

PROJECT SUMMARY

Overview:

The McMurdo Dry Valleys, Antarctica, are a mosaic of terrestrial and aquatic ecosystems in a cold desert that support microbial foodwebs with few species of metazoans and no higher plants. Biota exhibit robust adaptations to the cold, dark, and arid conditions that prevail for all but a short period in the austral summer. The MCM-LTER has studied these ecosystems since 1993 and during this time, observed a prolonged cooling phase (1986-2002) that ended with an unprecedented summer of high temperature, winds, solar irradiance, glacial melt, and stream flow (the "flood year"). Since then, summers have been generally cool with relatively high solar irradiance and have included two additional high-flow seasons. Before the flood year, terrestrial and aquatic ecosystems responded synchronously to the cooling e.g., the declines in glacial melt, stream flow, lake levels, and expanding ice-cover on lakes were accompanied by declines in lake primary productivity, microbial mat coverage in streams and secondary production in soils. This overall trend of diminished melt-water flow and productivity of the previous decade was effectively reversed by the flood year, highlighting the sensitivity of this system to rapid warming. The observed lags or opposite trends in some physical and biotic properties and processes illustrated the complex aspects of biotic responses to climate variation. Since then, the conceptual model of the McMurdo Dry Valleys has evolved based on observations of discrete climate-driven events that elicit significant responses from resident biota. It is now recognized that physical (climate and geological) drivers impart a dynamic connectivity among landscape units over seasonal to millennial time scales. For instance, lakes and soils have been connected through cycles of lake level rise and fall since the Last Glacial Maximum, while streams connect glaciers to lakes over seasonal time scales. Overlaid upon this physical connectivity among soils, glaciers, streams and lake are biotic linkages facilitated by the movement of genes, individuals and species through metapopulations and metacommunities. The 5th iteration of the MCM-LTER program (MCM5) includes superimposing biotic connectivity upon this linked, heterogeneous landscape. The hypothesis is: Increased ecological connectivity within the MDVs ecosystem will amplify exchange of biota, energy and matter, homogenizing ecosystem structure and functioning. This hypothesis will be tested with new and continuing monitoring and experiments that examine: 1) how climate variation alters connectivity among landscape units, and 2) how biota (species, populations and communities) are connected across this heterogeneous landscape using state-of-the-science tools and methods including ongoing and expanded automated sensor networks, analysis of seasonal satellite imagery, biogeochemical analyses, and next-generation sequencing.

Intellectual Merit :

The Intellectual Merit of MCM5 is understanding how the distinctive biotic communities that survive in the harsh environment of the McMurdo Dry Valleys respond to environmental change. This proposed research will test ecological theories describing how the resilience of ecosystems is related to the diversity and composition of resident biota, and how environmental changes that homogenize biological communities reduce the stability of ecosystem functioning. Results from MCM5 will transform understanding of ecosystem response to climate drivers and will be directly transferrable to other ecosystems, especially those that are undergoing rapid climate variation.

Broader Impacts :

In MCM5 a strong tradition of Broader Impacts will be continued by appointing a PI to lead and coordinate outreach and educational activities among the research community (LTER network, agencies, etc.) and professional educators. MCM-LTER education programs (K-12 instruction, incorporation of LTER-themed children's books into school curriculum) and outreach activities (e.g., Antarctic Library Lecture Series, interaction with the NSF Artists and Writers Program, and engagement with the media) will be continued, and expanded with new programs associated with the 200th anniversary of the discovery of Antarctica. These activities will advance societal understanding of how polar ecosystems respond to climate variation. MCM-LTER will continue its mission of training and mentoring students, postdocs, and early career scientists as the next generation of leaders in polar ecosystem science, and lead the development of international environmental stewardship protocols for human activities in the region.

LTER: Ecosystem response to amplified landscape connectivity in the McMurdo Dry Valleys, Antarctica

The McMurdo Dry Valleys (MDVs) (78°S, 162°E) represent the largest (4500 km²) ice-free area on the Antarctic continent (Fig 1, Levy 2012). The MDV landscape is a mosaic of glaciers, soil and exposed bedrock, and stream channels that connect glaciers to closed-basin, permanently ice-covered lakes on the valley floors (Fig 2). Mean annual air temperatures are cold (ranging from -15 to -30°C on the valley floors, Doran *et al.* 2002a), and precipitation is low (~50 mm annual water equivalent as snow; Fountain *et al.* 2010). Summer air temperatures typically hover around freezing and winter air temperatures are commonly < -40°C. While the water columns of the lakes are liquid and biologically active year round, glacial meltwater streams flow and soils thaw only during the austral summer. There are no vascular plants, but microbial mats are abundant in lakes and streams. Mat organisms are transported by wind onto glacier and lake ice surfaces where they actively metabolize in liquid water pockets (cryoconites) that form during the summer months. In the streams, which desiccate for ~10 months each year, cyanobacterial mats host extensive diatom and soil invertebrate communities. Lakes provide a habitat for diverse phototrophic and heterotrophic plankton communities that are adapted to annual light-dark cycles and temperatures near 0°C. Soils are inhabited by nematodes, rotifers, and tardigrades, all of which are metabolically active during summer. The McMurdo LTER (MCM) began studying this cold desert ecosystem in 1993 and showed that its biocomplexity is inextricably linked to past and present climate drivers. We propose to determine how the ecosystem responds to amplified landscape connectivity resulting from contemporary climate variation.

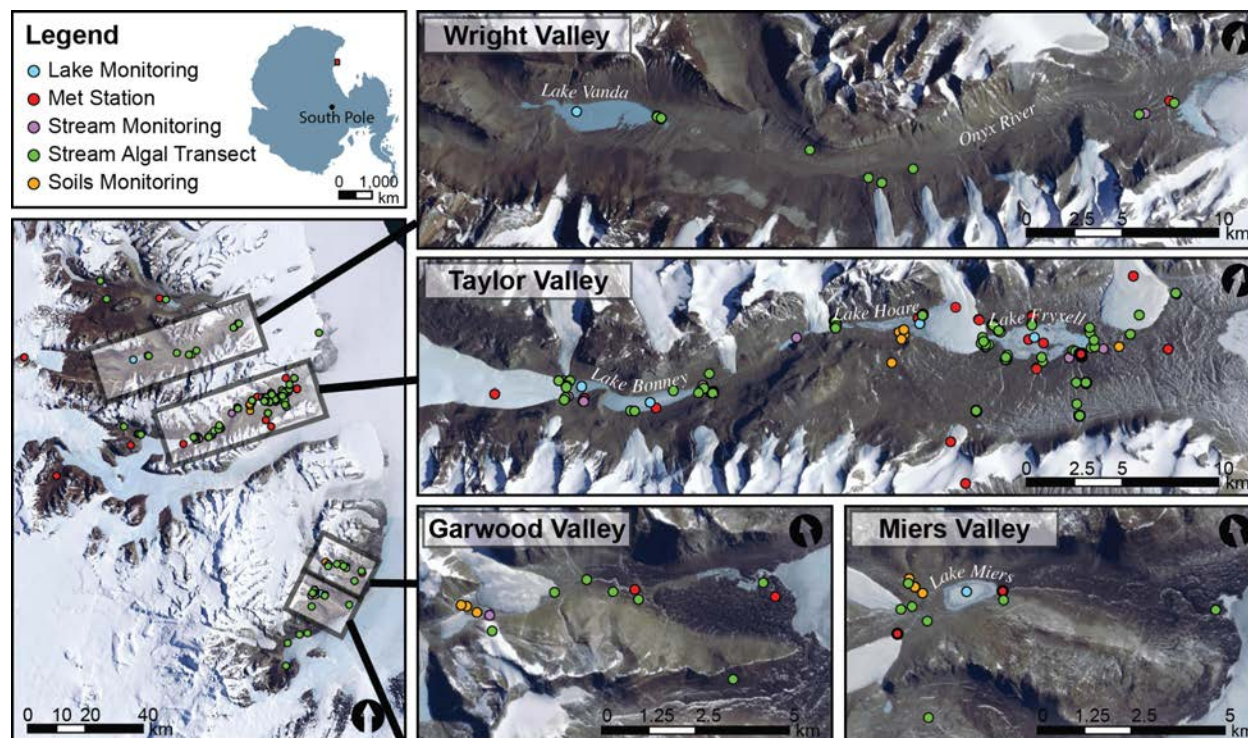


Figure 1. Map showing the 4 valleys where we primarily conduct our research. Monitoring and experimental sites are noted.

1. RESULTS FROM PRIOR SUPPORT

The MCM4 (4th funding period of MCM) team was: Adams (evolutionary ecologist), Barrett (soil ecologist/biogeochemist), Doran (hydrogeologist/paleolimnologist), Fountain (glaciologist/meteorologist), Gooseff (hydrologist/modeler), Howkins (environmental historian), Lyons (geochemist), McKnight (PI, stream ecologist/hydrologist), Priscu (limnologist/ biogeochemist), Takacs-Vesbach

(microbial ecologist), Virginia (ecosystem ecologist), and Wall (soil ecologist). During MCM4, we produced 138 papers in refereed journals (see supplementary table), 20 book chapters, 1 book, and 24 theses/dissertations (19 more in progress). Another 17 journal articles are in press. We involved 43 graduate students, 8 postdoctoral fellows, 88 undergraduates and 22 K-12 students and teachers. More than 34 collaborators were involved in MCM4.

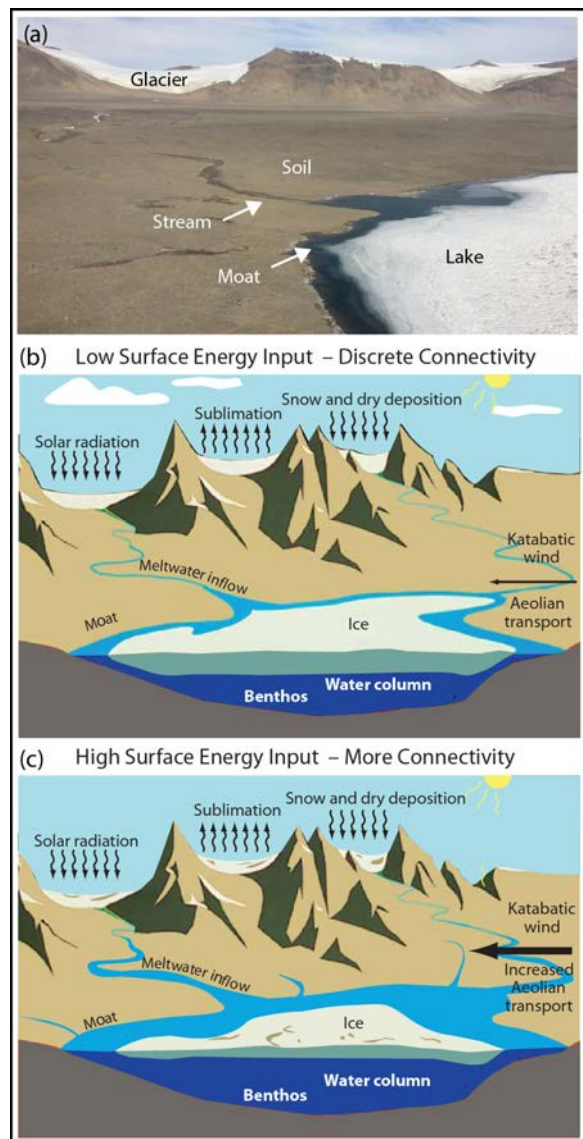


Figure 2. Image showing the MDV landscape (a) and our conceptual models of the physical differences across the landscape in summers with (b) low surface energy input (solar, wind, and temperature), and (c) high surface energy input to the system.

1.1 LESSONS FROM AN ECOSYSTEM RESPONDING TO ENVIRONMENTAL CHANGE

A key discovery from MCM3 was that cooling of the MDVs at a rate of $0.7\text{ }^{\circ}\text{C decade}^{-1}$ between 1986 and 2000 elicited distinct ecological responses including (i) thicker lake ice that reduced under-ice photosynthetically active radiation (PAR) and decreased phytoplankton primary productivity (PPR), (ii) reduced meltwater generation and associated streamflow, and (iii) declines in soil invertebrate populations (Doran *et al.* 2002b). This cool period ended in January 2002 when the MDVs experienced one of the warmest and sunniest summers on record (aka “the flood year”) resulting in significant thinning of the lake-ice cover and the highest stream flows recorded in Taylor Valley. We now have a post-flood year record approximately as long as the pre-flood year record (Fig 3), which allows us to examine the significance of the flood year in the context of long term trends on the structure and functioning of the MDVs ecosystem. Trend-break analyses on the full time series reveals that the flood year was indeed the end of a significant cooling trend, and after the flood year, ecosystem responses exhibited no trend or the trend was reversed compared to before the flood year (Gooseff *et al.*, in review). We have also modified our conceptual model to focus on climate influence in terms of surface energy balance, not just warm vs. cold conditions (Figs 2b, 2c, 3a). Below we highlight specific research areas from MCM4 that form the basis of our new conceptual model in MCM5. The remainder of this section highlights ecosystem responses in the context of what we learned from MCM4, which are applied to our current hypotheses (Section 2.2).

1.1.1 Physical Connectivity. The general topic of hydrological connectivity has recently generated a burst of new ideas and papers, to which our team has contributed. This focus on how water bodies are connected is stimulated by the US EPA potential modifications to the rules that govern the jurisdiction of the US Clean Water Act (e.g., Alexander 2015). We have interpreted our long-term stream gauging records by defining hydrologic connectivity in the MDVs (Gooseff *et al.* in revision, 2011; Wlostowski *et*

al. 2016). We have also quantified aeolian transport in our system, which connects all parts of the landscape (Nkem *et al.* 2006; Michaud *et al.* 2012; Šabacká *et al.* 2012).

1.1.2 Biological Connectivity. In MCM4, we investigated the biological connectivity among MDV landscape units by determining the biodiversity, distribution, and functional roles of the microbial communities within the environment (Geyer *et al.* 2013, 2014; Van Horn *et al.* 2013; Okie *et al.* 2015), and their responses to climate driven pulses and presses (Buelow *et al.* in review; Schwartz *et al.* 2014; Van Horn *et al.* 2014). These studies showed that bacterial diversity is greatest in streams (Van Horn *et al.*, in review), followed by lakes and soils (Fig. 4a). Significant habitat filtering is evident for bacteria communities (Fig 4b), indicating limited biological connectivity among habitats despite physical connectivity. Biotic connectivity (e.g., dispersal) is difficult to measure directly, but our past and ongoing work demonstrates significant biogeographic patterns that include a range of connectivity among organisms from very broadly dispersed panmictic taxa (e.g., nematodes, Adams *et al.* 2007) to fine-scale sorting in cyanobacteria (Michaud *et al.* 2012) and diatom communities (Sakaeva *et al.* 2016). We have developed a metacommunity simulation to model how niche and dispersal dynamics contribute to observed biodiversity patterns (Sokol *et al.*, 2013; in review). Understanding how biotic connectivity responds to climate variation and resulting changes in physical connectivity is the major focus of MCM5.

1.1.3 Permafrost Degradation as an Ecosystem Disturbance. The MDVs are underlain by continuous permafrost, which extends from ~50cm below the ground surface to >100m deep. Near surface permafrost can be dry (low

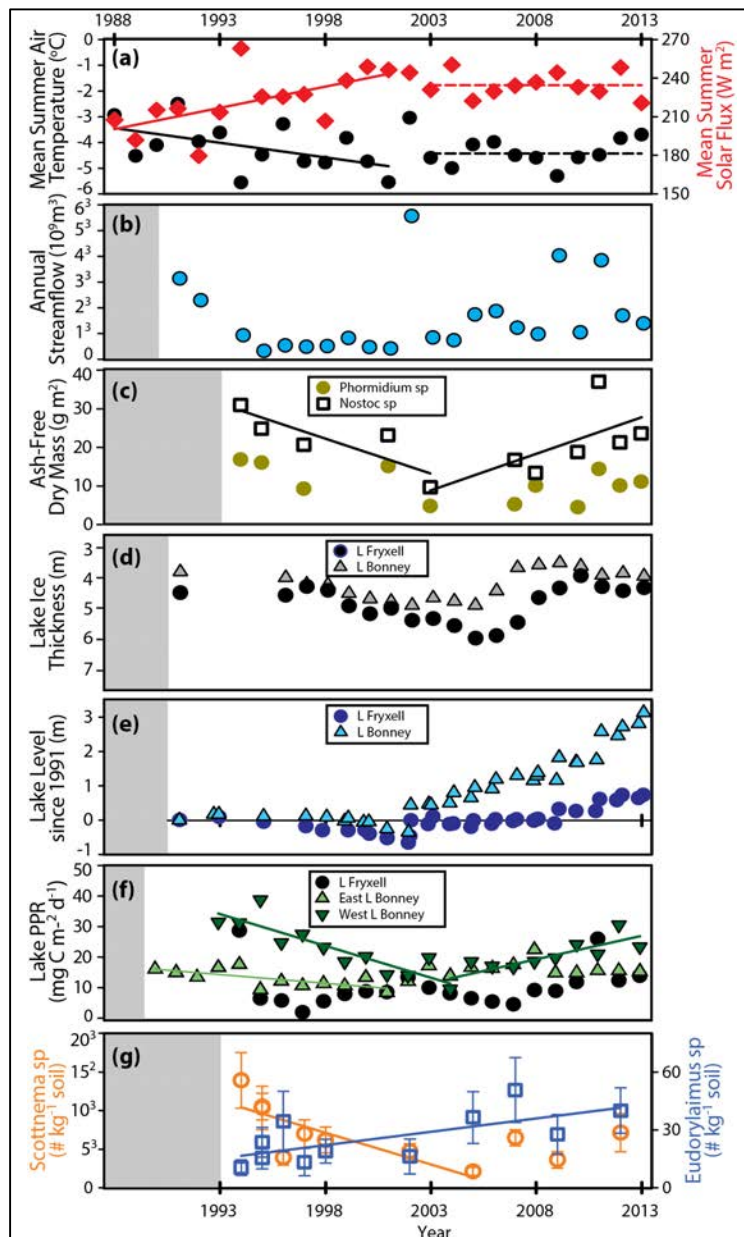
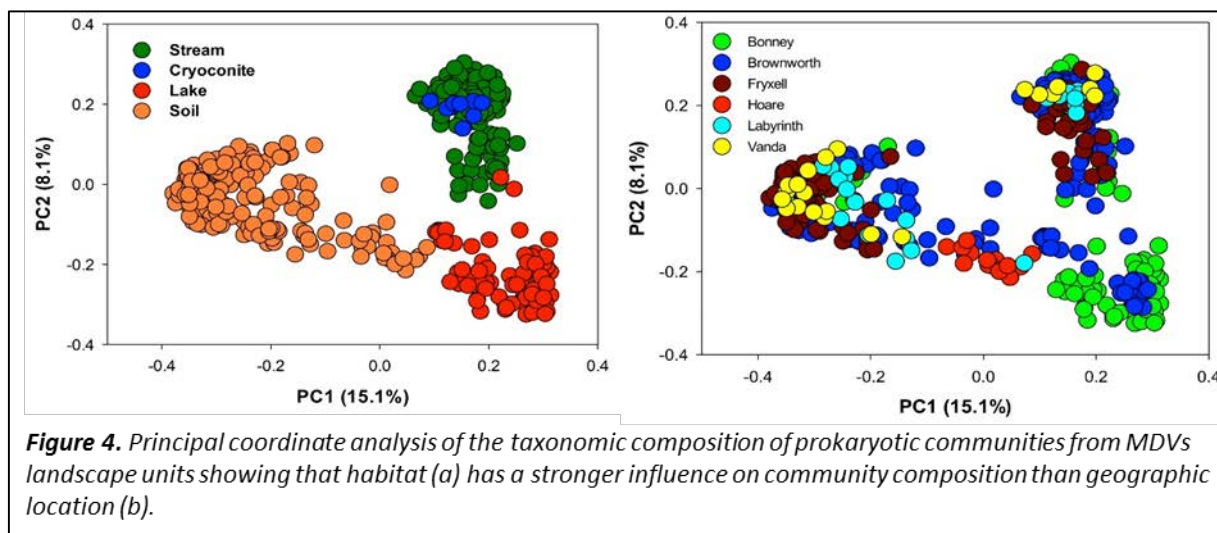


Figure 3. Climate drivers during the cooling trend (pre-2002) and the relative climate stasis post-2002: (a) mean summer air temperature and solar flux and associated ecosystem responses: (b) annual Fryxell basin stream inflow, (c) stream algal mat ash-free dry mass of the orange *Phormidium*-dominated and black *Nostoc*-dominated mats, (d) and (e) ice-thickness (inverted scale) and level changes for Lakes Fryxell and Bonney, (f) primary productivity in Lakes Fryxell and the east and west lobes of Bonney, and (g) soil invertebrate density. Significant ($p < 0.1$; Doran *et al.* 2002b) linear regressions are displayed as solid lines; dashed lines=average values over the period. Temporal trend in *Eudorylaimus* was significant for entire period of record, related to the overall increase of meltwater generation from 1994-2013.

water content), ice-rich, or contain buried ice (Bockheim *et al.* 2007). Recent permafrost degradation (thermokarst) has been discovered associated with streams (Gooseff *et al.* in press; Levy *et al.* 2013a; Sudman 2015). This degradation results in the transport of significant volumes of sediment and associated nutrients into streams. To examine the effects of permafrost degradation on soil physical and biological properties we experimentally manipulated hillslope soils to simulate different frequencies of permafrost thaw in MCM4 (Barrett 2014) and will continue this experiment in MCM5.



1.1.4 Hotspots and Hot Moments. Hotspot/hot moment phenomena describe discrete places or brief times in which elevated biogeochemical processing occurs (McClain *et al.* 2003). For example, MDV stream hyporheic zones, where surface and subsurface waters mix, are hotspots for microbial activity and N uptake (Koch *et al.* 2010). A hot moment occurred in the MDVs during the flood year in 2001-02, when record high stream flow sent a plume of organic matter and nutrients into lake water columns, altering lake productivity (Bowman *et al.* in review; Foreman *et al.* 2004) and improving soil habitability (Barrett *et al.* 2008a, c; Nielsen *et al.* 2012). Microbial mats within streams and cryoconites represent hotspots and hot moments for microbial diversity and activity (Van Horn *et al.* in review; Stanish *et al.* 2013a; Kohler *et al.* 2015b). Hot moments were also addressed experimentally in MCM4 in a manipulation experiment that measured the impact of nutrient loading on productivity and diversity of plankton communities (Takacs-Vesbach and Priscu in prep). We will expand our examination of the impact of hotspot/hot moments on the MDV ecosystem in MCM5 to provide new information that will allow us to test our hypotheses.

1.1.5 Synthesis and Significant Publications. Our understanding of the MDVs has evolved significantly from MCM1-4. The following synthesis products have documented this evolution: (1) the book *Ecosystem Processes in Antarctic Ice-Free Landscapes* (Lyons *et al.* 1997, Balkema Press), (2) the book *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica* (Priscu 1998, American Geophysical Union), (3) a special issue of *BioScience* (1999, vol 49, no. 12), and (4) the book *Life in Antarctic Deserts and other Cold Dry Environments* (Doran *et al.* 2010, Cambridge University Press). Six of our PIs also made contributions to the book *Polar Lakes and Rivers* (Vincent and Laybourn-Parry 2008) published for the International Polar Year (IPY). In addition, we have helped pioneer a new series of children's books with our publication of *The Lost Seal*. Recently, we have collaborated closely with the Palmer LTER group to generate 3 papers for a special section of *BioScience* focused on the response of Antarctic marine (PAL) and freshwater (MCM) ecosystems to climate variation (in review). MCM investigators organized a NSF-sponsored workshop to establish a Terrestrial Observation Network for the McMurdo Dry Valleys (Levy *et al.* 2013c), helped direct other international efforts aimed at understanding MDV organismal and ecosystem resilience (Gutt *et al.* 2013), and organized an

international workshop on environmental stewardship in the MDV that will be held in May 2016. Our most significant contributions to the ecological literature during MCM4 include new findings on ecosystem responses to disturbance, and demonstrate biological connectivity among our landscape units.

Table 1. Ten most important papers published in the past 6 years and their significance. Throughout the rest of this text, citation of these papers will be noted in **bold font**. See a full list of MCM4 peer-reviewed publications in Supplemental Table.

Paper	Significance
Kohler, et al. 2015. Life in the main channel: Long-term hydrologic control of microbial mat abundance in McMurdo Dry Valley streams, Antarctica. <i>Ecosystems</i> , 18: 310-317.	Stream algal mat biomass is sensitive to hydrologic regimes, in part based on where in a channel mats exist. High flows scour some in the main channel, but promote growth in side channels.
Šabacká, et al. 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. <i>Geomorph.</i> , 155-156: 102-111.	Quantified the aeolian transport of particulate organic C, N, and P in the MDVs, ~100, 5, and 5 mg m⁻² yr⁻¹ respectively, during katabatic wind events (>20 m s⁻¹).
Michaud, et al. 2012. Cyanobacterial diversity across landscape units in a polar desert: Taylor Valley, Antarctica. <i>FEMS Microbio. Ecol.</i> , 82: 268 - 278.	Diversity increases down-valley due to aeolian transport. 16S rRNA data indicate most phylotypes common to other polar/alpine systems.
Nielsen, et al. 2012. The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. <i>Ecosphere</i> , 3: art17.	Response to a flood event on soil communities reduces salinity, which reduces soil osmotic stress. Floods onto soils have an important role in conditioning soil habitat.
Stanish LF, et al. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. <i>Canadian J. Fisheries Aquatic Sci.</i> , 69: 1405 -1419.	Flow intermittency is a species filter that increases habitat heterogeneity in MDV streams. Diatom diversity was greatest in streams with intermediate flow intermittency and low in highly intermittent streams.
Fountain, et al. 2014. The McMurdo Dry Valleys: A landscape on the threshold of change. <i>Geomorph.</i> , 225: 25-35.	Previously very stable glacial and buried ice are beginning to degrade, accelerating geomorphic change of the MDVs.
Okie, et al. 2015. Niche and metabolic principles explain patterns of diversity and distribution: theory and a case study with soil bacterial communities. <i>Proc. Royal Soc.-B</i> , 282: 20142630.	General diversity theory proposed that integrates metabolic principles and niche-based community assembly. Expectation that taxon niche widths should decrease along environmental gradients in cold climates was confirmed along an elevation gradient in MDVs.
Morgan-Kiss, et al. 2016. Photoadaptation to the polar night by phytoplankton in a permanently ice-covered Antarctic lake. <i>Limnol. Oceanogr.</i> , 61: 3-13.	MDV lake microbial communities respond to the transition from summer to polar night using differential adaptive strategies.
Fierer, et al. 2012. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. <i>Proc. Nat. Academy Sci.</i> , 109: 21390-21395.	MDV soils have the lowest levels of abundance and taxonomic diversity, but MDV functional diversity can be as high as temperate forests.
Stanish et al., 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. <i>Env. Res. Letters</i> , 8: 045006.	Diatom diversity in cryoconite holes co-varies with diversity found in nearby streams suggesting strong biological connectivity between glacier and stream communities.

1.2 ECOSYSTEM RESPONSES IN THE MCMURDO DRY VALLEYS

Below we summarize the primary results of our research on each of the main landscape units and our progress in modeling and synthesis:

1.2.1 Meteorology. Meteorological data are a core part of the MCM data set. The MDVs are extremely sensitive to changes in summer temperatures given that the local climate is poised on a threshold between melting and freezing of water (Obryk *et al.* in review). Doran *et al.* (2002a) showed that air temperature decreased by 0.7°C per decade between 1986-2000 (Fig 3a). Nylen *et al.* (2004) examined the climatology of katabatic winds, which are important in transporting biological material across the ecosystem (Šabacká *et al.* 2012; Michaud *et al.* 2012), and concluded that the warmest summers are associated with increased frequency of katabatic winds (Doran *et al.* 2008). Fountain *et al.* (2010) defined the spatial and temporal variation of precipitation in the valleys and identified a strong gradient with much less precipitation in western Taylor Valley. Fountain *et al.* (2010) also showed that ~50% of the

snow accumulation on the valley floor is due to redistribution from the valley walls. On a larger scale, the Southern Annular Mode (SAM), a pressure oscillation between high and mid-latitudes of the Southern Hemisphere, has been shown to produce colder temperatures in the MDVs when positive, and warmer temperatures when negative (Fountain *et al.* in review). These authors also concluded that there is no clear ENSO response, or ENSO impact on SAM in the MDVs.

1.2.2 Soils. In MCM4 we characterized the role of soil biota in mediating biological and geochemical connectivity, both above- (Ball and Virginia 2014a,) and below-ground (Fierer *et al.* 2012; Van Horn *et al.* 2013; Geyer *et al.* 2014; Schwartz *et al.* 2014; Sylvain *et al.* 2014; Ball and Virginia 2014b; Okie *et al.* 2015), and at the interface of terrestrial-aquatic ecosystems (Knox *et al.*; Michaud *et al.* 2012; Smith *et al.* 2012; Ball and Virginia 2015). We also explored how geomorphological changes to landscape units affect hydrological and geochemical structure (Levy *et al.* 2011, 2012, 2013b, c; Levy 2014). This led to an improved understanding of relationships between hydrological connectivity, geochemical heterogeneity, and habitat suitability (Ball and Virginia 2012), and provided a physical context for interpreting patterns of phylogenetic and functional diversity (Fierer *et al.* 2012).

Additionally, we described the genetic mechanisms involved in niche breadth (Adhikari and Adams 2011) and organismal and community responses to transiently altered hydrologic and geochemical conditions (Buelow *et al.* in review; Nielsen *et al.* 2012; Van Horn *et al.* 2014). Results from these studies revealed how patterns of local geography and landscape development are correlated with distribution ecology (Wu *et al.* 2011; Hogg *et al.* 2014; Adams *et al.* 2014; Convey *et al.* 2014) and local and regional influences over metacommunities (Sokol *et al.* 2013), allowing us to make predictions about how these communities may respond to future climate-driven changes (Nielsen *et al.* 2011).

1.2.3 Streams. The structure and functioning of stream ecosystems was explored during MCM4 in relation to the connectivity of materials and biota across the landscape (Figs 3b,c). Stream mats, comprised of cyanobacteria, heterotrophic bacteria, chlorophytes, diatoms, tardigrades, and nematodes, represent hotspots of biological activity on the landscape (Van Horn *et al.* in review). Diatoms (>45 taxa) represent the most diverse eukaryotic community in the MDVs (Kohler *et al.* in press; Esposito *et al.* 2006). Stream ecosystems in the MDVs range broadly in their characteristics from stream reaches with abundant coverage of mats to those with unstable substrate and short duration of intermittent flow containing low mat abundance. A network of algal mat transects was designed to evaluate mat biomass changes by scouring due to floods and desiccation during low flows. Analysis of the 20-yr monitoring record (Kohler *et al.* 2015b) showed that cyanobacteria and chlorophyte mats occur in stream thalwegs and are more strongly influenced by flood induced losses than the cyanobacterial mats at the stream margin. Analysis of the diatom communities showed that dominant diatom taxa changed along a continuum of inter-annual flow frequency, with abundant endemic taxa in streams that flowed only 3 times in the 22 years of record (Stanish *et al.* 2012). Similar relationships to flow regime were seen in the cyanobacterial and microbial communities (Stanish *et al.* 2013b).

Studies of mat recovery following an experimental scour (i.e. removal from channel substrate), showed that regrowth was inherently slow, i.e., less than 20% re-growth of average mat biomass over a 2 month flow season (Kohler *et al.* 2015a), and that greater nitrogen availability favored green algae and certain diatom taxa (Kohler *et al.* in press). We have also quantified stream transport of particulate organic matter in response to the daily rise in the flow of these streams (Cullis *et al.* 2014). The diatom taxa from the mats that are transported by these diel pulses come not only from the stream thalweg, but also from mats on the margins (Stanish *et al.* in review).

1.2.4 Glaciers. There has been an overall loss of glacial ice since 1993, with lower rates of loss during the 1993-2000 cooling period than after 2002. Glacial margins remain stationary, though there is potential for some advance as glacier ice becomes more ductile when it warms (Fountain *et al.* 2004). Given the cold climate and cold state of glaciers, our models and observations indicate that meltwater generation is occurring exclusively at the glacier surface. One important advance in MCM4 was the development of a

new model that quantified the importance of meltwater generation within the top 20cm of the glacier surface (Hoffman *et al.* 2014) – a layer coincident with cryoconite holes that host microbial and algal communities (Bagshaw *et al.* 2011, 2013; Stanish *et al.* 2013a).

1.2.5 Lakes. Long term monitoring data showed that ice thickness in Lake Hoare increased (0.11 m a^{-1}) between 1986 and 1999 in association with an annual air temperature decrease (Doran *et al.* 2002b). This cooling period was terminated in January 2002 by one of the warmest summers on record (Barrett *et al.* 2008b; Doran *et al.* 2008). Following this warm pulse, lake-ice thickness in all lakes has been decreasing between 0.07 and 0.18 m yr^{-1} in response to warmer air temperatures (Fig 3d). Because the ice covers attenuate PAR reaching the water column, ice thickness is directly related to the rate of PPR (Obryk *et al.* in review; Morgan-Kiss *et al.* 2016). Water column productivity (Fig 3f) and biodiversity is therefore indirectly linked to air temperature via its role in regulating ice thickness. Lake benthic mat PPR is also largely controlled by PAR (Hawes *et al.* 2014), and the thinning ice cover has also increased biomass accumulation in recent years (Hawes *et al.* 2016). These perennial mats, comprised mainly of cyanobacteria and diatoms, represent a net sink for carbon and other nutrients (Sutherland and Hawes 2009). Recent rises in lake level (Fig 3e) have created more benthic habitat at the lake margins while reducing PAR reaching the deeper mats (Hawes *et al.* 2013).

In MCM4 we examined the molecular diversity of bacterial, archaeal (Takacs-Vesbach *et al.* 2010; Vick-Majors *et al.* 2014) and protistan (Bielewicz *et al.* 2011; Xu *et al.* 2014; Dolhi *et al.* 2015) communities in the lake water columns and found that community diversity is spatially distinct within and among lakes. Owing to the logistical difficulties of sampling the MDV lakes during winter, little is known about planktonic microbial community responses to the cessation of PPR during the polar night, with the exception of a few studies during the seasonal transitions (Priscu *et al.* 1999; Kong *et al.* 2012b, a, 2014; Morgan-Kiss *et al.* 2016). Vick-Majors *et al.* (2014) used pyrosequencing of the small-subunit ribosomal RNA gene and showed that these light (Lizotte and Priscu 1992, 1998) and nutrient-limited (Priscu 1995; Dore and Priscu 2001) ecosystems exhibit low diversity overall, but that the autumn decrease in solar radiation coincides with shifts in microbial diversity across all three domains of life.

1.2.6 Integrative Responses across Landscape Units. In MCM1-3, we focused primarily on individual landscape unit (soils, streams, glaciers, lakes) responses to resource legacy, stoichiometric controls or physical forcing. We took a more integrated approach in MCM4, focusing on the connections among the landscape units. For example, we characterized the distribution of several prokaryotic and eukaryotic groups across each of the landscape units, as influenced by physical and aeolian processes (Michaud *et al.* 2012; Šabacká *et al.* 2012). We also showed how a discrete climatic event involving glaciers, snow patches, subsurface ice, and streams impact habitat suitability and the structure and functioning of soil communities (Nielsen *et al.* 2012). The integrative factor behind these changes lies in the significant geomorphological linkages among all landscape units. These linkages are driven by increased sediment on ice and solar radiation, and are likely to trigger dramatic hydrological, geochemical and biological responses in the near future (Fountain *et al.* 2014). There is also substantial evidence for environmental filtering among habitats, e.g., diatom communities in cryoconite holes on glaciers (Stanish *et al.* 2013a) and in ponds (Sakaeva *et al.* 2016).

1.2.7 Ecological Modeling. Our first models in MCM4 addressed physical and biogeochemical processes in distinct landscape units. A new model was developed (HEMM, hyporheic end member mixing) that estimates the amount of stream water that has passed through the hyporheic zone of a stream, based on the electrical conductivity and discharge measurements made at our stream gauges (Wlostowski *et al.*, in press, in review). Given the importance of hyporheic exchange on nitrogen and phosphorous transport and fate in streams, this model provides a foundation to new stream biogeochemical models. We are currently developing a landscape surface energy balance model, extrapolating the findings of Knox *et al.* (in press), that soil nematode populations are in part dependent upon the number of freeze-thaw cycles in a given year. We are using this model to explore how freeze-thaw cycles change with dynamic soil moisture.

We developed a metacommunity modeling framework to explore hypothesized links between landscape heterogeneity, ecosystem connectivity, and emergent biodiversity patterns (Sokol *et al.*, 2015, in review). The model is a zero-sum individual oriented lottery model, based on Hubbell's neutral theory of biodiversity model (Hubbell 2001) and modified to allow interactions between local habitat and species' traits to affect recruitment probabilities. Simulations can be parameterized based on environmental data and estimates of local and regional field observations. We implemented this modeling approach to link mass effects dynamics to patterns indicative of biotic homogenization in ponds in the temperate Baltimore Ecosystem LTER (Sokol *et al.* 2015). We have collected similar empirical datasets for MDV soil nematodes, bacteria and diatoms (Sokol *et al.* 2013; Sakaeva *et al.* 2016) that will be used in MCM5 to parameterize and validate new metacommunity models to explore alternative community assembly hypotheses. By studying pond diatoms in the MDVs and Cape Royds across McMurdo Sound we will be able to evaluate influence of long distance aeolian transport of microbes on regional community structure.

1.2.8 Environmental History. Much of the environmental history research during MCM4 focused on evaluating how information from the early expeditions to Taylor Valley during the "heroic era" of Antarctic exploration at the beginning of the twentieth century can guide contemporary ecological research in the region (Howkins 2016). Photographs, sketches, maps, and diary entries from the sledging expeditions of Robert F. Scott, Griffith Taylor, and Raymond Priestley offer snapshots of the environmental conditions of the MDVs one hundred years ago. Although historical information is not immediately transferable into modern data sets, environmental history research provides unique insights into ecosystem change over time that have important implications for contemporary ecological research. For example, historical research was used to locate ponds studied by early explorers in the MDV and Cape Royds to allow for comparison with archived samples from these expeditions. Work has also begun on the modern period of scientific research in the MDVs, which began with the International Geophysical Year of 1957-58 (Howkins 2014). Archival research has been conducted in New Zealand, Australia, Great Britain and the United States. Twenty oral history interviews have been conducted and transcribed with scientists who have worked in the MDVs. Through this research we have started to build detailed data sets about where and when human activity has taken place in the MDVs, as well as the nature of these activities, in order to address questions about human impact and the effectiveness of environmental management strategies.

1.2.9 Education and Outreach. MCM4 included a program of outreach and education activities for K-12 teachers and students, undergraduates and early career scientists, and the broader public. We have made numerous school visits, both in the United States and overseas, including Skype calls from the MDVs, allowing students to get direct insight into life at an Antarctic field camp. The MCM has a strong tradition of involving REU students, graduate students, and post-doctoral students in our fieldwork and research, which was continued and strengthened during MCM4. For example, immediately before the LTER All Scientists Meeting at Estes Park in September 2015, students associated with the McMurdo and Niwot LTER sites held a joint workshop at the CU Mountain Research Station. A number of outreach and education programs targeted at the broader public have been held at our home institutions across the United States. Public outreach is amplified because of frequent media visits to the MDVs and popular interest in our work. Two of our PI's (Doran and Priscu) have given TEDx talks involving MCM results. Another form of high-profile public engagement is our collaboration with various NSF-sponsored Artists and Writers projects taking place in the MDVs. Through participation in monthly conference calls and ASM sessions of the LTER Education and Outreach Group, we have contributed to broader activities in this area within the Network.

A component of the education and outreach work in MCM4 has centered upon the *Lost Seal* Schoolyard LTER book. Taking advantage of the international nature of Antarctic research, the *Lost Seal* has been translated into six languages. Bilingual versions of each of these translations will be published in early 2016 and all versions will be available on the MCM website. In Spring 2016, the *Lost Seal* translations will be highlighted at a special event at the American Museum of Natural History in New

York City. MCM CoPIs have also played a leading role in promoting and developing the Schoolyard Book Series within the LTER Network.

1.3 INTEGRATING INPUT FROM THE MCM4 SITE REVIEW

Our MCM4 site review occurred in Jan 2014. The review team visited McMurdo Station and many of our field sites. The team offered constructive ideas that have been embraced in MCM5. For example, the review team encouraged our emphasis on connectivity and recommended that we clearly distinguish between physical and biological connectivity in interpreting our results. This recommendation has been addressed directly in subsequent publications and in our hypotheses for MCM5. We have included a new collaborator in MCM5, Dr. Shawn Devlin, to help us address physical and biological connectivity across lake moats, an important transition zone between the aquatic and soil landscapes. The review team also cautioned that the metagenomic data that we were collecting in MCM4 would be too much for one PI to process. In MCM4 we collaborated with other experts to synthesize these data (Bowman *et al.* in review; Kong *et al.* 2012b, a, 2014; Vick-Majors *et al.* 2014; Okie *et al.* 2015; Dolhi *et al.* 2015). Dr. Rachael Morgan-Kiss has been added to MCM5 as a new CoPI to focus specifically on the poorly understood role of microbial eukaryotes (primarily protists) across landscape units in the MDVs. Morgan-Kiss has experience studying *in situ* processes using biophysical and biochemical measurements combined with -omic studies to understand the diversity, evolution, and adaptation of microorganisms. The review team asked us to consider whether the MDVs are in fact an end-member ecosystem and how this insight could be applied to other ecosystems. To address this issue we became involved in several cross-site initiatives where our data were applied to larger scale ecological questions, and have framed our MCM5 work to be more broadly transferable to other ecosystems (see Section 3.6). Finally, the review team observed that a majority of the outreach and education responsibility fell on the lead PI and suggested that another CoPI lead the outreach efforts, and that we needed to build the outreach section of our website to be more than a list of events. CoPI Howkins is now responsible for the outreach and education activities of MCM4 and will continue to do so in MCM5. A plan has been developed and the resources needed have been identified to transform our outreach website into an educational site for school children, university students, educators, and the general public.

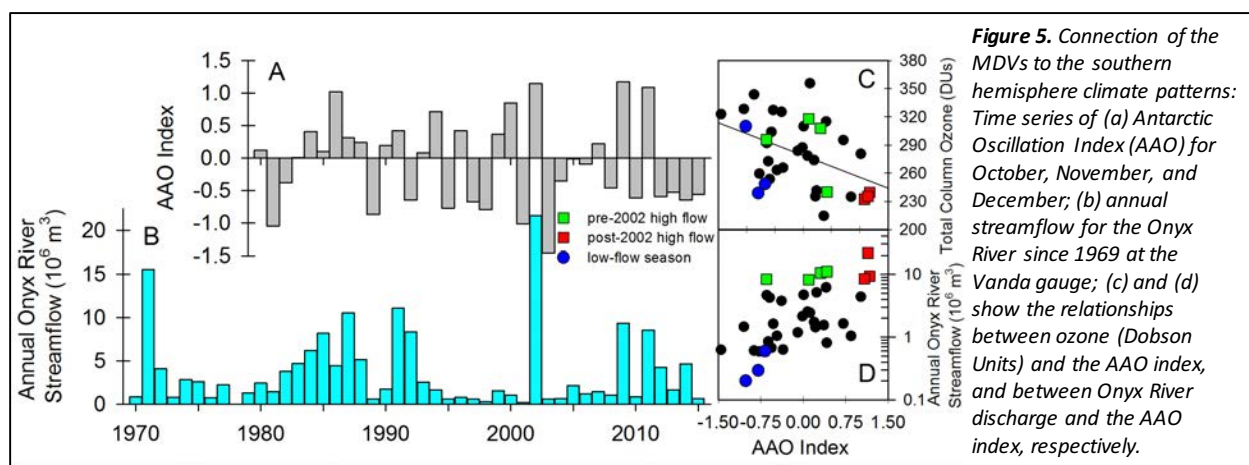
2. PROPOSED RESEARCH

The research proposed in MCM5 will be addressed by a team consisting of five early-mid career investigators (Adams, Barrett, Gooseff, Howkins, and Takacs-Vesbach) who joined the project in MCM4 and a new CoPI (Morgan-Kiss). These scientists will join Doran, McKnight and Priscu who have been with the MCM since its inception. A newly funded early career collaborator, Devlin, has been brought on to advance our new project objectives; we will strengthen our collaboration with Ian Hawes (University of Canterbury, NZ) to help address the new moat and benthic ecology questions.

2.1. INTRODUCTION

In MCM4 we hypothesized that climate warming would amplify ecosystem connectivity leading to enhanced coupling of nutrient cycles across landscapes and increased biodiversity and productivity throughout the system. Our previous hypotheses followed from our observations of synchronous and uniform ecosystem response to the cooling period of 1987-2001, which dampened connectivity among landscape units (Fig 3, Doran *et al.* 2002b). In the decade since the end of that cooling trend, streamflows and aeolian transport of material have increased, amplifying connectivity. The MDVs climate and surface energy balance is tightly coupled to regional atmospheric dynamics, specifically the Antarctic Oscillation (Fig 5), which appears to be at least partly correlated to the ozone hole.

Contrary to the predictions of some of our MCM4 hypotheses, not all ecosystem responses to increased connectivity have been synchronous or monotonic. For example, response of lake ice thickness and PPR to the flood year lagged behind the actual event. These lags were likely due to the thermal mass of the ice and the sediment inflow and reduced light levels (e.g., Foreman *et al.* 2004), but suggest that ecosystem level responses to future climate events will also be complex especially now that our research



focuses increasingly on the biotic responses. We also predicted that enhanced glacial melt would lead to increased liquid water availability and movement of nutrients across the landscape, stimulating biodiversity (Barrett *et al.* 2008b) and productivity (Foreman *et al.* 2004). However, soil wetting experiments and observed responses to natural events indicated that biotic responses could not be generalized for all taxa and that changes in hydrological connectivity were also associated with shifts in physical and chemical conditions such as sediment and solute mobilization and increased freeze-thaw cycles that also influence biotic communities (Fig 6a,b) (Knox *et al.* in press; Barrett *et al.* 2008b; Nielsen *et al.* 2012; Stanish *et al.* 2012; Kohler *et al.* 2015b). Thus, while our long-term records demonstrate synchronous responses of landscape units in the MDVs ecosystem to overarching climate drivers, discrete climate events (e.g., floods or katabatic wind storms) contribute to lagged responses of some biota and ecological processes.

As physical and biological connectivity increase across the MDV landscape, predicting the ecological responses to these changes becomes more difficult: *How does increased connectivity influence biological and functional diversity? How does physical and biological homogeneity affect ecosystem stability (resistance and resilience)?* These are fundamental ecological questions in the era of pervasive climate change and the MDVs provide a unique setting to explore these questions.

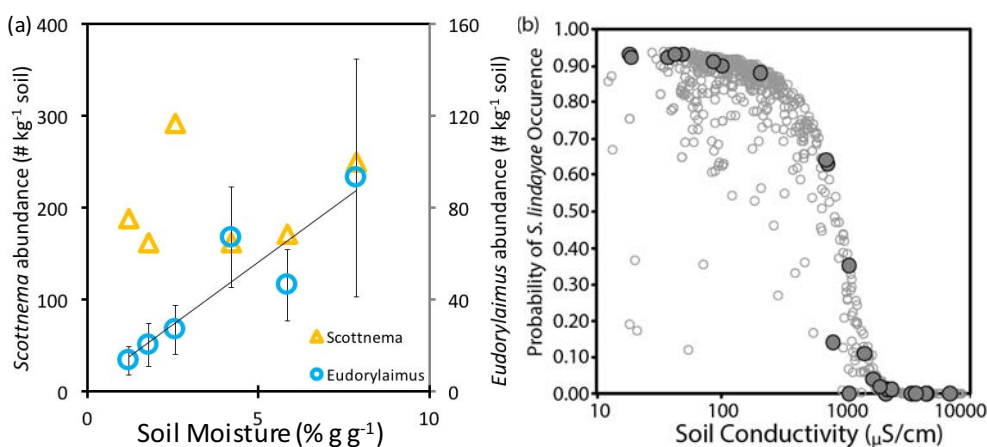


Table 2. Key Terms and Definitions:

Physical connectivity: The extent of abiotic interconnectedness. e.g., *the extent of water flow across landscape units and associated transport of solutes and materials.*

Biological connectivity: The extent of biotic interconnectedness. e.g., *the extent of gene flow across landscape units, movement of individuals among metapopulations and metacommunities.*

Disturbance: A biotic or abiotic *cause* which results in the ecological *effect* of either a stress at an individual (physiological) or ecosystem (functional) level, or a response at the population or community level; i.e., a perturbation (*sensu* Griffith and Philippot 2013). The disturbance can be temporally consistent (press) or episodic (pulse) and spatially isolated/patchy or uniform/widespread.

Stability: persistence of ecosystem structure and functioning following disturbance, a property of an ecosystem's resistance and resilience to disturbance (Holling 1973; Grimm and Wissel 1997; Gunderson and Holling 2001). e.g., *strong chemical stratification of the MDV lakes (Spigel and Priscu 1998) insulates deep waters from disturbances to the upper water column such as changes in ice thickness, stream flow and PAR.*

Resistance: The ability of an ecosystem to withstand a disturbance and associated stress (*sensu* Pimm 1984). e.g., *soil nematode populations are relatively unchanged by mild trampling disturbance (Ayres et al. 2008).*

Resilience: The capacity of an ecosystem to recover from disturbance and stress (Gunderson and Holling 2001); the magnitude of a disturbance (e.g., degrees of temperature, stream flow, or physical disturbance) tolerated by an ecosystem before significant change in structure and/or function is detected (Holling 1973). e.g., *rapid recovery of algal mat and diatom populations following removal (Kohler et al. 2015a).*

Homogenization: Any process that leads to a breakdown of ecological heterogeneity; a process of generating uniform patterns of ecosystem structure and functioning. e.g., *decreasing species diversity and evenness following resource subsidies (Van Horn et al. 2014, Schwartz et al. 2014).*

Synchrony: Simultaneous ecological responses or events. e.g., *simultaneous decreases or increases in air temperature, stream flow, lake levels and productivity.*

2.1.1 Evolution of the MCM Conceptual Model. Our overarching hypothesis in MCM1 was: **The structure and functioning of the MDVs are controlled by physical constraints.** This project developed the *legacy model* that helped us link geologic history to current ecosystem structure and functioning (Moorhead *et al.* 1999; Burkins *et al.* 2000a; Lyons *et al.* 2000a). The overarching hypothesis of MCM2 was: **Past climates in polar desert environments strongly overprint present ecosystem structure and functioning.** In MCM2, contemporary spatial distribution of biomass and biodiversity were explored in the context of legacies manifest across the landscape (e.g., soil salt accumulations, paleolimnologic evidence for valley-filling lakes and deposits of ancient lacustrine organic matter in soils). This idea of legacy resources, e.g., organic matter, as a driver of contemporary ecosystem structure and functioning was refined to balance ancient and contemporary controls in MCM3, which addressed the overarching hypothesis: **Biodiversity and ecosystem structure and function in the McMurdo Dry Valleys are dictated by the interactions of climate legacies with contemporary biotic and physical processes.** During MCM2, we observed an austral summer of abnormally high temperature and meltwater generation (the 2001-02 'flood year'), and since 2002 we have observed more saturated soils and water tracks across the landscape. The climate projections for the region predict warming over the next 50-100 years (Chapman and Walsh 2007; Walsh 2009). This projection led us to develop the MCM4 overarching hypothesis focused on connectivity of our landscape and ecosystem: **Climate warming in the McMurdo Dry Valley ecosystem will amplify connectivity among landscape units leading to enhanced coupling of nutrient cycles across landscapes and increased biodiversity and productivity within the ecosystem.** To address these predictions, we conducted several experiments to test the response of the ecosystem to wetting. We learned that increased meltwater movement across the landscape does not yield consistent (e.g., synchronous and monotonic) responses from biota and landscapes with the MDVs ecosystem, indicating that the response to increased connectivity is more nuanced than originally expected. In MCM5 we propose an evolved conceptual model of ecosystem responses to amplified connectivity (Fig 7), due to increased surface energy balance (Fig 2 b,c). These ecosystem responses include changes in biological connectivity, in which inter-patch dispersal is enhanced.

2.2. HYPOTHESES

2.2.1 Overarching Hypothesis. MCM5

incorporates an evolved conceptual model that explores ecosystem responses to amplified physical connectivity in the MDVs in response to changing climate. We will explore how those responses will be influenced by the resource legacies, such as the distinct biogeochemical patterns imparted by the history of lake inundation and recession. Anticipated outcomes of enhanced connectivity are changes in distribution of material (organic matter and nutrients) and biota toward greater homogeneity among and within landscape units, in effect dampening the influence of resource legacies. While the MDVs have undergone a decadal transition from summer cooling to a relatively stable summer temperature regime (Fig 3a), the forecast for the coming decades is regional warming (Chapman and Walsh 2007, Walsh 2009). Hence, our expectation is that summers of intense ice melt and permafrost thaw (as were observed in 2002, 2009 and 2011) will become more frequent and drive greater physical connectivity. We have evolved our overarching hypothesis from MCM4 to emphasize an expected shift toward biotic homogenization, in which some taxa will increase while others decrease their abundance, with unknown changes in ecosystem function. The overarching hypothesis for MCM5 is:

Increased ecological connectivity within the MDVs ecosystem will amplify exchange of biota, energy and matter, homogenizing ecosystem structure and functioning.

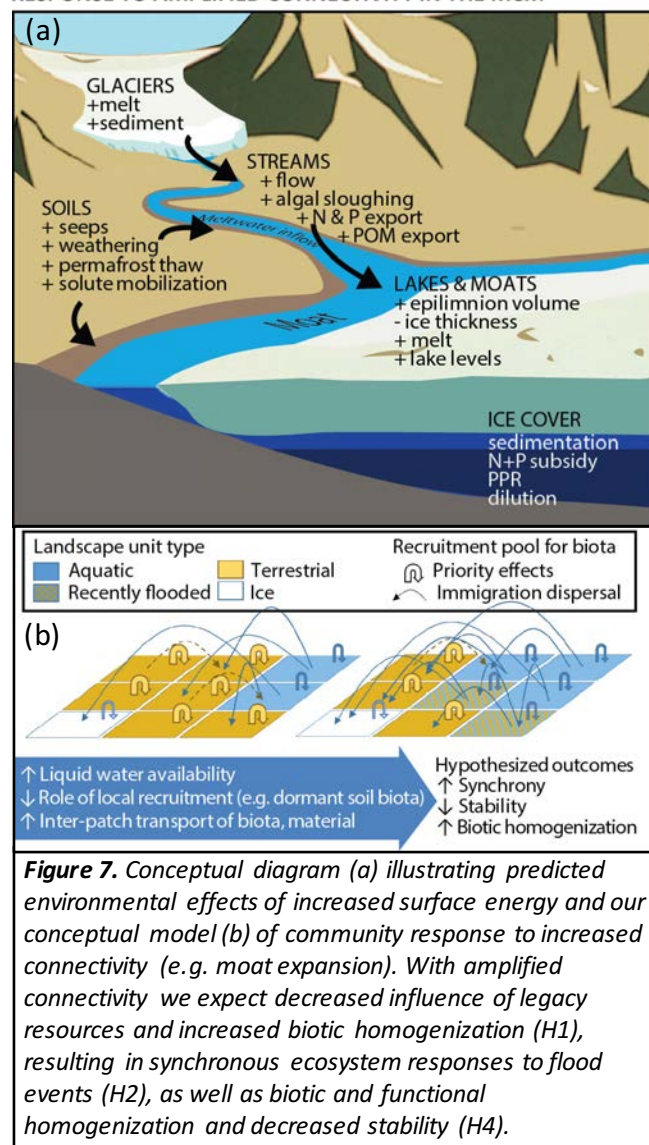
Whereas the MDVs ecosystem is specifically identified, this is a general hypothesis that could be tested in many different ecosystems. Hence, our contributions to ecosystem science from MCM5 are expected to be both fundamental and translational.

2.2.2 Working Hypotheses. Below we pose four working hypotheses, provide justification for each, and articulate expected outcomes that would provide confirmation. As stated, they are testable in any ecosystem (e.g., Arctic lakes, grasslands or arid lands), which positions our products (findings, evolution of conceptual models, publications, etc.) as tools that can inspire replicated experiments/approaches at other sites. The hypotheses will be tested with ongoing and new experiments, and monitoring activities.

H1. Enhanced exchange of energy and matter diminishes the influence of resource legacy, homogenizing spatial variability of ecosystem structure and functioning.

The increased exchange of energy and matter among landscape units will increase the homogeneity of ecosystem structure, thereby reducing the variability across landscape units. We expect that increased

RESPONSE TO AMPLIFIED CONNECTIVITY IN THE MCM



hydraulic connection between glaciers and streams will cause long streams to become more dilute in their major ion and nutrient chemistry. However, greater connectivity of streams and soils may also accelerate chemical weathering and enhanced biogeochemical transfer of some solutes. Lakes will respond to increased connectivity by continuing to increase in volume expanding and potentially diluting this habitat. Past soil wetting experiments and observational studies generally show shifts in relative abundance among soil species following wetting, with distinct responses among trophic levels. Climate driven shifts in soil moisture alter the structure of invertebrate communities (Fig 6, Barrett *et al.* 2008b). Soil bacterial communities exhibit less sensitivity to increased water availability, in stark contrast to dramatic shifts in bacterial diversity and community composition following organic matter additions (Buelow *et al.*; Schwartz *et al.* 2014; Van Horn *et al.* 2014). In all of these examples, we expect that the shifts of the conditions in the different landscape units will result in altered community composition, nutrient availability and productivity. We will test H1 with on-going and new experiments and monitoring activities. Our long-term monitoring program provides the opportunity to quantify ecosystem response to natural changes in connectivity across the landscapes, while contemporary experiments will test specific controls of changes in connectivity on ecosystem responses. For H1 to be accepted, community responses (e.g., diversity and species composition) across landscapes must begin to resemble each other as climate warms. For example, increased stream inputs into the lakes will preferentially stimulate specific groups of algae or bacteria (Section 3.2.4), or microbial communities in inundated soils will come to resemble moat sediment communities (Section 3.3.1).

H2. Amplified connectivity increases synchrony of ecological responses among landscape units.

Synchronous ecological responses were observed during the cooling period from 1987-2000, which ended in January 2002 (Fig 3a; Doran *et al.* 2002a). While the mean summer air temperatures have remained cool, the mean summer solar flux has remained high; no trend in either of these parameters has been detected for more than a decade. However, during this summer climate stasis, the landscape experienced increased connectivity, largely because of increased stream flow (Fig 3b) and increased winter katabatic winds. The MDVs ecosystem has responded with an end to and in some cases a reversal of trends previously observed during the cooling period (e.g., stream algal mat biomass has increased since 2003, Fig 3c). Temporal aspects of ecosystem responses are best evaluated in the context of long-term studies so that potential lags in the system can be evaluated (e.g., lags in stimulation of lake productivity in response to nutrient pulses). We will test H2 through a combination of long-term monitoring (Sections 3.1.2-8) and new (Sections 3.3.1, 3.3.2) and ongoing experiments (Sections 3.2.1, 3.2.3, 3.2.4). For H2 to be accepted, either natural increases in connectivity or experimental manipulations simulating increased physical connectivity (e.g., wetting experiments) will have to be shown to drive temporal changes in ecosystem functioning that are coincident and synchronous across landscapes.

H3. Disturbance increases connectivity and accelerates shifts towards homogeneity in ecosystem structure and functioning in the MDVs.

The MDVs experience two general types of disturbance – direct human impacts and disturbance due to climate variation. Direct, local human impacts include emissions from local fossil fuel consumption, chemical spills, distribution of non-native species, and physical disturbance associated with trampling (Ayres *et al.* 2008), vehicles or camps. Climate disturbances include for example flooding in streams (leading to scour and enhanced erosion) and soils (increased soil moisture and mobilization of salts). These disturbances can be caused by increased snow/ice melt, enhanced aeolian transport of soil/sediment, changes in albedo of ice and soil surfaces, and increased surface energy balance that results in permafrost degradation (Levy *et al.* 2013a). Some of these disturbances are discrete and some are more widespread in time and space (i.e., pulse vs. press events).

We will test H3 through long-term monitoring and two new experiments. Our continued long-term monitoring will capture climate variability as it occurs (as we have over the past 24 years) and long-term responses of ecosystem structure and functioning. Two new studies are proposed to explore

mechanistic ecosystem responses to (i) permafrost degradation on stream banks (Section 3.3.3), and (ii), human disturbance to the MDV system associated with occupation (Section 3.3.4).

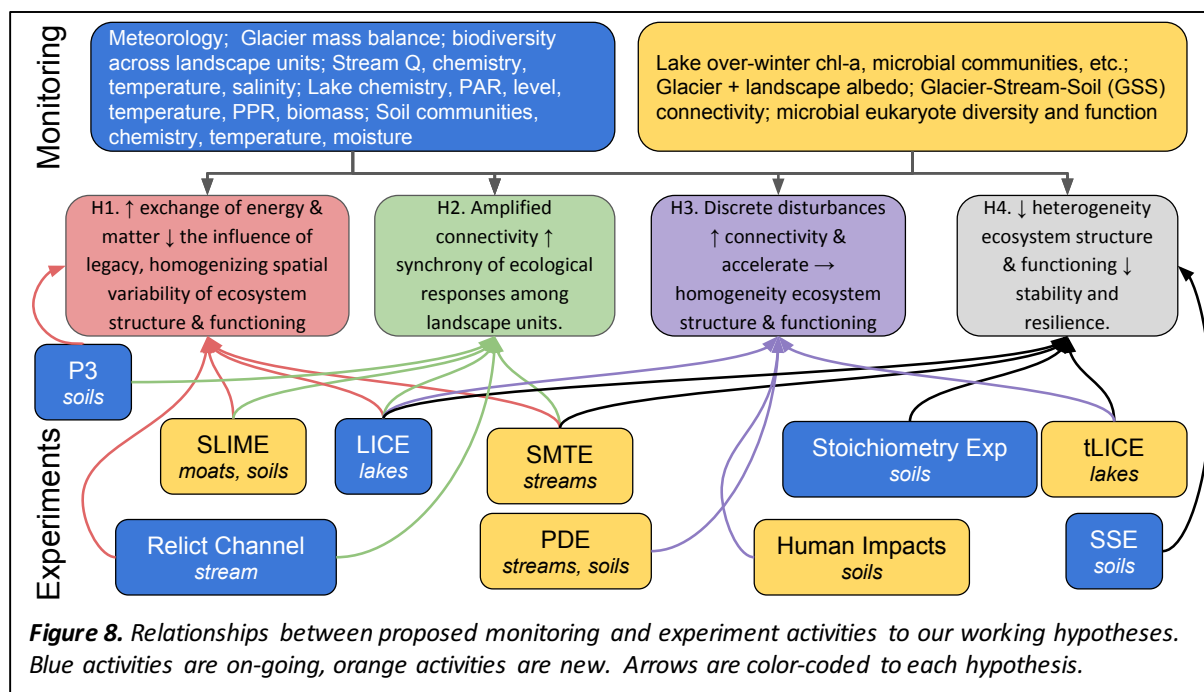
H4. Decreased heterogeneity of ecosystem structure and functioning reduces stability (resistance and resilience) of the MDVs ecosystem.

Ecosystem structure (e.g., species richness, standing biomass) and functioning (e.g., PPR, nutrient cycling) are expected to be strongly influenced by the diversity of biotic communities and the structure of food webs. As such, a negative impact to one element of the ecosystem will be compensated for, and the resultant system will become more resilient and stable (Micheli *et al.* 1999; Gonzalez and Loreau 2009). Despite low organismal diversity of upper trophic levels in the MDVs, homogenization is expected to result in even lower diversity. We propose that a simplified, homogenized community will be less resilient to changing conditions (e.g., Vasseur and Fox 2009) and therefore less stable. Similarly, ecosystem functions (e.g., nutrient cycling, metabolism) in a homogenized system will be conducted by fewer species. Hence, the stability of ecosystem functioning may be jeopardized by the diminished resilience of the ecosystem following species removal or populations declines, as has been observed for key species following dramatic climate events (Barrett *et al.* 2008a, b; Stanish *et al.* 2013a; Kohler *et al.* 2015a).

H4 will be tested by conducting transplant experiments in streams and lakes (Sections 3.3.2 and 3.3.5) in concert with continued long-term experimental amendments of soils (Section 3.2.2). Transplant experiments will consist of moving cyanobacterial mats between streams, and transplanting isolated (in dialysis tubes) plankton communities within lakes and between moats and lake water columns to determine community responses to physical and biogeochemical conditions that may occur as the MCM continues to warm. The long-term soil experiments (>10 yr) consist of amending soil plots with nutrients and water to study the impacts of homogenization of the soil nutrient and physical status on community structure and functioning.

3 RESEARCH PLAN

Each of the 4 working hypotheses will be tested with an integrated set of new and continuing studies (Fig 8) as described below.



3.1 CONTINUING AND NEW LONG-TERM MONITORING

3.1.1 Meteorology [Doran]. The MCM maintains one of the longest-running automatic weather station networks in Antarctica. The Lake Hoare meteorological station has been operating since 1987 with just one short data gap in 2012 (Fig 3a). There are currently 16 stations being run by the MCM (Fig 1). All stations are based on Campbell Scientific data loggers and have as their minimum sensor suite, temperature, relative humidity, wind speed and direction, and solar flux. Additional measurements depending on location include: soil temperatures at 0, 5 and 10 cm depth, PAR, longwave radiation, precipitation, snow on ground, air temperature at 1m (glacial stations), wind speed/direction at 1m, barometric pressure, and aeolian particle count. Data are saved both on memory cards and telemetered in near real time to satellite via Iridium phone. We propose to continue operating the network largely as is, but are assessing if we can decommission redundant stations to reduce the logistics and cost associated with maintenance.

We propose to initiate a regular examination of satellite imagery in MCM5 to augment our meteorological data. High-resolution satellite imagery will document snow cover on the ground, and the size of lake moats through the season. The Polar Geospatial Center at the University of Minnesota will assist in this effort by providing geo-rectified imagery (see letter from Paul Morin).

3.1.2 Lakes [Priscu, Morgan-Kiss, Doran, Hawes, Devlin, Takacs-Vesbach]. Core measurements in the water columns of Lakes Bonney (east and west lobes), Fryxell, Hoare, and Miers will continue and be combined with new methods that focus on collection of winter data and a more detailed analysis of protist communities. Benthic mat monitoring will also continue to examine long-term linkages between benthic and water column metabolic processes and biodiversity. Given the expanding moat area related to lake level rise, we will initiate new measurements of biogeophysical conditions in the moats to address our hypotheses related to ecosystem connectivity.

Autonomous Lake Profiling System (ALPS). The lakes of the MDVs are inaccessible for ~7 mo each year (during the dark when logistical support is not available). Limited studies during the spring and fall transitions (e.g., Lizotte *et al.* 1996; Takacs and Priscu 1998; Priscu *et al.* 1999; **Morgan-Kiss *et al.* 2016**) provided the first evidence that the lake communities remain metabolically and phylogenetically dynamic during winter. We recently initiated deployment of two ALPS which are comprised of three McLane Laboratories devices: one Phytoplankton Sampler (PPS), one Remote Access Sampler

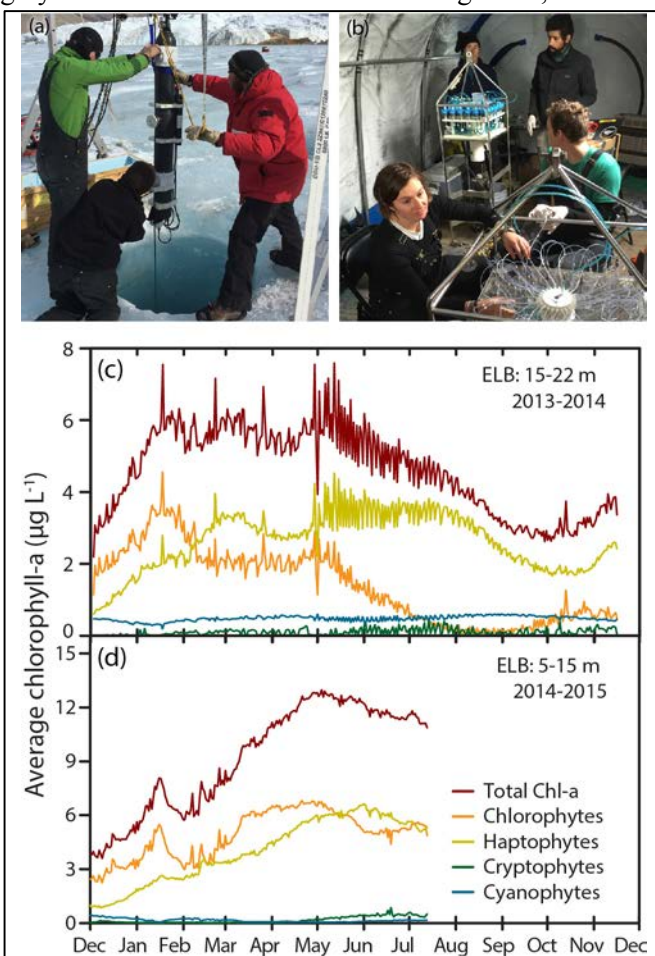
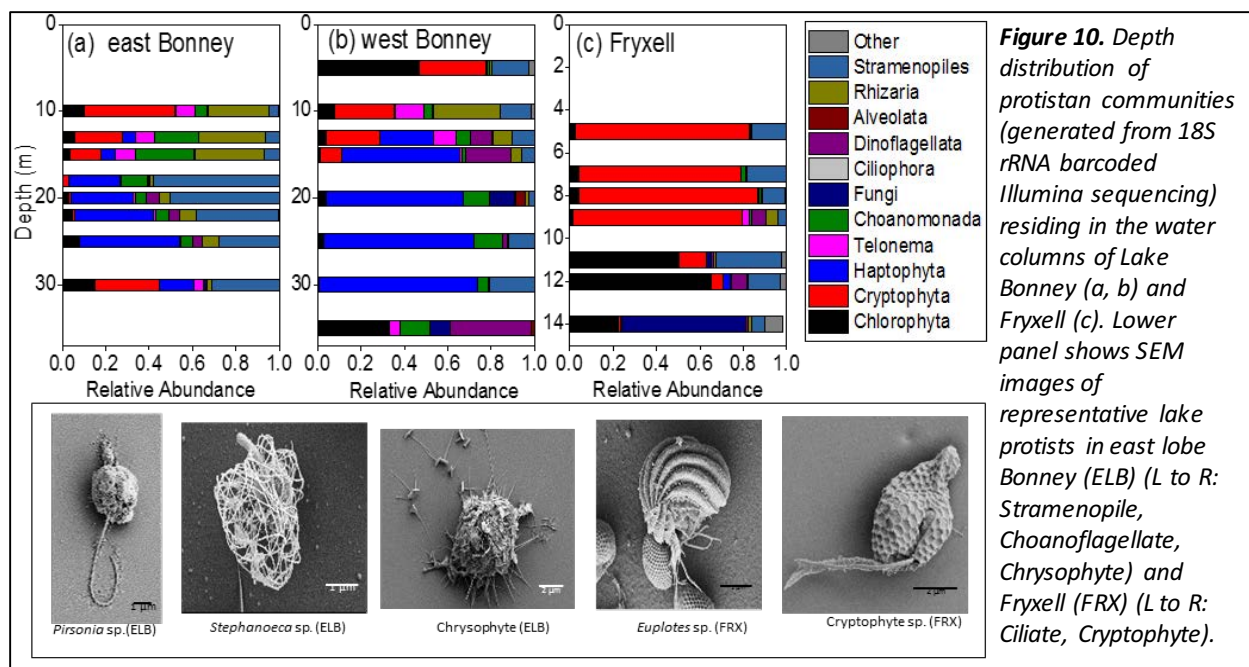


Figure 9. Year-round deployment of ITP and fluoroprobe (a), and RAS and PPS (b) in East Lobe Lake Bonney. Data from deep (c) and shallow (d) water fluoroprobe deployments show that total chlorophyll-a remains high through much of the polar night (April to late September) and that there is a general decrease in chlorophyte chlorophyll with a concomitant increase in haptophyte chlorophyll following the onset of total darkness (~May).

(RAS), and a modified Ice Tethered Profiler (ITP, Fig 9). The PPS and RAS instruments are programmed to collect and preserve lake water samples from the primary productivity maxima of Lake Bonney for community and biogeochemical analysis at 22-day intervals through the year. The ITP, which includes a CTD, a spectrofluorometer (fluoroprobe), and oxygen and CO₂ sensors, is set to profile a selected layer in the water column. Preliminary data show that chlorophyll *a* in the shallow (5-15m) waters increases for four months (February-May) following the onset of darkness whereas deep (15-22m) water chlorophyll remains relatively constant (east lobe) until late winter (August) (Fig 9c,d). Late winter loss rates are balanced by rapid phytoplankton growth in mid-October as solar radiation increases in the water column. Chlorophytes, which dominate the water column during summer, are replaced by Haptophytes during winter, indicating that Haptophytes persist in winter by alternative modes of metabolism while Chlorophytes may retain their photosynthetic apparatus long after solar radiation has disappeared. We will continue to deploy the ALPS in MCM5. *Data from the ALPS will expand the temporal scale of our lake monitoring program and provide critical information that will be used to test H1, H2, H4.*

Microbial Eukaryotes (Protists). Measurement of diversity and function of protists are a new focus in MCM5. While protists are ubiquitous across all aquatic ecosystems (Montagnes *et al.* 2012), their positions at both the bottom and the top of the foodweb in our study lakes (Priscu *et al.* 1999) makes them key players in the microbial loop (Laybourn-Parry 2009). Photosynthetic protists produce the vast majority of autochthonous organic carbon in the MDVs lake water columns, while heterotrophic nanoflagellates and ciliates are the top predators of bacteria and smaller protists (Fig 10) (Bielewicz *et al.* 2011; Kong *et al.* 2012b, 2014; Dolhi *et al.* 2015). We will use flow cytometry to characterize protist populations based on size, morphology and fluorescence characteristics (red, photosynthetic; lysotracker-green, heterotrophic), and will monitor protist taxonomic diversity (i.e., 18S rRNA) as described in Section 3.1.8. Preliminary data indicates that Lakes Bonney and Fryxell are occupied by taxonomically distinct protistan communities which possess diverse metabolic versatility, including mixotrophy and parasitism (Fig 10, Li *et al.* in review). This new focus on protists will expand our understanding of carbon and energy cycling in MDV food webs and *test hypotheses H1, H2, H4 in one ongoing (Section 3.2.4) and two new (Sections 3.3.1 and 3.3.5) experiments.*



Benthic Mats. Benthic mats are major contributors of biomass and diversity in the MDVs lake ecosystems and have been shown to be highly sensitive to environmental changes (Hawes *et al.* 2013, 2014, 2016; Mackey *et al.* 2015). We will continue to monitor productivity, diversity and

biogeochemistry of benthic mats in Lakes Fryxell, Hoare and Miers and integrate information on mat structure and functioning with soil and lake processes. *Ongoing research on benthic lake mats will be integrated with new research focused on lake moats to examine the spatial and temporal transitions in composition and function that occurs as soils are inundated with lake water (Section 3.1.3).*

3.1.3 Moats [Doran, Devlin, Hawes, Morgan-Kiss, Priscu, Takacs-Vesbach]. The moats are a new focus in MCM5. Moats form around the lakes during the austral summer in response to increased solar radiation and associated stream input (Fig 2). The moats are dynamic and their size varies from meters to tens of meters wide, and can occupy over 10% of the lake surface area (Fig 11). The open moat water represents the only part of the lakes that (i) interacts directly with the atmosphere where gases can diffuse across the air-water interface (Priscu *et al.* 1996), (ii) interfaces directly with inundated soils along the shoreline (Gooseff *et al.* 2011), and (iii) forms a mixing zone with inflowing stream water (Moore 2007). The degree of connectivity between the moats and the under ice water columns is poorly understood.

Thermistors and conductivity sensors will be deployed in horizontal arrays to measure timing of melt and temporal evolution of the size of the moat compartment. Moat biogeochemistry will be monitored using CTD, fluoroprobe and discrete water sampling in response to stream discharge. Benthic mats will be sampled using “catwalks” and/or through holes drilled in the ice allowing samples to be collected

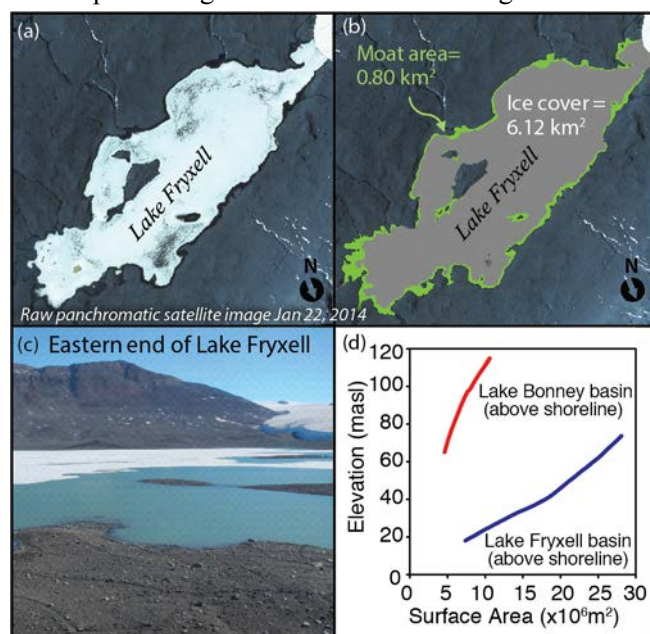


Figure 11. Satellite images of L. Fryxell showing (a) a raw satellite image, (b) lake ice and moat area, (c) expanded view of the moat in Fryxell, and (d) relationship between lake elevation and surface area in Bonney and Fryxell.

without disturbing the community. Particulate C, N, P, chlorophyll-a, phycobilins and AFDW of benthic biofilms will be analyzed as outlined in Hawes and Schwartz (2001). Gross and net PPR will be estimated as oxygen exchange using in situ light and dark benthic chambers (Devlin *et al.* 2016). The taxonomic composition of benthic communities (i.e., SSU rRNA gene diversity), functional diversity measured by qPCR of specific genes (i.e., proxies for biogeochemical cycles – e.g., carbon and N₂-fixation, methanogenesis), and the organization of organisms by microscopy and pigment analysis will be determined. Given the paucity of information on moats, these new long term investigations will determine *the degree of physical connectivity with the lake water column and the roles of cyclical (freeze-thaw dynamics), disparate (ice sheet grounding dynamics), and climatic disturbances responsible for increased melt, all of which will provide context for addressing H1 and H2.*

3.1.4 Streams [Gooseff, McKnight]. We maintain a network of 17 stream gauges in 3 valleys, including two on the Onyx River, the longest river in Antarctica (25 km). The Onyx record was initiated in 1968 by New Zealand scientists (MCM took over responsibilities for these in 1993). The gauges measure stage, electrical conductivity (EC), and temperature every 15 min. Seven of the gauges have real-time data telemetry (supported in part by UNAVCO; see letter of support). Our stream team deploys each season to operate and maintain these gauges to ensure accurate records are being collected. The team also collects chemistry samples (analyzed for major ions, nutrients, alkalinity, DOC) during gauge visits. The streamflow records are used to quantify connectivity dynamics (quantity and timing) between glaciers, streams, and lakes, and provide the opportunity to evaluate the response of surface energy balance changes in the MDVs. The EC records are further used to determine how much dilute glacial meltwater has interacted with sediments or soils en route to the stream gauge (Wlostowski *et al.* in review). *The*

stream records provide a direct measure of hydraulic connectivity among landscape units, providing important context and support for testing H1 and H2.

Algal Surveys. A total of 16 transects were established in MCM1 to conduct repeat monitoring of stream benthic mats (1-3 lateral transects on 10 streams representing both abundant and sparse mats). During MCM1-3, these sites were surveyed (topographic) and sampled (mat biomass and Chlorophyll *a*, preserved samples for diatoms and morphological analysis of algae, stream water quality) on a 2-3-year cycle. In the past 5 years we have incorporated Terrestrial LiDAR Surveys (TLS) at these transects (with support from UNAVCO; see letter of support) to quantify 3-D changes in the stream reaches due to scour and deposition in the streambed (Crisp 2015). Each transect section is scanned every ~3 years. These data provide insight into the persistence of different types of microbial mat communities as channels undergo geomorphic change due to floods (Crisp 2015). We propose to continue these regular survey activities through MCM5 with support from UNAVCO for GPS and TLS data collection. *The data from annual stream algal surveys directly supports testing H1-H4.*

3.1.5 Glaciers, Active Layer, and Permafrost [Gooseff]

Glacier Mass Balance. Our long-term (since 1993) monitoring of several glaciers in the MDVs has largely been focused on glacier mass balance with measurement locations distributed across each glacier to track accumulation at upper locations and provide an estimate of net ablation at lower elevations. These measurements provide one opportunity (albeit at a gross scale) to evaluate where meltwater is generated during the summer. *Combined with the streamflow records, these data provide direct quantification of glacier-stream connectivity, providing context for testing H1 and H2.*

Landscape Albedo. A new instrument package designed to be carried under a helicopter was used in the 2015-16 field season to measure the reflected shortwave radiation from glacier ice, soils, and lake ice that was. These data can be normalized to the incoming solar radiation (measured at met stations) to calculate distributed albedo. When collected several times through the season, these results will allow us to evaluate how snow distribution and physical changes to glacier and lake ice impact the amount of incoming radiation that is absorbed, and allow to track the influence of deposited sediment on ice surfaces. *These data are important for quantifying the long-term changes in energy connectivity between the atmosphere and the landscape (i.e., testing H1).*

Active Layer & Permafrost. Five active layer monitoring stations (ALMSs), equipped with temperature, soil moisture, and salinity sensors, have recently been installed. Each station has 4-6 sensor ‘chains’ allowing profiles to be obtained down into permafrost. Two ALMSs are located on streams (Green Creek, Von Guerard Stream), so they have sensor ‘chains’ installed from the thalweg out to the shoreline and dry soil beyond. Two ALMSs are similarly deployed on water tracks (zero-order drainages of snow/ice melt that rarely have surface flow). The 5th ALMS is deployed in dry soil (4 chains) near a long-term soil experimental site on the south shore of Lake Fryxell. A 6th will be deployed on the shoreline of Lake Miers during the 2016-17 field season. *These stations provide data to quantify the connection of the atmosphere with soils, especially the bidirectional fluxes of heat and moisture providing context to testing H1 and H2 in soils and streams.*

3.1.6 Soils [Adams, Barrett]. We propose to maintain long-term measurements of soil biodiversity and biogeochemical processes in soils of Taylor, Miers and Garwood Valleys. An elevational transect (established in Taylor Valley in 1993 and extended to Miers and Garwood Valleys in 2012), control plots in ongoing experiments such as the stoichiometry experiment (established in 2007), biotic effects experiment (established 1999), and long term manipulation experiment (established 1993) are at the core of MCM soil monitoring in which invertebrate communities, microbial biomass, soil chemistry and soil respiration are measured annually (Knox *et al.* in press; Barrett *et al.* 2008a, b; Nielsen *et al.* 2012; Smith *et al.* 2012). We also have a permanent transect established in the Lake Bonney catchment, a natural experimental site of previous warming pulses, to determine the long-term effect of increased water connectivity on biotic and soil/sediment variability across the landscape. New soil monitoring plots will be established at transects that extend from the lake moats to the dry soils to address our hypotheses

related to the effects of lake level rise on long-term soil dynamics in warmer valleys, and to help us predict the ecological transitions that may occur in Taylor Valley as climate warms. We will also establish a new monitoring study of moss and algal ground cover and production in near-stream environments and dry soils using similar protocol to the stream algal mat surveys described above and supplemented with analysis of satellite imagery from PGC to detect the active signal of Chlorophyll *a* in mat communities (Salvatore 2015). Such information is essential to refine production and C models for dry valleys soils (Burkins *et al.* 2000b, 2001; Barrett *et al.* 2008c; Ball *et al.* 2009; Ball and Virginia 2014a, b, 2015) and work toward closing the dry valley organic matter budget. *These data provide information that will allow us to test the soils component of H1-H4.*

3.1.7 Cross-Landscape Monitoring - Glacier-Stream-Soil (GSS) [Gooseff, Barrett, Adams, Devlin, McKnight]. Streams are intimately connected to their glacier sources, where meltwater is dilute in nutrients and major ions. As stream water flows downstream (longitudinally) it interacts laterally with hyporheic zones, with materials deposited into the channel, and surrounding soils, thus increasing solute load (Gooseff *et al.* 2002). Consequently, long streams tend to have higher solute concentrations than shorter streams (Gooseff *et al.* 2011; Wlostowski *et al.* in press). Longer streams provide greater opportunity for interactions between streams and surrounding soils because these connections are driven by mineral weathering and biogeochemical cycling in hillslope soils/sediments and by aeolian deposition in the stream channel, which are enhanced with greater stream length. Stream channels are incised into the landscape and therefore collect aeolian-transported material and accumulate windblown snow, which melts out early in the summer. Hence, greater lateral transfer of soil, associated biota, salts, and nutrients may occur in longer streams, which accumulate more snowpack than shorter streams. We have yet to investigate the influence of these lateral transfers from soils to streams on stream processes and biodiversity. GSS will provide new quantification of soil to stream connectivity, and over the long-term, its dynamic nature.

We propose a new study to examine lateral and longitudinal connections between glaciers, headwater ponds (a few streams have these), soils, and streams, and to build upon the current design and network of algal survey transects (Section 3.1.4). We will augment the algal survey network by establishing new sampling transects along 4 long streams and 4 short streams to document lateral connectivity of the stream corridors with the surrounding landscape, and the longitudinal evolution of stream communities and biogeochemistry. Two of each stream type will have a headwater pond. The stream margins are characterized by strong biogeochemical gradients that structure soil invertebrate and microbial communities (Fig 6, Treonis *et al.* 1999, Barrett *et al.* 2002, Zeglin *et al.* 2011). At each transect, we will conduct topographic surveys, sample the stream algal mats and make in-situ measurements of photosynthetic activity (PAM chlorophyll-*a* fluorescence), collect soil and sediment samples for soil moisture, chemical, biological (soil invertebrates, diatoms, SSU rRNA gene diversity), and quantify AFDM in the stream channel, riparian areas and in the area beyond the banks. Stream water samples will also be collected for nutrient and major ion analyses. For those streams with ponds in their headwaters we will collect similar samples (mat samples, soil/sediment samples, water samples) in the littoral areas near the pond outlets (Sakaeva *et al.* 2016), to relate pond communities and conditions to those downstream. At the beginning of each season, we will collect snow cores from snow packs within the channels, which occur in the same locations year to year, in order to estimate the deposition of aeolian sediment during the winter. Sediment collectors will be deployed in and near stream channels at these transects to collect deposition at these points.

We hypothesize that short streams with headwater ponds will demonstrate less evidence of connectivity to the surrounding soil communities than short streams without headwater ponds. Long streams without ponds should show the greatest connectivity to soils because of opportunity to receive more inputs from adjacent soils, and no buffer between the glaciers and channels and greater opportunity for downstream evolution of ecosystems (communities, biogeochemistry, etc.) than short streams. Whereas we can test H1 by conducting this set of surveys one time, we can test H2 by repeating these surveys through differing seasonal conditions (e.g., Fig 2) and comparing the temporal variance of

correlation of populations between soils and streams. *An explicit goal of MCM5 is to document and quantify the spatial and temporal connections between landscape units, and this new activity will allow us to directly characterize the connections between streams and glaciers and streams and soils, testing H1 and H2.*

3.1.8 Cross-Landscape Monitoring: Integrative Metagenomics [Takacs-Vesbach, Priscu, Adams, Morgan-Kiss].

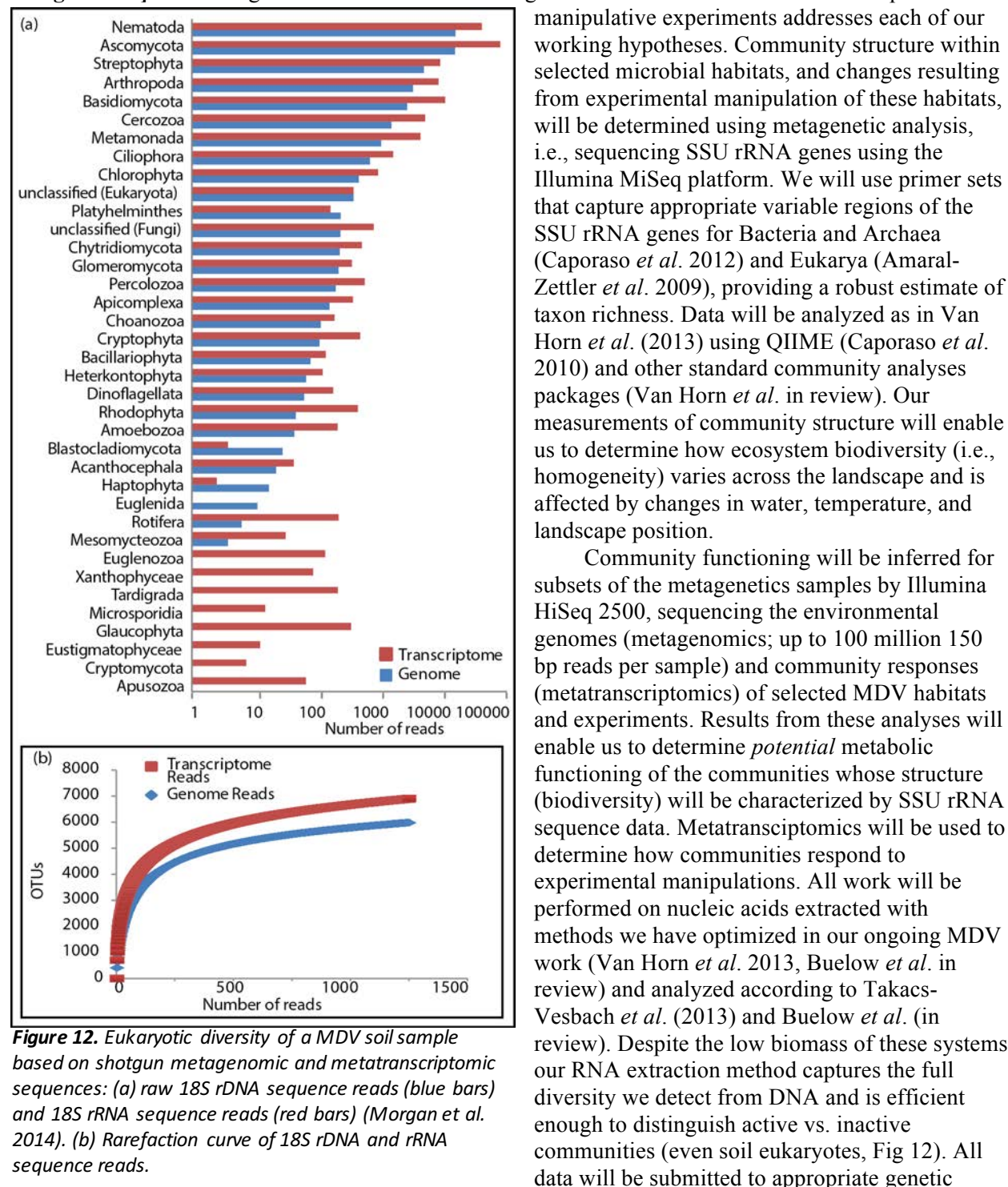


Figure 12. Eukaryotic diversity of a MDV soil sample based on shotgun metagenomic and metatranscriptomic sequences: (a) raw 18S rDNA sequence reads (blue bars) and 18S rRNA sequence reads (red bars) (Morgan *et al.* 2014). (b) Rarefaction curve of 18S rDNA and rRNA sequence reads.

databases in addition to being incorporated into the MDV relational database as described in the Information/Data Management Plan of the proposal. *This activity will specifically investigate biological connectivity of the MDVs ecosystem and provide information to test H1-H4.*

3.2 CONTINUING LONG-TERM EXPERIMENTS

3.2.1 Relict Channel Re-Activation Experiment [McKnight, Gooseff]. During MCM1, we began a long-term experimental manipulation, reactivating an abandoned stream channel by constructing a shallow sandbag wall to divert water into a channel that had not carried flow in about 3 decades (McKnight et al 2007). Although the original intent of the experiment was to quantify the rate of establishment of new benthic microbial mats, we observed that “relict” mats that had been preserved in a freeze-dried state began growing within several days, and these mats had higher productivity rates than those in streams with regular flow. During the 2001/02 flood event the upstream large perennial snowbank and sediment deposits that had formed a barrier to flow towards this channel were “blown out” and substantial flow with associated sediment entered the channel above the sandbag wall.

We continued to monitor the microbial mats in this reactivated channel in MCM3-4 as a way to understand how diatom communities develop over periods of flow and no-flow. The diatom communities in the abandoned channel were found to be very similar to those in intermittently flowing streams in the Bonney basin (Stanish *et al.* 2012). By sampling closely spaced sites (~100-200 m) in the reactivated channel we found that the within-stream and short-term variability in diatom community composition is much lower than the variability across a range of streams with different hydrologic regimes and habitat quality for persistence of microbial mats (Stanish *et al.* 2012). In MCM4, we studied the C and N isotopic composition of the microbial mats at these closely spaced sites to better understand the variation observed across Taylor Valley streams. *In MCM5, we propose to continue to monitor the microbial mats in the abandoned channel on an annual or biennial basis providing critical data to address H1 and H2.*

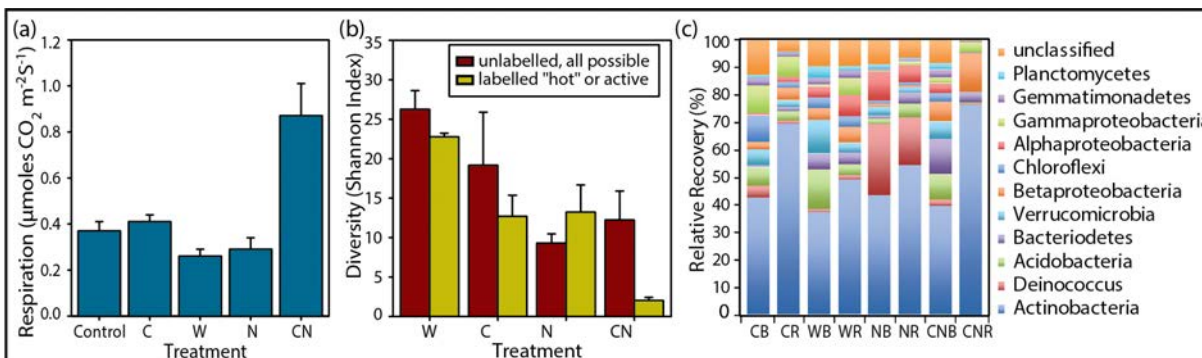


Figure 13. Microbial response to annual nutrient amendments over 4 years of stoichiometric nutrient amendments. (a) Field measurements of soil respiration 2 weeks after nutrient and water addition (C=carbon, W=water, N=nitrogen). (b) 16S diversity of labeled (active) and unlabeled responders to stable isotope probes (¹³C-DNA SIP with ¹³C-labeled mannitol, ¹⁵N-DNA with ¹⁵N- NH₄NO₃, ¹⁸O-DNA SIP with H₂¹⁸O, and a combination DNA SIP with ¹³C- and ¹⁵N); note that CN additions reduce diversity (and richness and evenness, data not shown). (c) Responses of specific taxa to water, N and CN addition relative to an unamended control (treatments with “B” represent baseline community; “R” represents the responders). Note that Actinobacteria (*Athrobacter* sp.) represents 45% of total recovered taxa.

3.2.2 Soil Stoichiometry Experiment (SSE) [Adams, Barrett]. This experiment was initiated in 2007 to examine how landscape history and its influence over nitrogen and phosphorus availability modulate the response of soil organisms and communities to carbon and nutrients added in stoichiometric proportions (e.g., Barrett *et al.* 2007). Our central hypothesis was that the response of organisms and ecosystems to these resource additions would be constrained by the influence of landscape history on evolutionary and ecological processes mediated through the relative availability of key limiting nutrients (Sturner and Elser 2002). After almost ten years of study, our results support this hypothesis; we found that soil communities

occurring in the phosphorus-rich soils in the Fryxell basin responded positively to C+N additions, manifest in elevated microbial biomass, increased soil respiration (Fig 13a) and higher abundances of nematodes (Fig. 14a). These amendments also resulted in changes in microbial community composition, including bacterial dominance, decreases in richness (Fig 13b), evenness and diversity. For example, C+N additions led to marked shifts in community structure by selecting for a single *Arthrobacter* species (Actinobacteria; 45% of recovered taxa, Fig 13c). In contrast, soils occurring on the nitrogen-rich, phosphorus-poor west Bonney basin responded to C+P additions, which stimulated soil respiration and nematode populations (Fig 14b). *This and several other soil amendment experiments involving decades of water and/or nutrient additions are now well-positioned to test H4. In MCM5, we predict that the plots that responded to disturbance via decreased heterogeneity in ecosystem structure and functioning will show decreased resilience (capacity to recover from experimental manipulations relative to controls) and resistance (capacity to withstand future disturbance).*

3.2.3 Pulse Press Permafrost (P3) Thaw Experiment [Barrett, Adams, Gooseff]. The impact of climate change is expected to be amplified in polar regions partially because of the sensitivity of the cryosphere to the phase change of ice to liquid water (Grebmeier and Priscu 2011). Thawing of permafrost contributes to significant changes in soil hydrology, biogeochemical cycling, the activity and composition of soil communities and connectivity among soil and aquatic landscapes. While climate warming can elicit such responses over years to decades, thawing events typically occur as discrete melt-water pulses.

In MCM4 we initiated an experimental manipulation of hillslope soils intended to simulate different frequencies of permafrost thawing events (i.e., pulse and press) and their impacts on soil physical and biological properties. Accordingly, we established a water diversion experiment, introducing two frequencies of water additions to the soil subsurface of three large permanent plots (each plot is 112.5m²) on a south-facing hillslope above a large, flow-through pond in Taylor Valley. Before the first treatment in 2014, we carried out high-resolution LIDAR imaging of each of the plots and three years of comprehensive pretreatment sampling. Instrumentation at the site consists of thermocouples, soil moisture probes and water activity probes buried at multiple active-layer depths every 2 m down-gradient from the water-addition trenches. Soil samples were collected for quantification of soil biota (invertebrates determined by microscopy and prokaryotic diversity by SSU rDNA sequencing) and intensive geochemical analyses. Preliminary results indicate that the pulses of water can be detected downslope at the plots instrumented as far as 7 m, but the additional water did not have a lasting effect on surface soil moisture content. We also noted an increase in available Ca⁺ in the treated soils, and a slight (but not significant) increase in Cl⁻ and NO₃⁻, which together with flooding may contribute to a slight decline in nematode abundance.

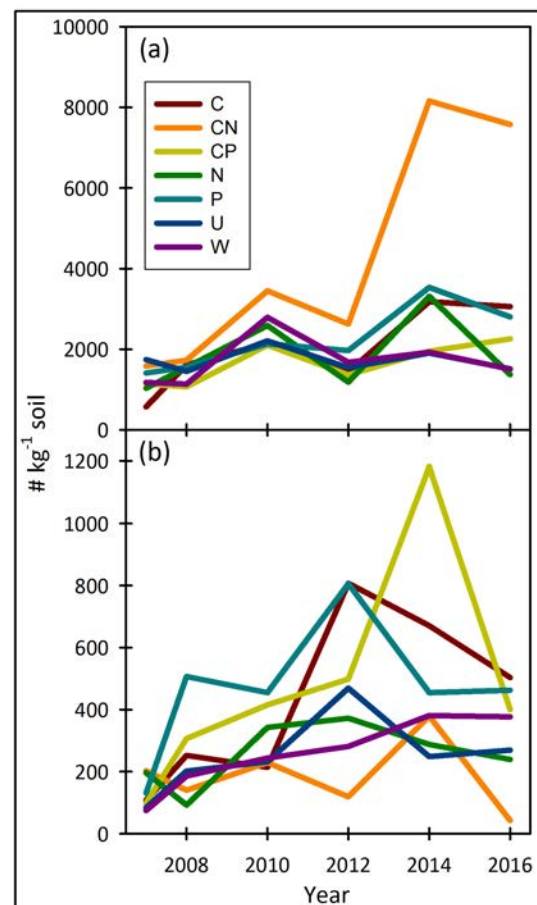


Figure 14. Soil nematode population responses (# of individuals kg⁻¹ dry soil) in the (a) Lake Fryxell and (b) Lake Bonney basins to aqueous additions of organic carbon (C), ammonium nitrate (N), and potassium phosphate (P) added in molar proportions of 100:10:1 C:N:P. W denotes a positive control for water and U refers to unamended or control treatments.

This experiment addresses H1 and H2 in MCM5. Simulated permafrost thaw is expected to mobilize solutes and nutrients within the active layer of treated plots, resulting in reduced influence of resource legacy and homogenization of the fine scale variation in surface geochemistry (e.g., Barrett et al. 2006b, 2009) (H1). As we continue to treat and monitor this experiment in MCM5, we predict that increased hydrological connectivity will alter habitat suitability uniformly, leading to synchronous, ecological responses, including changes in ecosystem structure and functioning (H2).

3.2.4 Lake Integrated Connectivity Experiment (LICE) [Takacs-Vesbach, Morgan-Kiss, Priscu].

Lakes represent the most productive landscape unit in the MDVs and, because of their location at the end of the hydraulic continuum, integrate all processes in the ecosystem. Therefore, the increased physical connectivity we hypothesize to occur during MCM5 should profoundly affect the structure and functioning of the lake ecosystems. In MCM4, we conducted a Lake Integrative Connectivity Experiment (LICE) to address our overarching hypothesis that climate warming in the MDVs will amplify physical connectivity among landscape units leading to enhanced coupling of nutrient cycles, increased productivity, and biodiversity (Takacs-Vesbach and Priscu, in prep). LICE was designed specifically to determine the effect of increased ecosystem connectivity on lake water productivity, as well as community composition and function. Under a scenario of increased connectivity, we expect lakes to experience increased nutrient input (either directly or indirectly) from streams, cryoconites, aeolian sediments, and fluvially introduced algal/cyanobacterial mats. The LICE experiment amended near surface water from Lake Bonney (east lobe) with leachate from selected landscape components from the surrounding basin (e.g., aeolian sediment collected from the surface of Lake Bonney, wetted sediments from the surrounding soils, *Nostoc* mats from ponds in the basin, cryoconite material collected from the Canada Glacier, stream water) to simulate increased material transport resulting from increased hydraulic connectivity. These materials were placed into 12,000 Dalton dialysis tubing to ensure that only macromolecules or exudates from the materials would be leached into the lake water microcosms. The tubing was incubated in 10 L microcosms for 2 days and removed to approximate a pulse event. Lake water productivity, biogeochemistry, and biodiversity were measured over the following six days. We observed an increase in primary and bacterial productivity in the microcosms in response to the treatments with significant N and P leaching. At the same time, bacterial 16S rRNA gene richness initially increased in many of the treatments relative to the controls, but then decreased in nearly every treatment by the end of the experiment. Changes in community composition were largely attributed to variations in the relative abundance of members of the Bacteroidetes, Proteobacteria, and Cyanobacteria. Results from this experiment indicate that MDV lake communities can rapidly respond to pulses of nutrients that can result from increased connectivity within the ecosystem. This experiment was conducted on only the surface water of Lake Bonney, which is known to be highly P-deficient (Dore and Priscu 2001). In MCM5, we will conduct LICE experiments in Lakes Fryxell and Miers which are N-deficient (Priscu 1995) and have different patterns of hydrological connectivity to the surrounding environment. *These experiments will test lake responses (biogeochemical, productivity, and community composition) to nutrient pulses in lakes with different nutrient status and located in basins with different hydrological connectivity and testing H1-H4. We anticipate that amplified physical/biological connectivity will result in homogenization of ecosystem structure and function (H1) and synchronize ecological responses (H2), effectively decreasing the influence of resource legacy (H1) on lake communities.*

3.3 NEW EXPERIMENTS

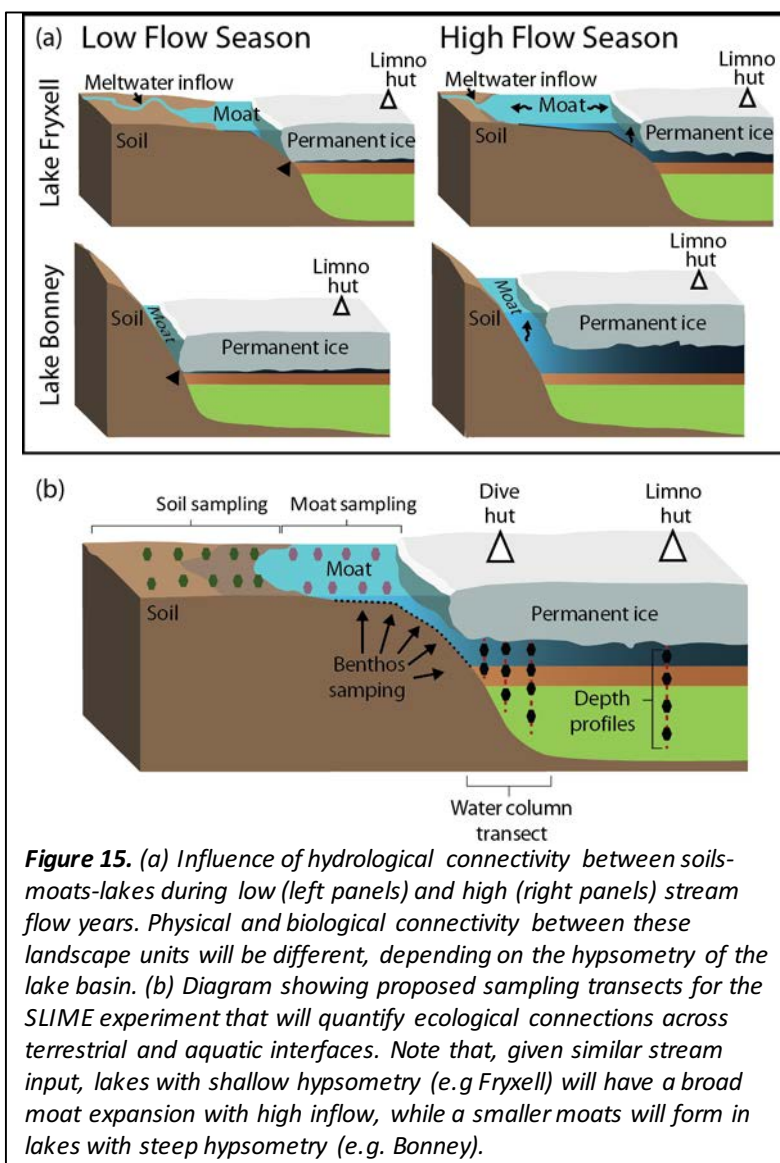
In addition to the above continuing and new monitoring activities, we propose several new experiments to test specific working hypotheses).

3.3.1 Soil - Lake Inundation Moat Experiment (SLIME) [Adams, Barrett, Devlin, Doran, Hawes, Morgan-Kiss, Priscu, Takacs-Vesbach]

Previous work has shown that high stands of paleolakes in Taylor Valley still exert a tremendous influence on the structure and functioning of current lake and soil ecosystems (Moorhead et al. 1999; Burkins et al. 2000; Hall et al. 2000; Lyons et al. 2000a). We

anticipate that increases in glacial meltwater will lead to continued lake level rise, expanded moat area, and a conversion of dry soils to benthic sediment in conjunction with seeding of the moat communities with inorganic nutrients and biota (Fig 15a). SLIME will quantify the ecological connections across aquatic-terrestrial interfaces (specifically soils to moats to lake water columns) and the biogeophysical properties of the soil and benthic ecosystems under the changes associated with lake level rise, and will determine if resultant changes from this restructuring influence nutrient cycling and NPP in the moats. Community structure of the planktonic and littoral moat communities will be measured across the soil to sediment transition as well as the extent this transition extends beyond the moats to the under-ice planktonic and benthic communities.

We will establish permanent sampling transects that span from the lake benthos through various depths of the moat onto the wetted hydrological margins of the lake, into dry soils at multiple positions to ensure dry reference transect positions through at least the duration of MCM5 (Fig 15b). Transect sampling will occur in Lakes Fryxell and Bonney, which differ significantly in their hypsometry (see Fig 11d), and will integrate with new long term monitoring activities in the moats (Section 3.1.3). Biological diversity will be measured at the organismal (taxonomic and organismal abundance) and functional (metagenomic) level, as described in 3.1.8. Biogeochemical and physical properties will be measured as described above for lakes, moats and soils (see Sections 3.1.2, 3.1.3, 3.1.6). NPP and nutrient transformations will be estimated by measuring oxygen and nutrient changes within in situ light and dark benthic chambers. Enzymatic assays (carboxylase and *B*-glucosaminidase; Li *et al.* in prep; Kong *et al.* 2012a) and functional gene qPCR (Dolhi *et al.* 2015) will be conducted on mat and sediment cores following removal of the chambers. *SLIME* will examine explicitly the link between community structure and nutrient cycling across the transitions (*i.e.*, soils to moat, moat to water column), quantify the flux of energy and matter across these transitions while determining whether these fluxes are linked to the homogeneity of physical, chemical, and biological parameters across the soil to lake transition, and determine whether the amplified physical and biological connectivity leads to increased synchrony of ecological responses, directly testing H1 and H2.



3.3.2 Stream Mat Transplant Experiment (SMTE) [McKnight, Takacs-Vesbach, Devlin]. Long and short streams have different conditions based on different flow regimes and differing interactions with hyporheic zones and the surrounding landscapes (see 3.1.7). Stream length is positively correlated with hyporheic zone volume, which must be filled (as they thaw) before water can keep moving down the channel. Thus, long streams also have greater capacity for biogeochemical cycling than short streams. Short streams tend to have more consistent flow and more dilute chemistry than long streams. Despite these differences, abundant benthic algal mats can be found in both types of streams, yet the mat distribution, biomass, and communities of diatoms vary between the two. For example, long streams tend to host more endemic diatom species than short streams (Esposito *et al.* 2006; Stanish *et al.* 2012). Short streams are generally more homogeneous than long streams, given their more consistent flow regime. Hence, we would expect, for example, increased dominance of cosmopolitan taxa in long streams to become more homogenous.

SMTE consists of several specific manipulations that build upon our experience studying in stream mat regrowth on scraped rocks (Kohler *et al.* 2015a) and growth on artificial substrates (Kohler *et al.* in press). In one set of manipulations we will collect large rocks and their associated mats (~10-20 cm in diameter) and surrounding sediment from one reach and transplant them to another reach in a different stream. This experiment takes advantage of the fact that freeze-thaw cycles (periglacial processes) cause the largest flat side of the rocks to be exposed on the streambed, which provides a stable habitat for the perennial microbial mats. We will also transplant rocks and sediment to a nearby upstream reach to be able to resolve transplantation effects. In a parallel set of manipulations we will establish microbial mats on substrates during one season in a stream reach. The following season we will transfer a subset to another reach in another stream, another subset to an upstream site in the same stream, and a third subset will remain in place. These substrates will include some augmented with nutrients that will diffuse over the course of the summer and some with no added nutrients. The N:P ratio of the nutrient diffusing substrates will match the host and the transplant stream. The goal of the SMTE is to track how mat abundance, biomass, Chlorophyll *a*, diatom communities, and primary productivity change through time in the contrasting habitats. *These experiments will test H1 and H2 within the context of long streams becoming more like short streams if glacial melt increases substantially in the coming decades as expected.*

3.3.3 Permafrost Degradation Experiment (PDE) [Gooseff, McKnight, Devlin]. Unlike aeolian deposition into stream channels from soils across the landscape, permafrost degradation along stream banks can introduce several m³ of sediment directly into the channel at one time, producing physical, chemical, and biological changes to the stream. We have observed several such occurrences recently and tracked some of the impacts – including increased stream nutrient concentrations and substantial modification of downstream channel form (Fig 16; Gooseff *et al.* in press; Sudman 2015). However, we have not had the opportunity to study this in a controlled manner with a discrete input of sediments.



Figure 16. Thermokarst (modified land surface) due to permafrost degradation and erosion along Crescent Stream (Lake Fryxell basin), as observed in January 2012. Thermokarst features were observed along 3+ km of the stream.

In this experiment, we will identify 3 locations in streams that have stable banks and explicitly remove thawed bank sediments ($\sim 10\text{m}^3$) and dump these into the channel at a single point to simulate the influence of permafrost degradation on the banks. The locations will be pre-selected and background data collected for 2 seasons prior to manipulation. TLS data (with support of UNAVCO; see letter of support) will be collected at this time to document the channel form up- and downstream, and benthic mat samples will be collected for AFDM, Chlorophyll *a*, diatom, and invertebrate analyses, and to estimate in-situ primary productivity using pulse-amplitude modulation (PAM) chlorophyll-a fluorescence at several locations up- and downstream of the location of the sediment input. Synoptic water chemistry samples up- and downstream will be collected; upstream conditions and water chemistry will serve as a control against which we can compare downstream changes to the channel, biology, and chemistry. We expect that after the sediment is added to streams, it will get transported and deposited downstream modifying channel form. Stream chemistry will become enriched in weathering solutes and nitrate (similar to Gooseff *et al.* in press) and mat, diatom, and invertebrate communities will become substantially different than conditions prior to the start of the experiment and different than those upstream of the sediment input. H3 will be confirmed if there is substantial homogenization of the communities and conditions downstream, and/or if these changes mimic those that are found in the GSS monitoring on long streams.

This experiment is different than the P3 permafrost thaw experiment in that this experiment specifically focuses on the consequences of physical degradation of stream channel banks on the aquatic system, whereas P3 is focusing on how the soil ecosystems are responding to wetting over different time intervals. Together, they provide strong complementary evidence *regarding how multiple landscape units will respond to disturbances from a warming climate, testing H3.*

3.3.4 Ecosystem Response to Human Impacts [Howkins, Adams, Takacs-Vesbach]

The relatively limited, but well-documented human presence in the MDVs make the region an ideal site for understanding ecosystem response to local human disturbance (H3). Some human activities in the McMurdo Dry Valleys constitute discrete disturbance events (walking), and some are prolonged (occupying a camp). Humans trample soils, disrupt sediments, increase the movement of materials around the valleys, and promote the introduction of nutrients, chemicals, and non-native biota to the MDVs. *We expect the net consequence of these anthropogenic disturbances to be an increase in physical connectivity and an acceleration in shifts towards homogeneity in ecosystem structure and functioning.* We expect human induced ecosystem homogeneity will be greatest in sites where human presence has been most intense and most recent (Fig 17).

To test H3 we will use information from environmental history research to evaluate how human activities accelerate shifts toward homogeneity in ecosystem structure and functioning. In MCM4 we began to document human activity in the MDVs since the arrival of Captain Scott in 1903 (Howkins 2016). Historical data provide information about the duration and intensity of human presence in the MDVs. By accumulating information from historical photographs, oral history interviews, publications, and archival records (such as field camp reports,

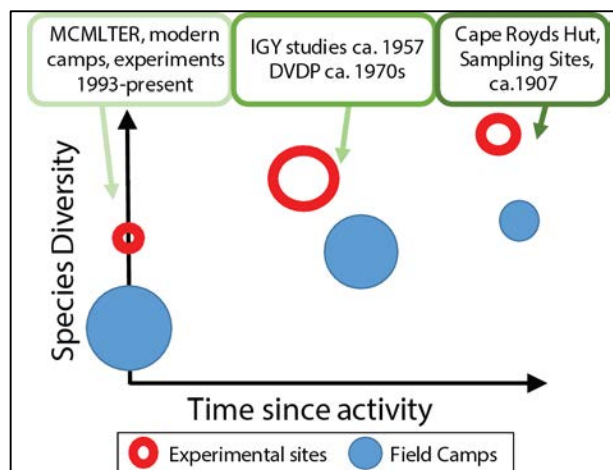
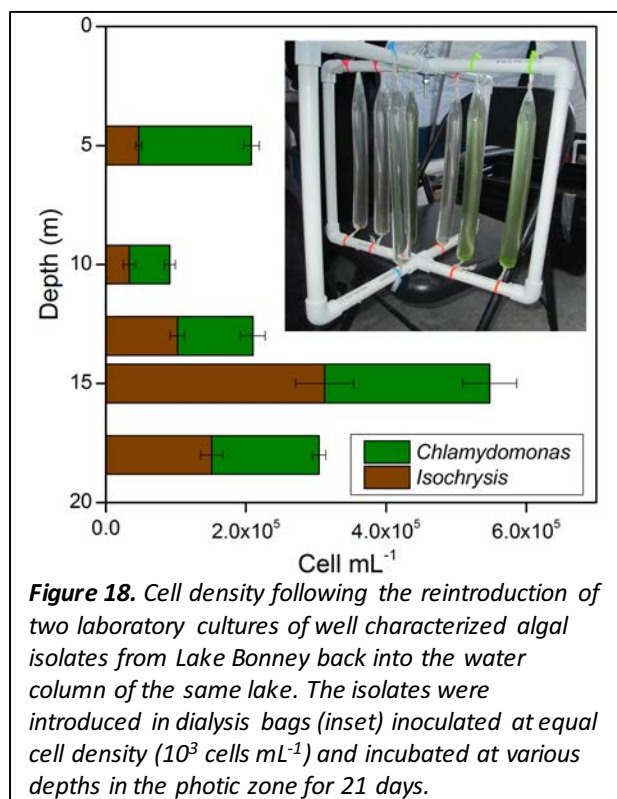


Figure 17. Predictions of soils species diversity related to sites of human disturbance at discrete locations since the time of the activity. Circle size indicates the magnitude of disturbance. We predict species diversity to be lowest at sites of current field camps (where human disturbance is more intense), and greatest at former experimental sites that have had most time to recover (where human disturbance is less intense). Green boxes provide examples of the specific locations (IGY = International Geophysical Year; DVDP = Dry Valley Drilling Project) that fit the two disturbance types, and time since occupation.

helicopter flight logs, etc.), and data from the US Antarctic Program, we are compiling a detailed picture of the nature of human activity in the region. This information ranges from the number of person days spent at different field camps and campsites in the MDVs, waste disposal practices in different places, and descriptions of activities that occurred at different sites. Although these historical data can never be fully complete, the carefully documented nature of human activities in the MDVs since the late 1950s offers an excellent opportunity to know what has occurred at different places, and thereby evaluate the potential for magnitude of impact.

Soils are sensitive indicators of the ecological consequences of human activity (Lyons *et al.* 2000b; Ayres *et al.* 2008). In MCM5 we will examine differences in invertebrate and microbial taxa richness and community structure in soils that vary as a function of disturbance type, magnitude and duration of impact. We will focus on two types of locations – areas adjacent to existing and former long-term experimental/monitoring sites and long-term (i.e., more than a few seasons) field camps that have been exposed to varying degrees of human activity. Reference sites with similar soil conditions, will be co-located with disturbed sites on proximate soils with no known significant past or present human activity. Community diversity will be determined according to Section 3.1.8. The results will enable us to evaluate how human activity impacts community structure in the MDVs (H3). *We expect the impacted sites to have greater homogeneity (i.e., reduced biodiversity) and decreased functional diversity relative to the associated control and reference sites.*

3.3.5 Transplant Lake Integrated Connectivity Experiment (tLICE) [Takacs-Vesbach, Morgan-Kiss, Priscu] In MCM4, the LICE experiment (Section 3.2.4) addressed the impact of increased MDV connectivity on lake productivity and community composition. In MCM5, the transplant LICE experiment (tLICE) will consider the impact of increased connectivity between MCM landscapes on community stability. Natural planktonic communities of Lakes Bonney (east lobe) and Fryxell collected from either the liquid moats or the under-ice communities will be diluted 10-fold in 0.2 μm -filtered lake water and transferred to dialysis bags (cutoff 12-14 kD; Fig 18, inset). Sealed bags will be suspended in the water column at various locations. Moat communities will be exchanged between the two lakes, while



under-ice communities will be suspended deeper in the water column to investigate the impact of lake level rise on microbial community diversity and function. Dialysis tubes carrying the original communities will serve as controls. The tubes will be incubated for up to 7 days in the moats (approximately 2 generation times) or multiple seasons (under-ice communities). Microbial community diversity (SSU rRNA) will be monitored, along with lake water productivity, and microbial eukaryote trophic diversity using flow cytometric methods (see Section 3.1.2). In a preliminary experiment, we incubated dialysis bags of two MDVs phytoplankton which differ in their metabolic strategies (*Chlamydomonas* – obligate photoautotroph; *Isochrysis* - mixotroph) at various depths in Lake Bonney. Phytoplankton abundance was dependent upon the incubation depth: *Chlamydomonas* dominated under-ice communities while *Isochrysis* abundance increased in the deep photic zone (Fig 18). In tLICE, we will expand this proof of concept experiment to investigate natural community responses. *The tLICE experiment will test the resistance and resilience of the lake*

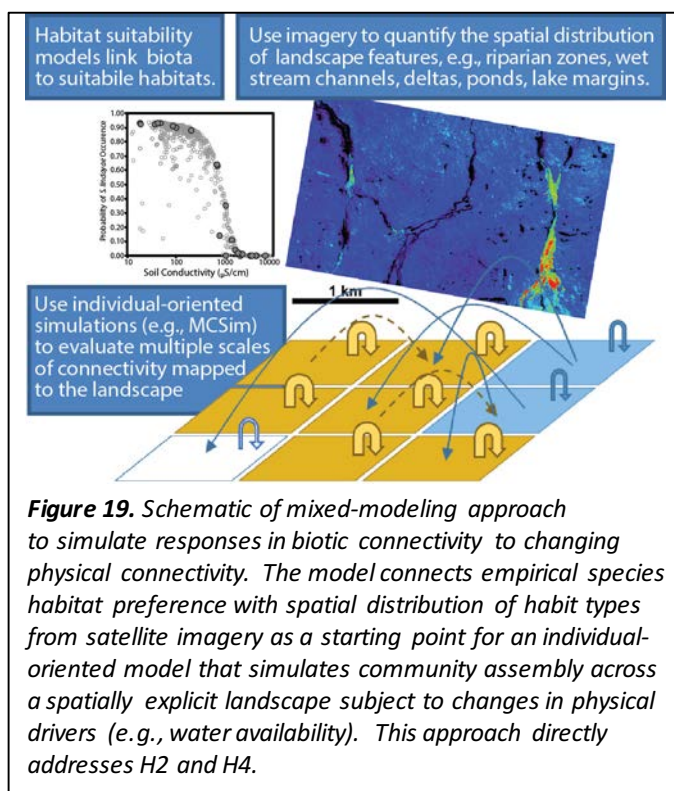
communities (H4) to increased lake connectivity (i.e., transplanted moat communities) and the press disturbance of lake level rise (i.e., shallow to deep transplanted communities).

3.4 MODELING [Gooseff, Barrett]

MCM investigators have used a combination of modeling approaches over the past 4 funding cycles to investigate the influence of climate variation on ecosystem structure and functioning. For example, we have used deterministic models to simulate the influences of physical drivers on soil water dynamics (Hunt *et al.* 2007, 2010), glacial melt (Ebnet *et al.* 2005; Hoffman *et al.* 2014), stream hydrology and biogeochemistry (Gooseff *et al.* 2002, 2004a, b; Koch *et al.* 2010, 2011), empirical models to describe major pools of lake and soil organic matter and nutrients and the biological, mineralogical and geomorphological drivers that influence them (Takacs and Priscu 1998; Burkins *et al.* 2000b; Takacs-Vesbach *et al.* 2001; Barrett *et al.* 2005, 2006a, b, 2007; Bate *et al.* 2008), empirical models that describe habitat suitability for soil organisms and stream diatoms (Freckman and Virginia 1997; Esposito *et al.* 2008; Poage *et al.* 2008; Kohler *et al.* 2015b) and stochastic individual-oriented models to simulate community assembly (e.g., Sokol *et al.* 2015).

Deterministic and empirical models provide a foundational understanding of energy transfer, biogeochemical pools and fluxes, and habitat suitability for biota at local scales. For example, earlier approaches at investigating patterns of diversity in MDV soil ecosystems utilized a combination of simple numeric models describing local climate (Doran *et al.* 2002a), empirically-based biogeochemistry models (Burkins *et al.* 2001; Barrett *et al.* 2006b) analytical population models (Moorhead *et al.* 2002) and statistical models (Poage *et al.* 2008) to describe habitat suitability for the dominant soil organism *Scottnema lindsayae*. This approach was useful for inferring major drivers (salinity, organic matter and water availability) over the spatial distribution of a single species and we can use these models to constrain predictions about how abiotic forcing factors may change in predicted climate scenarios. However, these models are limited in their ability to capture community-level dynamics because they are driven solely by observed correlation between environmental drivers and species composition and abundance; they do not explicitly include spatial or biogeographic processes that are also important drivers of diversity patterns (Sokol *et al.* 2013).

Individual oriented models provide a method for scaling local processes across a landscape to make predictions about the emergent properties of an ecosystem (Grimm and Railsback 2005). We will employ MCSim, which is a stochastic metacommunity simulation for R (Sokol *et al.*, 2015, in review), to model temporal dynamics in a network of sites interconnected by dispersal. Metacommunity dynamics are modeled using transition probabilities that are modified by local and regional species compositions, habitat characteristics, and species-specific traits (dispersal ability, habitat preference, and niche breadth) (Fig 19). For example, we demonstrated how MCSim could be used to model a zooplankton metacommunity in a system of interconnected temperate ponds to explore the underlying drivers of biotic homogenization in the Baltimore Ecosystem Study LTER (region-wide decline in beta-



diversity) (Sokol *et al.* 2015). In MCM5 we will use this approach to explore how different biodiversity patterns can emerge for metacommunities in the MDVs (e.g., pond diatoms, stream diatoms, soil bacteria, soil nematodes) under alternative landscape scenarios, such as increased liquid water availability. To this end, we have integrated the MCSim modeling platform with igraph for R (Csárdi and Nepusz 2006) to allow for alternative network connectivity topologies. We have also modified the modeling platform so that we can use empirical community composition data and environmental data to estimate habitat preferences and niche breadths using the outlying mean index (Doledec *et al.* 2000) implemented in the ADE4 package for R.

In MCM5 Gooseff, working with Barrett and Sokol (a postdoc on the project), will use a combination of deterministic, empirical, and stochastic individual-oriented models to integrate processes understood at local scales across habitat types to make predictions about how MDV ecosystems will respond to climate variation and changing connectivity at the landscape scale. *Specifically, these modeling exercises will explore how changes in the prevalence and patchiness of abiotic resources, such as liquid water and nutrients, will affect spatial heterogeneity and temporal stability of primary producer and consumer metacommunities (H1, H2).* Response metrics will include estimates of standing biomass, and species richness and compositional turnover across spatial gradients (e.g., patterns described in Sokol *et al.* 2013; Sakaeva *et al.* 2016). Using this modeling platform, we will explore how predicted future landscape configurations may result in shifts in the synchrony and stability of aggregate measures of ecosystem structure, such as standing biomass and species richness.

3.5 INTEGRATING ENVIRONMENTAL HISTORY AND ECOLOGICAL SCIENCE IN THE MCMURDO DRY VALLEYS [Howkins]

Environmental history research started during MCM4 and is proposed to continue in MCM5 with the central goal of using historical data to contribute to our understanding of ecosystem response to amplified landscape connectivity. Environmental history research will play a central role in addressing H3 (see Section 3.3.4). For example, how large are the differences in ecosystem resilience between sites that have been disturbed by human activity and sites that have not? How quickly do ecosystems “recover” after prolonged periods of human activity? Is there a correlation between the duration and intensity of human activity at a particular site and the speed of recovery (resilience)? Do we notice any particular human activities that have a particularly large impact on ecosystem structure and functioning? Answers to these questions will deepen our understanding of the environmental history of the MDVs by adding a quantitative element to the historical data that can contribute to wider studies of the impact of humans in Antarctica and effective environmental management (Terauds *et al.* 2012).

In addition to contributing to H3, the environmental history research will continue to add to our understanding of the relationship between science, human activity, and the environment in the MDVs over time. As demonstrated by the environmental history research conducted during MCM4, the relatively simplified human history of the MDVs makes it an ideal location for integrating the theory and practice of environmental history with contemporary ecological research (Howkins 2015, 2016). In MCM5 environmental history data will be collected through archival research in the United States and New Zealand, conducting oral history interviews with people who have worked in the MDVs, and gathering together other materials relating to the history of the region. The environmental history data will be organized in a geospatial database on the MCM website in order to facilitate access. *A major goal of this research will be the publication of a comprehensive history of the MDVs as an academic monograph (two leading university presses have informally expressed an interest in this project).*

3.6 INTERSITE COMPARISONS

In MCM4, we collaborated with the Palmer LTER group to fill an upcoming special section of *BioScience*. These papers focus on comparisons and contrasts of Antarctic marine and terrestrial ecosystems - climate drivers of the two systems (across the continent) (Fountain *et al.*, in review), the physical controls of seasonal and permanent ice (Obryk *et al.* in review), and microbial community dynamics (Bowman *et al.* in review). In MCM5 we plan to expand these collaborations with PAL

scientists to generate new directions in the frontiers of ecosystem responses to a changing regional climate.

Our group contributed to a cross-site comparison of NPP responses to climate variability (Smith et al. 2015), and led new collaborative efforts to compare applications and advancements in metacommunity understanding. Postdoc Sokol was a co-leader of a working group at the LTER All Scientists Meeting in 2015, which included participation from 19 LTER sites. This effort has continued with a planned workshop at the 2016 ESA annual meeting, and a planned submission to the LTER Communications Office synthesis competition (due March 2015). In MCM5 we will expand this work with new metacommunity modeling studies to test our hypotheses and continue to compare and contrast our applications to those at other LTER sites (and beyond).

In MCM5, we will hold our annual winter PI meeting (during which we debrief the past field season and plan for the next) at other LTER sites so that we can engage other LTER science groups and generate opportunities for collaboration. See details in Site Management Plan.

We also hope to contribute to a multi-site effort that was explored at the 2015 All Scientist Meeting session “*LTER based perspectives on analyzing microbial community structure, function, and process*”. This effort aims to conduct a cross-site analysis of aquatic and soil community composition and functioning shifts in response to nutrient and moisture (soils only) amendment experiments. MCM CoPIs Adams, Morgan-Kiss and Takacs-Vesbach will work to move this forward with the other session attendees and organizers by requesting support from the DOE Community Science Program in 2017.

CoPI Howkins will continue on-going work with historians and ecologists at other LTER sites to consider the challenges and opportunities for integrating historical research into our understanding of LTER ecosystems. He has helped to organize two ASM sessions (2012, 2015) on history and ecology, which began to develop a series of best practices for integrating historical information into LTER datasets. This history-focused integrative work will continue into MCM5.

4. RELATED RESEARCH PROJECTS

The MCM is the longest running research project in the MDVs, and there are no other contemporary research projects comparable to the MCM operating in the MDVs at this time. Hence, our approach to conducting research in the MDVs requires that we be able to accomplish our research and monitoring objectives from the resources of the LTER grant alone. Our PI group is therefore intentionally small compared to other LTER projects. We do, however, collaborate with a wide array of other research projects that have typical 2-3 year grant periods. These include US and foreign projects working in the MDVs on which our PIs and collaborators are involved, and we have taken the lead in establishing a Terrestrial Observation Network for the region (Levy *et al.* 2013). These collaborations have generated new technological and method capabilities. For example, the ALPS project was originally funded by NASA (to MCM4 PIs Doran, Takacs-Vesbach, and Priscu). The end of that project provided new equipment to be used in overwinter lake water sampling and monitoring.

5. EDUCATION AND OUTREACH ACTIVITIES

The history, landscapes, biota – even the *idea* of Antarctica – piques the curiosity and imagination of people across all age groups. We view this as an incredible asset that can vastly extend the influence of our work, and have designed of our education and outreach activities to take advantage of this.

A great strength of the MCM in general is that the site highlights the global interrelatedness of ecological research. The overarching goal of our education and outreach work at all three levels (K-12, Undergrad and Early Career, and Broader Audience) is to highlight this interrelatedness, and to use the MDVs to help students and the general public understand the global importance of ecological research. In particular, we plan to develop closer links with other LTER sites in order to develop a more integrated suite of education and outreach programs and materials. Our intention is to begin this integration with other cryosphere-dominant sites (Niwtot, Palmer, and the Arctic LTERs), and work closely with the new LTER Communications Office to coordinate our education and outreach activities with sites throughout the Network.

CoPI Howkins has taken leadership of this aspect of the project as the education and outreach PI for MCM5. We will partner with Science Discovery, a center at CU Boulder that specializes in science education for elementary and middle school children, to employ a quarter-time education and outreach coordinator (see letter of support). This partnership gives us access to a large range of existing education and outreach programs, and to the expertise of a staff of science education experts. Partnering with Science Discovery also positions us to apply for additional funding to support our outreach and education initiatives. The education and outreach coordinator will take a lead in developing a range of programs and materials that can be used by all members of the MCM community. These will include the development of “data nuggets” for inclusion in the growing LTER database, visits to schools, and participation in science cafes. An important role for the outreach PI will be to continue developing the outreach and education section of the MCM website to act as an attractive entry point for school children, university students, educators, and the general public to connect to our site, as well as to broader Antarctic educational opportunities. With assessment strategies developed by Science Discovery already in hand, the outreach PI will use these to evaluate and improve our education and outreach initiatives and monitor our progress. Particular attention will be paid to aligning activities, such as development of classroom activities, to the Next Generation Science Standards (NGSS) in order to make our work as broadly adoptable as possible.

Our aim is to provide opportunities for everyone associated with the MCM to participate in some form of education and outreach activity. Throughout the grant cycle we plan to train our scientists for full participation in the NSF-sponsored “Portal to the Public” program, a networked, informal science education (ISE) framework that facilitates face-to-face interactions between scientists and public audiences. ISE training activities will be conducted by Science Discovery at CU Boulder. Each year at our annual summer science meeting in Boulder, we will dedicate a day to outreach and education training for ten or more scientists connected to MCM, including coPIs, collaborators, postdocs, graduate students, and REU students. Over the course of the grant, this will allow us to train over sixty MCM scientists, thereby increasing our education and outreach capacity.

5.1 K-12 Outreach. Much of the general education and outreach work conducted by MCM scientists and overseen by the outreach coordinator (e.g. data nuggets, school visits, science cafes) will continue to focus on the K-12 audience and stakeholders. In keeping with the overall education and outreach aims of this proposal, there will be a particular emphasis on making connections to other sites in our K-12 activities. We have plans to partner with the Critical Zone observatory at the CU Mountain Research Station to participate in a summer program for middle school teachers focused on the cryosphere. This offers an ideal program to start developing our integrative education and outreach activities. We also plan to continue developing PolarTrec applications, for teachers to travel to Antarctica to participate in MCM research. We will continue to use *The Lost Seal* books in our outreach and education activities at the K-12 level. In particular, the translated versions will allow us to reach a more diverse community of children and educators, both in the United States and internationally. Within the United States we plan to use the bi-lingual Spanish-English and fully Spanish versions of the *Lost Seal* to reach out to Spanish speaking communities in places such as Denver and Albuquerque. Internationally, there will be a number of opportunities for MCM scientists to use the translations. For example, a number of our scientists also work in Greenland and can visit local schools to present the Greenlandic version of *The Lost Seal*. All our scientists fly through Christchurch, New Zealand on their way to and from Antarctica, presenting opportunities to use the Maori translations with local communities.

5.2 Undergraduates and Early Career Scientists. During MCM5 we plan to continue our emphasis on working with undergraduate and early career scientists. Throughout the grant, we will take our full allocation of two REU students per year. By making a sustained effort to include REU students, graduate students, and post doctoral students in our outreach and education program we will be helping train MCM scientists in an important component of a successful scientific career. In particular, training through the “Portal to the Public” program will better prepare our students both for participation in our activities and

for developing and implementing innovative education and outreach programs within their future projects. By highlighting the potential for collaboration with other LTER sites throughout our education and outreach initiatives, this component of MCM5 will give our students increased opportunities to make connections with scientists at other sites, helping to build an integrative component into their scientific careers from an early stage. We also plan to continue working closely with the Association of Polar Early Career Scientists (APECS).

5.3 Broader Impacts. During MCM5 we will continue to develop our outreach efforts to the broader public at our various home sites. These efforts will benefit from the more systematic training offered by our participation in the “Portal to the Public” program. We plan to collaborate with the Niwot LTER to develop an Antarctic display as part of a museum exhibit being developed at the CU Mountain Research Station, which will present MCM science to tourists visiting the Rocky Mountains. Our use of *The Lost Seal* translations will continue to offer opportunities for engagement with broader communities, as well as schoolchildren. The continuation of the environmental history work will provide additional opportunities for engagement with a wider public, especially through the planned publication of a book on the history of the MDVs and the upcoming 200th anniversary of the first recorded sighting of Antarctica (in 2020).

6. CONCLUDING REMARKS

The glaciers, streams, lakes and soils of the MDVs comprise a terrestrial ecosystem on the precipice of change. Through past work by the MCM-LTER, we now view the region as an integrated system that includes dynamic interactions among biotic and abiotic components of the environment. It is clear that ecosystem linkages driven by climate produce a cascade of tightly coupled events that ultimately leads to the biological production, diversity and biogeochemical dynamics that occur within the MDVs. Acutely sensitive to minor fluctuations in surface energy, these ecosystems are responding with increased biological and physical connectivity. The research proposed in MCM5 naturally follows results from MCM1-4 and will allow us to test new hypotheses that capture important elements of these responses at multiple temporal and spatial scales, and interpret them in the context of fundamental ecological theory that will be readily transferable to other ecosystems. Building on our existing long-term monitoring and experimental manipulations, our proposed work will contribute to cross-site syntheses of NPP, population and community processes, organic matter accumulation and decomposition, nutrient and hydrologic cycling, and the mode, frequency and magnitude of disturbance. MCM5 is based on a legacy of foundational scientific data that are well curated, accessible and easily disseminated. We have developed very strong outreach programs, trained new generations of scientists, and herein articulate clear plans for extending our influence even more effectively in the future.

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(bold font indicates 10 most important papers published from last 6 years)

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