

This document is our response to Dr. Twombly's request for more information on issues mentioned by the panel and reviewers. Those issues were: **(1)** Clarify how our past modeling work motivated the proposed research; **(2)** Briefly describe the models, justify their use in this context, and describe how they will be applied; and **(3)** Clarify how the proposed modeling addresses the theme of ecological openness and connectivity.

1. Motivation of proposed research based on past modeling: Our research goal is to develop a predictive understanding of the responses of arctic landscapes to disturbance and climate change, using the concepts of *biogeochemical and community openness* for arctic terrestrial and freshwater ecosystems and the *landscape connectivity* among these ecosystems. In terrestrial systems, this goal is motivated largely from our earlier analyses of tundra responses to disturbance and climate change using the Multiple Element Limitation (MEL) model (Pearce et al. 2015, Jiang et al. 2015a&b). In those analyses, we discovered that the observed rate of tundra recovery from fire and thermokarst failures was far too fast to be explained by the low, background rate of nutrient supply to these ecosystems. In other words, it appeared that the nutrient cycles were essentially closed, at least on the scale of a few decades. Based on uncertainty analyses of nutrient supply rates, amounts of residual soil organic matter, and turnover rates of soil organic matter (Pearce et al. 2015), we predict a two-phase recovery from disturbance. During the first phase, the observed rates of vegetation recovery are fueled by the redistribution of nutrients from the residual organic matter in soil and permafrost. During the second phase, which can take centuries, the ecosystems recover the nutrients lost in the disturbance by re-entraining them from the slow trickle of external sources. Based on similar MEL analyses, we also predict that responses to elevated CO₂ and warming are similarly constrained by the nearly closed nutrient cycles, and that the accumulation of vegetation and the sequestration of ecosystem C again depend on the redistribution of nutrients from soils to vegetation (Jiang et al. 2015b). These uncertainty analyses indicate that responses are far more sensitive to warming, which stimulates nutrient redistribution between soil and vegetation, than to even a twenty-fold increase in the current external nutrient supply because the current nutrient supply rate is so small (i.e., a nearly closed ecosystem). These biogeochemical responses also lead to major changes in soil communities, which we have analyzed with Jacobian Matrix models of food-web structure (Ch. 11 in Moore & de Ruiter 2012, Sistla et al. 2013). We are testing these predictions with our greenhouse and fertilizer experiments.

In aquatic systems, our models of key stream processes, in particular stream metabolism, nutrient uptake, and food webs, have informed and tested our hypotheses on the openness of stream nutrient cycles. Our modeling of stream metabolism has been based on continuous monitoring of reach-level oxygen budgets (e.g., Cappelletti 2006, Hury et al. 2014). Our understanding of nutrient uptake and the openness of aquatic nutrient cycles is based on models constrained with stable isotope tracer experiments (¹⁵N) as well as non-tracer nutrient enrichment experiments (N & P) operating in continuous and pulse modes (e.g., Wollheim et al. 1999, 2001, Edwardson et al. 2003, Gooseff et al. 2008). These models emphasize the importance of hydrology on openness as well as connectivity of these ecosystems, with nutrients moving only a few tens of meters downstream with each pass through the biogeochemical cycle in low discharge streams (<0.1 m³ s⁻¹) to several kilometers in high discharge streams (> 10 m³ s⁻¹; Wollheim et al. 2001). In contrast, nutrient uptake is highest at intermediate stream discharge, indicating that openness as defined by external supply relative to internal demand for nutrients is a complex function of hydrology as well as stream metabolism. In our stream food-web models (Wan et al. 2008, Wan & Vallino 2005) we found that food web energy and nutrient flows are a function of discharge, temperature, and nutrient inputs, and we use the long-term interannual variability to assess uncertainty. We are directly testing these model predictions in our stream experiments, by for instance, stopping the Kuparuk nutrient addition and tracking changes in the food web dynamics, nutrient cycling, and metabolism.

2. Model descriptions: a. Terrestrial biogeochemical model: The MEL model will continue to be the main tool in our proposed research for synthesizing and predicting changes in terrestrial biogeochemistry and assessing the consequences of biogeochemical openness. The model couples ecosystem C, N, P, and water cycles and operates at a plot scale on a daily time step (Rastetter et al. 2013, Pearce et al. 2015). It partitions vegetation allometrically into active (leaves plus fine roots) vs. woody biomass using a func-

tion that simultaneously fits the tissue distribution in all four major types of tundra in northern Alaska (heath, wet sedge, tussock, and shrub tundra). The model uses an aggregated representation of vegetation. As such, changes in species composition are represented by changes in the relative magnitudes of woody vs. active biomass. The heart of the model is a dynamic algorithm that allocates plant assets (such as biomass, enzymes, carbohydrates, etc.) to the uptake of eight resources from the environment (light, CO₂, H₂O, NH₄, NO₃, DON, N-fixation, and PO₄). These assets are implicitly represented as an aggregate uptake potential that is assumed to increase in proportion to the active vegetation biomass. The allocation algorithm calculates the fraction of these uptake assets (effort) allocated toward acquiring each resource based on the resource optimization hypothesis (Bloom et al. 1985). The model distributes the active biomass between leaves and fine roots based on the relative limitation by canopy (CO₂ and light) vs. soil resources (nutrients and water). The model partitions detritus into Phase I and Phase II soil organic matter (SOM; Melillo et al. 1989) and debris (debris and standing dead plant material). The debris is gradually converted to Phase I material where it begins to decompose. Phase I SOM represents the young, more active, organic matter and implicitly includes microbial biomass. Phase I SOM both mineralizes and immobilizes nutrients, and turns over relatively quickly. Phase II SOM does not immobilize nutrients, but continues to mineralize nutrients and release C at a slow rate. Thus, MEL is a detailed, well-validated model with the biogeochemical framework and underlying flexibility to address the questions in our proposed research (e.g., Proposal p. 15).

b. Aquatic biogeochemical model: We will continue and extend this analysis of biogeochemical openness to aquatic ecosystems contained within the landscape, by building on our previous aquatic modeling and including key aspects of and inputs from MEL. Specifically, we are applying models that integrate stream uptake and metabolism based on concepts of nutrient uptake velocity and nutrient spiraling (Wollheim et al. 2006, 2008, Peterson et al. 2013, Hale et al. 2014, Peterson & Ver Hoef 2014) to arctic streams to examine openness and connectivity. These models provide a fine-grained understanding of in-stream biological and geochemical processes that will help us understand how water flow, river network connectivity, and stream ecosystem processes interact. This is essential information that will help us predict how terrestrial exports of C, N, and P from the MEL model will be processed in arctic streams and is a necessary first step in our efforts to model connectivity of linked terrestrial-aquatic arctic systems.

Because the basic biogeochemical cycles of terrestrial and aquatic systems are similar, we will develop analogous model structures to facilitate comparing and contrasting the effects of biogeochemical openness on responses to disturbance and climate change among terrestrial, stream, and lake ecosystems. The basic MEL structure can be applied to aquatic systems by incorporating the effects of animals and top-down control and replacing components like tissue allometry, root-shoot allocation, water limitation, and formulations of photosynthesis based on light extinction through canopies vs. the water column. For example, in streams we have the analogous circumstance of rapidly and slowly processed organic matter (algae versus terrestrial detritus); thus we will use a similar MEL Phase I and II approach to organic matter dynamics. We should thereby be able to adapt a MEL-type model to the current biogeochemical budget models for streams and lakes (e.g., Whalen and Cornwell 1985, Peterson et al. 1985, 1986, 1997), and test the predictions of these models with the proposed research (Proposal p. 19, 24, 29).

c. Hydro-biogeochemical connectivity model: A major goal of the proposal is to examine the biogeochemical connectivity between terrestrial and aquatic ecosystems. This landscape-level connectivity is driven largely by hydrology. We are working with Bayani Cardenas (U. Texas) and Beth Neilson (Utah State) to develop a hillslope-riparian hydro-chemical model that can link the terrestrial biogeochemical responses predicted by the MEL model to aquatic ecosystems (e.g., Merck et al. 2011, Merck & Neilson 2012). The hydrology model for the hillslope-riparian areas uses a multiphysics approach incorporating unsaturated flow, surface energy balance, and reactive solute transport, integrated into one widely-used, generic, finite-element platform, COMSOL Multiphysics (see Cardenas et al. 2008a,b, 2010). COMSOL allows for coupling user-defined partial differential (conservation) equations, and thus can link directly to output of the MEL model and provide input directly to the stream model. The hillslope flow is comprised of explicit, distributed forms of the advection-diffusion/dispersion/conduction equations for water and heat, with user-defined source/sink/reaction terms for C and nutrients. Using the biogeochemi-

cal output of MEL, the model can move C and nutrients downslope and includes reactive transport. Thus, the connectivity of the terrestrial soil and vegetation to the groundwater to the riparian zone to the stream can be assessed in both space and time (that is, determining where the landscape is strongly or poorly connected). Perhaps more importantly, with this model we can conduct “experiments” that disturb the landscape at different time scales by changing climate, changing vegetation, or changing the depth of thaw into the permafrost. For each of these scenarios, which represent landscape-level changes that relate directly to our proposal questions, we can use the coupled models to make predictions that can be tested by various aspects of our proposed research. Overall, this approach will help us determine the effects of disturbance and climate on biogeochemical connectivity and system response (Proposal p. 29).

d. General community model: To compare and contrast plant and animal communities in terrestrial, stream, and lake ecosystems, we will analyze Jacobian matrix models of food webs (e.g., Rooney et al. 2006); we have developed and tested these models with Toolik data (Ch. 11 in Moore & de Ruiter 2012, Sistla et al. 2013). This approach melds empirical information into an abstract model structure that quantifies food web connections, feedback loops, and the effects of immigration and emigration in a way that can be compared across multiple, very different ecosystems (e.g., Rooney et al. 2006). Thus, the general model framework and common currency (energy, C, N, or P) will allow us to compare structural properties like openness to species loss, ecosystem-level functional attributes (C, N, and P input fluxes relative to mineralization rates; openness to nutrients), and dynamic characteristics derived from the Jacobian matrix (e.g., feedback loops, food-web stability, and vulnerability to nutrient loss or species additions or deletions). These comparisons will test the model predictions (see Proposal p. 14, 18-19, 22-23).

e. Community connectivity models: Community connectivity between terrestrial and aquatic ecosystems in this landscape includes micro and macro organisms (bacteria to fish). We have observed that small prokaryotes and eukaryotes move from soil waters to streams and lakes, and our characterization of this movement and modeling of its importance will be developed following the framework described in Crump et al. (2007, 2012), where stream and lake residence time are analyzed in relation to the rates of organism transfer and growth. There is also a very strong connectivity between stream and lake communities via fish migration. We know that lakes connected to stream systems (open) have more diverse communities and more trophic levels than isolated (closed) lakes. Budy and Luecke (2014) used an energetics approach to model size dimorphism in predatory fish in closed lakes. They predict climate warming will lead to stronger cycling between populations dominated by small individuals vs. by large individuals, which has ramifications that propagate to the rest of the community. Our research now needs to model how grayling migrations in and out of open lakes on a seasonal basis affects these cycles in size dimorphism and the propagated effects on community structure. Each of the project components (terrestrial, streams, lakes, landscape interactions) will test the predictions from these models with the research proposed in the Toolik, Kuparuk, and Oksrukuyik basins that have streams and lakes with different levels of organism connectivity (Proposal p. 19-20, 24-25, 28-29).

3. Role of models in addressing the theme of ecological openness and connectivity: A single, unified model of landscape biogeochemistry or of community dynamics is not needed to answer our proposal questions, but we are clearly heading in that direction. Our proposed approach is to first compare and contrast among ecosystems with very different physical and biological properties. To do this comparison we have selected general model structures (e.g., Jacobian matrix models) and similar model structures (e.g., MEL model and proposed aquatic version) to compare and contrast key aspects of openness and connectivity and their effects on responses to disturbance and climate change. The second objective is to model characteristics unique to the individual components of the landscape (e.g., hillslope hydrology, energetics and size dimorphism in fish) and address these unique aspects in their response to disturbance and climate change. Our long-term objective is to develop a comprehensive understanding of the biogeochemistry and the community ecology in a diverse arctic landscape, and to predict how these ecosystems will change in the face of climate warming and the resultant more frequent and punctuated disturbances (fire and thermokarst). The models we have selected will help us synthesize the large amount of data we have and are collecting for these systems, and the models were selected explicitly to address issues of openness and connectivity.

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