Greenhouse Gas Production and Consumption in Soils of the Canadian High Arctic

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By

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ABSTRACT

Micro-organisms living in the soils of the Canadian High Arctic produce and consume the greenhouse gases (GHGs) CO_2, CH_4, and N_2O, contributing to global nutrient and GHG cycles; however, different vegetation and soil communities differ in their net productions of each gas and the total emissions from the ecosystem. The range of Arctic vegetation communities spans wetlands, tundras, and deserts differing in their soil water contents and other properties such as organic matter content. Previous estimates of total GHG emissions are often imprecise relative to the scale of microbial processes that result in these emissions. Deserts have extremely low levels of both water and organic matter, yet I found that deserts produce nearly as much GHGs as wetter, more fully vegetated tundras. To test the hypothesis that this unexpectedly strong source of GHGs in deserts was a consequence of recently-thawed, organic-rich permafrost, I measured GHG net production throughout the active layer of polar desert soils; both production and consumption of CH_4 and N_2O, as well as soil respiration were found throughout the profile, indicating no link to thawed permafrost and suggesting these high GHG activities are characteristic features of Arctic polar deserts rather than transient effects of recent warming.

I studied the community of microorganisms of the Arctic deserts by examining DNA from soil samples collected from three deserts on Ellesmere Island using DNA microarrays targeted for the functional genes *AmoA* and *pmo*. Using Structural Equation Modeling (SEM) I evaluated the hypotheses that the community of ammonia-oxidizers would be causally linked to the observed patterns of N_2O net production, and that methane-oxidizers would be causally linked to CH_4 net production. The SEM showed the expected link for CH_4 production, but not N_2O production. Available nitrogen in Arctic desert soils is primarily in the form of ammonia/ammonium, thus I find it surprising that no link could be found to the nitrifying community. Subsequent analysis of the occurence patterns of nitrous oxide reductase, a gene present in denitrifying bacteria and the only known biological sink for N_2O, revealed only a weak association. Thus it remains unknown which organisms are responsible for the high levels of N_2O emitted from Arctic polar desert soils. Furthermore, I observed several cases of unusual GHG processes, including a positive correlation between net CO_2 and net N_2O production in only some soils and some soil layers that consumed both CH_4 and N_2O.

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DEDICATION

I dedicate this dissertation to Charlie Roy. Thank you, My Love.

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LIST OF ABBREVIATIONS

ACIA	Arctic Climate Impact Assessment
AmoA	Ammonia oxidase subunit A (gene)
ANAMMOX	Anaerobic ammonium oxidation
AOA	Ammonia-oxidizing archaea
AOB	Ammonia-oxidizing bacteria
AUC	Area under the curve
APL	Above permafrost layer
BD	Bulk density
BDL	Below detection limit
bgs	Below ground surface
CAVM	Circumpolar Arctic Vegetation Map
CFI	Comparative fit index
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CFC	Chlorofluorocarbon
CO_2e	Carbon dioxide equivalent
D_e	Effective diffusivity
DNA	Deoxyribonucleic acid
FTIR-TGA	Fourier transform infrared trace gas analyser
GC	Gas chromatograph
GHG	Greenhouse gases
GSMC	Gravimetric soil moisture content
H_2CO_3*	Sum of all chemical species that CO_2 forms when dissolved in water
IPCC	Intergovernmental Panel on Climate Change
MOB	Methane-oxidizing bacteria
NMS	Non-metric multidimensional scaling
NosZ	Nitrous oxide reductase (gene)
NPOC	Non-purgeable organic carbon
ns	Not significant
OMZ	Oxygen minimum zone
PCoA	Principal co-ordinates analysis

PCR	Polymerase chain reaction
PLFA	Phospholipid-derived fatty acid
qPCR	Quantitative polymerase chain reaction
PMO	Particulate methane monooxygenase (enzyme)
SDS	Sodium dodecyl sulfate
SEM	Structural equation model
sMMO	Soluble methane monoxygenase (enzyme)
SSC	Saline-sodium citrate buffer
TLI	Tucker-Lewis index
TN	Total nitrogen
WFPS	Water-filled pore space

1. INTRODUCTION

Greenhouse gas accumulation in the atmosphere leads to higher atmospheric temperatures and consequently climate change. While the majority of greenhouse gas emissions that drive current climate change are a direct result of human activity (IPCC 2007), such as the CO_2 released by burning carbon-based fuels, considerable quantities of the gases CO_2, CH_4, and N_2O reach the atmosphere from soils. These soil emissions are primarily biogenic in origin, the result of physiological processes undertaken by soil organisms, especially microorganisms including bacteria, archaea, and fungi (Burke et al., 2012; IPCC, 2007; Ludley and Robinson, 2008).

Abiotic factors including soil temperature, water, and available nutrients structure microbial communities (Burke et al., 2012; Ludley and Robinson, 2008). These microbial communties close global carbon and nitrogen cycles by performing key steps such as respiration of soil organic matter, nitrification and denitrification, and methanogenesis and methanotrophy. The contributions of these microbial communities to global greenhouse gas budgets – the sum total of greenhouse gas emissions associated with particular ecosystems and human activities – are the subject of considerable research, though these study efforts have not been spread evenly across different ecosystem types. Non-agricultural ecosystems such as Arctic tundras have been relatively poorly studied; considering these ecosystems are among those experiencing the most rapid climate change (ACIA, 2005; IPCC, 2007) it is imperative to understand how polar terrestrial ecosystems are both contributing to and reacting to ongoing climate change.

Polar deserts are a high-latitude biome characterised by rock and bare soil covering at least 95% of the surface. Vascular plants only survive in microclimates of increased shelter from wind and moisture accumulation, leading to most of the soil profile having very few roots and low organic matter content (Bliss and Gold, 1999). Cryoturbation has been widely observed in polar deserts (Bliss and Matayeva, 1992; Ugolini et al., 2006), and leads to mixing of soil layers, burial of organic matter and other materials, and texture sorting resulting in patches of finer

material surrounded by coarse pebbles and boulders that strongly effect plant habitat suitability (Ugolini et al., 2006). Together, these conditions lead to an impression of severe biological paucity in polar deserts, with soil C and N cycles occuring under restricted nutrient, water, and energy availability and reduced net ecosystem processes compared to warmer, wetter locations elsewhere in the polar regions.

Whereas the Antarctic ice-free landmass is small as a proportion of the total area of the contentinent (approximately 2%) and hosts no vascular plants outside of the Antarctic peninsula (Singh et al., 2010), the Arctic polar deserts are extensive, covering approximately 1.3 million square kilometres and are marginal habitat for tundra shrubs (e.g., *Dryas integrefolia, Salix arctica*), forbs (e.g., *Papaver radicatum, Draba spp.*), and graminoids (e.g., *Carex spp., Poa arctica*) (Ball and Virginia, 2014; Bridgland and Gillett, 1983). These large areas are poorly understood because they are difficult to access and many have supposed them to be minor contributors to global processes such as greenhouse gas emissions.

The emissions of CO_2 from soil are the product of soil respiration, the total respiration of all cells in soil including plant roots, microorganisms, and soil animals; the contribution of animals in most soils is negligible compared to that from plants and microorganisms, and in the polar deserts the lack of plants leads to the majority of respired CO_2 coming from single-celled organisms. In contrast to the diverse sources of CO_2, N_2O and CH_4 are products of a limited number of metabolic pathways in bacterial, archaeal, and fungal cells.

There are two main pathways that produce N_2O. Ammonia oxidation, also known as nitrification because the main products are nitrite (NO_2^-), may release N_2O as a by-product of enzymatic reactions that transform NH_3 into NH_2OH and further into NO_2^-. Denitrification, the process that transforms NO_2^- into N_2O and N_2, is responsible for considerable N_2O emissions when conditions and available microbial functional groups do not include strong expression of the *nosZ* gene, that encodes the enzyme that catalyzes the final step of denitrification, the reduction of N_2O to N_2. Because oxidized nitrogen species are used as electron acceptors by denitrifying microorganisms, strong N_2O emissions result typically from wet and anaerobic conditions that restrict the most-prefered electron acceptor, O_2 (Firestone and Davidson, 1989), and where other potential electron acceptors such as Mn^{4+}, Fe^{3+}, or SO_4^{2-} are limited (Achtnich et al., 1995).

The biological source of CH_4 is methanogenesis, a process undertaken by a number of archaea that use either CO_2 and H_2 or acetate to produce CH_4 (Conrad, 1989; Liu and Whitman, 2008). This process is inhibited by O_2 and occurs primarily in wet soils or aquatic and marine sediments under anaerobic conditions (Conrad, 1989; Conrad, 1999). Thus, the main terrestrial source of CH_4 is wetlands, especially wetlands rich in organic matter such as peatlands (Conrad, 2009).

While the known sinks for CO_2 in soils are regarded as negligible compared to the magnitude of soil respiration in most ecosystems, there are important sinks for both N_2O and CH_4 in many soils (Blagodatsky and Smith, 2012). Biological consumption of N_2O is catalyzed by the enzyme nitrous oxide reductase (NOS), typically under extremely anoxic conditions such as water-saturated soils. Approximately 80% of the global sink of CH_4 is abiotic oxidation in the atmosphere, while biological consumption accounts for most of the remainder (Conrad, 2009; Wang et al., 2004) and is mediated by methanotrophs, autotrophic bacteria that use CH_4 for energy and carbon under aerobic conditions (Conrad, 1999). Net consumption of N_2O is largely restricted to wet, anaerobic soils, whereas consumption of CH_4 is restricted to well-drained, aerobic soils, though cases of anaerobic CH_4 oxidation and aerobic N_2O reduction have been reported (Boetius et al., 2000; Miyahara et al., 2010; Wu et al., 2013).

Physical and chemical parameters such as the amount of water present in soil and the availability of oxygen and organic matter structure microbial functional groups such that key processes can be expected to occur only under particular conditions. The Arctic polar deserts are most often dry, cold, low in nutrients and high in oxygen, leading to modest respiration, N_2O production by ammonia oxidation, and CH_4 oxidation by methanotrophs. Through the course of this research, I have made measurements of Arctic polar desert greenhouse gas emissions using a chamber-based approach, and identified several cases of exceptional patterns of net production within the soil profile, including a positive correlation between CO_2 and N_2O emissions and co-consumption of both N_2O and CH_4 in some desert soils. These measurements and discoveries are detailed in following chapters.

1.1 Organization of the Dissertation

This dissertation is written as a collection of articles for submission to peer-reviewed Journals. Preceding the research chapters, Chapter 3, 4, and 5, are the Introdution to the

dissertation and a Literature Review that provides an overview of the topics covered by the dissertation as a whole. Each research chapter includes a brief Introduction and a detailed Materials and Methods section that allows the reader to repeat the described work, a summary of the results and statistical treatment of the data, and a discussion of the results including their context within the published literature, and my conclusions. Some information is repeated in the research Chapters, for example the calculations for estimating net production of soil gases appear in both Chapter 3 and Chapter 4 as they are central to the work described in each chapter, but all references have been collected into a single section at the end of the dissertation to limit redundancy.

Field work formed the basis of the research included in this dissertation, in the form of two major field campaigns to the Canadian High Arctic in the summer of 2009 and summer of 2010. The research chapters of this dissertation describe these field campaigns and the results of the investigations carried out in the field and in the laboratory. Each research chapter addresses one major topic: Chapter 3 details the results of the 2009 field campaign, Chapter 4 details the 2010 campaign, and Chapter 5 describes the follow-up investigations into the microbial ecology of the soil samples collected in 2010 and analyzed in light of the greenhouse gas production patterns. Each research chapter thus represents an extension of previously-discovered patterns and processes, moving from initial explorations of physical phenomena through comparisons across time and space, to a look at the microorganisms responsible for these phenomena.

The final chapter of this dissertation is a summary of the research as a whole, and a description of related research questions not fully pursued due to limited time and resources. Finally, I describe areas of future research that may build on the research conducted here, with an eye to both broadening the scope of my research and extending the reach into more focused topics.

2. LITERATURE REVIEW

2.1 Arctic Soils

Terrestrial ecosystems in the Arctic span a continuum of temperature and soil water availability from perpetually saturated wetlands to arid deserts (Chapin et al., 2000; Walker, 2000). Water is a major controller of soil processes and in the Arctic also represents latent heat because ice is water not available to organisms, and thaws only with addition of large amounts of heat. Flowing liquid water acts as a vehicle for the transport of heat because of this high heat of fusion (Illeris et al., 2003; Rouse, 2000; Sullivan et al., 2008), generating patterns on Arctic landscapes of wet soils in close proximity to dry soils. These juxtapositions of moisture and heat may be horizontal, as among the matrix of stream-side wetlands surrounded by barren dolomitic desert on Cornwallis Island (Cruickshank, 1971; Woo and Young, 2003), or vertical as in organic-matter-rich wetlands overlying permafrost composed of mineral soils (Muc et al., 1994).

Biological activity tends to correspond to water and heat in Arctic ecosystems (Bliss et al., 1973; Eugster et al., 2000; Rouse, 2000; Teeri, 1973). Wetter, warmer systems such as wetlands and moist tundras fix more carbon by photosynthesis (Muc et al., 1994) and have higher rates of nutrient cycling including nitrogen fixation, ammonia oxidation, and denitrification (Stewart et al., 2012). Because of these correlations, it has been proposed that remote-sensing methods that measure vegetation community parameters such as leaf-area index may be used to predict patterns of biological activity at the landscape or regional scale (Clein et al., 2000; Walker et al., 2002; Walker et al., 2005; Williams et al., 2000).

While any separation of categories is necessarily arbitrary, this dissertation will refer to ecosystems meeting the requirements of less than 5% vegetation cover and occurring either north of the Arctic circle (66° 33′ 44″ N latitude) or south of the Antarctic circle (66° 33′ 44″ S latitude) as polar deserts, and soils covered with more than 5% vegetation as tundras. In practice, I have encountered few Arctic soil ecosystems or areas of ground that were close to this dividing

value. Instead, most polar desert ecosystems considered in this dissertation have had sharp boundaries formed by steep elevation changes, flowing or ponded water, or glacier ice, though the desert portions at Okse Bay (77° 8’ 8” N, 87° 39’ 10” W) consist of the tops of raised beach crests; the tundra lying between crests has a distinct upper boundary on the slopes of the raised crests in which plant cover declines from above 50% to below 5% over a horizontal distance of 20-30 cm (pers. obs.), similar to the juxtaposition of raised beach crests and sedge-moss dominated meadows at Truelove Lowland on Devon Island (Bliss, 1977).

Polar deserts account for more than 1.3 million square kilometers of the ice-free land in the Arctic (Walker et al., 2002). The uncovered 95% of polar desert surface may be composed of a mixture of bare soil, rock ranging in size from pebbles to boulders, patches of moss and lichen, temporary pools of water, and a thin layer of microscopic organisms known as cryptogams (Bliss et al., 1994). At first glance, polar deserts may appear too barren to contribute to global cycles of nutrients and global greenhouse gas budgets, yet considerable below-ground stores of organic matter (Burnham and Sletten, 2010; Chapin et al., 2000) and some measurements of greenhouse gas flux (e.g., Jones et al., 2000) suggest these soils have a role to play in current and future scenarios of microbial greenhouse gas ecology.

Polar deserts and adjacent polar oases, areas of less harsh conditions where vegetation communities are typically associated with regions further from the pole, have been defined by others by measures such as vegetation cover, or the combination of vegetation with precipitation and evapotranspiration (Aleksandrova, 1988; Polunin, 1951; Tedrow, 2004; Walker and Peters, 1977; Walker et al., 2002). While tundra soils are sometimes considered permafrost-affected variants of temperate soils, polar deserts are not similar to soils of temperate or tropical deserts (Bliss et al., 1973; Bliss and Gold, 1999) due to cold winds in polar deserts as well as the tendency of fallen snow to move away from desert soils rather than melting in place; these features are qualitatively distinct from the hot, high-radiation and severe daily temperature cycles of temperate and tropical deserts.

Polar deserts in the Arctic occur largely in Canada, Greenland, Svalbard, and the Russian High Arctic islands and coast (Tedrow, 2004; Walker et al., 2002). Studies in these environments have characterized patterns of vegetation growth and contributions of various groups to net primary productivity (Henry et al., 1990; Svoboda, 1977), showing that the few plants that do grow in the harsh conditions are most often found in sheltered microhabitats where water and

nutrients accumulate and desiccation by wind is reduced (Bliss, 1956; Henry et al., 1990; Ugolini et al., 2006; Wilson, 1959). Furthermore, total productivity is low compared to tundras, what primary production does occur is almost completely restricted to the vascular plants; bryophytes and soil crust organisms contribute negligibly to soil organic matter contents (Henry et al., 1990; Richardson and Finegan, 1977), though these organisms play key roles in nutrient cycles including nitrogen fixation (Breen and Lévesque, 2008; Stewart et al., 2011; Stutz, 1977).

Cryoturbation, a process driven by freeze/thaw cycles and the expansion of ice in soils, leads to severely disrupted horizons in many polar desert soils (Szymański et al., 2013; Tedrow, 2004; Ugolini et al., 2006). In dolomitic deserts on Devon Island, Ugolini et al. (2006) describe soil texture sorting driven by cryoturbation, resulting in striped ground, sorted circles, and plugs. Furthermore, intense cryoturbation acts to bury plants and other surface features, leading to pockets of soil at depth with unusually high organic matter contents, visible as a marked darkening of the soil colour (Ugolini et al., 2006; Walker and Peters, 1977). Such buried organic matter may be a major driver of variation in microbial populations and activities observed at a range of spatial scales and depths in polar deserts (Burnham and Sletten, 2010; Czimczik and Welker, 2010). At the soil surface, a desert pavement or desert patina may form due to the extreme rarity of liquid water on the soil surface combined with primarily wind-driven erosion (Jahn and Manecki, 1991; Tedrow, 2004).

At the study areas included in this dissertation, the short Arctic summer typically thaws soil to a depth of 50 to 100 cm; this seasonally thawed soil is the active layer, and overlies the permafrost that may be tens or hundreds of meters thick (Ford, 1993; Stotler et al., 2011). Almost all Arctic polar deserts are located in the continuous permafrost zone, where the underlying permanently-frozen soil features few gaps in coverage (more than 90% of the land includes permafrost), extending under water bodies and under the ocean on the Arctic continental shelf in the western Canadian Arctic (Brothers et al., 2012; Portnov et al., 2013). Further south, tundra and some forest ecosystems may be underlain by discontinuous, sporadic, or isolated permafrost, varying degrees of underlying ice that lead to distinct permafrost-associated land features. Most permafrost is a relic of the Pleistocene ice ages, when sea levels were lower and surface temperatures were colder in the Arctic and massive surface ice and glaciers covered and penetrated soils in the western Canadian Arctic (Duk-Rodkin and Barendregt, 2011).

Permafrost is soil that remains below 0°C for at least two consecutive years; this definition includes a considerable number of marginal soils including a poorly-defined boundary layer between the active layer and deeper continuous permafrost. While most permafrost includes visible ice, dry soils may qualify as permafrost despite an absence of apparent ice. The defining condition is perpetual temperatures colder than 0°C; glaciers and other massive ice bodies may never reach warmer temperatures except within millimeters of the surface, and some parts of Antarctica such as University Valley (77°52' S, 160°40' E) feature a permafrost horizon actually above the soil surface; even stones lying upon the soil surface never achieve above-freezing temperatures and are thus counted as permafrost (Heldmann et al., 2013; Lacelle et al., 2013; Marinova et al., 2013).

Studies have reported measureable concentrations of living microbial cells (e.g., Price and Sowers, 2004; Gordon et al., 2000; Lanoil et al., 2009) or measureable biological activity (e.g., Lacelle et al., 2011) from permafrost and other perpetually-frozen ice habitats. Lack of liquid water may be the limiting factor on microbial activity rather than low temperatures *per se*; what little liquid water remains at -20°C carries high solute concentrations that further restrict microbes (Ponder et al., 2008). Active microbial populations have also been found in snow (Brooks et al., 2004; Buckeridge et al., 2010), and winter fluxes of greenhouse gases or dissolved nutrients have been observed in snow and in frozen soils (Brooks et al., 1997; Buckeridge et al., 2010). Microbial biomass peaks before winter ends and frozen soils thaw (Brooks et al., 2004), due to the osmotic effects of percolating meltwater lysing cells and the exhaustion of the previous summer's accumulated pool of nutrients during early spring (Jefferies et al., 2010).

Tundra ecosystems include large areas of wetlands, featuring complete or near-complete saturation of water in the soil of the active layer. Low temperatures, low oxygen availability, and rapidly-growing plants create conditions in which organic matter is deposited faster than it can be mineralized, leading to peatlands with organic soils up to 4 m thick (Jahn et al., 2010). These Arctic peatlands have been extensively studied to predict the effect of climate warming: increasing temperatures will speed decomposition processes and release large amounts of CO_2 and CH_4 (Juutinen et al., 2013; Ström et al., 2005; Tveit et al., 2013) as well as N_2O (Repo et al., 2009). Furthermore, in nearby moist tundras shrubs may be replaced by more rapidly-decomposing (i.e., their carbon is less stably sequestered) grasses, sedges, and mosses (Paré and Bedard-Haughn, 2013; Sistla et al., 2013), indirectly leading to higher GHG emissions.

However, ecological succession associated with warming temperatures is also predicted to expand the range of some shrubs (Hobbie et al., 2000) and alter patterns of both summer temperatures and winter snow cover. The effects of a warmer climate therefore include both increased temperature-dependent rates of greenhouse gas generation and increased water-dependent accumulation of recalcitrant carbon molecules such as lignin (Paré and Bedard-Haughn, 2013; Sistla et al., 2013). The net effect, therefore, of climate change in Arctic ecosystems is difficult to predict, and may involve increasing importance of CH_4 and N_2O compared to CO_2 or non-linear responses in ecosystem sensitivities to global patterns of change (McGuire et al., 2009; McGuire et al., 2000).

2.2 Greenhouse Gases

Three greenhouse gases account for the majority of the climate-forcing effects of the current composition of the atmosphere: CO_2, CH_4, and N_2O (IPCC, 2007). Other gases such as chlorofluorocarbons (CFCs) and particulate matter suspended in the air also have climate effects but are the result of only human activity or abiotic natural processes such as volcanic activity or forest fires (IPCC, 2007). In contrast, CO_2, CH_4, and N_2O have significant sources and sinks in biological processes, especially processes mediated by microorganisms (Conrad, 1989; Firestone and Davidson, 1989; Galchenko et al., 1989) in addition to the abiotic and human-activity-based sources. Indeed, these gases constitute important components of global C and N cycles; CO_2 is produced by nearly all living organisms and is fixed by photosynthesis, CH_4 provides a pathway for the movement of reduced carbon within some ecosystems (Raghoebarsing et al., 2005), and N_2O may be produced by many different organisms as the product of a metabolic pathway for the detoxification of nitric oxide (Arkenberg et al., 2011; Firestone and Davidson, 1989; Klotz and Stein, 2008; Stein and Klotz, 2011).

Total greenhouse gas net production in soil is determined by the presence and metabolic activity of microorganisms capable of producing or consuming these gases (Firestone and Davidson, 1989; Wertz et al., 2009) as well as the necessary substrates for the relevant enzymes and the nutrients required by the organisms for growth and survival. Soil respiration is the total of CO_2 production in soil; the majority comes from respiration, either aerobic or anaerobic, of bacteria, archaea, fungi, and plant roots, with small contributions from unicellular eukaryotes and animals. The major sink for CO_2 in most ecosystems is photosynthesis, in which plants and green

algae fix CO_2 to produce organic matter. Within the soil profile, there are some smaller sinks for CO_2, in the form of chemolithoautotrophic organisms that fix CO_2 using energy derived from inorganic molecules; this includes the autotrophic methanogens that combine CO_2 with H_2 to produce CH_4 (Conrad, 1999; Vogels et al., 1988). However, the magnitude of CO_2 fixation below the surface is several orders of magnitude smaller than soil respiration making it difficult to detect by monitoring CO_2 concentrations.

Soil respiration is controlled by a number of factors in soil ecosystems including temperature, water, and available nutrients (Fang and Moncrieff, 2001; Howard and Howard, 1993; Kowalenko et al., 1978; Shaver et al., 2006; Smith et al., 2003). Temperature affects soil respiration by altering the fundamental rates of biochemical reactions, with warmer soils having increased CO_2 production, both at the scale of individual pedons warming during the course of a day (Fang and Moncrieff, 2001; Risk et al.; Vanhala et al., 2011; Zeglin et al., 2013) and with warmer climates tending to have characteristically higher soil respiration (Davidson and Janssens, 2006). Lack of water inhibits biological activity and slows CO_2 production, while water saturation restricts oxygen diffusion into soils, causing some organisms to switch to anaerobic modes of respiration, reducing CO_2 production. Production of CO_2 may restrict itself, as gaseous CO_2 dissolves in soil water and lowers the pH; low pH inhibits some organisms (Li et al., 2007; Wang et al., 2013) and aerobic respiration consumes O_2 and leads to anaerobic conditions. The ratio of organic carbon to nitrogen in soils (Huang, 2004), may affect soil respiration if there is either too little nitrogen to support microbial growth, or too much for many organisms (Kaštovská et al., 2012). Most soil CO_2 is derived from the biological decomposition of organic matter, therefore the supply and characteristics of organic matter in soil is also a major driver of total CO_2 emissions (Jones et al., 2011; Shaver et al., 2006).

The addition of organic matter to soil, such as in the form of manure or organic fertilizers in agricultural systems leads to an increase in soil respiration (de Graaff et al., 2010). Organic matter includes a range of characteristics that alters their susceptibility to microbial decomposition, and more labile materials such as simple carbohydrates are typically attacked by soil heterotrophs more quickly than more recalcitrant materials such as lignin (Grogan and Jonasson, 2005). However, in some circumstances an increase in decomposition rates of more recalcitrant materials has been observed following the addition of relatively labile organic matter to soils (Farrar et al., 2012; Kuzyakov, 2010; Kuzyakov et al.; Nottingham et al., 2009). This

"priming effect" (Broadbent and Norman, 1947) that raises overall decomposition rates and CO_2 emissions by more than expected given the characteristics of the added organic matter may be due to general increased activity among heterotrophic organisms (Farrar et al., 2012; Fontaine et al., 2003; Nottingham et al., 2009).

In the diffusion-limited, complex three-phase matrix of soil, a very large surface area of water may be in contact with soil air. When CO_2 dissolves in water it speciates to carbonate (collectively considered as H_2CO_3*, the sum of all H_2CO_3, HCO_3^-, and CO_3^{2-} in aqueous solution) as well as dissolved $CO_{2(aq)}$. Carbonates are weak acids, and act to both buffer soil solution pH and drive it down. Highly acidic soils will not store large quantities of inorganic C as carbonates, but more alkaline soils may harbour more C in the form of dissolved H_2CO_3* than is present in air-filled pore spaces, even when soil water is low as in arid environments (Cheng et al., 2007). Thus, a small decrease in pH, as when snowmelt-derived water infiltrates soil may release stored CO_2 that could be mistaken for soil respiration (i.e., biological production) by an observer (Oren and Steinberger, 2008; Serrano-Ortiz et al., 2010; Shanhun et al., 2012).

Though there are a number of known non-photosynthetic CO_2 fixation pathways (Conrad, 2009; Kawaichi et al., 2013; Kletzin et al., 2004; Wang et al., 2014), the energy requirements of CO_2 fixation and the requirements for other resources such as H_2 in the case of CO_2-fixing methanogens (Conrad, 1999) lead to estimations that soil CO_2 consumption will be negligible compared to total soil respiration even in extremely oligotrophic systems (Schleper and Nicol, 2010); measurements of both dark chemolithoautotrophic fixation and light phototrophic fixation of CO_2 are sparse, though Wu et al. (2014) report accumulation of ^{14}C from labelled $^{14}CO_2$ within a soil profile and at the surface and show the overwhelming importance of photosynthesis to ecosystem-level CO_2 fixation. Net consumption of CO_2 *in situ* within soil profiles has been reported in a few cases (De Jong and Schappert, 1972; Risk et al., 2002; Shanhun et al., 2012). These measurements have been accounted for either as measurement error (De Jong and Schappert, 1972; Risk et al., 2002) or as CO_2 moving between gas and aqueous phases by abiotic carbonate cycling (Oren and Steinberger, 2008; Shanhun et al., 2012).

Most CH_4 emitted from soil is derived from biological methanogenesis, a process mediated by archaeal methanogens (Liu and Whitman, 2008). These organisms produce CH_4 from CO_2 and H_2 or from small organic molecules such as formate and acetate, in a process that also releases CO_2 (Conrad, 1999; Vogels et al., 1988; Zinder, 1993). Larger organic molecules

are not substrates for methanogens, and organic matter must first be decomposed by anaerobic bacteria or eukaryotes before it can be converted to CH_4 (Conrad, 1999; Liu and Whitman, 2008; Schink, 1997). All known methanogens are inhibited by oxygen, and consequently their activities are largely restricted to anaerobic environments such as water-saturated soils, marine and freshwater sediments (Chaban et al., 2006; Conrad, 1989; Liu and Whitman, 2008) and the guts of animals such as termites (Purdy, 2007) and ruminants (Wolin and Miller, 1988). In most cases the majority of CH_4 produced in soils and sediments is oxidized before it reaches the atmosphere (Bridgham et al., 2013; Conrad, 2009; Frolking et al., 2006). The total amount of CH_4 emitted from soils therefore depends on the balance between methane production and consumption.

Because of its high dimensionless Henry's constant (approximately 42 at typical Arctic soil temperatures) most CH_4 is in the gas phase rather than dissolved in water. As a consequence, CH_4 readily forms bubbles and may move through water much more quickly than diffusion through water would normally allow (Conrad, 1989; Kettridge et al., 2011; Tokida et al., 2007). Ebullition therefore represents a major pathway of CH_4 movement through ecosystems, a process that can be difficult to measure with chamber or probe based methods that may exaggerate or underestimate the effect on concentration measurements of rapid injections of CH_4 into the measurement space, depending on the point in the measurement period when the CH_4 bubble arrives or if bubbles are excluded from the measurement space (Kettridge et al., 2011; Mastepanov and Christensen, 2008; Stamp et al., 2013; Tokida et al., 2007). Strong, episodic ebullition also has important effects on wetland ecosystems, such as altering peat buoyancy (Strack et al., 2006) and hydraulic conductivity (Beckwith and Baird, 2001), and moves large quantities of CH_4 out of the soil and beyond the reach of methanotrophs that would otherwise consume it − although in cold climates CH_4 bubbles trapped in ice are subject to microbial oxidation (Walter et al., 2008). Estimates of the amount of CH_4 emitted from wetlands by ebullition range widely, from around 3% (Green and Baird, 2013) to 18% (Christensen et al., 2003) or as high as 89% (Lansdown et al., 1992). Other difficult-to-measure pathways of CH_4 emission include transport via the aerenchyma roots of some wetland plants such as rice (*Oryza sativa*); the air channels represent a gas phase that CH_4 readily moves into and diffuses rapidly through an otherwise aquatic medium (van Bodegom et al., 2001).

Net CH_4 production depends on both methanogenesis and methanotrophy, the oxidative consumption of CH_4 by bacteria (Conrad, 1996). Some soil parameters control total CH_4 emissions by affecting both production and consumption of CH_4; these include soil redox status and oxygen availability, pH, temperature, vegetation, and salinity (Conrad, 1999; Wang et al., 1996). Oxygen availability and a redox state above about -200 mV inhibit methanogenesis (Wang et al., 1996) but promote methanotrophy (Chowdhury and Dick, 2013). Most methanogens are most active at circumneutral pH, though some have been isolated and shown to be actively producing CH_4 from acidic wetlands with pH less than 4 (Williams and Crawford, 1985). Methanogens have been found to tolerate an extremely wide range of temperatures, including isolates from permafrost and near-permafrost soils (Wagner et al., 2007) and marine hot vents with water temperatures as high as 110°C (Pley et al., 1991) but broadly within ecosystems methane production follows an exponential response to temperature (Conrad, 1996; Dunfield et al., 1993). As described above, vegetation may include aerenchyma roots that permit the rapid passage of CH_4 to the atmosphere, though these aerobic microhabitats harbour methanotrophs that oxidize some of the CH_4 (Conrad, 1996; Conrad, 1989; Le Mer and Roger, 2001).

Methanotrophs are a diverse group of bacteria that are nearly all aerobic (McDonald et al., 2008), though a group of marine methanotrophs working as consortia with nitrate-reducing bacteria and capable of anaerobic oxidation of CH_4 have been discovered (Boetius et al., 2000; Raghoebarsing et al., 2006). Aerobic methanotrophs are autotrophic, using CH_4 as their sole source of carbon (Hanson and Hanson, 1996), with the fate of carbon split between respiration and release as CO_2 and incorporating it into cell biomass (Anthony, 1982; Chowdhury and Dick, 2013). Methanogens show patterns of diversity and abundance associated with soil concentrations and fluxes of CH_4, especially “high affinity” and “low affinity” types that appear to be specialized for CH_4 concentrations near ambient, or elevated concentrations as are found in the upper parts of wetlands and above landfills, respectively (Chowdhury and Dick, 2013; Reay and Nedwell, 2004). They also respond to other factors such as salinity (Bissett et al., 2012), pH (Kolb, 2009; Rahman et al., 2011), and temperature (Wartiainen et al., 2003). However, few methanotrophs have been cultured and studies of the environmental controls of their activity are needed to understand this important step in global carbon cycles and drivers of greenhouse gas emissions (Chowdhury and Dick, 2013; Kolb, 2009).

Methane oxidation in methanotrophs is catalyzed by the enzyme Methane monooxygenase, in either its particulate (PMO) or soluble (SMO) forms (McDonald et al., 2008); these two enzymes are not closely related but both are regulated by copper (Fru, 2011; Murrell et al., 2000) because PMO includes a dicopper active center (Balasubramanian et al., 2010) and some methanotrophs carry the genes for both PMO and SMO (Auman and Lidstrom, 2002; Murrell et al., 2000). Of the two enzymes, PMO is much more widely distributed, occurring in all aerobic methanotrophs except the genus *Methylocella* (Dedysh et al., 2001; Theisen et al., 2005) while SMO is found only in a few genera of Alphaproteobacteria and Gammaproteobacteria (Fuse et al., 1998; Murrell et al., 2000; Shigematsu et al., 1999). The reliance of PMO on copper makes copper distribution an important controlling factor for methanotrophy (Fru, 2011); when copper is absent or at levels below those needed for the synthesis of PMO, SMO is produced (Fru, 2011; Murrell et al., 2000). Both enzymes catalyze the conversion of CH_4 to CH_3OH, and the CH_4-oxidation activity of methanotrophs is stimulated by CH_3OH additions (Benstead et al., 1998); however, the two enzymes have different requirements and affinities for CH_4: PMO has higher affinity and requires copper, but SMO degrades a wider range of other hydrocarbons and does not require copper (Fru, 2011). PMO is closely related to ammonia monooxygenase (AMO), and NH_3, the usual substrate of AMO, may act as a competitive inhibitor of CH_4 oxidation (Bédard and Knowles, 1989; Carlsen et al., 1991).

The interaction between methanogens and methanotrophs in soils, especially wetland soils, results in CH_4 acting as a vehicle for the movement of carbon from organic matter in dark, anaerobic environments to CO_2 in light, aerobic environments. Methanotrophic bacteria have been found in hyaline cells of *Sphagnum cuspidatum*, a dominant wetland plant that benefits from the association by fixing the CO_2 produced by the methanotrophs through photosynthesis (Raghoebarsing et al., 2005). In addition, this methanotrophy appears to stimulate nitrogen fixation (Larmola et al., 2014), and methanotrophs may be an important food source for higher trophic levels in nutrient-poor freshwater systems (van Duinen et al., 2013). Cocultivation experiments have suggested some benefits to the methanotrophs ranging from metabolite exchange with heterotrophs (Stock et al., 2013) to a stable habitat with steady O_2 supply (Yoshida et al., 2014). Similar interactions have not been observed in other ecosystems where anaerobic methanogens may supply CH_4 to aerobic methanotrophs in nearby soil layers, such as

the polar deserts where water from thawing permafrost may create anaerobic conditions and CH_4 production that diffuses upwards to methanotrophs near the surface.

The release of N_2O from soil represents both a contribution to the atmospheric accumulation of an important greenhouse gas and ozone-depleting compound, and the net loss of reactive nitrogen from the soil ecosystem (IPCC, 2007). Efforts to prevent N_2O emissions from soil have thus emerged from soil fertility and agricultural efficiency concerns as well as climate change (Mosier et al., 1998; Nevison et al., 1996). Many measurements of soil-atmosphere exchange of N_2O have been made in an agricultural context, (e.g., Blackmer and Bremner, 1979; Ryden, 1981; Mosier et al., 1996; Bockman and Olfs, 1998; Kaiser et al., 1998; Liu et al., 2006; Reay et al 2012; Jat et al., 2012). Current research includes a move beyond agricultural and other directly managed ecosystems into soils that have not been used to produce crops or timber such as deserts (e.g., Hall et al., 2011; Abed et al., 2013; Zaady et al., 2013), as well as soils that have been severely modified by urbanization and other non-agricultural land-use activities (e.g., Hafeez et al., 2012) and soils and sediments downstream of urban drainages (e.g., Beaulieu et al., 2011).

As a greenhouse gas, N_2O has a climate-forcing potential approximately 300 times that of CO_2 (IPCC, 2007) and is thus sometimes considered in pooled estimates of total ecosystem greenhouse gas contributions as units of CO_2 equivalent, or CO_2e. This calculation of equivalency allows comparisons of ecosystems or processes that may produce relatively little CO_2, or be a net sink for CO_2, but account for a large fraction of regional greenhouse gas budgets by being a strong source of N_2O or CH_4. For example, peatlands are most often a net sink for CO_2, with photosynthesis fixing more CO_2 than is produced by soil respiration (Andert et al., 2011), but may be a net source of N_2O (Palmer et al., 2012; Repo et al., 2009), especially when partly or completely drained (Anderson et al., 2010; Andert et al., 2011).

Soils are the major global source of N_2O (IPCC, 2007). Biomass burning contributes some N_2O directly that may be partly offset when the ash is deposited on agroforestry soils because net N_2O production from those soils decreases following ash application (Klemedtsson et al., 2010). Together, all agricultural and soil sources of N_2O account for 56-70% of global N_2O emissions to atmosphere (Syakila and Kroeze, 2011).

There are several pathways for microbial production of N_2O (Butterbach-Bahl et al., 2013; Guo et al., 2013; Wrage et al., 2001). In terrestrial ecosystems the processes of ammonia

oxidation and denitrification dominate N_2O emissions (Butterbach-Bahl et al., 2013), and, together form a pathway from ammonia to nitrogen gas that may be present in a single organism or separated into multiple organisms occupying the same habitat (Wrage et al., 2001). Unlike CH_4, N_2O emissions to the atmosphere via ebullition seem to constitute a minor pathway, with low concentrations of N_2O recorded in bubbles in streams (Baulch et al., 2011).

Ammonia oxidation releases N_2O from the abiotic decomposition of the intermediate NH_2OH to NO and N_2O in what is sometimes referred to as the "hole-in-the-pipe" model of nitrifier N_2O production (Davidson et al., 2000; Davidson and Verchot, 2000; Firestone and Davidson, 1989). While this pathway has been well established in ammonia-oxidizing bacteria (AOB), there is an alternate hypothesis stating that ammonia-oxidizing archaea (AOA) cannot carry out this process (Schleper and Nicol, 2010). No NH_2OH-degrading enzymes have been found by gene prediction in the analyzed genomes of sequenced ammonia-oxidizing archaea (Walker et al., 2010); thus removing ammonia-oxidizing archaea from consideration among N_2O sources. However, this hypothesis awaits comprehensive testing by both further analysis of genomes and observations of pure-culture ammonia oxidizers, a difficult group of organisms to culture (Konneke et al., 2005). Contrary to the hypothesis that archaeal ammonia-oxidizers do not produce N_2O, Loscher et al. (2012) present clear evidence of AOA-mediated N_2O production in a marine system.

The proximal source of the nitrogen that is converted to N_2O by ammonia oxidation or denitrification is either NH_3 or NO_3^-, but the ultimate source may be organic matter, N-fixation, or the deposition of reactive N compounds such as NO_3^- from atmospheric sources that may themselves be the result of human activity or natural processes occurring thousands of kilometres away (Dise and Wright, 1995; Magill and Aber, 2000; Robinson et al., 2004). The available pool of NH_3 or NO_3^- in soils may therefore not be a reliable indicator of potential N_2O production due to replenishment of these pools from mineralization of organic N, release of NH_3 from N-fixation, or the downward movement of deposited reactive N (Elberling et al., 2008).

Only one biological sink for N_2O is known, the reduction of N_2O to N_2 by nitrous oxide reductase (nos), a copper-containing enzyme employed by some bacteria and archaea to use N_2O as an electron acceptor. Whereas this typically occurs under oxygen-depleted conditions (Chapuis-Lardy et al., 2007; Ciarlo et al., 2007; Clough et al., 2005; Vieten et al., 2009), though aerobic N_2O consumption has been reported (Wu et al., 2014; Wyman et al., 2013). The

mechanism for N_2O consumption under conditions in which O_2 is available is not clear; Miyahara et al. (2010) report on a strain of *Pseudomonas stutzeri* TR2 isolated from a wastewater treatment plant in Japan that constitutively expresses *nosZ*, though how often that organism encounters oxygenated conditions is unknown. Similarly, Wyman et al. (2013) report *nosZ* mRNA transcripts from a region of open ocean water adjacent to the oxygen minimum zone (OMZ) in the Arabian Sea; they speculate the responsible organisms may represent spill-over from the OMZ where complete denitrification is widely observed and O_2 is largely absent, or may be the result of anaerobic microsites inhabited by filamentous bacteria (Wyman et al., 2013).

Well drained soils and soils in arid and semi-arid ecosystems are usually aerobic, at least close to the soil surface. Several researchers have reported N_2O consumption in such aerobic soils; Donoso et al. (1993) observed consumption of approximately 26 μmol m^{-2} s^{-1}, though with considerable variation of similar magnitude to the mean. This sink was abolished by rewetting, either by experimental manipulation or by the end of the dry season and resumption of the rainy season in Venezuela (Donoso et al., 1993). Flechard et al. (2005), working in an agricultural grassland in Switzerland, report a net sink in unfertilized sites that they cannot attribute to anaerobic denitrification.

Vieten et al. (2008) tested the hypothesis that aerobic soil N_2O consumption may be the result of assimilatory reduction to NH_3, a thermodynamically favourable reaction compared to reduction to N_2 that is catalyzed by nos. No significant amount of the isotopically labelled $^{15}N_2O$ they applied to flow-through microcosms resulted in an enrichment of soil organic matter N, indicating at most a negligible role for this reduction pathway in soils; despite the apparent energetic and reactive-N advantages of NH_3 production from N_2O, this pathway does not seem to account for aerobic N_2O consumption in soils.

Goldberg and Gebauer (2009), working in a spruce forest subject to both natural and induced drought conditions observed a sink for N_2O in the upper, presumably well-aerated soil layers that was often of greater magnitude than the combined N_2O source observed in the litter layer above and in deeper soil layers below, suggesting net consumption of N_2O including atmospheric N_2O in this ecosystem. This sink was abolished by water addition, as was reported by Donoso et al. (1993), though in the case of the spruce forest it took up to four months after

resumption of normal soil water levels for the N_2O sink to completely disappear (Goldberg and Gebauer, 2009).

The overall strength of the global biological sink of N_2O may be declining; measurements of the $\delta^{15}N$ of atmospheric N_2O suggest a change in the ratio of biological production to biological consumption (Conen and Neftel, 2006). This may be caused by a change in the source of nitrogen that becomes N_2O: in addition to fertilizer applied at or near the soil surface, deposition rates of reactive nitrogen species have approximately doubled in many terrestrial ecosystems, leading to greater activity near the surface of the soil profile and thus a shorter distance over which diffusing N_2O may be captured by microbes as well as a greater availability of oxygen in the upper soil layers (Bol et al., 2003; Conen and Neftel, 2006; Decock and Six, 2013). Furthermore, the diversity of the denitrifier community is positively associated with the total sink for N_2O in some soils (Cavigelli and Robertson, 2001; Chèneby et al., 1998; Rich and Myrold, 2004), and some agricultural practices appear to reduce diversity of soil microorganisms (Huang et al., 2013; Kumar et al., 2012; Philippot et al., 2007; Philippot et al., 2013).

Denitrifying organisms capable of reducing N_2O to N_2 appear to be widespread, with global surveys of N_2O consumption reporting activity in many ecosystems (Chapuis-Lardy et al., 2007). These organisms even appear to have colonized animal guts in a manner similar to other gut flora such as methanogens. Majeed et al. (2012) report N_2O consumption in live xylophagous termites that feed on low-nitrogen substrates such as dry wood. Reduction of N_2O may be coupled to N_2-fixation in the guts of these insects, leading to assimilation into the tissues of the animal (Majeed et al., 2012; Tayasu et al., 1994).

Many soil microbes are capable of producing or consuming more than one of the gases CO_2, CH_4, and N_2O, and thus provide a biological link between these greenhouse gases. Nearly all organisms produce CO_2, including those organisms capable of fixing CO_2 by photosynthesis or chemolithoautotrophic activities because some portion of fixed CO_2 will be subsequently re-released as organic matter is digested. There are also biological associations between CH_4 and N_2O. Aerobic methanogens are critical components of the global carbon cycle because they convert CH_4 to CO_2, both directly and when their cellular components are digested by heterotrophs (Raghoebarsing et al., 2005; van Duinen et al., 2013). They are also active in the nitrogen cycle, with many methanotrophs possessing genes for ammonia oxidation (Klotz and

Stein, 2008; Stein and Klotz, 2011), and some have been shown to reduce nitrate at least as far as producing N_2O (Campbell et al., 2011; Kalyuhznaya et al., 2009; Stein and Klotz, 2011). In addition, one anaerobic bacterium, the first described representative of the phylum NC10, has been found to both oxidize CH_4 and reduce N_2O under anaerobic conditions (Ettwig et al., 2010). Methanotrophs are affected by nitrate addition; some are inhibited by nitrate (Reay and Nedwell, 2004; Yuan and Lu, 2009) while others require nitrate to oxidize CH_4 (Kalyuhznaya et al., 2009; Vecherskaya et al., 2009). Ammonia addition often inhibits methanotrophy (Cai and Mosier, 2000; Kravchenko et al., 2002) though it can also stimulate it (De Visscher and van Cleemput, 2003). Where a single organism does not have the capacity to directly influence both CH_4 and N_2O, consortia of two or more microorganisms, often a bacterium and an archaeon, may exchange metabolic intermediates and simultaneously consume or produce both gases (Knowles, 2005; Raghoebarsing et al., 2006).

Curiously, N_2O production may respond to light much as CO_2 production does as plants photosynthesize or respire depending on incident light, though the mechanism by which N_2O flux is regulated in plants is not clear (Stewart et al., 2012). Dissolved N_2O is transported in plants with transpired water (Chang et al., 1998) and released through open stomata, though in the Arctic deserts N_2O was consumed under light conditions, rather than produced as would be expected if soil-produced N_2O were moving upwards through plants during transpiration (Stewart et al., 2012).

2.3 Measuring Soil Gases

Net emissions to the atmosphere are measured using either chambers – either steady-state or non-steady state, in which gases effluxing from the soil accumulate over a pre-defined period (Butterbach-Bahl et al., 2011; Davidson et al., 2002) and concentrations are monitored over that period, or by eddy covariance towers that monitor larger areas (Nicolini et al., 2013). Concentrations of gases within soil pore space are measured using probes; a considerable diversity of probes have been described and used in various soils around the world, with some based on simple diffusion of gases into the interior of a metal or hard plastic probe (e.g., Risk et al., 2002; Kellman and Kavanaugh, 2008; Brummell and Siciliano, 2011) and others employing more sophisticated materials and designs that permit capture of gases travelling through soil or water by ebullition (e.g., Mastepanov and Christensen, 2008). Some study designs include field-

deployed gas chromatographs in parallel with an in-line infrared analyzer (e.g., Nishimura et al., 2005), and others may use both chambers and eddy covariance towers to study the ecosystem at two scales (e.g., Kabwe et al., 2005; Grondahl et al., 2008).

Chamber measurements are sensitive to a range of factors that affect the accuracy of the measurement. Strong winds distort flux estimates by advective pumping; wind effectively blows into and through the soil and flushes gas that would otherwise move only by diffusion (Amonette et al., 2013; Davidson et al., 2002; Lai et al., 2012; Suleau et al., 2009). Even the disturbance of placing or closing a chamber leads to a few minutes of chaotic gas movements; fortunately this small disturbance typically dissipates within a few minutes and can be compensated for by discarding the first few minutes of data following chamber closure (Davidson et al., 2002; Lai et al., 2012).

Diffusion of materials through porous media such as soil can be modelled using Fick's Law (Davidson and Trumbore, 1995; Maier and Schack-Kirchner, 2014; Risk et al., 2002). When other factors such as wind and water movement, or advection are not important for determining gas movements, diffusion dominates the behaviour of gases such as CO_2, CH_4, and N_2O in soils. These conditions are met on non-windy days and when water is not infiltrating soil. Gases produced by microbes will diffuse outwards from the source, and because soil concentrations of these gases are often higher than ambient atmospheric concentrations, the net direction of movement is typically upwards (Davidson and Trumbore, 1995; Kellman and Kavanaugh, 2008; Risk et al., 2002).

The rate of diffusion of a gas through soil is determined by both the intrinsic properties of the gas, including its Henry's constant (which describes its partitioning between water and air phases) and its rate of diffusion in free air and free water, and by the soil's porosity and tortuosity. Tortuosity describes the connections between soil pore spaces and the actual distance that must be travelled through pores compared to the straight-line distance; for simplicity, and because soil pore space usually varies over a narrow range within a particular soil type, tortuosity is often accounted for with a constant rather than by direct measurement (McCarthy and Johnson, 1995; Millington, 1959; Risk et al., 2002). Soil water contents have a large effect on diffusivity because materials diffuse through water approximately 10,000 times slower than through air; gases can become trapped in soil by infiltrating water (Clough et al., 2005), or by ice

in seasonally frozen soils, and may be released as large bursts as soil thaw and the active layer deepens (Mastepanov et al., 2008; Mastepanov et al., 2013).

3. GREENHOUSE GAS SOIL PRODUCTION AND SURFACE FLUXES AT A HIGH ARCTIC POLAR OASIS

3.1 Preface

Soils contribute to global greenhouse gas budgets, acting as either sinks or sources for CO_2, CH_4, and N_2O through plant- and microbe-mediated processes of production and consumption, and by physical transport processes such as diffusion that may move gases from soil layers to the surface. Arctic soils are relatively poorly understood in this context compared with the more intensively studied forest and agricultural biomes of temperate latitudes. Biological activity and thus greenhouse gas emissions are mostly restricted to the brief Arctic summer when the surface layer of soil (i.e., the active layer) thaws while underlying permafrost remains frozen. This chapter describes the net emissions from the surface and the concentrations and calculated net production of greenhouse gases within the soil profile of the active layer from six Arctic vegetation communities located at Alexandra Fjord on Ellesmere Island in the Canadian High Arctic. This site is a polar oasis, with vegetation communities representative of broad areas of the Arctic in close proximity to each other, and serves as a natural laboratory for this and other ecological investigations.

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3.2 Abstract

Arctic vegetation and soil biological communities interact with a range of biotic and abiotic factors to produce or consume the GHG CO_2, CH_4, and N_2O. In Arctic environments the parameters controlling these processes are not well understood. I measured soil GHG concentrations and surface fluxes from six vegetation communities at a High Arctic polar oasis and adjacent polar deserts in order to identify regions within the soil profile of production and consumption of these GHGs. Examined communities included two polar deserts differing in parent material and soil pH, and four lowland tundra communities: (1) prostrate dwarf-shrub, herb tundra; (2) prostrate/hemiprostrate dwarf-shrub tundra; (3) nontussock sedge, dwarf-shrub, moss tundra and (4) sedge/grass, moss wetland, representative of large areas in the low Arctic. Polar desert soils were net producers of greenhouse gases during the brief High Arctic growing season, including at depths close to the permafrost layer, and effluxes from the surface were of a similar magnitude to nearby mesic and hydric tundra soils including for CO_2, indicative of soil respiration in desert soils with few roots. Differences in water content, rather than calculated diffusivity, appear to drive gas transport in at least some soils, with all three GHGs appearing to move rapidly through, for example, the soil at 10 cm above permafrost in the Prostrate (dominated by *Dryas integrifolia*) plant community. Such physical processes may obscure or falsely suggest biological processes in soil ecosystems.

3.3 Introduction

Arctic soils are both producers and consumers of the greenhouse gases (GHG) dioxide, methane, and nitrous oxide; however, the net contribution of different Arctic vegetation and soil communities to the global atmospheric GHG inventory is not well defined (Elberling et al., 2004). This is especially true for polar deserts and semi-deserts. These landscapes, with less than 5% plant cover, are typically thought to contribute little to GHG exchanges because of the limited biological activity occurring in these systems and their arid nature. Covering a combined area of 1.4×10^6 km^2 within the Arctic, polar deserts are the dominant ecotype in the High Arctic area (Walker et al., 2002). The arid nature of polar deserts not only implies that these soils will respond rapidly to a shifting climate but also that GHG production in these deserts may differ from their tundra counterparts.

Soil GHG processes are mediated by biological communities interacting with each other over a wide range of soil conditions (Elberling, 2007). Water content and redox condition in soil play major roles in structuring soil communities, by constraining the physiologies and distributions of both the organisms themselves and the chemical substrates used by the soil communities (Conrad, 2007). Water is both the medium of exchange of materials between cells and the environment and a barrier to the diffusion of oxygen in soils. When soil pores are mostly or entirely filled with water, gas diffusion rates are low, preventing atmospheric oxygen from reaching deep into the soil and contributing to reducing environments at depth. Water filled pore space (WFPS) is often used as a surrogate for oxygen availability in soils. High WFPS prevents most aerobic respiration, lowering CO_2 production. Conversely, under saturated conditions, CH_4 production increases as the biochemical pathways involved in respiration shift from consuming oxygen to consuming CO_2, water, and H_2 (Conrad, 1999). Nitrous oxide emissions may increase or decrease with increasing WFPS, depending on which group of organisms and which biochemical pathways are present and active (Bremer et al., 2009; Corre et al., 1996; Ma et al., 2007).

Concentrations of GHG in the soil atmosphere vary with depth and with the communities of organisms in the soil. Thus, a profile of gas distribution in the soil can highlight regions of production and consumption of gases. This requires detailed compositional analysis of soil air samples, which are almost always obtained from air diffusion wells (Farrell et al., 2002). Moreover, because of the link between production/consumption processes within the soil and gas flux at the surface, many researchers have used the soil gradient method to estimate soil/atmosphere gas fluxes (Davidson and Trumbore, 1995).

Polar oases are isolated areas in the Arctic and Antarctic with local climate conditions milder than their surrounding area and include varied soil types and vegetation communities in close proximity to each other. Moreover, climate factors such as precipitation, near-surface air temperatures, and wind speed and duration are consistent with lower latitudinal locations. Alexandra Fjord lowland, on Ellesmere Island, Canada (78º53’N; 75º55’W), is a High Arctic oasis that harbours a range of vegetation communities that are found throughout the Arctic (Freedman et al., 1994; Walker et al., 2002) and is characterized by climatic conditions that are less severe than the surrounding polar deserts. This study examined belowground GHG profiles in six vegetation communities at the Alexandra Fjord polar oasis during one growing season.

Each community was assessed by examining soil gas profiles and the soil/atmosphere gas flux, with the lowland communities being sampled near the beginning and again at the end of the Arctic summer. The communities sampled represent some of the wettest landforms present in the terrestrial Arctic as well as some of the driest. As such, they encompass a wide range of GHG production/consumption processes occurring in Arctic vegetation communities and which contribute to the global GHG budget. In aggregate, these desert and tundra vegetation communities represent approximately 1.5 million square kilometres of land in the Arctic (Walker et al., 2002).

The objective of this study was to investigate patterns and distributions of subsurface GHG concentrations and how these profiles are linked to net gas production and flux in six vegetation communities during the summer of 2009. The vegetation communities included two polar deserts, three mesic tundras, and a depressional outwash plain wetland at the Alexandra Fjord polar oasis. Gas concentration profiles and soil physical properties were used to estimate microbially-mediated production and consumption of GHGs; surface fluxes were measured using non-steady-state chambers (Hutchinson and Livingston, 2002).

3.4 Materials and Methods

3.4.1 Study Location

The Alexandra Fjord lowland polar oasis is an 8 km^2 valley on the eastern coast of Ellesmere Island, Canada. The polar oasis includes a variety of vegetation types (vegetation communities) in close proximity to one another (Freedman et al., 1994). To the west, the valley is bordered by a mountain (the Dome) that harbours two distinct polar desert communities adjacent to one another, but separated by a sharp discontinuity in soil type. The valley itself encompasses several plant communities; the four major communities, with their Circumpolar Arctic Vegetation Map (CAVM; Walker et al., 2002) designations and the notation used in this paper being: prostrate dwarf-shrub, herb tundra (P1, “Prostrate”); prostrate/hemiprostrate dwarf-shrub tundra (P2, “Hemiprostrate”); nontussock sedge, dwarf-shrub, moss tundra (G3, “Sedge/dwarf-shrub”) and sedge/grass, moss wetland (W1, “Wetland”); the two polar desert communities of the Dome are cryptogam, herb barren (B1, “Barren”) and noncarbonate mountain complexes (B3b, “Mountain”) (Table 3.1). Although the CAVM designations are not

ideally suited for such small scale resolution, I use these designations so that readers can link other study sites to the communities studied here. Greenhouse gas fluxes and subsurface gas concentrations were measured in the six vegetation communities during the summer (late June to early August) of 2009.

The soils were determined in the field to be generally sandy , with low organic matter contents; the Wetland soils were the exception, with organic horizons overlying a sandy C horizon. All the soils were cryosols, with permafrost at depths (i.e., the depth of the active layer) of 30 cm to 60 cm, and most vegetation communities included soils with surface and profile features consistent with cryoturbation (i.e., turbic cryosols). Indeed, frost boils, or similarly patterned surface features, were found in all the lowland communities except the Wetland. Surface frost boils also were visible in the Barren polar desert community, but were not observed in the adjacent Mountain community. Because of the prevalence of these surface features, soil probe clusters and flux chambers were placed both inside and outside frost boils. Subsequent data analysis, however, revealed that both the profile gas concentrations (integrated over the depth of the profile) and the surface fluxes were not statistically different between positions (i.e., for boils *vs*. interboils within each vegetation community). The lone exception occurred in the Hemiprostrate community, where CO_2 effluxes from the interboil positions were marginally higher than those from the boils themselves (i.e., 118 ± 57 μmol m^{-2} s^{-1} *vs*. 40 ± 22 μmol m^{-2} s^{-1}; $p = 0.128$). Nevertheless, both the gas concentration and surface flux measurements from within and between frost boils were pooled within communities.

3.4.2 Soil Gas Profile and Surface Flux Measurements

Subsurface gas concentrations were measured in each vegetation community by inserting gas sampling probes into the soil to a set depth, typically to the top of the permafrost. The probes were inserted into undisturbed soil and allowed to equilibrate by diffusion for 24 hours before sampling the internal gases. For details of the construction and deployment of the probes, please see Brummell and Siciliano (2011). Multiple probes were required to obtain a single soil gas profile; indeed, each soil gas profile was a composite of measurements obtained using six probes installed in a cluster - with the sampling ports located at depths of about 5 cm below ground surface (bgs) to about 2 cm above the top of the permafrost. Within each vegetation community, clusters (n = 5) of soil gas probes were located in areas representative of the larger community.

Table 3.1 Vegetation communities included in the 2009 greenhouse gas study.

CAVM Classification†		User-defined Names		Estimated Area†
ID	**Description**	**Colloquial‡**	**Present study**	**(km^2)**
B1	cryptogam, herb barren	Dolomitic	Barren	225,000
B3b	noncarbonate mountain complex	Granitic	Mountain	69,000
G3	nontussock sedge, dwarf-shrub, moss tundra	Willow	Sedge/dwarf-shrub	569,000
P1	prostrate dwarf-shrub, herb tundra	Dryas	Prostrate	399,000
P2	prostrate/hemiprostrate dwarf-shrub tundra	Cassiope	Hemiprostrate	140,000
W1	sedge/grass, moss wetland	Wet sedge meadow	Wetland	101,000

† Taken from the Circumpolar Arctic Vegetation Map (Walker et al., 2002).
‡ Refers to names that have been used by other researchers working at Alexandra Fjord, and at similar sites in the Arctic.

Subsurface concentrations of CO_2, CH_4, and N_2O were measured simultaneously by connecting the soil gas probes to a Gasmet DX-4015 Fourier transform infrared trace gas analyzer (FTIR-TGA; Gasmet Technologies Oy, Helsinki, Finland). The gas analyzer collects a complete infrared spectrum at 100 ms intervals, with multiple spectra averaged over a pre-selected (180 s) measurement time. Gas concentrations are then calculated from the resulting sample spectrum using the on-board software (Calcmet™ ver. 2005.1), which employs a modified Classical Least Squares analysis algorithm; evaluations under laboratory conditions indicate a response time of the FTIR-TGA of approximately 40 s. The internal volume of the measurement cell in the FTIR-TGA (500 mL) is greater than that of the soil gas probes (112.5 mL); thus to increase the effective volume of the gas sampling probes, a 1.0 L polypropylene bottle was connected to each probe as described by Brummell and Siciliano (2011). Quick-disconnect fittings were used to connect the FTIR-TGA to the soil gas probes without introducing atmospheric air into the probe or reservoir bottle. After connecting a probe (including the reservoir bottle) to the FTIR-TGA, the air in the probe was cycled through a closed loop for 3 min at a rate of 5 L min^{-1}. The probe was then disconnected and the FTIR-TGA system flushed with ambient air for 2 min. Preliminary studies demonstrated that this yielded negligible carryover from one probe to the next, even at high gas concentrations, and that this arrangement applied negligible pressure differential and turbulence at the probe/soil interface.

The total gas concentration measured by the FTIR-TGA (C_T) includes a contribution from the ambient air in the measurement system (C_a) as well as the soil atmosphere (C_s); (Equation 3.1).

$$C_T = C_S\left(\frac{V_S}{V_T}\right) + C_a\left(\frac{V_{FTIR}}{V_T}\right) \quad \text{(Eq. 3.1)}$$

where V_S is the volume of the sample probe (1.1125 L, including the gas reservoir bottle); V_{FTIR} is the volume of the gas measurement cell and associated tubing (0.6455 L); and V_T is the total volume of the closed sample loop (1.7580 L). The gas concentration in the soil atmosphere is then calculated by re-arranging Equation 1 to solve for C_S (Equation 3.2).

$$C_S = \frac{C_T V_T - C_a V_{FTIR}}{V_S} \quad \text{(Eq. 3.2)}$$

Carbon dioxide, CH_4, and N_2O concentrations in the air above the soil surface also were determined on each sampling day (n = 5). Gas concentrations in the ambient air were measured by opening the FTIR-TGA gas circuit to the atmosphere, placing the intake hose at a height of 2 cm above the soil surface, and drawing air through the instrument for 3 min at a rate of 5 L min^{-1}.

Greenhouse gas fluxes at the soil/atmosphere interface were measured using opaque, vented, non-steady-state chambers (Li-Cor model 8100-104; Li-Cor, Lincoln, NB) connected to the Gasmet DX 4015 FTIR-TGA. One day prior to the start of data collection, PVC collars (20 cm i.d.) were pressed into the soil to a depth of *ca.* 7 cm; within each vegetation community, all flux chambers were deployed in close proximity to the soil probes. At each sampling event, a chamber was positioned over each collar, sealed onto the collar and the change in gas concentration measured over a 10 min period with the on-board software recording gas concentrations averaged over 60 s intervals. Small disturbances and pressure changes associated with the closing of the chambers (Davidson et al., 2002) consistently created noise in the initial measurements, and a clear accumulation of GHG in the chamber was not observed until this disturbance had passed. Gas concentrations in the chambers increased in near-linear fashion following this period of disturbance; thus, GHG fluxes were calculated by plotting gas concentration *vs*. time and fitting the data to a linear least-squares regression – after discarding the data obtained during the first 2 min following closure of the chamber. Preliminary studies

showed that instrument precision during a 60 s sampling interval, more than 2 min after chamber closing, was 0.006% for CO_2, 0.20% for CH_4, and 0.21% for N_2O. Repeatability of measurements of gas concentrations in probes are reported in Brummell and Siciliano (2011), and range from 2.5 to 33% for the three gases across the six vegetation communities.

Subsurface gas concentrations and surface fluxes were measured at the four lowland sites at the start of the season (June 26 to July 7, 2009) and again approximately 25 days later (July 18 to August 3); thus, providing a look at seasonal changes. Because the soil was disturbed by removal of the probes following the early season sampling, late-season measurements were made at nearby locations within each of the target plant communities. Profiles and surface fluxes were measured at the polar desert sites at the beginning of the snow-free season only (July 10 to July 14).

3.4.3 CO_2, CH_4, and N_2O Production

Production of each of the three GHG was calculated separately, using the concentration data obtained from the soil gas probes and estimates of soil gas diffusivity from bulk density and water content measurements for each profile. Concentrations of GHG in the soil atmosphere are usually much higher than ambient concentrations at the surface, thus GHG are assumed to be diffusing vertically through the soil profile, from regions of production to regions of consumption or to the surface (Equation 3.3) (Davidson and Trumbore, 1995; Risk et al., 2002).

$$P_{GHG} = D_{e_i}\left[\frac{C_i - C_{i-1}}{\Delta z}\right] - D_{e_{i+1}}\left[\frac{C_{i+1} - C_i}{\Delta z}\right] \qquad \text{(Eq. 3.3)}$$

where P_{GHG} is net production of either CO_2, CH_4, or N_2O; D_{ei} is effective diffusivity for layer i ($m^2\ s^{-1}$); C_i and C_{i-1} are the gas concentrations (mol m^{-3}) in layers i and i-1 below, respectively; and Δz is the difference in depth (m) between layers i and i+1 above. Positive values of P_{GHG} indicate production/accumulation of gas at a given depth; negative values indicate consumption/loss. Because of large uncertainties surrounding diffusion through the near-surface boundary layer and highly variable GHG concentrations close to the soil surface, production estimates for the shallowest layer of soil in each community (i.e., the uppermost 10 cm) were calculated based on the diffusivity of that layer of soil (D_{ei}) rather than the diffusivity of the layer above (D_{ei+1}), the free air overlying the soil.

Production in the deepest soil of the active layer was calculated by assuming zero flux from the permafrost immediately below, and considering only the diffusivity and gas concentration gradient to the soil layer above. While microbial activity has been detected in permafrost and other soil-ice structures (Katayama et al., 2010; Ponder et al., 2008), the contribution of these activities to the net soil gas processes of the active layer is unknown.

Effective diffusivity was calculated using the Millington relationship (Millington, 1959) as modified by McCarthy and Johnson (1995) and by Risk et al. (2002) to include a term for aqueous diffusion (Equation 3.4):

$$D_e = \frac{\frac{\Theta_w^{10/3}}{H} D_{fw} + \Theta_g^{10/3} D_{fg}}{\Theta_T^2} \qquad \text{(Eq. 3.4)}$$

where, for each gas D_{fw} is the diffusion coefficient in free water, H is the dimensionless form of Henry's solubility constant in water, D_{fg} is the diffusion coefficient in free air, and Θ_w is water-filled porosity, Θ_g is air-filled porosity and Θ_T total porosity.

Small errors in measurement of porosity of soils can result in large errors of estimation of effective diffusivity because the air-filled and water-filled porosities are raised to the power of 10/3 (Equation 3.4). Assuming a 10% random error of measurement of water-filled porosity, error propagation (Figliola and Beasley, 2006) leads to an uncertainty of approximately 22% in D_e, which, combined with random uncertainty of measurement of gas concentrations ranging from approximately 2.5 to 33% (Brummell and Siciliano, 2011) leads to the calculated errors for production estimates reported here. Please see Appendix 1 for details of the error propagation calculations.

Production estimates were calculated using median values of gas concentrations and porosities (Equation 3.3, Equation 3.4) for 10 cm depth bins because gas concentrations were typically non-normally distributed and for some pits, there were mismatches between soil sampling depths and gas sampling depths of up to approximately 5 cm.

4.3.4 Soil Sampling and Analysis

Upon conclusion of the gas sampling, the probes were removed from the soil and a soil pit excavated to the top of the permafrost. Pits were excavated after gas sampling at all lowland

and polar desert sites, and again after late-season gas sampling at one site (Hemiprostrate) in the lowlands. One pit at the Wetland site collapsed during excavation, reducing the total number of pits to 34. Soil samples were collected at six depths (corresponding to the depths of the sampling ports on the soil gas probes) using sterile polypropylene bottles (Thermo Fisher Scientific); bulk density samples were collected using stainless steel hand corers (100 cm^3; Eijkelkamp Agrisearch Equipment BV, Giesbeek, Netherlands). Soil samples were placed in a -20ºC freezer on-site as soon as was practical, and were kept frozen. Except in the Wetland site, where extremely high soil moisture contents led to rapid degradation of pit walls, temperature was measured at each depth position in the pits using a ProCheck digital sensor (Decagon Devices, Pullman, WA, USA) equipped with an ECH2O-TE combined moisture-temperature probe that was inserted into the soil and allowed to reach thermal equilibrium (ca. 2 min).

Frozen soil samples were processed for measurement of moisture content and WFPS, exchangeable nutrients, organic carbon, total nitrogen, and pH (Carter and Gregorich, 2008). Gravimetric soil moisture content (GSMC) was determined by drying the soil at 105ºC for 24 h and measuring weight loss; WFPS (%) was calculated using Equation 3.5:

$$WFPS = \frac{GSMC \times BD}{1 - (BD/PD)} \times 100 \qquad \text{(Eq. 3.5)}$$

where *BD* is bulk density and *PD* is particle density (2.65 g cm^{-3}). No soil samples composed largely of organic matter were collected; such soil was present in the upper few (< 10) cm of the Wetland site only.

Nutrients and organic matter were extracted from soils using a 1:10 soil:K_2SO_4 (0.5M) extract, followed by centrifugation at 500 × g and filtration through Whatman #1 filter paper (Whatman Plc, Maidstone, UK). The filtered extracts were analyzed for total non-purgeable organic carbon (NPOC) and total nitrogen (TN) using a Shimadzu TOC-V analyzer (Shimadzu Corporation, Kyoto, Japan) and a furnace temperature of 720ºC. Extractable NH_4^+ and NO_3^- plus NO_2^- were determined using a Smartchem 200 (Westco Scientific Instruments Inc., Brookfield CT, USA) following the manufacturer's instructions. Soil pH was determined using a 1:10 (w/v) soil:water suspension, allowing the suspension to settle and measuring the pH of the supernatant solution.

3.4.5 Data Analysis

Soil variability and variation in depth to permafrost made it impossible to insert the probes into the soil to exactly the same depth, either within or between sites. Thus, for the purposes of statistical analysis − and as a reasonable trade-off between sample size ($2 \leq n \leq 10$) and profile resolution − the samples were grouped into 10 cm depth increments, or bins.

Due to the importance of the permafrost layer for structuring my calculations of gas production, depths were expressed as distance above permafrost rather than the more typical depth below surface; this results in larger sample sizes for near-permafrost bins, facilitating analysis of this portion of the soil profiles.

Outliers within each depth increment were identified using the Q-test with a 90% confidence limit (Dixon, 1986). [Note: only five of 2400 gas concentration measurements were identified as statistical outliers.] The between-day variance for individual probes within a vegetation community was less than the variance between probes at similar depths, thus the gas measurements for each 2 d measurement period were pooled.

Integrated estimates of the subsurface gas concentration and production for CO_2, CH_4, and N_2O were calculated using area-under-the-curve (AUC) analysis (NCSS Statistical Analysis Software) (Hintze, 2009). The AUC analysis employed the trapezoidal rule to calculate the area under the gas concentration × depth curve – with the baseline set at ambient gas concentration – to yield a profile integrated net gas content balance. Positive values (mol m^{-3}) indicate that, on a profile-scale, gas concentration exceeds that of the overlying free atmosphere while negative values indicate depleted concentrations in the soil. Similarly, AUC analysis of the production × depth curve – with the baseline set at zero net production – to yield a profile integrated net production balance. Positive values (nmol cm^{-1} s^{-1}) indicate gas production exceeds consumption plus efflux; conversely, negative values indicate that gas consumption plus efflux exceeds production.

Significance of net GHG production was assessed by multiple comparisons, using post-hoc T-tests. Dunn-Šidák correction (Sokal and Rohlf, 1995) for 29 comparisons, the total number depth bins across all ecosystems for each gas, was applied to achieve an overall α of 0.05; critical values of one-tailed T, with between 1 and 9 degrees of freedom (n within bins 2 to 10) were used at $p < 0.0025$.

3.5 Results

3.5.1 Soil Characteristics

Most of the soils were in the slightly acidic to slightly alkaline pH range (6.0–7.4), with more acidic soils (pH 5.3–5.9) associated with the Sedge/dwarf shrub community and more alkaline soils (pH 7.6–7.9) associated with the carbonate-rich dolomitic soils of the Barren community (Table 3.2). Mineral N was lowest in the polar desert soils (i.e., in the Barren and Mountain communities), with virtually no detectable nitrate near the permafrost layer, but increasing concentrations of ammonium with depth. The highest mineral N levels were associated with the Sedge/dwarf shrub and Wetland communities.

Both polar desert communities include large areas of exposed soil nearly devoid of vascular plants and large bryophytes, but covered by a thin layer of cryptogams. Snowmelt occurred during the time of the gas measurements, with snow cover completely disappearing over the five day measurement period in these communities. This resulted in extremely high, but transient, soil water contents in some areas. Water contents were below saturation by the time the soil gas profiles and surface fluxes were measured, and the water contents presented in Table 3.2 were obtained when the pits were excavated, at least three days after most surface pools of water had drained away. Snowmelt was much further along in the lowland communities and by the time the gas concentration and flux measurements were made in the valley, the soils had been snow free for at least 14 days.

3.5.2 GHG Flux, Profile Concentration, and Net Production

Flux of gas did not vary through the growing season in the lowland tundra communities; the polar desert communities were measured only once each, shortly after snowmelt. Gross ecosystem CO_2 flux was consistent with plant biomass and previous estimates from these vegetation communities (Muc et al., 1994; Welker et al., 2004), with the polar deserts producing less CO_2 than some of the lowland tundras; all vegetation communities except the Barren produced significantly more than zero CO_2 (ANOVA, $p < 0.001$) (Fig. 3.1A). In contrast, CH_4 flux was significantly different from zero (t-test, $p < 0.001$) only for the Barren community, which emitted 0.38 ± 0.14 nmol m^{-2} s^{-1} during measurement. Not unexpectedly, CH_4 effluxes

Table 3.2. Depth profiles of soil variables in the vegetation communities at Alexandra Fjord.

Depth† (cm)	NH_4^+ - N (mg / kg)	NO_3^- - N (mg / kg)	PO_4^{2-} - P (mg / kg)	NPOC‡ (g / kg)	WEN§ (g / kg)	pH	WFPS¶ (%)
			Barren				
30	2.7 (1.2)	1.7 (0.5)	-#	4.4 (0.9)	0.032	7.6 (0.1)	45 (8.4)
20	3.5 (0.4)	3.8 (1.4)	-	4.1 (0.8)	0.006 (0.006)	7.8 (0.1)	31 (4.2)
10	3.6 (1.0)	2.5 (1.4)	-	5.0 (0.5)	0.014 (0.014)	7.7 (0.1)	36 (5.8)
0	6.4 (3.0)	2.5 (1.6)	-	5.2 (0.6)	††BDL	7.8 (0.1)	46 (7.1)
			Mountain				
30	6.6 (1.8)	0.2 (0.1)	-	5.2 (0.1)	-	6.6 (0.2)	47 (7.7)
20	6.1 (1.2)	0.7 (0.3)	-	5.1 (0.3)	0.055	6.6 (0.1)	47 (4.1)
10	7.8 (2.1)	1.0 (0.7)	-	3.5 (0.7)	BDL	6.5 (0.2)	53 (7.7)
0	12.4 (2.9)	3.5 (3.2)	-	5.3 (0.4)	0.033	7.0 (0.1)	55 (5.7)
			Prostrate				
40	47.0 (41.7)	7.1 (3.7)	BDL	15.4 (8.7)	4.518 (2.975)	5.5 (0.1)	74 (10.8)
30	1.0 (0.4)	3.0 (0.1)	0.1 (0.0)	5.8 (0.5)	1.277 (0.060)	5.9 (0.1)	58 (7.4)
20	0.5 (0.1)	2.7 (0.1)	BDL	4.8 (0.1)	1.198 (0.077)	6.2 (0.1)	67 (5.0)
10	0.1 (0.1)	2.5 (0.2)	BDL	4.0 (0.2)	1.237 (0.152)	6.6 (0.1)	79 (7.1)
0	BDL	2.9 (0.0)	BDL	3.5 (0.5)	0.989 (0.154)	6.9 (0.1)	76 (6.1)
			Hemiprostrate				
50	3.8 (0.8)	7.2 (2.8)	-	2.6 (1.2)	0.013 (0.013)	6.3 (0.4)	61 (12.0)
40	4.1 (0.7)	7.6 (1.6)	-	2.8 (1.1)	0.015 (0.008)	6.3 (0.2)	75 (11.8)
30	3.2 (0.7)	6.9 (1.7)	-	2.5 (0.9)	0.002 (0.002)	6.5 (0.2)	64 (4.3)
20	3.5 (0.9)	6.3 (1.6)	-	5.2 (1.0)	BDL	6.7 (0.2)	54 (6.5)
10	3.5 (1.0)	5.4 (1.6)	-	4.0 (1.0)	0.006 (0.006)	6.7 (0.2)	66 10.8)
0	4.6 (0.8)	10.5 (0.8)	-	2.9 (0.9)	0.007 (0.007)	7.0 (0.0)	75 (12.6)
			Sedge/dwarf-shrub				
30	68.1 (15.5)	21.2 (7.0)	0.2 (0.0)	41.7 (7.2)	7.975 (1.154)	5.7 (0.2)	47 (1.5)
20	37.8 (11.2)	13.1 (2.6)	0.2 (0.0)	30.7 (7.7)	6.274 (1.405)	5.2 (0.2)	43 (4.8)
10	15.5 (6.3)	7.5 (2.2)	0.1 (0.0)	16.7 (3.7)	3.212 (0.636)	5.8 (0.1)	51 (6.7)
0	5.8 (0.8)	5.2 (0.7)	0.1 (0.0)	11.6 (1.0)	2.373 (0.341)	5.6 (0.1)	43 (4.2)
			Wetland				
30	157.0 (30.1)	30.9 (3.8)	0.5 (0.1)	68.5 (7.5)	15.89 (1.532)	6.6 (0.1)	89 (3.7)
20	18.3 (9.1)	16.4 (9.3)	0.2 (0.1)	31.7 (18)	5.801 (2.589)	6.4 (0.1)	75 (2.9)
10	5.6 (2.2)	2.2 (0.8)	0.2 (0.1)	6.9 (1.3)	1.820 (0.180)	6.4 (0.1)	92 (16.7)
0	4.3 (1.6)	2.8 (0.5)	BDL	5.0 (0.5)	1.475 (0.156)	6.6 (0.1)	75 (14.9)

†Above deepest permafrost measurement in the vegetation community
‡NPOC: non-purgeable organic carbon
§WEN: water extractable nitrogen, including both NH_4^+ and NO_3^-
¶WFPS: Water Filled Pore Space
#- not measured due to limited sample volume.
††BDL: Below Detection Limit.

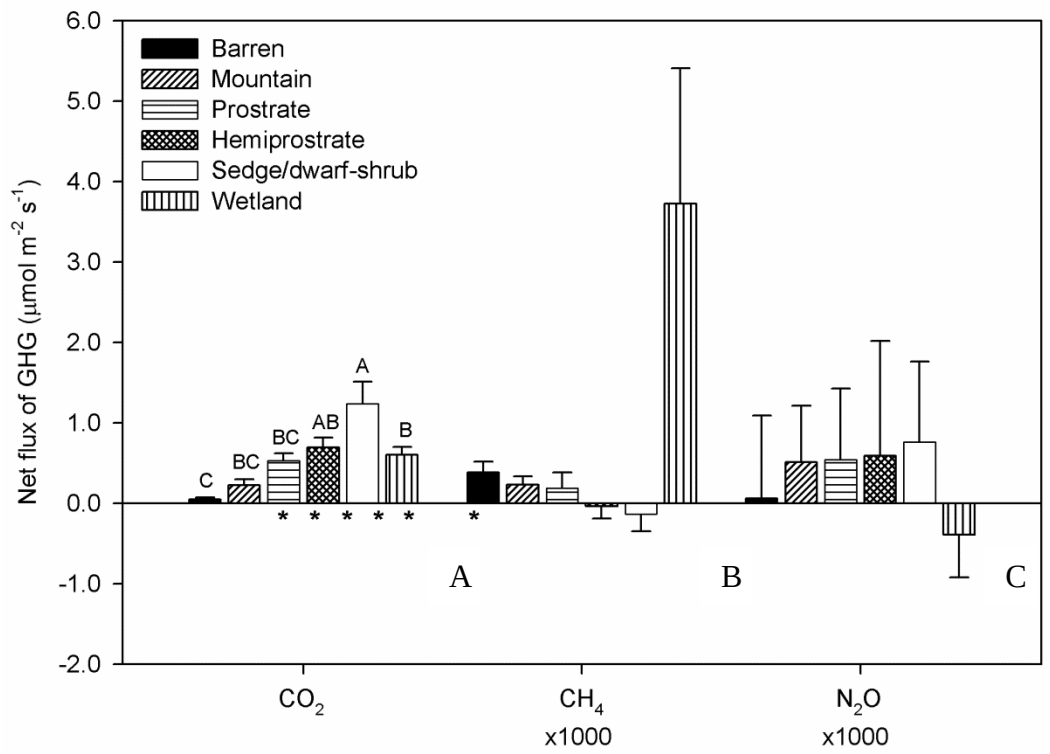

Fig. 3.1. Net ecosystem gas fluxes (n = 8 per community) for CO_2 (A), CH_4 (B), and N_2O (C) of six vegetation communities at Alexandra Fjord; positive values indicate movement of gas from soil to the atmosphere, i.e., net production, while net consumption is indicated by negative values. Communities differed significantly only in their fluxes of CO_2 (ANOVA, $p < 0.001$), letters in common indicate CO_2 flux estimates that do not significantly differ. Fluxes significantly ($p < 0.05$) different from zero are indicated by *.

were greatest in the wetland community, but were also highly variable (-17.2 to 36.4 nmol m^{-2} s^{-1}); consequently, the mean flux was not significantly different from zero ($p = 0.197$) (Fig. 3.1B). Fluxes of N_2O were highly variable for all vegetation communities and, as a result, the mean fluxes were not significantly different from zero (Fig. 3.1C).

3.6 Discussion

The largest N_2O efflux observed for a single measurement, 11.1 nmol m^{-2} s^{-1}, is more than 10 times the highest mean N_2O efflux reported by Dalal and Allen (2008) in a review of N_2O emissions from natural ecosystems. The highest mean N_2O efflux observed in this study, 0.76 nmol m^{-2} s^{-1} in the Sedge/dwarf-shrub community, or 10.56 kg N_2O-N ha^{-1} y^{-1}, while not significantly different from zero is similar to reported mean values from tropical rainforests in Australia (Kiese and Butterbach-Bahl, 2002) and Brazil (Silver et al., 2005), and about 50% more than the log-normal mean reported N_2O efflux of 0.5 nmol m^{-2} s^{-1} from an Antarctic desert

(Gregorich et al., 2006). My observed negative fluxes of N_2O are similar to other previous estimates based on alpine and Antarctic sites, which range from -0.008 to -0.80 nmol m^{-2} s^{-1} (Dalal and Allen, 2008; Holst et al., 2008). A previous estimate obtained from a different vegetation community at Alexandra Fjord ranged from -4.4 to 2.0 nmol m^{-2} s^{-1} (Lamb et al., 2011) while an estimate based on opaque static chamber measurements at a slightly lower latitude mesic site at Truelove Lowland, Devon Island varied between -0.18 and -2.9 nmol m^{-2} s^{-1} (Ma et al., 2007). Fluxes of N_2O from soils are highly variable and often skewed, with rare high-magnitude emissions dominating average measurements (Yates et al., 2006), and while the mean values reported here are not significantly different from zero, I think the mean values are representative of real patterns of N_2O emissions that are hidden by high variability. I measured GHG fluxes only during the brief High-Arctic growing season, not the full year, thus meaningful comparisons with annual emissions from other ecosystems are difficult, and are only included here to suggest the scale of activity in the soils studied here during the short Arctic summer.

Flux of CO_2 was weakly ($p = 0.110$, $r = 0.716$) correlated with belowground gas concentrations, averaged using the AUC method (Brummell and Siciliano, 2011) (Fig. 3.2A). The correlation for CH_4 was also weak ($p = 0.193$, $r = 0.616$) (Fig. 3.2B), while N_2O was not correlated ($p = 0.284$) (Fig. 3.2C). There was no correlation between total belowground gas production, averaged using the AUC method and the measured surface flux (Fig. 3.2 D-F). If I include all ecosystems, fluxes calculated from the gas concentrations at 10 cm depth below ground surface and ambient (2 cm above soil surface) were not correlated with measured fluxes (Fig. 3.2 G-I). Removal of the Barren community from the comparison of calculated and measured fluxes of CO_2 (Fig. 3.2 G) renders the correlation significant ($r = 0.919$, $p = 0.028$); the apparent outlier status of the Barren site may be due to changes in diffusivity associated with water movement within the soil between the time of measurement of surface flux (July 10), profile gas concentrations (July 11), and pit excavation and soil sampling (July 12). Similarly, the Wetland community is a clear outlier on the comparison of CH_4 fluxes (Fig. 3.2 H); removal of that community improves the correlation ($r = 0.857$, $p = 0.064$); as discussed below, my methods for measuring gas concentration in profiles and gas fluxes at the surface may be unsuitable for very wet conditions where gas transport processes other than diffusion, such as

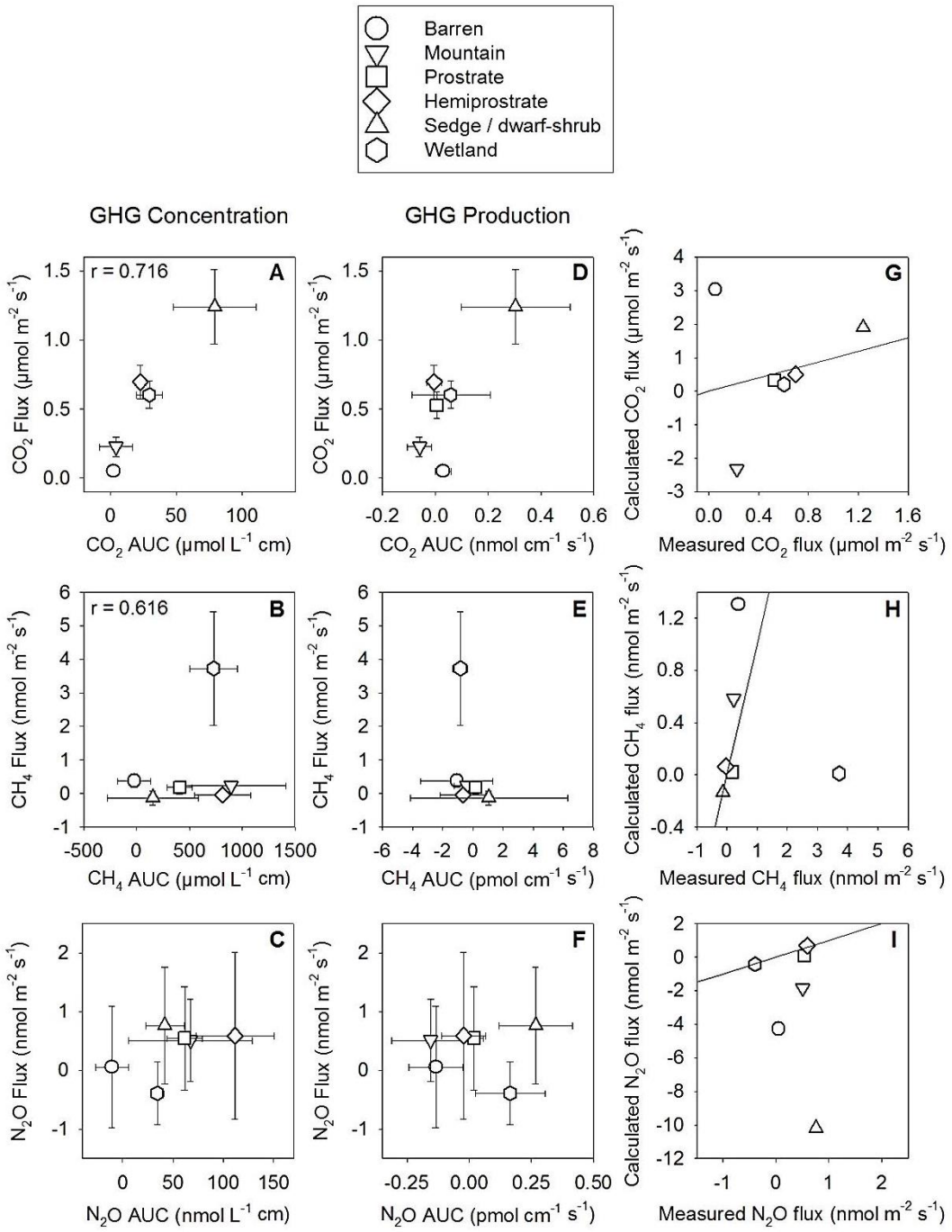

Fig. 3.2. Surface fluxes of GHG were weakly correlated with area-under-the-curve (AUC) measurements of subsurface gas concentrations relative to ambient levels, for CO_2 (A: p = 0.110) and for CH_4 (B: p = 0.193), but not correlated for N_2O (C: p = 0.284). Measured fluxes of GHG were not significantly correlated with AUC estimates of net belowground gas production (D: CO_2 p = 0.273; E: CH_4 p = 0.708; F: N_2O p = 0.390). Error bars indicate ±1 standard error. Calculation of flux from estimates of the diffusivity of the shallowest 10 cm of soil and measurements of GHG concentrations at 2 cm above the soil surface and -10 cm below were not significantly correlated with measured flux (G: CO_2 p = 0.762; H: CH_4 p = 0.764; I: N_2O p = 0.536). Lines in G, H, and I are 1:1, indicating the distribution of data if calculations perfectly matched measurements.

ebullition may be important. Nitrous oxide (Fig. 3.2 I) shows no obvious pattern. Discrepancies between calculated and measured GHG flux may be due to variation in effective diffusivity through the soil profile, leading to misestimates when calculating flux from a single soil layer, or transport processes other than diffusion that my soil gas probes are unable to adequately capture, leading to overestimates. Thus I speculate that the non-significant correlations between subsurface production and surface flux likely arise due to the high variability and additional ecosystems and samples would need to be evaluated to fully explore the use of AUC as a predictive model of GHG fluxes from soil.

The Wetland community is by far the wettest examined in the course of this study and had the second highest above ground plant biomass (the same vegetation community as "sedge-cushion plant-dwarf shrub" of Muc et al., 1994) and with the largest concentration of labile organic matter in the soil (Muc et al., 1994). Production of CH_4 in wet soils is closely related to soil water content (Conrad, 1989; Ponnamperuma, 1972; Smith et al., 2003), with strong production when water contents create anaerobic conditions and electron acceptors such as nitrate, iron (III) and sulphate have been reduced (Conrad, 1989; Ponnamperuma, 1972). However, the Wetland had non-significant overall CH_4 flux (t-test, $p = 0.197$; Fig. 3.1) due to very high variation in measurements, including some negative fluxes. One possible explanation for this high variation and unexpected negative flux (i.e., into soil) of CH_4 is the occurrence of bubbles rich in CH_4 inside my chambers during measurement. As gas flux is calculated from the slope of the line of accumulation or depletion of gas inside the chamber over an 8 min period (10 min chamber closed minus first 2 min due to disturbance of chamber closing), a sudden increase in gas concentration may lead to an erroneous estimate of negative gas flux if the bubbles emerge early in the measurement period or an erroneously large estimate of gas efflux if the bubbles emerge near the end of the period.

My gas probes appeared to suffer a loss of accuracy at very high soil water contents. Under conditions of very high water content as are found in the Wetland soil, CH_4 production is expected to be high, leading to high gas concentrations in the soil as well as large surface effluxes. However, my calculation of gas production relies on my calculation of gas diffusivity, which may be less accurate where water filled pore space dominates, particularly for a gas such as CH_4 with both a high Henry's constant (42; Liss and Slater, 1974) at the range of soil temperatures observed in this study and a biochemical production pathway highly sensitive to

soil pore fluid contents and local redox state. Movement of CH_4 from soil to atmosphere or overlying free water is dominated by ebullition in at least some systems (Kusmin et al., 2006; Rothfuss and Conrad, 1998; Strack et al., 2005), and it is unlikely my probes accurately sample gas concentrations from such bubbles. In addition, plant cover was complete at Wetland, with an extensive root network established by the plants, providing a channel for vascular transport of CH_4.

Previous studies of N_2O fluxes from Arctic soils (e.g., Rodionow et al., 2006; Repo et al., 2009; Elberling et al., 2010) have found generally low emissions from tundra soils, but very high N_2O emissions from Arctic wetlands following thaw, warming, draining and rewetting as may be expected to occur during the course of the short arctic summer (Elberling et al., 2010); the study site of Elberling et al. (2010) at Zackenberg, Greenland, appears to be similar to the Wetland and Hemiprostrate sites here, but the direct comparison of results is difficult due to unknown differences in water movements at the two locations. The wetland examined in this study did not experience drying during the study period, with surface water present at all measurement locations in this community throughout the summer. Cryoturbation, a soil mixing process that results in patches of bare soil in many Arctic ecosystems, may also contribute to N_2O emissions (Repo et al., 2009); the Wetland community at Alexandra Fjord does not show such bare patches and appears not to be mixed by cryoturbation while the other lowland communities and one of the polar deserts do show signs of cryoturbation.

While other studies have used sub-surface gas concentrations and surface fluxes to develop models of soil respiration and efflux (Elberling et al., 2004), or have used long-term monitoring of permanent probes to examine seasonal or other changes in respiration (Fang and Moncrieff, 1998; Kammann et al., 2001), relatively few studies have directly compared subsurface profiles and surface fluxes (e.g., Kellman and Kavanaugh, 2008; Risk et al., 2008). Kellman and Kavanaugh (2008) report consumption of N_2O within the soil profile, weakening the connection between subsurface concentrations and surface flux. Risk et al. (2008) report consistent and close correlation between measured subsurface production of CO_2 and surface fluxes. I speculate that differences between gases in the ability of subsurface production to predict fluxes or vice-versa may be the result of sinks for gases such as N_2O and CH_4 which are not present in soil for CO_2.

3.6.1 Soil Carbon Dioxide Production Profile

Significant production of CO_2 was detected only at the deepest layer of the Barren community, where 5.3 ± 1.2 pmol m^{-2} s^{-1} (mean ± SE) of production was calculated from an observed concentration gradient from 14.32 to 14.15 μmol L^{-1} of CO_2 (gas concentration values are medians) (Fig. 3.3A). Significant negative production, i.e., consumption, of CO_2 was detected in all soil profiles except at the Hemiprostrate community (Fig. 3.3D). However, sinks for CO_2 within the soil profile are not expected to contribute to overall profile production; chemolithoautotrophic organisms capable of fixing CO_2 under dark conditions have been reported from some permafrost soils (e.g., Sizova and Panikov, 2007), but their contributions to net soil CO_2 production are unknown.

A power analysis based on these measurements of GHG production indicated that 13 replicate pits in each vegetation community, rather than the five used here, would likely be needed to robustly statistically differentiate between zero and the production values I observed here. Significant differences from zero represent post-hoc tests based on critical values of T (see Methods). For all comparisons, only bins with sample sizes of at least nine showed net production significantly different from zero.

3.6.2 Methane and Nitrous Oxide Production

Production of CH_4 in the near-permafrost Mountain soil is likely a transitory phenomenon in this desert system, driven by increased soil water content in the days or weeks following snowmelt. The source of this water may be either infiltrating snowmelt from above or melting ice from below, or some combination of those; neither the duration of this water in the lowest layers of soil nor its source were examined in this study. Examinations of these polar desert soils for the length of the growing season would help to quantify their contributions to broader patterns of soil emissions of this gas.

Apparent consumption of all three GHG was observed at approximately 10 cm above the permafrost in the Prostrate soils. The metabolic pathways that would result in the biological consumption of these three gases are distinct, and respond to physical parameters such as soil water content in different ways. Calculated effective diffusivity (D_e) for each gas at this depth does not strongly differ from D_e for the layers above and below (Table 3.3), yet water contents show an increase moving down from 20 cm above permafrost to the permafrost layer (Table

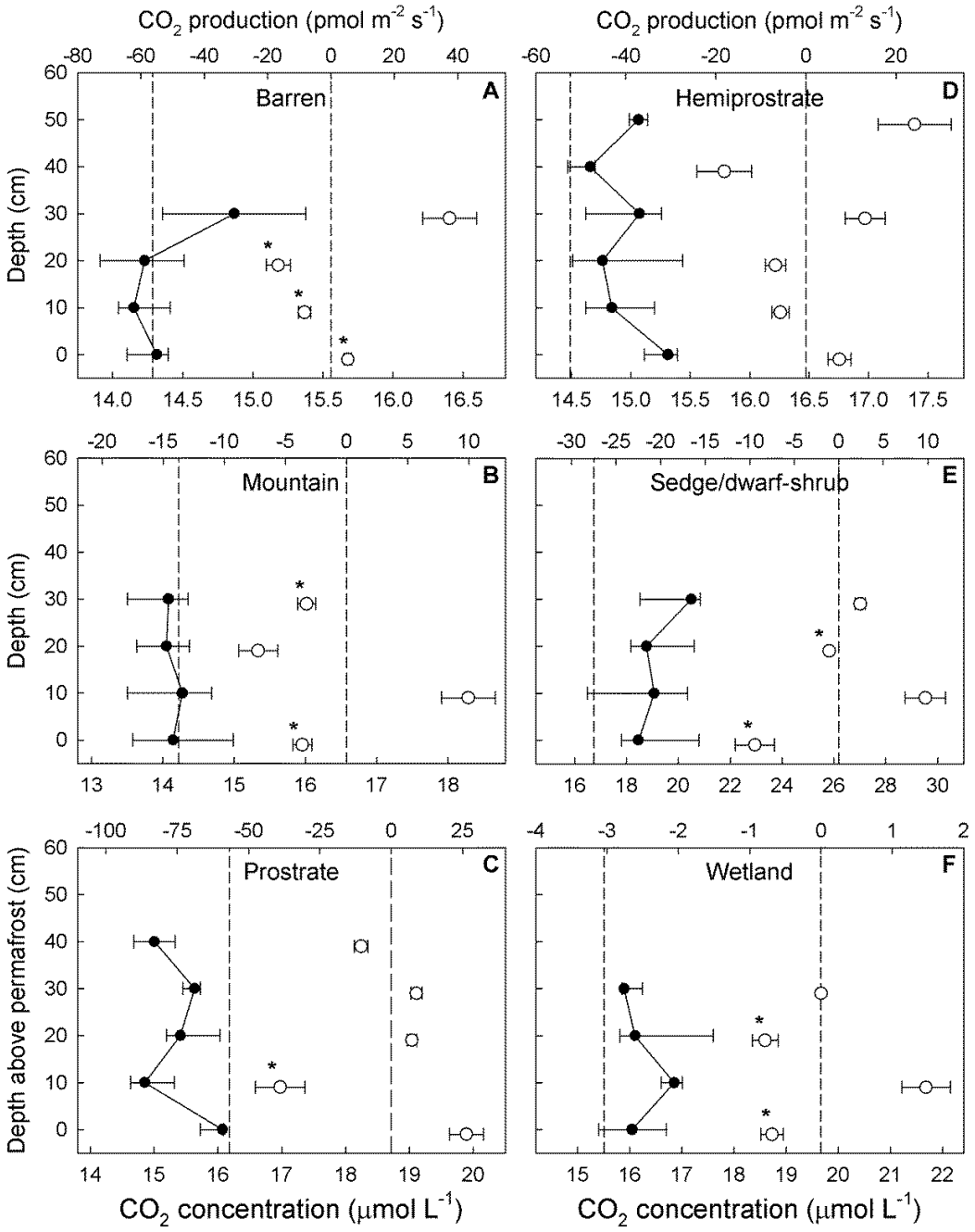

Fig. 3.3. Soil profile concentrations of CO2 (closed circles) and production (open circles) both show differences between vegetation communities. Dashed lines at left in each panel indicate mean ambient concentration, at right indicate zero production. Production profiles of CO2 showed significant production at the deepest layer of the Barren community (A), indicated by * (multiple comparisons of means, overal $p < 0.0025$), near the permafrost layer. Significant CO2 consumption, at various depths at all vegetation communities except Hemiprostrate (D), is enigmatic. Values for concentration are medians, error bars are ±1st and 3rd quartiles ($2 \leq n \leq 10$), for production values shown are calculated from means of gas concentration gradients and diffusivities, error bars are ±1 SE as calculated by error propagation. Production means are positions 1 cm deeper to avoid overlap with the concentration data.

3.2); bulk density similarly increases slightly with proximity to the permafrost (Table 3.3). Thus, I speculate the significantly negative net production here is the result of gases diffusing upwards out of the 10 cm above permafrost layer more rapidly than they are produced or are entering from the layer below, rather than consumption *in situ*. Positive, though not significant, production measurements for all three gases in the layer above, 20 cm above the permafrost, further suggests relatively large rates of upward transport from the 10 cm layer.

Significant production of CH_4 was found at the near-permafrost layer of the Mountain soil (Fig. 3.4B), with significant consumption in the Prostrate soil at approximately 10 cm above the permafrost (Fig. 3.4C). Despite occasional large effluxes of CH_4 from the Wetland soil (Fig. 3.4F), no depth at that site showed significant production. As discussed above, my probes may not accurately sample soil gases where water contents are high, as the probes rely on diffusion to reach equilibrium between gas concentrations within the probe and in the surrounding soil.

Consumption of N_2O was also observed in the Mountain soil at near-surface and near-permafrost depths (Fig. 3.5B); this soil also shows CO_2 consumption (Fig. 3.3B) but not CH_4 consumption (Fig. 3.4B) at the near-surface layer. I am puzzled by the apparent co-consumption of N_2O and CO_2, though recent work in nearby environments has suggested a plant-mediated link between these two GHG (Stewart et al., 2012).

Table 3.3. Mean calculated diffusivities (D_e) for each studied gas in the soil profiles.

Depth* (cm)	Mean D_e CO_2 (m^2 s^{-1})	Mean D_e CH_4 (m^2 s^{-1})	Mean D_e N_2O (m^2 s^{-1})	Mean Bulk Density (g cm^{-3})
		Barren		
30	0.031	0.030	0.051	1.492
20	0.039	0.038	0.065	1.248
10	0.033	0.032	0.054	1.438
0	0.032	0.031	0.052	1.481
		Mountain		
30	0.029	0.028	0.048	1.455
20	0.029	0.028	0.048	1.483
10	0.028	0.027	0.046	1.523
0	0.025	0.025	0.042	1.565
		Prostrate		
40	$5.87x10^{-3}$	$5.77x10^{-3}$	0.010	1.252
30	0.024	0.023	0.040	1.455
20	0.022	0.022	0.037	1.524
10	0.022	0.021	0.036	1.630
0	0.020	0.019	0.033	1.646
		Hemiprostrate		
50	0.025	0.024	0.041	1.689
40	0.020	0.019	0.033	1.541
30	0.016	0.016	0.027	1.601
20	0.023	0.022	0.038	1.497
10	0.016	0.016	0.026	1.487
0	0.021	0.021	0.036	1.477
		Sedge/dwarf-shrub		
30	$4.39x10^{-4}$	$4.28x10^{-4}$	$7.15x10^{-4}$	0.479
20	$1.10x10^{-3}$	$1.08x10^{-3}$	$1.82x10^{-3}$	0.599
10	0.016	0.016	0.026	0.854
0	0.025	0.025	0.042	0.967
		Wetland		
30	$2.03x10^{-5}$	$1.15x10^{-5}$	$3.49x10^{-7}$	0.245
20	$1.05x10^{-3}$	$1.03x10^{-3}$	$1.74x10^{-3}$	0.733
10	$8.52x10^{-4}$	$8.36x10^{-4}$	$1.41x10^{-3}$	1.086
0	0.012	0.012	0.020	1.236

†Above deepest permafrost measurement in the vegetation community

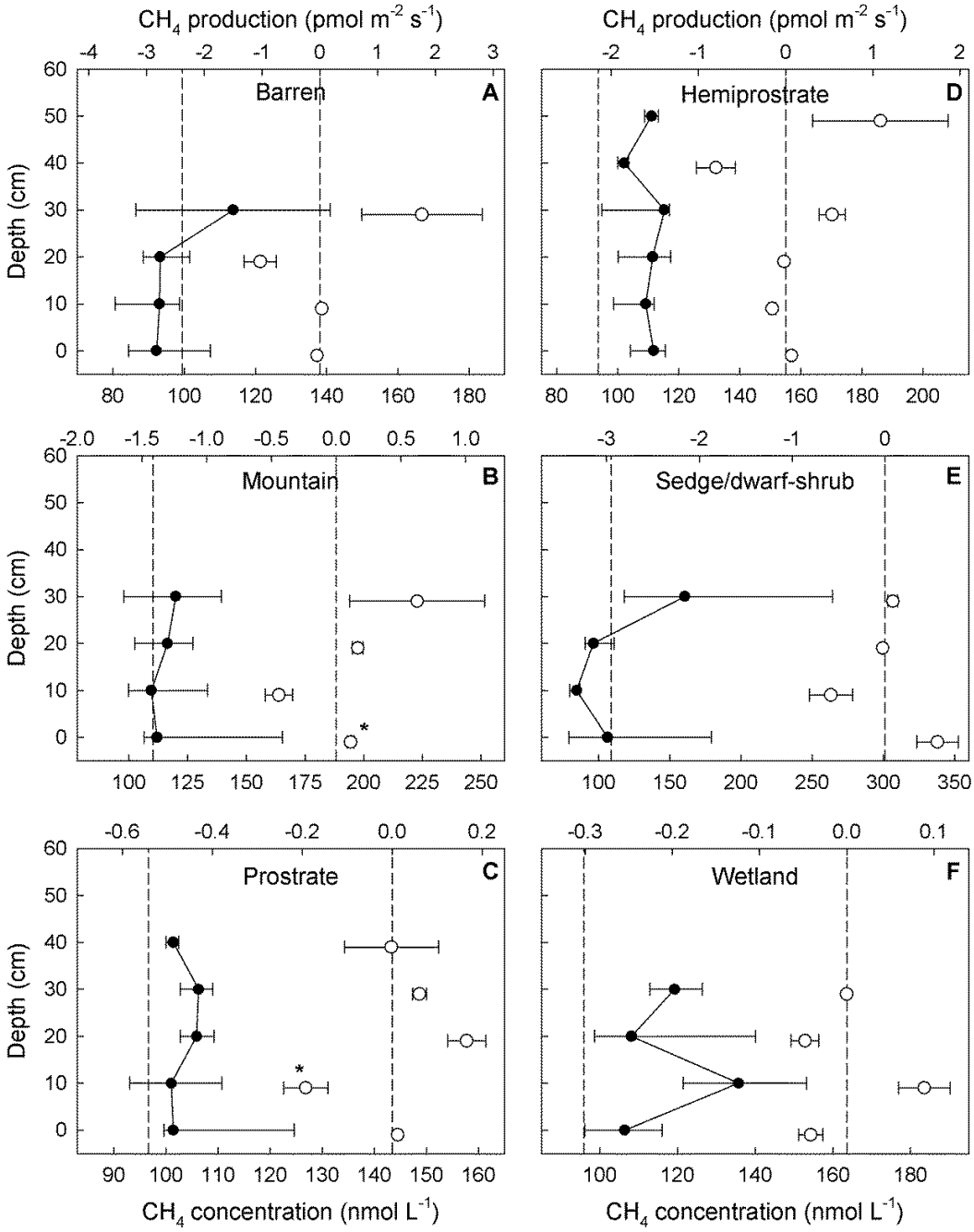

Fig. 3.4. Soil profile concentration of CH_4 (closed circles) and production (open circles) both show differences between vegetation communities. Dashed lines at left in each panel indicate mean ambient concentration, at right indicate zero production. Significant (multiple comparisons of means, overall $p < 0.0025$) production of CH_4 in the Mountain community (B), indicated by *, was found at the deepest soil layer, immediately above the permafrost layer. Significant consumption of CH_4 was found at 10 cm above the permafrost in the Prostrate community (C). Values for concentration are medians, error bars are ±1st and 3rd quartiles ($2 \leq n \leq 10$), for production values shown are calculated from means of gas concentration gradients and diffusivities, error bars are ±1 SE as calculated by error propagation. Production means are positions 1 cm deeper to avoid overlap with the concentration data.

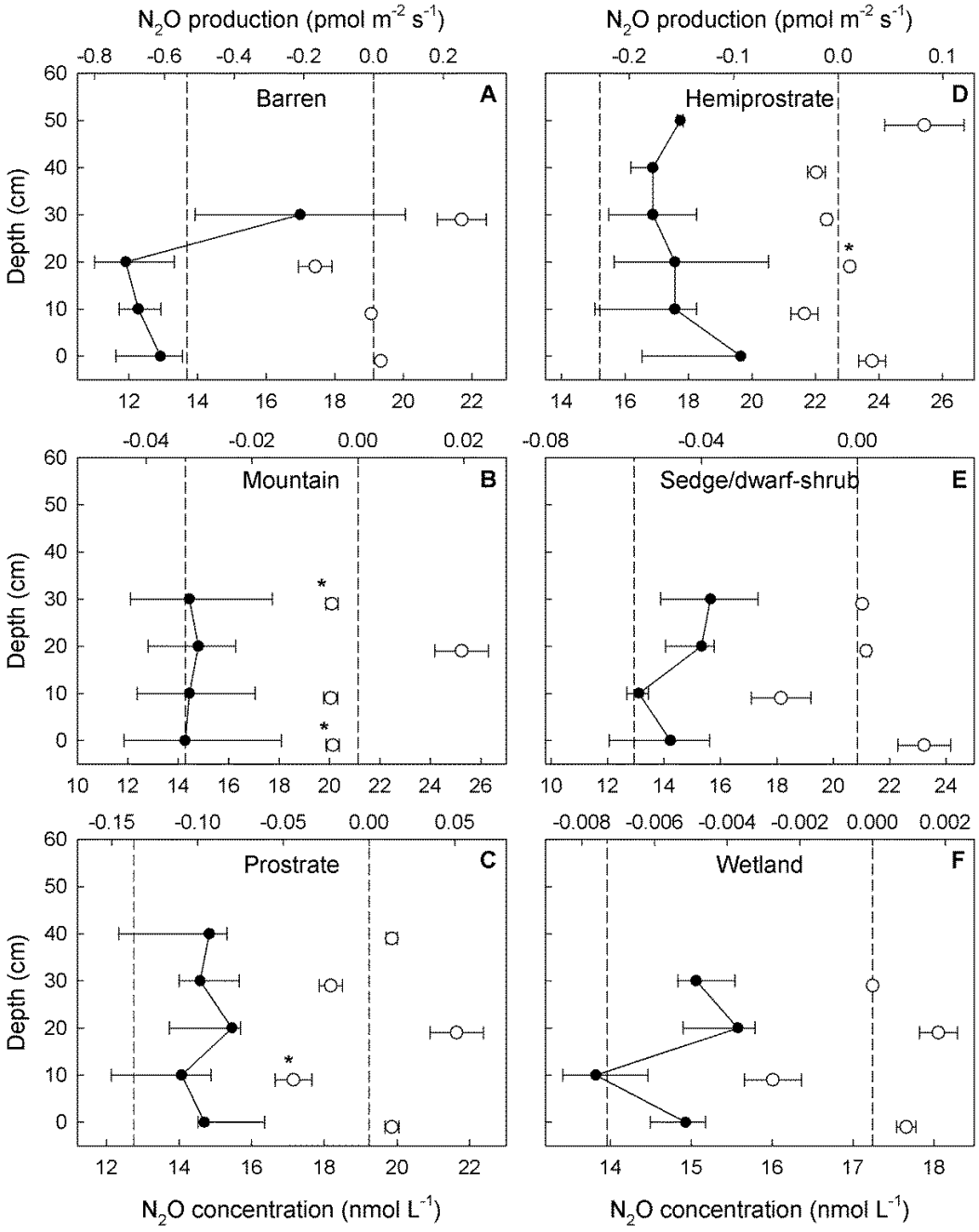

Fig. 3.5. Soil profile concentration of N_2O (closed circles) and production (open circles) both show differences between vegetation communities. Dashed lines at left in each panel indicate mean ambient concentration, at right indicate zero production. Significant (multiple comparisons of means, overall $p < 0.0025$) production of N_2O in the Hemiprostrate community (D), indicated by *, was found at the intermediate depth of 20 cm above the permafrost layer. Significant consumption of N_2O was found at the near-surface layer and the deepest layer in the Mountain community (B) and at 10 cm above the permafrost in the Prostrate community (C). Values for concentration are medians, error bars are ±1st and 3rd quartiles ($2 \leq n \leq 10$), for production values shown are calculated from means of gas concentration gradients and diffusivities, error bars are ±1 SE as calculated by error propagation. Production means are positions 1 cm deeper to avoid overlap with the concentration data.

3.6.3 Conclusions

Polar desert soils were net producers of greenhouse gases during the brief High Arctic growing season, including at depths close to the permafrost layer, and effluxes from the surface were of a similar magnitude to nearby mesic and hydric tundra soils. In particular, soil respiration was similar in deserts and tundras, indicating the role of soil microorganisms in soils lacking extensive plant cover. Production and consumption of GHG at depths from near the surface to just above the permafrost combined with increasing soil organic matter and available nitrogen at depth suggests active populations of microorganisms maintained by soil mixing by cryoturbation and related processes in the polar deserts, with implications for the contributions of these ecosystems to global carbon and nitrogen cycles. A lack of correspondence between surface effluxes and production in soil profiles suggests these soils are variable in effective diffusivity, and that differences in transport across soil layers obscures biological processes. Thus, physical limitations on gas flux, rather than rapid biological processes, may explain the variations in GHGs from soils. That is, changes in climate including especially drying of near-surface soil layers and consequent increased diffusion of soil gases may allow more rapid efflux of GHG to the atmosphere.

4. GREENHOUSE GAS PRODUCTION AND CONSUMPTION IN HIGH ARCTIC DESERTS

4.1 Preface

The 2009 field campaign, described in Chapter 3, showed us the large potential role of the Arctic deserts in GHG budgets, but this role needed to be more precisely quantified, and extended beyond the single point represented by the Dome at Alexandra Fjord. The return to the Dome combined with data collected at Okse Bay and Patterson River led to the confirmation that the patterns of net GHG production were occuring broadly in the other deserts and were persistent features of the polar deserts at the Dome. In addition, the findings of significant net production of all three GHG at positions throughout the active layer at each site as well as the rare appearance of co-consumption of CH_4 and N_2O at each site strongly argue that these patterns of GHG production are the result of processes inherent to the Arctic polar deserts and not the result of instrument or experimental errors, nor are they likely to be transient phenomena resulting from ongoing changes in arctic climate.

This chapter, with minor formatting changes, was published as Brummell, M.E., R.E. Farrell, S.P. Hardy, and S.D. Siciliano. 2014. Greenhouse gas production and consumption in High Arctic deserts. Soil Biology & Biochemistry 68: 158-165. Dr. Farrell again provided critical equipment, advice, and discussion, Sarah Hardy provided critical assistance with field work and logistics, and Dr. Siciliano provided necessary operating funds, a great deal of very useful advice and guidance at each step of the field campaign, and critical assistance with data analysis.

4.2 Abstract

Polar deserts dominate the High Arctic covering over 1 358 000 km^2 (Walker et al., 2002) but little is known about greenhouse gas (GHG) production or flux in polar desert soils. I measured soil-atmosphere GHG exchange for CO_2, CH_4, and N_2O, and net production of these gases in the active layer at 30 sites across three polar deserts in the High Arctic on Ellesmere Island, Canada for a total of 180 production/consumption estimates. There was inter-annual consistency in patterns of GHG net production and a consistent, significant, positive relationship (r^2 = 0.91 - 0.93; $p < 0.05$) between CO_2 production and N_2O production in Arctic desert sites. This differs from the negative correlations found in wet or moist tundra ecosystems and may arise from the large N_2O emissions in dolomitic desert ecosystems. I predict that global change processes that increase microbial activity in deserts will likely increase N_2O emissions but increases in microbial activity in wetter tundra will decrease N_2O emissions due to increased consumption by denitrification. However, given the unusual co-consumption of CH_4 and N_2O in the deserts, it is not clear if models of GHG production developed for other ecosystems will apply to these unique Arctic environments.

4.3 Introduction

Polar deserts cover 1 358 000 km^2 in the Arctic, or approximately 26% of land not covered by ice (Walker et al., 2002). These ecosystems are predicted to change rapidly under a warming climate (IPCC, 2007), and until recently their contributions to global greenhouse gas (GHG) budgets have not been considered. Burnham et al. (2010) found that these deserts may have more stored carbon than had been previously thought. Recent work revealed that GHG emission rates in the deserts were surprisingly high and similar to wetter Arctic tundra soils (Chapter 3). Despite the importance of desert soils to global climate change models, polar deserts remain poorly understood ecosystems and it is not understood how ecosystems such as polar deserts can produce such large quantities of GHGs.

Quantification of GHG emissions from a range of Arctic vegetation communities may allow estimation of landscape-scale soil GHG emissions through the use of remote sensing and other tools based on measurement of the extent of vegetation communities such as the CAVM (Walker et al., 2002). Furthermore, consideration of each major GHG individually may not provide necessary insight into the underlying processes responsible for total emissions

(Blagodatsky and Smith, 2012; Brummell and Siciliano, 2011; Singh et al., 2010); different conditions in each vegetation community or region will drive microbial activity in varying ways (Elberling et al., 2008), creating associations between GHG and structuring biological communities.

Observed rates of soil profile GHG production and efflux to the atmosphere were comparable to those of fully-vegetated tundra at nearby sites (Chapter 3), though it was not clear if such rates could be generalized to other Arctic polar deserts, or were unique to the Alexandra Fjord area adjacent to the polar oasis. Here, I report a follow-up field season in 2010, in which I studied three different deserts in the Canadian High Arctic. These deserts were selected to represent degrees of polar desert harshness in the Canadian Archipelago. These ecosystems correspond to the B1 designation of the Circumpolar Arctic Vegetation Map (CAVM, Walker *et al*., 2002), with extremely low vegetation cover, low soil water and organic matter contents, and high pH and carbonate. I hypothesized that rates of GHG production and consumption in the soil profiles of the three deserts would be more similar to each other than to any tundra site, indicating a more general characteristic of Arctic polar deserts that could be used for broad estimation of patterns across the large area covered by these soils. I also hypothesize that the relationships between the three GHG would qualitatively and quantitatively vary between desert and non-desert tundra soils due to the presence or near-absence of vascular plants.

4.4 Materials and Methods

4.4.1. Study Sites and Field Sampling

Three polar deserts corresponding to the B1 Barrens vegetation community of the CAVM (Walker et al., 2002), characterized by less than 5% vegetation cover and dolomitic parent materials, were chosen on Ellesmere Island in the Canadian High Arctic Archipelago (Fig. 4.1). Each desert site represents a different landform. Okse Bay (Fig. 4.1, A) is a connected series of raised beach crests with moist tundra in the lower areas between. The tops of the raised crests, 4-5 m wide, exhibit the characteristics of B1 polar deserts, including very sparse vegetation, low soil moisture contents, and coarse texture with a desert polish on the surface stones. Sampling sites at Okse were located on these raised beach crests. The Dome at Alexandra Fjord (Fig. 4.1, B) has been described in previous publications (Walker et al., 2008). It is an alpine semi-desert

composed of soils with either dolomitic or granitic parent material; only the dolomitic desert was examined in the present study. Patterson River (Fig. 4.1, C) is a fluvial outwash plain adjacent to a small river draining glaciers of the mountains of the United States range. The soil is extremely coarse textured, often with a layer of larger pebbles (2-10 cm) on the surface. Okse Bay was sampled July 13 to 17, 2010, The Dome July 20 to 21, and Patterson River July 30 to August 1.

Within each site, sampling positions were chosen at least 70 m apart. Analysis of previous results (Chapter 3) indicated this exceeded the minimum distance between sampling positions needed to avoid autocorrelation in measurements of soil parameters in High Arctic polar deserts. The vegetation community was characterized using 50 cm × 50 cm grids and visual estimation of the percent cover of bare soil, lichens, bryophytes, and each species of vascular plant (Lamb et al., 2011).

At each site, the gas flux was measured using both transparent and opaque chambers (Brummell and Siciliano, 2011; Stewart et al., 2012). Soil gas probes were then installed in clusters of six probes to sample gas at depths from near the surface to the permafrost; the probes were allowed to reach gas-concentration equilibrium with the soil by diffusion over at least 24 hours (Brummell and Siciliano, 2011). Gas concentrations in the probes were measured using a Gasmet DX-4015 Fourier-Transform Infrared Gas Analyzer (FTIR-TGA) (Gasmet Technologie Oy, Helsinki, Finland), following the procedures described previously (Brummell and Siciliano, 2011). Finally, soil pits were excavated at each cluster and soil samples were collected from depths corresponding to the gas-sampling depths of the probes; additional data regarding soil temperature and depth to permafrost were also recorded. Sampling of the soil profile was destructive and no repeated measurements were made except the use of two different chambers over an interval of approximately 20 minutes. Soil samples were frozen at -20ºC and transported to the laboratory at the University of Saskatchewan for analysis.

4.4.2 Data Analysis

Gas concentrations and fluxes were analyzed following the procedures described in Chapter 3. Briefly, gas fluxes were calculated from the accumulation or depletion of each gas inside a non-steady state, vented chamber during a 10-min deployment. Non-significant ($p > 0.05$) regressions of gas concentration *vs*. time were set to zero flux.

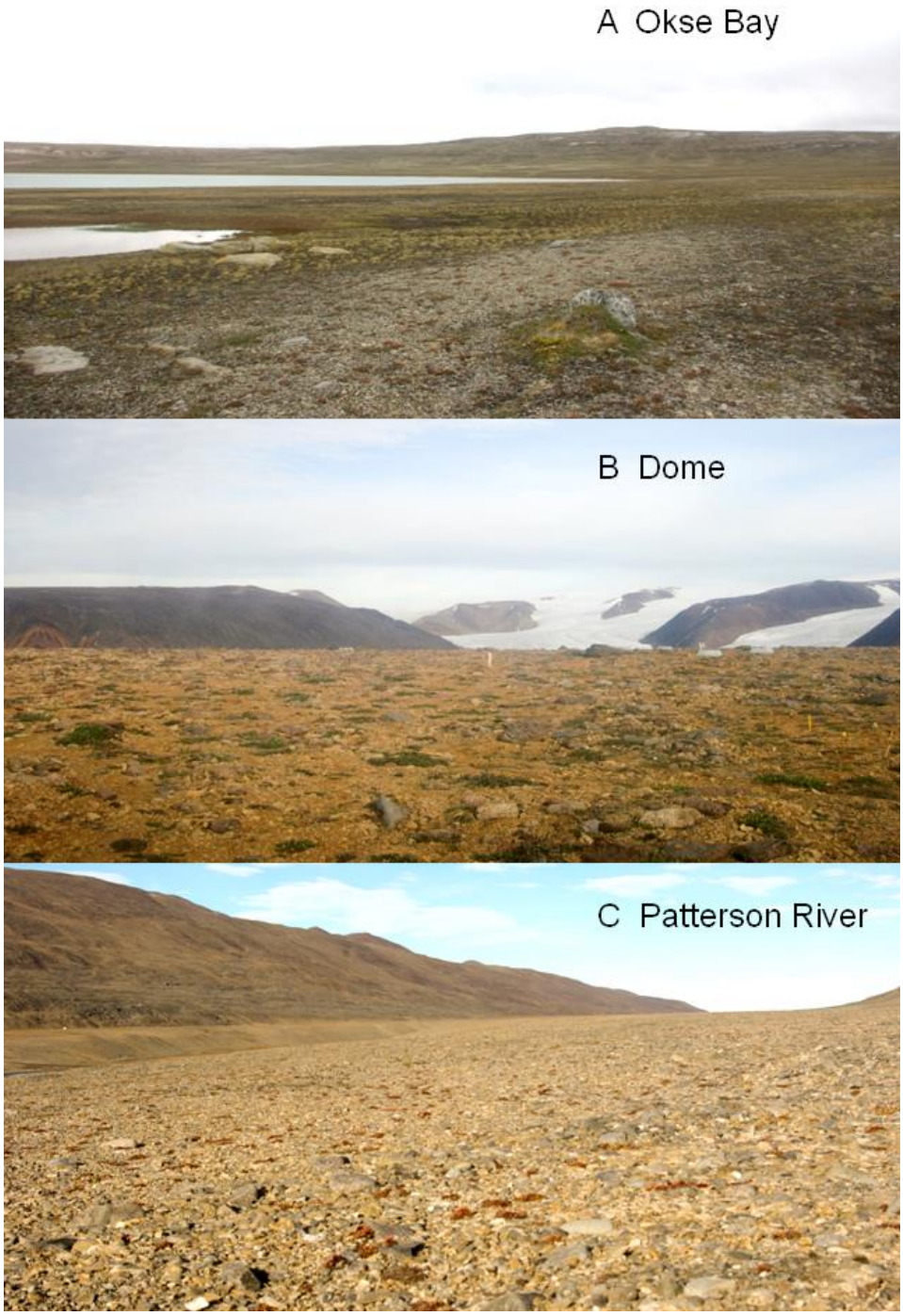

Fig. 4.1. (A) Okse Bay, on southeastern Ellesmere Island (77º 8' 8" N 87º 39' 10" W), consists of a series of raised beach crests, 4-5m wide, composed of polar desert soil. (B) Dome, near Alexandra Fjord (78º 51' 31" N 75º 55' 37" W), is an alpine plateau approximately 540m above sea level, with a cryoturbated soil of dolomitic parent material. (C) Patterson River, near the northern coast (82º 35' 47" N 63º 45' 32" W), is a fluvial outwash plain composed of very coarse soil with high gravel content.

Probe gas concentrations were pooled into 10 cm depth bins within each site, measured from the permafrost layer upwards to reflect the importance of the underlying permafrost in structuring these soils. Because the concentration data were not normally distributed, median gas concentrations within each bin were used to calculate gas concentration gradients. Effective diffusivity was calculated for each of the three GHG (Equation 4.1) using constants (diffusivity of each gas in free air and in free water) from the literature (Liss and Slater, 1974) and Henry's coefficient (H) corrected for temperature in the range observed (0-11°C) (Dean, 1999).

$$D_e = \frac{\frac{\Theta_w^{10/3}}{H} D_{fw} + \Theta_g^{10/3} D_{fg}}{\Theta_T^2} \qquad \text{(Eq. 4.1)}$$

For each gas D_{fw} is the diffusion coefficient in free water, H is the dimensionless form of Henry's solubility coefficient in water, D_{fg} is the diffusion coefficient in free air, and Θ_w is water-filled porosity, Θ_g is air-filled porosity and Θ_T total porosity.

Gas production (Equation 4.2) was calculated using the gas concentration gradients and the effective diffusivity of each soil layer (here, 10 cm thick):

$$P_{GHG} = D_{e_i}\left[\frac{C_i - C_{i-1}}{\Delta z}\right] - D_{e_{i+1}}\left[\frac{C_{i+1} - C_i}{\Delta z}\right] \qquad \text{(Eq. 4.2)}$$

where P_{GHG} is net production (pmol m^{-2} s^{-1}) of either CO_2, CH_4, or N_2O; D_{ei} is effective diffusivity for layer i (m^2 s^{-1}); C_i, C_{i-1} and C_{i+1} are the gas concentrations (mol m^{-3}) in layers i and i-1 below, and i+1 above, respectively; and Δz is the difference in depth (m) between layers i and i+1 above, or between i and i-1 below. Positive values of P_{GHG} indicate production/accumulation of gas at a given depth; negative values indicate consumption/loss. Because of large uncertainties surrounding diffusion through the near-surface boundary layer and highly variable GHG concentrations close to the soil surface, production estimates for the shallowest layer of soil (i.e., the uppermost 10 cm) in each community were calculated based on the diffusivity of that layer of soil (D_{ei}) rather than the diffusivity of the layer above (D_{ei+1}); i.e., the free air overlying the soil. The deepest layer of unfrozen soil was assumed to receive zero gas flux from the permafrost

below; productions for the deepest layer were thus calculated with the first term of Equation 4.2 set to zero.

Due to high variability and measurement error in porosity estimates, and the high sensitivity of the calculation of effective diffusivity to such errors, mean porosities including water-filled, air-filled, and total, were used for each depth bin at each site; in these soils, low water contents led to high sensitivity of the calculations to small errors of water-filled pore space estimation. Combined with the use of median gas concentrations, the resulting production calculation cannot include typical calculations of error, such as standard error. Thus to provide estimates of error for the calculated GHG production, error propagation was employed in which the maximum extremes of each parameter were estimated and carried through each calculation (Figliola and Beasley, 2006). The resulting error terms are analogous to standard deviation, which was converted to an approximation of standard error by dividing by the square root of the sample size. I report standard error or this calculated approximation except where otherwise noted.

Significant differences from zero production were tested by comparing the calculated production value for each soil depth layer to zero using the propagated error and critical values of Student's T. Where the absolute value of the production minus critical T times the propagated error was greater than zero, the net production was deemed significant at $p \leq 0.05$ and using the number of observations in the bin as the sample size.

4.4.3 Soil Analysis

Soil water content was measured by subsampling from each soil sample and determining water loss after 24 hours at 105ºC in a soil-drying oven. Soil-solution components were extracted in 0.5M K_2SO_4 and analyzed for soluble organic carbon (SOC) and soluble total nitrogen (STN) using a Shimadzu TOC-V and TN / Ozone-generation Module (Kyoto, Japan) with furnace temperature set to 720ºC, following the manufacturer's instructions. Dissolved NH_3 and NO_3^- and NO_2^- were analyzed using a Smartchem colorimetric analyzer (Westco Scientific Instruments, Inc., Brookfield CT, USA) following the manufacturer's instructions. Measurements of pH were made by mixing 10 mL of water with 10 g of thawed soil, allowing most particles to settle, and measuring with a pH electrode (SevenMulti, Mettler Toledo, Mississauga, Canada).

Biological consumption of CO_2 within the soil profile is unlikely, but concentration gradients within some soils suggest the loss of CO_2 from the soil atmosphere. A model of carbonate cycling (Equation 4.3), in which CO_2 reaches equilibrium between gas phase and carbonate species within soil water was constructed based on assumptions of closed systems and K_H values corrected for measured soil temperatures in soil pits (Dean, 1999); Shanhun et al. (2012) present a similar model.

Total dissolved CO_2 (C_T) which includes the species H_2CO_3, HCO_3^-, and CO_3^{2-}, is a function of CO_2 in the atmosphere (as partial pressure, pCO_2), temperature via Henry's Law and the temperature-dependent Henry's coefficient (K_H), and pH (Dean, 1999) by Equation 4.3:

$$C_T = \left(\frac{\mathrm{pCO_2}}{k_H}\right)\left(1 + \frac{k_{a1}}{[\mathrm{H^+}]} + \frac{k_{a1}k_{a2}}{[\mathrm{H^+}]^2}\right) \quad \text{(Eq. 4.3)}$$

where k_{a1} and k_{a2} are the equilibrium constants for $[H^+][HCO_3^-]/[H_2CO_3] = 5.01 \times 10^{-7}$ and $[H^+][CO_3^{2-}]/[HCO_3^-] = 5.01 \times 10^{-11}$, respectively (Dean, 1999). Where Equation 4.2 results in estimates of negative net CO_2 production, the largest sink (i.e., most negative) within each site was added to each production estimate at that position, under the assumption that the strongest sink represents the total abiotic sink throughout the soil profile at that position, with zero biotic production; other positions in the soil profile then represent total biotic production of CO_2. For all three GHG, net production is the sum of all sinks and sources within the soil layer, though abiotic sinks for CH_4 and N_2O are assumed to be negligible, and biotic sinks for CO_2 are assumed to be negligible.

A subset of soil samples was examined using Phospholipid Fatty Acid (PLFA) analysis, using the procedure of Helgason et al. (2010); only those samples that yielded sufficient total PLFA for analysis were used. Low microbial biomass of polar desert soils compared to agricultural soils led to low masses of biomarkers, with some expected biomarkers absent and others present in quantities near the minimum detection limits of the technique. The PLFA profiles were analyzed by Nonmetric Multidimensional Scaling (NMS) after data-trimming to remove outliers and samples showing on a single PLFA signal.

4.5 Results

The relationship between CO_2 production and N_2O production within the active layer at the Arctic desert sites differs from that at other Arctic ecosystems. Unlike the negative correlations between the productions of these two gases found in wet or moist tundra ecosystems (data analyzed here are from Chapter 3 but were not analyzed in this way previously), there is a positive correlation in the deserts (data from both the current chapter and Chapter 3), as well as in some dry tundras (Fig. 4.2). Estimates of net CO_2 production include abiotic sinks, and have not been corrected by addition to show only presumed biotic production and to allow direct comparison between rates of net production of CO_2 and of N_2O. Orthogonal regression analysis indicates a strong negative correlation for the Wet Sedge ($r^2 = 0.99$, $p < 0.05$) (Fig. 4.2, A) and Willow ($r^2 = 0.93$, $p < 0.05$) (Fig. 4.2, B) sites and a weak positive correlation at Cassiope ($r^2 = 0.45$, $p < 0.05$) (Fig. 4.2, C); all three of these vegetation communities had moderate to high soil water contents at the time gas production was measured in 2009 (Chapter 3). The Dryas community was the driest tundra in 2009 (Fig. 4.2, D; Chapter 3), and did not show a significant correlation between CO_2 production and N_2O production. Among the deserts, Granite (Fig. 4.2, E) studied in 2009 did not show a significant correlation, while Patterson (Fig. 4.2, G) was weak and marginal ($r^2 = 0.46$; $p = 0.060$). Okse (Fig. 4.2, F) shows a strong, significant positive correlation ($r^2 = 0.91$, $p < 0.05$), as does Dolomite / Dome (Fig. 4.2, G) when measurements from both years are pooled ($r^2 = 0.93$, $p < 0.05$). Maximum net CO_2 production varied over nearly two orders of magnitude from approximately 1.5 pmol m^{-2} s^{-1} at the Wet Sedge site (Chapter 3) to approximately 120 pmol m^{-2} s^{-1} at Okse Bay. Similarly, maximum net N_2O production was highest at Okse Bay and lowest at Wet Sedge (Fig. 4.2). Photosynthesis by plants in the wetter ecosystems apparently lowered net CO_2 flux compared to the nearly unvegetated deserts, and N_2O net production was also lower, suggesting a role for plants in net N_2O flux (Stewart et al., 2012).

The three deserts studied represent a wide range of soil parameters within the B1 vegetation community of the CAVM (Walker et al., 2002). All were moderately to strongly alkaline (with pHs between 7.7 and 8.7) and had less than 5% vegetation cover, but differed in other parameters including gas flux at the soil surface (Table 4.1), abundance and community composition of plants (Table 4.2), soil moisture, and nutrient availability (Table 4.3).

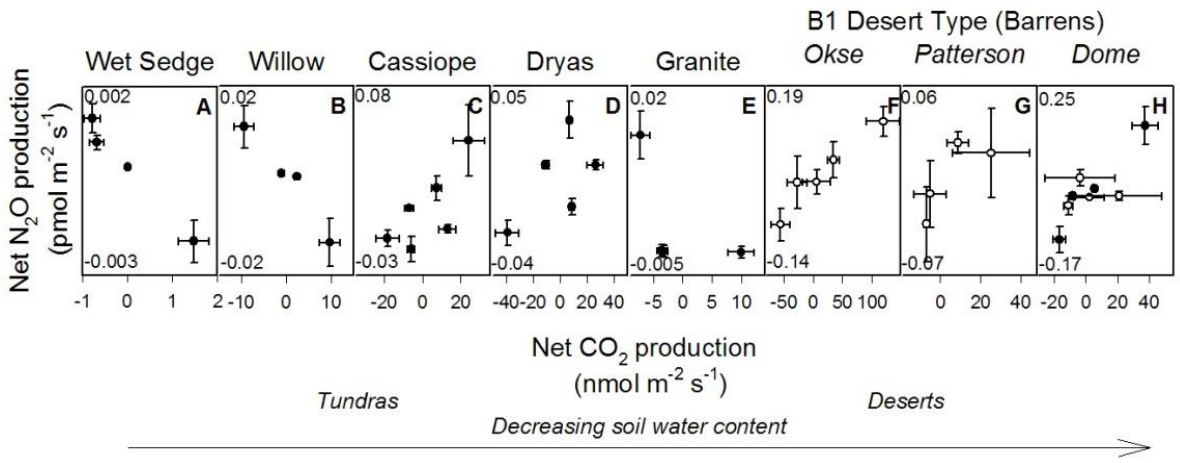

Fig. 4.2. The relationship between production of CO_2 and of N_2O varied across a soil moisture gradient at Alexandra Fjord. Gas flux data for the tundra sites (Panels A–E) were obtained in 2009 (see Chapter 3); data for the polar desert sites were obtained in 2010. Significant negative correlations (orthogonal regression, $p < 0.05$) between the two gases were observed in the hydric/mesic tundras; i.e., the Wet Sedge (A) and Willow (B) sites. Conversely, significant positive correlations (orthogonal regression, $p < 0.05$) were observed in the mesic tundra Cassiope (C) and the three B1 deserts (F, G, H; (●; Chapter 3) and 2010 (○) in the B1 desert of the Dome site). Data collected in 2009 had not previously been analyzed in this way. For clarity, minimum and maximum observed production values for N_2O are shown for each vegetation community rather than labeled axes; values shown represent the end-points of the net N_2O production axis. To allow comparison with 2009 (Chapter 3) values and between gases, CO_2 sinks were not eliminated by addition.

Equation 4.3 and measurements of soil pH and temperature were used to calculate C_T; the low temperature and high pH of the soils of the Arctic polar deserts studied here leads to C_T values 5 to 10 times their pCO_2, and likely exist as carbonates dissolved in the soil water (Table 4.2). These large values of C_T relative to measured pCO_2 indicate a large potential abiotic sink for CO_2 within the soil. The magnitude of these sinks was assumed to be equal to the magnitude of the largest CO_2 sink estimated from Equation 4.2 for each position, and that value was added to all CO_2 production estimates for each position to estimate total biotic CO_2 production (Fig. 4.3, A-C).

Production and consumption of GHG were not restricted to the near-permafrost layer at any of the three deserts studied. Instead, those processes were identified at depths throughout the

Table 4.1. Surface characteristics of three deserts on Ellesmere Island.

Site	Bare rock	Gravel	Sand/ silt	Litter	Dung	Bones	Animal Disturbance	Bryophytes	Lichens	Vasc. Plants	Most Abundant Vascular Plants
Okse Bay	4.3	0.0	51.4	27.4	7.9	7.7	1.2	0.0	0.0	0.1	*Saxifraga oppositafolia, Salix arctica*
Patterson River	0.0	70.9	19.6	1.1	0.0	0.0	0.0	2.4	5.9	0.0	*Saxifraga oppositafolia, Salix arctica, Papaver radicans, Cerastium alpinum*
Dome	†										*Salix arctica, Dryas integrefolia*

Classes of surface cover are % cover averages across the measurement positions within each site.
†All measurement positions at the Dome site were placed on areas of bare soil and gravel. The vegetation of the site is described in Walker et al., (2008), as community UD.

Table 4.2. GHG fluxes at three deserts on Ellesmere Island.

Site	Depth to Permafrost (cm)	Dark Flux CO_2 (SE) nmol m^{-2} s^{-1}	Dark Flux CH_4 (SE) nmol m^{-2} s^{-1}	Dark Flux N_2O (SE) nmol m^{-2} s^{-1}	Light Flux CO_2 (SE) nmol m^{-2} s^{-1}	Light Flux CH_4 (SE) nmol m^{-2} s^{-1}	Light Flux N_2O (SE) nmol m^{-2} s^{-1}
Okse Bay	49.7	312 (52)	-1.112 (0.296)	0.009 (0.053)	154 (46)	-1.781 (0.441)	0.001 (0.047)
Patterson River	35.5	154 (29)	-0.592 (0.123)	-0.159 (0.164)	159 (61)	-0.134 (0.257)	-0.270 (0.035)
Dome	42.4	53 (37)	-1.497 (0.309)	0.092 (0.070)	-30 (27)	-1.859 (0.562)	-0.148 (0.144)

Values in parentheses are ±1 Standard Error. GHG flux was measured one day prior to measurement of within-profile gas concentrations. Positive values represent net movement of gas from soil to atmosphere, negative values indicate soils are net sinks.

Table 4.3. Soil parameters in the active layer at three polar desert sites on Ellesmere Island.

Site	Depth APL†	pH (SE)	NPOC‡ (SE) g kg^{-1}	WEN§ (SE) g kg^{-1}	NO_3^- (SE) mg kg^{-1}	NH_4^+ (SE) mg kg^{-1}	BD¶ (SE) g cm^{-3}	WFPS# (SE) %
Okse Bay	40	8.1 (0.20)	32.18 (5.15)	4.12 (1.19)	1.57 (0.37)	2.12 (0.31)	1.27 (0.06)	38 (0.59)
	30	7.8 (0.15)	32.87 (2.87)	5.37 (1.37)	2.16 (0.19)	2.29 (0.22)	1.30 (0.06)	5.2 (0.40)
	20	8.0 (0.14)	33.80 (4.34)	5.45 (0.73)	2.13 (0.19)	2.21 (0.30)	1.29 (0.04)	6.8 (1.7)
	10	7.9 (0.23)	33.15 (1.95)	5.70 (1.40)	1.80 (0.23)	2.63 (0.59)	1.28 (0.05)	6.2 (0.57)
	0	7.7 (0.38)	33.22 (2.95)	6.77 (1.75)	1.96 (0.23)	2.26 (0.22)	1.41 (0.04)	5.8 (0.55)
Dome	30	8.5	31.75	5.39	BDL††	2.47	1.26	6.2
	20	8.6 (0.06)	53.72 (12.43)	22.37 (7.37)	BDL	0.95 (0.46)	1.30 (0.05)	5.8 (0.53)
	10	8.6 (0.04)	47.72 (9.83)	16.34 (6.26)	BDL	0.79 (0.40)	1.32 (0.05)	5.0 (0.48)
	0	8.6 (0.02)	36.10 (7.93)	9.27 (4.46)	BDL	1.58 (0.50)	1.30 (0.04)	5.9 (0.41)
Patterson River	30	8.6 (0.09)	65.66 (13.37)	32.08 (7.25)	0.54 (0.36)	0.49 (0.33)	1.17 (0.03)	5.2 (0.77)
	20	8.5 (0.09)	64.48 (11.24)	25.40 (4.95)	0.35 (0.24)	0.27 (0.19)	1.15 (0.07)	4.9 (0.62)
	10	8.6 (0.05)	71.73 (6.83)	33.30 (3.96)	0.68 (0.26)	0.52 (0.22)	1.22 (0.02)	4.5 (0.43)
	0	8.7 (0.10)	51.82 (10.13)	24.15 (6.87)	0.65 (0.34)	0.80 (0.34)	1.11 (0.12)	4.1 (0.89)

Values in parentheses are ±1 Standard Error. The near-surface depth, 30cm above the permafrost layer at Dome included only one measureable soil sample, thus no error is presented for that depth.
†APL: above permafrost layer
‡NPOC: soluble organic carbon
§WEN: water extractable nitrogen
¶BD: bulk density
#WFPS: Water-Filled Pore Space
††BDL: Below Detection Limit.

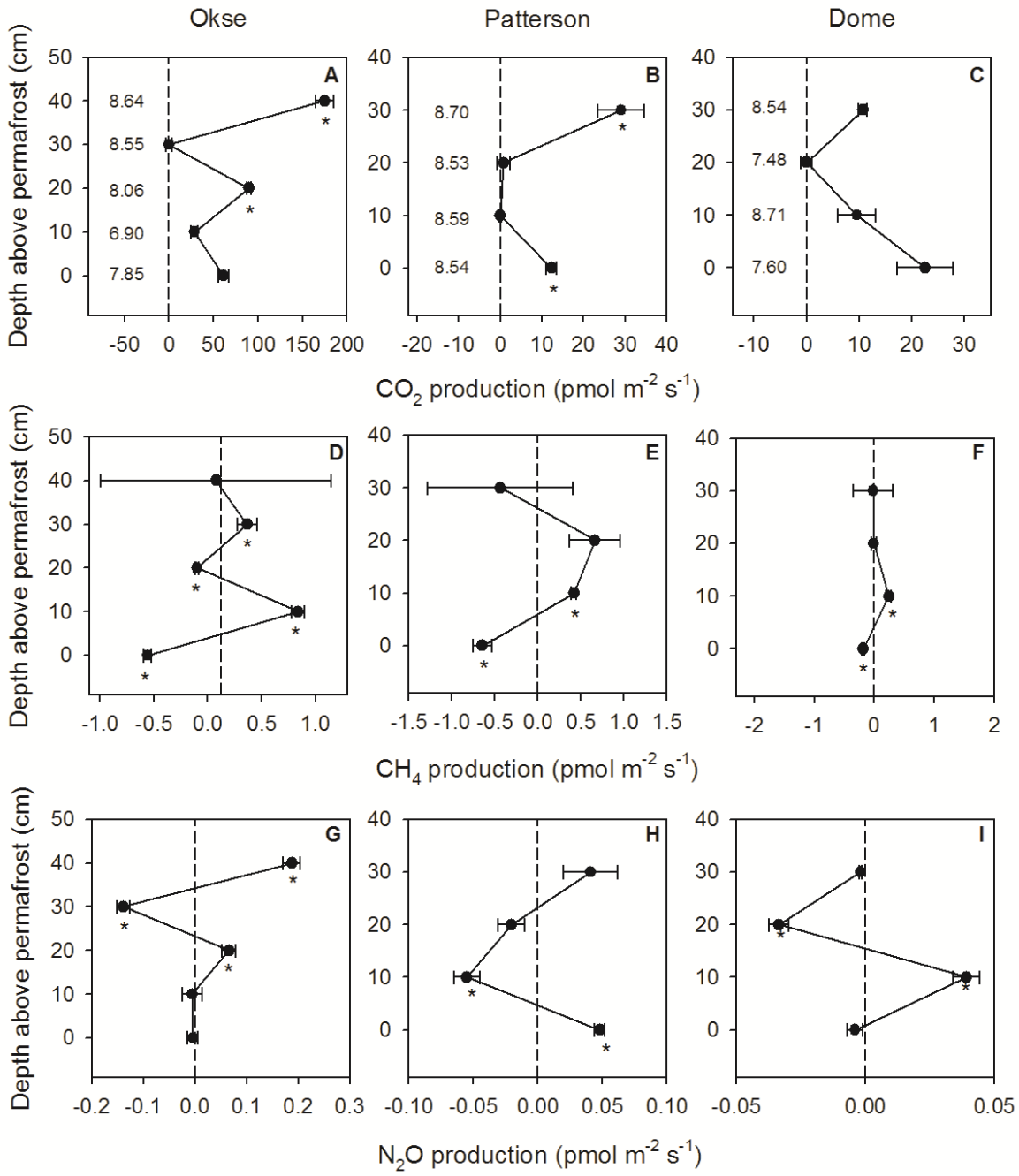

Fig. 4.3. Significant ($p < 0.05$; indicated by *) net production of CO_2 (panels A–C), CH_4 (panels D–F) and N_2O (panels G–H) was observed throughout the active layer of the soils at the three study sites. Values on panels A-C are mean pH for each depth bin. To show only biotic production, CO_2 net production has been rescaled by addition of the most-negative net production, here presumed to represent abiotic removal from the gas phase by carbonate cycling; significant CO_2 production without addition is indicated by * for panels A-C.

soil profile, from near-surface to near-permafrost (Fig. 4.3). Consumption of CH_4 was found in the near-permafrost layer at all three desert sites, with CH_4 production in the overlying adjacent layer in both the Okse and Patterson soils (Fig. 4.3, D, E, F). Of 180 soil positions measured, 22 showed consumption of both CH_4 and N_2O. For example, four of the 16 measurements in the 30 cm Above Permafrost Layer at Okse Bay had calculated CH_4 consumption ranging from 0.28 to 0.76 pmol m^{-2} s^{-1} and N_2O consumption ranging from 0.040 to 0.13 pmol m^{-2} s^{-1}. No soil layer had a negative average net production of both CH_4 and N_2O across a site (i.e., co-consumption), thus no soil layer consistently shows this co-consumption at any one site, even though individual soil samples co-consumed these GHG at all three sites and at depths ranging from near-surface to near-permafrost.

I used PLFA analysis to examine the broad characteristics of the microbial communities in a subset of the soils showing GHG activity, hypothesizing some of the variation in GHG production could be explained by microbial community differences. Ordination of the PLFA results combined with best subsets regression revealed no significant correlation between net production of any of the three GHG, either individually or in combination, with microbial community differences (Appendix 2). However, the three desert sites clustered separately in the ordination, suggesting that differences in microbial community composition did occur between the sites.

4.6 Discussion

The Arctic polar deserts showed apparent aerobic consumption of N_2O, an observation at odds with other N_2O-consuming environments where oxygen limitation drives complete denitrification. Furthermore, the relationship between rates of CO_2 net production and rates of N_2O net production, positive in the deserts but negative in the wet tundras, suggests an unusual process is at work in these cold, dry, organic-matter-poor soils.

4.6.1 Production and Consumption of Gases

Gas production profiles obtained at the Dome Dolomite desert in 2010 were similar to those obtained in 2009 as part of an earlier study of the soils near Alexandra Fjord (Chapter 3) (Fig. 4.4). In general, the direction of the change in net production of the GHGs as one moves up the profile from the permafrost to the near-surface was consistent between years. For example, the

net production of CO_2 decreased as the distance above the permafrost increased from 0 to 10 to 20 cm (Fig. 4.4, A); 2010 CO_2 production estimates have not been corrected for abiotic sinks to allow direct comparison with 2009 results (Chapter 3). In the two instances where the change in net production between years was in opposite directions (i.e., net CH_4 production in the uppermost layer and net N_2O production just above the permafrost), the overall changes were very small and were not significantly different from zero (Fig. 4.4, B & C). Moreover, given that the sampling dates varied between years — July 10 and 11, 2009 and July 19, 2010 (corresponding to 3–5 days past snowmelt in 2009, at least 10 days past snowmelt in 2010) — the GHG production profiles appear to be robust features of the Dome dolomite soils during the growing season.

Production of GHG in Arctic polar desert soils is not restricted to the most recently thawed layer adjacent to the permafrost, rather it is found throughout the active layer. Similar to non-permafrost soils, cycling of both C and N are distributed throughout the profile (Kellman and Kavanaugh, 2008; Müller et al., 2004; Risk et al., 2002). Furthermore, I observed that there are sinks for CH_4 and N_2O — including a CH_4 sink adjacent to the permafrost — in the polar deserts. However, because these deserts differ significantly from Arctic peatlands that have been well described recently (Bäckstrand et al., 2010; Christensen, 2004), my finding that the permafrost layer is not an active site of GHG production, may not reflect the dynamics of thawing Arctic peatlands or other Arctic ecosystems.

The negative correlation between CO_2 and N_2O production in wet tundra systems suggests strong expression of nitrous oxide reductase (NOS), the enzyme responsible for the reduction of N_2O to N_2. In hydric tundra systems, CO_2 production was much lower than that found in arid desert ecosystems, reflecting the anaerobic nature of wet soils. I think that the negative correlation arises because as CO_2 production increases, NOS activity increases resulting in a decrease in net N_2O production. In contrast, desert ecosystems are largely aerobic ecosystems with high concentrations of ammonia. I hypothesize that total N_2O production is driven by NH_3 oxidation (Hayatsu et al., 2008; Stein, 2011; Zumft, 1997) as has been seen in other Arctic ecosystems (Ma et al., 2007). Ammonia oxidation pathways do not include NOS and thus, as CO_2 production increases, general microbial activity increases, presumably

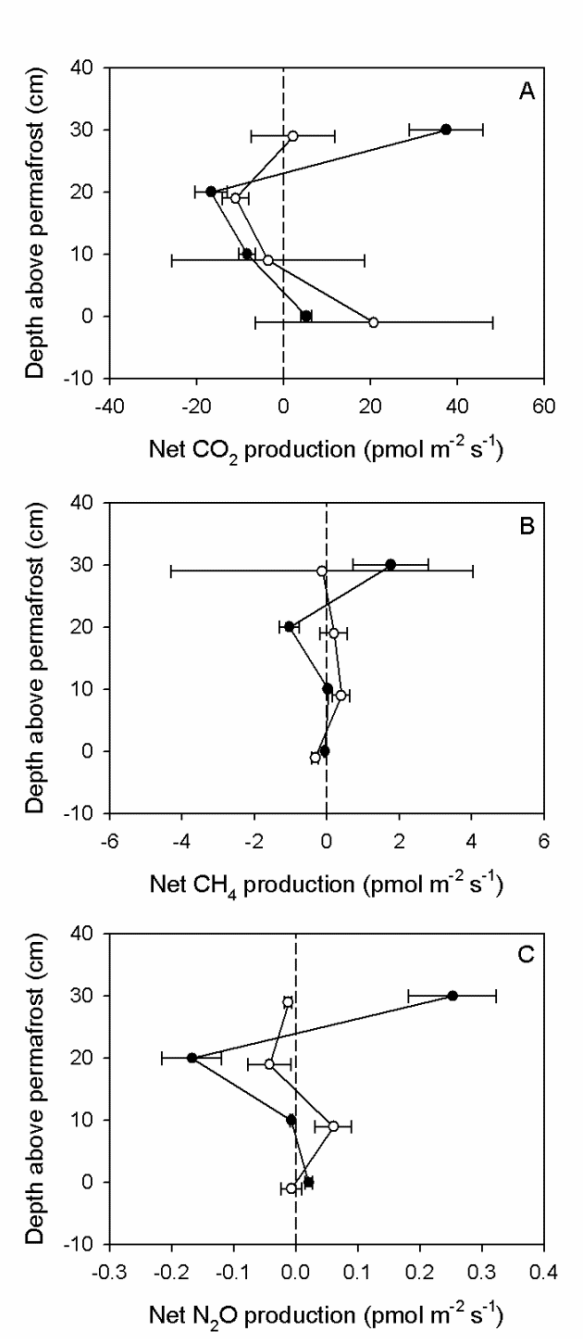

Fig. 4.4. Soil GHG production profiles constructed from data obtained in 2009 (●; Chapter 3) and 2010 (○) in the B1 desert of the Dome site. Net production of CO_2 (A) has not been rescaled to set maximum consumption (i.e., most negative production) to zero to facilitate comparison between years and between gases; apparent consumption of CO_2 within soil profiles is generated by carbonate cycling in these high-pH soils. In both years, significant ($p < 0.05$) production of CO_2 was detected near the surface and near the permafrost. Net production of CH_4 (B) was highly variable in both years, especially near the soil surface. Net production of N_2O (C) near the surface was significant in 2009 but not in 2010, though relationships between soil layers were largely consistent across years.

increasing NH_3 oxidation and, thus, N_2O production. My data suggest that it may be possible to model the N_2O/CO_2 relationship as a function of the vegetation communities identified on the CAVM (Walker et al., 2002). Specifically, global change processes that increase microbial activity in deserts (B1, B3b in the CAVM nomenclature) will likely increase N_2O emissions. In contrast, global change that increases microbial activity in wetter tundra ecosystems such as W1 or G3 will result in decreased N_2O emissions. Given the high CO_2 equivalency of N_2O (i.e., 300 CO_2 equivalents per N_2O), processes that increase N_2O emissions from Arctic soils must be carefully considered.

Co-consumption of CH_4 and N_2O does not correspond to current knowledge of the biochemical pathways and environmental conditions associated with these processes (Conrad, 2009; Stein and Klotz, 2011). The only known sink for N_2O is reduction via NOS, associated with oxygen-limited environments which are also typically a source of CH_4 (Stein and Klotz, 2011). Recently, the existence of methanotrophic bacteria that may also produce N_2O has been suggested, though a homologue to *nosZ* has not been identified in those genomes (Stein and Klotz, 2011).

Carbon dioxide partitions to the carbonate species H_2CO_3, HCO_3^-, and CO_3^{2-} upon dissolving in water; at high pH, the total inorganic carbon in the aqueous phase can be an order of magnitude larger than the mass present in the gas phase, even with water-filled porosities as low as are found in these arid soils (Table 4.2). In the soils of the polar deserts of Ellesmere Island, signals of consumption of CO_2 are generated by movements of CO_2 between soil air and soil water, as well as between soil layers.

I assume a high, effectively infinite, buffering capacity in these soils due to the presence of Ca^{2+}, Mg^{2+}, and alkaline surface sites derived from weathering of dolomitic parent material, leading to fixed pH. Under this assumption, net production of CO_2 estimated by Equation 4.2 is the result of the balance between production of CO_2 by respiration, and consumption (from the gas phase) of CO_2 by abiotic processes. In order to compare between all three GHG, I add the most-negative CO_2 net production estimate to all CO_2 production estimates at each position, thereby setting the most negative to zero. While other authors, working in slightly-acidic and non-permafrost soils, ascribe a similar addition to errors of measurement because the magnitude of estimated sinks is small relative to the magnitude of estimated sources (e.g., Risk et al., 2002, De Jong and Schappert, 1972), I assume the estimated CO_2 sinks, which are of a similar

magnitude to uncorrected sources, are not due to errors of measurement of gas concentration, but due to abiotic processes particular to these cold, alkaline soils (Shanhun et al., 2012).

The addition of the largest sink was not included in the inter-year comparison (Fig. 4.4A) because the 2009 data did not include such a procedure in the estimates of CO_2 production. The addition was not included in the comparisons between CO_2 and N_2O for the same reason, and because the factors that create strong abiotic sinks for CO_2 in soils may be relevant for biological net N_2O production, though through effects on the microorganisms responsible for consumption or production of N_2O rather than directly on the fluxes of N_2O.

The calculation of production includes local ambient concentrations of each gas, which varied considerably across my sites and required site-specific normalization. The coefficient of variation of ambient GHG concentrations was 9.0% for CO_2, 24.5% for CH_4, and 10.5% for N_2O across the three polar deserts considered here. Within each site, ambient concentrations were generally less variable (CO_2, 0.8-7.5%; CH_4, 3.0-15.8%, N_2O, 4.2-12.8%). A second source of uncertainty is that associated with the estimation of effective diffusivity, which is sensitive to errors of measurements of bulk density (a difficult parameter to measure precisely in the very coarse and rocky soils of the polar deserts). For these reasons, diffusivity and production were calculated using average values of input parameters whenever possible, minimizing the effects of large errors of measurement. Despite these sources of error, I observed strong annual stability, suggesting the observations of production and consumption are robust to these considerations.

My model of gas production in the soil includes an assumption that the permafrost underlying the active layer contributes zero net flux of gas to the active layer, specifically to the production calculated in the deepest, near-permafrost soil of the profile. It is conceivable that permafrost does contribute slightly to active-layer gas production, given recent discoveries of microbial activity in frozen soil including measurements of soil respiration at temperatures as cold as -39ºC (Panikov et al., 2006). If I assume the diffusivity of the frozen permafrost immediately below the deepest part of the active layer is similar to the estimates of diffusivity of frozen Antarctic soils [i.e., 7.0×10^{-5} cm^2 s^{-1}; (Harvey-Schafer et al., 2012)], and use estimates of microbial respiration in frozen Arctic soils from Panikov et al. (2006), the effect on the production estimates of the deepest soil layers is approximately ± 2.0 pmol m^{-2} s^{-1} for CO_2 or roughly 10% of the estimated production in the above permafrost layer. It is not clear what effect severely limited liquid water availability would have on the effective diffusivity of CH_4 and N_2O

and the net production of those gases, though it seems likely that at sub-zero temperatures enzymatic activity responsible for fixing or producing these GHG would be slowed in addition to the limiting effect on diffusivity of layers of ice forming in the frozen soil.

I find the lack of correspondence between microbial community composition, as estimated by PLFA profiles, and patterns of GHG net production puzzling. With the exceptions of the release of stored gas and abiotic carbonate cycling, the production and consumption of GHG in soils is primarily due to biological activity. The three sites I studied differ in several respects, including landform, vegetation community, and microbial community composition, yet largely do not differ in GHG net production; examples of co-consumption of CH_4 and N_2O were observed in soils from all three sites, and significant net production of each gas was found throughout the soil profiles at all three sites (Fig. 4.3). I speculate that more precisely targeted investigations of the microbial community, for example examination of the abundance and distribution of genes involved in GHG production and consumption such as *nosZ* and *pmoA*, may reveal functional relationships between the organisms living in the soils and the GHG being released and/or fixed.

4.6.2 Conclusions

The polar deserts were both quantitatively and qualitatively different from other Arctic terrestrial ecosystems. There appears to be at least one fundamentally different process giving rise to GHG in arid versus hydric Arctic ecosystems, that is, the aerobic consumption of nitrous oxide. I did not detect this in my study of lowland Arctic tundra ecosystems (Chapter 3). Given that above ground vegetation is a surrogate for soil moisture in the Arctic (Walker, 2000; Walker et al., 2002), I suggest that the Circumpolar Arctic Vegetation Map (Walker et al., 2002) can serve to identify regions of the Arctic with fundamentally different biology giving rise to N_2O in these ecosystems. The production and consumption of GHG occurred throughout the soil profile. Thus, I speculate the key importance of melting permafrost may be how an increased active layer alters GHG production and consumption processes occurring throughout the entire profile, in addition to the release of carbon as previously frozen soil layers thaw (McGuire et al., 2009). Until we understand how an increased active layer will influence these processes, it is not certain that the GHG sink I have observed will be an enduring feature of Arctic deserts.

5. SOIL FACTORS INFLUENCE ARCHAEAL AMMONIA OXIDIZERS BUT NOT METHANOTROPHS IN ARCTIC POLAR DESERT SOILS

5.1 Preface

Soil samples were collected from each sampling position in each excavated pit during the 2010 field campaign. DNA from these samples was extracted and the microbial community composition compared against the GHG net production dataset from Chapter 4. This paired dataset approach, combining a molecular-biological investigation of the community of microorganisms hypothesized to be causal factors in the observed patterns of the GHG production dataset allowed a direct test of causal, microbial-ecological hypotheses that combine both abiotic and biotic soil factors.

There are many techniques available for studying microbial community composition in soils. Through contact with the Environmental Genomics team at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Hobart, Tasmania, I chose to use DNA microarrays built around observed patterns of diversity of functional genes including genes coding for two enzymes directly related to microbial GHG processes: particulate methane monooxygenase, used by methanotrophic bacteria to consume CH_4, and ammonia monooxygenase, used by ammonia-oxidizing bacteria and archaea to consume NH_3, a process that may also release N_2O.

5.2 Abstract

Polar deserts are a vast, 1 358 000 km^2, barren, (less than 5% plant cover), xeric, Arctic ecosystem with CH_4 and N_2O emissions similar to mesic Arctic ecosystems dominated by heaths or willows. It is not clear how the microbial communities of these polar deserts are linked to these unusual soil conditions or to the production of greenhouse gases. Here, I investigated the link between methane-oxidizing bacteria and ammonia-oxidizing archaea, soil environmental conditions, and patterns of net gas production using community-composition DNA microarrays and structural equation modelling across three Arctic polar deserts, located between 77° and 82° N latitude. Surprisingly, ammonia-oxidizing bacteria were not found in sufficient abundance to support detailed analysis, while their archaeal counterparts were found throughout the study area. Methane-oxidizing bacteria were significant drivers of observed patterns of CH_4 production, but did not vary with edaphic factors such as organic carbon or total nitrogen. In contrast, ammonia-oxidizing archaea did not drive patterns of N_2O production, but were responsive to edaphic factors. Despite this edaphic dependence, neither methane-oxidizing bacteria nor ammonia-oxidizing archaea differed between sites. In this study, N_2O production was not linked to archaeal or bacterial nitrifiers, though bacterial denitrifier abundance was too low to analyze. My results highlight two key uncertainties in the biogeochemistry of Arctic climate change modelling: (1) drivers of methanotrophic activity and prevalence in xeric Arctic soils are not known, and (2) the biological source of N_2O in deserts is unknown.

5.3 Introduction

The biogenic greenhouse gases (GHGs) CO_2, CH_4, and N_2O are components in global cycles of carbon and nitrogen. The production or consumption of one gas is often directly associated with either the production or consumption of another, for example the synthesis of CH_4 from CO_2 and H_2 (Conrad, 1999). Which GHG-relevant metabolic pathways are active in a soil depends on the presence of capable organisms (e.g., methanotrophic bacteria, denitrifying bacteria or ammonia oxidizing bacteria), soil conditions especially water and oxygen, and the availability of the substrates of gas-metabolizing enzymes (e.g., CH_4, NO, N_2O).

Polar desert (i.e., an Arctic ecosystem with less than 5% plant cover) soils are typically aerobic, cold, dry and have organic carbon contents less than 5 kg m^{-2} in the active layer (Burnham and Sletten, 2010; Gregorich et al., 2006). However, some of these vast ecosystems

(covering approximately 1,358,000 km^2 of the Earth's surface), have GHG production rates similar in magnitude and vertical distribution to wetter, more carbon-rich tundra soils (Siciliano et al., 2009). Characterized by low biomass and plant diversity (Jones et al., 2000; Klady et al., 2011; Muc et al., 1994), polar deserts serve as a relatively simplified natural system in which to investigate patterns of microbial diversity and activity and their relationship to GHG production.

Biological consumption of methane is primarily catalyzed by membrane-bound particulate methane monooxygenase (PMO), the gene for which is found in nearly all methane oxidizing bacteria (MOB) (Dedysh, 2009; Kizilova et al., 2013; Kolb, 2009; Murrell et al., 1998) and serves as a useful phylogenetic marker (Bodrossy et al., 1997; Pacheco-Oliver et al., 2002). These organisms are an important sink of CH_4 globally, accounting for 30 Tg yr^{-1} of atmospheric CH_4 removal, or 6% of the global sink (Dalal and Allen, 2008; IPCC, 2007). Recently, a DNA microarray targeting a wide range of sequences of *pmo* has been developed that allows rapid, low-cost, high-throughput examination of the community structure and composition of MOB using the gene directly involved in the process of CH_4 oxidation (Stralis-Pavese et al., 2011).

There are two major pathways for the production of N_2O in soils, during nitrification via the chemical decomposition of NH_2OH to NO and N_2O (Braker and Conrad, 2011), and as the penultimate step of denitrification that typically occurs only under anaerobic conditions (Firestone and Davidson, 1989; Hochstein and Tomlinson, 1988; Wrage et al., 2001). The first step in nitrification, the oxidation of NH_3 to NH_2OH is catalyzed by ammonium oxidase (AMO) a multi-subunit enzyme encoded by distinct but related genes in ammonia oxidizing bacteria (AOB) compared to ammonia oxidizing archaea (AOA) (Hatzenpichler, 2012); furthermore, *pmo* and bacterial *Amo* are themselves closely related (Bodrossy et al., 1997; Holmes et al., 1995). Examination of the diversity of sequences of *AmoA*, the gene encoding the A subunit of AMO, present in a sample is informative regarding relationships to biogeochemical processes such as GHG production because of the direct metabolic link between gene, enzyme, and gas-producing process; in addition, phylogenetic analyses of ammonia oxidizing arachaea and bacteria show strong congruence between *16s* and *AmoA* genes (Aakra et al., 2001; Calvó et al., 2005; Nicol et al., 2008). As for methane-oxidizers, a functional gene DNA microarray targeting *AmoA* sequences has been developed for both ammonia-oxidizing bacteria and ammonia-oxidizing archaea (Abell et al., 2012), allowing rapid characterization of these largely uncultured groups (Ward and Bouskill, 2011).

The link between functional groups of soil microorganisms and edaphic factors is unclear, especially in Arctic ecosystems (Lamb et al., 2011). Soil water content is a driver of community composition by its effects on redox state and oxygen diffusion, with obligate aerobic bacteria including aerobic methanotrophs (McDonald et al., 2008) restricted to habitats with available O_2 (Chowdhury and Dick, 2013); the reliance of nitrification on available O_2 similarly restricts AOA and AOB to aerated environments (Bartossek et al., 2010; Schleper and Nicol, 2010). However, the environments where methanotrophy and nitrification have been observed include a wide range of pH, water, temperature, and other factors (Kolb, 2009; Ma et al., 2007; McDonald et al., 2008; Rahman et al., 2011; Schleper and Nicol, 2010; Sullivan et al., 2008).

Methanotrophs are the only biological sink for CH_4, and their sum contribution to CH_4 net emissions from soils and other environments depends on their abundance, activity, and ability to acquire CH_4 at atmospheric concentrations of a few parts per million (Bull et al., 2000; Knief and Dunfield, 2005). While it is difficult to measure the activity of methanotrophs *in situ*, it is clear that a greater diversity of methanotrophic bacteria is usually associated with a stronger local sink (Bárcena et al., 2011; Bárcena et al., 2010; Bengtson et al., 2009; Horz et al., 2002; Knief and Dunfield, 2005), though in some cases variation in the strength of CH_4 sinks may be decoupled from the community composition of microbes by the influence of vegetation or other factors (e.g., (Menyailo et al., 2010; Menyailo et al., 2008; Reay et al., 2005). Similarly, net emissions of N_2O are driven by the total community of organisms capable of either or both the production or consumption of the gas (Lamb et al., 2011; Ma et al., 2008). Arctic soils including polar deserts produce N_2O largely through the actions of nitrifiers (Ma et al., 2007; Siciliano et al., 2009), a functional community in which archaea are critical components in high-latitude soils and in which patterns of N_2O emissions may be associated with microbial community composition (Alves et al., 2013; Banerjee and Siciliano, 2012; Daebeler et al., 2012; Lamb et al., 2011).

In dolomitic Polar Deserts, there are very high levels of NH_3 and O_2 but low organic carbon, water, and temperatures (Burnham and Sletten, 2010; Horwath et al., 2008; Sullivan et al., 2008). Thus, nitrification is expected to be the major source of emitted N_2O (Klotz and Stein, 2008; Ma et al., 2008; Siciliano et al., 2009; Stein and Klotz, 2011), and net CH_4 emissions are expected to be negative, that is consumption of atmospheric CH_4 in the soil (Angel and Conrad, 2009; Bárcena et al., 2010). The goal of this study was to evaluate the hypothesis that patterns of

variation in GHG net production in Arctic polar desert soils are driven by variation in microbial community composition among methane oxidizers and ammonia oxidizers. Furthermore, community composition of microorganisms would be driven by edaphic factors thus affecting GHG emissions indirectly. These hypotheses were tested using Structural Equation Modelling and measurements of community composition obtained from DNA microarrays targeting the functional genes *pmo* and *AmoA*.

Structural equation modeling allows estimation of the relative strength of causal relationships between variables and the construction of synthetic "latent" variables to ease simulation and visualization of complex relationships within systems (Grace, 2006; Lamb et al., 2011). In this study, prior expectations regarding methanotroph physiology and ecology led to the hypothesis that community composition of MOB would be a causal factor of previously observed patterns of net CH_4 production. In addition, I hypothesized MOB would be driven by variations in edaphic factors such as water, organic carbon and porosity that are related to the processes of biological CH_4 generation and oxidation (Angel and Conrad, 2009; Conrad, 1999, 1989).

5.4 Materials and Methods

5.4.1 Soil Collection Locations

Three polar deserts on Ellesmere Island in the Canadian High Arctic were visited in July and early August, 2010. Okse Bay (77° 8' 8" N 87° 39' 10"W), Dome (78° 51' 31" N 75° 55' 37"W), and Patterson River (82° 35' 47" N 63° 45' 32"W) were sampled for GHG flux and below-ground concentration *in situ* and soil samples were collected from pits excavated after gas probes had been measured (Chapter 4). The results of the analysis of GHG and edaphic factors are described in Chapter 4, and the present chapter describes an analysis of the microbial communities of the soils by DNA microarrays, Fast Unifrac (Hamady et al., 2010), and structural equation modelling (SEM).

Soil samples were collected from the walls of pits at depths matching the sampling depths of soil gas probes deployed in clusters of six where soil-atmosphere gas flux had recently been measured by non-steady-state chambers (McDonald et al., 2008). Collection of soil was sometimes difficult in the extremely coarse and rocky soils of many pits; Fig. 5.1 shows an

example of a pit at Patterson River, where glaciofluvial parent material included relatively little sand, silt and clay, and large amounts of pebbles and larger stones. Soil collected for DNA extraction and microbial analysis included smaller pebbles and their surface-adhered fine material.

Soil DNA was extracted from each soil sample (total n = 180) from the three polar deserts using approximately 1.0 g of bulk soil (avoiding pebbles larger than 5mm) and the FastDNA Spin Kit for Soil (MP Biomedicals, Santa Ana, USA). DNA extracts were frozen at -80°C before transport, packed in dry ice (i.e., solid CO_2) to the CSIRO laboratories at Hobart, Australia. The extracts had been thawed for an unknown period of no longer than three days when they reached CSIRO facilities, but tests of concentration and amplification success by PCR and standard primers for 16S (Abell et al., 2013) suggested negligible degradation in DNA quality.

5.4.2 Amplification of Target Sequences

The genes *pmoA* for methanotrophic bacteria and *AmoA* for bacteria and for archaea were amplified by PCR from subsamples of the soil DNA extracts after adjusting DNA concentration to between 10 and 20 ng uL^{-1} from raw extraction concentrations ranging between 10 and 100 ng uL^{-1}. All reverse primers included the T7 promoter site (5' – TAATACGACTCACTATAG – 3') at their 5' end, which enabled T7 RNA polymerase-mediated *in vitro* transcription using the PCR products as templates. Amplification of *pmoA* was accomplished using a two-step nested, touch-down PCR design that allowed amplification of difficult samples in which traditional non-nested PCR did not yield products. The forward primer pmoA189 was used with the reverse primer mb661 (Costello and Lidstrom, 1999) in the first round (11 cycles T_{ann} = 65-55°C, then 24 cycles T_{ann} = 55°C) or with the reverse primer A682 (Bourne et al., 2001) in the second (10 cycles T_{ann} = 65-56°C, then 25 cycles T_{ann} = 56°C). The modification included the addition of two tags, T3c and T7c, based on the T3 and T7 promoter sites, to the forward and reverse primers, respectively (Stralis-Pavese et al., 2011). Amplification of *AmoA* was accomplished using the primers Arch-amoAF and T7-Arch-amoAR (Abell et al., 2012) (35 cycles, T_{ann} = 53°C). PCR products were purified using an Agencourt AMPure XP magnetic beads kit (Beckman Coulter Australia Pty Ltd, Lane Cove, Australia), according to the manufacturer's instructions. Purified DNA was dissolved in sterile, ultrapure water to a DNA concentration of 50 ng uL^{-1} and stored at -20°C

Fig. 5.1. An example profile from Patterson River, the northernmost of the three studied polar deserts. No horizonation and no soil structure are visible, due to the young age of the soils, cryoturbation, and extremely coarse texture. The tape measure on the left shows depth from the bottom of the pit, excavated to the permafrost, in cm. Soils in the other polar deserts were similar in appearance and physical and chemical characteristics, though varied in color due to differences in parent material.

prior to reverse-transcription and fluorescent labelling. Working under RNA-ase free conditions, reverse transcription was carried out using the procedure of Stralis-Pavese et al., (2011), including purification of RNA product with Agencourt AMPure XP magnetic beads and post-transcription fragmentation and storage at -20°C.

5.4.3 DNA Microarrays

I used two DNA microarrays, recently developed and refined for examination of microbial communities of methane-oxidizing bacteria (Stralis-Pavese et al., 2011) and ammonia-oxidizing archaea (Abell et al., 2012), based on bacterial *pmoA* and archaeal *AmoA*, respectively. Detailed procedures for these microarrays are described in Stralis-Pavese et al., (2011) and Abell et al., (2012), respectively. Briefly, RNA transcripts mixed with a hybridization solution containing sodium dodecyl sulfate, Denhardt's solution, and saline-sodium citrate buffer were

hybridized to each DNA microarray, a glass microscope slide with single-stranded DNA oligonucleotides printed in a hexagonal grid pattern, in triplicate within each hybridization well. Microarrays were incubated in a rotating hybridization oven overnight at either 55°C (*pmoA*) or 60°C (*AmoA*), then non-adhered RNA was washed away and the microarrays were allowed to air-dry for one hour.

Microarrays were stored in microscope slide boxes to avoid unnecessary exposure to light that can degrade fluorescent signal intensity prior to being scanned with an Axon Genepix 4000B microarray scanner (Molecular Devices LLC., Sunnyvale, USA). Images were analyzed using GenePix Pro version 7.0 (Molecular Devices) and a custom MS Excel spreadsheet macro that standardized all signals to a set of standard probes included in each DNA microarray.

5.4.4 Data Analysis

After setting each microarray point brightness relative to the control points, microarray signals were compared to a threshold value equal to 10% of the reference value for each probe (Abell et al., 2012; Stralis-Pavese et al., 2011); this conservative threshold value was intended to minimize the occurrence of false-positive signals indicative of the presence of sequences not actually found in the polar desert soils. Probes that included zero values above the 10% threshold were eliminated from further analysis, and soil samples that showed no signals except in control microarray points were also eliminated from further analysis. When comparing between the two microarray datasets, samples that were present in one dataset only were eliminated from the overall comparison; 16 samples showed at least one signal on the *pmoA* microarray but zero signal on the *AmoA* microarray.

Due to the overlapping and nested structure of the probe design and sequence targeting (Abell et al., 2012; Stralis-Pavese et al., 2011), a non-reticulated (Philippe et al., 2011), full phylogenetic relationship among all probes on each microarray was not possible. Probes that could be unambiguously assigned to a phylogeny that included several polytomies were included in Fast Unifrac analysis as one of the inputs (Hamady et al., 2010). Datasets that included all phylogeny-assigned probes and all positive-signal soil samples were assembled with available soil chemical and physical factors data (McDonald et al., 2008) including location, depth, pH, non-purgeable organic carbon (NPOC), water-extractable total nitrogen (TN), (NO_3^- + NO_2^-), NH_4^+, soil bulk density, water content, and gas concentration and net production for CO_2, CH_4,

and N_2O and were then submitted to Fast Unifrac analysis to cluster soil samples by their biotic and abiotic dissimilarities and to produce principle co-ordinates analysis (PCoA) visualizations of these relationships between multivariate samples.

Structural equation models (SEM) were constructed to test causal hypotheses regarding the role of the microbial communities of methane-oxidizing bacteria and ammonia-oxidizing archaea to the observed patterns of net production of the GHG CH_4 and N_2O, respectively. Construction of SEM proceeded by first defining observed and latent variables and ascertaining the most well-supported relationships among those variables, then refining input instructions to obtain a model that satisfied the criteria of a p-value associated with a χ^2 test of $p > 0.001$ and CFI and TLI values each greater than 0.995. If a model with those criteria could not be obtained, the hypothesized causal relationships were rejected as incongruent with observations.

5.5 Results

Extractable organic carbon ranged between 15 and 176 g kg^{-1} (or 0.15 to 1.8 %) except at four near-surface soils with detected amounts less than 1 g kg^{-1}. Extractable nitrogen was also low, ranging from less than 1 to 74 g kg^{-1}. Measured NO_3^- was very low (below detection limits in more than half of soils sampled) but ranging up to 4.1 g kg^{-1}. More details of the physical and chemical characteristics of the soils of these polar deserts can be found in Chapter 4. Compared to most soils in temperate and tropical zones, the polar deserts are exceptionally dry, with water filled pore space ranges from 0.64% to 12.4% and very coarse; soils could not be sieved without the loss of the majority of the material due to the high proportion of pebbles and larger stones, and with the permafrost layer occurring approximately 50 cm below the surface. The pH of the polar desert soils ranges from 6.5 to 9.2, roughly equal to the pH range of greatest change in proportions in a $NH_3 \leftrightarrow NH_4^+$ system; most inorganic nitrogen is in the form of ammonia or ammonium. This pH range also results in a strong potential inorganic sink for CO_2 as considerable quantities can dissolve in even the sparse but alkaline water (McDonald et al., 2008; Shanhun et al., 2012).

Sequences corresponding to 126 DNA oligonucleotide probes on the *pmoA* microarray were detected in at least one soil DNA extract each; 42 probes were detected in only one soil extract. Of the 126 probes, 34 could be unambiguously classified in a dendrogram for Fast Unifrac analysis with a mean of 56 soils showing a positive signal per probe (Fig. 5.2) while 29

probes were detected in at least 10 soil extracts and were included as candidate indicators for the latent variable MOB in the structural equation model. Probe richness, the sum of probes showing an abundance greater than zero for each soil sample (*i.e*, the sum of rows counting all non-zero as 1 in the heatmap), ranged from zero to 43 for the *pmoA* microarray, with a mean of 10.9. Samples with relatively high richness are clustered on the heatmap, as do samples with low richness, including a set of samples that showed zero abundance for all probes and were thus not classifiable by the clustering function of Fast Unifrac (Fig. 5.2). Some probes were detected in nearly all samples, including USCG-225b and Nit_rel470, probes associated with upland soils and sequences closely related to ammonia-oxidizing bacteria, respectively. Nit_rel652, previously associated with Arctic soils (Stralis-Pavese et al., 2011), was detected in only one sample, PK34 from Patterson River 34 cm below the ground surface.

No PCR amplification of bacterial ammonia oxidase was successful for any polar desert soil samples. Sequences corresponding to 60 DNA oligonucleotide probes on the *AmoA* (archaeal) microarray were detected in at least one soil DNA extract each and 26 probes were detected only once. Twenty-four probes could be unambiguously classified in a dendrogram for Fast Unifrac analysis with a mean of 65.25 samples showing a positive signal per probe (Fig. 5.3). Three major clades and three minor clades of samples are formed by the clustering function of Fast Unifrac; the major clades, accounting for the first 121 samples are distinguished by the presence or absence of the first six probes, AmoA-50, AmoA-51, AmoA-59, AmoA-44, AmoA-43, and AmoA-42 (Fig. 5.3). The first three probes are associated with soils and estuarine sediments, while AmoA-44, AmoA-43, and AmoA-42 are associated with grassland soils (Abell et al., 2012; Pester et al., 2012). Probe richness on the *AAmoA* microarray ranged from 2 to 26 out of the set of 60 probes with at least one positive signal. Sample PM19, from Patterson River, is part of the second major clade and has the highest richness, 26; it shows the only positive signal for three of the 26 probes detected only once. Fast Unifrac could not adequately classify 18 out of 163 soil sites due to the presence of zeroes in the abundance of every *pmoA* probe analyzed by Fast Unifrac (Fig. 5.2); these samples were included in the analysis because they showed significant probe signals in other probes that could not be associated unambiguously with the dendrogram of probes (Abell et al., 2012).

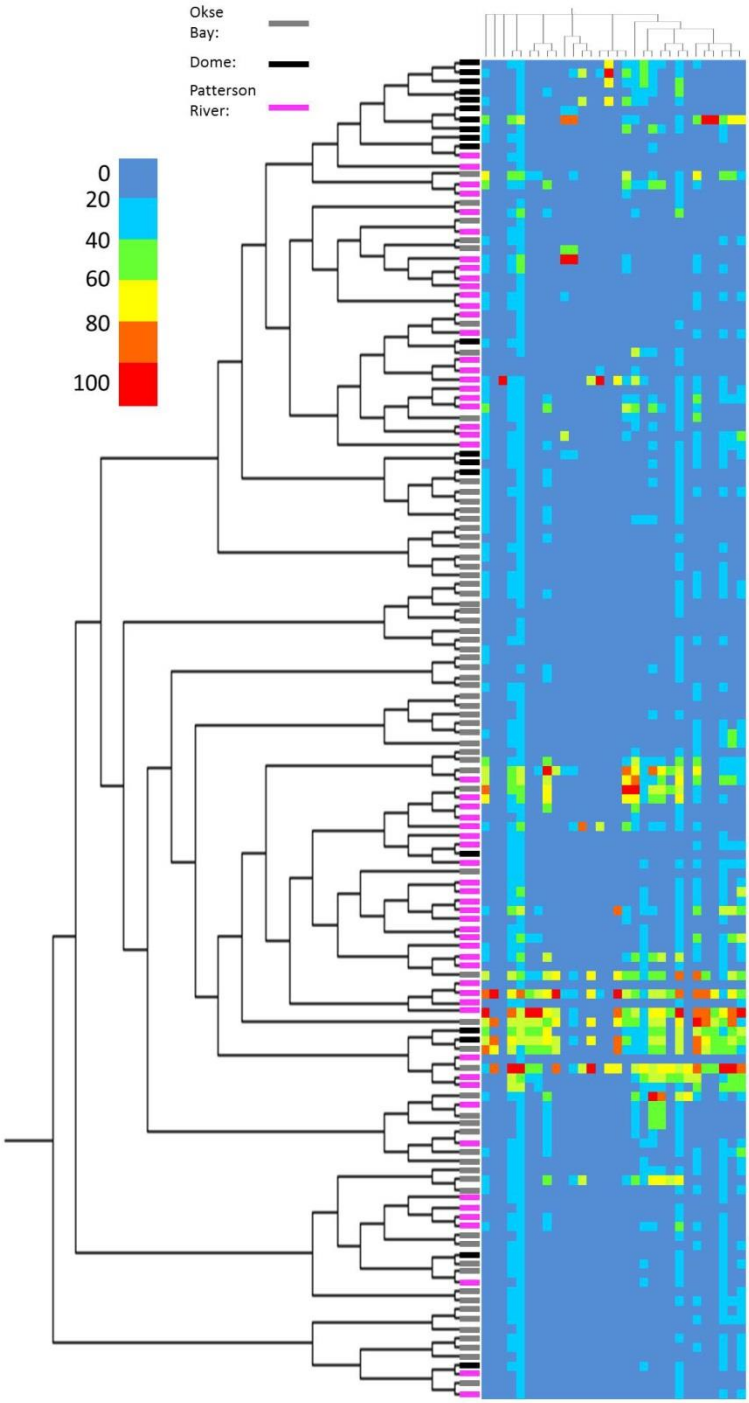

Fig. 5.2. Results of the DNA microarray for *pmoA* sequences represented as a heatmap, with dendrograms showing relationships among samples (right) and microarray probes (top). Soil samples from pits in the polar deserts form rows, with *pmoA* probes (McDonald et al., 2008; Stralis-Pavese et al., 2011) forming columns. Probes from left to right: Mmb 562, DS2-220, WC306_54-385, USCG-225, USCG-225b, Mcl408, Mcl404, 501-375, 501-286, Peat264, Msi423, MsS475, MsS314, Mm229, MsQ290, LP20-607, Mmb304, Nit_rel351, Sed585, Sed422, Nit_rel419, Nit_rel471, Nit_rel470, Nit_rel417, TUSC409, B2all343, B2all341, RA14-591, RA14-594, RA14-299. Dendrograms were created by ladderise-left function in TreeView X (Page, 1996).

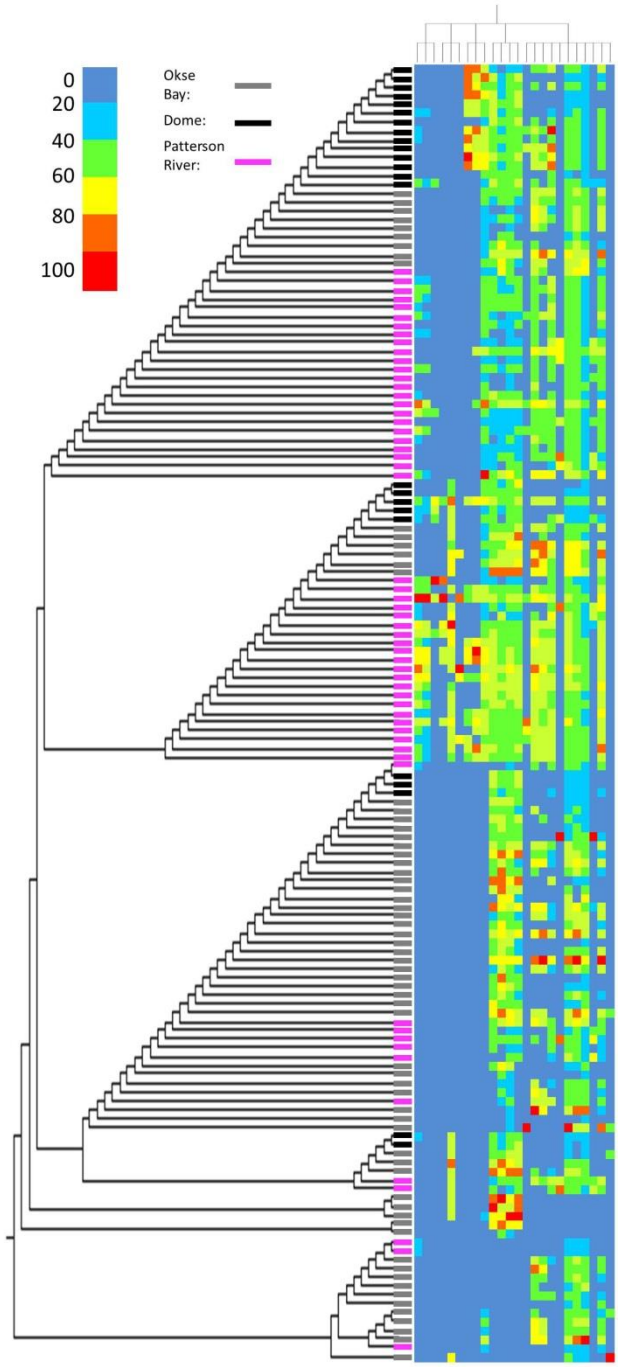

Fig. 5.3. Results of the DNA microarray for *AAmoA* sequences represented as a heatmap, with dendrograms showing relationships among samples (right) and microarray probes (top). Soil samples from pits in the polar deserts (McDonald et al., 2008) form rows, with *AAmoA* probes that could be unambiguously classified (Abell et al., 2013) forming columns. Probes from left to right: AmoA-50, AmoA-51, AmoA-59, AmoA-44, AmoA-43, AmoA-42, AmoA-85, AmoA-90, AmoA-84, AmoA-27, AmoA-19, AmoA-23, AmoA-26, AmoA-17, AmoA-7, AmoA-8, AmoA-9, AmoA-4, AmoA-1, AmoA-2, AmoA-3, AmoA-6, AmoA-12, AmoA-10. Dendrograms were created using the ladderise-left function in TreeView X (Page, 1996). No probe with only a single positive signal is included.

My conceptualization of the links between edaphic factors, MOB functional composition and net CH_4 production was congruent with the observed data (Fig. 5.4). The high values for CFI and TLI, higher than 0.95, are indicative of a good fit between the model parameters and the correlation/covariance matrix derived from the observed data. The community composition of MOB was linked (0.203 ± 0.090, $p = 0.024$) to the observed net production of CH_4. Net CH_4 production was also linked to CH_4 concentrations (0.312 ± 0.075, $p < 0.001$) and depth (0.240 ± 0.064, $p < 0.001$) and to a greater degree than MOB. MOB community composition was not significantly linked to Fertility (0.266 ± 0.184, $p = 0.149$) or pH (-0.009 ± 0.119, $p = 0.938$) but was weakly significantly linked to CH_4 concentration (-0.094 ± 0.053, $p = 0.077$). Water-filled pore space (WFPS) was not significantly related to any other variable in the model but this is readily explained because WFPS did not vary significantly between deserts, averaging $5.4\% \pm 0.19\%$ (Fig. A3.1).

In contrast to MOB, the community composition of AOA was not associated with any other measured parameter when analyzed by SEM (Fig. A2.2). Similar to MOB, a latent variable based on the functional genotypes was constructed (SEM $\chi^2 = 5.317$, $p = 0.26$, CFI = 0.997, TLI = 0.992) using a set of five probes from the archaeal *AAmoA* microarray [AamoA-1, AamoA-7, AamoA-8, AamoA-9, AamoA-84; (Abell et al., 2012)], this latent could not be linked with either the Fertility latent or with soil parameters directly as observed variables, nor with any measured soil or gas parameter; attempts to construct SEM with these variables failed to result in models congruent with observations or failed to converge.

Supporting the SEM interpretation, taxon richness, the sum of detections of probes on the microarrays regardless of relative abundance, was correlated with net CH_4 production for MOB ($r = 0.194$, $p < 0.05$), but not with net N_2O production for AOA. No measured soil parameter was significantly correlated with MOB richness, while pH, depth below ground surface, extractable organic carbon, extractable nitrogen, and NO_3^-, were all significantly ($p < 0.05$) correlated with AOA richness (Fig. A3.3). Neither dissimilarity matrix, for MOB or for AOA, was significantly associated with the dissimilarity matrix for edaphic factors (Mantel, MOB: $p = 0.21$, permutations = 9999; AOA: $p = 0.16$, permutations = 9999). The latent variable MOB from the SEM was significantly correlated with each of the first three axes of the PCoA for the MOB community as analyzed by Fast Unifrac ($r = 0.36 – 0.39$, $p < 0.001$); similarly, the latent

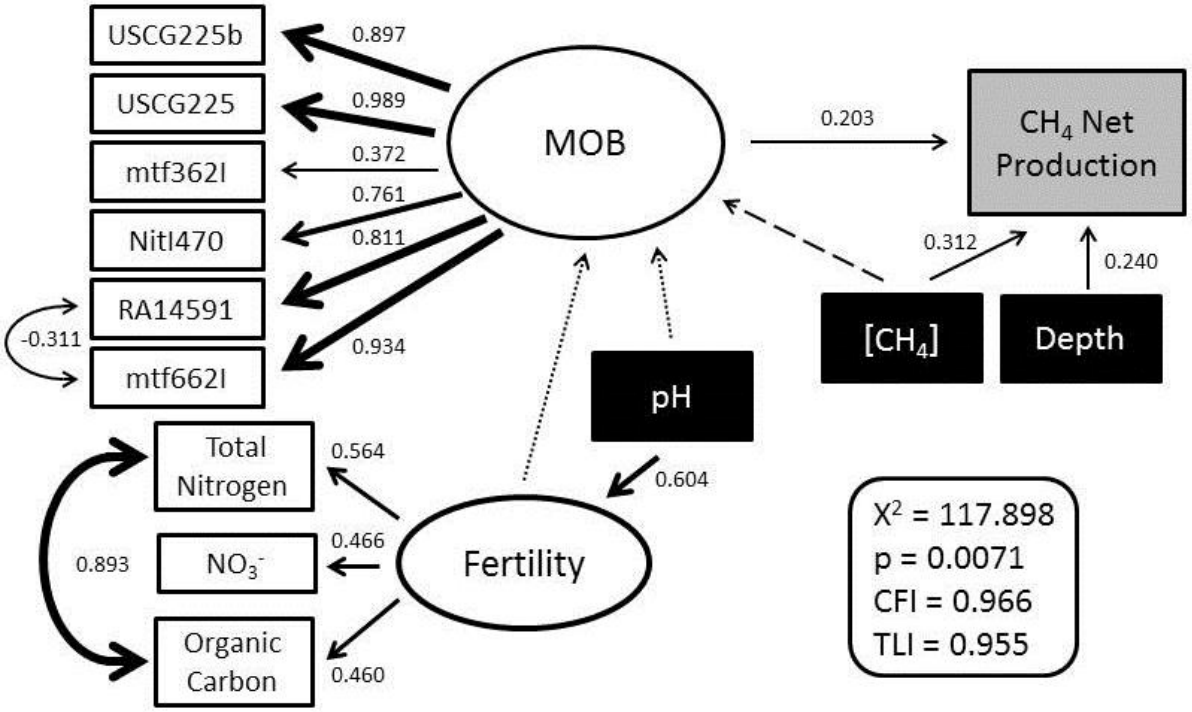

Fig. 5.4. The structural equation model for methane-oxidizing bacteria (MOB) was congruent with observed data. The community composition of MOB is a significant causal factor for net CH_4 production in these Arctic polar deserts. The latent variable MOB is indicated by a set of six sequence probes of the DNA microarray for *pmoA* but is not significantly affected by the latent variable Fertility, itself indicated by NO_3^-, total nitrogen, and organic carbon (i.e., non-purgeable organic carbon) and driven by pH. Other edaphic factors including pH and depth below the soil surface do not directly affect the community composition of MOB, though depth and the concentration of CH_4 within soil atmosphere also affect net CH_4 production. Thicker arrows represent stronger correlations or causal pathways; dashed arrows are not significant at $p < 0.05$. Standardized co-efficients are shown for each significant path. Concentration of CH_4 may weakly affect MOB, $p = 0.077$.

variable AOA was significantly correlated with the first two axes of the PCoA (r = 0.187, 0.228, $p < 0.05$).

Principal Coordinates Analysis of the Fast UniFrac dissimilarity matrices successfully represented the data set but did not reveal separation among soil samples by location (i.e., three polar deserts on Ellesmere Island) nor by net GHG production (Fig. 5.5). In the SEM, MOB are not strongly affected by soil factors such as NO_3^- or extractable organic carbon (Fig. 5.4), and likewise neither of the first two axes of the PCoA are significantly correlated with those and other soil parameters (Table 5.1). In contrast, AOA are correlated with most measured soil parameters when analyzed by Fast Unifrac and PCoA (Table 5.1).

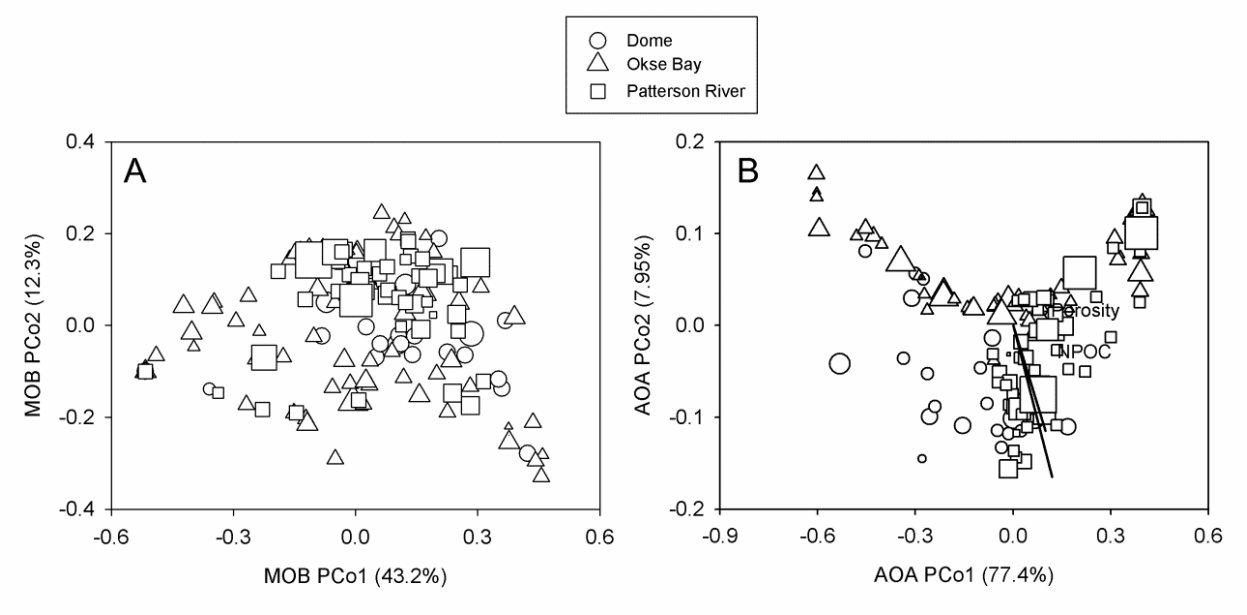

Fig. 5.5. (A) PCOA ordination for MOB showed no correlation with observed patterns of CH_4 production in soils. The size of symbols represents relative net CH_4 production; small symbols are soils with zero or net consumption of CH_4, large symbols are close to the maximum observed net CH_4 production, with values binned into 10% intervals of the maximum after scaling by adding the value of the strongest CH_4 sink to all net CH_4 production estimates. PCo1 accounts for 43.2% of the variance, PCo2 for 12.3%. (B) Ordination of PCoA for AOA showed no relationship with observed patterns of net N_2O production in soils. The size of symbols represents relative net gas production, as in A, but for N_2O. NPOC and porosity were correlated with both axes of the AOA PCoA; lines on (B) show a vector from (0,0) to ½ the value of r for each correlation (Table 5.1). PCo1 accounts for 77.4% of the variance, PCo2 for 7.96%.

Table 5.1. Correlations between Fast Unifrac PCoA axes and edaphic variables.

	pmoA				***AamoA***			
	PCo1	**PCo2**			**PCo1**		**PCo2**	
		r		*p*	*r*	*p*	*r*	*p*
pH	ns	0.25		**	ns		-0.36	***
NPOC	ns	ns			0.24	**	-0.33	***
NO_3	ns	ns			ns		0.38	***
TN	ns	ns			ns		0.23	**
Porosity	ns	ns			0.20	*	-0.23	**
WFPS	ns	-0.23		**	ns		0.22	**

NPOC: non-purgeable organic carbon
TN: total nitrogen
WFPS: water-filled pore space
ns: not significant ($p > 0.05$); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

5.6 Discussion

The two functional communities of microorganisms studied in the polar deserts of Ellesmere Island differ from each other in their relationship to GHG production and to edaphic factors such as soil carbon and nitrogen. The methanotrophs are a driver of patterns of net CH_4 production in these ecosystems, yet they do not respond to variations in NO_3^-, extractable nitrogen, or organic carbon. In contrast, the ammonia oxidizing archaea are linked to all measured soil properties, but do not play a significant role in patterns of net N_2O production.

The main results of the SEM, that MOB community composition is a predictor of net CH_4 production but that community composition is not driven by edaphic factors (Fig. 5.4), are supported by two independent comparisons. Community composition as constructed by principle coordinates analysis by the Fast Unifrac method (Hamady et al., 2010) showed no correlations between major axes of the MOB PCoA and edaphic factors with the exception of pH and soil moisture, two variables reported to be drivers of methanotroph populations (Conrad, 2009; Dunfield, 2007; Kolb, 2009; Op den Camp et al., 2009; Semrau et al., 2010), though a similar lack of correlation with abiotic factors was observed in methanotrophs collected from a landfill cover soil (Kumaresan et al., 2009). Furthermore, probe richness, a simplified measure of community composition, was significantly correlated with net CH_4 production but not with any edaphic factor. These consistencies across analytical methods provide high confidence that the SEM is congruent with the reality in these soils.

In much the same way a lack of correlation between edaphic factors and MOB is supported by independent analyses, the dependence of AOA on edaphic factors is indicated by the strong correlations between PCoA axes, AOA richness, and edaphic variables (Fig. A3.2). Similar findings from a range of terrestrial environments show clear responses by AOA communities to soil moisture content (Gleeson et al., 2010), water and nitrogen (Di et al., 2010; Szukics et al., 2012), pH (Gubry-Rangin et al., 2011; Nicol et al., 2008), topography (Stewart et al., 2014), and patterns of land-use across gradients of pH and other factors (Hu et al., 2014). Ammonia-oxidizing archaea and bacteria appear to segregate by habitat under contrasting pH (Nicol et al., 2008; Shen et al., 2014), and nitrogen (Di et al., 2010), as well as responding to interactions between soil biotic and abiotic factors (Hatzenpichler, 2012; Yao et al., 2013). It is not surprising, therefore that the AOA community of the Arctic polar deserts appear to be responsive to the range of soil parameters measured here.

Denitrifying organisms are drivers of net N_2O production in many soil ecosystems (Banerjee and Siciliano, 2012; Bateman and Baggs, 2005; Chapuis-Lardy et al., 2007; Ma et al., 2007, 2008; Philippot et al., 2009, 2013), but conditions in the Arctic polar deserts are particularly poorly suited to their activities because of low water and organic carbon, poor availability of NO_3^-, low temperatures, and high oxygen (Siciliano et al., 2009). Repeated ^{15}N tracer investigations in Arctic systems have demonstrated that in the mesic and xeric ecosystems, nitrifiers dominate N_2O emissions (Ma et al., 2007; Siciliano et al., 2009; Stewart et al., 2012). An estimation of *nosZ* gene-copy abundance by qPCR (Fig. A3.4) revealed no correlation with either N_2O concentration or net N_2O production, further suggesting the denitrifying organisms in the Arctic polar deserts are not the driver of net N_2O production. For similar reasons, especially the abundance of oxygen and low NO_3^-, the ANAMMOX process is not currently thought to be a major factor in these cold, dry, aerobic and nutrient-poor soils (Francis et al., 2007; Simon and Klotz, 2013). The remaining possible driver of N_2O emissions is heterotrophic nitrification such as by fungi (Hora and Iyengar, 1960; Spott et al., 2011), which has not been reported from cold, dry, low-organic-content, high-pH soils.

The ecological relationship between MOB and AOA may be primarily competition for ammonia, as reported in Icelandic grassland soils (Daebeler et al., 2014) with initial NH_4^+ concentrations (0.64 – 1.42 g NH_4^+ kg^{-1} soil) within the range of NH_4^+ concentrations found in these polar desert soils (0.27 – 2.63 g NH_4^+ kg^{-1} soil) (McDonald et al., 2008). Methanotrophic bacteria have been shown to be responsible for a large fraction of total ammonia-oxidation activity in a number of environments, though to date these reports have included conditions of considerably higher levels of water and nitrate than are found in the Arctic polar deserts (Acton and Baggs, 2010; Bodelier and Frenzel, 1999; Nyerges et al., 2010; Stein et al., 2012).

The three polar deserts studied are separated from each other by approximately 370 km between Okse Bay and Dome, and 500 km between Dome and Patterson River; Okse Bay and Patterson River are both near sea level, while Dome is at 540 m asl. Despite differences in local climate, the responses of the communities of microorganisms to local variations was not different across the three sites, reflecting work at other spatial scales and in other ecosystems that has found soil microbial communities respond strongly to local factors, especially soil carbon and pH (Fierer et al., 2009; Fierer and Jackson, 2006; Geyer et al., 2013; Sokol et al., 2013), but not in a

manner consistent with the latitudinal gradients of diversity and abundance found among plants and animals (Allen et al., 2002; Fierer and Jackson, 2006; Gaston, 2000; Hawkins et al., 2003).

5.6.1 Conclusions

The soils of the polar deserts of Ellesmere Island are exceptionally dry, with low nutrient levels and high pH. I used recently-developed DNA microarrays to analyze the communities of methane- and ammonia-oxidizing microorganisms in this harsh environment, and found these two groups of organisms respond differently to local conditions and while the methanotrophs are drivers of patterns of net CH_4 production, the ammonia-oxidizing archaea could not be linked to net N_2O production that includes both sinks and sources in these deserts (Chapter 3). The sinks for GHG I have observed (Chapters 3 and 4) are of particular interest, and their maintenance as features of these ecosystems is not assured, though the apparent separation of methanotrophs from most soil parameters suggests any changes to that community will be driven by different factors than those that drive changes to the ammonia-oxidizing archaea.

6. SUMMARY, CONCLUSIONS, AND FUTURE CONSIDERATIONS

6.1 Summary of Methodology and Findings

This dissertation was built from a process of incremental addition to an existing body of knowledge, through the application of both novel and well established methods to a series of questions regarding the ecology of Arctic polar deserts and adjacent tundra ecosystems. Three main themes run through this dissertation. First, while the essential information about the climate and geology of Arctic polar deserts is well established, my research explored the patterns, processes, and causes of greenhouse gas production and consumption in these soils. Second, this dissertation represents progress along a research trajectory, from the discovery of the patterns of GHG emissions, to investigation of the processes of GHG production and consumption, and to an examination of the causal microorganisms that drive soil GHG processes. Third, methods both new and old were applied to the study of the Arctic polar deserts, including recently-developed technological advances in the field of gas measurement, the analysis of datasets composed of both biotic and abiotic parameters, and cutting-edge molecular-biological tools and techniques.

The results similarly build upon both previous works by others and the progress of this research effort. Early discoveries, such as the magnitude of GHG emissions by polar deserts (Chapter 3), both motivated and provided a necessary foundation for later discoveries including the extent and persistence of those GHG emissions (Chapter 4) and the distribution of functional microbial community compositions across Ellesmere Island (Chapter 5). Other discoveries were not fully explored, and remain as intriguing possible avenues for future research efforts studying the enigmatic polar deserts.

6.1.1 Novel and Refined Methods

Prior to the start of my dissertation work, I developed the methods needed to employ a Fourier-Transform Infrared trace gas analyzer ("FTIR-TGA" hereafter) in field studies in cooperation with Dr. Siciliano (Brummell and Siciliano, 2011), who later became my PhD

advisor. This device provides the capacity to study gas concentrations in near-real-time; it is possible and practicable to analyze gas concentration data produced by the FTIR-TGA within minutes of collection, which allows the researcher to modify plans and research efforts in the field to quash errors before they propagate and to take advantage of opportunities. The opportunities that can be tackled with near-real-time data in this case includes unusual fluxes as are driven by unusual conditions below ground, such as the pockets of soil with highly enriched organic matter contents that are the result of cryoturbation in many Arctic landscapes and are otherwise difficult to detect.

With the FTIR-TGA able to function under arctic field conditions, I also developed a probe that would allow measurement of gas concentrations by the FTIR-TGA from within the soil profile (Brummell and Siciliano, 2011). There is a rich tradition in Soil Science of measuring soil gas concentrations – please see the Literature Review (Chapter 2) of this dissertation. My contribution was in the design and use of a probe robust enough to be deployed into otherwise undisturbed polar desert soils, notable from the perspective of a soil scientist for their extremely coarse texture and abundance of large stones. A steel tube with a heavy point and a strong cap can be driven into the soil with a hammer; more delicate designs cannot be emplaced without excavating pits. These probes proved their use in generating data found in Chapter 3 and Chapter 4, and further analyzed in Chapter 5.

An anonymous reviewer of the manuscript that became Chapter 3 provided the push needed to fully take advantage of the data generated by the probes and the FTIR-TGA. Spurred by this reviewer's comments, I used the calculations that allow estimation of soil gas production *in situ* based on the probe gas concentrations and the soil parameters routinely measured including bulk density and water content. Further investigations ranging across much of the sub-discipline of Soil Physics further provided the necessary calculations for error propagation (Figliola and Beasley, 2006) that allow interpretation of the significance of calculated gas production. These calculations provide the leap from pattern − the measured gas concentrations across polar vegetation community profiles − to process in the form of an analysis of gas net production within those soils.

The calculation of gas production allows for both production (positive values) and consumption (negative values) in each soil layer. Consumption of CH_4 or N_2O suggests the presence of microorganisms capable of oxidizing or reducing those gases, respectively, but no

known biological sink for CO_2 is plausible when belowground consumption of that gas is detected. In previous studies in temperate soils that detected apparent belowground sinks for CO_2, the soil conditions of slightly acidic pH and a weak sink compared to the observed sources of CO_2 allow the assumption of spurious CO_2 consumption and an adjustment of calculated values throughout the profile to set such values to zero (Risk et al., 2002). Calculated CO_2 sinks in the Arctic polar deserts, as reported in Chapter 3 and Chapter 4, do not satisfy such assumptions: the magnitudes of CO_2 sinks are as large as the magnitudes of CO_2 sources such that an assumption of high error of measurement would remove all gas production estimates, for all three studied gases. The solution to this problem is found in the high pH of the polar desert soils. Some desert soil samples had pH as high as 9.0, with nearly all samples in the alkaline range. This range of pH, from around 7.5 to 9.0 coincides with aqueous solutions that can dissolve large quantities of CO_2 under "closed" conditions; low diffusivity of gases through soil supports the use of calculations of CO_2 aqueous speciation based on closed conditions. Applying this model of soil gas / water exchange, I calculated stores of CO_2 in the aqueous phase as H_2CO_3* of at least 10 times as much as what I detected in the gas phase through the probes. Such large amounts of H_2CO_3* in solution suggest a large abiotic sink in soil water that may remove CO_2 from soil air as it diffuses through soil layers of varying water content and local pH.

Several approaches to analyzing the microbial communities of the polar deserts were considered, but due to fortunate circumstances and excellent contacts with international researchers, I was able to employ DNA microarrays through a partnership with Dr. Stan Robert, Dr. Levente Bodrossy, and Dr. Guy Abell, as well as others in their research team at Commonwealth Science and Industrial Organization (CSIRO) facilities in Hobart, Tasmania, Australia. Their team had recently developed DNA microarrays designed to quantify the functional microbial communities of ammonia oxidizers and methanotrophs using sequences corresponding to parts of the genes for ammonia-monooxygenase (*Amo*) and particulate methane monooxygenase (*pmo*), respectively. Chapter 5 applies these DNA microarrays to the soil samples collected during the 2010 field season that resulted in Chapter 4, based on the gas production dataset. Functional gene microarrays of this type had not been previously applied to Arctic polar desert soils, and the opportunity to combine this novel application with an existing dataset of GHG production was appealing to the CSIRO team.

In addition to the two datasets derived from field work and DNA microarrays, Chapter 5 includes the use of two sophisticated analytical methods to study the relationships between soil factors, microbial communities, and GHG production. First, structural equation modelling (SEM) was used to test causal hypotheses I had generated during the process of data collection and initial analysis for Chapter 4. Second, Fast Unifrac was used as an independent confirmation of the broad patterns identified by the SEM. I used this approach of confirming results with independent methods throughout the work described in this dissertation; initial experiments with the FTIR-TGA were compared with the performance of a laboratory-based gas chromatograph system, and an area-under-the-curve (AUC) based approach was compared with both profile production and flux at the soil surface in Chapter 3. In Chapter 4, methods that I had found unsuitable or of relatively low usefulness were discarded; comparing the FTIR-TGA against a GC was unnecessary, and an AUC approach did not provide any additional avenues of analysis or inquiry.

As much a part of the progress of this dissertation as the addition of novel methods has been the process of removing unworkable or unsuitable methods. The Q-test (Dixon, 1986), employed in Chapter 3 to detect outliers among the gas concentration dataset, was not used in Chapter 4 or Chapter 5 due to my increased confidence in the data supply from the FTIR-TGA; outliers were detected and eliminated using less quantitative but more robust methods involving comparison among multiple variables associated with an individual sample point. The use of error-propagation and the realization of the importance of CO_2 interacting with soil water at high pH allowed a streamlining of error-control methods in later chapters.

Some techniques have been developed by other authors that would have been usefully deployed in this dissertation but I learned of these advances too late to include them in field work or laboratory analyses. Solving the problem of gas ebullition in wetlands, a major route of gas emission from water-saturated ecosystems especially for CH_4, Mastepanov and Christensen (2008) have developed a membrane-based soil gas probe capable of detecting both dissolved and bubble-bound CH_4 in Arctic wetland soils, though such a probe in the wetlands, dry tundras, and deserts at the polar oasis at Alexandra Fjord would require significant modification. Incremental advances in gas detection technology such as the FTIR-TGA I used throughout this dissertation continue, with improvements to software analysis of spectra as well as recent improvements in competing technologies that allow partitioning of trace gases in environmental samples by their

isotopic content; the ability to measure natural abundance or enriched samples of $^{15}N\text{-}N_2O$ or $^{13}C\text{-}CH_4$ provides a powerful tool for studying the microbial processes that produce and consume such gases.

6.1.2 Summary of Findings

In Chapter 3, I describe the quantification of total GHG emissions from Arctic polar deserts and the discovery that these apparently barren and nearly lifeless ecosystems are contributing almost as much GHG as the more verdant tundras and wetlands nearby, on a per-unit-area basis when the CO_2 equivalents of CH_4 and N_2O are taken into account. This discovery was surprising because of the large role of vascular plants in regulating GHG emissions and other aspects of microbial functional ecology in tundra ecosystems, and the consequent expectation that the absence of these plants in the Arctic polar deserts would lead to severely reduced overall GHG emissions. In addition, polar deserts occupy a large fraction of the non-ice-covered land in the Arctic, suggesting their total contributions in aggregate to global GHG cycles are also large.

Chapter 4 represents both the confirmation of the main results described in Chapter 3 and an examination of patterns across a range of polar deserts on Ellesmere Island. Patterns of GHG emissions and net production in the soil profile were similar both across the three study locations and between years at the Dome where measurements had been made in 2009. This confirmation allows me to state with greater confidence that the unusual aspects of Arctic polar desert GHG dynamics, such as the positive correlation between CO_2 and N_2O observed only in the deserts, are intrinsic features of these deserts. In addition, the discovery and confirmation of GHG net production throughout the active layer allows me to discard the hypothesis that most or all of the GHG activity in these soils is the result of recent warming; were that the case, I would expect to observe net GHG production concentrated at the active layer / permafrost boundary where long-frozen organic matter and other nutrients have recently been made available to microbes, in a climate-change scenario that includes a gradual thickening of the active layer.

Chapter 5 adds the investigation of the microbial communities of the soils to the GHG production of Chapter 4, and employs structural equation modelling to test the hypothesis that the patterns observed are best explained by the community composition of functional groups of microorganisms that are also responding to soil factors such as organic matter content. In this

way, Chapter 5 serves to complete the story of my dissertation, by carrying the research from the initial exploration of patterns, through the processes of microbial GHG metabolism, to the causal factors of edaphic parameters and microbial community composition.

6.2 Unexplored Avenues

During the course of this research, several interesting phenomena were observed that have not been described elsewhere or are poorly understood. These avenues of inquiry were beyond the scope of this dissertation, though I present here what information I can regarding the co-consumption of CH_4 and N_2O, the relationship been soil emissions of CO_2 and N_2O and soil water, the puzzling role of light in regulating N_2O emissions, and the uncertainty surrounding the processes of ice formation and melting in permafrost soils and the resulting effects on gas transport.

6.2.1 Co-consumption of CH_4 and N_2O

Simultaneous consumption of CH_4 and N_2O was observed in some soil layers at Alexandra Fjord Dome in 2009 (Chapter 3) and again at Okse Bay and at Patterson River as well as at the Dome in 2010 (Chapter 4); these observations span the entire field season from shortly after snowmelt until shortly before the onset of autumn persistent snow and across all depths within the active layer. A follow-up field campaign in 2013, which included work largely beyond the scope of this dissertation, targeted these co-consuming soils with the goal of enriching and isolating the organisms responsible for this unusual GHG flux. Where CH_4 consumption in soils has been observed, conditions are typically dry and well-aerated, consistent with the physiological requirements of methanotrophic bacteria that consume CH_4 for both energy and carbon (Conrad, 2009). In contrast, where N_2O consumption has been observed, conditions are almost always very wet, often saturated when in soil rather than aquatic or marine environments, and oxygen levels are extremely low (Chapuis-Lardy et al., 2007), consistent with the physiology of complete denitrifiers that express nitrous oxide reductase when other electron acceptors are absent (Philippot et al., 2007). To observe both gases being consumed at the same time in the same soil is therefore indicative of one of three possibilities: (1) anaerobic CH_4 consumption, which has been observed (e.g., Conrad, 2009; Thauer, 2011); (2) aerobic N_2O consumption,

which has not been confirmed; (3) a previously unknown process in which N_2O and CH_4 consumptions are directly coupled to each other.

While anaerobic CH_4 consumption has been described by other researchers (Conrad, 2009), it is unlikely to be responsible for the co-consumption observed in the Arctic polar deserts studied in this dissertation because these deserts are very dry and therefore it is unlikely that large regions of severely anaerobic conditions suitable for normal complete denitrification exist anywhere above the permafrost layer. Transient high-water-content conditions exist, especially in the days immediately following snowmelt, but the observed cases of co-consumption are distributed apparently randomly throughout the soil profile and have been observed several weeks past snowmelt in soils with water contents as low as 5% (Chapter 3, Chapter 4).

Biologically-mediated reduction of N_2O to N_2 under conditions with plentiful O_2 has been suggested in several cases (Chapuis-Lardy et al., 2007; Jones et al., 2014), though the mechanism by which this occurs is not clear. An organism that constitutively expresses *NosZ* has been identified in a Japanese water-treatment plant (Miyahara et al., 2010). Though it is not clear how often *Pseudomonas stutzeri* TR2 experiences aerobic conditions or whether its continuous expression of *NosZ* represents a competitive or physiological disadvantage under aerobic conditions. Such a simple change in gene regulation could potentially create co-consuming conditions in polar desert soils, though I do not yet know enough about the physiological or ecological ramifications of constitutive expression of *NosZ* in a psychrophillic or psychotolerant organism living in the oligotrophic polar deserts to be able to speculate about such evolutionary events.

Under conditions of elevated pressure and temperature, CH_4 and N_2O can be made to react with each other, especially in the presence of certain metallic catalysts (Kögel et al., 1999; Pietrogiacomi et al., 2014). Indeed, the ability of N_2O to enhance combustion of organic molecules has been long known (Priestley, 1772), and N_2O shares with O_2 the ability to re-kindle a glowing splint. The reaction is exothermic, but requires a high activation energy in the form of temperatures of approximately 300°C or higher, depending on other factors such as the nature of the catalyst and the presence of water vapour (Pârvulescu et al., 1998; Pietrogiacomi et al., 2014). To my knowledge no enzyme or biological metabolic pathway has been described that catalyzes this reaction, nor has such an enzyme or pathway been described involving other,

similar compounds such as NO, CH_3OH, C_2H_6, or other small hydrocarbons. The net reaction may be represented as:

$$N_2O + O_2 + CH_4 \rightarrow N_2 + CO_2 + H_2O + H_2$$

I do not know, nor am I proposing, that this reaction actually occurs in nature, mediated by living organisms using enzymatic catalysts, but I speculate that a biologically-driven reaction similar to this one is possible because I can see no reason why this reaction cannot occur. All of the reactants and products are common materials in Earth's biosphere, the reaction is thermodynamically favourable and could potentially supply energy to a cell, and the half-reactions that make up this reaction, the oxidation of CH_4 and the reduction of N_2O to N_2, already occur in a wide variety of organisms.

6.2.2 CO_2, N_2O, and Light

In Chapter 4, I describe a positive correlation between CO_2 and N_2O fluxes in the Arctic polar deserts I studied, but a negative correlation in the wetland soil at Alexandra Fjord lowland and no correlation at all in the mesic tundras in the lowland, based on data collected in 2009 and partly described in Chapter 3; I arranged the vegetation communities I studied along an axis of decreasing average soil water content to emphasize the hypothesized driver of this pattern. Wetlands are among the most anaerobic environments I studied, and the N_2O net consumption observed there is likely the result of strong activity by NOS overpowering assumed high production of N_2O through nitrification or the earlier stages of denitrification. Under anaerobic conditions, total respiration is likely to be lower than nearby areas with more oxygen availability, and thus CO_2 production will be reduced. However, in the polar deserts a different relationship probably dominates: increased production of N_2O associated with regions in the soil of increased organic matter availability that drives higher respiration. High organic matter availability might be expected to increase CH_4 production as well, especially in the anaerobic conditions at the wetland, but no correlation with CH_4 and either CO_2 or N_2O was observed.

I contributed to a paper published in 2012 (Stewart et al., 2012) that describes the shift from source to sink of N_2O under varying light conditions in the polar deserts studied in Chapter 4 and Chapter 5. The net production of CO_2 shifts from source under dark conditions in which respiration dominates to sink under light conditions sufficient to drive photosynthesis; the net production of N_2O follows the same pattern but cannot be explained by photosynthesis. Soil

moisture and other factors play roles in regulating N_2O consumption but I do not understand the mechanisms or drivers of this unexpected pattern (Stewart et al., 2012).

6.2.3 Measuring Gases in Freezing Soil

Soils of the cold-temperate regions, alpine areas around the world, and the polar regions are subject to seasonal freezing as temperatures lower than 0°C lead to the formation of ice within soil. From a biological perspective, ice is not water; it does not dissolve and transport nutrients or waste, and it does not flow into and out of cells in response to concentration gradients. In non-permafrost soils, ice forms near the surface of the soil first and deeper soils may not experience freezing temperatures due to the thermal insulation of soil. In permafrost soils, however, ice may form both at the bottom of the active layer and at the soil surface in autumn as air and soil temperatures decline. Ice formation drives water movement, as liquid water freezes around growing ice crystals and releases latent heat that facilitates further water movement; the expansion of ice compared to the volume of liquid water pushes on the mineral component of soil and leads to cryoturbation and other soil-movement processes.

The effects of these freezing processes on the production and movement of gases such as GHGs in soil is difficult to study. Besides the challenges of working in remote Arctic areas with continuous permafrost, most techniques for measuring changes in soil moisture cannot account for the phase change of ice formation, and assume instead that decreasing water contents are the result of a net movement of water out of the soil, such as by deeper infiltration or evaporation and gaseous diffusion, rather than the smaller movements of freezing. Large ice pieces, such as the wedges that form in some wet Arctic soils may be directly observed, but the centimetre-scale (and smaller) ice that forms in the dry polar deserts is more cryptic. Small ice crystals distributed through the soil are subject to local freeze/thaw cycles and may act as a source or sink for liquid water during winter. Furthermore, the ice/water mixtures within soil will alter patterns of movement by diffusion in ways that are beyond the scope of the physical models I have used to estimate net diffusivity of soil.

6.3 Future Research Directions

The trajectory of this dissertation, from patterns through processes to causes of soil GHG emissions, can be continued in several ways. Further study of the interactions between different

GHG may illuminate further the links between the global carbon and nitrogen cycles. Deeper understanding of the microbial ecology of soils will contribute to the study of such links as well as the roles of different microbial groups and their responses to both biotic and abiotic factors. The Arctic remains largely unknown, with the deserts particularly enigmatic regarding their ecology and contributions to global processes.

6.3.1 Gas-Gas Interactions

While the only microbial metabolic pathway that directly links two of the three GHG studied in this dissertation is the production of CH_4 by reduction of CO_2 with H_2 in some methanogens (Conrad, 2005), there are correlations between all three GHG in the Arctic polar deserts. The positive correlation between CO_2 and N_2O, for example, suggests a relationship between nitrification, denitrification, and respiration in well-aerated, cold, dry soils with limited organic matter content. Ammonia-oxidizing bacteria and archaea are typically described as autotrophs (Bergmann et al., 2005), but their activity may increase CO_2 production directly if at least some nitrifiers are heterotrophic or mixotrophic, or indirectly if their activity promotes the activity of nearby heterotrophic organisms. Alternatively, heterotrophic denitrifiers may dominate that N-reduction pathway in Arctic desert soils, and increase both the production of N_2O and respiration in microhabitats enriched in organic matter, particularly if oxidation of organic matter leads to the release of either NO_3^- or NH_3.

The co-consumption of CH_4 and N_2O described above is one of six combinations of net production of these two GHG observed in the Arctic deserts; at the level of measurement I employed, in which it is impossible to distinguish between sinks and sources of each gas based on concentration gradients alone, the net production of CH_4 appears to be independent of that of N_2O across the desert landscape. Each gas may be produced, consumed, or not be significantly different from no production at a particular soil layer, and indeed the combination of a source of N_2O found in conjunction with a sink for CH_4 is consistent with expectations for aerobic, low-organic-matter soils and was often found in both 2009 (Chapter 3) and 2010 (Chapter 4).

There are numerous links between the carbon and nitrogen cycles globally, but it is not yet apparent how these two critical cycles interact in the Arctic deserts. Water and light further interact with the microbial communities and metabolic processes thriving in these harsh ecosystems.

6.3.2 Microbial Ecology

The scale of investigation throughout my dissertation ranged from centimetres to metres, with a comparison between sites separated by a few hundred kilometres. Soil microbes exist in a world of micrometres and smaller, in a three-dimensional complex matrix of minerals, organic matter, water and gas carrying a wide range of dissolved compounds, and other organisms. The ecology of these systems is not well understood in any natural soil system, and most bacteria and archaea have never been isolated, cultured, or described as species (Rappé and Giovannoni, 2003).

The GHG studied here are the products or substrates of microbial enzymes, and as such measuring their concentrations and fluxes provides insight into the characteristics of those enzymes and the microorganisms that create and use them. Functional microbial ecology relies on measurements of enzymes and their substrates and products to investigate the characteristics and interactions of microorganisms, partly in an effort to sidestep issues of species identity or food-web position that dominate the ecology of larger organisms. While it is difficult or impossible to directly observe soil microorganisms *in situ* in natural systems, I can gather clues to their activities, requirements, physiologies, and community interactions through measurement of their enzymes.

Climate and soil conditions in the Arctic are broadly similar to those in the Antarctic and in alpine areas around the world, with low temperatures for much of the year and a large fraction of precipitation falling as snow and then variously accumulating or blowing away under the influence of strong winds before it melts and can be used as liquid water by organisms. Permafrost underlies the Antarctic and many alpine soils, and the extreme conditions severely limit plant growth and diversity such that most of the ice-free Antarctic and some alpine areas are cold deserts. However, despite the broad similarities, there are important differences between Arctic, Antarctic, and cold alpine deserts. The Arctic polar deserts include at least 37 species of vascular plants even at the extreme northern edge of Ellesmere Island and Greenland (Vincent et al., 2011), but Antarctica is home to only two species of vascular plants, neither of which occurs south of the Antarctic Peninsula, while tropical alpine areas may be home to a much higher diversity of arid-adapted and cold-tolerant plant species. Future studies of Arctic soils, vegetation communities, and microbial activities will benefit from comparison with studies of alpine and Antarctic regions, but major differences should be expected across such widely-distributed areas.

6.3.3 The Changing Arctic

The polar regions are currently experiencing climate change that is faster and of greater magnitude than other parts of the planet. Much of the Arctic includes features that sit on the edge of drastic changes, such as glaciers and permanent snowfields that melt more each summer than they accumulate each winter; many smaller snowfields have disappeared, with large implications for the soils and vegetation communities that developed in their downstream melt areas. While most of these are small in area, covering only a few hectares, in aggregate they represent the reduction or loss of an important Arctic community of organisms. The unique features of Arctic polar deserts may be lost as vegetation and soil microbial communities shift and change under warming Arctic. The next few years or decades may be the last opportunity to observe and study these communities and ecosystems.

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APPENDICES

APPENDIX 1

Error Propagation

Error propagation allows estimates of random error associated with measurements to be carried through equations to provide estimates of random error for calculated variables as are commonly encountered in Soil Science. The general form of the error propagation calculation is in Equation A1.1:

$$R = f(X_1, X_2 \ldots X_i) \qquad R_{error} = \left(\sum_{i=1}^{J} {X_{error}}^2\right)^{1/2} \tag{A1.1}$$

where R is a function of measured or calculated variables X_1 to X_i. The error of R is the square root of the sum of squares of errors of variables X_1 to X_i; this is known as the root sum of squares method of error propagation (Figliola and Beasley, 2006). In this case, the error of Production is a function of the measured gas concentration, measured depth, and calculated effective diffusivity, which is itself a function of measured water-filled and total porosity (Equation A1.2); air-filled porosity is the difference between total and water-filled porosity.

$$D_e = \frac{\frac{\Theta_w^{10/3}}{H} D_{fw} + \Theta_g^{10/3} D_{fg}}{\Theta_T^2} \tag{A1.2}$$

The measurement errors are most commonly expressed as standard deviation. To propagate these errors, the range of possible values is carried through the calculation, one variable at a time, and the effect of these errors assessed on the value of the calculated variable. For example, calculation of effective diffusivity, D_e (Equation A1.2), is a function of total porosity (Θ_T), water-filled and gas filled porosity (Θ_w, Θ_g, respectively), and the constants H, D_{fw}, and D_{fg} (Henry's constant, diffusivity in free water, diffusivity in free gas, respectively).

First, estimate the measurement error of each measured variable; in this case, my measurements of porosity have 10% random error. Second, the value of D_e is calculated using the measured values of Θ. This is the operating point. Third, the value of D_e is calculated using the highest value of Θ, or Θ + 10%, and with the lowest value of Θ. The range of D_e

proportionate to the operating point value of D_e (i.e., (D_e + error – D_e – error)/D_e) is the propagated error for D_e, in this case approximately 22%.

This process is repeated for calculation of production (Equation A1.3):

$$P_{GHG} = D_{e_i}\left[\frac{C_i - C_{i-1}}{\Delta z}\right] - D_{e_{i+1}}\left[\frac{C_{i+1} - C_i}{\Delta z}\right] \quad \text{(A1.3)}$$

Because production is a function of both diffusivity and gas concentrations, each with their associated random error, the effect of both errors must be assessed; errors of measurement of depth will lead to categorical errors in bin assignment for a small fraction of the measurements of other variables and are ignored under the assumption the average effect of such bin mis-assignments is negligible. The error of D_e is propagated, holding gas concentrations at their measured values. Then the error of gas concentration measurements, ranging from approximately 2.5 to 33% depending on the gas and the vegetation community (Brummell and Siciliano, 2011), is propagated while holding D_e constant at its calculated value. Finally, the propagated error of production is calculated by Equation A1.1, using the propagated errors of D_e and gas concentration, their effect on the value of production, as the values of $Xerror_i$.

Appendix 1 References

Brummell, M.E. and S.D. Siciliano. 2011. Measurement of carbon dioxide, methane, nitrous oxide, and water potential in soil ecosystems. Methods Enzymol. 486: 115-137.

Figliola, R.S. and D.E. Beasley. 2006. Theory and design for mechanical measurements. 4th ed. John Wiley and Sons Hoboken, NJ, USA.

APPENDIX 2

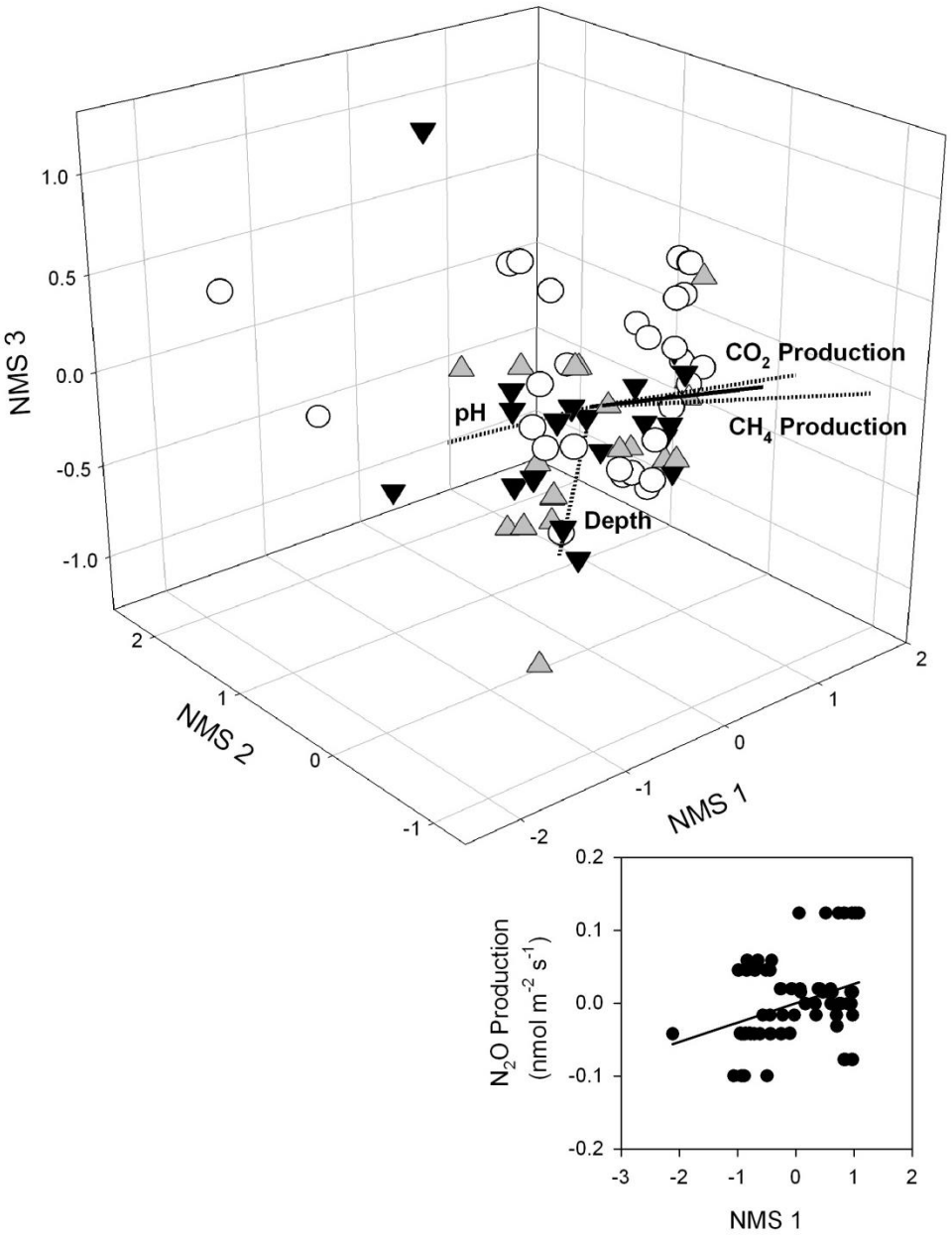

Fig A2.1. Ordination of PLFA data by NMS did not show any significant relationships with net GHG production.

APPENDIX 3

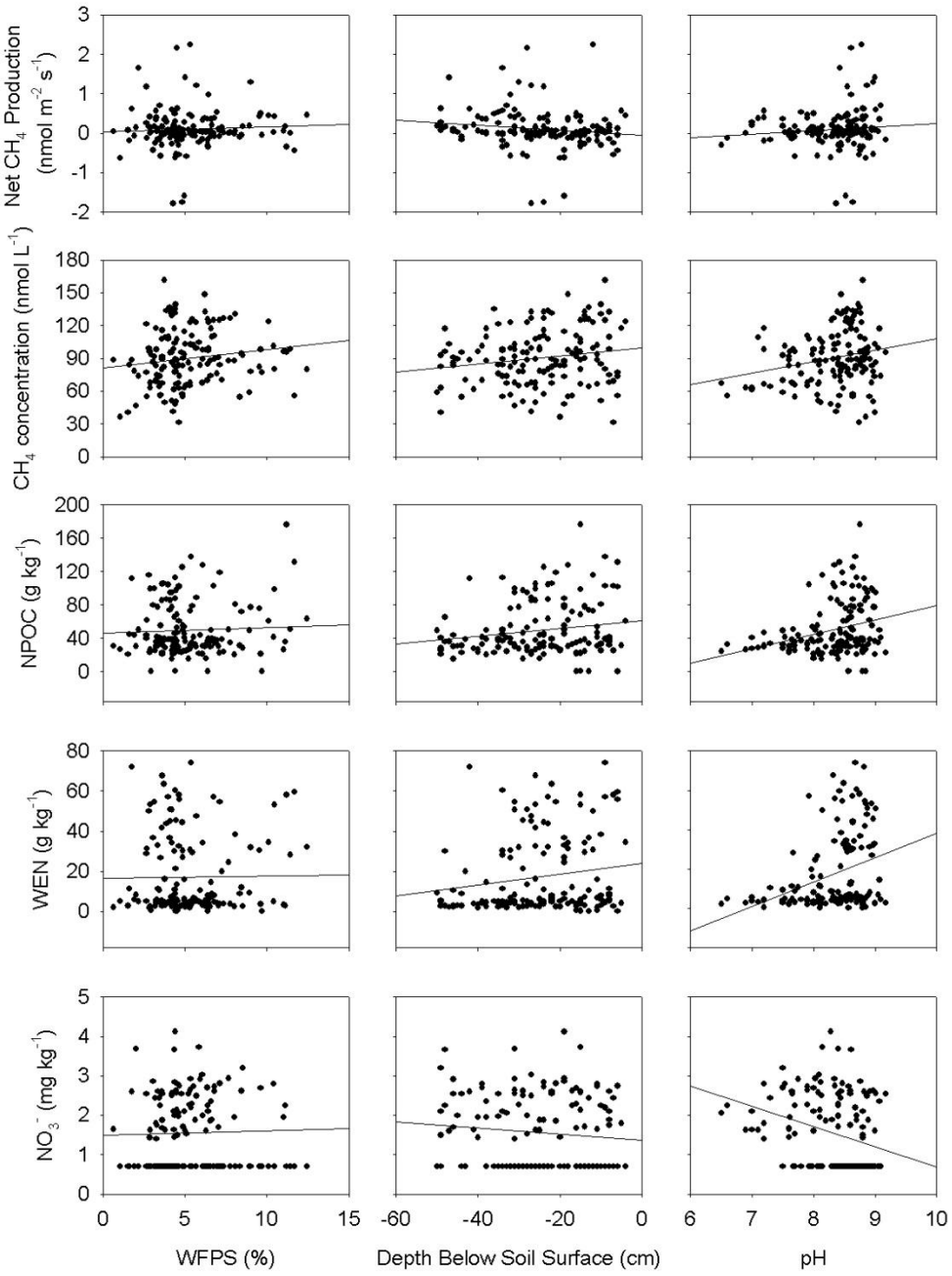

Fig. A3.1. Bivariate plots for relationships between observed variables evaluated during construction of the MOB structural equation model. The trend lines ($p < 0.05$) were plotted using univariate linear regression. WFPS: Water-filled pore space; NPOC: non-purgeable organic carbon; WEN: water-extractable nitrogen; NO_3^-: total nitrate plus nitrite.

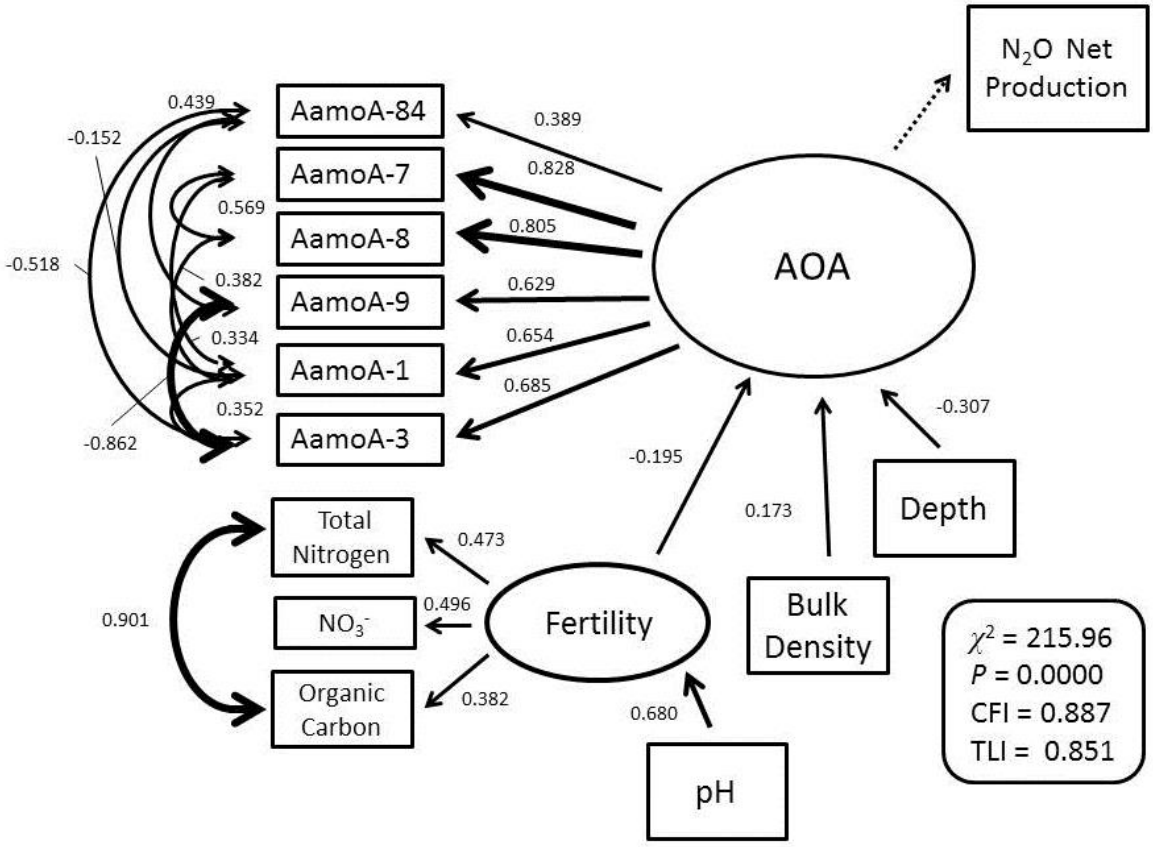

Fig. A3.2. Probe richness for AOA was not significantly associated with net N2O production in any structural equation model. This model has an unacceptable χ2 value and CFI and TLI values, but is shown here for illustration.

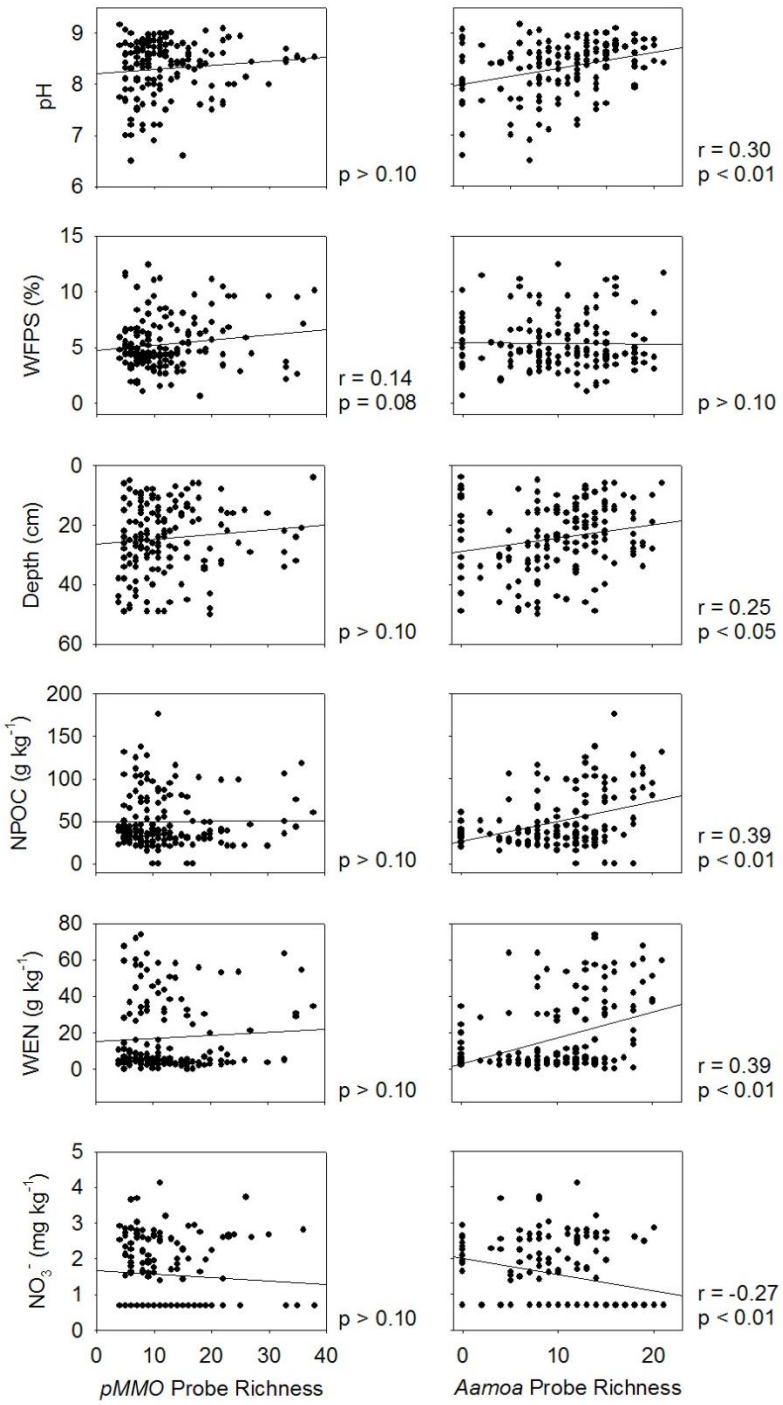

Fig. A3.3. Probe richness for MOB was not significantly correlated with any measured soil variable. Probe richness for AOA was significantly ($p < 0.05$) correlated with pH, Depth below soil surface ("Depth"), non-purgeable organic carbon ("NPOC"), water-extractable nitrogen ("WEN"), and total nitrate plus nitrite ("NO_3^-").

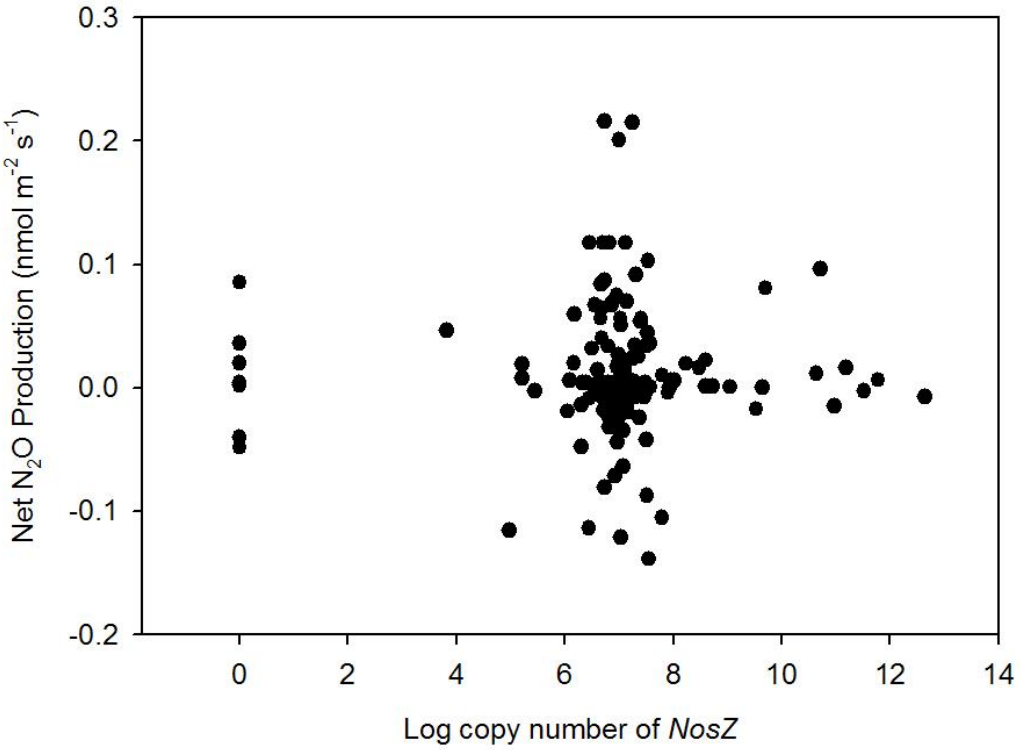

Fig. A3.4. NosZ copy-number abundance as determined by qPCR was not significantly correlated with net N_2O production.