

Overview

Understanding the resilience of ecological systems is a fundamental goal in ecology, and essential for delivering ecosystem services in the face of change. KBS LTER scientists have studied ecological processes in agricultural systems since 1989, using long-term datasets informing ecological principles mediating resilience under various land uses. These studies have been important for revealing, understanding, and optimizing the delivery of ecosystem services in agricultural landscapes. Recently, KBS LTER has pivoted to a specific focus on the resilience of ecosystems to climate and land use changes, motivated by long-term observations documenting differences in resilience across land use intensities, in addition to projections of increasing climate variability that threaten the long-term integrity of agricultural systems. In the US Midwest, short droughts during the growing season are projected to become more common, associated with greater precipitation variability and warmer temperatures. Based on three decades of research showing that some land uses are more resilient to climate disturbance than others, three classes of mechanisms were identified that underlie agroecosystem resilience – resources, diversity, and adaptation. The overarching hypothesis is that knowledge of these mechanisms and their interactions can allow prediction of the resilience of key ecosystem processes at field, landscape, and regional scales. Specific hypotheses focus on soil resources that can drive the resilience of water availability, carbon storage, and greenhouse gas emissions; on diversity that can drive the resilience of microbial and arthropod communities at plant and landscape scales; and on farmer and evolutionary adaptation, respectively influenced by beliefs and values and genetic plasticity. These hypotheses will be addressed with strategically designed new and existing experiments, including a large-scale rainout shelter experiment across three land uses, the implementation of perennial prairie strips within agricultural fields, and a major regional farmer survey. Finally, KBS LTER scientists will introduce new tools to explicitly address how resilience scales across landscapes, extrapolate site-specific measurements to the region, and quantify the potential regional impact of changes in management to enhance ecosystem services.

Intellectual Merit

KBS LTER is uniquely positioned to build a mechanistic understanding of the resilience of agricultural ecosystems and landscapes in response to projected climate changes against the backdrop of a gradient of land use intensities. This mechanistic approach will reveal generalizable principles about ecological resilience, which inform theory and develop much-needed predictions of resilience of communities and ecosystem processes in the face of global change. Coordinated, long-term measurements spanning diverse organisms, biophysical resources, and biogeochemical processes will uniquely reveal linkages among ecosystem components that may be key to enhancing system-level resilience. At the same time, modeling and remote sensing will expand the spatial applicability of this work, while surveys of regional farmers identify socioeconomic conditions and increase the ability to project results across the Midwest and include farm-scale social factors in future climate scenarios.

Broader Impacts

The agricultural setting of KBS LTER provides an exciting potential to connect with people and translate fundamental research findings into opportunities to increase public scientific literacy and engagement. Through an extensive strategic planning process in 2021, KBS LTER has identified three priority areas that will best impact conservation and environmental decision-making: Carbon for Croplands, which aims to disseminate knowledge of carbon sequestration to stakeholders and policymakers, Farmscapes for Biodiversity, which emphasizes findings that incorporation of perennial conservation lands can enhance ecosystem services at field and landscape scales, and Ecology for All, which identifies new areas for KBS LTER to reduce barriers for underrepresented groups in STEM. These initiatives are centered on the formation of bi-directional relationships with stakeholder groups and new strategic partnerships, both regional and national. KBS LTER will also continue well-recognized programs – Data Nuggets and its K-12 Partnership – that focus on student understanding and educator development, with a new emphasis on broadening representation.

LTER:KBS – Ecological and social mechanisms of resilience in agroecosystems

1.0 Project Overview and Results from Prior Support

1.1 Project Overview

Anthropogenic changes increasingly impose stress on natural and working ecosystems. If ecological systems become unable to resist or rapidly recover from such perturbations, global change will impair critical ecosystem functions and services. Determining which processes mediate resilience is crucial, particularly in agroecosystems, where ecosystem processes translate to societal services (Novick et al. 2022). While agricultural intensification can help meet human demand for food, fiber, and fuel, it can come with severe tradeoffs, including ground- and surface water contamination (Cooper 1993, Syswerda et al. 2012), eutrophication (Hamilton 2015), increased greenhouse gas emissions (Gelfand and Robertson 2015), and biodiversity declines (Benton et al. 2021). Adoption of certain practices may lessen some of these harmful effects, but in order to predict how and when this occurs, we need a basic understanding of the ecological processes involved. In the future, agricultural systems will be subjected to increased climate variability, which will compromise both food production and other ecosystem services. A pressing global challenge, which provides the backdrop to KBS LTER, is to elucidate the mechanisms by which intensive agriculture and climate change affect ecosystem functions, and to identify how to mitigate those effects to make agriculture both less environmentally harmful and more resilient to global change.

At the KBS LTER, we use long term, well-replicated experiments to test hypotheses about how land use and other global changes alter productivity, soil carbon (C) balances, greenhouse gas (GHG) emissions, nutrient transformations and transport, pest and natural enemy dynamics, and other ecosystem functions. These experiments, some of which have run continuously for 33 years, have directed us to three central mechanisms that mediate resilience. **In our proposed research, we use both ongoing and new experiments to describe not only how ecosystem processes change, but also to test how these central mechanisms - resources, diversity, and adaptation - mediate ecosystem resilience.** Throughout the proposal, we define *resilience* as the ability of a system to maintain function, or to return to a steady state (Holling 1973), in the context of ecosystem responses to disturbances (Elmqvist et al. 2003, Standish et al. 2014, see Fig. 1)

We study responses to two of the most intense global changes - climate and land use change, including the interaction between the two. To study resilience with respect to climate change, we increase rainfall variability and drought using rainfall manipulations. Drought serves as an excellent model of disturbance because it both impacts critical agroecosystem services and increasingly threatens the sustainability of agricultural systems worldwide. It also affects the attitudes and behaviors of farmers managing these systems, allowing us to study ecological and social mechanisms of resilience simultaneously. Our drought manipulation occurs on KBS LTER's hallmark long-term experiment that documents ecological and evolutionary responses to a gradient of land use intensity from intensive agriculture to conservation lands. Using this study as a foundation, we test how mechanisms of drought resilience change across land use intensities. We will also directly study resilience to land use change by investigating the potential for agronomic practices to promote resilience. In two treatments in the same long-term land use experiment, we introduce native plant species via "prairie strips" within row crops, testing the hypothesis that higher diversity will enhance resilience of ecological systems in managed lands. In our proposed research, we introduce new themes of how *interactions* among the three mechanisms mediate resilience, and explicit efforts to scale knowledge of resilience using remote sensing, farmer surveys, and process-based modeling.

1.2 Historical Context

As the only cropland agriculture site in the LTER Network, KBS LTER explores and tests the application of ecological theory to the cropping systems that underpin U.S. agriculture. We investigate both classic theories, such as biodiversity-ecosystem function relationships, and new questions motivated by our long-term data about the mechanisms that underpin the resilience of key

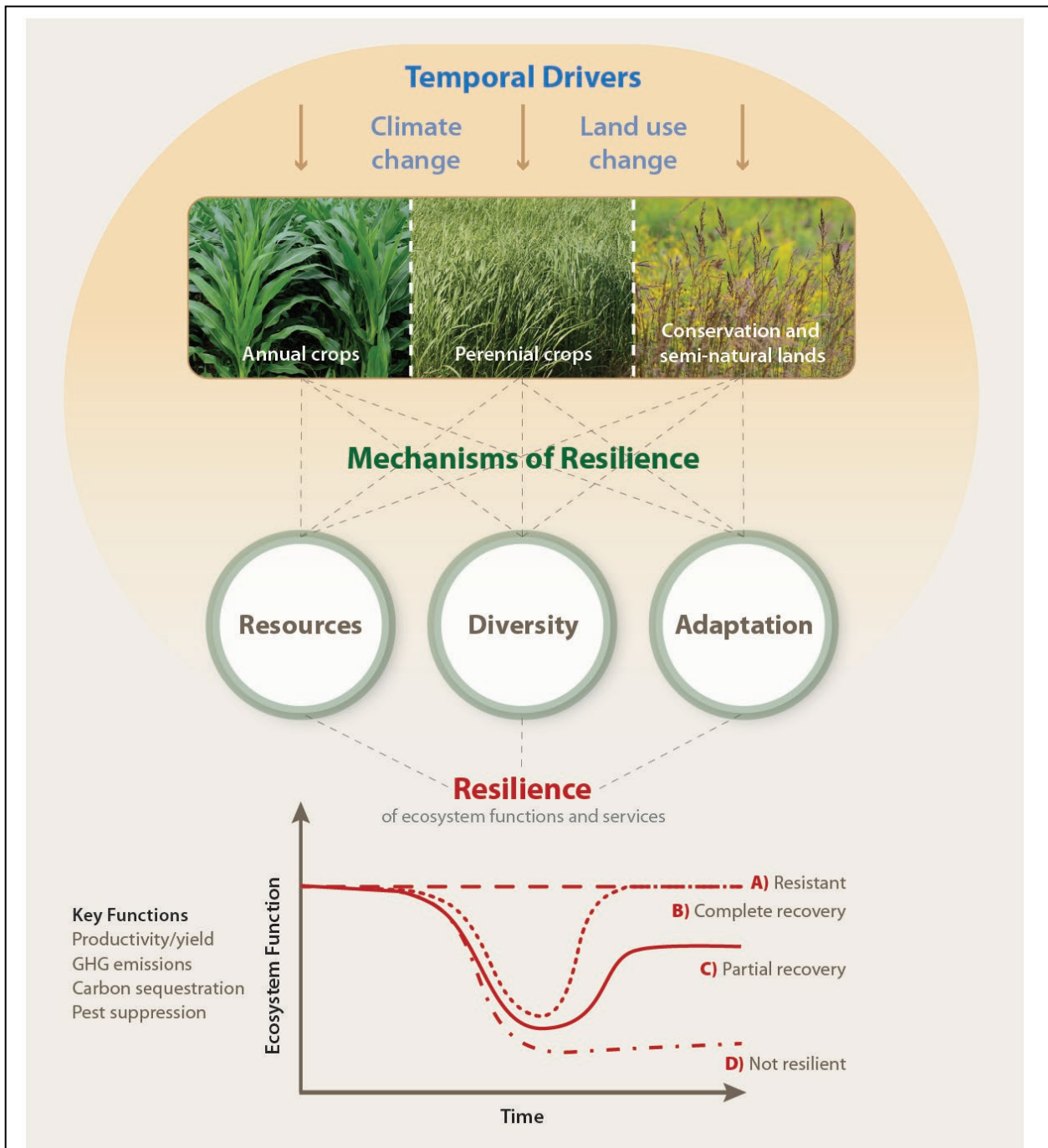


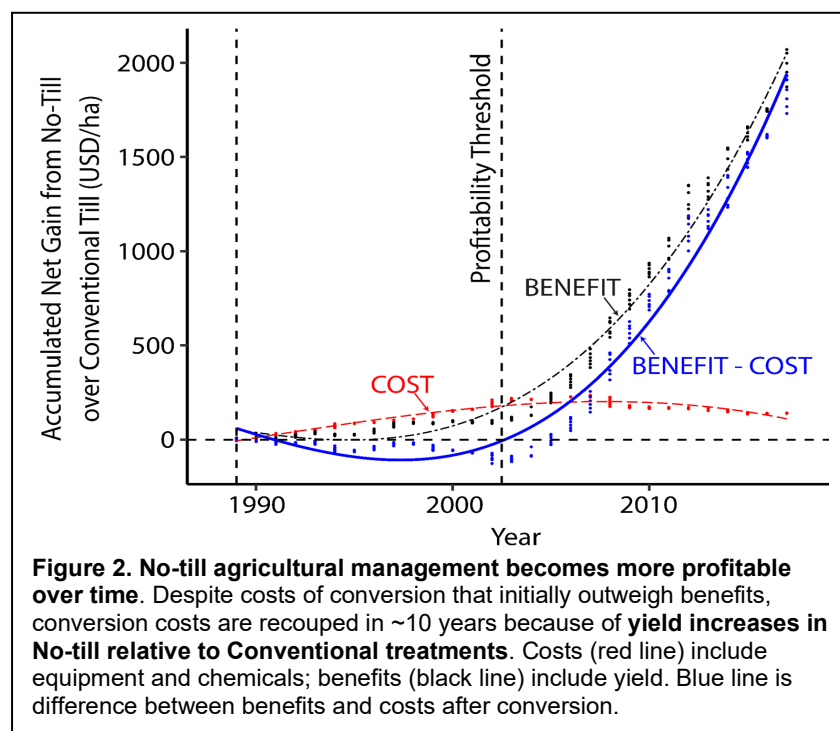
Figure 1. KBS LTER will study mechanisms that mediate resilience along a gradient of land-use complexity that represents the dominant landscapes in our region: annual cropping systems, perennial cropping systems, and conservation lands. Climate and land use change drive ecological processes in these farmscapes. We focus on three classes of mechanisms: Resources, Diversity, and Adaptation that we hypothesize are key determinants of resilience of ecosystem function to large-scale drivers and associated short-term disturbances (e.g., growing-season water stress). Bottom graph modified from (Oliver et al. 2015).

ecosystem services. Since our site's inception, we have added studies to test hypotheses about the functioning of these human-dominated ecosystems, bridging the natural and social sciences. Hallmark studies include experimental tests of: greenhouse gas costs of intensive agriculture (since

1989); interactions between N cycling and rainfall (since 2000); agricultural land use change and pest suppression (since 1989); benefits of crop rotational and non-crop plant species diversity (since 2000); applicability of predictions generated in plot-level experiments to the scale of entire farm fields (since 2006); plant species diversity impacts on biomass production for bioenergy (since 2008); and prairie plant species richness and origin (across a latitudinal gradient) on ecosystem functions (since 2015). In addition, our ongoing socioecological studies test how changing farmer perceptions affect their decisions regarding crop and environmental management (with our region-wide Panel Farmer Survey, PFS; since 2017).

KBS LTER's signature experiment, established in conjunction with our original proposal, is the Main Cropping System Experiment (MCSE, see Major Experiments), which spans a gradient of land use intensity, from row crop agriculture (four levels of intensity) to perennial crops (switchgrass and hybrid poplar), to native habitats (perennial grasslands, deciduous forest). Within our main plots, we set aside space to conduct additional manipulative sub-plot experiments including nutrient addition, water addition, disturbance, species removal, cover cropping, and herbicide-free treatments. More recently, in 2019, we introduced native plant communities (prairie strips) into the Reduced Chemical Inputs and Biologically Based treatments. In 2021, we initiated a major subplot Rainfall Exclusion Experiment (REX) to test resilience hypotheses.

1.3 Treatment effects still accruing after three decades



Findings from the KBS LTER demonstrate why long-term studies are essential to understand the effects of environmental change. We found, for example, that yields in no-till agriculture - a lower intensity land use - can exceed those of conventional agriculture while providing more environmental services. Even more surprising, the gap in yield between the two treatments is still increasing after three decades (Cusser et al. 2020). We showed that at least fifteen years were required to generate patterns consistent with 29-year trends in yield differences, and economic analysis showed that 10 years of implementation were needed

for a farmer to recoup the costs of conversion from conventional tillage (Fig. 2). Higher yields in no-till could be due to higher soil water holding capacity, changes in soil pore architecture, or C accrual at depth, but will require future investigation.

Long-term studies also have been essential in understanding plant and animal communities, as exemplified by work on the predatory coccinellid (ladybird beetle) over the past 33 years. Our moving-window analysis (Bahlai et al. 2021) found that it takes, on average, 9.4 years to identify the long-term trend in coccinellid abundance, and that a 2%/yr decline (30% decline over the duration of KBS LTER) was consistent across native and exotic beetle species (Fig. 3). Moreover, the decline in coccinellid abundance has not abated, and is more pronounced in annual vs. perennial habitats (e.g., herbaceous and forest). In future work, we ask what is causing the ladybird beetle decline,

investigating aphid prey abundance, the effects of neonicotinoid insecticides, and changing habitat suitability (see *Diversity Question 4 (D-4)* below).

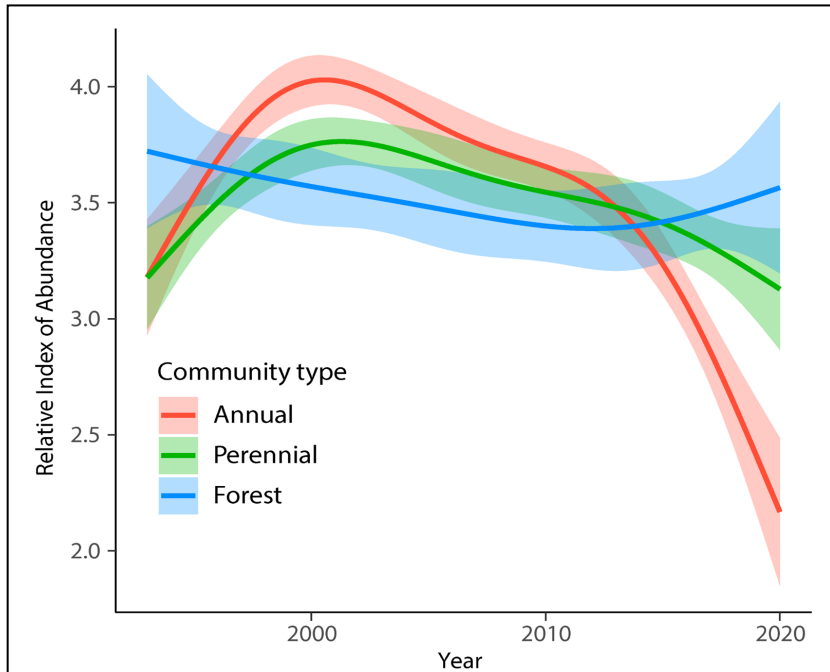


Figure 3. Normalized coccinellid abundance, including native + exotic species sampled weekly during the growing season, have **declined for the last two decades** in annual and perennial herbaceous habitats, with precipitous declines in annual habitats in recent years. Populations have remained relatively stable in forest plots during this same time period.

These two examples demonstrate the need for sustaining our long-term observations and experimentation, and also motivate our future investigation of the mechanisms that underlie differences in resilience that we have captured over multiple decades.

1.4 Key drivers of environmental change at KBS LTER

KBS LTER research focuses on two primary drivers that affect responses in our landscapes: climate change (specifically precipitation and warming) and land use change (specifically, intensification).

Our most recent research on climate change focuses on altered precipitation regimes, particularly regimes during the growing season (see *REX in Major Experiments*). Although total precipitation in the Midwest is predicted to remain stable or even increase, rainfall patterns are predicted to become more variable, with a greater frequency and duration of dry periods during the growing season, and more intense rainfall events (Pryor et al. 2013, Tomasek et al. 2017). Precipitation in 2021 illustrated this trend: while cumulative rainfall at the end of June was the lowest recorded over the last ninety years, that period was followed by 20 cm of rainfall over nine days, effectively raising the cumulative precipitation above average levels (Fig. 4). This is consistent with patterns observed at KBS and with

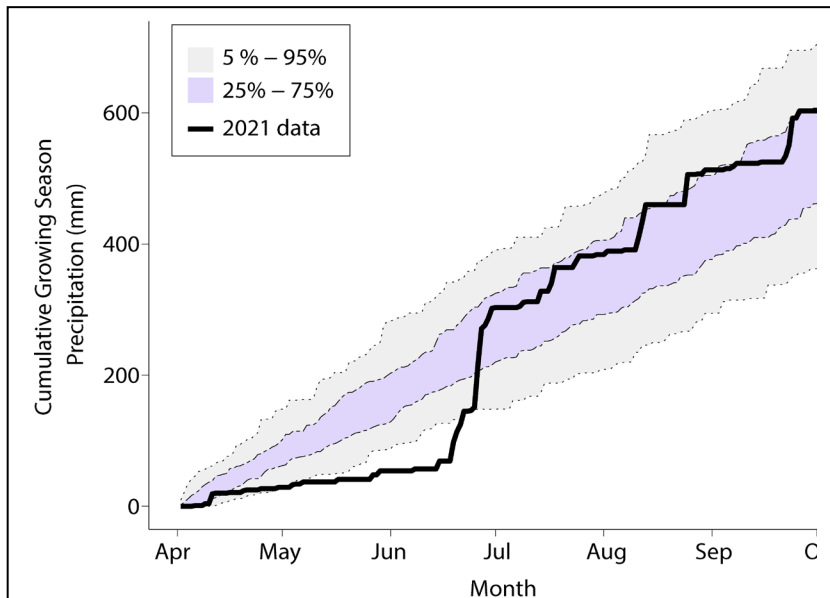


Figure 4. Cumulative 2021 rainfall (black line) demonstrates **extended spring drought and a late summer flash drought despite total growing season rainfall resulting in a “wet” year**. Confidence intervals based on daily KBS weather station data from 1931-2021.

projections of future climate change (USGCRP (U.S. Global Change Research Program) 2018, IPCC 2022). Indeed, farmers across the Midwest report increasing concern over unusually heavy rainfall events (see PFS in Major Experiments). Over the past forty years, we have observed rising temperatures (Robertson and Hamilton 2015), especially minimum temperatures (Senthilkumar et al. 2009), and declining duration of snow cover (Ruan and Robertson 2017) - trends expected to continue (Basso et al. 2021).

The second driver of environmental change we investigate is the effect of land-use change (e.g. the increasing intensity with which land is managed). Our landscape - indeed the entire U.S. Midwest - has undergone wholesale simplification in recent decades, with increased extent of croplands and reduced crop species richness (Hemberger et al. 2021). While increasing the diversity of species and habitats can increase ecosystem services, including pollination, biocontrol, erosion control, and nutrient retention (Chaplin-Kramer et al. 2019), linkages between diversity and ecosystem function have been found to be inconsistent. Studies that focus on how and why diversity enhances long-term ecosystem services could help fill this gap (Tscharrnke et al. 2016, Dainese et al. 2019). An innovative approach to increasing diversity within intensely managed agricultural landscapes is the introduction of native plant species via “prairie strips.” These prairie strips, which are intended to increase resilience of biodiversity and ecosystem services in working landscapes (Schulte et al. 2017), feature prominently in our Proposed Research.

1.5 Intellectual Merit of Prior Support

Since 2016, 340 researchers (including 82 faculty, 70 postdocs, 112 graduate students, 69 undergraduate interns, and seven K-12 teachers) have conducted research utilizing KBS LTER. Collectively in this period, we have produced 230 publications and 40 MSc and PhD theses. Over 83 projects (totalling \$73M in external funding) have leveraged our site and its infrastructure, data, and experiments to conduct research in this period.

Mechanisms of resilience

We organize both our current and proposed research according to our conceptual model (Fig. 1) and its core mechanisms of resilience: Resources, Diversity, and Adaptation. These themes map onto the five LTER Core Areas: primary production, organic matter accumulation or utilization, and inorganic inputs and movements of nutrients through ecosystems (*Resources*); population dynamics and trophic structure (*Diversity*); and patterns and frequency of disturbances (*Resilience*). Themes also follow NSF’s guidance to integrate Core Areas with social, economic, or cultural processes to examine effects of human-environment interactions on ecosystem dynamics.

In the next sections, we highlight our most impactful research from the current funding period, which has demonstrated the recurring importance of Resources, Diversity, and Adaptation at KBS LTER in explaining resilience. This work sets the foundation for new studies that will answer questions about resilience conferred by these mechanisms, as well as by interactions between these mechanisms, and about scaling this knowledge from plots to the region (Fig. 5).

Resources

One of the primary resources we hypothesize mediates resilience to environmental stressors is soil organic carbon (hereafter, soil C). Soil C can improve soil structure and aggregation (e.g., Grandy and Robertson 2007, Grandy and Robertson (in press)), thereby increasing soil water retention and soil fertility, decreasing erosion, and enhancing other ecosystem functions (Amézketeta 1999). We have established that, relative to conventional tillage, no-till management increases soil C by ~20% in the top 1 m of soil (Syswerda et al. 2011), and that this corresponds to increased water availability during dry periods in the growing season (Robertson et al. 2014). Notably, our simulations of long-term yields and soil C changes under the corn-soybean-wheat rotation in the MCSE under future climate scenarios (+2°C warming and 500 ppmv CO₂ Basso and Ritchie 2015) demonstrate that no-till management ameliorates climate impacts on yield via increased soil C levels (Liu and Basso 2020). *In Proposed Research, we test how soil C mediates resilience in REX by manipulating labile*

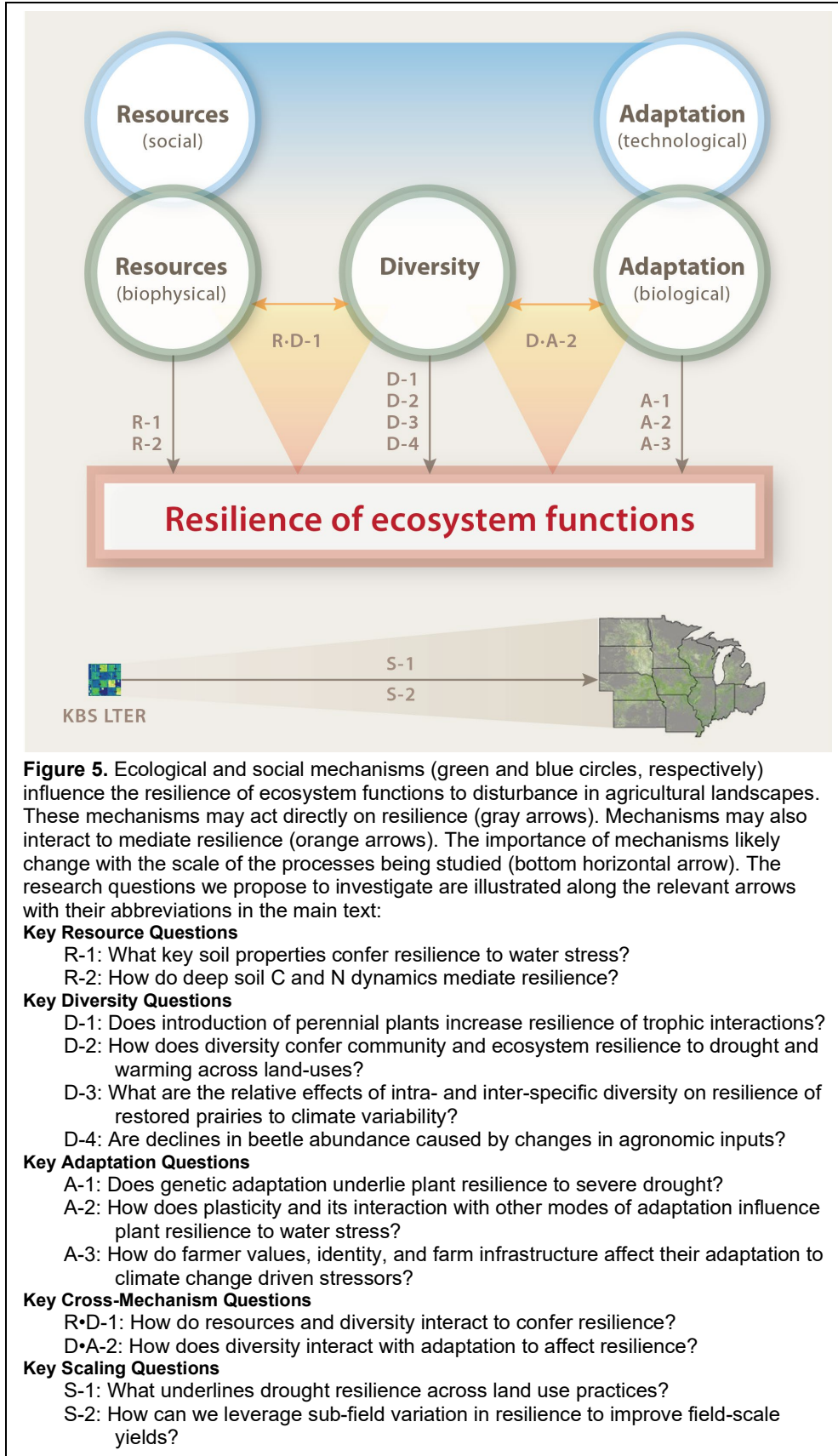


Figure 5. Ecological and social mechanisms (green and blue circles, respectively) influence the resilience of ecosystem functions to disturbance in agricultural landscapes. These mechanisms may act directly on resilience (gray arrows). Mechanisms may also interact to mediate resilience (orange arrows). The importance of mechanisms likely change with the scale of the processes being studied (bottom horizontal arrow). The research questions we propose to investigate are illustrated along the relevant arrows with their abbreviations in the main text:

Key Resource Questions

- R-1: What key soil properties confer resilience to water stress?
R-2: How do deep soil C and N dynamics mediate resilience?

Key Diversity Questions

- D-1: Does introduction of perennial plants increase resilience of trophic interactions?
D-2: How does diversity confer community and ecosystem resilience to drought and warming across land-uses?
D-3: What are the relative effects of intra- and inter-specific diversity on resilience of restored prairies to climate variability?
D-4: Are declines in beetle abundance caused by changes in agronomic inputs?

Key Adaptation Questions

- A-1: Does genetic adaptation underlie plant resilience to severe drought?
A-2: How does plasticity and its interaction with other modes of adaptation influence plant resilience to water stress?
A-3: How do farmer values, identity, and farm infrastructure affect their adaptation to climate change driven stressors?

Key Cross-Mechanism Questions

- R•D-1: How do resources and diversity interact to confer resilience?
D•A-2: How does diversity interact with adaptation to affect resilience?

Key Scaling Questions

- S-1: What underlines drought resilience across land use practices?
S-2: How can we leverage sub-field variation in resilience to improve field-scale yields?

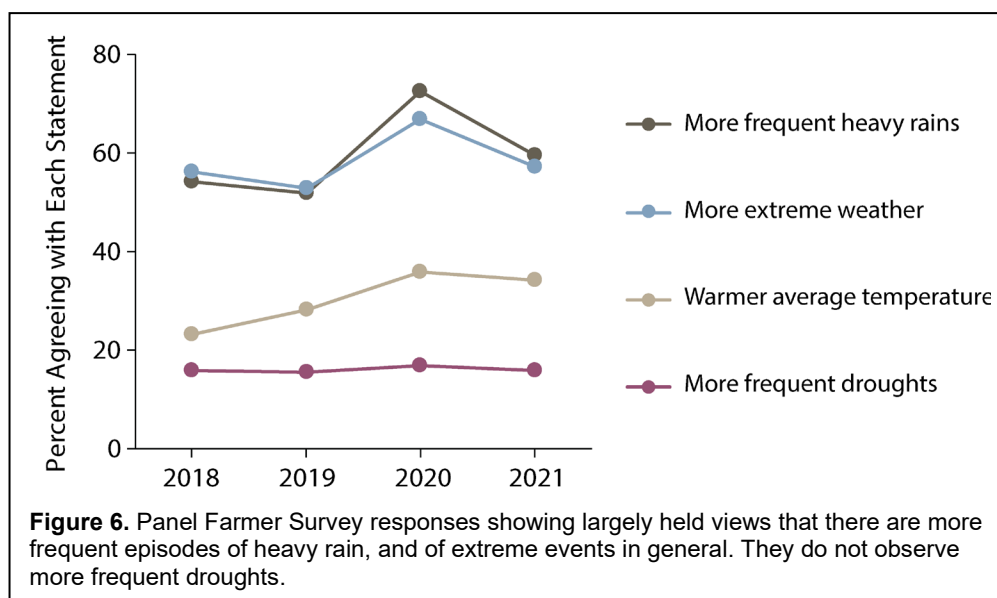
C resources, and comparing land uses with different soil C levels (Resources Q1, or, as noted in Fig. 5 and for all questions from here forward, R-1).

We are also investigating the process-level mechanisms responsible for enhanced soil C accrual under no-till, cover cropped, and diverse perennial vegetation. Soil aggregate stability is known to play a key role. Diverse vegetation promotes the turnover of microbial biomass and the association of cell metabolites with soil mineral surfaces, which also benefits soil C accrual (Kallenbach et al. 2015, Kallenbach et al. 2016). Polycultures, such as annual cropping systems that are cover-cropped and perennial systems with mixed species, enhance the development of pore systems favorable to soil C gain. This soil pore architecture

is beneficial for the long-term stabilization of mineral-associated organic matter (Kravchenko et al. 2019). *In our Proposed Research, we explicitly test how spatial structure of soil drives soil C accrual, particularly at depth (R-2). This work has also revealed how resilience can be mediated by interactions between mechanisms (Resources and Diversity Q1, or, as noted in Fig. 5, R•D-1), motivating a new theme in Proposed Research (Resilience across Mechanisms).*

We have shown surprisingly important effects of rainfall variability and warming on biogeochemical cycles, even over short periods. For example, we documented a doubling of cumulative N₂O emissions when soils that dried *in situ* for four weeks were re-wet, compared to those re-wet at historically normal 2-3 day intervals (Glanville 2020). This phenomenon only occurred in annual cropping systems where N₂O reductase enzyme activity was slow to respond post-drought. In another rainfall exclusion study, longer intervals between heavier rainfall events increased water percolation rates in conventional, no-till, and perennial cropping systems, but nitrate leaching increased only in tilled systems, which were less resistant to rainfall effects on nutrient loss (Hess et al. 2018, Hess et al. 2020). *In our Proposed Research, we will investigate how water stress interacts with land use, soil resources, and diversity to affect resilience of ecosystem functions such as N₂O emissions and plant community productivity (R-1).*

Of course, changes in rainfall intensity also affect ecological systems through changes in how a farmer's financial resources are allocated, as demonstrated by our PFS, that reaches 2500 regional farmers annually (see Major Experiments). The PFS revealed that farmer concern about deleterious extreme rainfall events increased from 2018 to 2021 (Fig. 6). Surprisingly, despite expressing little concern about drought, farmers increased irrigation infrastructure over this same time period (Das Bhowmik et al. 2020). Interviews with corn growers revealed two main decision-making strategies to address uncertainty. While some farmers rely on previous personal experience, others used a data-intensive approach with increased use of field- and farm-scale data collection and management to minimize uncertainty (Reimer et al. 2020). From interviews, we developed PFS questions to gauge how pervasive these knowledge and information gains are across watershed, landscape, and regional scales. *In our Proposed Research, we will use a decade of farmer responses to ask how a*



farmer's financial resources and values interact to determine practice adoption and their farm's resilience to suboptimal weather or market conditions (A-3).

Increasingly, KBS LTER research applies the processes uncovered from studies at KBS LTER to regional scale questions.

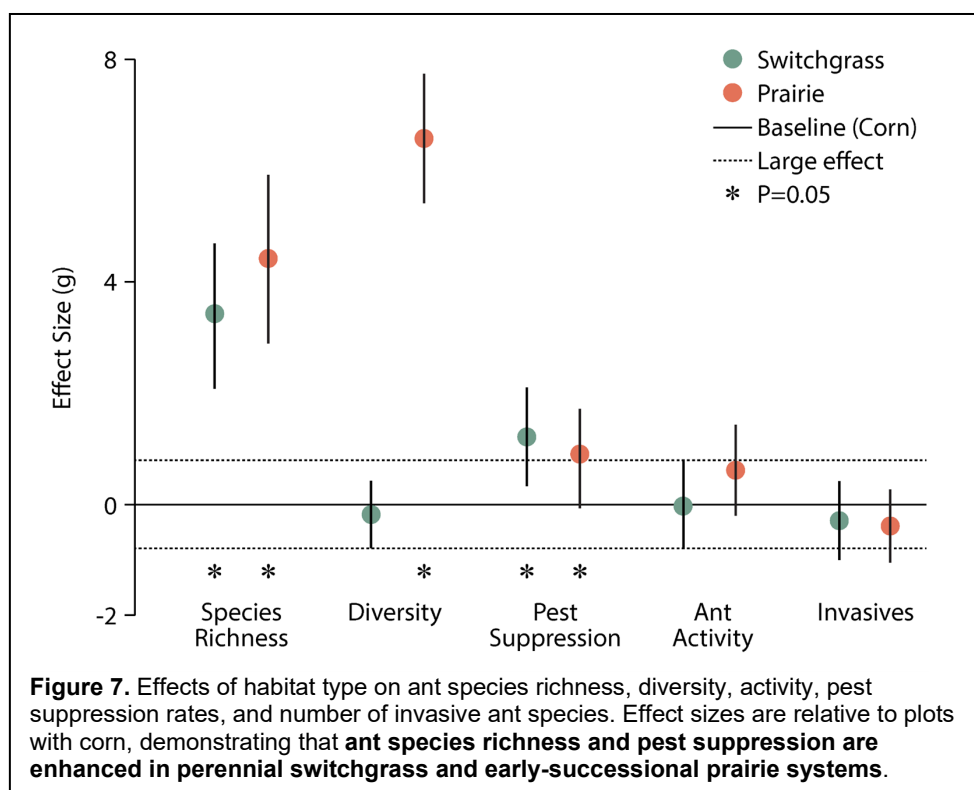
We integrate knowledge from plot scale studies and satellite imagery, and have demonstrated novel relationships between interannual yield variability, terrain features, and water availability across the Midwest (Basso et al. 2019, Martinez-Feria and Basso 2020). In doing so, we can identify areas that lack natural resources, do not benefit from nutrient amendments, and therefore can be removed from production and allocated to biodiversity conservation, perhaps without adversely impacting a farmer's income (Basso and Antle 2020, Basso 2021). *In our Proposed Research, we will investigate*

how farmers' knowledge of yield stability on their fields alters their management decisions (A-3), and to scale such findings in a new theme (S-2).

Diversity

Our agricultural landscape provides a unique lens through which to examine how land use change and farmer decision-making alter biodiversity. Our recent work illustrates 1) how diversified landscapes affect arthropod and potentially microbial communities; and 2) what values or incentives motivate farmers to adopt conservation strategies such as converting annual row crops to perennial bioenergy grasses or prairies - practices which increase biodiversity, but may reduce yield.

We have pioneered research on how landscape-scale habitat diversity alters the diversity and function of arthropod communities. Arthropod predators and parasitoids provide a valuable ecosystem service in suppressing crop pests. We have shown that the abundance and activity of these beneficial organisms depend on habitat composition of the local agricultural landscape (Gardiner et al. 2009, Gardiner et al. 2010, Woltz et al. 2012). In a recent synthesis, we explored how landscape spatial configuration (i.e., the size, shape, and spatial arrangement of fields and other habitat patches) affects pest suppression services. We found that natural enemies are more abundant in agricultural landscapes made up of smaller habitat patches than in those with larger homogenous patches, and that the effects of landscape configuration on pest suppression depend on organismal traits such as overwintering strategies and dispersal modes (Haan et al. 2020).



In addition to showing effects of landscape diversity, we have demonstrated that greater within-field diversity enhances ecosystem services. Bioenergy crops can take the form of monocultures (i.e., switchgrass) or diverse mixtures of native species. In studies manipulating plant diversity, we found that diversified bioenergy crops (converted to prairie, as compared to corn) support higher ant diversity and

enhanced services (as predators of common pests and nuisance seeds) (Fig. 7, Helms et al. 2020). Conversion to switchgrass (which, in fact, results in a mixed plant community) or prairie can support high pollinator diversity, and can do so while achieving yield for bioenergy comparable to the highest yield produced by native grass species alone (Fig. 8, Kemmerling et al. 2021). *In our Proposed Research, we will analyze yield-stability relationships to assess which farmlands across the Midwest could most benefit from conversion to perennials capable of providing ecosystem services to surrounding croplands (D-1).*

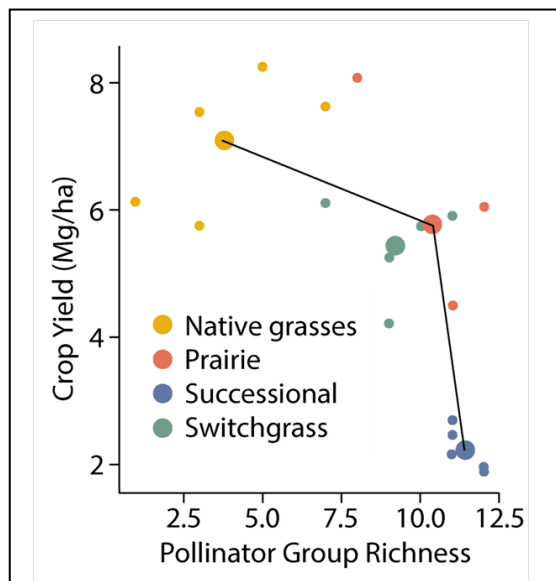


Figure 8. Prairie supports high yield and pollinator richness. A Pareto frontier (black line) for mean bioenergy crop yield (Mg/ha) and mean pollinator group richness across bioenergy crop treatments. The frontier describes the optimal values for crop yield and pollinator group richness over a range of preferences. Large dots are means across replicates.

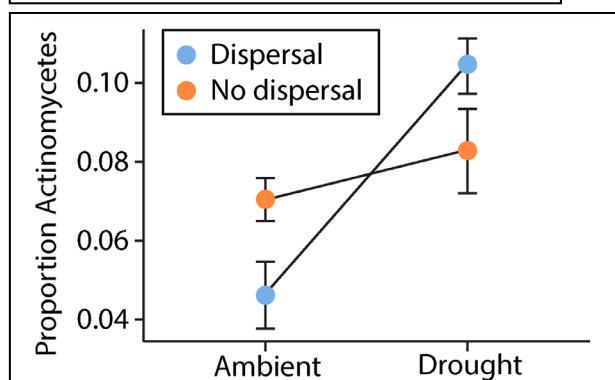


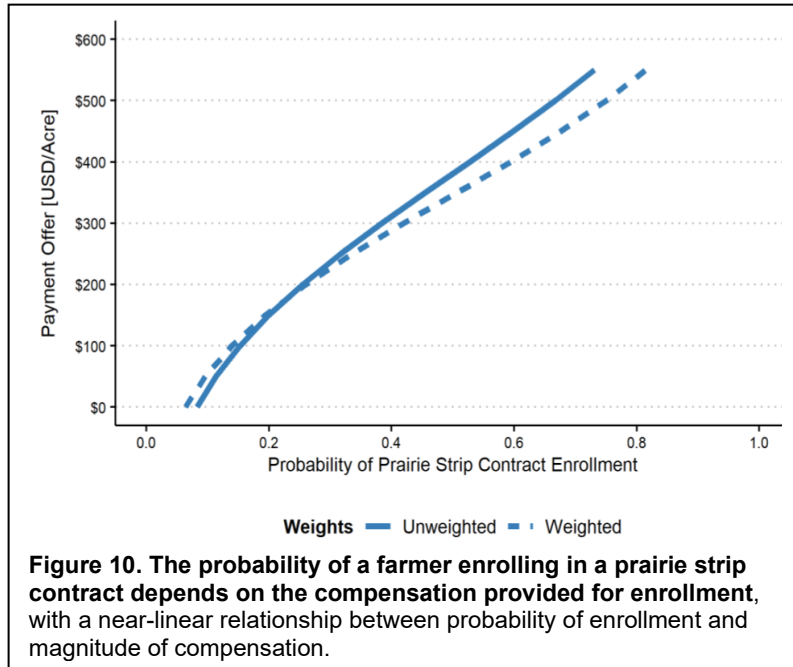
Figure 9. Relative abundance of the soil bacteria Phyla Actinomycetes under drought and dispersal soil manipulations. The relative abundance of this drought tolerant group was greater under drought only when aerial dispersal was permitted in the mesocosms, **demonstrating how microbial dispersal and diversity can increase the resilience of microbial communities.**

Microbial communities can also be sensitive to changes in landscape diversity, including diversity over time. First, more diverse crop rotations can increase soil health by enhancing microbial diversity and aggregate stability (Tiemann and Grandy 2015), and enhance microbial disease suppression (Peralta et al. 2018). Second, exchange of microbes from one land use type to another adjacent field may be important. When we excluded colonists introduced to soils via aerial dispersal, we observed large changes in microbial composition, diversity, and biomass, sometimes as large as induced by experimental drought treatments (Evans et al. 2020). Allowing dispersal also increased the resilience of some taxonomic groups to drought (Fig. 9). We have also experimentally demonstrated how aerial microbes contribute to assembly of the leaf microbiome (Bell-Dereske and Evans 2021). *If plant diversity alters microbial dispersal patterns, it could alter the resilience of microbe-mediated services, which we investigate using prairie strips in Proposed Research (D-2).*

Diversifying management or croplands can also be a mechanism underlying a farm's resilience to market and climate uncertainty. Using the PFS, we have shown that those Midwestern corn-soybean farmers most likely to diversify their croplands - in this case, through adoption of cover crops - have certain characteristics: they are younger and care more about environmental stewardship. They also acquire information from agricultural extension, independent crop consultants, grower associations or other farmers, rather than from seed and agrochemical dealers. *In our Proposed Research we will determine how farmer values interact with their financial resources and also new knowledge about their fields to influence their adoption of diverse management strategies (A-3, D•A-2).*

These prior results motivated us to further test mechanisms by which increased diversity within fields affects ecosystem function. Much of our proposed research does this using prairie strips, or native communities planted as within row crop treatments. Strips were planted in two MCSE

treatments in 2019 (see *Major Experiments*) and will take 6 years to fully develop. We initiated studies of diversity and abundance of many species within and near the strips, including ants, beetles, butterflies, and microbes, as well as ecosystem services, including soil C and nitrogen (N), microbial function, and pollination, and have already seen effects during the establishment phase. For example cumulative ground beetle (carabid) abundance across many species decreases with distance from strip, and responds to land use legacies.



Our documented benefits of prairie strips will only be relevant to society if farmers choose to adopt them. We conducted an economic experiment with a subset of the PFS farmers surveyed, exposing them to different potential payment levels for converting 5% of their largest corn or soybean field to prairie strips. We found that if paid 100% of the Conservation Reserve Program (CRP) rent, 20% of respondents are willing to take cropland out of production and introduce strips (Fig. 10 Luther et al. 2021). *Our Proposed Research will utilize prairie strips to simultaneously study social and ecological resilience, identifying what underlies farmer decisions to adopt strips (D-1).*

Adaptation

Our work on the evolution of mutualisms in response to long-term N-addition (Weese et al. 2015) illustrates the power of KBS LTER experiments for studying evolutionary adaptation in agroecosystems. We have used long-term treatments to test classic mutualism theory about the evolution of resource mutualists, to investigate the evolutionary responses of plants to N-addition and determine whether commonly observed plant trait responses to N-addition are adaptive, and to explore the mechanisms that can result in microbe-mediated adaptation (the capacity for microbial communities to shift in response to stress in ways that promote plant stress tolerance). We are also building long-term socioecological datasets to investigate the drivers of human adaptation.

Our original work tested classic mutualism theory and demonstrated that 20+ years of N addition caused the evolution of less cooperative rhizobia that provide fewer growth benefits to their plant hosts (Weese et al. 2015). We have since expanded this work on the evolutionary effects of N fertilization to plant populations. We capitalized on what is now a 30+ year N addition experiment in annual plant communities to test how replicated *Setaria faberii* (giant foxtail) populations have evolved in response to N, and to identify which plant traits are under differential selection in high vs. low N environments (Waterton et al. (in review)). We found that N-addition affects the strength of natural selection on plant traits, in part because of the indirect effects that result from N-addition increasing light asymmetry and reducing diversity. While this has elicited evolutionary responses, the direction of effect is not always what we would predict based on plant community responses to N-addition. For example, even though taller species are typically favored under N-addition at the community level (e.g., Suding et al. 2005), N-addition reduces selection for increased plant height. Furthermore, many commonly observed phenotypic shifts in plant traits in response to N actually appear to be maladaptive.

Recent work suggests that plants and animals are not adapting to environmental stressors on their own; but are assisted by diverse microbial communities. Microbe-mediated adaptation can occur when microbial communities respond to stress in ways that increase plant fitness in stressful environments (Petipas et al. 2021). However, why plants would rely on microbes for adaptation remains a mystery. One possible mechanism that can explain this phenomenon is “by-product benefits”. By-product benefits occur when a trait that benefits microbes in a particular environment happens to provide an incidental benefit to the plant host. Using 14 bacterial taxa isolated from KBS

LTER, we found that bacteria with traits that are associated with bacterial success under dry conditions (low optimum water potential, high biofilm production) also improve plant growth under dry conditions (Bolin et al. (in prep)). Other studies suggest that microbial communities cause greater effects on plant traits than plant genetics, potentially allowing plants to evolve to rely on microbial communities (Hawkes et al. 2020). *Identifying the existence and magnitude of such microbe-mediated adaptation is a focus of our Proposed Research (A-1, R•D-1).*

Agroecosystems cannot be understood without considering the role of people. Adaptive behavior by people in response to changing stressors (what we call 'social adaptation') will determine ecosystem resilience as much as biological adaptation. Our studies of social adaptation ask how farmers assess changing environments on their farm, and what practices they use to address such changes. We expect farmer adaptation to climate change will depend on how changes affect profitability, income risk, and other farmer objectives, as well as existing and new technologies. For profitability risk, climate change adaptation decisions will pivot on two key factors: 1) farmer perceptions of the changing probability of production outputs like grain yields, and 2) farmer risk attitudes.

The PFS enables us to determine what farmers think about climate change, management practices, and agronomic policy over time, both in response to our questions as well as the changing environment they experience. We found farmer objectives other than income, such as preferences for environmental amenities or social status, were important adoption drivers for conservation and precision technologies, respectively (Luther et al. 2020). Whereas livestock farms were less likely to adopt precision soil testing technologies, farmers who participated in working lands programs were more likely to do so. Both groups were likely to adopt cover cropping practices. Policies and messaging to encourage voluntary adoption of practices to reduce agricultural nutrient loss should account for farmer objectives, farming systems, and existing policy incentives. Our results identify decision-makers, willing audiences, targets of program expansion, and information sources, to whom new research and policies could be delivered to effectively promote beneficial practices. *Our Proposed Research builds on this, assessing how farmer decision-making (flexible or rigid), identity, and knowledge affects their ability to remain profitable under economic or climatic stress (A-3).*

Broader Impacts

Increased public scientific literacy and public engagement with science and technology. Through our public engagement activities since 2016, over 6,700 individuals had direct experience with KBS LTER. Direct interactions took place on-site through scientist-led or self-guided walking tours or field days, and even a public showcase of visual art and poetry by the KBS community and a farmer Artist in Residence in 2019. Visitors included members of the local community and Midwest region, educators and students, politicians and local leaders, and international visitors. We also hold events off-site in community spaces, on local farms, and virtually. We produce videos, blog posts, and press releases which we disseminate to over 7,000 followers via KBS and KBS LTER newsletters and active social media accounts, including Twitter, Instagram, YouTube, and Facebook (@KBSLTER). Our most recent video production, in partnership with the North Central Climate Collaborative and MSU Extension, showcases the first year of REX and interviews with LTER scientists studying climate change and soil health.

Our program directly engaged farmers and farm advisors to better understand barriers to adoption and help stakeholders work toward improving conservation practice implementation. From 2018-2020, a collaboration between the LTER, Michigan Agri-Business Association, Michigan Environmental Council, and National Wildlife Federation led to discussions across Michigan focused on sustainable agriculture, nutrient management, and conservation (e.g., Doll and Reimer 2017, Reimer et al. 2017, Doll et al. 2018, Doll and Bode 2019, Reimer et al. 2022). We hosted seven roundtable discussions in three regions; 33 producers and farmer advisers attended. In addition, we develop soil health and climate change programming for extension educators across the Midwest in partnership with MSU Extension and the Soil Health NEXUS, and hosted their 2021 in-service training event.

Improved STEM education and educator development. KBS LTER is a network leader in curriculum development, teacher professional development, and assessment. The Data Nuggets program began at the KBS LTER and has built network-wide involvement, with 34 activities from 11 LTER sites. Data Nuggets bring authentic research, datasets, and scientist stories into K-12 and undergraduate classrooms (Schultheis and Kjellvik 2015, Schultheis and Kjellvik 2020), while increasing student interest in STEM careers, self-efficacy in data related tasks, and ability to construct scientific explanations (Schultheis et al. in press). In the past year, over 120,000 users visited the Data Nuggets website, and we maintain a mailing list and social media following of over 12,000 educators (@Data_Nuggets). Data Nuggets were even more utilized by teachers and students during the COVID-19 pandemic, with website traffic peaking in 2020. In response to teacher requests, we developed virtual programming and online resources: (1) teacher webinars attended by hundreds of educators, including a cross-site event with Harvard Forest LTER, (2) a Network-wide Education & Outreach Committee initiative that identified and curated datasets from each site for use in education settings, and (3) creation of new Digital Data Nuggets on DataClassroom that allow students to work with larger, long-term datasets and expand their data literacy abilities.

The KBS K-12 Partnership for Science Literacy, supported since 1996 with Schoolyard LTER (sLTER) funds, annually connects with hundreds of Michigan-based K-12 teachers while hosting professional development workshops and co-designing curricular materials. Our teachers hail from small, underserved, farming communities. sLTER funds were leveraged to fund additional programs: (1) *Teaching Science Outdoors - Urban Partnerships program* which researches the implementation of Next Generation Science Standards by urban elementary teachers, utilizing nearby outdoor spaces for science inquiry, (2) *Outreach Fellowships* for at least two KBS affiliated graduate students to participate in a year-long program that includes professional development in science communication while coordinating and creating content with and for the Partnership, and (3) *Research Experiences for Teachers* (described below).

Development of a diverse, globally competitive STEM workforce. Since 2016, 112 graduate students and 69 undergraduates (38% from historically excluded groups, 25% first generation college, 61% women) have conducted research at KBS LTER. Undergraduates are mentored by LTER scientists, assist with research, and conduct independent research; many go on to present at national scientific meetings (>20 since 2016) and publish their KBS LTER research in peer-reviewed journals (>18 since 2016). In the summer, students engage in a series of professional development activities to benefit their careers: (1) a public symposium where they present their research, (2) creation of blog posts for our website and social media, (3) creation of Data Nuggets and other outreach materials, (4) diversity, equity, and inclusion (DEI) training, (5) the option to take summer courses, and (6) a weekly colloquium that provides training on careers in academia, proposal writing, science communication, analyzing data, and presenting research. Our undergraduate mentors

Box 1 – ReGrow: Mowing for Monarchs

KBS LTER research demonstrated that strategically timed disturbance -- mowing common milkweed patches -- reduced predator communities and increased monarch butterfly oviposition and survival on regenerating stems (Haan and Landis 2019, 2020). However, a subsequent community science study failed to replicate the result, potentially because participants used varying methods to create disturbance. In 2021, LTER researchers partnered with RET participants – Whitehall, MI elementary school teachers Gabe Knowles and Britney Christensen – to test methods of disturbance (clipping versus mowing) at eight schoolyard sites. Their results showed that more aggressive disturbance improves outcomes for monarchs, likely via slowing predator recolonization of regenerating stems. Knowles and Christensen incorporated their students into the study, teaching observation and data collection skills. They also published a Data Nuggets activity titled “Mowing for Monarchs” including a Teacher Guide, Student Activities, and Grading Rubric.



commit to mentor training activities and a long-term relationship with students, including support navigating academia and STEM careers. LTER undergraduates are integrated in the broader KBS field station community and live and learn with other student researchers from around the country.

1.6 Results of Supplemental Support

Since 2016, we have received three RET supplements. In 2016, we received RET supplemental funding (\$22,000) to support two teachers to work with LTER scientists Jennifer Lau and Elena Litchman. In 2019, we received RET supplemental funding (\$10,000) that was deferred to 2022 and will support a teacher to work with LTER scientist Carmella Vizza. In 2020-2021 we received RET supplemental funding (\$66,212) to fund two teachers (Gabriel Knowles and Britney Christensen) with LTER scientist Doug Landis for Mowing for Monarchs - an ambitious combination of research by scientists, community scientists, and RETs that reveals patterns behind monarch and milkweed interactions and brings the story into classrooms (Box 1).

1.7 The 10 most significant publications resulting from the last 6 years of funding (Box 2)

Box 2. Recent papers selected for known or expected impact and to illustrate the diversity of KBS science and scientists.

- Basso, B., Shuai, G., Zhang, J., and Robertson, G. P. 2019. Yield stability analysis reveals sources of large-scale nitrogen loss from the US Midwest. *Scientific Reports* 9:1-9.
- Cusser, S., Bahlai, C., Swinton, S. M., Robertson, G. P., and Haddad, N. M. 2020. Long-term research avoids spurious and misleading trends in sustainability attributes of no-till. *Global Change Biology* 26:3715-3725.
- Evans, S. E., Bell-Dereske, L., Dougherty, K., and Kittredge, H. 2020. Dispersal alters soil microbial community response to drought. *Environmental Microbiology* 22:905-916.
- Helms IV, J. A., Ijelu, S. E., Wills, B. D., Landis, D. A., and Haddad, N. M. 2020. Ant biodiversity and ecosystem services in bioenergy landscapes. *Agriculture, Ecosystems & Environment* 290, 106780.
- Hess, L. J., Hinckley, E. L. S., Robertson, G. P., and Matson, P. A. 2020. Rainfall intensification increases nitrate leaching from tilled but not no-till cropping systems in the US Midwest. *Agriculture, Ecosystems & Environment*. 290, 106747.
- Kravchenko, A. N., Guber, A. K., Razavi, B. S., Koestel, J., Quigley, M. Y., Robertson, G. P., and Kuzyakov, Y. 2019. Microbial spatial footprint as a driver of soil carbon stabilization. *Nature Communications* 10:1-10.
- Kravchenko, A. N., Snapp, S. S., and Robertson, G. P. 2017. Field-scale experiments reveal persistent yield gaps in low-input and organic cropping systems. *Proceedings of the National Academy of Sciences* 114:926-931.
- Luther, Z. R., Swinton, S. M., and Van Deynze, B. 2021. Potential Supply of Midwest Cropland for Conversion to In-Field Prairie Strips. *Land Economics* 082020-0129R1.
- Robertson, G. P., S. K. Hamilton, B. L. Barham, B. E. Dale, R. C. Izaurralde, R. D. Jackson, D. A. Landis, S. M. Swinton, K. D. Thelen, and J. M. Tiedje. 2017. Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science* 356:eaal2324.
- Zettlemoyer, M.A., Schultheis, E.H., and Lau, J.A. 2019. Phenology in a warming world: differences between native and non-native plant species. *Ecology Letters* 22:1253-1263.

1.8 Response to Previous Reviewers

Our midterm review panel felt that “*the overriding sentiment of the review report [was] extremely positive.*” They had four primary suggestions that we have implemented in our current or proposed work. The panel suggested that we 1) take advantage of “*...the potential to rethink the design of the drought experiment to more comprehensively address changing precipitation patterns,*” 2) “*...further integrate land-use change into the conceptual framework to be more adaptive in response to what farmers’ practice,*” 3) pursue “*...opportunities to more strongly link socio-economic research to long-*

term ecological data, and 4) develop “...more formalized training in best practices for data creation, management and sharing for early-career scientists.”

We used COVID-induced delays in REX implementation to modify its experimental design to manipulate rainfall. This addresses the panel’s concerns by enabling us to investigate the effects of variability in rainfall patterns. We are also leveraging the multi-lab aspect of this project to develop a new model workflow for data creation and management that provides structure and support for individual researchers to develop their own data skills; this will eventually be the *modus operandi* for all KBS LTER (see *Data Management Plan*). Although we are constrained in our ability to modify long-term treatments at a rate similar to farmers, we have added co-PI Basso to bring expertise modeling ecological processes and mechanisms discovered at KBS LTER under varied agronomic management (see **R-1, S-1, S-2**). Finally, to directly link socio-economic research to long-term ecological data, we propose to leverage pre-existing PFS data to identify farmers that may differ in their personal values, and investigate how these values interact with knowledge of yield stability of their operations that we provide (see **A-3**).

2.0 Proposed Research

For 33 years, the guiding question of KBS LTER has been: How can we effectively use ecological knowledge to better generate ecosystem services, including yield, greenhouse gas mitigation, soil health, water quality, pollination, and pest control? The question we recently pivoted to, which drives our current and future research is: **How can ecological knowledge - and specifically mechanistic knowledge of resources, diversity, and adaptation - improve the resilience of cropping land and natural habitats to multiple and interacting stressors like climate and land use change?** We address this question using both existing and new experiments. Within the MCSE treatments, which vary in land use intensity, we now include two new experiments: a rain exclusion experiment (REX) established in 2021 to investigate climate-focused hypotheses, and a prairie strips experiment established in 2019 to test hypotheses about land-use change and habitat diversity. With the initiation of these two experiments, we are poised to investigate specific resilience hypotheses over the coming six years in concert with on-going regionalization research, including our longitudinal survey of farmers in the Midwest.

2.1 Major experiments and related research projects

Here we describe our focal LTER experiments and three other experiments that complement, leverage, and strengthen our LTER research.

Focal experiments

Main Cropping System Experiment (MCSE)

The MCSE was established at KBS LTER’s inception in 1989 to test hypotheses about land use intensity and ecosystem function and services (Robertson and Hamilton 2015). The experiment includes eleven replicated treatments. There are four corn-soy-wheat row crop treatments, including **Conventional** agriculture with tillage, conventional **No-till**, conventional tillage with **Reduced Inputs** (30% the fertilizer and herbicide inputs), and conventional tillage that is **Biologically Based** (certified organic). Both the reduced input and organic treatments also have a cover crop. In addition to these row crops, there are two perennial bioenergy crops, **Poplar** and **Switchgrass**, and a perennial-dominated **Successional** grassland maintained by annual burns and limited shrub removal. Four additional treatments replicated in the surrounding landscape provide additional context: a never-tilled grassland, mid-successional forest, late successional forest, and planted conifer stands.

Prairie Strips

Within the MCSE Reduced Input and Biologically-Based treatments, we increased plant diversity by introducing 5-m wide x 100-m long areas of native, perennial vegetation, called prairie strips (Fig. 11). We seeded prairie strips in spring 2019 with 22 species chosen to optimize community function, including variation in plant functional groups, timing of production (to



Figure 11. Prairie strips were planted in 2019 in Reduced Input (foreground) and Biologically Based (background) treatments of the MCSE. Strips are 100m long; plots are 1ha. REX shelters can be seen in the upper left and upper right.

benefit predatory arthropods), and timing and amount of flowering (to benefit pollinators Rowe et al. 2021). We optimized our species mix to be both relevant to new USDA Conservation Reserve Program (CRP) rules and affordable. On an annual basis we reduce unwanted herbaceous and woody vegetation through mowing and burning.

We expect an establishment period of 6 years (by about 2024) to attain full species diversity and functional capacity. This could provide a growing source of ecological benefits that will spill over to adjacent crops. Although our hypotheses are not contingent on this temporal dynamic, time enters both in the development of strips and in the interaction of strip's effects on adjacent, disturbed land and resilience to climate extremes.

Rain Exclusion eXperiment (REX)

To test the effects of resources and diversity on resilience to water stress, REX was deployed in the 2021 growing season within three treatments of the MCSE. REX consists of 48 5.5 x 4.3 m rainfall exclusion structures with galvanized steel supports,



Figure 12. Rain Exclusion eXperiment (REX) shelter footprint during irrigation. Water in tank on left is pumped through sprinklers via solar power.

plexiglass roofing, gutters, and an integrated sprinkler system for controlled watering (Fig. 12). Shelters are deployed in three plot-level treatments: our Conventional and No-till cropping systems, and Successional grasslands. Within all plots, there are three shelter treatments: 1) intense **drought** through continuous rain exclusion for six weeks; 2) **variable** rain exclusion, with three, 3-week drought periods attenuated by two days of re-wetting wherein three weeks-worth of precipitation (6 cm) is applied; and 3) **controls** irrigated once a week to 30-yr average rainfall (2 cm). In drought treatments, shelters are deployed in one location for one year only, and then are moved to different locations in subsequent years to study effects of drought on each of the three crops in our rotation, as well as legacy effects in areas that experienced drought in previous years. Variable treatments are deployed in the same location annually, and simulate predicted climate changes in our region. This experiment allows us to examine the resilience of many response variables to rainfall shifts, which is a strong - and regionally relevant - disturbance that is a major driver of ecosystem function.

Under each shelter, there are four 1.5 x 2m experimental subplots, within which we manipulate resources and diversity to test their effects on resilience. We focus on carbon additions because of the observed differences in soil C across long-term MCSE treatments that differ in resilience to drought (see Proposed Research: Resources). In Conventional treatments, we test the effects of four different types of C resources: 1) biochar (recalcitrant C), 2) switchgrass residue (labile C but low in N), 3) sorghum residue (labile C with higher N), and a no-added-C control. We added C to soils before planting via roto-tilling. In our No-till and Successional treatments, we added sorghum residue to one subplot by surface application, and reduced diversity in two other subplots. We manipulate diversity in two ways, applying: 1) fungicide to reduce fungal diversity and abundance, and 2) nematicide to reduce nematode diversity and abundance. Biocides are applied as liquid solution twice before placing shelters.

In the Successional treatment, we created additional treatments to test resilience to additional stressors, including water stress, warming, and insecticides, and their interactions. Subplots were warmed with open-top chambers (OTCs) installed in ambient conditions and under shelters. Tall-stature OTCs, designed at KBS LTER, raise daytime air temperatures 1.8 C on average during the growing season (Welshofer et al. 2018). The insecticides are applied in subplots every two weeks, beginning two weeks prior to shelter deployment.

As we delayed implementation by one year due to COVID-19, the initial results from REX are still in progress; however, our rainfall treatments were effective. For example, soybean yield under shelters was reduced by 43% in Conventional plots and 30% in No-till plots, similar to the reduction in response to natural droughts observed in our long-term data.

Panel Farmer Survey (PFS)

In 2017, we initiated a set of long-term sociological observations to complement our long-term ecological measures to allow us to better address important socioecological questions. Today, this study is one of the largest longitudinal datasets in existence concerning farmer perceptions, sources of information, and practices. Our goal is to understand long-term farmer knowledge of and attitudes towards the three global drivers of our conceptual model (Fig. 1): large-scale resources (e.g., financial, land, equipment), diversity (e.g. number of crop species, conversion of row crops to prairie strips or conservation land), and adaptation (e.g., irrigation, crop types). To begin the study, we contacted a cohort of producers in Michigan, Illinois, Indiana, and Ohio. The survey has been completed by ~2500 farmers per year since 2017. Response rates are ~25% for the cross-sectional, static annual samples and >55% for the cohort, longitudinal sample (same farmers surveyed annually). The PFS allows us to assess social mechanisms of resilience to climate and land use change at farm and regional scales: collecting responses from the same individuals over time provides insight into changing views and farming practices, and allows for interpretation of long-term trends. We use this longitudinal approach to determine how resources, diverse practices, and adaptive capacity are evolving in a way that a single static or cross-sectional response cannot. We modify questions to address new hypotheses relevant to our conceptual model that emerge from survey findings or are informed by our field experiments.

Other experiments central to KBS LTER research

Bioenergy Cropping System Experiment (BCSE)

The BCSE, initiated in 2008, includes 10 bioenergy cropping systems arranged along a biodiversity and management intensity gradient. Treatments include continuous corn, sorghum, switchgrass, miscanthus, and poplar monocultures, and polycultures of native grasses, successional grassland, and restored prairie. The BCSE complements the LTER by encompassing different (but overlapping) gradients of management intensity and biodiversity, and hypotheses generated in one experiment can be tested in the other.

Conservation Lands Experiment (CLE)

The CLE was established in 2015 to expand our capacity to address diversity questions. Unlike the MCSE, in which diverse plots are the result of unmanaged succession, diversity in the CLEs is intentionally designed. Plots are planted with 12 or 75 native plant species sourced from regions that extend from the northern Midwest (Minnesota/Wisconsin) to the southern Midwest (Kansas/Missouri). This allows for more involved tests of diversity-mediated mechanisms of resilience in a field setting. To increase our gradient of land use intensity relative to MCSE, we will quantify productivity and GHG emissions, allowing us to build the long-term dataset necessary to study resilience to natural climate variability.

Long-Term Agroecosystem Research (LTAR) Common Experiment

The LTAR Common Experiment at KBS, created in 2021, offers additional opportunities to test KBS LTER resilience hypotheses. In this experiment, an Aspirational cropping system, co-designed with stakeholders, is compared to a Business-as-Usual system representing prevailing practices in the region, and similar to our MCSE Conventional treatment. Plot and field scale treatments allow the fundamental research of LTER to inform the co-design of systems directly relevant to farmers and other agricultural stakeholders, effectively enhancing the broader impacts of LTER research, and providing another controlled setting in which to test resilience hypotheses.

2.2 Proposed research under major focal areas

Our proposed research is guided by our global question: **How can ecological knowledge - and specifically mechanistic knowledge of resources, diversity, and adaptation - improve the resilience of cropping land and natural habitats in the face of multiple and interacting stressors such as climate and land use change?** This question frames thirteen other questions (Fig. 5), which themselves guide hypotheses by which the aforementioned mechanisms, both ecological and social, explain resilience of ecosystem functions. Building on our current research, our proposed research addresses new questions about effects of individual mechanisms on resilience. In our proposed research, we expand our scope to include novel tests of how interactions among these mechanisms affect resilience, and explicitly examining how these mechanisms scale across landscapes.

Resources

The performance of cropping systems is dependent in part on the biophysical attributes of soil (a key biophysical resource) and on the technologies, equipment, and information (key social resources) that farmers have at their disposal. **We hypothesize that these resources can play key roles in buffering agroecosystems against negative perturbations by promoting resilience to stresses imposed by climate and land use change.** Because these resources can be managed, a better knowledge of their contributions and interactions might allow us to design agricultural systems able to better withstand stress. While farmers have long-intuited such knowledge – indeed, the current regenerative agriculture movement is based in large part on soil's conferring such resilience (Robertson and Harwood 2013) – the specific mechanisms underlying these functions and the ways in which they interact to magnify or diminish resilience is largely unknown. The ways that resources

impact resilience have also not been closely examined in a larger ecological context that includes how resources interact with Diversity and Adaptation, and this is a focus of our proposed research.

Of the manageable soil properties valued most for resilience, none are more important than soil C. Well-documented impacts of soil C on soil structure, water availability, nutrient supply and retention, and soil biological communities make soil C a master variable for soil health and farm success (Grandy and Robertson (in press)). This has long been appreciated by organic growers (Robertson 2015) and is a lever influencing many natural processes (e.g., Furey and Tilman 2021). We have a long history of soil C research at KBS LTER, including links to climate resilience: In 2012 (Robertson et al. 2014) and again in 2020, our no-till system with its higher soil C content (Syswerda et al. 2011) was better able to withstand dry periods by storing more water at the onset of the growing season compared to the conventional system, resulting in higher yields under drought. The exact mechanisms underlying this response are unclear, but improved soil structure associated with higher soil C levels seems likely. Indeed, it is precisely this SOC-mediated buffering in the no-till system that could explain the long-term enhanced crop productivity in no-till treatments (Cusser et al. 2020), especially against the backdrop of more frequent dry periods (Pryor et al. 2013).

We propose to examine the role of soil C for conferring resilience to climate variability, addressing questions revealed by prior results. First, we will experimentally test the role of soil C against other soil attributes for buffering productivity and greenhouse gas responses to rainfall variability while manipulating labile C inputs in REX, and by examining responses across three contrasting MCSE land use treatments. Second, based on earlier research (Kravchenko and Robertson 2011, Kravchenko et al. 2017, Shcherbak and Robertson 2019), we suspect soil C at depth could play an important role in climate mitigation, both by sequestering atmospheric CO₂ and influencing nitrous oxide (N₂O) emissions. We will thus examine how different cropping systems contribute to large-scale climate resilience via greenhouse gas mitigation, focusing on deep-soil dynamics that are often ignored.

Resources Q1) What key soil properties confer resilience to water stress?

Resources H1.1: Soil C buffers ecosystem drought stress through its influence on soil physical properties

Our land use treatments across the MCSE contain a gradient of soil C concentrations (Syswerda et al. 2011, Córdova et al. (in prep)), allowing us to test how soil C levels confer resilience under experimental drought. Other soil attributes (in particular physical structure) may separately or together confer resilience. Thus we will attempt to separate the influence of soil C changes vs. other processes by testing the short- and long-term effects of C additions that differ in lability in REX subplots within Conventional, No-till, and Successional treatments. More specifically, we will quantify differences in patterns of soil moisture and water retention, aboveground net primary productivity (ANPP), soil C fractions (especially particulate organic matter (POM), and mineral-associated organic matter (MAOM)), and soil physical structure (e.g., aggregate stability and porosity) in drought and control treatments of each agronomic treatment, and within C-addition subplots in REX.

We will also test our ability to scale results from REX in two ways. First, we will study whole-system water dynamics by modeling differential responses to drought using the System Approach to Land Use Sustainability (SALUS) model (Box 3). We will be able to test the likely effects of soil C versus other factors such as deep roots and changes in

Box 3. The System Approach to Land Use Sustainability

(SALUS) is a validated process-based crop and soil biogeochemical model designed to simulate daily plant growth and soil conditions (during growing seasons and fallow periods) using historical and projected weather. SALUS has been extensively applied to quantify the systems (soil-plant-atmosphere continuum) interactions under different management strategies on yield and C, N, and P dynamics. It accommodates various crop rotations, genotype characteristics, planting dates and densities, irrigation, fertilizer (mineral and organic), tillage practices and simulates plant growth and changes in soil conditions every day and across multiple years (Bruno & Ritchie 2015).

soil structure and subsequent water storage that might contribute to drought resilience. Deep (1 m) cores taken at the conclusion of the experiment will validate predictions. We will also assess whether and which soil properties explain within-field variation in plant water stress, which we have mapped via aerial drone thermal imagery for our 1 ha MCSE plots as well as larger fields (to 25 ha) at KBS. We predict that drought-resilient subfield areas in similar slope positions will be predictable from the attributes identified by our site-scale experiments. We will use this knowledge as a base upon which to scale across habitats and landscapes in Resilience across Scales (**S-1**).

Resources H1.2: Variable rainfall will result in greater cumulative greenhouse gas fluxes

Greater rainfall intensities (longer dry periods bookended by heavier rain events) can increase cumulative N₂O gas emissions (Glanville 2020, Glanville and Robertson (in review)), creating the potential for a positive feedback as rainfall becomes more variable due to climate warming. However, we do not know precisely what mechanisms control this phenomenon, whether it differs across land uses, nor how it scales to an entire agricultural system. We will test this hypothesis by comparing N₂O emissions and CH₄ oxidation in REX Variable and Control rainfall treatments across land use treatments. In addition, we will probe the mechanisms of this pattern using subplots that manipulate resources by adding labile C substrates.

We will use this knowledge to predict the impact of variable rainfall at scale by modifying our machine learning predictors of N₂O emissions (Saha et al. 2021) to include the impact of variable rainfall, and then use SALUS to scale emissions to Midwest annual cropland. Our machine learning model to predict N₂O emissions, when coupled with a process-based model of moisture and soil inorganic N status, can provide over three times the predictive power of quantitative models such as DAYCENT and DNDC for untrained, novel sites. A comparison of fluxes under historical versus contemporary rainfall patterns may help to explain the growing global atmospheric N₂O burden, driven mainly by agricultural soils (Shcherbak et al. 2014, Tian et al. 2020).

Resources Q2) How do deep soil C and N dynamics mediate resilience?

Resources H2.1: Physical properties of deep soil impact soil C gain under different land uses

Carbon storage within deep horizons of the soil profile may be key to plant resilience, yet it remains insufficiently understood, in part due to measurement difficulties and slow C accumulation rates. However, the C gains that occur in the subsoil can be sizable because the volume of subsoil can be much greater than that of surface soil and, importantly, relatively insensitive to surface management and direct climate variations. Deep roots and preferential flow paths for dissolved organic C are the main mechanisms of C inputs into the subsoil, both exhibiting extremely high spatial and temporal variability (Franklin et al. 2021). Physical characteristics, e.g., soil pore size distributions and architecture, within and around these C entry pathways, influence the fate and protection of the newly added C. Understanding the mechanisms of deep soil C storage requires learning about functioning of such pathways and their interconnections with the surrounding soil.

We hypothesize that precipitation patterns and inherent soil C and physical structure formed under different land uses interact to enable accessibility of deep soil layers to C inputs and enhanced C storage. We have the opportunity to test this hypothesis by measuring responses in deep-soil cores collected across the MCSE in 2023 as part of our decadal deep (1m) soil C sampling protocol. In addition to routine measurements of soil C and N, intact soil cores will be subjected to X-ray computed tomography scanning to quantify pore architecture as a function of agronomic treatment and depth. Moreover, POM and MAOM measurements will shed light on the physical and physico-chemical mechanisms of soil C storage and protection that contribute to C accrual.

Resources H2.2: High N₂O fluxes in subsurface horizons result from low sink strengths due to little soil C at depth

Fluxes of N₂O are highly variable and sensitive to land use. Most of what we know about N₂O production and the responsible taxa (mainly denitrifiers in KBS soils) is derived from surface soils (Liang and Robertson 2021). While N₂O production and consumption are known to occur in

subsurface horizons, their magnitude is poorly known. At KBS LTER, subsurface sources of N₂O have been measured in situ only, where we have shown that over 50% of surface fluxes can derive from subsurface horizons (Shcherbak and Robertson 2019). We suspect that the large fluxes from subsurface horizons may be related to the lack of soil C at depth (Syswerda et al. 2011) and its extreme variability (Kravchenko and Robertson 2011), such that more of whatever N₂O is produced remains unconsumed due to low electron demand (Robertson and Groffman 2022). If so, encouraging soil C accretion at depth (*R-2.1*) might lead to greater N₂O consumption and lower surface emissions.

We will test the hypothesis that low concentrations of deep soil C limit N₂O consumption by incubating soil from different horizons of MCSE treatments in the presence of different C additions. We will test alternative hypotheses by characterizing denitrifier communities and conducting cross-inoculation experiments across MCSE treatments and horizon depths, including, for example, the hypothesis that denitrifier populations with different N₂O consumption capacities (Cavigelli and Robertson 2001) are responsible for differences.

Diversity

Supporting and managing biodiversity in agricultural landscapes is key to the provision of resilient ecosystem services including crop yield, soil C sequestration, pollination, and pest suppression. However, agricultural landscapes globally are experiencing unprecedented biodiversity losses due to climate change, land use change, and intensification of agriculture (Dudley and Alexander 2017, Wepprich et al. 2019, Wagner et al. 2021). Understanding how crop production practices influence biodiversity has been a hallmark of KBS LTER research. Our proposed work continues to focus on diversity's role in resilience, expands our purview to include biotic interactions, and focuses on functional traits, making our proposed research more integrative across taxonomic and functional scales.

Biodiversity increases ecosystem function stability (e.g., Tilman et al. 2006, Gross et al. 2014), and shapes trophic dynamics (Haddad et al. 2009). Of relevance to our site and proposed research, diversity also stabilizes ecosystem response to water stress (Tilman and Downing 1994), and stabilizes ANPP and associated ecosystem services via increasing resistance to climate extremes (Isbell et al. 2015). In some ways, the effects of plant diversity on stability in natural habitats translates to the same relationship in agricultural systems (Elton 1958, Davis et al. 2012, Tiemann et al. 2015, Isbell et al. 2017). Yet, the range of plant diversity in crop fields is typically much lower than that in natural systems. One way to increase plant diversity in agricultural fields and landscapes is by the addition of prairie strips, which can reduce erosion, increase water quality, and increase pollinator abundance (Schulte et al. 2017).

In agricultural landscapes, we are interested in not only how diversity of species mediates resilience, but also how diversity of habitat types (and their spatial distribution) mediates resilience (Bianchi et al. 2006). Habitat diversity at field and landscape scales has been shown to increase pollination and biocontrol (Ricketts and Imhoff 2003, Tscharntke et al. 2016, but see Karp et al. 2018, Winfree et al. 2018, Albrecht et al. 2020). More attention is needed to resolve the mechanisms by which diversity of habitats affects ecosystem function, and to characterize the stability of those functions as climate changes, as can be done in a long-term experiment. Diversified landscapes can affect stability on working farms. Through our PFS, we can assess farmer knowledge about increasing diversity on their farms, including its role in stabilizing agroecosystems, and the factors that affect farmer willingness to introduce new habitat types, and where.

Long term biodiversity datasets - Long-term biodiversity monitoring at KBS LTER is one way we can probe the role of diversity on resilience. We have decades-long datasets on plant and coccinellid beetle communities, and we are now adding two groups to our core monitoring. First, we will sample soil and root bacterial and fungal diversity annually across the MCSE, employing new standardized methods that better allow longitudinal comparisons, and provide openly accessible soil microbe data (Smith et al. 2020). Although we have not previously had a standardized microbial sampling plan, we

have frozen samples archived and/or data analyzed across the MCSE spanning KBS LTER's 33-year history, with approximately ten years of samples analyzed to date. Second, we will monitor nematode communities to better understand linkages between soil food web structure and ecosystem function. Free-living nematodes are Earth's most abundant metazoa and mediate key soil functions. Nematode diversity determines food web complexity, which is responsive to land use and predicts ecosystem function (Freckman and Ettema 1993, Culman et al. 2010, Dupont et al. 2014, Sprunger et al. 2019). All of these core datasets lay groundwork for future investigators to address how diversity mediates resilience to interannual variation and to land use.

Diversity Q1: Does introduction of perennial plants increase resilience of trophic interactions?

Diversity H1.1: Plant diversity in prairie strips increases biodiversity in strips and nearby crops.

To test the effects of diversity on trophic dynamics (Diversity H1.2), we must first establish the effects of our experimental treatments on diversity (Diversity H1.1). Plant diversity increases diversity of higher trophic levels (e.g., arthropods Haddad et al. 2009), as we have found within prairie strips so far (Kemmerling et al. (in revision)). We expect diversity and abundance to change over time as strips mature, and this could act to stabilize trophic interactions. We propose to continue and expand studies to include species that have strong effects on ecosystem function and services, especially ants, carabid beetles, bees, nematodes, and microorganisms.

A novel aspect of our hypothesis is that higher diversity within the strips will spill over to the rest of the plot, increasing the resilience of diversity and trophic interactions. We expect diversity and abundance of arthropod consumers to be higher near strips. Over time as strips mature and more species establish, the strength of the effect will increase, even at larger distances from the strip. But we expect the potential for spillover to depend on species' traits (e.g. persistence, dispersal ability). For instance, preliminary data suggest that microbial communities in prairie strips are diverging each year from those in crops, and that certain taxa have traits that allow airborne dispersal to nearby crops. Additionally, management practices (e.g. tillage) may reduce successful spillover.

Diversity H1.2: By increasing plant diversity, prairie strips increase resilience of trophic interactions in crops adjacent to strips.

Our previous research demonstrated that landscape diversification increases species diversity, thus influencing trophic dynamics like pest control and pollination (Albrecht et al. 2020, Haan et al. 2020). We propose to test the mechanisms by which prairie strips affect the resilience of trophic interactions in agricultural landscapes. First, we will test the effects of prairie strips on pest suppression using sentinel prey deployed at different distances from strips. Ant, carabid, and rodent predation and parasitoid pressure will be contrasted using differentially accessible containers. Second, we will test for effects of strips on weed suppression by ground-dwelling insects by deploying seed trays with representative weed species at different distances from strips. Third, as pollinators can increase soybean yield (Garibaldi et al. 2021), we will test the effects of strips on pollination and seed set of soybeans at varying distances from strips.

We will expand our investigation into the trophic roles and influence of nematodes on soil microbial communities and plant-microbe interactions. Nematodes are extremely abundant in soils and include species spanning a broad range of trophic roles. Pilot studies show that nematode communities in perennial systems have a greater capacity to contribute to key ecosystem processes (e.g., carbon sequestration) as the system becomes fully established (Sprunger et al., 2019). Thus, tracking nematode community changes within and adjacent to prairie strips will elucidate early changes in ecosystem function and key processes. Compared with strips, we expect much less structured soil food webs in cropland adjacent to strips; however, the distance over which strips affect nematode food webs could expand with time.

Diversity H1.3: Farmer adoption of prairie strips increases with knowledge of available incentives and their benefits for ecosystem services.

By the time our prairie strips have matured, we will have completed nine years of longitudinal surveys of farmer views. This will include the time since federal programs have incentivized strips to increase resilience of agricultural ecosystems, including through introduction of the USDA Conservation Reserve Program's CP-42 and designation in the 2018 USDA Farm Bill. In 2018, we asked farmers about their familiarity with and views of prairie strips (Luther et al. 2021). We will assess changes in attitudes by repeating some questions, and with new questions about attitudes about policy knowledge and land management interest. We will focus on establishing a farmer's history of participation in CRP programs, since this is a key factor in willingness to adopt prairie strips. New questions will also target the potential ecosystem service benefits that may motivate farmers to adopt prairie strips (pollination services, erosion control, water quality, forage), and how these benefits correlate with farmer perceptions of climate change and economic risk. We can then investigate whether farmers who are willing to adopt prairie strips are motivated by a desire to enhance the resilience of their operations, and whether this corresponds to their operations' resilience (i.e., their profits are not being as negatively affected by adverse conditions).

Diversity Q2) How does diversity confer community and ecosystem resilience to drought and warming across land uses?

We will move beyond a focus on diversity *per se*, to focus on how biotic interactions, networks, and especially trophic interactions impact ecosystem function and resilience. Soil trophic cascades, and not simply species richness, are key mediators of ecosystem resilience (Sprunger et al. 2019), including in response to land use (Banerjee et al. 2019) and under drought (De Vries et al. 2018). A diversity of trophic levels is required to support multifunctional working landscapes (Mitchell et al. 2014, Lefcheck et al. 2015, Soliveres et al. 2016).

Diversity H2.1: Soil food webs composed of more connections will increase resilience of ecosystem functions and services under water stress.

We predict that higher trophic groups will be key to increasing connectivity and maintaining resilience of biodiversity and ecosystem services. Certain groups (e.g. fungi, nematodes) may be particularly critical to maintain stable networks in these systems, preventing collapse under disturbances (Eisenhauer et al. 2012). Nematode communities can serve as bioindicators because different groups have different sensitivities to stress and environmental change (Banerjee et al. 2019). For instance, nematode omnivores and predators are extremely sensitive to abiotic stress, including drought (Neher 2001). Thus, we might expect systems under stress to be more dominated by other nematode specialists that can withstand disturbance (Siebert et al. 2020). Such shifts in the soil food web could reduce soil food web complexity and could lead to reductions in ecosystem function. Moreover, systems with increased plant diversity may support increased resilience to support functional belowground food webs when under water stress (Yan et al. 2018). Thus, we will measure changes in nematode community structure and function in REX, one subplot of which is a nematicide manipulation. We expect that higher trophic complexity will cause more rapid recovery of ecosystem processes (e.g., N cycling) after drought.

Diversity H2.2: Water stress will reduce the functional diversity of arthropod communities, including pest suppression potentials

We will test the effects of growing season water stress on ant community diversity, abundance, and potential for pest regulation. Ant activity, and potential pest regulation, varies through the growing season; ant ability to suppress pests depends on when stresses are imposed relative to crop productivity (winter wheat is harvested earlier than corn and soy). We predict that water stress will reduce ant activity and potential pest suppression, and will have more intense effects on wheat than corn or soy crops (Helms et al. 2021).

Diversity H2.3: More diverse above-ground (arthropod predator & herbivore) and below-ground (microbe) communities will increase resilience of warmed plant populations (fitness) and plant communities (ANPP) to drought, additional warming, or both stressors.

We propose to test for network effects on resilience to climate change. To do this, we will integrate studies across plant, arthropod, and microbial communities that we have studied largely in isolation in the past. The sensitivity of these networks to stressors like drought differs across groups like fungi and bacteria (De Vries et al. 2012, De Vries et al. 2018), and between aboveground and belowground communities (Le Provost et al. 2021). To test interactions between warming and above- and below-ground communities, we will manipulate microbes (soils) and arthropods living in conjunction with plants from warmed environments, in a factorial design during the growing season. We will leverage REX by establishing potted plant community mesocosms under REX treatments (drought, warming, and the combination) with seeds originating from nearby old field communities that have been warmed with OTCs since 2015 (Welshofer et al. 2018). Plant communities will consist of common old field forb and grass species grown in soil communities inoculated with soils from warmed or unwarmed OTC treatments, or with sterile soil. We will control arthropod abundances within cylindrical cages enclosed by insect mesh (following Schmitz 2008, Rosenblatt et al. 2019). Insect treatments will include: no insects (plant-soil treatments only), grasshopper herbivores (herbivore-plant-soil), and sit-and-wait spider predators (predator-herbivore-plant-soil). We will measure plant phenology by species (flowering, seed set onset and duration), plant fitness (number of undamaged seeds and mean seed mass per species), total and species-specific ANPP, plant and insect tissue C:N, and herbivory damage.

Diversity Q3: What are the relative effects of intra- and inter-specific diversity on resilience of restored prairies to climate variability?

Diversity H3.1: Plant intra-specific diversity will increase resilience to natural climate variation

Just as interspecific diversity promotes resilience and stability, intraspecific diversity can also promote resilience through similar mechanisms, such as compensatory dynamics, mean-variance scaling relationships, and dominance (e.g., Grman et al. 2010). The effects of intraspecific diversity on community processes rival the effects of interspecific diversity (Crutsinger et al. 2006). In an experiment capitalizing on the CLE, intraspecific diversity shifted interspecific plant-soil feedbacks from negative to neutral, reducing the strength of plant-soil feedbacks as a species coexistence promoting mechanism. This could result in increased dominance of abundant species (Bolin and Lau (in press)). Given the role of dominance in contributing to stability in similar KBS landscapes (Grman et al. 2010), we predict that intraspecific diversity will reduce the strength of interspecific diversity-stability relationships. In the CLE, we will test the effects of both inter- and intraspecific diversity on resilience of ecosystem functions, including pollination, ANPP, and N₂O emissions, to natural water stress events.

Diversity Q4) Are declines in beetle abundance caused by changes in agronomic inputs?

Diversity H4.1: Coccinellid populations, once maintained by competitive interactions between native and invasive species, are now declining rapidly in response to pesticide use.

Long-term studies of the coccinellid communities in our treatments provide an ideal model system to elucidate competitive interactions among a set of closely related species and the community responses to new stressors. The dynamics of native coccinellid (lady beetle) abundance at KBS LTER have been driven in part by competitive exclusion by the arrival of two invasive lady beetle species (Bahlai et al. 2015) whose niches are separated by phenology, temperature, and humidity (Arnold et al. 2022). However, recent, rapid declines in both native and exotic coccinellid species point to new drivers that threaten community resilience (Fig. 3). Specifically, coccinellid declines occurred in annual and perennial crops in the MCSE, but not in forest plots. Concomitant with this decline is the widespread adoption of neonicotinoid seed treatments by farmers; we use the same pesticides to effectively control aphids, prey for coccinellids, on all MSCE crops. With repeated use, neonicotinoids build up in the soil and can cause direct and indirect toxicity to herbivores and their predators (Frank and Tooker 2020). Using KBS LTER data in part, Crossley et al. (2021) showed that aerially transported aphids are in decline globally and especially in the North Central US.

To test the effects of neonicotinoids on coccinellid abundance and community structure, and on coccinellid predation, we will sample aphid abundance and levels of neonicotinoid insecticides in soil from all MSCE and unmanaged habitats. We will test potential routes of toxicity by exposing lady beetles on plants with aphids grown on soils from neonicotinoid treated (Conventional, No-till, Reduced Input) and untreated (Successional) plots. We will also artificially increase aphid abundance using sentinel prey in MCSE subplots to determine how coccinellid abundance and community composition respond to prey availability.

Adaptation

Adaptation, whether biological, technological, or behavioral, can promote resilience by enabling populations or human systems to adjust in ways that maintain function during disturbance or restore function after disturbance. We focus on four modes of adaptation: genetic adaptation, adaptive phenotypic plasticity, microbe-mediated adaptation, and human adaptation. First, genetic adaptation results from rapid evolutionary changes in response to strong selection and can cause shifts in the community or ecosystem level functions provided by dominant species (e.g., Bassar et al. 2013) or result in evolutionary rescue (sensu Gomulkiewicz and Holt 1995) of declining populations and the functions they provide. Second, phenotypic plasticity is the main mode by which plants and animals are adapting to climate change (Hendry et al. 2008). Variation in the capacity for plasticity among species can explain which decline and which persist or even increase in abundance with climate change (Willis et al. 2008). Plastic trait shifts can also affect ecosystem function (reviewed in Miner et al. 2005). Third, microbe-mediated adaptation occurs when disturbance shifts microbial community composition in ways that buffer the effects of disturbance on hosts (Petipas et al. 2021). For example, microbe-mediated adaptation can promote individual plant resilience to water stress (e.g. Lau and Lennon 2012). General explanations of why and when such microbe-mediated adaptation occurs are developing (e.g., Hawkes et al. 2020). Finally, human adaptation describes the strategies farmers use to adapt to suboptimal conditions, like drought. Farmers may respond by making decisions to alter management, or adopt certain technologies or practices that might increase resilience. Such decisions and strategies will be affected by farmer values, identities, and knowledge, by available incentives and subsidies, and by farm attributes.

For some modes of biological adaptation, ecological theory predicts when rapid adaptation will be observed (genetic adaptation, plasticity) and even how modes might interact (e.g., phenotypic plasticity and genetic adaptation, Kirkpatrick and Barton 1997). These studies typically focus on single populations (e.g., how genetic adaptation or phenotypic plasticity influence a population's response to climate change). Here, we test these theoretical predictions, but also extend this framework to the resilience of whole communities and suites of ecosystem functions, focusing on dominant species since their population dynamics can explain long-term stability (Grman et al. 2010).

Adaptation Q1: Does genetic adaptation underlie plant resilience to severe drought?

Adaptation H1.1: The potential for rapid adaptation to promote plant resilience to drought is swamped by the genetic reservoir in the seed bank.

In 2021, a long, early-season drought dramatically reduced *Setaria faberii* abundance, and we suspect this intra-seasonal drought was a strong agent of selection. The few plants that germinated pre-drought and managed to survive produced innumerable seeds, while plants germinating post-drought produced very few. Building on seed collections from 2019, 2020, and 2021, we will conduct a resurrection experiment (e.g., Franks et al. 2007) to compare the pre-drought *S. faberii* populations (2019, 2020) with post-drought populations (2021).

Genetic adaptation can be buffered by persistent life stages. For example, seed banks can serve as reservoirs of genetic diversity, and in species with abundant seed banks, even strong selective events can result in little evolutionary change. We will investigate the role of such seed reservoirs in the evolutionary response by comparing our populations derived from seed collections with the population emerging from the seedbank.

Adaptation Q2: How does plasticity and its interaction with other modes of adaptation influence plant resilience to water stress?

Adaptation H2.1: Plasticity and microbe-mediated adaptation act synergistically to increase plant resilience to drought.

Adaptive phenotypic plasticity results from shifts in plant traits. Microbe-mediated adaptation results from two processes: 1) the microbial community can respond to environmental changes in ways that buffer plants from environmental changes (e.g., by altering soil structure and increasing water holding capacity in the case of drought) or 2) the microbial community can alter plant phenotypes in ways that promote plant fitness (Angulo et al. 2022). This latter mechanism is a special case of adaptive phenotypic plasticity whereby the microbial community is the environmental factor eliciting the plastic plant response. When microbe-mediated plasticity occurs through this mechanism, then microbe-mediated adaptation and adaptive plasticity can act synergistically or antagonistically. Synergistic interactions result if the plastic responses to microbes increase the magnitude of plant plasticity under drought. Such an effect could occur if microbial communities adapted to drought conditions are better cues of drought stress than the abiotic environment. Alternatively, microbe-mediated adaptation and plasticity may act antagonistically if shifts in microbial communities reduce the realized effects of drought on plants or the cues plants use to elicit plastic responses (e.g., by promoting soil water holding capacity). We will test the interaction between microbe-mediated adaptation and adaptive plasticity by testing how microbial community shifts in response to REX treatments in the field and simulated REX treatments in the greenhouse affect the expression of plant traits associated with drought tolerance (e.g., SLA, root morphology, leaf pubescence, epidermal conductance, stomatal conductance, osmotic adjustment).

Adaptation Q3: How do farmer values, identity, and farm infrastructure affect their adaptation to climate change driven stressors?

Adaptation H3.1: Flexible decision-making by farmers will buffer farm profitability against disadvantageous climatic conditions.

Unlike the other organisms we study, adaptive responses of farmers are social and technological, and the extent to which farmers are able to embrace change in response to emerging stressors may be analogous to the biological plasticity discussed above. We expect that farm resilience will be determined by the complex interactions among a farmer's ability to alter their management strategies including weather extremes, price and market fluctuations in the face of climate change, and new information and technologies. Using the PFS, we will examine why and how farmers become responsive to changing conditions, and what attributes confer greater flexibility in decision-making. While we expect farm-scale economic factors to influence farmer ability to respond and innovate, farmer attributes including beliefs, identities, values, and attitudes are also critical factors that influence which conservation (resilience-conferring) practices are adopted, and key for farmers to move from intended to actual behavior (Prokopy et al. 2019, Perry and Davenport 2020). Using PFS, we will measure both farm-scale and farmer attributes as predictors of decisions and practice adoption. Since such factors vary over time and place and involve weighing perceived costs and benefits of different courses of action, we will employ models in which numerous pathways are specified to impact behavior (Epanchin-Niell et al. 2022).

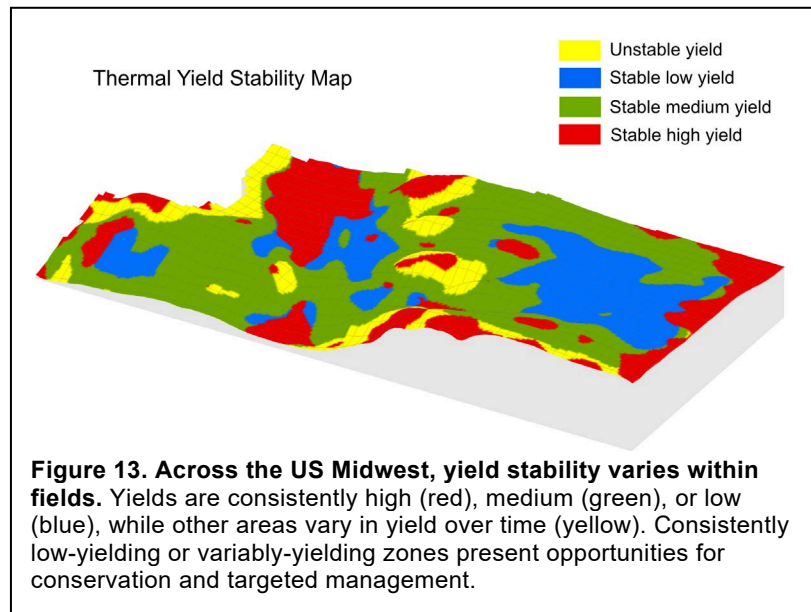
Taking resilience to drought as an example, farmers might adapt to greater drought frequency by doing nothing, by paying more for drought-tolerant crop seed, or by investing in irrigation infrastructure. Farm and farmer attributes are likely to underlie these decisions, and knowledge of what predicts whether or what they adopt is needed. Such decisions have cumulative effects and may be influenced by both the biophysical conditions present on a farm and the social relationships and values of an individual farmer.

Adaptation H3.2: A conservationist identity in farmers is a strong predictor of adoption of agricultural practices that will enhance the resilience of their operations.

Determining why and how farmers adopt new technologies or practices is critical for determining how that practice affects farm profits or resilience. It is also critical for designing effective policies that aim to incentivize adoption. A baseline constraint on farmer's ability to adopt new practices is their capital, which is why so many policy incentives are financial. However, there are some farmers (including those surveyed in our PFS) that adopt new sustainable agricultural practices in the absence of economic incentives. These farmers have increased their operational responsiveness and resilience and are not exclusively motivated by financial resources. We expect this subset of farmers to have a higher conservationist identity, which we assess as a combination of the percentage of their operations given over to conservation practices already, the information sources they are most willing to turn to for advice, and their perceptions of climate change and the benefits of biodiversity. We will examine what drives the adoption of multiple practices, including cover cropping, no-till, prairie strips, and diverse crop rotations, separately and in combination, and examine the role of identity in driving adoption (Burton et al. 2020, Dixon et al. 2022). We expect greater uptake in practices at the farm scale for those farmers who exhibit a more conservationist mindset. As farmer values shift from profit-maximizing to stewardship, operations will shift toward more resilient profiles where complementary adaptive practices are employed, leading to greater likelihood of mitigative practice adoption.

Adaptation H3.3: Given information about underperforming areas in their fields, farmers with a conservationist identity will convert low-yielding zones to perennials.

By using the PFS to identify farmers with different value orientations (e.g. conservationist identity and profit-maximizers), we can test how motivation affects willingness to adopt resilience-enhancing operation practices. We will do this through an information treatment, to test whether this information affects behavior. We will provide farmers with yield stability maps - digital images of their agricultural field that demonstrate which regions within that field produce consistently high yields and consistently low yields (Fig. 13, Basso et al. 2019). These maps offer a novel tool through which



to study resilience; typically developed across multiple years of crop rotations, yield stability maps provide a crop-independent, spatially-resolved metric of resilience over timeframes that might also influence practice adoption. These maps demonstrate: 1) zones that are consistently unproductive no matter the management, and thus waste resources like fertilizer, and 2) zones that vary each year with management or climatic conditions (ie, are unstable), and can potentially benefit from targeted management. Critically, these maps can be constructed for the field of any farmer across the Midwest using pre-existing remotely-sensed data, without requiring farmers to share information about their yields.

We will use farmer responses to questions about practice adoption in previous PFS waves to select a subset with different identities and past experiences with conservation programs. We will provide these farmers with yield stability maps of their own fields and technical assistance on the potential benefits for various management solutions for low- and unstable-yield zones. The long-term profile of each farmer that we have from the PFS will enable us to determine whether they change their operations after the incorporation of yield maps into their decision-making, and how their values

interact with a) available financial resources, b) the diversity of information sources they rely on, and c) adaptations they make in response to changing climate and economic conditions.

This effort provides a powerful opportunity for KBS LTER research to have broader impacts among regional land managers. Farmers chosen for the study will engage in multiple educational workshops hosted at KBS LTER or at local participant's farms, and will have the opportunity to co-develop educational materials and how-to guides for each successive year of the workshop. This cohort of farmers will become a long-term network of land managers that we can continue to rely on for more detailed involvement than the PFS allows, providing ongoing benefits to both the intellectual merit and broader impacts of the research we perform.

Resilience across Mechanisms

Work in the current funding cycle revealed many instances in which resources, diversity, and adaptation potentially interact to confer resilience. We will test the nature of these interactions, and how they affect resilience of communities and ecosystem functions, bridging gaps between ecosystem, community, and evolution ecology.

Across Mechanisms Q1) How do resources and diversity interact to confer resilience?

Resources x Diversity H1.1: Plant and soil microbiota diversity enhance soil C by creating optimal soil pore architecture

Recent work by Kravchenko et al. (2019) suggests that diverse plant communities generate soil pore architecture optimal for belowground C accumulation. Diverse plant roots in perennial systems led to formation of dense pore networks interspersing the soil matrix, generating optimal environments for microbial functioning (Kravchenko et al. 2021) and soil C accrual. This may be an additional mechanism by which diversity enhances C accrual and resilience, along with others such as greater primary production (Paustian et al. 1995) and stoichiometry (Furey and Tilman 2021). Notably, perennial polyculture crops produce more fine roots than monoculture perennials (Sprunger et al. (2017), further evidence of how plant diversity can enhance rhizosphere dynamics and C accrual.

So far, this phenomenon has been explored only in perennial systems (Zheng et al. 2022). We have documented greater carbon accumulation in cover crop systems, with C gains demonstrated not only in surface but also in subsurface horizons (Córdova et al. (in prep)). Yet, the underlying mechanisms remain unknown. We will explore the role of deep rooting patterns in diverse cover crop systems and direct and indirect influences through deep core sampling, X-ray computed micro-tomography (μ CT) of intact cores, and micro-scale geo-referenced soil sampling for C (e.g., Quigley and Kravchenko 2022).

Soil biota is one of the five pillar factors of soil formation (Jenny 1941) and an extensive literature exists on the role of fungi and nematodes in soil C-cycling (Ingham et al. 1985, Fitter and Garbaye 1994). Yet how the modifications of pore spaces by these soil architects interact with their impact on soil C processing and what that translates to in terms of C protection and subsequent gains remains unknown (Martin and Sprunger 2021). Nor is it known how these physical-biological interactions will be affected by changing precipitation patterns and water stress. Using the combination of micro-scale sampling and μ CT approaches, we will test how the presence of functioning soil fungal or nematode communities interacts with water stress over multiple growing seasons to affect soil pore formation and associated C protection mechanisms in soil profiles under REX.

Resources x Diversity H1.2: Resource availability and diversity interact to affect the resilience of microbial community function under drought

Under drought, microbial functions maintain ecosystem services such as plant growth, nutrient mineralization, and C sequestration. The specific traits of the microbial community will determine their response to stress and resultant effects on functions. Yet, we lack a generalizable framework for predicting the resilience of microbial function to drought. We know microbial drought response can be mediated by C availability because C is required for microbes to express traits that help them

tolerate stress, such as the production of osmolytes (proteins to maintain osmotic balance), biofilm formation, and dormancy (Schimel et al. 2007, Lennon and Jones 2011, Lennon et al. 2012). Drought can also alter other traits that affect functions, like C accrual. For instance, drought causes microbes to decrease C use efficiency (growth per unit resource Tiemann and Billings 2011) and produce more enzymes that degrade recalcitrant C (Bouskill et al. 2016). Drought may also interact with the effects of plant diversity on soil pore architecture; as soils dry, the heterogeneity and distribution of pore spaces that continue to hold moisture create “hotspots” of microbial activity that impact bulk nutrient mineralization rates (Kuzyakov and Blagodatskaya 2015). Together these trends suggest that there may be microbial trade-offs between stress tolerance, C acquisition, and growth, which could help develop a generalizable, predictive framework for how microbial function changes under drought (Malik et al. 2020). Whether such trait changes can occur under drought will also depend on the diversity of the resident or surrounding community. While it is known that diversity and C availability interact to determine microbial function, how these linkages determine response to drought and outcomes for carbon cycling is unknown.

We will test this by measuring microbial functional traits with shotgun metagenomics under drought in REX subplot treatments. We will also examine microbial traits in subplots in which we vary community diversity (nematicide and fungicide) and resources (labile carbon additions). Functional traits are a powerful way to understand stress response, since these traits can affect organism fitness and also contribute to ecosystem processes (Nock et al. 2016). By characterizing microbial trait trade-offs, the trait shifts we describe will be testable outside KBS LTER to identify general constraints on microbial community response to drought, and implications for C storage.

Resources x Diversity H1.3: Farmers that adopt cover-cropping are motivated by a desire to enhance soil C for its perceived ecosystem services.

We will investigate whether farmers perceive cover-cropping as a viable way to increase soil C, and whether they value soil C as a mechanism by which to increase operational resilience. For example, we will investigate whether farmers that express more concern about future climate change put more value on soil C as an ecosystem service. We leverage insights gained from the PFS into farmer's willingness to expand cover-cropping by developing new questions about motivations for engaging in different types of cover-cropping (multi-species, inter-cropping). Based on known farmer interest in soil health (Carlisle 2016, O'neill et al. 2021, Wade et al. 2021) and the results of our PFS, we conducted in-depth interviews and found that farmers link soil health and soil C (Irvine et al. (in prep)). Even so, it is unclear what mechanisms they believe underpin soil C, particularly C sequestration. We will investigate whether farmers see engagement in C markets and measures to promote soil C sequestration as a mechanism of resilience for their farm operations, for example if these policies provide additional income to buffer against volatility in crop production, or by providing actual ecophysiological resistance to environmental stress. To address this hypothesis, we will present farmers with measures of soil C in tandem with maps of stability zones, and evaluate whether this knowledge increases likelihood of cover-cropping adoption, expansion, or diversification.

Across Mechanisms Q2) How does diversity interact with adaptation to affect resilience?

Diversity x Adaptation H2.1 Plant diversity limits the capacity for microbe-mediated adaptation to promote ANPP resilience to drought.

We are currently testing microbe-mediated adaptation to water stress in agricultural crops in REX and will test how microbial diversity affects the capacity for microbe-mediated adaptation in a parallel study in 75 farm fields selected among PFS respondents. We propose to expand this approach to our Successional treatment to test whether microbe-mediated adaptation is similar in diverse plant communities. Previous work in simplified greenhouse systems suggests that microbial communities can respond to drought stress in ways that promote plant resilience to drought (Lau and Lennon 2012), and preliminary data from REX suggests that microbial communities respond to REX treatments in ways that affect soybean growth (Fig. 14). Even in diverse plant communities, microbe-

mediated adaptation may occur if it acts through general processes (e.g., a shift in the microbial community towards high biofilm production, which generally increases soil water holding capacity) likely to benefit most plant taxa. However, it is also possible that any drought-caused shifts in microbial communities could actually reduce the capacity of other resilience mechanisms (e.g., plant diversity increasing resilience via compensatory dynamics). Such effects might be likely given that drought seems to affect the strength of plant-soil feedbacks (e.g., Fry et al. 2018), which can determine the outcome of competitive interactions between plant taxa and ultimately their coexistence.

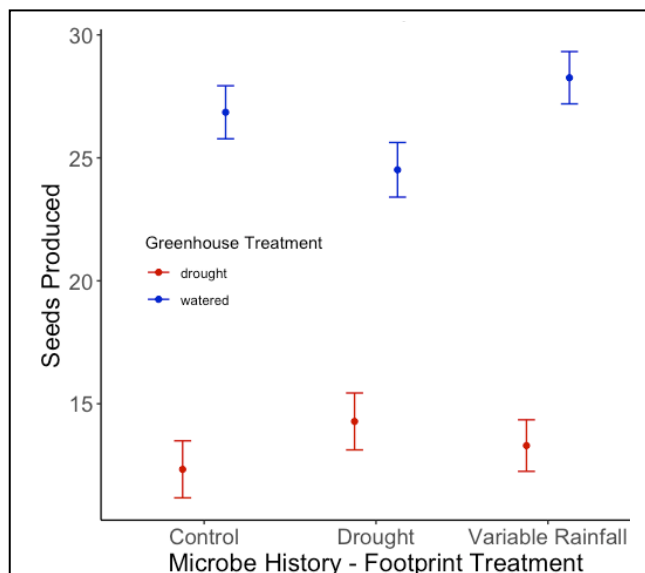


Figure 14. Plants inoculated with microbial communities from REX Variable Rainfall treatments were more affected by experimentally imposed drought stress in the greenhouse, both because they tended to grow more poorly under drought stress (red symbols) and because they were better able to take advantage of well-watered conditions (blue symbols).

We will use two approaches to test how plant community diversity affects microbe-mediated adaptation. First, we will leverage observed natural variation in diversity across REX Successional plots. By collecting microbial communities from REX treatments within these plant communities, we will test how plant diversity influences the capacity for microbe-mediated adaptation to reduce the negative effects of experimentally imposed drought in the greenhouse. Second, we will explicitly manipulate plant diversity in large experimental mesocosms in the greenhouse and impose droughted or well-watered conditions upon these communities. The resulting soils with a legacy plant diversity and drought treatment will be used to test how plant diversity affects microbe-mediated adaptation to drought. If plant diversity inhibits microbe-mediated adaptation, then we would predict that microbes from droughted soils will provide the strongest benefit to drought resilience of plants when those microbes also originate from low diversity mesocosms.

Resilience across Scales

We propose to expand the impact of KBS LTER's site-based research by scaling the processes that we investigate in local experiments to the landscape and to the US Midwest. Ultimately we will address the question: **Can mechanisms of resilience we have identified at the scale of REX or MCSE confer resilience to biodiversity and ecosystem functions elsewhere (e.g., other soil types or climatic conditions)?** We will address this by using a multi-faceted approach. First, building on *R-1*, we will identify and measure salient features of our system that are amenable to scaling. This includes within-plot heterogeneity of soil properties and ecosystem services. This will help us accurately scale aspects of resilience, including those that are nonlinear. Second, we will account for unmeasured (or unmeasurable) aspects of our sites using our process-based spatial modeling (SALUS, see Box 3), and simulate a diversity of approaches to land management. Importantly, simulations will allow us to project system dynamics into future climates and land uses, allowing us to examine resilience of ecosystems under different climate and land management scenarios.

To answer our overarching question, we will investigate scaling hypotheses in three ways. First, we will test predictions using REX data at the field scale. Second, we will test whether mechanisms of resilience predict yield stability of our MCSE treatments. Third, we will use measures of ecosystem responses in stability zones across the MCSE to test the ecosystem-wide effects of alternative management on yield stability.

Scaling Q1) What underlies drought resilience across land use practices?

Scaling H1.1: Practices that maintain high C stocks will display greatest drought resilience across a diversity of land-use settings

In REX, we expect soil C content to be a major predictor of drought resilience across land use treatments. To understand whether soil C predicts resilience at landscape and regional scales, we can compare SALUS outputs to measurements under shelters in REX to validate the model for the KBS LTER setting (see **R-1**). We will also be able to factor in processes likely to affect drought resilience that are omitted in our field design. These include properties that are difficult to measure, like root and shoot dynamics, or practices that are not manipulated in tandem at KBS LTER, like the combined impacts of tillage and cover crops.

Using REX-validated SALUS simulations, we can explore drought resilience of a greater breadth of land use types and broader climate scenarios than our experimental treatments. Importantly, in comparison to REX we can much more flexibly investigate how changes in the timing and severity of drought impact ecosystem resilience. For instance, we can test whether no-till or other practices increase resilience to drought in the short term, or whether resilience is (as hypothesized) mediated through more gradual and protracted increases in soil C content. We can also examine mechanisms other than C resources. Increased water infiltration and reduced evaporation both confer drought resilience. We could not measure these directly in REX, but we can simulate in SALUS. Finally, we will be able to estimate the impacts of drought on common land use types and understand how increased climate variability will affect both yields and ecosystem services in the region.

Scaling Q2) How can we leverage sub-field variation in resilience to improve field-scale yields?

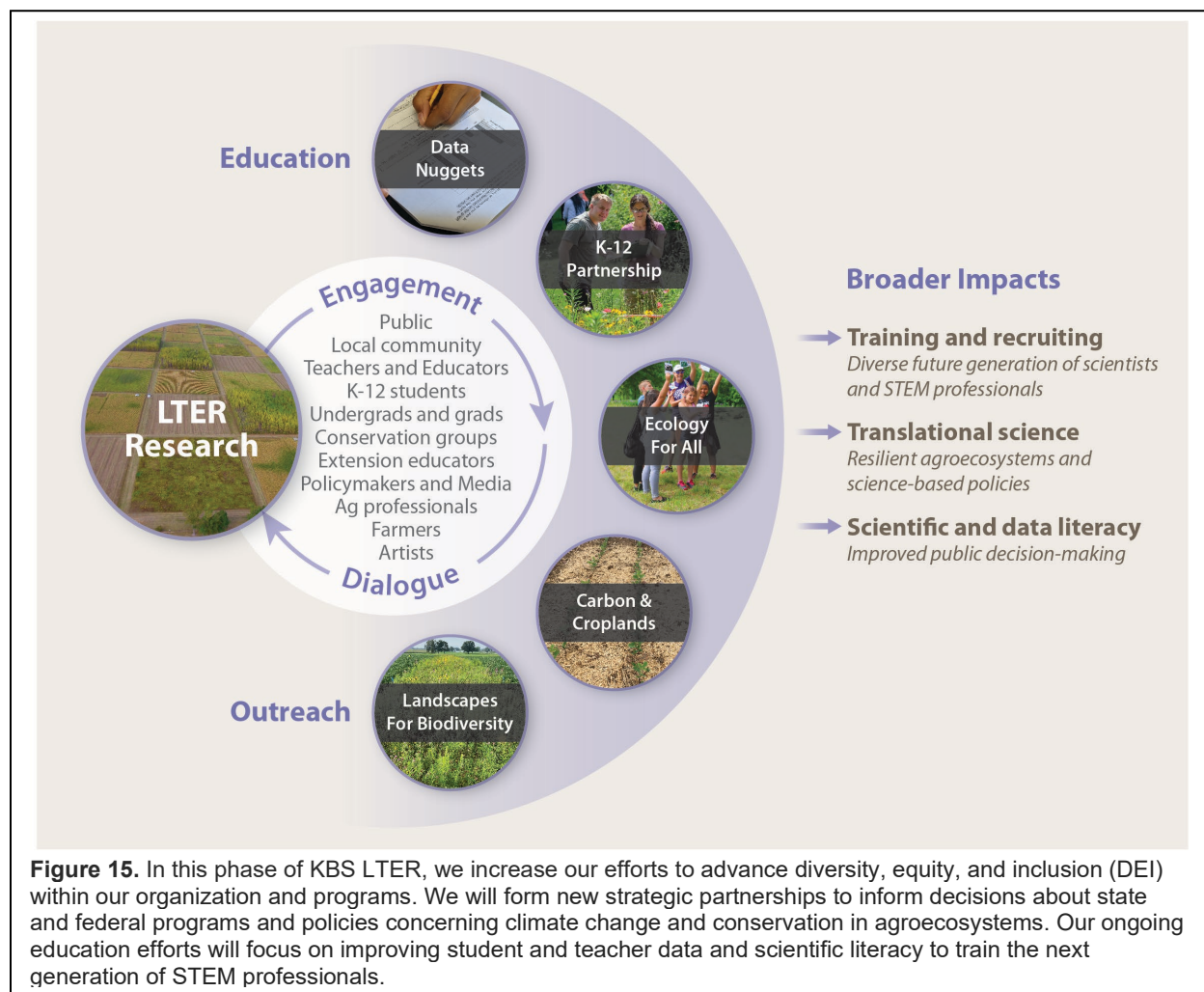
Scaling H2.1: Fields contain zones that differ in resilience, and accounting for this heterogeneity improves field-scale predictions of resilience.

Yield stability maps provide spatially-resolved proxies for the resilience of key ecological processes within agricultural fields. The high variation of yield stability within an individual field (Fig. 13) presumably underpins the large inter-annual fluctuations in field-scale yields observed in the MCSE. Using our geolocated harvest data, we will generate yield stability maps across the MCSE and investigate how knowledge of sub-field heterogeneity in yield stability allows us to improve our predictions of yields at the scale of our MCSE plots in varied future climatic conditions. Using the SALUS model, we can then capture the mechanisms that drive variation in yield stability we observe within our fields, and establish which of these processes are enhanced or inhibited as a result of the long-term agronomic treatments (e.g, no-till, cover crops, or prairie strips) that we have imposed.

Scaling H2.2: Changing management practices can improve resilience of sub-field zones.

Descriptions of yield stability zones can help us understand how sub-field heterogeneity influences spatial scaling, but it does not tell us if these zones will be responsive to changes in management, and over what timescale. To predict this, we need to understand the mechanisms that underlie resilience (or lack of it) in these zones, and to measure a broader array of responses than yield. Within different yield stability zones of the MCSE, we will measure soil properties, including GHG flux, nitrate leaching, C accrual, and yield, in subfield zones of varying crop performance. We will then use SALUS to simulate mechanisms that confer resilience of these responses, and project how they will change in different soil types, topographies, and management practices across the region. We can also test resilience of these zones to varied climatic conditions. In the end, we will quantify the net potential benefits to agroecosystem resilience that can be achieved through alternative management practices tailored to the subfield scale. For instance, these zones, if converted from row crops to perennial areas, will increase plant and animal diversity, which could contribute to field-scale resilience that can enhance pollinator visitation, pest suppression, carbon sequestration, and other ecosystem services.

We can improve this analysis further by taking into account the constraints that particular settings pose for land managers. For instance, even if no-till management can generally increase resilience of yields and soil water retention, soils with high sand or clay content will not benefit from conversion to no-till and should not be managed as such. And, as we have established, if herbicide-resistant weed pressure exceeds a certain threshold, farmers will be unwilling to implement no-till management for fear of reduced yields (Van Deynze et al. 2021). These constraints must be modeled accurately to provide meaningful projections of enhanced agroecosystem functions via novel practice.



Broader Impacts

Educating decision makers and landowners about climate change and biodiversity

The agricultural setting of KBS LTER gives us the exciting potential to conduct basic science and directly translate research to increase public scientific literacy and engagement with science and technology. Through an extensive strategic planning process in 2021, we identified two key areas where we can impact conservation and environmental decision making (Fig. 15). Our “Carbon and Croplands” and “Farmscapes for Biodiversity” initiatives are centered on the formation of bi-directional relationships with stakeholder groups and new strategic partnerships. Involvement with the LTER Network Education & Outreach Committee, MSU Extension, Michigan Agriculture Advancement (MiAA), North Central Climate Collaborative, and the Soil Health NEXUS will help

connect and expand our efforts, while KBS LTAR will serve as a key partner in stakeholder engagement.

The Carbon and Croplands initiative will explore opportunities to use KBS LTER science to inform decisions, for example about state level programs and policies (e.g., the Michigan Climate Action Plan), federal climate legislation, and the 2023 Farm Bill reauthorization. We will collaborate with MSU's Institute for Public Policy and Social Research to explore opportunities to increase the use of science in carbon accounting and monitoring in voluntary and regulatory markets as well as corporate supply chain sustainability efforts. In addition, the initiative will promote soil health practices to increase carbon storage in soils. We will begin with a formative engagement process where we reach out to local and federal policymakers (e.g. Michigan Environmental Council, congressional staff, USDA) to seek input on key questions that KBS LTER science can address.

Farmscapes for Biodiversity will explore the potential for KBS LTER research to inform decisions related to state and federal funding priorities for conservation programs (e.g., Conservation Stewardship Program and EQIP). This includes working with landowners to develop evidence-based land rental contracts for sustainable cropping; encouraging landowners/managers/farmer advisors to think more about biodiversity at both field and landscape perspectives; keeping edges of fields wild; and management plans for large-acreage farms. This initiative led to a new collaboration with Iowa State University, MiSTRIPS, which aims to promote the adoption of prairie strips in farms across the Midwest and promote research to understand the benefits of native spaces, and barriers to adoption (Luther, et al. 2021). MiSTRIPS will work with farmers to plant their own prairie strips, hold field days for farmers on these farms, and disseminate research findings through press releases, learning circles, videos, and KBS LTER field days.

Building data and scientific literacy to promote interest in STEM

Building on the success of Data Nuggets and K-12 Partnership programs, we will focus on increasing representation in our educational products by highlighting scientist role models from historically excluded groups in STEM, an effective strategy to increase student interest in STEM careers (Shin et al. 2016, Gladstone and Cimpian 2021). Data Nuggets are written by scientists, enabling them to serve as role models, and share their stories about and passion for their research and careers. Current work, in partnership with Project Biodiversify, will create new Data Nuggets from LTER scientists from under-represented groups and pair these with profiles sharing humanizing elements of scientists' lives. We will continue formal evaluation of Data Nugget efficacy, including with an assessment tool to determine the effects of scientist role models on student interest in STEM careers and self-efficacy.

The K-12 Partnership will continue to involve KBS LTER scientists in teacher training activities. We will invite teachers and students to participate in professional learning opportunities, for approximately 40 hours of instructional time each year for ~75 teachers, and we will offer RET positions as funding opportunities allow. Each RET will partner with our scientists to create new Data Nuggets and share their research broadly. We will strengthen our communication by engaging and training our scientists, students, and RETs to promote LTER science via our social media, website, and place-based outreach opportunities.

To ensure full participation of women, persons with disabilities, and underrepresented groups in STEM, we will work to ensure KBS is a welcoming community that benefits from a diversity of perspectives. Our new Ecology for All initiative permeates all aspects of our organization, beginning with effective, inclusive recruitment and retention of students, staff, and faculty from underrepresented groups. Most importantly, these members of our community must be represented in the activities we perform and the products we produce, and in roles that let them demonstrate leadership. We have established a new relationship with a Michigan tribal college to facilitate these efforts. This initiative has already resulted in KBS LTER hiring (in conjunction with KBS) a DEI Advocate for long term research programs. This Advocate has been hired to enhance KBS LTER's efforts to have a diverse, inclusive, and equitable community.

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8.1 Data Management Plan (continued from page 8-1)

Our data management system is designed to curate and distribute accurate research data for multiple projects in a consistent, accessible, and timely way. The KBS Information Management System (KBS IMS; lter.kbs.msu.edu/datacatalog) serves local, Network, and community-based users for both research and education.

Our goal is to deliver data and data products that

1. have long-term integrity
2. are freely and publicly available in acceptable, standardized formats
3. include both data collected by project personnel and specific data used in site publications
4. are Findable and Accessible (by archiving the data in public repositories), and Interoperable and Reusable (by having structured metadata accompanying the data).

Data management is included at the proposal stages of research projects. We encourage investigators to include the KBS IMS in data management plans of proposals submitted to NSF, DOE, and USDA. We require all investigators working on site or with samples from the site to affirm in writing that they will contribute their data to the KBS IMS.

IM Personnel. Our KBS IMS team consists of several people. Sven Bohm, a full-time professional Information Manager (IM), coordinates data-related activities. Project Manager Stacey VanderWulp is responsible for QA/QC, synthesis, and summary of the core datasets, protocols, and metadata. Assistant Information Manager Hsun-Yi Hsieh manages spatial data and remote sensing products and assists in metadata and data curation. Education and Outreach Coordinator Liz Schultheis and Science Coordinator Nameer Baker coordinate and update website content. This general model has been in place since 1997 and has worked well. An IM Committee composed of graduate students, postdocs, and faculty meets once each year to advise the IMs and PIs of issues with the discoverability and usability of data products.

The IM team works with researchers to assist in data and metadata collection by providing advice and training on using appropriate tools to aid in the collection and documentation process. We use the following tools:

- We hold regular office hours to offer individual advice and training.
- To establish common data and metadata collection patterns, we hold data meetings with larger research groups (REX, for example).
- We encourage labs to share data internally, early, and with the information management team.
- Where appropriate, we find the resources to automate the collection and annotation of data and metadata.
- We offer help and advice for submitting data and metadata to repositories.

KBS LTER data life cycle

KBS LTER data management is designed to facilitate data use as formalized in the DataONE life cycle with its eight components: planning, collection, quality assurance, description, preservation, discovery, integration, and analysis.

Planning

We include data management at the outset of planning KBS LTER experiments and observations. During planning for new experiments and observations, expected data and metadata to be collected are identified, and the data management team is involved in vetting the plan. We use existing data, knowledge, experience, and, where applicable, statistical power analysis to estimate the time and replication needed to address specific hypotheses. The IM is a member of the Executive Committee and has input into the early stages of planning new experiments and data collection efforts. The data

management team then works with the researchers to determine a collection and documentation workflow that will result in the expected data and metadata being ready for curation and publication while fitting within the researchers' workflow.

We offer advice on data collection template design, naming conventions, and metadata collection strategies that enable users to produce reusable data packages.

Data collection and description

The best time to document data is at the time of collection when all of the relevant information is fresh. Therefore, data collection and description activities are interlinked and must happen simultaneously. Observational data are generally collected into either MSExcel templates or small web applications to standardize data collection. Using web apps also allows us to catch data entry errors early. Custom apps process data from instruments, for example, GCs, elemental analyzers, and gas analyzers, to transform the data into usable forms and merge them with the required metadata. For activities that are not part of our standard sampling program, we promote the use of individualized templates to facilitate incorporation into the data catalog. Sensor data (e.g., from our weather stations and soil moisture monitoring network) are typically collected via radio or cell modem link and automatically processed and uploaded into our database. We use Postgresql, an open-source relational DB, as our primary data store.

Spatial data are collected via handheld GPS units, GPS-equipped agricultural equipment such as combines and tractors, uncrewed aerial vehicles (drones), fixed-wing aircraft, and satellites. Using PostGIS, lidar and ground-based GPS surveys are managed alongside the non-spatial data in our Postgresql database. A commercial operator collects annual aerial images (visible, infrared, and thermal), and the resulting images are stored on our image server. All air photo missions and metadata are detailed on the web; orthorectified digital images are available at full resolution on request. Survey-grade GPS is used to track sampling locations. In addition, thematic maps are available in our spatial data catalog and GIS layers for the local area are available on a shared drive to facilitate greater use by local researchers. We will make these spatial data available through EDI.

We will save two copies of the X-Ray tomography data on external hard drives, with one copy stored off-site as a backup. Because the storage capacity for these data is so high, they will be made available on EDI as an off-line data source.

Social-science data from the Panel Farmer Survey (PFS), other surveys, and data from focus groups and interviews are handled by individuals trained in responsible research conduct and human subject protocols, complying with MSU IRB standards. Personal identifying information is removed, and data stored in secure locations. Anonymized datasets with human subjects data are otherwise treated the same as other research data.

We maintain a catalog of archived samples – primarily stored dried soil, plant, and seed material – dating from project inception in 1988 and stored in two purpose-designed archive rooms in the LTER field lab. The current collection holds approximately 18,000 plant and 13,000 soil samples. The building has backup power and a C3HF7-based fire suppression system to protect the archive from water damage. This building is currently nearing capacity, and we will be submitting a Building Capacity proposal to support the needed expansion of the facility. Plant and soil samples destined for archiving are dried, placed in rodent-proof containers, and cataloged before storage.

We maintain a public project log to document and report on daily research activities and an agronomic log to document field activities relating to the agronomic management of the site.

Other data products include research protocols for project data collection and processing, as well as a site bibliography (Iter.kbs.msu.edu/publications) that provides direct links to pdfs of open access publications and data publications, and indirect links to all others. In 2017 we began depositing copies of publications in the NSF-PAR database within 12 months of publication. The site bibliography database also cross-references papers to specific LTER experiments and field sites.

The KBS IMS also includes the KBS LTER web site (lter.kbs.msu.edu), which provides access to the data catalog, site bibliography, personnel directory, information about research, education, and outreach activities, data and site access policies including site use request forms, information for prospective researchers and students, and meeting abstracts and posters.

Data Assurance

Primary responsibility for data quality rests with individual scientists. The Project Manager checks project data with a secondary review by the information manager. We provide QA/QC apps for regular data flows to streamline QA/QC and reduce the load on the data management staff. We generate graphs as part of the curation cycle and provide them to specific investigators to ensure that the data are consistent with previous measurements and correctly transferred. The information manager checks automated data flows, such as sensor data, and provides graphical summaries to the lead investigators and other interested parties as a secondary check. We encourage researchers to use scripts to document their QA/QC decisions on the raw data. We are implementing a new model workflow starting with our multi-investigator (nine PIs) REX, whereby all project-specific scripts are publicly accessible on GitHub.

Data Description

We provide metadata documents in the Ecological Metadata Language (EML). We collect metadata as part of the data collection workflow in MSEXcel templates or via web apps and amend it with project-level metadata stored in our database. Common project-level metadata improves description consistency across datasets, freeing researchers to concentrate on the specific metadata for their study. In REX, we use templates to collect common metadata and suggest information to be collected, which will facilitate generating structured metadata for individual datasets.

Data Preservation

Data preservation has short- and long-term aspects. For "in-flight" data protection, it depends on preventing accidental or intentional loss of research data. Implementing security protocols, backup strategies, and redundancy ensure data and metadata are available for archiving. We will preserve long-term access to the data by submitting the data to nationally recognized archives such as Dryad, EDI, or other community accepted repositories.

Data in the KBS LTER Data Catalog are pushed to the Environmental Data Initiative (EDI), our primary national repository, which is federated by DataONE. For distribution to EDI we bundle related tables into more comprehensive datasets, composed of all of the related tables; this provides a more self-contained archive although it reduces the number of apparent KBS contributions to EDI. KBS LTER datasets in EDI have their own DOIs

All data and metadata are made available online as specified in the Data Access Policy for the LTER Network. Our data use policy, posted publicly at lter.kbs.msu.edu/data/terms-of-use/, relies on ethical behavior by data users, and we put no restrictions on use of data by others except for preserving the primary investigators right to first publication, and we do not track data access. Our site use policy requires that data be made available within two years from collection and no later than the publication of the main findings from the dataset.

Security

Access to the database and other servers is only allowed with key-based ssh connections from campus or the MSU VPN. Servers only expose the minimally necessary ports. The computer systems used by KBS LTER undergo monthly security scans by the MSU IT team to probe for vulnerabilities. To date, these scans have not revealed any issues. Program access to databases is always routed through standard libraries to prevent SQL injection attacks. Daemons are running with the lowest possible permissions, and we stream logs to a central logging server for analysis, intrusion detection, and auditing. To shorten incident recovery time and ensure continuity in the case of the departure of crucial personnel, we use "infrastructure as code" principles for system administration and for managing the setup and deployment of hardware and software systems.

Capturing the details of the system configuration in code ensures that the steps required for maintaining and updating the software and systems are automated and repeatable.

Data Backup

Weekly backups and daily incremental backups of the servers and data are maintained jointly by the Kellogg Biological Station (KBS) IT staff and the KBS LTER IM staff to ensure data and infrastructure availability and continuity. Daily backups are kept for three months and weekly backups for six months, except that every six weeks one weekly backup is retained for at least two years. In addition, annual snapshots of the database are stored indefinitely. KBS IT or individuals handle backups on individual investigators' computers. If needed, we provide help in setting up an automated backup scheme.

Redundancy

Data from our servers are replicated to a server on the MSU campus (~ 60 miles away) to ensure continuity. Disks are configured as RAID 5 or RAID 6 to minimize downtime due to hardware failures.

Data Monitoring

We use Grafana dashboards to monitor infrastructure performance and data flows. The IM team is automatically alerted about issues such as downtime or lagging data collections.

Analysis and Integration

While we do not prescribe the type of workflow and tools that researchers use during their analysis, we do encourage the use of scripting languages (R, SAS, SPSS) to document the analysis workflow and aid in reproducibility. We encourage researchers to make the analysis pipeline part of their data submission. As part of the new model workflow developed for REX, we have established a KBS-LTER Github organization to share and version control such analysis scripts.

Data Discovery

Data and Metadata are available online in repositories (EDI, Dryad, Genbank, and others) and our local catalog under terms compatible with the Data Access Policy for the LTER network. Our data policy found on the "terms of use" web page of the KBS LTER site relies on the ethical behavior of users. It puts no restrictions on use except for preserving the primary investigator's right to first publication. In 2022, we plan to start using the Creative Commons CC-BY license for our long-term datasets, which complies with the LTER Network data access policy.

For baseline data collected by the project team, we push the data periodically to EDI. We generate the EML metadata from our metadata catalog and bundle up the dataset for archiving at EDI.

Promoting data contributions from investigators

We have implemented the following procedures to ensure that data from individual investigators and projects become available in the LTER databases and on nationally recognized repositories:

1. We include a section on data contributions to our annual email to collaborators reminding them to submit new publications and data. This email from Science Coordinator Nameer Baker has successfully collected publication information over the years.
2. We schedule short annual interviews by the IM staff with collaborating researchers to help researchers keep data in shape for archiving.
3. We run periodic data management workshops and encourage investigators to plan for data management at the outset of their research.
4. We use the IM committee to detect issues and provide feedback to the IM team.
5. We encourage and assist researchers in depositing data specific to their publications into the Dryad digital data repository.

6. We reach out to researchers during office hours, offer advice, and help with data and metadata handling and repository submissions.
7. We require agreement to share data as part of our site use request processes.

Anticipated Datasets. With the current proposal we anticipate the following data catalog additions:

1. Extension of our long-term datasets on yield, soil resources, water, and GHGs
2. Additional datasets of arthropod abundances and distributions in relation to the proposed prairie strips.
3. Farmer survey datasets on attitudes toward implementing different management practices
4. Plant, microbe, and ecosystem effects of the drought × soil C × microbial diversity treatments.
5. A dataset of pore spaces in soil and connectivity in soil.

Contribution to LTER Network and community activities. IM Bohm and Assistant IM Hsieh attend all national LTER IM meetings and are active in LTER working groups. Bohm is currently a member of the Unit working group, and Hsieh has been involved in the Non-Tabular Data working group.

Response to Previous Reviews

The mid-term review team encouraged us to put more of the data management responsibilities on individual researchers and remove the role of the data manager as a single point of failure. We have worked on providing data processing applications and workflows for ongoing data collection efforts, such as the baseline sampling carried out as part of the project infrastructure. These applications and workflows reduced the need for intervention by the data management team for the ongoing baseline sampling at the site. However, it did not address datasets resulting from individual research projects that were not part of the baseline sample collection. To address this issue, we have

1. Increased our data management training efforts by offering more frequent presentations, regular office hours, and outreach efforts.
2. Trialed a guided data collection approach in the REX. This experiment provided an excellent platform to develop a more decentralized data management capability for project data since it includes researchers from nine research labs across three institutions. We have adopted a workflow where researchers contribute data to a shared storage location and use a series of standard transformation steps to convert the raw data (L0) to quality controlled, common harmonized data (L1) and then implement further transforms for specific analysis. The transformation scripts are versioned on GitHub to facilitate sharing among the group and repeatability of the data cleaning and analysis steps and provide documentation on the decisions made during the research.
- 3.

Key features of the KBS Information Management System.

Feature	Details
Network connection	Gigabit fiber optic connections between buildings and to the LTER field lab and MCSE. Wireless radio connections to sites within 2 km of the MCSE
Data Storage	Raid 5 + 1 or Raid 1 + 0 on all servers, hot spare database server on campus (60 miles away). Approx 40 Tb of storage space.
Monitoring	Uptime monitoring of servers, databases websites and data loggers, with notifications to the IM team.

8.3 Project Management Plan

Leadership will transition from a single lead PI to co-lead PIs in the cycle beginning December, 2022. Nick Haddad will be joined by Sarah Evans as co-lead PI. This new approach was arrived at after consideration of successful co-Lead models at other sites, and of the different disciplinary and leadership strengths that co-Leads would bring. An Executive Committee (EC) composed of the 10 principal investigators (PIs) and key personnel meets monthly to oversee KBS LTER. The EC will be chaired by co-lead PIs Haddad and Evans. Members include co-PIs Bruno Basso, Doug Landis, Sasha Kravchenko, Jen Lau, Sandy Marquart-Pyatt, Phil Robertson, Christine Sprunger, Phoebe Zarnetske, as well as Information Manager (IM) Sven Bohm, Science Coordinator Nameer Baker, and Education and Outreach Coordinator Liz Schultheis. Scott Swinton and Steve Hamilton will not remain as co-PIs. Kravchenko, Sprunger, and Zarnetske are new to the leadership team in this renewal, and will bring new strengths in soil physical properties, soil trophic dynamics, and spatial ecology.

EC members participate in all substantive decisions regarding project coordination, management, and scientific direction. They also support site promotion by hosting visiting researchers, making presentations to interested academic and professional groups, and promoting site use by students and colleagues. EC members actively participate in LTER-funded research and are expected to seek outside research funding. EC members also serve on site committees (see below) and participate in site and Network All Scientists Meetings, workshops, and committees.

Members of the EC have specific responsibilities. Haddad and Evans, as co-lead PIs and co-chairs, provide overall project leadership; they will be the principal contact for NSF, the LTER Network, and the University, and will supervise Science Coordinator Baker and Education and Outreach Coordinator Schultheis, IMs Sven Bohm and Hsun-yi Hsieh, and Agronomic Manager Joe Simmons. Co-PI Robertson will share responsibility with Haddad and Evans for supervision of Project Manager Stacey VanderWulp.

Co-PIs collaboratively lead the research outlined in this proposal and maintain the core datasets; the Biogeochemistry team led by Evans, Kravshenko, Sprunger, and Robertson; Biotic Interactions led by Haddad, Landis, Lau, Sprunger, Zarnetske, and Evans; Scaling led by Basso, Landis, and Zarnetske; and Human Decision-making led by Marquart-Pyatt. Co-lead PIs Haddad and Evans will receive 1 month of summer salary; the other co-PIs will receive two weeks except for Landis and Kravchenko who have 12-month appointments. Each research team is allocated a modest budget, described in Section 5.2, to support the long-term experiments and observations in their research area and to promote cross-project integration.

Project coordinators include two PhD-level academic specialists, funded by the University since 2009 (see Section 7.2), who provide administrative support and leadership for research coordination and education and outreach activities. As Research Coordinator, Baker coordinates the implementation of multi-lab studies, most notably overseeing the implementation of REX (see Proposed Research), promotes research opportunities to prospective investigators, including graduate students; coordinates KBS participation in network partnerships and initiatives; organizes with graduate students the annual KBS All Scientists Meeting; coordinates annual reports of sampling, agronomic, and information management activities; and helps to coordinate the Agronomy Advisory Committee (below). Baker chairs the network DEI committee, where he contributes to development and dissemination of best practices across the network, and of DEI-centered programming for the Network All-Scientists Meeting.

To meet our broader impact goals, our Education and Outreach Coordinator (Schultheis) works closely with LTER scientists at KBS and across the network and leads the implementation of our Broader Impacts Strategic Plan. Schultheis created and now leads Data Nuggets, a platform that brings real data from scientific research into K-12 and undergraduate classrooms. Data Nuggets is actively used across the LTER Network and in thousands of classrooms. Her work on Data Nuggets includes teacher professional development, STEM curriculum development, science communication training for scientists, science education research, and assessment. Schultheis' membership on the

LTER Network Education and Outreach Committee will help connect to and expand our efforts. She organizes and writes press releases for our researchers and disseminates these via social media and newsletters. Working in the MiSTRIPS program, Schultheis works to educate farmers about the use of prairie strips in their agricultural fields. Schultheis works closely with Kara Haas, the sLTER Coordinator, who is responsible for coordination of the KBS K-12 Partnership. Haas previously chaired the LTER Network Education and Outreach Committee. Schultheis coordinates LTER research internships for K-12 teachers (RETs) and undergraduates (REUs). She also coordinates and gives tours to a broad audience that includes educators at all academic levels, students, non-profit organizations, farmers, and farm industry, among others.

Committees advise the EC in specific areas. The *Agronomy Advisory Committee*, chaired by co-PI Landis, reviews agronomic practices and provides advice on agronomic management issues. This committee includes Extension educators and university field crop specialists. An *Information Management Committee*, chaired by IM Bohm, provides advice on data access, training, and management issues as described in Section 8.1. A *Graduate Student Committee*, co-chaired by two LTER graduate students (one campus-based and one Station-based), works with Baker to provide advice on recruiting and enhancing graduate student participation in the project and contributes to organizing the all scientist meetings.

Technical staff include Project Manager VanderWulp, who oversees core sampling and analytical activities, and supervises a research technician and 2–3 seasonal employees; Agronomy Manager Simmons, who is responsible for all farming activities with two full-time technicians; and IM Bohm, who has overall responsibility for data management, with full-time assistance of Hsun-yi Hsieh for spatial and remote sensing data (satellite, aerial, and UAV imagery; GPS and GIS).

KBS LTER Investigators include all researchers and educators who work with samples or data from the site. Since 2016, there have been 130 Investigators, including 82 faculty from MSU and elsewhere and 182 postdocs and graduate students, based on approved site use requests (below). Investigators are provided priority access to baseline data, are eligible to host REU students and RET teachers (if faculty), and are invited to attend both the national (every three years) and the local (every year) LTER All Scientists Meetings. Graduate students affiliated with the project can apply for research fellowships and small grant awards (see below). The annual KBS LTER All Scientists Meeting, which is held on campus or at the Station and attracts 75–110 LTER and non-LTER participants, includes research presentations, poster sessions, and project-related break out discussions. At the 2019 KBS LTER All-Scientists Meeting, we organized around a “network of networks” theme, and the program included talks by and discussions with program officers of three major, ecological networks, LTER, LTAR, and NEON. We organized breakout discussions on how to bridge datasets collected in different networks. Emerging from these activities was a workshop, led by co-PI Robertson and others, that brought together researchers from LTAR, LTER, and NEON to identify ways to use long-term data to address questions on working lands.

Graduate student participation is a KBS LTER priority. We support their participation in site level research by providing fellowship opportunities and encouraging them to attend Network-level programs and activities. Funding from the MSU Graduate School (Section 7.2) allows us to offer summer fellowships to graduate students conducting LTER-related research. In the past three years, Graduate School support for LTER has gone to 29 graduate students from 22 labs, 11 departments, and 5 colleges (Natural Sciences, Ag and Natural Resources, Engineering, Education, and Social Sciences). We also fund small grants (up to five \$2,000 awards per year for travel and research expenses) to promote site use by graduate students (MSU and other). This round, we will focus on funding researchers who will diversify the type of research conducted by KBS LTER (e.g., plant physiological ecologist), consider other drivers influencing our system, and build connections to other MSU research centers such as the Plant Resilience Institute. Current graduate students at KBS and on campus are excellent ambassadors for recruiting others to work at the site.

Use of the KBS LTER site is actively encouraged through our web site (<http://lter.kbs.msu.edu/>), which includes information on how to access data and develop research at the site. During 2017–

2022, we hosted 83 non-LTER research projects on site; these ranged from unfunded data exploration and synthesis projects to graduate student research awards to several >\$1M/y collaborations. Non-MSU researchers have led 25 of these projects. Funding agencies include USDA (NRI/AFRI, SARE, NRCS, and NCR Regional Projects), NSF (Ecology, Ecosystems, GRFP, IGI, DDBI, RTG, EHR, ICEB, Geobiology, CNH2 programs), DOE (Office of Science and EERE), state of Michigan agencies, and private foundations. Since 2008, MSU and UW-Madison have partnered in the DOE Great Lakes Bioenergy Research Center; a major focus of the Center's sustainability research is based at KBS and a new 5-year phase of the Center is being proposed. We also promote site use by providing tours to research teams and individuals, and overviews to science visitors; we host a field tour for prospective investigators every fall.

Site Access is assured by making the KBS LTER site a national research facility available to all scientists with a legitimate research interest in agricultural ecology. Access to the site is limited only as necessary to protect the integrity of existing experiments. We welcome additional experiments and sampling activities that: 1) are relevant to overall project goals of understanding ecological interactions in row-crop ecosystems, 2) are best answered in a stable long-term experimental setting such as that provided by the LTER site, and 3) meet the project's data-access expectations. We have set aside specific microplots in our MCSE to accommodate short-term manipulative experiments and sampling that cannot be done as part of our core sampling activities. We require all researchers working on site or who use samples from the site to provide written assurance that they will follow specific sampling, data access, and acknowledgement protocols. Requests to work on site are submitted annually via an LTER Site Use Request Form (SURF) that is reviewed and approved by the Project Manager and lead PI; the Executive Committee reviews requests when they involve a significant manipulation.

Diversity is promoted by welcoming the participation of scientists, educators, and students of diverse backgrounds in LTER research and education activities. We define diversity by race, nationality, ethnicity, age, gender, gender identity, sexual orientation, language, religion, disability, veteran status, geographic origins, first-generation college student, and socio-economic status. We have successfully partnered with the Station's NSF-funded REU site program to recruit underrepresented students to our REU positions. Since 2016, KBS LTER has hosted 69 undergraduates, of whom 38% were from historically underrepresented groups and 25% first-generation college students. Site scientists are required by MSU to participate in diversity, equity, and inclusion training offered by the University. Science Coordinator Baker is chairing the LTER Network's Diversity Working Group. Going into this next phase, we have teamed with KBS to hire a Diversity, Equity, and Inclusion Coordinator, a quarter of whose time will be dedicated to LTER activities. The DEI Coordinator will work to build relationships with the Saginaw-Chippewa Tribal College and with the Kalamazoo Promise (specifically, students in the program who are from historically underrepresented groups or are first generation college students). Taking advantage of our successes in diversifying KBS LTER at the undergrad/postbac level, we will devote attention in the coming cycle to diversity of graduate students, postdocs, staff, and faculty. Six faculty members of our EC are women, and one is black.

Network participation is a priority for KBS LTER. Haddad is a member of the Science Council, Lau served on the LTER Network 40-year review committee, Bohm serves on the Network IM Executive Committee and Network Information System Advisory Committee, Schultheis and Haas serve on the Education & Outreach Committee (that Haas chaired until recently), Baker serves as chair on the DEI Committee, and Julie Doll chaired the Communication Committee. KBS sent 36 scientists and educators to the Network All Scientists Meeting in 2018 (6 faculty, 11 graduate students, 8 postdocs, and 7 science staff). KBS scientists continue to participate in long-standing cross-site science initiatives, including recent cross-site special issues associated with the 40-year review, *Bioscience* and *Ecosphere* (co-led by KBS LTER coordinator Julie Doll).