High spatial resolution remote sensing models for landscape-scale CO₂ exchange in the Canadian Arctic

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ABSTRACT
Climate warming is affecting terrestrial ecosystems in the Canadian Arctic, potentially altering the carbon balance of the landscape and contributing additional CO₂ to the atmosphere. High spatial resolution remote sensing data can enhance models of net ecosystem exchange (NEE) and its component fluxes, gross ecosystem exchange (GEE), and ecosystem respiration (ER) by quantifying vegetation structure and function over time. In this study, we explored the variability of daytime CO₂ exchange rates for three vegetation types along a natural moisture gradient at ecologically distinct mid- and high Arctic sites. We demonstrated that for the two sites studied, there was no statistically significant variation in CO₂ exchange rates for the vegetation types through the peak growing season. Hence, the capacity to model these rates with a limited number of satellite data acquisitions is feasible. Simple bivariate models relating the Normalized Difference Vegetation Index (NDVI) to CO₂ exchange processes (GEE, ER, and NEE) were developed independent of vegetation type and geographic location and validated using independent data. The spectral models explain between 33 and 94 percent of the variation in CO₂ exchange rates at each site, indicating a high level of functional convergence in ecosystem-level structure and function within Arctic landscapes.

Introduction
The Arctic provides a crucial moderating effect on global climate, yet the extent of the impact of high-latitude warming on Arctic and global ecosystems is still uncertain (Arctic Monitoring and Assessment Program 2017). Over the past millennium, the Arctic has been a net sink for carbon dioxide (CO₂) as a function of photosynthetic uptake exceeding ecosystem respiration. With the northern circumpolar permafrost region accounting for more than half of the global soil carbon pool in the upper three meters (Hugelius et al. 2014; Strauss et al. 2017), the nature of CO₂ exchange through the balance of photosynthesis (gross ecosystem exchange, GEE) and plant (autotrophic) and soil (heterotrophic) respiration (ecosystem respiration, ER) may be altered with a changing climate. There may be a shift in Arctic net ecosystem CO₂ exchange (NEE) from a carbon sink to a carbon source, thereby creating a positive feedback mechanism and further enhancing climate warming (Oechel et al. 1993; Shaver et al. 2007; Dagg and Lafleur 2011; Lafleur et al. 2012; Arctic Monitoring and Assessment Program 2017).

Different factors influence the patterns and processes of Arctic ecosystems at different scales. At the regional scale, climate, topography, parent material, and time govern the distribution of ecosystems and their biophysical processes (Chapin, Matson, and Mooney 2002). At the landscape scale, vegetation types exhibit extreme patchiness due to the primary controls of macro- and micro-topography on local soil hydrological regimes (Bliss and Matveyeva 1992; Walker 2000; Shaver et al. 2007; Nobrega and Grogan 2008; Spadavecchia et al. 2008). It has long been understood that vegetation is both an integrator and indicator of climate and ecosystem function (Braun-Blanquet 1965). However, the spatial heterogeneity within the landscape can complicate the assessment of landscape-level carbon fluxes and how they may be altered in the future (Shaver et al. 2007). It has been demonstrated that GEE and ER vary in relation to patterns of vegetation (Nobrega and Grogan 2008; Emmerton et al. 2016). This variance is a result of many...
factors, including vegetation type, soil organic matter, soil moisture, nutrient availability, macro- and microtopography, temperature, thaw depth, and natural disturbances (Chapin, Matson, and Mooney 2002; Shaver et al. 2007; Dagg and Lafleur 2011). With an overall warming of the climate in the Arctic (Bintanja 2018) coupled with large pools of soil carbon (C), it is essential to quantify CO₂ exchange at regional and landscape scales (Shaver et al. 2007) to determine ecosystem responses across scales.

Spectral vegetation indices, specifically the Normalized Difference Vegetation Index (NDVI), can be used to quantify and monitor vegetation patterns that in turn can be used to predict patterns of CO₂ flux (Ostendorf and Reynolds 1998; Goetz and Prince 1999; McMichael et al. 1999; Boelman et al. 2003; Shaver et al. 2007; Huemmrich et al. 2010). Arctic field studies have applied the NDVI (derived from ground-based spectrometers) at the plot level to determine the relationships between ecosystem biophysical properties and CO₂ exchange (McMichael et al. 1999; Boelman et al. 2003; Shaver et al. 2007; Huemmrich et al. 2010). At the regional scale, the application of satellite remote sensing data such as the Advanced Very High Resolution Radiometer and Moderate Resolution Imaging Spectroradiometer have been sources of high temporal frequency NDVI data, albeit at coarse spatial resolutions (Oechel et al. 2000; Markon and Peterson 2002; Walker et al. 2002; Kimball et al. 2007; Sitch et al. 2007; Emmerton et al. 2016). However, biophysical remote sensing applications of high spatial resolution satellite data have been limited at the landscape scale in the Arctic (Laidler, Treitz, and Atkinson 2008; Fuchs et al. 2009; Atkinson and Treitz 2012) and have only been applied to a few studies for modeling CO₂ fluxes (Vourlitis et al. 2000; Williams et al. 2000; Lafont et al. 2002; Ueyama et al. 2013). In the Canadian Arctic, observations of CO₂ exchange have only been conducted relatively recently at a few sites (Lafleur and Humphreys 2008; Nobrega and Grogan 2008; Dagg and Lafleur 2011; Lafleur et al. 2012; Emmerton et al. 2016; Virkala et al. 2018). Shaver et al. (2007) reported that the NEE of low Arctic ecosystems may be predicted with acceptable accuracy (~80 percent of the variance) without identifying species or delineating vegetation types; for example, by simply using a multivariate approach with NDVI-derived leaf area index (LAI) and in situ measures of photosynthetically active radiation (PAR) and air temperature. Their results support a strong functional convergence with vegetation type (Field et al. 1998; Goetz and Prince 1999). It has been demonstrated that CO₂ flux varies significantly across soil moisture regimes, as well as seasonally (Nobrega and Grogan 2008; Dagg and Lafleur 2011; Emmerton et al. 2016).

Though satellite imagery allows for the study of large areas overtime, a major challenge with high spatial resolution satellite imagery can often be the timely acquisition of frequent images, particularly in the high Arctic. A short growing season coupled with summer cloud cover can render the acquisition of satellite data difficult and multiple intraseason images a rarity, particularly at peak growing season. Given these challenges, high spatial resolution satellite data may be limited to a single acquisition date for modeling the spatial variability of carbon exchange rates at landscape scales. Broader applicability for modeling carbon fluxes with high spatial resolution imagery could be achieved if intraseasonal data can be acquired or, alternately, if peak growing season fluxes have minimal temporal variability, allowing a single image to represent a larger portion of the growing season.

This research examines the temporal and spatial variability of GEE, ER, and NEE across three vegetation types distributed along a moisture gradient at two study sites (e.g., mid- and high Arctic sites spanning five degrees of latitude) in order to determine the applicability of high spatial resolution satellite data for modeling peak growing season CO₂ fluxes. The following research questions are addressed: (1) Do rates of GEE, ER, and NEE differ within and between vegetation types through the peak summer season at two independent geographic locations? (2) Is functional convergence demonstrated between vegetation types through their CO₂ exchange rates, and is this variation represented through differences in NDVI? and (3) Can high spatial resolution NDVI data be used to successfully model GEE, ER, and NEE at the landscape scale for two independent locations? The following specific hypotheses are tested to address the above questions:

Hypothesis 1: The rates of daytime CO₂ exchange (GEE, ER, and NEE) within dry, mesic, and wet vegetation types do not differ through the growing season.

Hypothesis 2: Daytime CO₂ exchange rates (GEE, ER, and NEE) between vegetation types are strongly correlated with NDVI.

Hypothesis 3: NDVI data alone can be used to model landscape-scale CO₂ exchange rates (GEE, ER, and NEE) at two independent study sites in the mid- and high Arctic.

Study site and methods
Study sites
In order to address these research questions across a latitudinal gradient, two study sites representative of the mid- and high Arctic were selected. The high Arctic
site is located on the south-central coast of Melville Island (74°55′ N, 109°35′ W) at the Cape Bounty Arctic Watershed Observatory (CBAWO; Figure 1a). CO₂ fluxes were measured initially in July 2006, with validation data collected in July 2008. Maximum active layer depth varies from 0.5 to 1 m across the study area. The mean daily July temperatures for the CBAWO in 2006 and 2008 were 6.2°C and 7.6°C, respectively; the long-term July temperature average since the start of monitoring at the CBAWO is 5.3°C (i.e., 2003–2018). Rainfall in 2006 was infrequent and of low intensity, with a total rainfall of 4.8 mm recorded for July 2006. The July 2008 season saw a total rainfall of 27.4 mm, approximately five times the average of the preceding four years. The long-term July climatic averages from 1986 to 2005 for temperature and rainfall at the closest meteorological station in Mold Bay are 3.83°C and 12.23 mm (Environment Canada 2019). Low stratus cloud and fog are common during the summer months, often hindering satellite image acquisition. Walker et al. (2005) characterize the CBAWO as being within Bioclimatic Zone B, which is dominated by low-lying dwarf shrubs and a mean July temperature of 3°C to 5°C (Walker et al. 2002). The vegetation classification for the area is P1: prostrate dwarf shrub, herb tundra (Walker et al. 2005).

Vegetation types

At each study site, three tundra vegetation types were identified along a summer season soil moisture gradient (dry, mesic, and wet) with replicate plots established for each type. These vegetation types were characterized by Atkinson and Treitz (2012), where species composition, percentage vegetation cover (PVC), aboveground biomass, and gravimetric soil moisture (GSM) were quantified at peak growing season. The Circumpolar Arctic Vegetation Map (Walker et al. 2005) was applied to describe the vegetation classifications for the CBAWO and SL (Table 1). The dry vegetation types (dry tundra, DT) at the CBAWO and SL are most closely related to P1: prostrate dwarf shrub and herb tundra (Walker et al. 2005). At the CBAWO and SL, microscale topographic features (e.g., frost cracks) create moisture gradients that influence the pattern and distribution of vegetation. Plant growth is limited to these frost cracks and depressions where wind speeds are reduced, thereby decreasing rates of evaporation and facilitating the accumulation of plant detritus (organic matter), which increases soil water-holding capacity and nutrient availability (Oberbauer and Dawson 1992). Though they are similar, the DT at each site is distinct. Although the predominant exposed surface material for DT at the CBAWO and SL is glacial till (~60 percent), the secondary cover types vary (CBAWO, bryophytes [18.5 percent]; SL, Dryas spp.)
Table 1. Classification summary for dry, mesic, and wet vegetation types at the Cape Bounty Arctic Watershed Observatory (CBAWO) and Sanagak Lake (SL).

| Ecosystem | CBAWO | SL |
|-----------|-------|----|
|           | Dry P. radicatum and till tundra | Mesic Nostoc spp. and till tundra | Wet sedge tundra | Dry Dryas spp. and till tundra | Mesic Dryas spp. and till tundra | Wet sedge tundra |
| Soil moisture (%) | 17.1 | 37.3 | 123.9 | 17.2 | 41.2 | 123.3 |
| Percent vegetation cover (%) | 50.2 | 101.7 | 154.0 | 30.4 | 80.4 | 144.8 |
| Bryophyte cover (%) | 11.6 | 57.7 | 88.0 | 8.8 | 1.3 | 59.7 |
| Graminoid cover (%) | 0.0 | 21.8 | 71.4 | 0.5 | 16.8 | 38.1 |
| Shrub cover (%) | 4.3 | 0.0 | 2.9 | 25.0 | 57.9 | 32.1 |
| Lichen cover (%) | 11.4 | 9.0 | 1.6 | 1.0 | 1.1 | 1.4 |
| Forb cover (%) | 0.7 | 4.1 | 0.8 | 0.3 | 1.2 | 0.0 |
| Biomass (g m⁻²) | 348.5 | 1,477.3 | 1,561.6 | 298.2 | 521.7 | 825.6 |
| Cover (%) | 26.9 | 89.9 | 141.0 | 41.0 | 87.0 | 131.3 |
| Primary cover | Till | Nostoc spp. comm., mosses | Sphagnum spp. | Till | Dryas spp. | Sphagnum spp. |
| Secondary cover | Mosses | Mosses | Eriophorum spp. | Dryas spp. | Carex spp. | Eriophorum spp. |
| Indicator species | P. radicatum | Nostoc spp. comm. | Eriophorum spp. | n/a | Dryas spp. | Eriophorum spp. |
| Bioclimatic class (Walker et al. 2005) | P1 | G1 | W1 | P1 | G2 | W1 |

Notes. P1 – prostrate dwarf shrub and herb tundra; G1 – rush/grass, forb, cryptogam tundra; G2 – graminoid, prostrate dwarf shrub, forb tundra; W1 – sedge/grass, moss wetland.

[18.4 percent), and the overall PVC for each DT is 25.4 and 30.4 percent, respectively. The CBAWO is distinct in that Papaver radicatum is a major species in the DT. The CBAWO dry sites are referred to as dry P. radicatum and till tundra, whereas SL sites are referred to as dry Dryas spp. and till tundra (Atkinson and Treitz 2012). The mesic tundra (MT) sites at the CBAWO and SL—for example, mesic Nostoc tundra (G1, rush/grass, forb, cryptogam tundra) and mesic Dryas spp. tundra (G2, graminoid, prostrate dwarf shrub, forb tundra), respectively—are similar in terms of total PVC (101.7 and 80.4 percent). However, the primary cover at the CBAWO is Nostoc commune (48.6 percent), a nitrogen-fixing cyanobacteria that forms a black crust on the soil (Liengen and Olsen 1997), typically found in association with bryophyte species and Salix arctica. In contrast, Dryas spp. is found in the majority of SL sites in varying percentages but rarely at the CBAWO. Dryas spp. (46.0 percent) and Carex spp. (10.6 percent) were the primary and secondary cover types of the SL MT sites, along with extensive Saxifraga oppositifolia. The wet vegetation types (wet tundra, WT) at the CBAWO and SL were extremely similar in species composition and PVC. At the CBAWO and SL, WT sites (most closely related to W1: sedge/grass, moss wetland) are often located in areas exhibiting high levels of soil moisture throughout the growing season, often due to the proximity of large upslope snow banks. The total PVC for these sites was 154 percent, due to the layering of vegetation, with Sphagnum spp. (69.3 percent) and Eriophorum spp. (47.5 percent) comprising the main cover types. Dryas spp. was present in some SL WT sites. Replicate vegetation plots (100 m × 100 m) were selected for each vegetation type at both sites (CBAWO [n = 7]: two DT, two MT, three WT; SL [n = 5]: one DT, two MT, two WT).

Environmental measurements

Soil temperature, GSM, air pressure, air temperature, and precipitation were all measured during the sampling period. Soil temperatures were recorded (using the Thermor stem thermometer model PS100, Themor Limited, Newmarket, Ontario, Canada) at 5 and 10 cm depths in the soil/organic layer simultaneously with each CO₂ exchange measurement at three random positions adjacent to each chamber. GSM was determined on each measurement day by collecting three 5-cm-depth, 5.3-cm-diameter soil cores. These samples were weighed wet in the field and returned to the lab for oven drying at approximately 110°C for 48 hours; GSM was determined as the mass of water expressed on a volumetric basis. Air pressure was measured during each CO₂ measurement cycle with a handheld Kestrel weather meter (Kestrel Meters, Sylvan Lake, Michigan).

CO₂ exchange measurements

Static chambers (~35 cm height, 285 cm² area, ~8.7 L) equipped with a Vaisala GMP343 infrared gas analyzer (Vaisala, Vantaa, Finland) were used to make CO₂ exchange measurements. The chamber was also instrumented with a Vaisala HMP75 temperature and relative humidity sensor (Vaisala) to adjust for relative humidity variation in real time. Temperature corrections were done manually using the ideal gas law during postprocessing (Equation (1)). The chamber was also fitted
with a pressure equalization vent and a small circulation fan (Hutchinson and Mosier 1981). The chamber was allowed to achieve equilibrium with ambient CO$_2$ and temperature prior to any measurement. CO$_2$ concentrations, temperature ($T$), and relative humidity (RH) were logged as the average value for each sensor every 5 seconds for a 5-minute period. NEE measurements were derived from measurements using the transparent chamber. After NEE measurements were completed, the chamber was removed, allowed to return to ambient conditions, fitted to the collar, and covered with an opaque hood to collect “dark” readings (ER).

A PVC collar (inner diameter 19.9 cm, height ~15 cm) was inserted at the center of each plot at a minimum of 24 hours prior to the initial sampling, but in most cases this period was 24 to 72 hours before sampling and conforms with other studies of arctic gas exchange (Stewart et al. 2013). The collars were then left in place and revisited during the growing season. The collars were inserted after cutting rings into the soil and vegetation; all attempts were made not to damage vegetation or root systems within the collar. Approximately 4 cm of the collar remained above the surface and was fitted with a rubber gasket to create an airtight seal between the collar and the flux chamber. In dry plots, where there was extensive exposed soil, two collars were inserted: one in bare soil and one within a vegetated area. CO$_2$ exchange measurements at the CBAWO began on 5 July 2006 and continued until 30 July 2006, resulting in six to seven sampling cycles per plot. At SL, measurements were collected from 18 July 2006 to 3 August 2006, resulting in four to five sampling cycles per plot. Each plot was sampled systematically every two to three days. Sampling began at 8 a.m. and was repeated every four hours (8 a.m., 12 p.m., 4 p.m., 8 p.m.) for a 12-hour cycle, resulting in four measurements per plot per sample day.

**CO$_2$ flux calculations**

CO$_2$ flux rates were calculated using a custom Matlab script (Matlab 2012). All CO$_2$ concentrations were converted from CO$_2$ concentration (ppm) to micromoles of CO$_2$ per square meter using the ideal gas law after Shaver et al. (2007):

\[ n = C \left( \frac{\rho}{RT} \right) \left( \frac{V}{A} \right) / 5 \]  

(1)

where $n$ is the converted concentration (µmol m$^{-2}$), $C$ is the concentration of CO$_2$ (ppm), $\rho$ is air pressure (hPa), $R$ is the ideal gas constant (0.08314 hPa m$^3$ mol$^{-1}$ K$^{-1}$), $\tau$ is the temperature (K), $V$ is the volume of the chamber after insertion into the collar (m$^3$), and $A$ is the projected horizontal surface area of the chamber (m$^2$). Because of the possibility of sampling artifacts at the beginning and ending of each measurement cycle, the rate was calculated using an iterative multiple regression search algorithm, which searches for a linear set of readings that create the best possible coefficient of determination ($R^2$) for the longest time period (minimum 60 seconds) with the highest level of significance. The slope of this linear regression was then recorded as the flux rate (µmol CO$_2$ m$^{-2}$ s$^{-1}$) for each measurement. Finally, GEE was calculated as

\[ \text{GEE} = \text{NEE} - \text{ER} \]  

(2)

Hence, we adopt the sign convention that net CO$_2$ uptake to the vegetation type is negative, whereas net CO$_2$ flux to the atmosphere is positive (Dagg and Lafleur 2011).

**Satellite remote sensing data**

IKONOS multispectral data (4 m spatial resolution) were acquired for the CBAWO on 22 July 2004 and 2 August 2008 and for SL on 23 July 2001. The 2004 and 2001 images respectively for the CBAWO and SL were used for modeling CO$_2$ exchange, and the 2008 image of the CBAWO was used for model validation. The spectral characteristics of the three images are similar, with almost identical time of year, time of day, and solar angle. Though these images do not correspond with the field sampling year, it is assumed that they are representative of the peak growing season. Image bands (blue: 0.45–0.52 µm; green: 0.51–0.60 µm; red: 0.63–0.70 µm, and near-infrared [NIR]: 0.76–0.85 µm) were calibrated to top of atmosphere reflectance following procedures outlined by Taylor (2005). The images were geo-referenced with an overall root mean square error (RMSE) of less than 3 m horizontally. NDVI data were derived from the difference in reflectivity of the land cover in the NIR band, where vegetation structure reflects strongly, and the red (R) band, where vegetation absorbs strongly as a function of chlorophyll concentration. NDVI for each image pixel was calculated as follows:

\[ \text{NDVI} = (\text{NIR} - R) / (\text{NIR} + R) \]  

(3)

NDVI data were extracted from individual sample locations; for example, sample site NDVI data were interpreted from adjacent cells ($n = 8$) using bilinear interpolation, which minimizes the effects of misregistration errors (Fuchs et al. 2009).
Statistical analyses

Site and vegetation type differences
Collecting flux data four times per day provided a more robust daily average flux value compared to single measurements. We explored possible vegetation effects on diel fluctuations using two-way repeated measures analysis of variance (ANOVA) with vegetation type and time of day as between-subjects factors. The interaction between vegetation type and time of day was nonsignificant ($p = .893$), allowing us to compute a daily average flux for subsequent analyses. We used two-way repeated measures ANOVA to then examine differences among sites ($n = 2$) and vegetation type ($n = 3$) as well as seasonal variability using time (dates of measurements) as the within-subjects variable. Average values were tested for homogeneous variance (Levene’s) and normality (Shapiro-Wilk) and found to satisfy both assumptions in most cases ($p > .05$).

Regression modeling with environmental variables
Stepwise multiple linear regression was used at each site to test the importance of averaged environmental variables on mean 12-hour daytime CO$_2$ fluxes for each vegetation type. Simultaneous measures of air temperature, 5-cm and 10-cm depth soil temperatures, daily soil moisture, and PAR were examined. Significance of .10 was used for variable selection. Data were tested for normality using Shapiro-Wilk’s test ($n < 50$) and for homogeneous variance using Levene’s test. The data did not satisfy these assumptions; thus, values were transformed using a natural log transformation on scaled fluxes. Data were also tested for multicollinearity using variance inflation factor values.

Modeling CO$_2$ with NDVI
Linear bivariate regressions were generated with NDVI as the independent variable and the averaged seasonal CO$_2$ flux values as the dependent variable. Though NDVI would be considered a function of the biophysical variables, the reversal of the variables allows for the calculation of spatial models (Shippert et al. 1995; Laidler, Treitz, and Atkinson 2008). With regression equations derived for each flux component and for each study site, we used analysis of covariance (ANCOVA) to determine whether relationships between NDVI and the component fluxes differed significantly across sites. If no significant difference in the relationships between NDVI and the components fluxes is found—for example, the empirical models exhibit equal slopes ($H_0 : \beta_{1CB} = \beta_{1SL}$) and equal intercepts ($H_0 : \beta_{0CB} = \beta_{0SL}$)—the data can be pooled from each independent site to derive a single model ($Y = \beta_0 + \beta_1X + E$) to describe the relationship between NDVI and a component flux.

Model validation
Statistical model validation was based on data collected at the CBAWO during the 2008 summer season. CO$_2$ and environmental measurements were collected for six of the vegetation plots (two DT, two MT, and two WT) sampled in 2006 and an additional five vegetation plots not previously sampled (two DT, two MT, one WT) for a total of four DT, four MT, and three WT vegetation plots. CO$_2$ exchange measurements were made between 24 June and 4 August 2008. Each plot was sampled weekly during weeks 1, 2, 5, and 6 and biweekly during weeks 3 and 4. The only significant difference in the sampling methodology in 2008 from 2006 was that only peak daytime fluxes were measured in 2008, whereas 12-hour samples (every 4 hours) were collected in 2006. All data collection and processing of the 2008 data (CO$_2$ exchange measurements, environmental data collection and measurements, and image preprocessing) was performed in the same manner as for the 2006 data. All statistical analyses were conducted in SPSS Version 25.0 (IBM Corp 2017).

Results

CO$_2$ exchange
Based on results from the two-way repeated measures ANOVA, site had no significant effect on any of the CO$_2$ fluxes (Table 2). Across all sites, rates of ER were generally highest in the WT sites and lowest in the DT sites ($p < .1$; Table 2, Figure 2). Similarly, GEE was also generally highest in the WT and lowest in the DT sites. These patterns were consistent across both study sites (i.e., SL and the CBAWO); there were no significant Site × Vegetation type interactions (Table 2). Rates of ER were generally consistent over the different sample dates at both study

| Flux  | Site$_{(1,7)}$ | Veg$_{(2,7)}$ | Site × Veg$_{(2,7)}$ | Time$_{(2,21)}$ | Time × Site$_{(3,21)}$ | Time × Veg$_{(6,21)}$ |
|-------|---------------|---------------|---------------------|-----------------|-------------------|-------------------|
| GEE   | 0.65          | 0.004         | 0.32                | 0.06            | 0.22              | 0.89              |
| ER    | 0.89          | 0.097         | 0.63                | 0.22            | 0.02              | 0.73              |
| NEE   | 0.86          | 0.078         | 0.36                | 0.27            | 0.77              | 0.50              |

Table 2. $p$ Value results from two-way repeated measures analysis of variance (ANOVA) testing the effect of site (Cape Bounty Arctic Watershed Observatory versus Sanagak Lake), vegetation type (dry tundra versus mesic tundra versus wet tundra), and time on gross ecosystem exchange (GEE), ecosystem respiration (ER), and net ecosystem exchange (NEE). Numbers within the brackets signify degrees of freedom between and within groups respectively.
sites (Table 2; Figure 2), but they did exhibit different ($p = .02$) patterns in ER over time (Figure 2). GEE varied significantly over time (Table 2, Figure 2), showing strong seasonal patterns at the CBAWO compared to SL (Figure 2).

Given the small overall time differences, we compared vegetation types and study sites using linear interpolation of each vegetation type flux rate to get one representative flux for the entire growing season (Figure 3). ER rates at SL and the CBAWO were similar in each of their comparable vegetation types. The WT had the highest GEE, and it was higher at the CBAWO compared to SL (Table 3, Figure 3). As a result, WT was the only vegetation type demonstrating net uptake (e.g., negative NEE) across the sampling period at the CBAWO. The MT at the CBAWO, though it was a modest source, had a somewhat lower GEE rate than MT at SL, where it was a modest sink. At both study sites, DT proved to be a source of CO$_2$ across the growing season even though GEE was stronger at the CBAWO than at SL.

**Regression modeling with environmental variables**

Daily average ecosystem carbon fluxes were generally poorly correlated with daily average environmental variables, generally explaining roughly 50 percent of the variability in each CO$_2$ flux (Table 4). Temperature (air or soil) was generally the most important predictor for the daily fluxes regardless of vegetation type and was a significant variable in most of the multiple regression models. Soil temperature predicted rates of ER significantly, explaining 60 to 70 percent of the variability in ER at both sites. Environmental variables were generally poor predictors of NEE (Table 4). It should be noted that some multiple regressions had a small sample size (e.g., SL-DT, where $n = 4$).

**Modeled CO$_2$ exchange using NDVI**

Bivariate linear regressions were derived to examine relationships between NDVI and average seasonal daytime GEE, ER, and NEE at the CBAWO ($n = 7$) and SL.
The ANCOVA results for each of the regression equations indicates that none of the slopes were significantly different between the two study sites ($p < .05$) and thus the fluxes vary with NDVI equally across the sites. Given that the regression equations for the CBAWO and SL are statistically similar, the data were combined into a single equation ($n = 12$) for each flux and applied to both sites (Figure 4, Table 5). NEE was the hardest to predict from NDVI alone, whereas NDVI explained over 70 percent of the variation in both GEE and ER (but not for all vegetation types (Table 5)).

**Model validation**

CO$_2$ flux measurements and NDVI values for 2008 ($n = 11$) were examined using the same methods of bivariate linear regression as discussed above and were

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**Table 3.** Averaged carbon dioxide (CO$_2$) flux rates for the duration of the study period (mmol CO$_2$ m$^{-2}$ s$^{-1}$) with standard error in parentheses (by vegetation type and geographic location).

| Vegetation type | CBAWO GEE | SL | CBAWO ER | SL | CBAWO NEE | SL |
|----------------|-----------|----|----------|----|-----------|----|
| DT             | $-0.58 \ (\pm 0.11)$ | $0.02 \ (\pm 0.14)$ | $0.03 \ (\pm 0.08)$ | $0.66 \ (\pm 0.14)$ | $0.74 \ (\pm 0.05)$ | $0.64 \ (\pm 0.09)$ |
| MT             | $-1.09 \ (\pm 0.13)$ | $-1.27 \ (\pm 0.13)$ | $0.15 \ (\pm 0.11)$ | $-0.24 \ (\pm 0.12)$ | $1.25 \ (\pm 0.08)$ | $1.04 \ (\pm 0.06)$ |
| WT             | $-2.15 \ (\pm 0.14)$ | $-1.51 \ (\pm 0.15)$ | $-0.87 \ (\pm 0.12)$ | $-0.21 \ (\pm 0.15)$ | $1.29 \ (\pm 0.09)$ | $1.31 \ (\pm 0.06)$ |

Notes. Dry tundra (DT), mesic tundra (MT), wet tundra (WT), gross ecosystem exchange (GEE), ecosystem respiration (ER), net ecosystem exchange (NEE), Cape Bounty Arctic Watershed Observatory (CBAWO), Sanagak Lake (SL).

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**Table 4.** Multiple linear regression analysis for plot-level daily averaged carbon dioxide (CO$_2$) exchange rates in relation to averaged environmental variables ($p < .05$).

| Site  | Flux Type | Predictor                          | Slope  | $R^2$ adjusted | RMSE  | F       | $p$ Value | df  |
|-------|-----------|------------------------------------|--------|----------------|-------|---------|-----------|-----|
| CBAWO | GEE       | DT Air temperature                  | 0.65   | 0.595          | 0.10  | 15.69   | .003      | 1, 9 |
|       | ER        | DT Air temperature                  | −0.45  | 0.542          | 0.08  | 12.81   | .006      | 1, 9 |
|       | NEE       | MT Soil moisture, air temperature   | 4.02   | 0.651          | 0.06  | 9.38    | .010      | 2, 7 |
|       |           | MT Photosynthetically active radiation (PAR) | 2.84 | 0.331 | 0.12 | 5.46 | .048 | 1, 8 |
|       |           | SL ER DT Soil temperature (10 cm)   | 0.24   | 0.996          | 0.00  | 729.49  | .001      | 1, 2 |
|       |           | MT Air temperature                  | 0.42   | 0.212          | 0.07  | 4.77    | .048      | 1, 13 |
|       |           | WT Soil temperature (10 cm)         | 0.42   | 0.676          | 0.04  | 19.77   | .002      | 1, 8 |
|       |           | NEE SL MT Soil temperature (10 cm)  | −1.23  | 0.259          | 0.09  | 5.890   | .030      | 1, 13 |

Notes. Dry tundra (DT), mesic tundra (MT), wet tundra (WT), gross ecosystem exchange (GEE), ecosystem respiration (ER), net ecosystem exchange (NEE), Cape Bounty Arctic Watershed Observatory (CBAWO), Sanagak Lake (SL)
all found to be significant \( (p < .01; \text{Table 5}) \). The regression equations for each flux rate were similar to the 2006 pooled data, though the \( R^2 \) values were lower. The lower \( R^2 \) values can be attributed to fewer samples with a greater variability (one at peak of day as opposed to four daily samples). ANCOVA was performed to test the similarity of the 2008 validation equations with the 2006 pooled data. Again, both equations showed parallelism (similar slopes) and similar intercepts, indicating that the 2008 validation equations are statistically similar to the 2006 pooled data.

The NDVI model for ER had the lowest percentage error (6.4 percent) of all of the \( \text{CO}_2 \) fluxes (Table 6). ER is a combination of autotrophic and heterotrophic respiration, and the ability for a spectrally based model to predict this flux illustrates the integration of various environmental variables within the NDVI signal. In a 1:1 comparison of actual versus NDVI predicted ER flux, WT tends to be overpredicted, whereas MT is underpredicted (Figure 5). The error estimates for the GEE model were moderate at 27.2 percent (Table 6). In a 1:1 comparison for the GEE regression model, the situation is reversed from ER, where MT was underpredicted and WT was slightly overpredicted (Figure 5). For the NEE model, which had the largest percentage error (57.6 percent; Table 6), we see that DT is an overpredicted source, WT is an overpredicted sink, and MT is highly variable (Figure 5).

**Table 5.** Bivariate linear regression \( (Y = \beta_0 + \beta_1X + E) \) and analysis of covariance (ANCOVA) results for carbon dioxide (\( \text{CO}_2 \)) exchange components gross ecosystem exchange (GEE), ecosystem respiration (ER), and net ecosystem exchange (NEE) with the normalized difference vegetation index (NDVI) for the Cape Bounty Arctic Watershed Observatory (CBAWO) and Sanagak Lake (SL).

| CO\(_2\) flux \((Y)\) | Site | Slope \((\beta_1)\) | Intercept \((\beta_0)\) | \( R^2 \) | RMSE | Slope \((p \text{ value})\) | Intercept \((p \text{ value})\) |
|---------------------|------|----------------------|-----------------------|----------|-------|-----------------------|-----------------------|
| GEE                 | CBAWO | −8.41                | 0.04                  | 0.64     | 0.23  | .695                  | .528                  |
| SL                  | −7.72 | 0.15                 | 0.72                  | 0.14     |       |                       |                       |
| Combined            | −8.15 | 0.10                 | 0.65                  | 0.48     |       |                       |                       |
| Validation          | −7.85 | 0.15                 | 0.48                  | 0.96     |       |                       |                       |
| Combined            | −8.05 | 0.13                 | 0.54                  | 0.70     |       |                       |                       |
| ER                  | CBAWO | 3.97                 | 0.58                  | 0.66     | 0.06  | .391                  | .199                  |
| SL                  | 4.07  | 0.38                 | 0.94                  | 0.02     |       |                       |                       |
| Combined            | 4.03  | 0.49                 | 0.70                  | 0.21     |       |                       |                       |
| Validation          | 3.81  | 0.43                 | 0.75                  | 0.26     |       | .847                  | .337                  |
| Combined            | 3.97  | 0.46                 | 0.73                  | 0.23     |       |                       |                       |
| NEE                 | CBAWO | −4.28                | 0.57                  | 0.33     | 0.14  | .485                  | .916                  |
| SL                  | −3.25 | 0.36                 | 0.48                  | 0.08     |       |                       |                       |
| Combined            | −3.87 | 0.48                 | 0.35                  | 0.42     |       |                       |                       |
| Validation          | −3.85 | 0.54                 | 0.26                  | 0.75     |       | .994                  | .815                  |
| Combined            | −3.91 | 0.51                 | 0.30                  | 0.57     |       |                       |                       |

**Figure 4.** Combined bivariate linear regressions for carbon dioxide (\( \text{CO}_2 \)) exchange rates: gross ecosystem exchange (GEE), ecosystem respiration (ER), and net ecosystem exchange (NEE).

**Table 6.** Normalized difference vegetation index (NDVI) model-based carbon dioxide (\( \text{CO}_2 \)) exchange rates for the Cape Bounty Arctic Watershed Observatory (CBAWO) and Sanagak Lake (SL).

| Site | Area \((\text{km}^2)\) | Flux \(\text{Mg CO}_2 \text{ day}^{-1}\) | SMAPE estimate \(\%\) |
|------|-----------------------|-------------------------------|---------------------|
| CBAWO| 80.74                 | GEE −141.16                   | 27.2                |
|      |                       | ER 244.77                     | 6.4                 |
|      |                       | NEE 64.19                     | 57.6                |
| SL   | 74.32                 | GEE −338.14                   | 27.2                |
|      |                       | ER 305.77                     | 6.4                 |
|      |                       | NEE −36.76                    | 57.6                |

**Notes.** Gross ecosystem exchange (GEE), ecosystem respiration (ER), net ecosystem exchange (NEE), Symmetric mean absolute percentage error (SMAPE).
Figure 5. One-to-one comparisons of actual calibration values and normalized difference vegetation index (NDVI) modeled values for gross ecosystem exchange (GEE), ecosystem respiration (ER), and net ecosystem exchange (NEE).

Figure 6. Spatially-explicit models of (a) gross ecosystem exchange (GEE) and (b) ecosystem respiration (ER) for the Cape Bounty Arctic Watershed Observatory (CBAWO) (left) and Sanagak Lake (SL) (right). White indicates no flux data.
reasoning for this may be that with NEE exhibiting such small values (i.e., close to zero), there is a greater potential for error. Alternatively, with the NDVI models for ER and GEE, it is possible to derive NEE from the models, thereby potentially reducing the overall error.

Watershed-scale estimates of CO\textsubscript{2} exchange

The regression equations generated for the 2006 data and validated with the 2008 data were applied to the NDVI images of SL (2001) and the CBAWO (2004), generating spatially explicit estimates of CO\textsubscript{2} flux for each site (Figure 6). Based on CO\textsubscript{2} exchange rates per pixel, summary statistics were calculated for each flux model, resulting in estimates of total CO\textsubscript{2} exchange per day during the summer peak season (Table 6). Symmetric mean absolute percentage error (SMAPE) was selected as a non-scale-dependent estimate of error for the regression equations’ relative error statistics. SMAPE is a variation on the mean absolute percentage error (MAPE) and is calculated using the average of the absolute value of the actual and predicted values in the denominator. This statistic is preferred when low values are problematic because they could skew the overall error rate higher (Chen et al. 2009; Tofallis 2014). Based on this model, the CBAWO is an overall source of CO\textsubscript{2} (64.19 Mg CO\textsubscript{2} day\textsuperscript{-1}) and SL is an overall sink (−36.8 Mg CO\textsubscript{2} day\textsuperscript{-1}).

Discussion

Variability across vegetation types and sites

Though numerous studies have examined carbon dynamics across vegetation types distributed along moisture gradients, few have studied these responses across bioclimatic zones, and fewer have done so in the high Arctic (Wüthrich, Moller, and Thannheiser 1999; Emmerton et al. 2016). Recent pan-Arctic studies have not examined vegetation types north of Bioclimatic Zone C (Shaver et al. 2013). Within each of our sites, environmental variables differed by vegetation type. However, soil temperature (5 and 10 cm depth), GSM, and PVC were not statistically different in comparable vegetation types between the CBAWO and SL despite the large latitudinal and bioclimatic difference. This lack of variability in environmental conditions between sites is interesting because species composition differed greatly between the CBAWO and SL in each of the three corresponding vegetation types. A major species compositional difference between the CBAWO and SL was the dominance of the shrub Dryas spp. at SL, where it was found in all vegetation types, whereas shrub cover at the CBAWO was limited. Additionally, there was a greater abundance (e.g., cover) of bryophytes at the CBAWO than at SL, except for the WT. These similarities were confirmed spectrally, in that NDVI values for all vegetation types at the CBAWO and SL were similar.

Temporal variation in CO\textsubscript{2} fluxes within a given vegetation type is important. There were no statistically significant variations in GEE, ER, or NEE over the sampling periods at either site, with the exception of ER in MT and WT at SL. The variation in ER rates in these vegetation types appears to be linked to unseasonably cool temperatures during a specific ten-day period (temperature decreased with the ER rate for MT and WT). These findings support Hypothesis 1 for the CBAWO: Daytime CO\textsubscript{2} exchange rates (GEE, ER, NEE) within DT, MT and WT are consistent through the peak summer growing season. On the other hand, the results cannot definitively support Hypothesis 1 for SL, although the majority of sites and CO\textsubscript{2} fluxes exhibited consistency (e.g., no statistically significant differences) when seasonal conditions prevail.

Although CO\textsubscript{2} flux studies for the high Arctic are limited, Wüthrich, Moller, and Thannheiser (1999) also noted that there was no statistical variation within DT, MT, or WT during a study on West Spitzbergen (78°22′ N; 12°44′ E; through early- and mid-season plant activity [8–26 July]). Environmental conditions during the growing season at the West Spitzbergen coastal site are similar to the CBAWO with low cloud and frequent fog. Conversely, studies in the mid- and low Arctic have noted extensive variability within vegetation types in terms of GEE, ER, and NEE fluxes (Nobrega and Grogan 2008). The greatest variability is observed during the early and late growing season (e.g., shoulder seasons), coincident with the greatest temperature fluctuations (Nobrega and Grogan 2008). This contradiction with respect to vegetation type may be a product of latitude and its impact on PAR and temperature. The high Arctic climate is cooler, with a short growing season through the summer months, compared to the mid- and low Arctic. Hence, increases in temperature and PAR may have a greater impact on the processes connected to CO\textsubscript{2} exchange rates at more southern sites. Regression modeling in this study indicated that air or soil temperature were the best predictors for the most successfully modeled fluxes. It has been shown that temperature and soil moisture have been key predictors of NEE, GEE, and ER for high Arctic DT, MT, and WT (Emmerton et al. 2016). The results of this study may be dependent on the conditions at these sites being relatively stable during the measurement period, so additional seasons should be examined.
**CO₂ exchange model**

Extensive research has been devoted to defining plant functional groups for the modeling of CO₂ exchange (Hobbie and Chapin 1996; Chapin and Shaver 1996; Callaghan et al. 2005; Wullschleger et al. 2014). This method of modeling requires detailed knowledge of vegetation distribution, which can be derived from remotely sensed data at a range of spatial resolutions (Shaver et al. 2007). The spatial model for CO₂ exchange in this study was independent of vegetation type and based solely on the spectral reflectance characteristics of vegetation. The NDVI model developed here demonstrates a functional convergence of vegetation types, in that the model is independent of species composition or functional type and builds on the relationships between vegetation cover, structure, and spectral reflectance (Shaver et al. 2007).

To examine Hypothesis 2, which posits that CO₂ exchange rates illustrate functional convergence and are captured in the NDVI data, we need to examine a number of ecological components. First, vegetation types, based on a soil moisture gradient at the CBAWO and SL, were composed of different species and functional groups, yet there was no statistically significant difference in CO₂ exchange across vegetation types (DT, MT, and WT) and site (CBAWO and SL). This may in large part be due to NDVI being strongly correlated with biogeophysical variables (e.g., PVC, aboveground biomass, leaf area, and soil moisture; Shippert et al. 1995; Walker, Auerbach, and Shippert 1995; Rees, Golubeva, and Williams 1998; Stow et al. 2004; La Puma, Philippi, and Oberbauer 2007; Laidler, Treitz, and Atkinson 2008; Atkinson and Treitz 2013). Hence, the NDVI values for similar vegetation types at both sites were not statistically different from one another. When NDVI was used to model carbon fluxes, the coefficient of determination \( R^2 \) illustrated that NDVI explained between 66 and 94 percent of the variation in GEE and ER at the CBAWO and SL. All regression equations confirmed coincidence, indicating that they were statistically similar and could be combined into one equation for both sites, thereby supporting Hypothesis 2. NEE was the weakest of the regression models at both sites; NEE was relatively low, because it was balanced by opposing GEE and ER values. However, NDVI did explain 35 percent of the variation in NEE at both sites. The results suggest that a simple model based on NDVI can be applied to accurately predict carbon exchange processes.

Hypothesis 3 states that NDVI alone can model landscape-scale CO₂ exchange rates at two independent sites. This hypothesis has been confirmed, in that all regression equations were coincidental and allowed one equation for each component, regardless of site, and that 35 to 70 percent of the variations in GEE, ER, and NEE rates were explained by NDVI. Additionally, the application of independent data collected in 2008 at the CBAWO reinforces the robust nature of these equations, because they were statistically similar to the pooled data. Thus, these models contribute to our understanding of functional convergence for CO₂ flux models.

Functional convergence models have been explored for the low Arctic (Shaver et al. 2007), and pan-Arctic models for NEE have been developed recently (Shaver et al. 2013). These models have had success with modeling NEE with \( R^2 \) values of 0.70 (RMSE = 1.16) for high Arctic sites (though no sites were at the latitude of this study). These models are multiple regression equations, requiring air temperature, PAR, and LAI. LAI values are derived from NDVI as a primary model input (Shaver et al. 2013). LAI is a quantifiable and straightforward measure for vascular plants and is preferable, at times, to other, more abstract variables (Street et al. 2007). Furthermore, LAI is estimated from NDVI using empirically based models (van Wijk 2005). However, NDVI values have been shown to vary based on sensor, so LAI models are often sensor specific (Laidler, Treitz, and Atkinson 2008). Additionally, it is difficult to incorporate nonvascular plant cover, an important component in high Arctic tundra CO₂ exchange, in LAI models (Shaver et al. 2007). For this research, a simple bivariate model with NDVI was optimal, in that it alone captures the spectral difference between red and NIR reflectance of all aboveground biomass. The results of the simpler bivariate models for GEE and ER developed here have similar \( R^2 \) values (0.70 and 0.65) and lower RMSE (0.21 and 0.48). The benefit of this bivariate model is that future estimates can be generated through the acquisition of new satellite imagery and not require in situ data, such as PAR and air temperature.

**Study limitations and recommendations**

Although the NDVI models developed here do explain a large portion of variance in CO₂ exchange rates (33 to 94 percent), there is additional variance left unexplained. However, this study illustrates that NDVI can be used quite simply to model CO₂ component fluxes, which can allow for the estimation of CO₂ exchange across large spatial scales without the need for additional in situ measures (e.g., soil moisture and temperature). It is anticipated that the inclusion of additional variables, such as PAR, air temperature, and water table depth, will improve
model development and predictions (Oechel et al. 1998; Street et al. 2007; Huemmrich et al. 2010; Olivas et al. 2010; Virkkala et al. 2018). Modeling peak growing season CO₂ dynamics can be valuable for understanding the ongoing changes to these processes with climate warming; however, more and more research is showing the importance of studying Arctic systems during non-growing seasons to fully understand the trajectory of change. Laboratory incubation studies have found evidence of microbial activity and subsequent CO₂ release at −10°C (Mikan, Schimel, and Doyle 2002). In situ evidence of CO₂ release under snowpack during the winter and spring periods has also been observed in the Alaskan Brooks Range, and these CO₂ effluxes were quite variable across different vegetation types (Fahnestock et al. 1998). Though NDVI models cannot be used accurately to model non-growing season CO₂ due to winter solar conditions, knowledge of the relationships between CO₂ dynamics and other influencing factors like temperature, moisture, and soil carbon quality can be included in these models to better develop our understanding of annual landscape-scale CO₂ processes.

Conclusions

A warming climate in the Arctic impacts terrestrial ecosystems directly and further complicates our understanding of how Arctic terrestrial ecosystems behave with respect to carbon and energy exchange (as a net source or sink for carbon). In a changing climate, we need to model and monitor CO₂ exchange rates throughout the Arctic at a variety of spatial and temporal scales (Virkkala et al. 2018). The application of high spatial resolution remote sensing data makes it possible to model CO₂ exchange rates where limited environmental data exist by capturing the heterogeneity of biophysical properties of tundra ecosystems based on their spectral reflectance. The ongoing challenge with intermediate and high spatial resolution data is the value that a single image can provide regarding processes occurring over longer timescales. Here, we have demonstrated that there was no statistically significant variation in GEE, ER, or NEE during the three- to five-week peak growth period at two independent study sites. These results illustrate that a single image captured within that time frame can be used to extrapolate temporally across the peak photosynthetic period. Additionally, the fact that GEE and ER can be predicted reasonably well for DT, MT, and WT in the mid- and high Arctic using NDVI demonstrates a strong functional convergence for these vegetation types.

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