limitation. In this concept, dispersal ability is assumed to be equivalent between species, but in reality dispersal ability is highly different among co-occurring species (Nathan and Muller-Landau, 2000; Muller-Landau, 2003; Gilbert et al., 2009) and could have a significant impact on the spatial patterns of communities. However, due to the difficulties in quantifying the dispersal ability of the meta-community structure, a limited number of studies have considered

species-specific dispersal ability in meta-community experiments (De Bie et al., 2012; Aiba et al., 2012; Jones et al., 2015).

In this study, to detect the effect of the dispersal process on the community, I performed research on “unique patchy vegetation areas” in sub-arctic tundra. In this region, vegetation exists only at the hollow on the parabolic dunes (Bégin, 1985). At these spatially separated vegetation patches, the way to establish the community is limited to dispersal methods. By using these unique vegetation types, I tried to identify which factor is most important for community assembly. 1) Hypothesis for the environmental affinity: Due to the harsh sub-arctic condition, the environment greatly explains the community structure and species distribution consistent with the former study presented. 2) Hypothesis for the dispersal ability: Since all patches are spatially separated, dispersal ability (traits) is important for the spatial distribution of species. To examine these hypotheses, I first used a variation partitioning method to detect what determines community composition (environment vs. spatial distance). After that, I also performed variation partitioning per species by using the method described by Aiba et al. (2012). From this result, I could determine the strength of environmental filtering and dispersal limitation per species. If this dispersal limitation per species is explained by dispersal traits, I can confirm the importance of dispersal ability in species spatial patterns.

Recently, reports on the importance of the effect of environmental gradients and those based on scale dependence of the relative importance have been reported (Chase, 2014; Garzon-Lopez et al., 2014; Brown et al., 2016). Chase (2014) clearly reviewed the scale dependence of community assembly patterns. Even in the same study system, as the sampling extent becomes larger, habitat associations become stronger and determine compositional shifts when environmental conditions change. As the sampling scale declines, the importance of environmental conditions decreases because of less habitat heterogeneity. On the other hand, there is an opposite theory, distance decay of the similarity; that is, the compositional similarity between paired assemblages generally decreases with increasing geographical isolation between them (Nekola and White, 1999; Morlon et al., 2008). According to this theory, it is predictable that if the scale becomes larger, community dissimilarity will be higher. To deal with these scale issues, I examined the analysis at three scales.

## 3.2 Materials and methods

### *Study site*

I conducted this study at the adjacent Whapmagoostui-Kuujuarapik, southeastern part of Hudson Bay ( $55^{\circ} 16' 50''$  N,  $77^{\circ} 45' 10''$  W) in northern Quebec, Canada (Fig. 3.1). Mean annual temperatures were  $-2.6 \pm 1.2^{\circ}$  C for 2001-2010. Mean annual precipitation was 656 mm, 40% of which fell as snow (Bhirt et al., 2011). This area is known as a forest-tundra ecotone, consisting of forest stands in the lowlands and treeless tundra on hills (Payette, 1976; 1983; Caccianiga et al., 2008). Most of this area is characterized by consolidated smooth granitic outcrops (Payette and Gauthier, 1972). Boreal coniferous forests exist only in the deep valley, which is facilitated by the accumulation of unconsolidated deposits and sheltered from extreme weather conditions (Payette and Gauthier, 1972). On the hills of the study site, due to the harsh environmental conditions (strong wind, low temperature, and smooth granitic ground), the vegetation can only establish at small hollows with thin organic deposits (Bégin, 1985). This condition contributes to the characteristic “patchy” distribution of the prostrate shrub heath tundra.

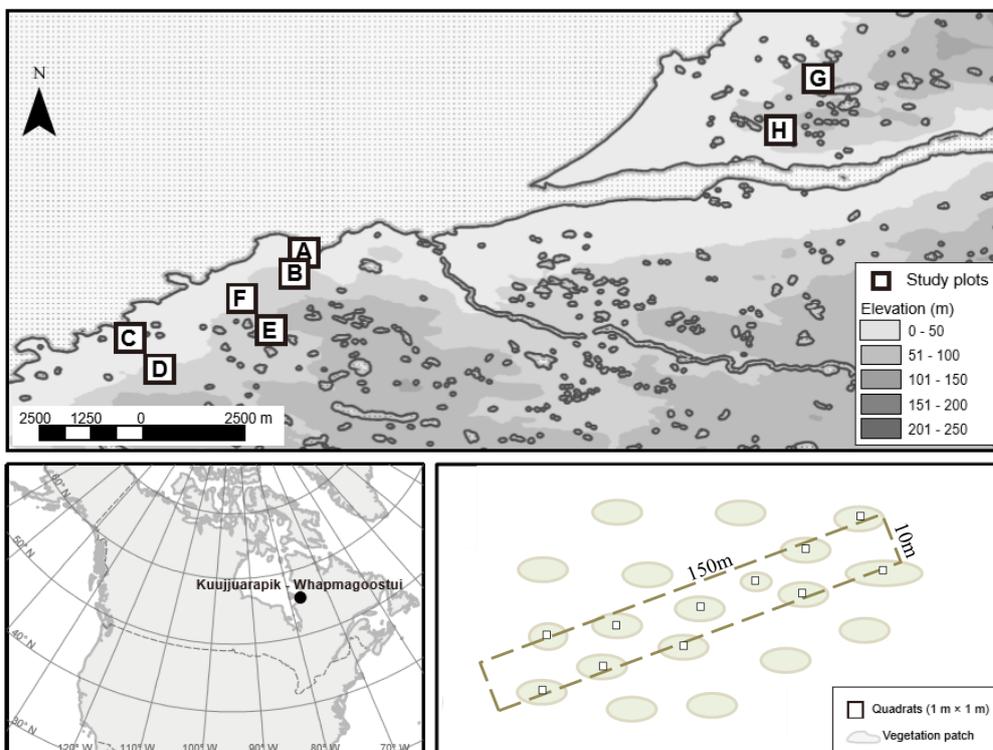


Fig. 3.1

Location, sampling design, and landscape of the study area. (a) the location of transect. (b) Location of Kuujjuarapik/Whapmagoostui. (c) Sampling design in the transects established in the patchy tundra habitats.

### *Field data collection*

Biological communities rarely occur in complete isolation, but often exist as part of a meta-community of local patches connected by dispersal (Wilson, 1992; Jones et al., 2015). Island and pond systems are classic examples of meta-communities, but in terms of vegetation, most of the meta-community theories are examined by using continuous systems like a forest at a broad scale (e.g. Myers et al., 2013).

To deal with scale issues in assessing the community assembly processes (Chase et al., 2014; Steinbauer et al., 2012; Tuomisto et al., 2012), our plots were set to analyze plant communities on three scales. First, on the outcrop that contains many areas of patchy vegetation, I set eight 10 m × 150 m plots (A-H). These plots are paired by two, each located closely, in a total of 4 pairs (AB, CD, EF, GH). Most distant plots were over 10 km apart. The vegetation survey quadrats (1 m × 1 m) were established at the center of every vegetation patch in every one of the 10 m × 150 m plots. In each plot, I surveyed every plant species appearing in the quadrat and estimated its percent cover by a guided visual observation using a 1 m × 1 m nylon mesh that was divided into 10 cm × 10 cm grids. This survey was conducted from late July to early August 2016.

In addition to the vegetation data, I also measured local environmental conditions in each quadrat (patch). In this study, I measured six environmental variables: soil water content (%), soil depth (cm), soil electrical conductivity (EC), soil pH, coverage of cryptogams (%), and patch size (m<sup>2</sup>). Soil water content was measured at three random positions using a soil moisture sensor (HH2, DeltaT Devices Ltd., Cambridge, UK). Soil depth was also measured at three random positions in each quadrat. The average of these three values for each of the environmental conditions was used. Soil at each plot was sampled from 0.5 to 2.0 cm depth after removing plant litter, and samples were returned to the laboratory to measure the pH and EC. These values were obtained using EC and pH meters (Twin EC and Twin pH, HORIBA Ltd., Kyoto, Japan) after extraction with ion-exchanged water (soil: water 1:5, 30 min. shake).

As plant functional trait data related to dispersal, seed mass (g), dispersal syndromes (gravity, zoochory, wind, and water) and plant height were obtained from the TRY database (Kattge et al., 2011; Kattge et al., 2020).

### *Data analysis*

The order of seed dispersal distance is sorted into four categories (Gallagher 2013), short-distance (<25 m), medium-distance (25 – 250 m), long and very long-distance (250 m – 10 km and >10 km, respectively), I performed the analysis at three spatial scales: broad scale (>10 km), medium scale (2 km), and fine scale (150 m). The broad scale included all 433 quadrats (1 replication), and the most distant quadrats are over 11 km in size. Medium scales include around 100 quadrats in two paired lines (AB-GH: 4 replications), and the most distant quadrats are approximately 2 km. Fine scales include around 50 quadrats in one line (A-H: 8 replications), and most distant quadrates are 150 m in size.

I performed variation partitioning (Borcard et al., 1992) for these three spatial scales to quantify the contribution of the environmental and spatial variables separately (Peres-Neto et al., 2006). While variation partitioning is generally performed at the community level, it was also performed at the species level based on multiple regression methods following Aiba et al. (2012). This approach is an application of variation partitioning based on a canonical redundancy analysis (RDA), as the result of variation partitioning based on RDA is the weighted means of  $R^2$  of multiple regressions for each of the constituent species (Peres-Neto et al., 2006). I used the values of adjusted  $R^2$  as the explained variance because normal  $R^2$  is strongly affected by the number of samples and explanatory variables (Peres-Neto et al., 2006).

Environmental variables included soil water content (%), soil depth (cm), soil electrical conductivity (EC), soil pH, coverage of cryptogams (%), and patch size (m<sup>2</sup>). These variables were log-transformed before the analysis. As spatial variables, I used principal coordinates of neighbor matrices (PCNM) that characterize spatial structure at multiple scales (Borcard and Legendre, 2002; Dray et al., 2006). The PCNM analysis produced a set of orthogonal variables derived from the geographical coordinates of the sampling locations (position of the sampling plot). Species used for this analysis were sorted only when the species appeared over 10 times.

First, I performed forward selection (999 permutations with an  $\alpha$ -

criterion of 0.05) for environmental and spatial explanatory variables to ensure that only significant variables were used in the final models. To avoid overestimation of the adjusted  $R^2$ , forward selection of variables was performed using the adjusted  $R^2$  of the full model as a second requisite, in addition to the significance of each variable (Blanchet et al., 2008). This step was only performed at the community level, and the same suite of variables was used for all species in later regressions at the species level to minimize the risk of selecting needless variables through repetition of variable selection.

I then performed three multiple regressions for each species to obtain the percentage of variance explained by environmental variables, spatial variables, and a combination of the two. Finally, total variances of species abundances in the quadrats were divided into four fractions: the unique contribution of environment (variance explained by environment independent of space), the unique contribution of space (variance explained by space independent of environment), the contribution of a spatially structured environment (variance shared by environment and space), and residuals by sequential subtractions. These fractions can be negative, and in such cases, the fractions are bounded to zero. I also performed variation partitioning at the community level based on the RDA. Later, procedures were conducted in the same manner as those of the species-level analysis.

Relationships between the unique contributions of space and functional traits were tested using the Kruskal–Wallis rank-sum test (for dispersal mode) or Spearman’s rank correlation (for seed mass and plant height).

### 3.3 Results

Species richness per quadrat (alpha diversity) was 2 to 14 species and 54 species in total (gamma diversity) in this study. As a result of variation partitioning at the community level, environmental control was a relatively stronger determinant in this study system. Scale dependence of the results was consistent with previous studies (Steinbauer et al., 2012; Tuomisto et al., 2012; Chase et al., 2014). As the spatial extent increased, the unique contributions of environment increased, and unique contributions of space decreased (Fig. 3.2).

The contribution of the spatially structured environment was higher at the local scale. Here, the  $R^2$  values of the middle scale are the mean of four replications and the local scale is the mean of eight replications.



(broad, middle, and fine). Black bars are purely explained by environments, gray bars are purely explained by space, and white bars are spatially structured environments. The values of middle and fine spatial scales are mean values of four sites and eight lines, respectively. Environmental variables mainly explain species distribution at every spatial scale. The proportions of spatial variables are gradually increased with a decrease in scale.

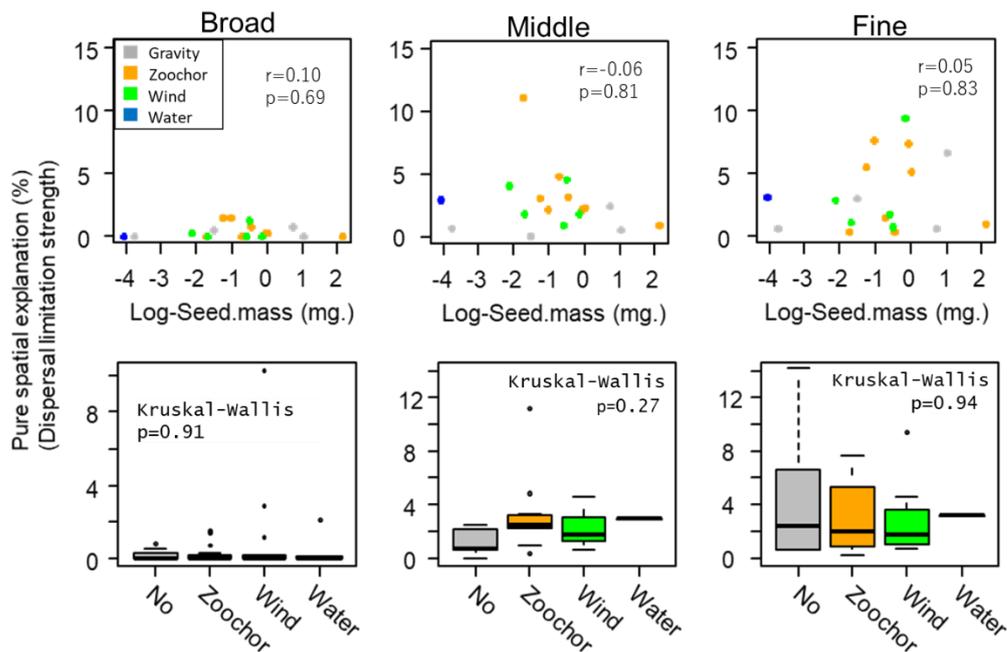


Fig. 3.4

The relationships between pure spatial contribution (i.e. the strength of dispersal limitation) and dispersal traits at three spatial scales (broad, middle, and fine). Upper panels show the relationships between seed mass and pure spatial explanation. Lower panels show boxplots of the dispersal syndromes. There were no significant relationships between dispersal limitation and dispersal traits.

### 3.4 Discussion

In this study, I examined how the community in environmentally harsh sub-arctic patchy distributed tundra vegetation is determined. First, I partitioned the importance of environmental affinity and spatial distance by using variation partitioning methods. After that, from the functional trait information, I assessed how the spatial patterns are generated, determined by dispersal ability or

demographic stochasticity.

Environmental conditions greatly explained community composition compared to spatial variables. This means that species characteristics related to environmental affinity are important community assembly processes (Fig. 3.2). Although some empirical studies have suggested that the contribution of environmental conditions is higher in harsh environments (Gough et al., 2001; Myers et al., 2013), these results are surprising. I set the plots on the homogeneous outcrop and plots were not set along the environmental gradient. Moreover, the number of measured environmental variables was limited due to logistical constraints. Such a low number of variables decreases the explanatory power of the environment (Brown et al., 2016). This result emphasizes how micro environmental conditions are important for community development.

Spatial factors had a relatively smaller explanation power than the environment. Even at broader spatial scales (10 km), spatial factors scarcely explained the community structure (Fig. 3.2). This result suggests that dispersal limitation is not strong in this region. The pure explanation power of the space was highest at the local scale. This result was consistent with the pattern introduced by Chase (2014), a niche-structured community at larger scales, and a neutrally structured community at smaller scales (Fig. 3.5). The report explained that as sampling scale declines, habitat heterogeneity declines and the importance of demographic stochasticity increases. Thus, there is a possibility that spatial structures are generated through demographic stochasticity.

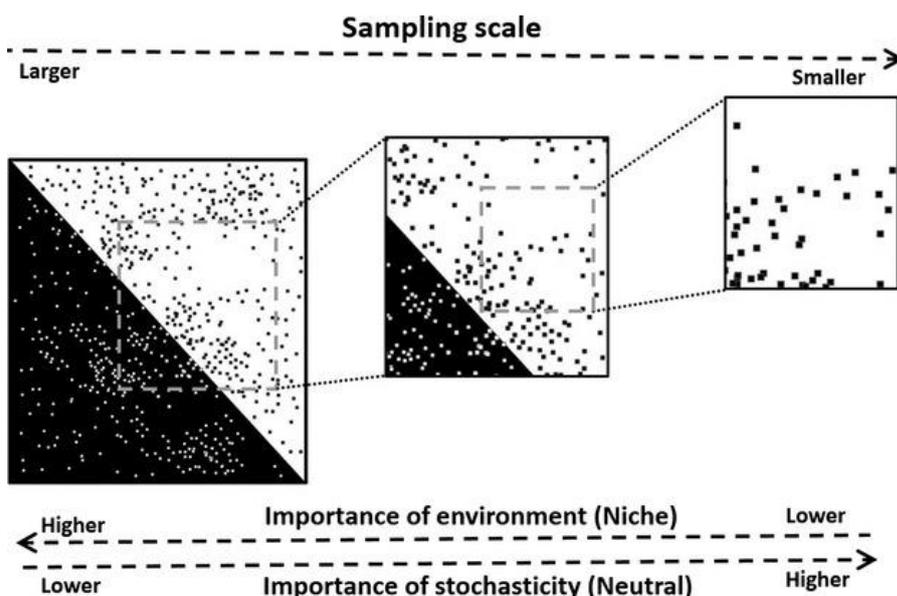


Fig. 3.5

Hypothetical depiction showing how sampling scale can influence the perception of the relative importance of environmental (niche) factors vs stochastic (neutral) factors. As the size of the sampling plot decreased, the relative importance of environmental factors declined while the relative importance of stochastic factors increased (Chase, 2014).

Theoretically, a pure spatial structure could emerge not only by demographic stochasticity but also by differences in species dispersal ability. To test that, I performed variation partitioning for species level and calculated the strength of dispersal limitations per species (Fig. 3.3). If these dispersal limitations per species were explained by traits related to dispersal ability, it was assumed that species spatial distribution patterns were determined by dispersal ability. However, there were no significant relationships between species-specific dispersal limitations and dispersal ability (Fig. 3.4).

The priority effect highlights the order of arrival to a habitat as being important in dispersal processes. This ordered assemblage promotes spatial patterns (Fukami et al., 2005; Fukami et al., 2016); however, there were no strong spatial patterns found in this study. It is said that the importance of establishment order is related to the habitat nutrient conditions, and the priority effect becomes weak in low-nutrient environments (Kardol et al., 2013). In such a harsh, nutrient-limited environment, environmental affinity is more important than dispersal orders, that is, priority effects are weak. This suggests that even if the dispersal ability is important to the order of arrival, it is eventually replaced by more environmentally suitable species. It is also said that the importance of habitat affinity is not detected at sites where dispersal is insufficient (De Bie et al., 2012; Soinen, 2016). Even if the site is suitable for certain species, they cannot be established without dispersal. This indicates that the species in this study area would be sufficiently dispersed. Taken together, the importance of dispersal ability is limited to existing community patterns in environmentally harsh conditions.

In summary, the patchy vegetation found in the sub-arctic tundra study site was mainly explained by environmental affinities, but dispersal ability did not influence the plant community composition. The small existing spatially explained influences on communities could be explained by demographic stochasticity at small spatial scales.

# 4

## **Deer herbivory affects functional diversity of forest floor plants via changes in competition-mediated assembly rules**

### 4.1 Introduction

In terrestrial ecosystems worldwide, large ungulates (e.g. deer) have created some major problems that have impacted biodiversity in addition to the properties of the ecosystems that they inhabit (Rooney, 2001; Côté et al., 2004). In forest ecosystems, herbivory by ungulates is an inherent part of natural consumptive processes, but their overabundance has been attributed to human activities and has been proposed to have adverse effects on vegetation (Côté et al., 2004; Takatsuki, 2009). Deer have direct and indirect effects on biotic interactions among coexisting plant species (Rooney and Waller, 2003). The former includes selective herbivory associated with the palatability of plants (Augustine and McNaughton, 1998), while the latter is exemplified by altered habitat conditions through their browsing that can result in gap formation and the alteration of nutrient cycling (Wardle et al., 2002; Bardgett and Wardle, 2003). As a result, the structure, composition and diversity of plant communities can be substantially altered (Russell, 2001; Horsley et al., 2003). To safeguard vegetation from overgrazing by ungulates, fences designed to exclude these large herbivores have often been established in various regions, and the resultant effects on local plant diversity are mixed (Côté et al., 2004; Inatomi et al., 2012). To face this complication, rigorous assessment of how intense herbivory alters

the organization of biodiversity is necessary. In doing so, it is worth focusing on the theory of community assembly; however, while most research on the consequences of establishing ungulate fences have primarily described patterns of biodiversity change, the underlying assembly processes have not been fully assessed. In order to guide conservation and management activities in the face of ungulate overabundance, such a gap in our knowledge should be urgently addressed.

There are two possible mechanisms of community assembly: deterministic and stochastic assembly (Chase et al., 2011). The deterministic process is based on the niche theory (Hutchinson, 1959). When this process is dominant, community composition should depend on local biotic and abiotic environmental conditions. On the other hand, when stochastic processes are dominant, community assembly is primarily shaped by randomness (Chase et al., 2011). The biotic interactions among species often act strongly at a fine scale (de Bello et al., 2013), and these interactions are affected by local factors such as environmental conditions or disturbance. Disturbance has been shown to have various effects on community assembly through altering the relative importance of deterministic and stochastic processes (Chase, 2007; Vellend et al., 2007; Chase et al., 2011). This may be the case for deer herbivory (Begley-Miller et al., 2014; Ohashi and Hoshino, 2014).

Recently, there has been a rapid expansion of trait-based approaches to reveal community assembly processes at local scales (Kraft et al., 2008; Angert et al., 2009; Cadotte et al., 2011; Weiher et al., 2011; Götzenberger et al., 2012; Kraft et al., 2014). Functional traits are any measurable feature that potentially affects performance or fitness (Cadotte et al., 2011). Traits determine if species can survive (Lavorel et al., 1997) and how species interact with one another, which provides information on the strength of competition and the efficiency of consumptive interactions (Davies et al., 2007). When multiple trait dimensions are considered, ecological differentiation between species may emerge. These sets of traits that are likely relevant to ecological tolerance, ecological niches and competitive abilities (Cadotte et al., 2011; Mouillot et al., 2013). Importantly, functional diversity (FD), the dispersion of species in multidimensional trait space, provides information on how ecologically similar or dissimilar species are assembled (Petchey and Gaston, 2007; Laliberte et al., 2010). In theory, a significant departure from random assembly can generate two opposing patterns that suggest some deterministic processes. These patterns can emerge as either a

low or a high FD, which indicates trait clustering or overdispersion, respectively. Under the classical assumption, ecologically dissimilar species can coexist through niche partitioning (MacArthur and Levins, 1967), leading to trait overdispersion. On the other hand, shared adaptive characteristics among syntopic species promotes the co-existence of species with similar traits. Under intense abiotic interactions, traits related to ecological tolerances are important (Cornwell et al., 2006; Grime, 2006). Under resource rich conditions, species with high competitive ability are superior to those with a poorer ability to compete with others (Mayfield and Levine, 2010). These processes promote trait clustering. Likewise, the trait-based approach allows important mechanisms underlying community assembly (Götzenberger et al., 2012) and the response of biodiversity (Mori et al., 2013) to be inferred.

Serious ecological concerns driven by the overabundance of sika deer (e.g. overgrazing/browsing) have been frequently expressed in Japan (Takatsuki, 2009). Such concerns exist even for areas with pristine vegetation, which have been designated as protected areas. In Shiretoko National Park (located on the northern island of Japan), deer overabundance has resulted in numerous ecological issues, including negative impacts on forest understory plant communities (Kaji et al., 2004). For the purpose of conserving forest vegetation, deer exclosure fences were established in the early 2000s. As more than a decade has passed since then, I expect that both the presence and absence of selective deer herbivory has considerably changed the biotic interactions among plant species in these forests. This is because the situation in these areas is now characterized by an over-abundance and an under-abundance of deer, which expectedly have some impacts on forest understory communities. Here, by assessing differences in community assembly processes between these two ecological extremes (i.e. deer overgrazing and no-grazing), I aim to detect the ecological roles of sika deer on the mechanisms of plant species coexistence and its consequences for the organization of biodiversity. I envision that this study will provide important information for management and policy to cope with deer overabundance in the study region as well as in other regions.

## 4.2 Materials and methods

### *Study site*

This study was conducted in Shiretoko National Park, which is located in northeastern Hokkaido, the northernmost island of Japan (Mori et al., 2016). This place is registered as a UNESCO (United Nations Educational, Scientific and Cultural Organization) World Natural Heritage Site because of its high biodiversity. The mean annual temperature and precipitation at the study site between 2004 and 2014 were 6.5 °C and 1271 mm, respectively (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). In this region, the population of sika deer (*Cervus nippon yesoensis*) has increased since the late 1980s, and the ground layer of the plant community has transformed in areas of high deer density. To address this problem, deer enclosure fences have been placed in these regions. Horobetsu, one of the most highly populated areas in Shiretoko Peninsula, is located in northcentral Shiretoko Peninsula (44°06'00"N 145°01'42"E). The forest floor is typically covered with snow from November to May (Kubota, 2000). The forest is characterized as a mixed coniferous and broad-leaved natural forest, dominated by *Abies sachalinensis*, *Quercus crispula* and *Kalopanax septemlobus*. Since around 2000, the deer density of this area has been as high as approximately 5~10 deer/km as estimated by light censuses in autumn (<http://dc.shiretoko-whc.com/>). To reduce deer grazing on vegetation, the deer enclosure fences were constructed in 2003. As a decade has passed since the construction of enclosure fences, the coverage of ground layer plants inside the boundaries of the fence has been recovering.

### *Field data collection*

To quantify the effects of deer foraging on the compositional characteristics of the ground layer plant community, I established two plots in the forest. The enclosure plot had fences to protect vegetation from deer herbivory. The control plot, which was located outside the boundaries of the fence, was exposed to deer herbivory. The sizes of the enclosure and control plots were 80 m × 120 m (0.96 ha) and 100 m × 100 m (1.00 ha), respectively. These plots were located close together so that there was little difference in the species composition of canopy trees (The Forestry Agency of Japan, 2004). These plots were partitioned into 96 and 100 10 m × 10 m subplots in the enclosure and control plot, respectively. At the center of each 10-m<sup>2</sup> subplot, I established a 1 m × 1 m quadrat (i.e. 96 and 100 quadrats in the enclosure and control plots, respectively). Taxonomic identification and percent cover of each plant species smaller than 50 cm in height within each

quadrat were estimated through visual observation guided using a nylon mesh divided into one-hundred 10 cm divided int. This survey was conducted in June 2014, the season during which most herbaceous species appear on the forest floor after thawing.

To evaluate the effects of biotic and abiotic conditions on plant community structure, I relied on several environmental variables, including three soil variables (water content (WC), electrical conductivity (EC) and pH) and four stand structural variables (tree species richness, stem number, total basal area of trees, and canopy openness) of the 10 m x 10 m quadrats. To evaluate local crowdedness, which restricts species distributions through, for example, the prevention of seed colonization and the restriction of light availability at fine scales (Berntson and Wayne, 2000; Mori and Takeda, 2003), I used vegetation ground cover on the forest floor as an additional environmental variable. This metric was arcsin-transformed to improve normality (Snedecor and Cochran 1967; Sokal and Rohlf 2012). Soil WC (%) and soil EC (mS/cm) were the mean of three repeated random measurements in the 1 m × 1 m quadrat, using a soil moisture meter (DM-18, TAKEMURA DENKI, Tokyo, Japan) and an EC tester (soil test HI 98331, Hanna Instruments, Chiba, Japan), respectively. Soil pH was measured with a pH meter (LAQUA twin B-71X, HORIBA, Ltd, Kyoto, Japan). I calculated canopy openness with CanopOn2 (<http://takenaka-akio.org/etc/canopon2>), using hemispherical photographs taken by a Sony NEX-5 camera (SONY, Tokyo, Japan) mounted with a fish-eye lens (MADOKA, YASUHARA Co., Ltd., Tokyo, Japan) at the center of each subplot. The stand structural variables were sourced from the Forestry Agency of Japan (2014), which measured size and species identity of all trees taller than 2 m in tree height. Vegetation ground cover of each 1 m<sup>2</sup> quadrat was measured to the nearest 1% using a mesh divided into a 10 cm × 10 cm scale.

### *Trait data collection*

I used ten plant functional traits, which were related to growth, survival and responses to environmental change (Pérez-Harguindeguy et al., 2013). They included leaf area (LA; mm<sup>2</sup>), specific leaf area (SLA; mm<sup>2</sup>/g), chlorophyll content (SPAD units), plant maximum height (plant height; cm), leaf phenology, life form, growth form, herbaceous or woody species, seed mass (g), and dispersal mode. For LA, SLA and chlorophyll content, I collected and measured five

samples from five individuals for each plant species (25 leaf samples for each species). First, I collected a fully formed adult leaf and measured chlorophyll content using a Minolta SPAD-502 (Osaka, Japan). I immediately scanned leaves before drying and calculated LA from scanned images using Image-J (Rasband, 1997–2008). For plant species with compound leaves, I used leaflets. To calculate SLA, I then dried leaves for 72 hours at 80 degrees Celsius to obtain the dry weight of leaves. Other traits were extracted from the literature and encyclopedias. Trait measurement and collection followed protocols outlined in Pérez-Harguindeguy et al., (2013).

### *Data analysis*

To describe the effect of deer presence/absence on plant communities, I calculated species richness and Shannon's diversity for measures of species diversity (Magurran and McGill, 2011). To examine changes in plant community structure, I also measured compositional dissimilarity using the Bray-Curtis index, which is one of the most commonly used measures of vegetation dissimilarity (Anderson et al., 2011). For evaluating differences in species-abundance distribution between the two plots, I plotted the frequency of occurrence of each plant species within all quadrats (the frequency of occurrence across all quadrats) with their dominance rank within the meta-community (hereafter, species dominance-rank curve). I visually checked for differences in the curve and the list of dominant species between the two plots.

I additionally calculated community-weighted mean (CWM) trait values, which is the mean trait value of all species in the community weighted by their relative abundance (Garnier et al., 2004) for five numeric plant traits, which are likely to affect by deer herbivory: LA, SLA, chlorophyll content, plant height and seed mass. LA has been variously related to climatic variation (Pérez-Harguindeguy et al., 2013). Furthermore, deer selectively graze large leaves of *Trillium grandiflorum* (Knight, 2003). SLA indicates the thinness of the leaf. Leaf longevity and leaf N content are related to SLA (Reich et al., 1997). Chlorophyll is one of the most important chemical substances for photosynthesis and is highly correlated with tissue N (Markwell and Blevins, 1999). These traits, which are related to the resource abundance in leaves, are likely vulnerable to deer herbivory. Plant maximum height is also associated with competitive ability (Vojtech et al., 2008) and vulnerability to deer herbivory. Seed mass is related to

survival and establishment in the face of environmental hazards (Pérez-Harguindeguy et al., 2013).

I calculated functional diversity using the functional dispersion ( $FD_{is}$ ) index, developed by Laliberte and Legendre (2010).  $FD_{is}$  is the mean distance of all species in the community in multidimensional trait space, weighted by their relative abundance. I selected this index because  $FD_{is}$  is independent of species richness, can take into account species abundances, and can be used for multiple traits (Laliberte and Legendre, 2010). In this study, I calculated  $FD_{is}$  using all functional traits I collected (ten traits) to express ecological differentiation between species (Cadotte et al., 2011; Mouillot et al., 2013). To evaluate the magnitude of deviation from random assembly, I calculated the Standardized Effect Size (SES) of  $FD_{is}$ . SES was defined as  $(FD_{isobs} - FD_{isnull}) / FD_{issd}$ , where  $FD_{isobs}$  is observed  $FD_{is}$  in actual communities, and  $FD_{isnull}$  and  $FD_{issd}$  are the mean and standard deviation of  $FD_{is}$  values calculated by 999 randomizations, respectively. I repeated this procedure for both enclosure and control plots. Randomization was based on the independent swap algorithm (Gotelli, 2000), which maintains species occurrence frequency and sample species richness based on meta-community. Positive and negative values of SES indicate greater and lower functional diversity than random expectation (trait overdispersion and trait clustering), respectively. To examine how biodiversity was structured, I tested a correlation between diversity measures (SES of  $FD_{is}$  and Shannon's diversity) and environmental variables across quadrats. I used Standardized major axis (SMA) regression to describe how these variables were related (Warton et al., 2006; Sokal and Rohlf, 2012).

### 4.3 Results

#### *Field sampling*

There were 54 total species out of all the study sites. Thirty-five species were found inside the fence (enclosure), and 43 species were found outside the fence (control). Twenty-four species were held in common. The four dominant species were *Dryopteris expansa*, *Maianthemum dilatatum*, *Sasa kurilensis* and *Toxicodendron orientalee*. The coverage of all four of these species was low in the control plot (Fig. S4.1). In addition, almost all of the other species common to both plots had lower coverage in the control plot than in the enclosure plot.

## Species diversity

Mean species richness and Shannon's diversity were significantly higher in the control plot ( $p < 0.001$ ; t-test) (Figs. 4.1a, 4.1b). The mean Bray-Curtis dissimilarity value was also significantly higher in the control plot ( $p < 0.001$ ; t-test) (Fig. 1c). On the other hand, mean vegetation ground cover was significantly higher in the exclosure plot ( $p < 0.001$ ; t-test) (Fig. 4.1d). The dominance-rank curve showed different forms between the two plots (Fig.4.2). In the exclosure plot, the dominance of each species decreased sharply as species rank decreased. Species were thus divided into dominant and rare species. On the other hand, the control exhibited a smooth curve that had more species with an intermediate frequency.

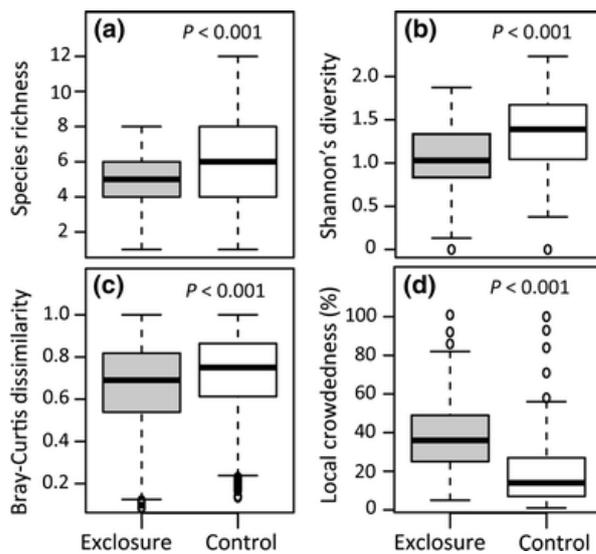


Fig. 4.1. Comparison of (a) species richness and (b) Shannon's diversity index and (c) Bray-Curtis dissimilarity index and (d) Coverage (%) values for each quadrat between the exclosure and control plots. Number of samples used in (a), (b), and (d) is 96 and 100, and in (c) is 4560 and 4950 in the exclosure and control plots, respectively. Significance was assessed with a t-test.

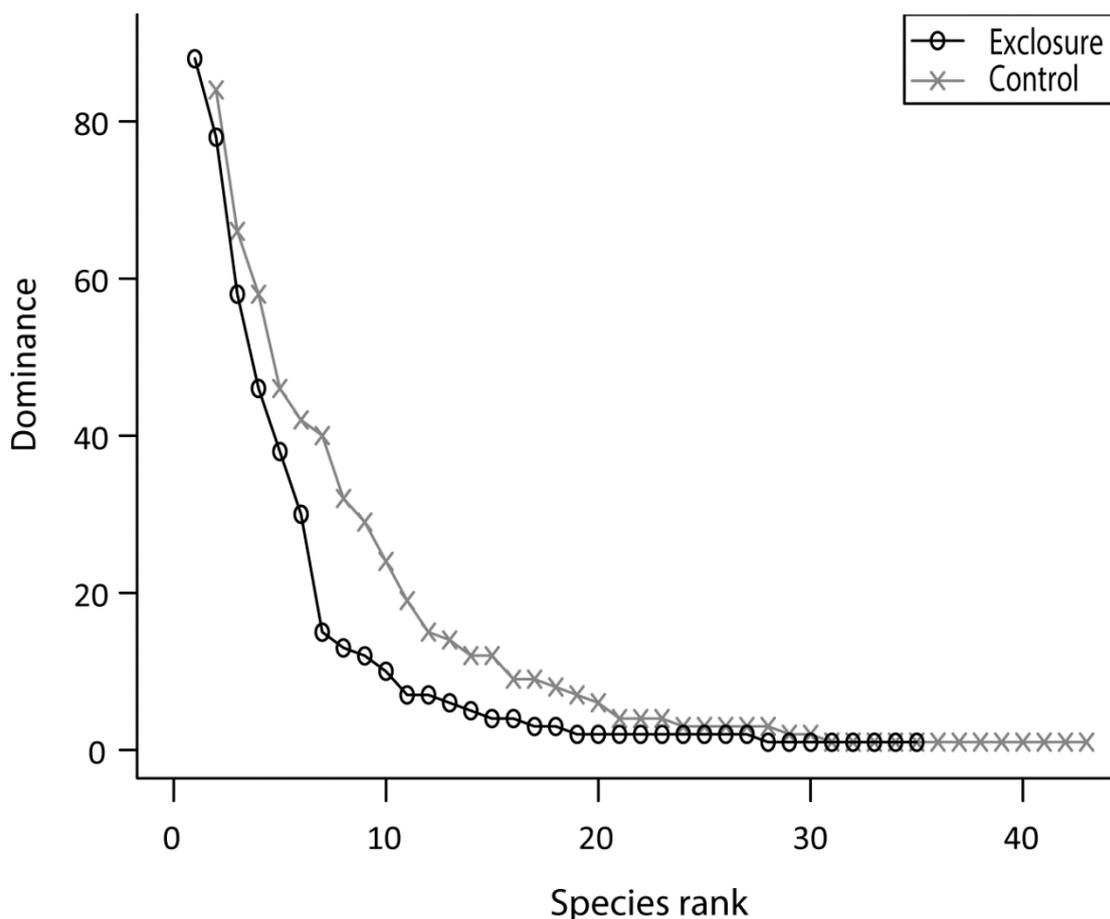


Fig. 4.2. Species dominance-rank curve of the enclosure and control plots. The number of occurrences across all quadrats.

### *Functional diversity*

The control had significantly lower LA and chlorophyll content value compared to the enclosure plot (Table 4.1). Other traits (SLA, plant height, seed mass) were not significantly different. There was no significant difference between the enclosure and control plots in functional diversity (SES) (the mean values of SES were -0.09 and 0.09 and the variances were 0.97 and 0.51, respectively).

In terms of relationship between SES and environmental variables, there was significant negative correlation between SES and local crowdedness in the enclosure plot ( $r = -0.248$ ,  $p < 0.05$ ) (Table 4.2, Fig. 4.3a). On the other hand, there were no other significant correlations between SES and environmental variables in both plots (Table 4.2), including local crowdedness in the control plot ( $r = -0.110$ ,  $p = 0.285$ ) (Fig. 4.3b). In the enclosure plot, there was a significant negative correlation between environmental variables and Shannon's diversity ( $r$

= -0.317,  $p < 0.01$ ) (Fig. 4.4a). In the control plot, however, there was no significant correlation between environmental variables and Shannon's diversity ( $r = -0.116$ ,  $p = 0.254$ ) (Fig. 4.4b).

Table 4.1. Differences in the community-weighted mean trait value between exclosure and control plots. P-values are from t-tests.

Functional trait	Exclosure CWM		Control CWM		P-value
	Mean	SD	Mean	SD	
Leaf area (cm <sup>2</sup> )	57.92	12.243	46.9	14.842	<b>&lt; 0.001</b>
SLA (cm <sup>2</sup> g <sup>-1</sup> )	398.18	78.342	412.58	67.008	0.171
Chlorophyll content (SPAD)	32.1	2.104	31.38	2.65	<b>&lt; 0.05</b>
Plant height (cm)	7.72	4.011	8.06	3.43	0.529
Seed mass (g)	16.29	8.967	19.65	18.627	0.11

Table 4.2. The correlation coefficient (r) between the standardized effect size of functional diversity and environmental variables.

Environmental variables	Exclosure		Control	
	R	P-value	R	P-value
Soil water content	-0.162	0.117	0.171	0.096
Soil EC	0.027	0.794	0.033	0.751
Soil pH	0.010	0.920	-0.040	0.702
Tree species richness	0.032	0.758	-0.048	0.643
Stem number	0.195	0.058	0.020	0.845
Total basal area of trees	-0.095	0.359	-0.082	0.428
Canopy openness	-0.034	0.745	0.075	0.465
Local crowdedness	-0.248	<b>0.016</b>	-0.110	0.285

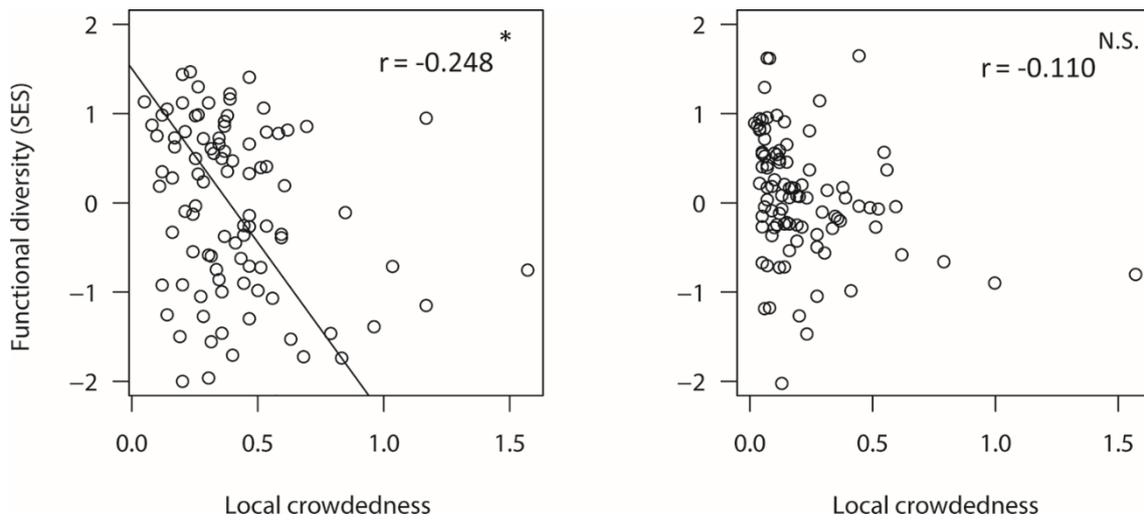


Fig. 4.3. The correlation between standardized functional diversity and local crowdedness index, which is arcsin transformed, of the (a) exclosure plot and (b) control plot. The regression line is the standardized major axis (SMA) between two components.

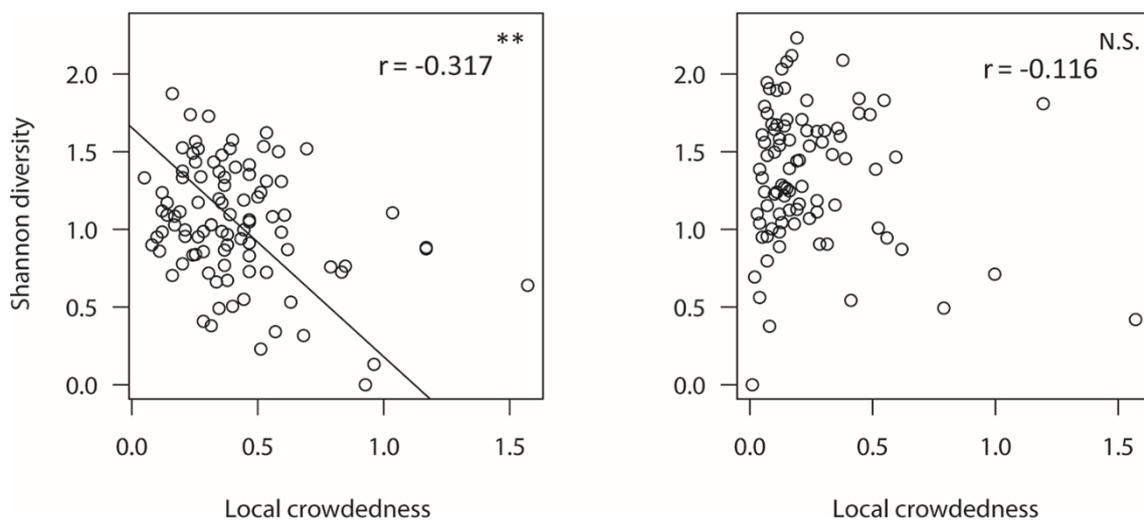


Fig. 4.4. The correlation between Shannon's diversity and local crowdedness index, which is arcsin transformed, of the (a) exclosure plot and (b) control plot. The regression line is the standardized major axis (SMA) between two components.

## 4.4 Discussion

By focusing on taxonomic and functional characteristics of local plant communities on the forest floor, I found that deer herbivory played a significant role in shaping local plant communities. Importantly, with the help of a trait-based approach, I detected changes in community assembly processes at a local scale, which may explain the underlying mechanisms of biodiversity organization.

### *Taxon- and trait-based evaluation*

I compared several community metrics of forest floor plants between the two plots with (exclosure plot) and without (control plot) fences. The significantly lower local crowdedness in the control plot than in the exclosure plot (Fig. 4.1d) suggests that deer herbivory plays a significant role in suppressing the growth and survival of plants on the forest floor. Species richness, Shannon's diversity and Bray-Curtis dissimilarity all showed higher values in the control plot than in the exclosure plot (Figs. 4.1a-c). Previous reports on the effects of deer herbivory on plant diversity have provided mixed results, depending on whether deer primarily consume dominant species or not (Côté et al., 2004). At this study site, some dominant species, which have higher levels of abundance (Fig. S4.1) could interrupt the prosperity of others in the exclosure plot, likely leading to a more skewed dominance-rank curve in the exclosure plot than in the control plot (Fig. 4.2). These results are consistent with the work of Schütz et al., (2003), who reported that the reduction of dominant species by deer herbivory could enhance plant species richness. Taken together, I speculate that dominance reduction by deer herbivory is one of the most important determinants for the maintenance of species diversity, likely leading to the relatively low and high levels of species diversity in areas with and without fences, respectively. Additionally, the lack of herbivory likely decreases the dissimilarity among local assemblages, leading to the homogenization of communities through the disproportionate representation of dominant species.

I additionally used the trait-based approach to evaluate compositional characteristics of forest floor plant communities in response to under- and overgrazing by deer. Here, I observed higher CWM trait values in LA and in chlorophyll content in the exclosure plot than in the control plot (Table 4.1). Deer are known to selectively graze large-leaved plants (Knight, 2003), which likely

results in selection favoring smaller CWM trait values of LA. For chlorophyll content, which is highly correlated with tissue N (Markwell and Blevins, 1999) and is thus likely vulnerable to deer herbivory (Ammer and Mei, 1996), I infer that species with high N tissue decreased in abundance and that the CWM value of chlorophyll was lower in the control plot than in the enclosure plot. From the skewed dominance-rank curve, CWM trait values are likely to be highly influenced by dominant species in the enclosure plot. Both high values of leaf area and chlorophyll content provide enhance photosynthetic abilities. Although the survival of these species cannot be explained by only these traits, I speculate that high values of these traits are more advantageous in situation lacking deer herbivory. In summary, plants with large leaves and high chlorophyll content are more competitive, but they are also more vulnerable to deer herbivory.

### *Community assembly processes*

Because functional diversity deviated from random expectation, I examined community assembly processes at the local scale. In the control plot, values of standardized functional diversity were distributed around zero (Fig. 4.3b), and there was no significant relationship between standardized functional diversity and environmental variables (Table 4.2). These results suggest that deterministic assembly processes, such as interspecific competition or environmental filtering, were weak in this plot. That is, stochastic processes predominated in the control plot. When vegetation coverage is reduced by deer, the likelihood of competitive exclusion (i.e. species exclusion by some species with competitive traits) might decrease, and opportunities for species establishment may thus increase (Grime, 2006; Mayfield and Levine, 2010). This finding is consistent with the idea that disturbance promotes random assembly processes (del Moral, 2009). When food resources are depleted through selective herbivory, deer are known to graze on plants regardless of their palatability (Balgooyen and Waller, 1995; Waller and Alverson, 1997; Takahashi and Kaji, 2001; Côté et al., 2004). I infer that intensive deer herbivory has reduced vegetation coverage (Fig. 4.1d), regardless of species traits at the study site. Stochastic processes often enhance species diversity (e.g. Chase, 2010), allowing various species to emerge independent of their traits.

In the enclosure plot, a significant shift in community assembly processes of plant communities was observed according to local habitat conditions. Specifically, the magnitude of deviation of trait diversity from the random

assemblage was significantly negatively correlated with local crowdedness (Fig. 4.3a). This result implies that plant communities in the enclosure plot were structured along a gradient of trait overdispersion as opposed to trait clustering. That is, there was a gradual change in the relative importance of these different assembly processes along a gradient of local crowdedness. Trait overdispersion within the enclosure plot suggests that species in each quadrat were functionally less similar than expected by chance. The underlying mechanism for this pattern may be limited similarity (MacArthur and Levins, 1967). Coexisting species with similar traits are often limited by interspecific competition (MacArthur and Levins, 1967; MacArthur, 1972). Consequently, coexistence of functionally distant species is permitted in local habitats, as a result of their niche differentiation (Chesson, 2000). These niche differences can arise from species specific interactions with resources, specialist consumers, pathogens, mutualists or temporal environmental heterogeneity (Tilman, 1982, 1988; Chesson, 2000; Sammul et al., 2006; Chesson and Kuang, 2008). In this study, with decreasing local crowdedness, more niches became available to more species. By using multivariate functional diversity, I aimed to evaluate high dimensionality of niches, which cannot be explained simply by single traits (Mouillot et al., 2013). Niche partitioning promotes the coexistence of various species, resulting in higher species diversity in less crowded localities (Fig. 4.4a). On the other hand, I found that species with similar traits were assembled (trait clustering) in quadrats characterized by high local crowdedness. Considering that few species became dominant and that the majority of species decreased their abundance (Fig. 4.2), the observed trait clustering could be explained by differences in species competitive ability. When a habitat is crowded, competition for light and nutrients becomes intense (Berntson and Wayne, 2000). I speculate that weaker competitors had been excluded by competitively superior species that had functional traits associated with high competitive ability (e.g. Kunstler et al., 2012; Kraft et al., 2014), leading to trait clustering (Mayfield and Levine, 2010). This disappearance of weaker competitors could result in lower species diversity in more crowded localities (Fig. 4.4a).

In the enclosure plot, only local crowdedness was correlated with the functional diversity patterns of each quadrat. To understand the mechanisms underlying the functional diversity gradient further, I need to determine which factors cause differences in local crowdedness among localities (i.e. quadrats). Unfortunately, our snapshot datasets do not provide a complete picture, but the

monitoring data support our interpretation of the factors that caused variability in local crowdedness among localities. According to a report of the Forestry Agency of Japan (2014), the abundance of dominant species has sharply increased since the establishment of the fence (Fig. S4.2). This result suggests that crowded localities have continued to expand up to the present day. From these data, I infer that the observed spatial difference in crowdedness among localities could reflect a temporal difference in vegetation change since deer herbivory was excluded (i.e. space-for-time substitution). By constructing the fence, deer herbivory has reduced local crowdedness and relaxed interspecific competition among plants, likely leading to deterministic community assembly based on the competitive ability of each species. As a consequence, plant communities in these areas have been homogenized and biodiversity has decreased (i.e. species and functional diversity) in the absence of deer herbivory.

### *Implications*

I studied two extremes: deer overgrazing and no-grazing areas where the assembly processes of forest understory plants were substantially affected. In overgrazing areas, community assembly was independent of species traits through deer-induced competitive relaxation among species. In contrast, in the area free from deer herbivory, competitive relationships were a major determinant of community assembly. In particular, I speculate that underlying assembly processes have been gradually dominated by species that have several functional traits reflecting high competitive ability, such as high chlorophyll content and large leaf area. Based on this finding, I emphasize that promoting species coexistence via niche partitioning through the natural, consumptive process of deer grazing is necessary. High and low species richness and species diversity and dissimilarity in the control and exclosure plots, respectively, can be explained by such an alternation of community assembly processes.

Deer overabundance has been caused by human activities, which include anthropogenic warming (Forchhammer et al., 1998; Loison et al., 1999), land-use change (Bobek et al., 1984; Roseberry and Woolf, 1998), reduction in hunting pressure (Brown et al., 2000; Riley et al., 2003) and loss of keystone predator species (Rooney, 2001). To mitigate the negative consequences of deer overabundance, deer exclosure fences aimed at conserving vegetation have been commonly constructed around the world. Fences have been reported to be

efficient in promoting the regeneration of trees in forests (Shimoda et al., 1994; Nomiya et al., 2002; Kumar et al., 2006) and conserving specific species (Fletcher et al., 2001; Tamura et al., 2005) and vegetation ground cover (Kurten and Carson, 2015; Tamura, 2015). From the perspective of ecosystem-based management, I envision that establishing fences is not an ideal solution. Recently, the importance of considering natural processes has been recognized for the conservation of biodiversity and the sustainability of forest ecosystems (Christensen and Bartuska, 1996; Lindenmayer and Franklin, 2002; Mori, 2011). I reaffirmed that deer herbivory is a natural and crucial process for species coexistence and community assembly through the relaxation of competitive relationships among plant species. While deer overabundance can surely negatively impact vegetation, the unrealistic scenario of completely eradicating grazing is insufficient for restoring and conserving the natural processes underlying plant diversity. My study suggests that to conserve vegetation in areas that are currently threatened by the overabundance of large herbivores, it will be necessary to employ some proactive measures, such as controlling populations of large herbivores, in addition to passive measures, such as fence establishment.

## Appendix 4.1

**Fig. S4.1**

Comparison of the coverage of four dominant species between exclosure and control plots. Coverage (%) is the mean value of all quadrats (96 and 100, respectively) from the visual estimation of data in this research. The exclosure plot shows higher coverages of these four species than the control plot.

Fig. S4.1

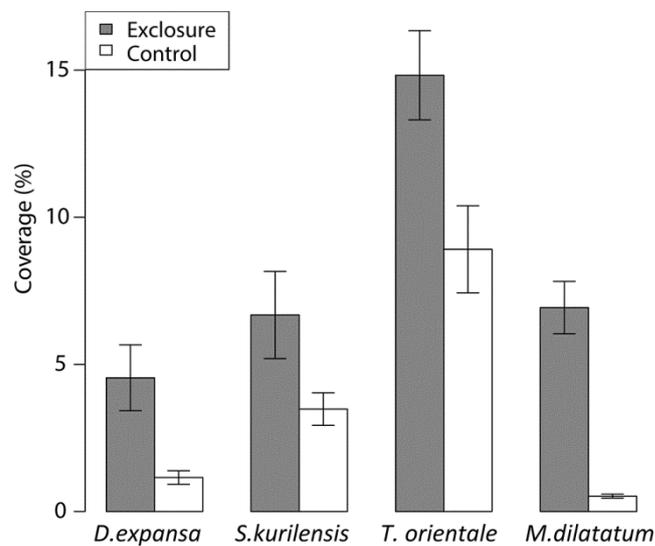


Fig. S4.1. Comparison of coverage (%) in the exclosure (gray bars) and control (white bars) plot for four dominant species, *Dryopteris expansa*, *Sasa kurilensis*, *Toxicodendron orientale* and *Maianthemum dilatatum*. Coverage (%) is the mean value of all quadrats in the exclosure and control plot (96 and 100, respectively). Standard error is used for error bars.

**Fig. S4.2**

The transition in the abundance of dominant species in Horobetsu, Shiretoko Peninsula, from the report by The Forestry Agency of Japan (2014). Since the establishment of deer exclosure fences in 2001, surveys of understory plant coverage have been conducted every 2-4 years. The data I used were the mean of 4-5 permanently surveyed quadrats and were written in percentages. The survey quadrats are in the same plots that I used, but these plots do not overlap with ours. *Toxicodendron orientale*, the most abundant species, has been increasing rapidly. *Dryopteris expansa* and *Maianthemum dilatatum* are steadily increasing in abundance and appear likely to continue to do so in the future.

Fig. S4.2

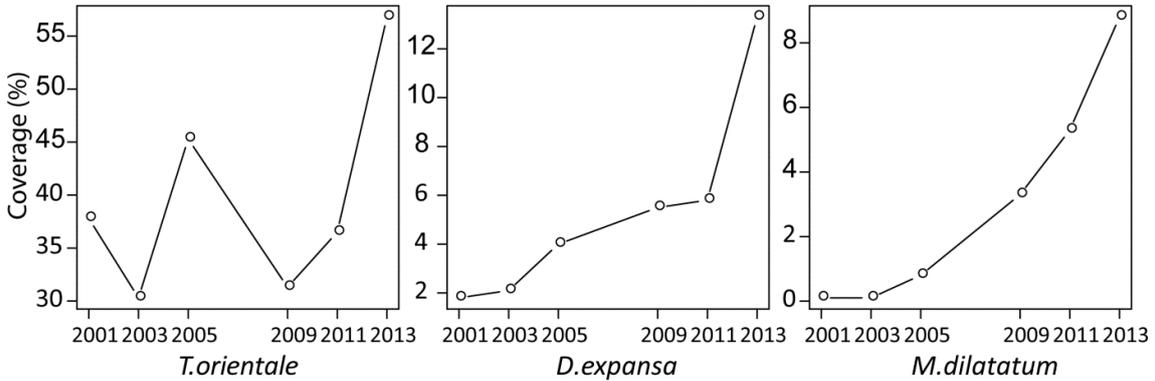


Fig. S4.2. The transition in coverage of three abundant species (*Toxicodendron orientale*, *Dryopteris expansa*, *Maianthemum dilatatum*) from 2001 to 2013 in the exclosure plot.

### **Appendix 4.3 (Reference list: trait data collection)**

- Asao S (2005) Sadao Asano's Biological Flora of Japan (In Japanese) Zenkoku Noson Kyoiku Kyokai, Tokyo, Japan
- Iwatsuki K (1999) Wild Flowers of Japan Ferns (In Japanese) Heibonsha, Tokyo, Japan
- Satake Y, Ohwi J, Kitamura S, Watari S, Tominari T (1982) Wild Flowers of Japan Herbaceous Plants Vol. I (In Japanese), Heibonsha, Tokyo, Japan
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# 5

## **The interactive effects of press and pulse disturbances on plant community reassembly**

### **5.1 Introduction**

Disturbance is an important ecological process that greatly influences plant diversity and community assembly processes, especially for settled organisms such as plants (Watt, 1947; Cadotte, 2007; Limberger et al., 2011). Classically, a disturbance is grouped into two types, “press” and “pulse,” based on its temporal and ecological characteristics (Bender et al., 1984; Glasby and Underwood, 1996). A press disturbance is considered as a continuous disturbance, along with a permanent change in species abundance and density. Generally, a long-term disturbance acts as a filter and selects species according to their traits such as stress (e.g., an environmental filter: Nishizawa et al., 2016). A pulse disturbance is considered a short-term disturbance that can cause a sudden change in the number of individuals and species with likely recovery after the disturbance. A sudden removal of many individuals results in an increase in available space, and other resources are freed, which promotes the colonization of new species. If species can survive a pulse disturbance (i.e., disturbance-tolerant species), they may have the opportunity to colonize patches created in the disturbed area (Slatkin, 1974; Hasting, 1980; Tilman, 1990).

Disturbance processes involving mammalian herbivores are one of the most studied due to their high impact on plant community composition and biodiversity (Cote et al., 2004, Koerner et al., 2018). Herbivory can also be classified into two types, “press” and “pulse,” based on the differences in ecological characteristics of herbivore species. These different types of coexisting

mammal herbivory could contribute to the maintenance of the diversity of plant species. Although there are multiple herbivore species in almost all ecosystems, and these species have evolved with the system, the combined effects of different types of herbivory are not well understood (Parikh et al., 2018).

Functional traits are based on ecological features of species and functional trait-based approaches offer a mechanistic understanding of how communities change due to disturbances (Diaz et al., 2001; Cornelissen et al., 2003; Moulliot et al., 2013). For plants, measurable functional traits are defined as morphological, physiological, or phenological features that potentially affect individual performance, organism fitness, and life-history strategy (Violle et al., 2007; Cadotte et al., 2011). Considering such information greatly helps to understand specific processes such as environmental filtering, competitive exclusion, and patch dynamics.

In this chapter, I investigated the effect of pulse and press disturbances on plant community dynamics using two intrinsic mammalian disturbances at Shiretoko National Park (located on the northeastern tip of Hokkaido, Japan). First, as a press disturbance, chronic deer herbivory was assessed. An overabundance of sika deer (*Cervus nippon yezoensis*) has been reported since the 1980s based on long-term enclosure experiments using fences. The ground layer plant community is transformed by chronic deer herbivory (Nishizawa et al., 2016). Second, as a pulse disturbance, I assessed short-term herbivory caused by an irregular rodent interval outbreak. In the study area, *Quercus crispula* is one of the most dominant tree species, and its irregular huge acorn production induces an extremely high density of forest-dwelling rodents such as *Apodemus speciosus* and *Clethrionomys rufocanus* once every several years (Jensen, 1982). In this region, 2015 was the most extreme masting year of *Q. crispula* in the past 30 years (<https://www.rinya.maff.go.jp/hokkaido/siretoko/donguritop.html>). Concurrent rodent outbreaks with this masting had intense effects on the ground layer plant community both inside and outside of the deer enclosure fence, acting as a pulse disturbance. Both types of disturbances could have changed plant community compositions and community assembly mechanisms.

In this study, by using 6 years of community monitoring data collected from inside and outside of the fenced area, I assessed the effects of press, pulse, and the combination of the two types of disturbances respectively (i.e., control in 2014–2016 experienced press and pulse disturbance, control in 2017–2019 experienced press and pulse disturbance, enclosure in 2014–2016 experienced

pulse disturbance, and exclosure in 2017–2019 experienced no-disturbance). To detect the mechanisms generating temporal community changes such as species sorting and patch dynamics, information on plant functional traits was included.

## 5. 2. Materials and methods

### *Study site*

This study was conducted in Shiretoko National Park (44°06'00" "N 145°01'42" E), which is located in northeastern Hokkaido, the northernmost island of Japan (Mori et al. 2016). The mean annual temperature and precipitation at the study site between 2005 and 2015 were 6.5°C and 1301.4 mm, respectively (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). The forest floor in this region is typically covered with snow from November to May (Kubota, 2000). The forest is characterized as a mixed coniferous and broad-leaved natural forest, dominated by *Abies sachalinensis*, *Q. crispula*, and *Kalopanax septemlobus*.

### *Press disturbance*

Since the late 1980s, damage to vegetation caused by the high density of sika deer (*C. yessoensis*) has been recognized. The study plot, the Horobetsu Plateau, is one of the most highly populated areas, with approximately 5–10 deer/km. Deer populations were estimated by light census surveys conducted each autumn from approximately the 2000 (<http://dc.shiretoko-whc.com/>). Considering the high densities of sika deer, it is deemed that the ground layer plants in this region are continuously exposed to the relatively intense deer herbivory. To protect natural vegetation and promote tree regeneration, many deer exclosure fences have been established in this peninsula. The fenced area used as the study site was established in 2003. A decade has passed since the construction of the exclosure fence, and chronic deer herbivory has caused significant differences in coverage and taxonomic-functional composition of ground layer plants inside and outside of the fenced area (Nishizawa et al., 2016). By using this experimental design, I assessed the effect of press disturbance (chronic deer herbivory) on the plant community assembly process.

### *Pulse disturbance*

In this study area, there are four rodent species: *C. rufocanus*, *C. rutilus*, *A. speciosus ainu*, and *A. argenteus*. The gray-sided vole (*C. rufocanus*) is the most dominant rodent species in this region and in the Hokkaido forest (Ota, 1968; Saitoh et al., 1998). Gray-sided voles mainly use plant resources and are known to consume the most abundant plant species in an area (Suga, 1980). As the monitoring research of The Forestry Agency of Japan reports (<http://www.rinya.maff.go.jp/hokkaido/siretoko/gyoumu/tyousa/donguri/tyousakekka/4tyousakekka1.html>), 2014 was the most productive year of the *Q. crispula* seed since this monitoring was started in 1989: about 25,000 seeds per stand in this region. This plentiful acorn production in 2014 caused an extremely high rodent population in 2015 (Fig. 1). The large extent of herbivory by large numbers of rodents caused an obvious decrease in vegetation coverage both inside and outside of the exclosure fence. After that, the populations of rodents crashed due to a lack of food resources and a high intensity of predation, possibly by foxes (*Vulpes vulpes*) or owls (*Strix uralensis* and *Ketupa blakistoni*), in a density-dependent manner (Saitoh et al., 1997; 2008). This periodic massive disturbance (pulse disturbance) historically affects plant community assembly as an ecological process in this region. Here, from the results of this outbreak, I assessed the effect of pulse disturbance (periodic rodent herbivory) on the plant community.



Fig. 1

The photos of the study site from 2014 to 2019. Rodent outbreak occurred in 2015, and gradual recovery can be observed after the outbreak. The left side of each photo is inside of the fence and the right side is outside of the fenced area. Although inside of the fence shows high plant coverage, there were minimal differences in 2015 (Rodent outbreak).

### *Field data collection*

I surveyed the ground layer plant community in the exclosure and control plots maintained in the forest for six years (2014–2019). The exclosure plot had a fence to protect vegetation from deer herbivory. The control plot, which was located outside the boundaries of the fence, was exposed to deer herbivory. The sizes of the exclosure and control plots were 80 m × 120 m (0.96 ha) and 100 m × 100 m (1.00 ha), respectively. These plots were located close together so that there was little difference in the species composition of canopy trees (The Forestry Agency of Japan 2004). These plots were partitioned into 96 and 100 10-m<sup>2</sup> subplots in the exclosure and control plots, respectively. At the center of each 10-m<sup>2</sup> subplot, a 1 m × 1 m quadrat was used (i.e., 96 and 100 quadrats in the exclosure and control plots, respectively). Taxonomic identification and percent cover of each plant species smaller than 50 cm in height within each quadrat were estimated through visual observation guided using a 100-point grid. Saplings and juveniles of the tree species were not counted in this study. This survey was conducted from late June to early July during all six of the collection years, which was the season during which most herbaceous species appeared on the forest floor due to warming temperatures (after thawing).

### *Trait data collection*

I used five plant functional traits related to growth, reproduction, and responses to disturbances (Pérez-Harguindeguy et al., 2013). They included leaf area (LA; mm<sup>2</sup>), specific leaf area (SLA; mm<sup>2</sup>/g), chlorophyll content (SPAD units), plant maximum height (plant height; cm), and leaf toughness (toughness; N cm<sup>-1</sup>). For LA, SLA, and chlorophyll content, five samples from five individuals for each plant species were collected and measured (25 leaf samples for each species). First, I collected a fully formed adult leaf and measured the chlorophyll content

using a Minolta SPAD-502 (Osaka, Japan). The leaves were immediately scanned before drying, and LA was calculated from the scanned images using Image-J (Rasband, 1997–2008). For plant species with compound leaves, I used leaflets. To calculate SLA, leaves were dried for 72 hours at 80°C to obtain the dry weight of leaves. Toughness is the maximum force to tear a leaf divided by the width of the leaf. The force was measured using a tearing machine (Kanagawagikenn Co., Ltd., Kanagawa, Japan) connected to a force gauge (DS2-50N, Imada Co., Ltd., Aichi, Japan).

### *Data analysis*

First, I calculated species richness, vegetation coverage (%), and Shannon diversity index per plot as community indices to determine the temporal changes over the six years. I also calculated community-weighted mean (CWM) trait values, which are the mean trait values of all species in the community weighted by their relative abundance (Garnier et al., 2004) for the five numeric plant traits, LA, SLA, leaf chlorophyll content, leaf toughness, and plant height.

Next, the temporal beta indices (TBI), as shown in Legendre (2019), were measured to assess the effect of the two types of disturbances. Each index, which compares data from a quadrat at Time1 and Time2, is composed of three parts: temporal species dissimilarity [ $b+c / (2a+b+c)$ ], species losses [ $b / (2a+b+c)$ ], and species gains [ $c / (2a+b+c)$ ]. Here, a is the number of common species between Time1 and Time2, b is the number of species that exist only in Time1, and c is the number of species that exist only in Time2. The B and C statistics will be used to produce B-C plots, with B (losses per quadrat) on the X axis and C (gains per quadrat) on the Y axis, as described in Legendre (2019). B-C plots visually display the relative importance of the loss and gain processes over each time span.

I also assessed the vegetation recovery processes after the disturbance to determine how these disturbances (press, pulse, and a combination of press-pulse) contribute to temporal fluctuations in the plant community. The rodent outbreak occurred in both plot types in 2015 alone. Although there were some vegetation-free sites just after the pulse disturbance, vegetation can emerge the following year (2016 here) if the plants only lost structures that were above ground because almost all plant species at the study sites are perennial. Here, I assumed that the community changes between 2014 and 2016 were the effects of

the pulse disturbances. The area outside of the fence (control) has been affected by a chronic press disturbance throughout the sampling period. I defined that community changes from 2014-2016 at the exclosure site (pulse period) were the result of a pulse disturbance, 2014-2016 at the control site (press period) were press and pulse disturbance (press-pulse period), 2017-2019 at the exclosure site (no-disturbance period) were no-disturbance, and 2017-2019 at the control site were press disturbance (press period). During all time periods, I measured temporal species dissimilarity, species losses, and species gains indices.

Further, to detect the community changes, I also calculated functional differences between each time period (no-disturbance, pulse, press, and press-pulse). Since simply calculating index of temporal functional beta diversity (functional dissimilarity) may fail to detect the detailed processes because the indices use only mean values and they do not distinguish what kind of species increased or decreased, I investigated the use of an irregular method.

Here, by comparing the abundance data from a quadrat at Time1 and Time2, I could separate the species into groups of those that increased and decreased in abundance. Using that, I calculated two metrics: the mean trait values weighted by species abundance increment (increment weighted mean: IWM), which contains the species that increased in abundance and mean trait values weighted by species abundance decrement (decrement weighted mean: DWM), which contains those species that decreased in abundance. IWM and DWM between Time1 and Time2 (IWM<sub>12</sub> and DWM<sub>12</sub>) are calculated as follows:

$$IWM_{12} = \frac{\sum_i^S (a_{i2} - a_{i1}) \times t_i}{\sum_i^S (a_{i2} - a_{i1})} \quad \text{for } (a_{i2} - a_{i1}) > 0$$

$$DWM_{12} = - \frac{\sum_i^S (a_{i2} - a_{i1}) \times t_i}{\sum_i^S (a_{i2} - a_{i1})} \quad \text{for } (a_{i2} - a_{i1}) < 0$$

where, S in regional species richness ( $\gamma$ ),  $a_{i1}$  and  $a_{i2}$  are the abundance of species  $i$  at Time1 and Time2, respectively.  $t_i$  is the trait value of species  $i$ . The mean values of five functional traits (leaf toughness, plant height, chlorophyll content, leaf area, and SLA) at each time period (no-disturbance, pulse, press, and press-pulse) were calculated. The abundance increment and decrement data matrix were Hellinger-transformed before calculating means (Legendre and Gallagher, 2001).

### 5.3 Results

The total number of understory species was 60 in this six-year study (2014–2019). I found 41 and 50 different types of species in the exclosure and control plots, respectively. *Toxicodendron orientale* was the most dominant plant species in all study periods (2014–2019 in exclosure and control plots).

I found considerable effects on the plant community due to the rodent outbreak in 2015 both in the exclosure and control plots. The temporal changes in plant community composition clearly indicated that many species were lost in 2015 but that they recovered in 2016 (Fig. 2). Although plants outside of the fenced area suffered a press disturbance every year, the balance of species loss and species gain did not differ from that within the fence (Fig. 2: 2016–2019). The species richness (alpha and gamma diversity) and vegetation cover were significantly decreased by the rodent outbreak in 2015 (Fig. 3). Changes in CWM trait values were highly affected by the existence of press disturbance, especially for the traits related to competition and/or vulnerability to herbivory (Fig. 4). Temporal dissimilarities in plant community composition were higher during the press-pulse period and lower during the no-disturbance period. Species losses seemed to be related to the pulse disturbance, and species gains seemed to be related to the press disturbance (Fig. 5). No-disturbance increased LA, plant height, and SLA, whereas, press disturbance centrally increased those species with low heights, small leaves, and low chlorophyll needs. Pulse disturbance generally increased the species with increased toughness and chlorophyll content. Interestingly, the trend observed for press and press-pulse disturbances showed the opposite pattern (Fig. 6).

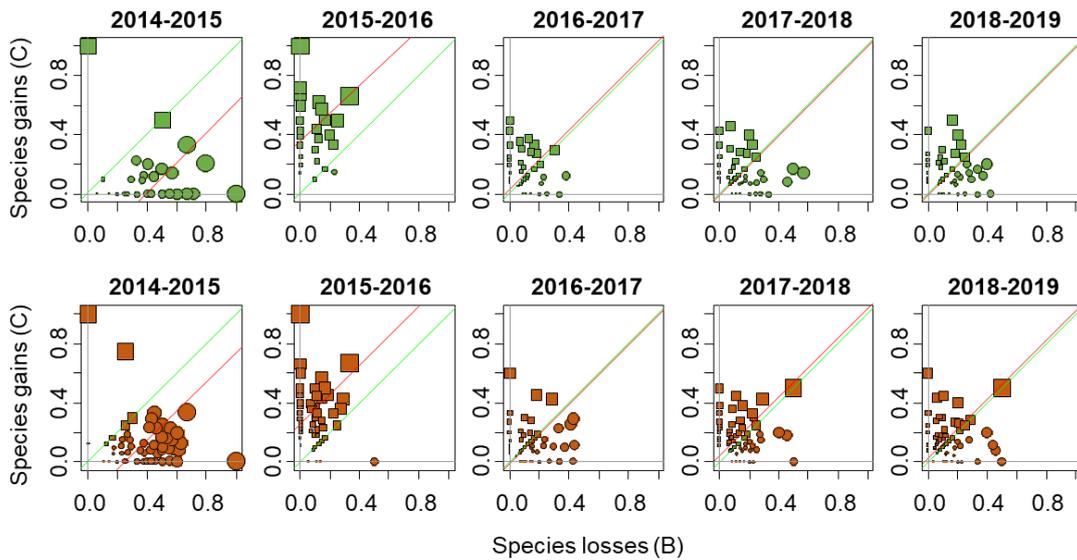


Fig. 2

Changes in plant community compositions every year. The X and Y axis are the indices of species losses and gains (B-C plots). This indicates that the changes before and after 2015 (rodent outbreak) are notable. Both inside and outside of the fence, rodent outbreak increased species losses in 2014–2015 and increased species gains during 2015–2016 as a recovery from the disturbance. Contrary to the pulse disturbance, the press disturbance did not cause conspicuous changes in species gains and losses.

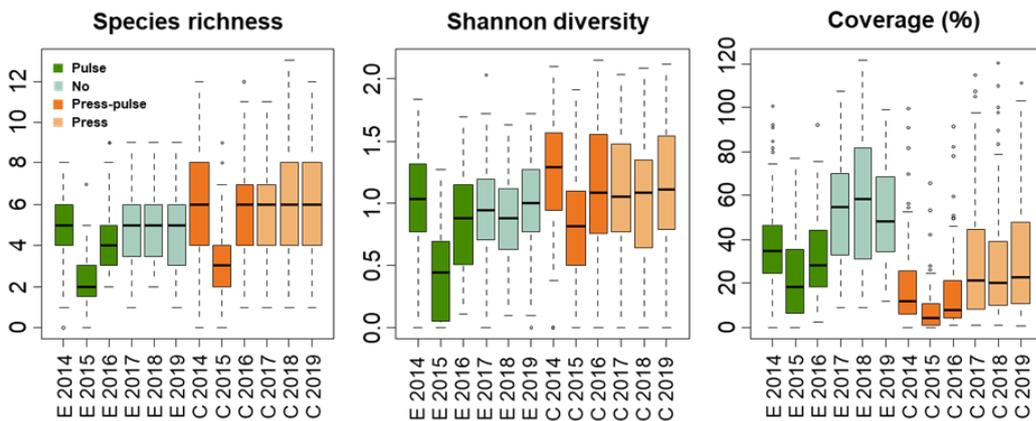


Fig. 3.

Comparison of (a) Species richness, (b) Shannon's diversity index, and (c) Coverage (%) values for each quadrat among all study periods at both enclosure and control plots. Number of samples used was 95 and 100 in the enclosure and control plots, respectively.

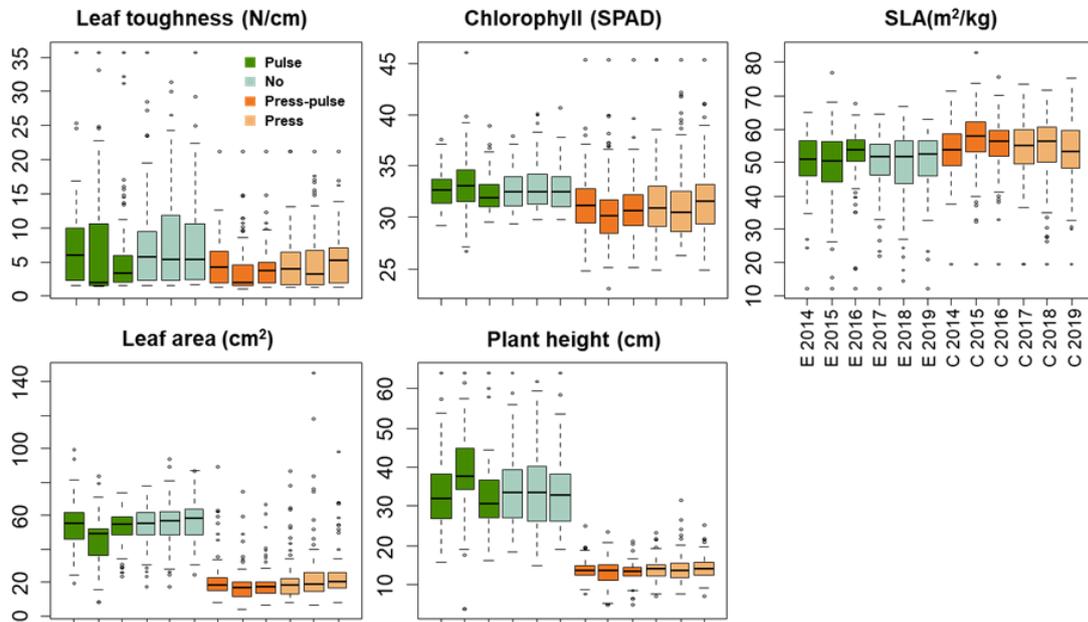


Fig. 4. Comparison of community weighted mean trait values include Leaf toughness, Chlorophyll content, specific leaf area (SLA), Leaf area and Plant height for each quadrat among all study periods at both exclusion and control plots. Number of samples used was 95 and 100 in the exclusion and control plots, respectively.

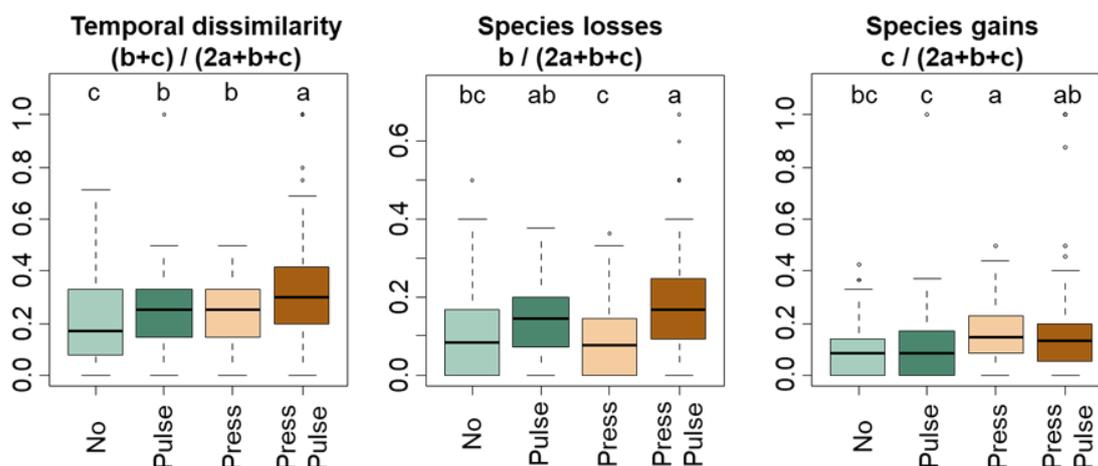


Fig. 5

Dissimilarity of the community composition among no-disturbance (2014–2016 in exclosure), Pulse disturbance (2017–2019 in exclosure), Press disturbance (2014–2016 in control), and Press and pulse disturbances (2017–2019 in exclosure) time periods. Each dissimilarity index, which compares data from a quadrat at Time 1 and Time 2 (here pulse and press-pulse are between 2014 and 2016, no and press are between 2017 and 2019), is composed of three parts: temporal dissimilarity, species losses, and species gains in given time periods. Number of samples used was 95 and 100 in the exclosure (no and pulse) and control (press and press-pulse) plots, respectively.

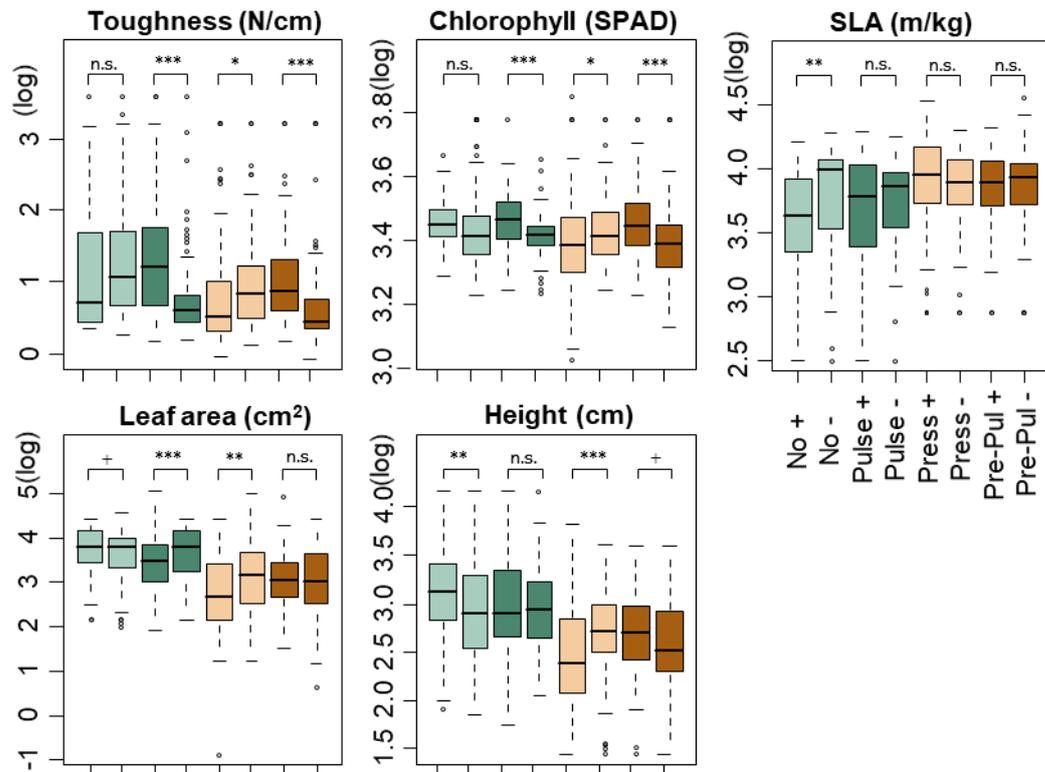


Fig. 6

The mean trait values weighted by species abundance increment (increment weighted mean) and decrement (decrement weighted mean) at each time periods. Increment weighted mean and decrement weighted mean trait values include Leaf toughness, Chlorophyll content, specific leaf area (SLA), Leaf area, and Plant height at no-disturbance periods (No + and No -), Pulse period (Pulse + and Pulse -), press period (Press + and Press -), and Press-pulse period (Pre-Pul + and Pre-Pul -). Number of samples used was 95 and 100 in the exclosure (no and pulse) and control (press and press-pulse) plots, respectively. T-test differences: \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ ,  $P < 0.1$ , and n.s.  $P > 0.1$ .

Table. 1.

The comparison of increment weighted mean and decrement weighted mean trait values for each time periods. Traits are Leaf toughness, Chlorophyll content, specific leaf area (SLA), Leaf area, and Plant height. t and P-values are from t-tests.

	No		Pulse		Press		Press-Pulse	
	t	p-value	t	p-value	t	p-value	t	p-value
Leaf Toughness	-1.627	0.105	5.758	>0.001	-2.172	0.031	3.753	>0.001
Chlorophyll content	0.686	0.494	4.757	>0.001	-2.065	0.04	3.691	>0.001
SLA	-2.83	0.005	-1.646	0.102	0.984	0.326	-0.487	0.627
Leaf area	1.88	0.062	-3.387	>0.001	-3.094	0.002	-0.214	0.831
Plant height	2.864	0.005	0.832	0.406	-3.39	>0.001	1.764	0.079

## 5.4 Discussion

Disturbance is a well-studied ecological process that highly influences plant community assembly and species diversity patterns (e.g., Petraitis et al., 1989; Bongers et al., 2009). Disturbances are classified into two types, “press” and “pulse,” based on its difference in ecological meaning (Bender et al., 1984; Glasby and Underwood, 1996). This “press and pulse” framework has been used for many years, but often considered separately (Harris et al., 2018). By focusing on a system where press and pulse disturbances occurred simultaneously, I could investigate how these disturbances affect the plant community assembly and diversity.

### *The effect of press disturbance*

The difference between deer presence and absence shows the effect of deer herbivory. At any research period, deer absence site (control) showed significantly high species richness (alpha diversity) and total species richness (gamma diversity) and a high value for the Shannon diversity index (Fig. 3). Deer absence contributed to relatively high vegetation cover in all study periods. In terms of CWM of functional traits, there were conspicuous differences in plant height, leaf area, and chlorophyll content between inside and outside of the fenced area (Fig. 4). This indicates that deer herbivory acts as a stressor and filters

species based on their characteristics. These trends are consistent with those of a previous study (Nishizawa et al., 2016). These existing patterns did not change much during the entire sampling period. The area inside of the fence was more static during the no-disturbance periods. This indicates that although there is an intense disturbance occurring, the plant community is stable in some way.

I could not detect all changes over time from the existing patterns. However, from the temporal analysis, I could detect that press disturbance promotes some sort of species turnover (Fig. 5). Analysis of temporal functional change at the plot scale (IWM, DWM) also revealed novel findings. During the period of press disturbance, the increased species have consistent features to those of the abundant species under herbivory, such as small leaf, low height, and low nutrient content species (Wakatsuki et al., in review) and are considered disturbance-tolerant. This indicates that abundant species increase their abundance even under strong herbivory.

As mentioned above, although the existing patterns of the no-disturbance and press disturbance periods were completely different, the temporal dynamics of the processes could be similar. The species that were already abundant, with highly competitive abilities such as large leaf area and plant height, were increased during this period. This pattern was the same for the press disturbance, and the species that were adapted to certain environments increased if there were no changes in the environment or habitat.

### *Pulse disturbance*

Although this study site (Shiretoko) suffers from an overabundance of deer, the effects on plant community fluctuation were limited and looked as stable as the inside of the fence. Here, the deer herbivory acted like an environmental stressor and facilitated species with disturbance tolerance.

With the rodent outbreak disturbance, both deer presence and absence plots resulted in significantly decreased species diversity and vegetation cover in 2015. After that, following the population crash of rodents (Saitoh et al., 1997; 2008), species diversity and vegetation cover were recovered to the same extent as that before the outbreak. This recovery was not observed for vegetation cover alone, and existing patterns of CWM trait values were also not significantly influenced by pulse disturbance. Since almost all species existing here are perennial species, they can regrow the following year even if they lose their aboveground organs.

This is one of the reasons that, although the vegetation suffered serious damage, the effects of the existing differences were limited.

On the other hand, I found interesting results from the small-scale analysis of community temporal dynamics. Although the effects on the existing community pattern were limited, the pulse disturbance greatly changed community compositions at the local scale. Moreover, assessing the temporal functional dynamics at the plot scale (IWM, DWM) revealed certain effects on community composition. The pulse disturbance had opposite effects on the existing patterns both inside and outside of the fence. The species that exist in both treatments are largely determined by the environment, and species adapted to certain conditions are abundant and keep increasing in abundance. Since herbivores are known to eat the more abundant species, I could infer that the abundant species under stable conditions (no and press disturbance) were eaten prior, which caused the decrease in their abundance. In addition to the differences in the features of pulse and press disturbances, the differences in body size of herbivores also affected my results. Press herbivory by deer increased small-sized species. However, pulse disturbances reduced these, which were outside of the dominating species.

### *Conclusion*

Deer herbivory and rodent herbivory are seemingly very similar types of disturbances. In the study site, herbivory intensity is higher for abundant species as mentioned by a previous study (Koerner et al., 2018). The effects were considerably different, and in some cases, they had opposite effects on the plant community. The effects on the existing community patterns (i.e., CWM) were considerably higher in press disturbance, and pulse disturbance changed community features. However, the effects of pulse disturbance were considerably higher for the community dynamics. Since the total effects were small, existing patterns could not be observed. However, by assessing the temporal functional dynamics at plot scale (IWM, DWM), I could detect these effects. Interestingly, the opposite effects on stable existing patterns generated by stable conditions (no and press disturbance) were observed.

# 6

## General discussion

Plant community compositions are determined through numerous processes, and such complexity contributes to local-scale biodiversity. Moreover, the dominant processes determining diversity patterns vary depending on the conditions of target systems, such as differences in regions (arctic or tropic), with or without herbivory, with or without human impact, island or continental scale, dynamic or static system, etc. To understand the mechanisms generating local diversity, there is a need to disentangle the dominating processes carefully along the purpose of the study. Therefore, ecological information of plant species (functional traits) could be a powerful tool. Here, I outlined how functional traits contribute to disentangle the focal community assembly processes in three existing diversity generating patterns.

### *Environmental diversity patterns and functional traits*

Although studies on differences in environment (habitat conditions) and biodiversity were examined in many cases, such as niche partitioning (Hutchinson, 1957) or environmental filtering (Cornwell et al., 2006), assessing functional traits offers lots of new mechanistic insights for assembly processes, including abiotic (Cornwell et al., 2006), biotic (Mayfield and Levine, 2010), disturbance (Mouillot et al., 2013), dispersal (Cadotte et al., 2011), and stochastic processes (Chase, 2007, 2010).

The existence of effective herbivory (disturbance) is one of the most studied processes that affect plant community compositions and diversity patterns. Many empirical studies assess the effects of herbivory, but since in most cases considering species taxonomic information. Mechanistic knowledge is

lacking. In Chapter 4, I have addressed the mechanisms of how herbivory generates differences in biodiversity by assessing functional trait diversity patterns (the dispersion of species in multidimensional trait space) in a local community. The results showed that the dominant community assembly processes were different with and without herbivory (Nishizawa et al., 2016). With herbivory, the functional diversity patterns were not significantly different from the random expectation, which means that stochastic (trait-independent) processes were dominant. In contrast, without herbivory, from the clustering pattern of functional diversity patterns, I inferred that communities are generated by competitive exclusion, leading to low diversity. In this way, the comparison of functional diversity patterns offers a mechanistic explanation for diversity pattern differences with and without herbivory. These findings were consistent with the global pattern obtained by meta-analysis of herbivory effects on biodiversity (Koerner et al., 2018).

The effects of herbivory have no direct impact on community composition, while indirect effects in nutrient conditions have been reported (Bardgett and Wardle, 2003), especially in nutrient-limited low productivity area. However, knowledge on long-term effects of herbivory is lacking. In Chapter 2, I assessed the effects of long-term disappearance of large herbivorous birds and fertilization experiments simultaneously in an extremely nutrient-limited Arctic ecosystem. From the community composition and weighted mean functional trait values, I could disentangle the direct disturbance and indirect fertilization effects. Assessing functional traits tells us how the differences in habitat generate diversity in various ways.

### *Spatial diversity patterns and functional traits*

Although ecologists have long focused on the importance of niche differences, spatial distances also influence biodiversity maintenance, especially after the publication of Hubbel's "Unified Neutral Theory of Biodiversity and Biogeography" in 2001. In this paper, he explained the maintenance mechanisms of highly diverse plant communities in tropical rainforests without considering species ecological features, and only from demographic stochasticity (Hubbel, 2006). This means that community differences are created through spatially limited dispersal. After that, the method to test the relative contribution of habitat differences and spatial distances in community compositions and variation

partitioning (Legendre et al., 2005, Legendre et al., 2008) rapidly prevailed. Although these studies provided us with a lot of important information on how spatial distances are important for community assembly and biodiversity maintenance, species differences are generally not incorporated. However, in reality, the differences in dispersal ability are also important factors in determining species distributions and community composition. In Chapter 3, by combining the strength of dispersal limitation resulting from variation partitioning, and species traits related to dispersal ability, I disentangled the effects of stochastic processes (demographic stochasticity) and dispersal ability-related deterministic processes on community assembly. The results showed that the interspecific differences in dispersal ability were not that significant for spatial distribution of species in the Arctic study sites. On the contrary, some studies have shown that dispersal ability may contribute to species spatial distribution patterns in tropical regions (Seidler et al., 2006). These differences between the regions suggest that trait-related dispersal processes have global patterns

#### *Temporal diversity patterns and functional traits*

Temporal differences in community composition are theoretically suggested from an old age. As the principal theory of competitive exclusion suggests, species compositions are convergent by a few selected species from interspecific competitions, like equilibrium. However, Pickett and White (1985) denied it by focusing on the disturbances. In the real world, a community near equilibrium is rare (Huston, 1994). Most communities experience disturbances before reaching equilibrium, and early succession called patch dynamics develops thereafter. Although disturbances are key processes in temporal community dynamics, the effects of disturbances are not necessarily uniform. Disturbances are classified according to strength and duration, such as press and pulse. In Chapter 5, we tested how the differences in disturbance types influence community temporal fluctuations. The results showed that the changes in community functional trait values indicated that press disturbances mainly contributed in species sorting. On the contrary, pulse disturbances in communities led to a different state. This indicates that press disturbances contribute to diversity, as habitat differentiation, and pulse disturbance contribute to temporal coexistence. Both disturbances contribute differently to local scale biodiversity patterns.

## *Outro*

To understand the mechanisms of biodiversity generation, it is important to disentangle the promoting processes from the differences in a local community. Functional traits offer a lot of mechanistic insights that strongly help solve ecological questions. The expansion of functional trait-based analysis is still ongoing.

The technology to measure plant traits rapidly and safely is currently developing. Kuhlert et al. (2016) introduced the low-cost instruments that enable us measure environmental conditions (light intensity and quality, temperature, humidity, CO<sub>2</sub> levels, time, and location) and useful plant photosynthetic parameters without destruction. Petit Bon et al. (2020) proposed a method that enables the measurement of various leaf chemical traits from spectral information using near-infrared reflectance spectroscopy. Moreover, the method using spectral information enables remote sensing of functional trait diversity from space.

The prevalence of these databases also promotes studies. TRY is the most prevalent plant trait database (Kattge et al., 2011; Kattge et al., 2020), which contains 279,875 plant taxa and 11,850,781 trait record data (Database version 5 (2019-03-26): <https://www.try-db.org/TryWeb/Home.php>). There are also more specific databases, including “Tundra Trait Team” (TTT), the database specialized in arctic plant traits (Bjorkman et al., 2018), and Seed Information Database (Royal Botanical Gardens KEW, 2008). These developments in databases and novel methods have stimulated global scale analysis (Kunstler et al., 2016; Bjorkman et al., 2018; Bruelheide et al., 2018; Moreno-Martinez et al., 2018; Sitzia et al., 2019).

The processes generating ecological community and biodiversity are outrageously complex. Owing to this complexity, structuring the complete general theory at the local scale is difficult. However, recent developments in novel technologies, and expansion of cooperation around the world have improved the knowledge, new insight, and methodology. This study contributes to the accumulation of empirical studies for better understanding of local diversity.

# 7

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