Final Scientific/Technical Report

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Recipient: The Regents of the University of California

Project title: Can microbial functional traits predict the response and resilience of decomposition to global change?

Institution: University of California Irvine

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Executive summary

The role of specific micro-organisms in the carbon cycle, and their responses to environmental change, are unknown in most ecosystems. This knowledge gap limits scientists' ability to predict how important ecosystem processes, like soil carbon storage and loss, will change with climate and other environmental factors. The investigators addressed this knowledge gap by transplanting microbial communities from different environments into new environments and measuring the response of community composition and carbon cycling over time. Using state-of-the-art sequencing techniques, computational tools, and nanotechnology, the investigators showed that microbial communities on decomposing plant material shift dramatically with natural and experimentally-imposed drought. Microbial communities also shifted in response to added nitrogen, but the effects were smaller. These changes had implications for carbon cycling, with lower rates of carbon loss under drought conditions, and changes in the efficiency of decomposition with nitrogen addition. Even when transplanted into the same conditions, microbial communities from different environments remained distinct in composition and functioning for up to one year. Changes in functioning were related to differences in enzyme gene content across different microbial groups. Computational approaches developed for this project allowed the conclusions to be tested more broadly in other ecosystems, and new computer models will facilitate the prediction of microbial traits and functioning across environments. The data and models resulting from this project benefit the public by improving the ability to predict how microbial communities and carbon cycling functions respond to climate change, nutrient enrichment, and other large-scale environmental changes.

Objectives

The objective of our project was to link functional traits that influence carbon cycling with individual microbial taxa in order to build predictive models of ecosystem responses to global change. Specifically, we aimed to address four main questions with our research: 1) How do microbial taxa respond to environmental changes? 2) How are extracellular enzyme genes distributed among microbial taxa? 3) Can we predict enzyme function and carbon cycling rates by combining enzyme gene distributions with the environmental responses of specific microbial taxa? 4) Are microbial communities and their functions resilient to environmental change? Overall, we were successful in addressing each of these questions and have so far published over 30 peer-reviewed articles and given 45 conference presentations on our findings. Raw data from the project are available on GitHub (https://github.com/stevenallison/DOE-microbes-and-global-change).

Objective 1

We used multiple approaches to address objective 1. Our main approach involved an experimental manipulation in California grassland in which we transplanted entire microbial communities into different environments (Allison et al. 2013). Environmental differences resulted from a long-term manipulation of precipitation and nitrogen inputs established by co-I Goulden. The main result here was that drought treatment (and its indirect effects through plant communities) altered microbial community abundance and structure. In particular, bacteria responded negatively to drought treatment, with negative consequences for the rate of litter decomposition under drought conditions. Effects of nitrogen manipulation on microbial communities and functioning were more subtle. We also measured the potential activities of extracellular enzymes involved in decomposition and found that they were less efficient under drought conditions and when microbes were transplanted out of their native environment (Alster et al. 2013).

In addition to measuring microbial responses to transplantation, we surveyed microbial communities over time in drought and nitrogen treatments. Although the treatments had a clear and significant effect on microbial community composition, most of the variation in composition could be explained by seasonality (Matulich et al. 2015). In our Mediterranean grassland system, ~95% of precipitation falls between October and May, and this seasonality has a stronger effect on microbial communities than our experimental manipulations (50% precipitation reduction or addition of 6 g N m^{-2} yr^{-1}).

We also found evidence that environmental change treatments alter numerous functional components of microbial communities. Bacterial taxa with genes involved in cellulose degradation tended to respond negatively to reduced precipitation (Berlemont et al. 2014). Using a novel approach with nanotechnology (quantum dots), we found that the nitrogen uptake preferences of fungi depended on their prior history with nitrogen inputs (Hynson et al. 2015). We also found that the diversity of genes involved in nitrogen cycling pathways varied substantially with seasonality in precipitation, and that microbial taxa vary in the number of nitrogen cycling pathways contained in their genomes (Nelson et al. 2015).

This grant supported some studies that addressed objective 1 outside of our southern California experimental system. Co-I Treseder mentored PhD graduate

Sandra Holden to examine microbial responses to fire in a range of ecosystems (Holden and Treseder 2014). This work showed that microbial abundance and activity respond negatively to fire, implying that post-fire losses of soil carbon are lower than previously expected (Holden et al. 2013). A reciprocal transplant study (similar to our California design) showed that despite fire-induced changes in fungal community composition, reductions in decomposition following fire are primarily due to abiotic effects (Holden et al. 2015). Finally, a comprehensive biogeographic study of fungal distributions and traits showed that high latitude ecosystems host more derived fungal taxa, potentially because colonization of these systems requires evolutionary adaptation to drought and cold stress (Treseder et al. 2014).

Objective 2

Our second objective focused on analyzing the distribution of extracellular enzyme genes across microbial taxa. We made major advances in this area in both technical approaches and fundamental understanding. On the technical side, we developed a high-throughput approach for screening soil metagenomes for extracellular enzyme function. We constructed fosmid libraries and discovered hundreds of extracellular enzyme genes from multiple bacterial (and some fungal) phyla (Nyyssönen et al. 2013). This technique allowed us to relate enzyme function to specific microbial taxa without making assumptions about gene annotation and functionality (Nyyssönen and Brodie 2014).

In addition to experimental approaches, we also made computational advances. Co-I Adam Martiny developed the consenTRAIT algorithm for extracting the phylogenetic depth of traits from a range of data sources (Martiny et al. 2013). By applying this algorithm, we showed that more complex traits (those requiring more genes, like photosynthesis) are conserved more deeply in the phylogenetic tree than simple traits underpinned by few genes (e.g. use of specific carbon substrates). These ideas are being revisited and advanced in a review article that was recently accepted by *Science* magazine (Martiny et al. 2015).

In particular, we have advanced fundamental understanding on the distribution of glycoside hydrolases among microbial taxa. A series of studies based on new bioinformatics pipelines that we developed shows that glycoside hydrolases, such as cellulases, are broadly distributed among bacteria, but there are important phylogenetic patterns (Berlemont and Martiny 2013, 2015, Berlemont et al. 2014). The genes required to degrade complex cellulose are predictable from bacterial taxonomy, and different taxa exhibit different genetically-based strategies for metabolizing carbohydrates. Some taxa appear to be opportunists with a narrow complement of oligosaccharide-processing genes, whereas other genomes may contain hundreds of distinct glycoside hydrolase genes.

Other project efforts related to extracellular enzymes focused on evolutionary tradeoffs and improving methods of measuring expressed enzymes. Using a meta-analysis approach, we found that microbes able to metabolize more complex carbon substrates are more abundant in high nitrogen environments, presumably because degrading these substrates requires a greater investment in nitrogen-rich enzymes (Treseder et al. 2011). We published two papers that provided a set of best practices for

improving the accuracy and consistency of extracellular enzyme assays in soils (German et al. 2011, Bach et al. 2013).

Objective 3

Our third objective focused on prediction: can we combine information on enzymatic traits and environmental responses of microbial taxa to predict how carbon cycling process respond to global change? This objective is probably the most challenging for us (and the field of microbial ecology) to address, so our efforts are ongoing in this area with additional publications expected to appear after this report. Still, we made substantial progress toward meeting our objective over the past five years, and our research team is often called upon to speak about incorporating microbes into predictive models (see conference proceedings section).

Based on data from our experimental system, we have been able to establish linkages between enzyme genes and the environmental responses of microbial taxa. We now know that microbial responses to drought treatment and nitrogen addition are phylogenetically conserved and correlated with the frequencies of some glycoside hydrolase genes (Amend et al. 2015a). We also found that microbial respiration of carbon substrates can vary based on an interaction between microbial community composition (i.e. the presence of specific taxa) and environmental conditions (such as water or nitrogen availability) (Matulich and Martiny 2015). Together these results suggest that different microbial taxa are not functionally redundant, and that environmental change will have different effects on functioning depending on which taxa are present in a community. However, this conclusion may not be universal, as we also found that phylogenetic diversity in fungal communities did not affect substrate respiration or response to N addition in microcosms (Amend et al. 2015b).

Another major goal under objective 3 was to develop and test predictive models. We have succeeded in developing spatially-explicit, trait-based models of complex microbial communities that produce enzymes (Allison 2012, 2014, Folse and Allison 2012). A key result from these models is that combining spatial structure with trait-based interactions can lead to interesting feedbacks at the community to ecosystem level. Incorporating tradeoffs among traits reveals potential constraints on potential microbial adaptation to temperature change (Allison 2014). When microbes specialize on different nutrient resources, these models suggest that microbes self-organize into cooperative consortia (Folse and Allison 2012).

Work on this project stimulated our interest in prediction of microbial processes at the global as well as local microbial scale. The project partially supported the PhD research of Kathe Todd-Brown who published a series of papers evaluating soil carbon outputs from Earth system models. Early on in the project, we observed that all current Earth system models represent soil carbon decomposition as a first-order process with implicit microbial mechanisms (Todd-Brown et al. 2012). We offered general recommendations for altering this model structure to directly couple microbial biomass pools with soil carbon pools, while making microbial biomass a function of environmental parameters. We then analyzed Earth system model outputs and found that they do not match observational data on soil carbon distributions (Todd-Brown et al. 2013), and future projections of soil carbon stock changes differ dramatically in sign and magnitude across models (Todd-Brown et al. 2014). When we incorporated the model

structure proposed in Todd-Brown et al. (2012) into models at the global scale, we found that they were better able to match current soil carbon stocks (Wieder et al. 2013). Furthermore, including microbial physiology directly in soil carbon models resulted in a much wider range of soil carbon responses to global change in the 21st century.

Objective 4
Our final objective was to assess whether microbial communities and functions were resilient to environmental change. Because the data collection required to address this objective was completed most recently, we are still in the process of finalizing products on this objective. Still, our initial results indicate that distinct microbial communities do require substantial time to recover in terms of composition and functioning, even when transplanted into the same environmental conditions. Decomposition rates were not resilient until the second year of our litterbag manipulation (Allison et al. 2013), and fungal communities required more time to recover (2-3 years) than bacterial communities. During the project period, we contributed to a review article/synthesis on microbial communities that discussed multiple mechanisms that constrain and contribute to resilience (Shade et al. 2012).

Additional objectives
In the course of addressing our original objectives, we engaged in several studies that were supported by DOE funding and provided additional context, scope, or new perspectives related to our project. In the course of testing if our litterbag technique had any effects on ultraviolet-mediated decomposition of litter, we discovered that microbes interact positively with UV to promote decomposition and enhance the efficiency of extracellular enzymes (Baker and Allison 2015). In the course of isolating bacterial and fungal strains to assess microbial traits, we analyzed cellular stoichiometry and found that average C:N:P ratios of microbes in our system were substantially greater than expected based on previous analytical techniques (Mouginot et al. 2014). We invited a self-funded postdoc to participate in our project and measure trace gas fluxes in our experimental plots. As expected, we found that nitrogen addition increases N_2O emissions from soil, and we conducted a meta-analysis to verify if this pattern is universal at the global scale. Interestingly, we observed that the response of N_2O emissions to fertilization has been declining globally in recent years, potentially because of higher background levels of nitrogen deposition (Aronson and Allison 2012). Finally, co-I Treseder coauthored a commentary for *Science* on the role of fungi in sequestering soil carbon (Treseder and Holden 2013).

Networks or new collaborations fostered:
This project led to the establishment of a long-term collaboration amongst the co-investigators. Recently Allison, Brodie, J. Martiny, A. Martiny, and Treseder were awarded a $1M grant from the National Science Foundation to test the climate response of microbial communities across an elevation gradient in southern California. This project uses a suite of approaches pioneered for our DOE-funded project, including microbial community transplants, metagenomic sequencing, bioinformatics pipelines, and trait-based modeling. We view the ongoing collaboration between UC Irvine and

Eoin Brodie at LBNL as a particularly valuable outcome of our DOE-funded project. In addition, we are engaging with co-I Goulden to continue and augment the ecosystem-scale climate and nitrogen manipulation that hosted our project and was originally funded by DOE-PER.

Computer modeling:

For this project, PI Allison developed the Decomposition Model of Enzymatic Traits (DEMENT, version 0.7.2). DEMENT is an agent-based numerical simulation model, open-source, coded in R, and available for all operating systems. The model uses microbial trait values and correlations to predict rates of organic matter decomposition. The most recent model version represents traits related to enzyme kinetics, enzyme production, growth efficiency, stoichiometry, and responses to moisture availability. During a model run, a large number (>100) of bacterial and fungal taxa are allowed to compete on a spatial grid representing the surface of decomposing organic material. Each taxon possesses a suite of physiological traits that are assigned based on trait correlations. Enzymes produced by the microbial taxa interact locally with substrates to generate monomers that are available for uptake. The model predicts microbial community trait distributions by simulating the abundances of the initial taxa at a daily time step. Enzymatic degradation is a Michaelis-Menten process with Arrhenius temperature sensitivity functions built into Vmax and Km kinetic parameters.

DEMENT was validated with litter decomposition data from Hawaiian rainforest, and was able to explain up to 69% of the variation in litter decay rates. Model validation results, equations, and detailed explanations of the underlying theory are available in two peer-reviewed publications (Allison 2012, 2014). The model code and documentation is available on GitHub at https://github.com/stevenallison/DEMENT.

Publications:

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Allison, S. D. 2014. Modeling adaptation of carbon use efficiency in microbial communities. Frontiers in Microbiology **5**:571.

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Berlemont, R., and A. C. Martiny. 2013. Phylogenetic distribution of potential cellulases in bacteria. Applied and Environmental Microbiology **79**:1545–1554.

Berlemont, R., and A. C. Martiny. 2015. Genomic potential for polysaccharide deconstruction in bacteria. Applied and Environmental Microbiology **81**:1513–1519.

Folse, H. J., and S. D. Allison. 2012. Cooperation, competition, and coalitions in enzyme-producing microbes: social evolution and nutrient depolymerization rates. Frontiers in Microbiology **3**:338.

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Holden, S. R., and K. K. Treseder. 2014. Soil microbial responses to disturbance events and consequences for carbon cycling in terrestrial ecosystems (PhD thesis).

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Conference papers:

Tradeoffs between growth and enzyme production in bacteria strains from plant litter. Ramin, K. and S. D. Allison. Annual Meeting of the Ecological Society of America, Baltimore. 2015.

Why Earth system modelers should care about microbial ecology. Allison, S. D. Annual Meeting of the Ecological Society of America, Baltimore. 2015.

Modeling microbial responses to drying and rewetting. Allison, S. D. and Aronson, E. Annual Meeting of the Ecological Society of America, Baltimore. 2015.

Predicting microbial community function based on physiological traits. Allison, S. D. UC Irvine Microbiome Connections, Irvine. 2014.

Microbial processes in global change models. Allison, S. D. Society for General Microbiology Focused Meeting, Loughborough, UK. 2014.

Factors influencing the relative contribution of stochastic and deterministic processes in microbial community assembly: results from a trait-based model. Evans S. E., J. B. H. Martiny, and S. D. Allison. Annual Meeting of the Ecological Society of America, Sacramento. 2014.

Drought and N addition control soil GHG flux and microbial composition. Aronson, E., and S. D. Allison. Annual Meeting of the Ecological Society of America, Sacramento. 2014.

Microbial feedbacks to climate change on local to global scales. Allison, S. D. Annual Meeting of the Ecological Society of America, Sacramento. 2014.

New models based on microbial control over soil carbon. Allison, S. D. Research Coordination Network Workshop, Breckenridge CO. 2014. Sponsored by NSF.

Microbial biogeography: Limits and new avenues for investigating dispersal. J. Martiny. International Society of Microbial Ecology, Seoul, South Korea. 2014.

The resilience of microbial composition and its functioning in response to global change manipulations. Jennifer B. H. Martiny, Claudia Weihe, Ying Lu, Renaud Berlemont, Michael Goulden, Adam C. Martiny, Kathleen K. Treseder and Steven D. Allison. Ecological Society of America, Sacramento, CA. 2014.

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Discoveries in microbial ecology. Treseder, K. 2014. Annual Meeting of the Ecological Society of America, Sacramento. 2014.

Dry-season ultraviolet radiation primes litter for wet season decomposition in a Mediterranean grassland. Baker, N. R. and S. D. Allison. Annual Meeting of the American Geophysical Union, San Francisco. 2013.

Changes in soil organic carbon storage predicted by Earth system models during the 21st century. Todd-Brown, K. E. O., J. T. Randerson, F. Hopkins, V. Arora, T. Hajima, C. Jones, E. Shevliakova, J. Tjiputra, E. Volodin, T. Wu, Q. Zhang, and S. D. Allison. Annual Meeting of the American Geophysical Union, San Francisco. 2013.

Scaling up microbial responses to climate change. Allison, S. D. and S. E. Evans. Annual Meeting of the American Geophysical Union, San Francisco. 2013.

Incorporating microbial traits into Earth system models. Allison, S. D. Annual Meeting of the Ecological Society of America, Minneapolis. 2013.

Resilience of extracellular enzymes to environmental change. Allison, S. D., C. J. Alster, Y. Lu, and D. P. German. Annual Meeting of the Ecological Society of America, Minneapolis. 2013.

Increased N deposition in a grassland stimulates soil N_2O release while drought decreases *Nitrospirae* abundance. Aronson, E. L., and S. D. Allison. ICoN3 conference, Tokyo, Japan. 2013.

Succession of Microbial Phylogeny and Function During Plant Litter Decomposition. Brodie, E. L. , Nyyssonen, M., Tran, H. M., Karaoz, U., Weihe, C., Hadi, M. Z., Martiny, J. B. H., Martiny, A. C., Allison, S. D. JGI Annual User Meeting, Walnut Creek, CA, March 2013. Sponsored by Department of Energy, Genomic Sciences Program.

Burn severity influences soil microbial responses to wildfire in Alaskan boreal forests. Holden, S., B. Rogers, J. Randerson, and K. Treseder. Annual Meeting of the Ecological Society of America, Minneapolis. 2013.

Fires as global change: Responses by mycorrhizal fungi. Holden, S., and K. Treseder. Joint Meeting of the American Phytopathological Society & The Mycological Society of America, Austin. 2013.

Metagenomic analysis of soil litter microbial populations in response to global changes. R. Berlemont & A.C. Martiny. SoCal Evolutionary Genetics & Genomics Meeting, UC-Irvine, CA. September 2013.

Metagenomic analysis to reveal how global changes impact the plant litter deconstruction by microorganisms. R. Berlemont, S.D. Allison, J.B.H. Martiny, E. Brodie and A.C. Martiny. 10th Southern California Geobiology Conference, Caltech, Pasadena. April 2013.

Metagenomics for plant litter deconstruction in natural and perturbed environments. R. Berlemont, S.D. Allison, J.B.H. Martiny, E. Brodie and A.C. Martiny. DOE JGI, Genomics of Energy & Environment – User Meeting, Walnut Creek, CA. March 2013.

Metagenomics of microbial communities from the leaf litter - Insights into the plant-polymers degradation. R. Berlemont, S. Allison & A. Martiny. DOE Genomic Science, System Biology for Energy and Environment, Bethesda MD. February 2013.

Season drives precipitation and N deposition impacts on nitrous oxide, methane and carbon dioxide emissions in a CA grassland. Aronson, E. L., and S. D. Allison. Annual Meeting of the American Geophysical Union, San Francisco. 2012.

Integrating microbial traits into ecosystem models. Allison, S. D. Annual Meeting of the American Geophysical Union, San Francisco. 2012.

Evaluating soil carbon in global climate models: benchmarking, future projections, and model drivers. Todd-Brown, K. E., J. T. Randerson, W. M. Post, and S. D. Allison. Annual Meeting of the American Geophysical Union, San Francisco. 2012.

Reconciling phylogeny and function during plant litter decomposition by high-throughput functional metagenomics. Nyyssönen, M., C. Weihe, M. L. Goulden, K. K. Treseder, J. B.H. Martiny, A. C. Martiny, S. D. Allison, and Eoin L. Brodie. International Society for Microbial Ecology Meeting, Copenhagen. 2012.

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Extracellular enzymatic response to drought and nitrogen deposition in southern California. Beasley, S. and S. D. Allison. NSF REU program in Earth System Science, UC Irvine. 2012.

Emergent spatial structure in a community of extracellular enzyme-producing microbes. Folse, H. J., III, and S. D. Allison. Annual Meeting of the Ecological Society of America, Portland. 2012.

Evaluating soil carbon in global climate models: How good are the models and what drives model variability? Todd-Brown, K, J. Randerson, W. Post, and S. D. Allison. Annual Meeting of the Ecological Society of America, Portland. 2012.

Linking microbial enzyme genes with community responses to drought and nitrogen. Allison, S. D. US DOE Contractors and Grantees Workshop, Bethesda, MD. 2012.

Post-fire changes in soil microbial communities constrain heterotrophic respiration following wildfires. Holden, S., and K. Treseder. 2012. Annual Meeting of the Ecological Society of America, Portland. 2012.

Percent mycorrhizal root length is a reliable indicator of benefits to host plants: Results from a meta-analysis. Treseder, K. Annual Meeting of the Ecological Society of America, Portland. 2012.

Distribution of potential for cellulose utilization in bacterial lineages. R. Berlemont & A. C. Martiny. 4th Argonne Annual Soil Metagenomics Meeting, Chicago, IL. 2012.

Phylogenetic distribution of Potential Cellulases in Bacteria. R. Berlemont & A. Martiny. DOE Genomic Science, Systems Biology for Energy and Environment, Bethesda, MD. February 2012.

Phylogenetic conservatism of functional traits in microorganisms. A.C. Martiny. International Society for Microbial Ecology Meeting, Copenhagen. 2012.

Assessing variability in belowground carbon for CMIP-5 models. Todd-Brown, K. E., F. M. Hoffman, J. T. Randerson, W. M. Post, and S. D. Allison. Annual Meeting of the American Geophysical Union, San Francisco. 2011.

Trait-based modeling of microbial decomposition. Allison, S. D. Annual Meeting of the Ecological Society of America, Austin. 2011.

Can microbial functional traits predict the response and resilience of decomposition to global change? Allison, S. D., E. L. Brodie, M. Goulden, Y. Lu, A. Martiny, J. B. H. Martiny, M. J. Nyyssonen, K. K. Treseder, C. Weihe. US DOE Contractors and Grantees Workshop, Crystal City, Washington DC. 2011.

Fire and fungi: Changes in soil fungal abundance and community composition across a fire chronosequence in an Alaskan boreal forest. Dooley, S., and K. Treseder. Annual Meeting of the Ecological Society of America, Austin. 2011.

How do microbial responses to global change influence ecosystem carbon cycling? Treseder, K., S. Kivlin, S. Allison, and K. McGuire. 2011. Annual Meeting of the Ecological Society of America, Austin. 2011.