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A test of functional convergence in carbon fluxes from coupled C and N cycles in Arctic tundra

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ABSTRACT

Arctic ecosystems exhibit functional convergence in Net Ecosystem Exchange (NEE's) of CO_2 response to light, air temperature, the Normalized Difference Vegetation Index (NDVI), and Leaf Area Index (LAI), potentially simplifying predictions of climate change impacts on the arctic C cycle over space and time. This convergence is hypothesized to be induced by tightly coupled carbon and nitrogen cycles, but has never been explicitly tested. We used model-data fusion on a mass balance model (i.e. the Coupled Carbon and Nitrogen; CCaN) to determine whether functional convergence in NEE results from tightly coupled carbon (C) and nitrogen (N) cycles. CCaN captured a majority, but not all, of NEE and NDVI observations across eight growing seasons, and MODIS NDVI observations across a tundra latitudinal gradient in Alaska. The hypothesis of temporal functional convergence was challenged by model-data disagreements for NEE during shoulder seasons and low light. The hypothesis of spatial functional convergence was challenged by the underestimation of NDVI in warm tundra. CCaN structure and parameter uncertainty analyses revealed that factors controlling leaf litter rate, the proportion of N in leaves, and net N mineralization rate are critical knowledge gaps in predicting pan-arctic NEE and NDVI in a future warmer climate.

1. Introduction

Arctic tundra ecosystems illustrate surprising convergence in the net uptake of CO_2 from the atmosphere (i.e. the Net Ecosystem Exchange of CO_2 (NEE)), despite large variability in soils climate, and vegetation cover (Shaver et al., 2007, 2013). This functional convergence is demonstrated by the ability to accurately model the spatial and temporal dynamics in the Net Ecosystem Exchange of CO_2 with a single functional response to light, temperature, and the Normalized Difference Vegetation Index-a spectral reflectance based proxy of Leaf Area Index (LAI) (Shaver et al., 2007; Loranty et al., 2011; Shaver et al., 2013). Understanding functional convergence is important because it can simplify C cycling predictions in a rapidly changing environment and help determine whether increased temperatures will make the arctic a future C source or sink. A limitation of the functional convergence model, however, is that it requires LAI to predict NEE, which is often difficult to predict in ecosystem models. Hence, a mechanistic understanding of C uptake and allocation to LAI is needed to predict future carbon cycling with the functional convergence model.

In arctic ecosystems, a simple and strong relationship exists between foliar N and canopy LAI across a wide variety of tundra communities (Fig. 1). This relationship arises as a unique emergent property at the plant community level and reflects both the strong N limitation in arctic systems and a stoichiometric N cost of producing canopy leaf area and increasing photosynthetic potential (Williams and Rastetter, 1999; van Wijk et al., 2005). This relationship is important because it may allow for the prediction of both LAI and NEE in the functional convergence model provided knowledge of N cycling. Arctic ecosystems are thought to have relatively closed N cycles, where N internally recycles among biomass, soil organic matter, and available N pools due to the low rates of deposition, runoff, and mineralization of N (Shaver et al., 1992; Williams and Rastetter, 1999; Pearce et al., 2015; Jiang et al., 2015). N can impose substantial biological constraints on soil and plant C cycling that may contribute to the observed functionally convergent responses of NEE to light, temperature, and LAI. Consequently, we hypothesize that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI.

Simple ecosystem models provide a means to further understand the dependence of functional convergence on tightly coupled tundra C and N cycles. Such models provide quantitative frameworks to corroborate or challenge our current understanding of ecosystems (Ågren and Bosatta, 1990; Rastetter, 2003; Rastetter et al., 2003; Dietze et al., 2013). Agreement between models and data indicate a parsimonious understanding of ecosystem function, while disagreement between

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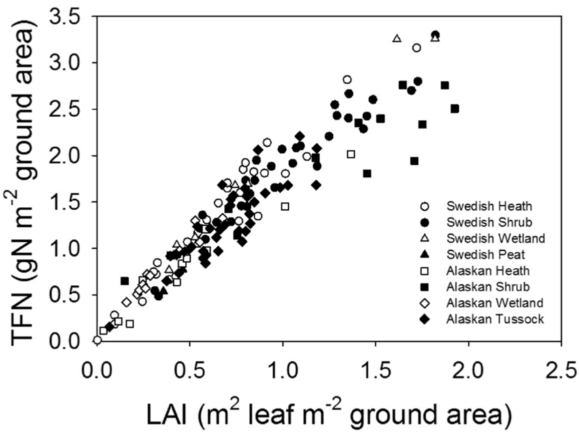

Fig. 1. Relationship between total foliar N (TFN) and the Leaf Area Index (LAI) of arctic ecosystems (Redrawn from Williams and Rastetter, 1999; van Wijk et al., 2005).

models and data highlights gaps in model structure and current understanding (Rastetter et al., 2003; Rastetter, 2017). Assessing model-data agreement is challenging however because uncertainty can be as large as the measurement itself, model parameters regulating ecosystem processes can be biologically unrealistic, and model parameters can offset one another through covariation, resulting in correct model predictions for the wrong reasons (Raupach et al., 2005; Luo et al., 2009; Keenan et al., 2011). One way to overcome these issues is to incorporate model and data uncertainty during parameterization through model-data fusion (Williams et al., 2005; Keenan et al., 2012; Dietze et al., 2013; LeBauer et al., 2013). Model-data fusion is an iterative technique used to find the best set of parameters that fit a proposed model to data with quantified uncertainties. Since model-data fusion statistically characterizes both model and data uncertainty and incorporates biological constraints into model parameterization, it provides a robust method to detect model-data disagreements.

We used model-data fusion with a simple mass balance model (i.e. the Coupled Carbon and Nitrogen model; CCaN) to test the hypothesis that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI. We developed CCaN instead of using other more commonly used C cycling models for several reasons. First, CCaN's simplicity allowed us to avoid issues of overfitting and equalfinality that can limit process based understanding from more complex models. Second, CCaN's simplicity also allowed us to relate model processes to actual field measurements to constrain model parameters within realistic and biologically valid limits during CCaN model-data assimilation. Third, CCaN's simplicity allowed us to better diagnose processes that resulted in model-data disagreements with statistical certainty, and thus, highlight ecosystem process that require further understanding. Lastly, CCaN is the only model to link the tight relationship between foliar N and LAI in van Wijk et al., 2005 and Williams and Rastetter (1999) to the functional convergence in NEE as proposed by Shaver et al., 2007, 2013. Further understanding how the functional convergence of arctic CO_2 fluxes is related to tightly coupled C and N cycles will not only help to predict tundra C cycling, but also help constrain the responses of plants and soils to climate change.

2. Methods

2.1. Research Approach

We developed and parameterized a Coupled C and N mass balance model (CCaN) using model-data fusion with eddy covariance NEE and daily NDVI. Our approach followed the code of best practices for model-data fusion (Keenan et al., 2011) by: 1) quantifying measurement uncertainties, 2) testing our model-data fusion framework against synthetic data, 3) assimilating multiple data sources (i.e. NDVI and NEE) to estimate parameters, 4) testing model output with independent observations, 5) minimizing equifinality by choosing a simple model and carefully selecting free-parameters, and 6) incorporating quantified model and data uncertainties into model predictions. Our hypothesis was that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI. The test of this hypothesis is whether the CCaN model, using a single parameter set estimated with model-data fusion, can replicate the temporal and spatial dynamics of arctic NEE and NDVI provided both model and measurement uncertainty. The model and model-data fusion code were written in R and can be found on a GitHub page (https://github.com/kkremers/CCaN_MS2016.git).

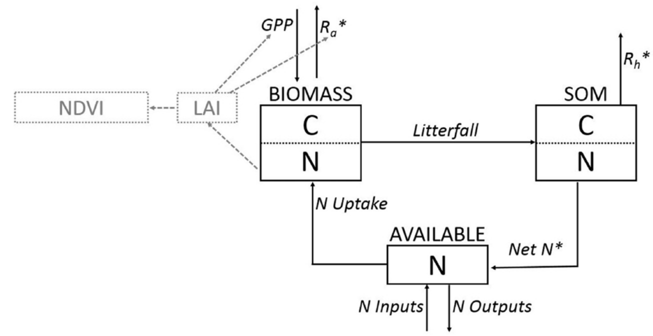

Fig. 2. CCaN model diagram. Boxes represent pools and solid arrows represent fluxes. Fluxes denoted with a "*" are temperature sensitive. Gray dashed boxes indicate other relevant model outputs, and the gray dashed arrows indicate their use in flux calculations.

2.2. CCaN Model

CCaN (Fig. 2) is a spin-off of the Simple Arctic Model (SAM, Shaver et al., 1992) in terms of its simplicity and N limitation on C fluxes. CCaN is consistent with the view of a relatively closed N cycle, where N is internally recycled among biomass, SOM, and available N pools (Shaver et al., 1992; Williams and Rastetter, 1999; Pearce et al., 2015; Jiang et al., 2015). CCaN was driven with daily light and air temperature and predicted daily NEE, LAI, and NDVI. CCaN equations and details can be found in the appendix and in Table 1, but we will briefly describe the model framework in the following section. CCaN pools are plant biomass C and N, soil organic matter (SOM) C and N, and available N (Table 1).

The functional convergence model for NEE controlled C moving into and out of the system. C inputs (GPP) were controlled by PAR and LAI. C is respired from biomass as autotrophic respiration (R_a), which is controlled by temperature and LAI, and from SOM pools as heterotrophic respiration (R_h), which is controlled by temperature alone. LAI is estimated by CCaN using a linear relationship with Total Foliar N (TFN) that is sensitive to biomass N, temperature, and vegetation phenology (Williams and Rastetter, 1999). LAI is converted to NDVI by inverting the exponential relationship derived from Shaver et al. (2007) and Rocha and Shaver, 2009 [Equation 3]. All parameters associated with the functional response of GPP, R_a, and R_h are derived from Loranty et al. (2011), which is a temporally scaled version of the original functional convergence model described in Shaver et al. (2007).

Along with the tight relationship between TFN and LAI, C and N cycles are coupled by several other processes in CCaN. Both biomass C and N moved to soil organic matter (SOM) through a shared litterfall rate. Plant uptake of N from the available N pool is limited by root biomass C and the amount of available N. Net N mineralization (Net N) transferred N from SOM to the available N pool, and is sensitive to temperature, the amount of SOM N, and a net mineralization rate. The available N pool also is influenced by smaller fluxes that included N