Overview:

Resilience of ecological processes in the face of environmental change is paramount to maintaining the ecosystem services on which we depend. KBS LTER has quantified ecosystem functions and services provided by agricultural landscapes since 1988. Long-term experimental treatments have diverged in soil resources and biodiversity, and likely differ in the adaptive potential of important taxa, all of which may affect the resilience of both agricultural and unmanaged systems to disturbance. Growing-season drought is a case in point: our systems differ in resilience to drought, one of the most important disturbances in agricultural systems and expected to increase with climate change. At the landscape scale, expected changes in the relative cover and distribution of cropland, perennial biomass crops, and grasslands will affect the resilience of ecosystem functions to droughts and other disturbances. A mechanistic understanding of how ecosystem functions can be resilient to future changes in rainfall regimes and land use will advance our fundamental knowledge of ecosystems while providing information that farmers and land managers can translate into practice.

Proposed research draws on our long-term data to motivate hypotheses about the mechanisms contributing to resilience to drought, allowing us to ask: What mechanisms contribute to the resilience of key ecosystem functions and services in agricultural landscapes? We will combine our long-term experiments and observations with new experiments that simulate growing-season droughts. We will test the importance of three classes of hypothesized resilience mechanisms: resource availability (soil resources and social resources), diversity (including species richness and intraspecific genetic diversity), and adaptation (both biological and technological). Evolutionary responses will be explicitly considered. In managed ecosystems, these ecological and evolutionary mechanisms interact with social mechanisms to influence resilience. We will continue longitudinal farmer surveys to reveal how decision-making contributes to resilience.

Intellectual Merit:

KBS-LTER is uniquely positioned to build a mechanistic understanding of the resilience of agricultural ecosystems and landscapes in response to projected long-term changes in rainfall regimes and land use. This comprehensive examination of both ecological and social mechanisms underlying the resilience of ecosystem functions (e.g., primary productivity, greenhouse gas exchanges, nutrient export, pest suppression) is a novel and powerful aspect of our proposed research. By examining mechanisms of resilience in each major land use in our spatial domain--annual crops, perennial biomass crops, and successional and conservation lands--we lay the foundation for understanding how changing land use and climate will interact to affect ecosystem functions.

Broader Impacts:

KBS LTER strives to increase the understanding of the ecology of agricultural systems for the public, students, K-12 teachers, farmers, and policy-makers. To foster scientific literacy, we will 1) continue to connect K-12 teachers with LTER research through workshops and Data Nuggets (short datasets for teaching quantitative science skills); 2) reach museum and nature center educators through Informal Educators Field Days; and 3) collaborate with MSU's Knight Center for Environmental Journalism to create research highlights accessible to the general public. To engage a broad spectrum of stakeholders we will expand our successful Roundtable Discussion series by bringing together a diverse group of scientists, agencies, NGOs, civic and faith groups, farm organizations, farmer advisors, and farmers. This Resilient Ag Coalition (RAC) will create a vision for a more resilient, sustainable Midwest agriculture and serve as a sounding board for LTER scientific endeavors, policy initiatives, and educational and outreach efforts. We will host an RAC Roundtable Discussion each year (2019-2021), leading to a capstone symposium in 2022, our 35th anniversary.

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LTER: KBS – Mechanisms of resilience in agricultural landscapes

1.0 Project Overview and Results from Prior Support

1.1 Project Overview

Both natural and managed ecosystems face increasingly novel conditions driven by anthropogenic changes, especially those related to climate and land use. Ecosystems in some landscapes appear resilient to many changes, while others are severely affected (e.g., Walker et al. 2017, Lucash et al. 2017). Understanding the causes and consequences of resilience (defined in Box 1) is especially propitious in agricultural landscapes, where findings inform both basic ecological theory and the maintenance of ecosystem services on which we so fundamentally depend. Over the past three decades KBS LTER researchers have tested long-term hypotheses about productivity, soil carbon (C) balances, greenhouse gas (GHG) emissions, crop water use, nutrient transformations and transport, pest and natural enemy dynamics, and other ecosystem functions in well-replicated experiments. Our results motivate new hypotheses about 1) the *mechanisms* determining resilience of these ecosystem functions to climate variability and change, 2) how these mechanisms differ in annual crops, perennial crops, and conservation lands, and 3) how and why different mechanisms might influence the resilience of different ecosystem functions.

We seek to answer the overarching question: **What mechanisms contribute to the resilience of key ecosystem functions and services in agricultural landscapes?** Specifically, we aim to elucidate the mechanisms that mediate ecosystem responses to increased frequency and severity of growing-season drought events projected for the U.S. Midwest (Fig. 1). Our proposed research is organized around three major classes of mechanisms that we hypothesize most contribute to resilience in these landscapes (described in detail in Section 2.1): 1) resource availability, 2) biodiversity, and 3) adaptation. These mechanisms are not mutually exclusive, likely interact, and include both ecological and sociological factors (Fig. 2). We build on our long-term research quantifying ecosystem services in row-crop systems by expanding observations to cover a broader array of land uses (annual crops, harvested perennial grasslands, and unharvested conservation lands) and installing new long-term experiments to explore one of the most consequential environmental disturbances in our landscape—growing-season drought. And we pair our experiments with longitudinal surveys of farmer attitudes and behaviors to investigate socioeconomic mechanisms that contribute to resilience in agricultural landscapes.

Box 1. **Resilience** has been a central tenet of ecology since Holling (1973) defined it as the capacity of a system to maintain function in response to disturbance and has been characterized in a number of ways (e.g., Standish et al. 2014, <u>Mumby</u> et al. 2014, Hodgson et al. 2015, <u>Nimmo</u> et al. 2015). Resilience has gained prominence in natural resource management (e.g., Resilience Alliance 2018; <u>CGIAR</u> 2014). KBS LTER will generate basic knowledge needed to understand the resilience of ecosystem functions and services to climate variability and change. We use growing-season drought, one of the most important climatic stressors of agricultural ecosystems, as our model disturbance to test mechanisms of resilience, which we evaluate by the following metrics: (Fig. 1; Hodgson et al. 2015; <u>Angeler</u> & Allen 2016):

- 1. **Resistance**: the proportional change in function caused by a disturbance compared to the long-term mean
- 2. **Recovery**: proportional change in function from the long-term mean to the equilibrium postdisturbance. This includes the possibility of regime shift (Fig. 1d in <u>Scheffer</u> et al. 2001)
- 3. Duration: time to recovery (Pimm 1984)
- 4. **Temporal stability**: the inverse of the coefficient of variation, reflecting the general susceptibility of a system to temporal variation, e.g. to interannual variation in climate anomalies.

For some disturbances and ecosystem functions, resilience may not necessarily be an ecological or societal benefit (Zhang et al. 2007). For example, GHG emissions may decline during a drought event (Gelfand et al. 2016), and as a result, systems in which GHG emissions are more resilient (i.e., decline less in response to drought) may have higher total emissions than less resilient systems.

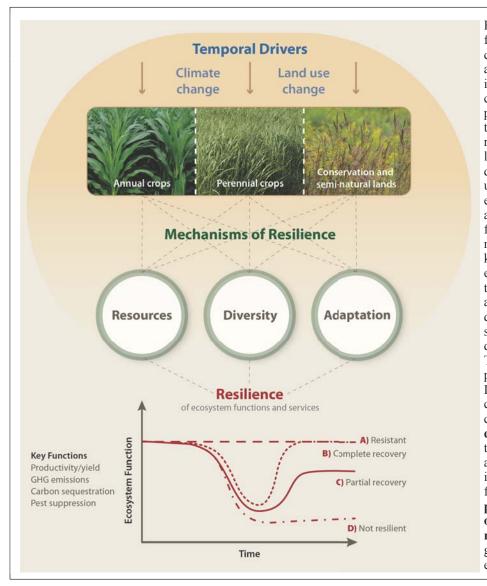


Fig. 1. KBS LTER will focus on mechanisms contributing to resilience along a land use complexity gradient of annual cropping systems to perennial cropping systems to conservation lands, representing the dominant land uses in our spatial domain. Climate and land use change strongly affect ecological processes in agricultural landscapes. We focus on 3 classes of mechanisms we believe are key to the resilience of ecosystem functions to these large-scale drivers and associated short-term disturbances (e.g., growingseason drought): resources, diversity, and adaptation. This framework incurporates the **5 core areas** of LTER research—climate change (e.g., drought) and changes in land use are disturbances that threaten the viability of **populations** and **biodiversity** and influence ecosystem functions, including primary production, organic matter and nutrient cycling. Bottom graph modified from Oliver et al. 2015.

1.2 Historical context

KBS LTER, the only LTER site focused on agricultural cropping systems, has grown into a complex transdisciplinary research program examining key ecological interactions and ecosystem functions in agricultural landscapes (Robertson & Hamilton 2015). At project inception in 1987, we focused on a limited number of ecological processes such as productivity, nutrient cycling, and species interactions in individual cropping systems and successional fields. In 1992 we added more unmanaged ecosystems to consider longer-term ecological succession from abandoned croplands to forests, and in 1998 expanded to landscapes with the addition of watershed biogeochemistry and hydrology (Hamilton 2015, Hamilton et al. 2015a Hamilton et al. 2018) and insect predator-prey dynamics (Landis & Gage 2015). In 2004 we added a socioeconomic component focusing on the valuation of ecosystem services (Swinton et al. 2015a), further expanded in 2010 with a socio-ecological model (Robertson & Hamilton 2015) to examine how alternative cropping systems provide different ecosystem services and how farmers make decisions to adopt practices to promote those services.

Historically, KBS LTER research has addressed the hypothesis that agronomic management based on ecological knowledge can better deliver ecosystem services, including yield, than can management based on synthetic chemicals. To this end, much of our research has been conducted in the context of our Main **Cropping System** Experiment (MCSE): replicated systems spanning a gradient of management intensities that include four annual cropping systems (cornsoybean-wheat rotations under Conventional. No-till. Reduced Input, and **Biologically Based** management), two perennial cropping systems (Alfalfa and Hybrid Poplar), and

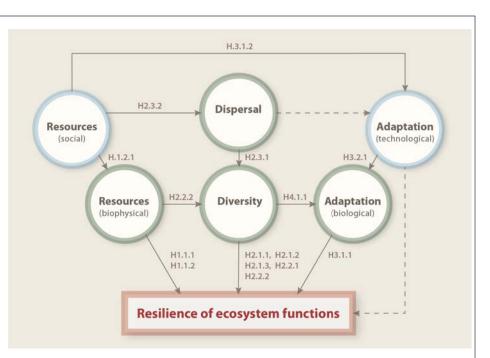


Fig. 2. Ecological and social mechanisms (green and blue circles, respectively) individually and interactively influence the resilience of ecosystem functions to disturbance in agricultural landscapes. We hypothesize that many mechanisms act directly on resilience: biophysical resources, diversity, and adaptation (both biological and technological). Other mechanisms may act indirectly to influence resilience: biophysical resources and dispersal will increase microbial and arthropod diversity; 2) genetic diversity will enhance the capacity for biological adaptation, and 3) technological adaptations like irrigation may inhibit biological adaptation by reducing selection for tolerance to disturbances such as growing-season drought. The labels along each arrow refer to the hypothesized paths that will not be addressed in the core proposed research; however, we will lay their foundation by initiating new collaborations and planning future waves of our CMSP survey (see Section 2.2).

an Early-Successional unmanaged plant community (See Section 2.2). The MCSE also includes unmanaged mid-successional fields, conifer plantations, and late successional deciduous forests. The power of this design lies in its long-term measurements of organisms and processes in communities along a management intensity gradient, complemented by short- and long-term experiments to test mechanistic hypotheses. Our experiments have manipulated climate stress (e.g., warming, snow removal, and precipitation variability), irrigation, nutrient availability, and biodiversity. At the landscape scale we sample surface waters within the broader watershed to address questions related to water quality, and we sample multiple terrestrial habitats to address questions related to the movement of crop pests and predators. Our socio-ecological analyses—informed by farmer focus groups, experimental auctions, and mail surveys—are conducted at regional scales.

1.3 Intellectual Merit of Prior Research

Since 2010 research based at or involving KBS LTER has involved 338 researchers (including 102 faculty, 51 postdocs, 108 graduate students, 77 undergraduate students, and 16 K-12 teachers) and resulted in 390 publications, 41 masters' and PhD theses, and collaborations with 88 separately funded projects.

4 0

next phase of our research. Specifically, our long-term data point to strong effects of interannual climate variability, and particularly water availability, on productivity, Yield (Mg ha⁻¹) GHG emissions, and other responses, and these effects differ among MCSE treatments. For example, soybean yields in No-till annual cropping systems are more resilient to growing-season drought than Conventional cropping systems (Fig. 3, Robertson et al. 2014); growing-season N₂O fluxes are sensitive to changing rainfall intervals in annual but not perennial cropping systems (Glanville & Robertson 2017); and the productivity of annual-dominated grassland communities has been more resilient in the face of interannual climatic variation than perennial-

A)

Key findings since 1988

volume (Hamilton et al.

2015b), available online

at the KBS LTER

measures of many ecosystem services and

website, and include

functions over three decades. MCSE

treatments have

intentionally, or

unintentionally.

resources, and other

to resilience, and

mechanisms contributing

motivate hypotheses to

be explicitly tested in the

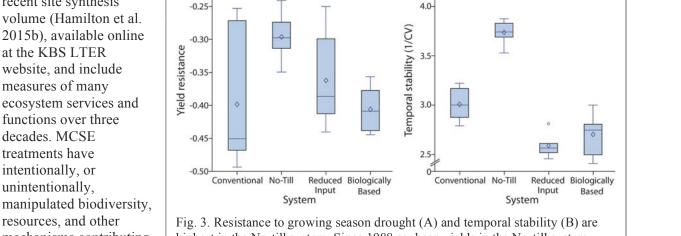
are summarized in our recent site synthesis

al. 2010). These and other findings based on long-term measurements illustrate that some treatments are more resilient than others for a variety of important ecosystem functions. In this proposal, we ask why, and in the following sections we describe prior findings

dominated early successional communities (Grman et

Key Drivers of Environmental Change: Climate and land use change are prominent drivers of environmental change in agricultural landscapes. For example, our short-term experiments have shown that warming influences decomposition, the phenology of invasive (but not native) plant taxa, and plant-microbe interactions (Lau, unpub. data), and that increasing

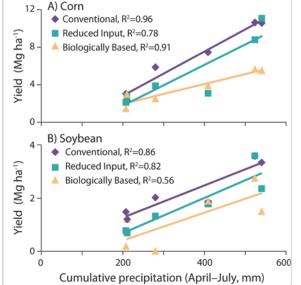
that motivate our proposed new directions.



B)

highest in the No-till system. Since 1988 soybean yields in the No-till system have been significantly less variable (and ~10-20% higher, see Fig. 6 below) than in other annual cropping systems, and the 2012 drought reduced soybean yields in the No-till system compared to the other treatments (Robertson et al. 2014).

Fig. 4. Cumulative growing season precipitation strongly predicts corn (A) and soybean (B) yields of Conventional, Reduced Input, and Biologically Based systems in 27 scale-up fields simulating MCSE treatments in commercial-size agricultural fields, further illustrating the potential negative consequences of drought in our system (Kravchenko et al. 2017). Notably, corn yields in the Biologically Based system are more resistant to drought than other systems; yields in the Biologically Based system are lower than other systems in wet years, but equivalent in dry years.



frequency of winter thaws can double wintertime N₂O fluxes from annual cropping systems (Ruan & Robertson 2017). An important future disturbance in our system is likely to be increasing precipitation variability, and in particular heavier rainfalls and more severe growing-season droughts (Pryor et al. 2013, Tomasek et al. 2017). Multi-week growing-season droughts affect both crop yields (Figs. 3A & 4) and the productivity and species composition of natural systems (Fig. 5). The timing and amount of precipitation are important to both nitrate leaching and N₂O emissions from KBS annual crops (Hess et al. 2016, Hess 2017, Glanville & Robertson 2017). Our proposed research builds on our many years of observations of the responses of our treatments to natural climatic variability by adding new rainfall manipulation experiments to test hypotheses about resilience mechanisms.

In the coming four years, we will also be laying the groundwork for an increased future focus on the resilience of ecosystem services to changes in land use. Land-use change is a major driver of environmental change in agricultural landscapes (Foley et al. 2005) and in our region is commonly accompanied by agricultural intensification including increased use of chemical inputs, genetically improved crops, and irrigation (Matson et al. 1997). Intensification leads to further simplified landscapes containing fewer crop types, less non-crop habitat, and reduced structural diversity (Tscharntke et al. 2005), biotic homogenization (Gaméz-Virués et al. 2015), and resultant reductions in ecosystem functions and services (Meehan et al. 2011, Raudsepp-Hearne et al. 2010). For example, we previously showed that aphid suppression in soybean and wheat fields is primarily related to landscape complexity (local diversity of crop and non-crop habitats) as it affects the immigration and abundance of coccinellid aphid predators (Gardiner et al. 2009, Woltz et al. 2012, Safarzoda et al. 2014). By manipulating coccinellid immigration rates in soybean fields, we determined that landscapes that support the early-season arrival of only 2-3 beetles m⁻² week⁻¹ are

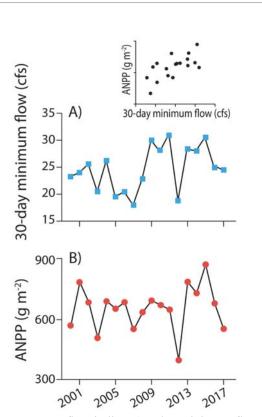


Fig. 5. Stream flow indices (30-day minimum flow rates) for nearby Augusta Creek provide an integrative indication of landscape water availability (A) that correlates well with agriculturally important droughts in our system. Productivity (ANPP) of the MCSE Early Successional treatment (B) also varies across years, with particularly large reductions in ANPP in years with severe growing-season droughts and resultant low stream flows (inset). Since 2000, when productivity and community composition stabilized in the Early Successional treatment, growingseason droughts most strongly reduced productivity in 2003, 2007, 2012 and 2017. These drought events were characterized by long-intervals without significant rainfall during the growing season and reduced productivity by ~40% in the Early Successional grassland. Note y-axis does not meet the origin.

sufficient to suppress aphid population growth (Woltz & Landis 2013). Motivated by the observed importance of landscape complexity for certain ecosystem functions (e.g., pest suppression), our proposed research includes establishing diverse perennial plant strips in selected treatments. Such strips have been shown to alter dispersal and community assembly, and increase the resilience of multiple ecosystem functions (Menalled et al. 1999, Lee et al. 2001, Garibaldi et al. 2014).

<u>Temporal Patterns of Focal Ecosystem Functions & Services:</u> KBS LTER has focused on the measurement of primary ecosystem functions including productivity, nutrient conservation, GHG mitigation, maintenance of high water quality, and pest suppression. Our long-term data on these

functions allow us to investigate resilience to seasonal and interannual variation in precipitation, including growing-season drought events that have varied widely in timing and severity.

Productivity has been the function measured in the vast majority of studies investigating resilience in terrestrial systems (e.g., diversity-stability relationships in grasslands: Tilman & Downing 1994), and crop productivity is central to the study of agricultural systems. Relative to the Conventional system, over a 24-year period the Notill system has provided an 8-15% yield benefit. The Reduced Input system, which receives 1/3 of the synthetic chemicals applied to the conventional system, has had equivalent yields to the Conventional system. The Biologically Based system has had equivalent soybean yield but lower corn yield (80% of Conventional) and much lower wheat vield (60%), largely owing to insufficient N acquisition (Fig. 6). The finding that long-term vields follow the pattern No-till > Conventional =

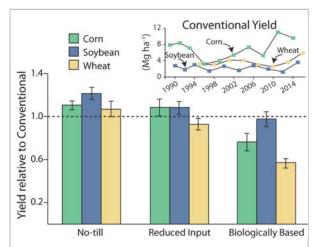


Fig. 6. Long-term yields (1989-2016) of three alternative management systems relative to the Conventional system (annual Conventional treatment yields are shown in inset). The Reduced Input system receives 1/3 of the chemicals applied to Conventional and No-till; Biologically Based receives no chemical inputs. Updated from Robertson et al. (2014).

Reduced Input > Biologically Based supports our original global hypothesis that ecological processes can help replace synthetic inputs (Robertson et al. 2014). In addition to differing in long-term mean productivity, these systems also differ in resilience to drought, including resistance to extreme growing-season drought and temporal stability in the face of interannual variation in precipitation and other factors (Fig. 3). A possible mechanism, which we propose to test, is related to differences in soil C (see below). Similarly, in the Early Successional system interannual variation in plant productivity is largely determined by growing-season precipitation (Fig. 5; Gross et al. 2015).

Greenhouse gas emissions and N leaching losses will be primary biogeochemical response variables for assessing mechanisms of resilience in our proposed research. We have shown how soil drying and rewetting enhance N transformations that lead to N_2O emission and nitrate leaching (Gelfand et al. 2015, Glanville & Robertson 2017, Hess et al. in review-a and b), but we cannot yet predict how this may change with future changes in rainfall regimes and drought events. Better understanding the mechanisms underpinning N cycling responses is imperative because globally agriculture is responsible for 8-14% of GHG emissions (IPCC 2014, Robertson 2014), and N_2O is the main GHG emitted from cropping systems.

Our long-term GHG measurements allow us to evaluate trade-offs between other ecosystem services and emissions, and generate hypotheses to be examined with our new experiments. Our GHG measurements allowed the first full-cost GHG accounting for intensive agriculture (Robertson et al. 2000), and have also led to more recent insights that could only result from sustained long-term measurements: 1) over time, cover crops can create soil C sinks equal to no-till management (Syswerda et al. 2011, Ladoni et al. 2016), likely from effects on plant-derived microbial metabolites rather than additional plant biomass (Kallenbach et al. 2015, Tiemann et al. 2015); 2) agricultural lime, added to soils to counteract acidity generated by accelerated nitrification, is a much weaker source of emitted CO₂ than originally thought (Hamilton et al. 2007, Gelfand & Robertson 2015), especially under irrigation (Hamilton & McGill 2017); 3) conversion of former croplands to cellulosic biofuels can provide substantial climate change mitigation by building soil C and minimizing N₂O losses (Gelfand et al. 2011, 2013; Robertson et al. 2017). The installation of conservation strips or conversion of low-yielding portions of fields to cellulosic biofuels (see Section 2.2) could have similar effects.

Pest suppression of aphids, which are globally important crop pests (Van Emden & Harrington 2017), by

key predators (Coccinellidae) constitutes an informative model system (Aquilino et al. 2005, Landis & Gage 2015). Our prior research has documented that aphid suppression can be resilient in the face of species invasions and shifting patterns of insecticide use. Since 1989, we documented the arrival of three new exotic coccinellids, associated with declines in abundance of native species via competitive interactions and habitat compression (Bahlai et al. 2015a). However, overall pest suppression by coccinellids has been resilient to these invasions (Bahlai et al. 2013). More recently, we have discovered changes in the abundance of the invasive multi-colored Asian ladybeetle (*Harmonia axyridis*) driven by a combination of new prey resources (invasive aphids) and shifting farmer practices, primarily adoption of neonicotinoid seed treatments (Bahlai et al. 2015b). Following the initial invasion of soybean aphids in 2000, *H. axyridis* populations increased dramatically, which led to an alternate year predator-prey cycle

(Fig. 7). The decline in *H. axyridis* abundance and a return to pre-2000 aphid population dynamics followed the widespread adoption of neonicotinoids in 2005 (Bahlai et al. 2015b). Collectively these results suggest that while predator communities shift in response to invasion and pesticide use, pest suppression has been remarkably resilient. Motivated by our longterm observations showing the effects of landscape composition on pest suppression (Woltz & Landis 2013), we propose new manipulations within our reduced input treatments to test effects of conservation strips on pest suppression services.

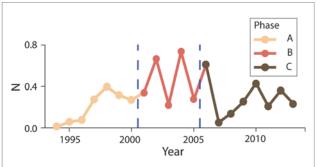
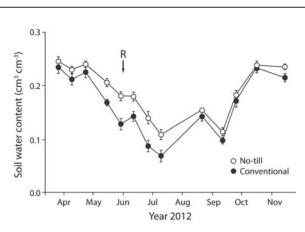


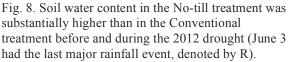
Fig. 7. Population density of *H. axyridis* from 1994-2012. Best-fit Ricker model defines 3 phases: presoybean aphid (1994-2000), peak soybean aphid (2001-5), and post-adoption of neonicotinoid insecticides (after 2005) (Bahlai et al. 2015b).

Mechanisms of Resilience

Resources. Our data indicate that soil C is likely a primary driver of resilience in our system, and variability in soil C across our MCSE treatments leads to testable predictions about when and how soil C influences resilience of yield and other ecosystem functions to drought. Soils in the No-till system contain \sim 20% more C (to 1 m depth) than do those in the Conventional system (Syswerda et al. 2011); by improving soil structure and stabilizing aggregates (Grandy & Robertson 2007), no-till management improves plant water-availability. In drier years this benefit becomes especially valuable: e.g., a severe Midwest drought in 2012 (6 weeks without summer rainfall) reduced Conventional yields in the MCSE

by 50% but No-till yields by only 25% (Robertson et al. 2014). Soil water content measurements show that there was more water stored in No-till soils at the drought's beginning, which appeared to mitigate the rainfall deficit (Fig. 8; Robertson et al. 2014). This pattern repeated almost exactly for corn in 2017 with another 5-week rainless period during midsummer. These long-term results point to a potential major mechanism (soil resources, and particularly soil C) explaining variability among treatments in resilience. Our new research will explicitly test the hypothesis that biophysical resources contribute to resilience of productivity to drought and will provide two fundamental advances: 1) we will compare the strength of resources as a mechanism promoting resilience across land uses and ecosystem functions, and 2) we will investigate how soil resources interact





with other mechanisms (in particular, microbial diversity and adaptation) to influence resilience to growing-season drought.

Diversity. Past biodiversity research at KBS LTER targeted three taxa of particular importance to ecosystem functions in agriculture: plants as they drive productivity, microorganisms as they decompose plant inputs, recycle nutrients, and mediate GHG exchanges, and arthropods as they suppress pests.

Plant diversity and composition: Through involvement in PDTNet, a cross-site LTER synthesis project, we have studied how grassland communities respond to predicted changes in climate, particularly precipitation (Cleland et al. 2013, Hallett et al. 2014), and how this relates to species composition and diversity. Results suggest that diversity promotes resilience (measured as temporal stability), but that the underlying mechanism (portfolio effects vs. negative species covariances) vary across a gradient of precipitation variability and mean annual precipitation (Hallet et al. 2014). The MCSE was not originally created with a plant diversity gradient, but we have one that was created via N fertilization (Dickson & Gross 2013), and we have added new experiments that manipulate plant species richness (see Conservation Lands Experiment, Section 2.2). Because other ecosystem functions have been or will be measured in these plots, this allows us to go beyond tests of the effects of plant functional diversity on resilience of productivity to examine responses of other ecosystem functions to drought.

Microbial diversity and composition: We have previously shown that richness of particular microbial taxa

(methanotrophs) was associated with increased methane consumption and increased resilience (measured as temporal stability) of methane consumption (Fig. 9: Levine et al. 2011, Schmidt & Waldron 2015). This finding underscores the apparent importance of microbial diversity for more specialized biogeochemical functions in soils, and suggests a role for microbial diversity as a modulator of resilience for ecosystem processes such as specific GHG fluxes in our landscape.

Microbial community composition also affects rates and stability of C turnover in our soils, leading to microbial communities that convert resources into biomass at different efficiencies (Roller & Schmidt 2015). Bacterial growth efficiency (the % of C consumed that becomes cell biomass) varies greatly among MCSE treatments, ranging from 23–63%. Some treatments such as our Conventional cropping system show strong seasonal variation (Lee & Schmidt 2014). Seasonal variation in bacterial growth efficiencies in cropping systems implies that climate change, specifically longer warm seasons and more extreme rain events, may accelerate soil C consumption because the composition of soil bacterial communities influences the relative amount of C that is sequestered in microbial biomass vs. respired to CO₂ (Roller & Schmidt 2015). Together these findings suggest new experiments that test how microbial diversity and composition can influence the resilience of methane and CO₂ emissions to summer drought

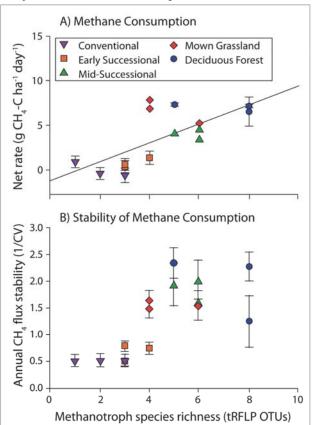
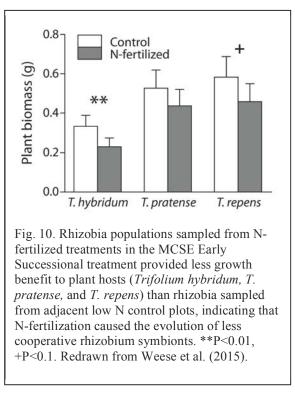


Fig. 9. Methanotroph (bacteria that oxidize methane) taxonomic richness was positively associated with both the net rate (A) and temporal stability (B) of methane consumption, suggesting that microbial diversity increases both the mean value and the temporal stability of this ecosystem function. Redrawn from Levine et al. (2011).

and interannual variation in other climatic factors.

Arthropod dispersal: Dispersal is known to influence species diversity in complex ways that depend on spatial context (Cadotte 2006). Our prior research focused on the invasive soybean aphid *Aphis glycines* and its top-down control by coccinellids (Costamagna & Landis 2011, Ragsdale et al. 2011). We have also shown that adding annual monoculture floral strips (buckwheat) to the margins of fields consistently increased coccinellid abundance (Gardiner et al. 2009, Woltz et al. 2012, Safarzoda et al. 2014). Collectively, these are among the few studies that have helped to define how dispersal affects biodiversity and ecosystem functions in agricultural landscapes (Tscharntke et al. 2012). Diverse perennial plant strips have been shown to alter dispersal and community assembly and increase the resilience of pest suppression functions for a wider range of taxa (Menalled et al. 1999, Lee et al. 2001). Motivated by these findings, we propose new manipulations of conservation strips to test the importance of landscape complexity on dispersal and pest suppression.

Adaptation. Although not explicitly designed for such purposes, LTER experiments provide unique opportunities for studying adaptation (Kuebbing et al. 2018) and for investigating the importance of adaptation to resilience in the face of long-term environmental change. For example at KBS LTER, 20+ years of nitrogen fertilization caused microevolutionary reductions in rhizobium quality (plant growth benefit; Fig. 10; Weese et al. 2015). Much weaker effects were observed in sovbean. likely because soybeans are not typically fertilized, and the fertilizer applied to preceding corn crops is largely consumed before the soybean phase of the rotation (Schmidt et al. 2017). Both horizontal gene transfer (Gordon et al. 2016) and selection at known symbiosis genes contribute to the observed reduced cooperation (Klinger et al. 2016). These evolutionary changes have ecological consequences, as the evolution of reduced cooperation alters soil N availability (Lau et al., in revision), illustrating the link between evolution and ecosystem functions and the potential for rapid adaptation of microbial populations to greatly increase (or decrease) resilience in our system.



Parallel to biological adaptation, in agricultural systems technological and management adaptation (e.g., irrigation, bioinoculants, cover crops, and complex crop rotations) can influence resilience. Our recent socioeconomic research on human decision-making has advanced understanding of farmer willingness to change agricultural practices to produce multiple ecosystem services. Many ecologically beneficial changes to cropping systems entail costs borne by farmers and benefits that extend beyond the farm. We have shown that Michigan citizens are willing to pay for reductions in GHG emissions and lake eutrophication at levels that would cover the average private costs of ecological cropping practices (Swinton et al. 2015a), and many corn and soybean farmers are willing to add cover crops to a cornsoybean rotation that would reduce GHG emissions and nutrient loss in exchange for an average payment of \$18-19 per acre (Ma 2011). Separate work on ecological pest management introduced a natural-enemy-adjusted economic threshold for pest control and economically optimal landscape configurations to advance pest control by natural enemies (Zhang et al. 2009, 2010). Our 2017 large-scale survey suggests that a better understanding of evolving farmer knowledge, attitudes, and technologies promises avenues for technological adaptation that are ecologically beneficial.

way for better understanding farmer decisions that influence resilience to climate and land use change.

1.4 Top 10 Papers Since 2012.

Box 2 shows recent papers selected for known (already highly cited according to Essential Science Indicators^{*}) or expected impact and to illustrate the diversity of KBS science and scientists. Associated data publications appear in the Table of Datasets (Section 8.5).

Box 2: Top 10 papers

Bahlai, CA, M Colunga-Garcia, SH Gage, DA Landis. 2013. Long term functional dynamics of an aphidophagous coccinellid community remain unchanged despite repeated invasions. *PLoS One* 8: e83407
*Gelfand, I, R Sahajpal, X Zhang, RC Izaurralde, KL Gross, GP Robertson. 2013. Sustainable bioenergy

production from marginal lands in the US Midwest. *Nature* 493:514-517

Hamilton, SK, MZ Hussain, AK Bhardwaj, B Basso, GP Robertson. 2015. Comparative water use by maize, perennial crops, restored prairie and poplar trees in the US Midwest. *Environmental Research Letters* 10:064015

Kravchenko, AN, SS Snapp, GP Robertson. 2017. Field-scale experiments reveal persistent yield gaps in lowinput and organic cropping systems. *Proceedings of the National Academy of Sciences USA* 114:926-931

Palm-Forster, LH, SM Swinton, RS Shupp. 2017. Farmer preferences for conservation incentives that promote voluntary phosphorus abatement in agricultural watersheds. *Journal of Soil & Water Conservation* 72:493-505

Robertson, GP, KL Gross, SK Hamilton, DA Landis, TM Schmidt, SS Snapp, SM Swinton. 2014. Farming for ecosystem services: an ecological approach to production agriculture. *BioScience* 64: 404-415

- Stuart, D, B Basso, S Marquart-Pyatt, AP Reimer, GP Robertson, J Zhao. 2015. The need for a coupled human and natural systems understanding of agricultural nitrogen loss. *BioScience* 65:571-578
- Tiemann, LK, AS Grandy, EE Atkinson, E Marin-Spiotta, MD McDaniel. 2015. Crop rotational diveristy enhances belowground communities and functions in an agroecosystem. *Ecology Letters* 18:761-771
- *Weese, DJ, KD Heath, BTM Dentinger, JA Lau. 2015. Long-term nitrogen addition causes the evolution of lesscooperative mutualists. *Evolution* 69:631-642

 *Werling, BP, TL Dickson, R Isaacs, H Gaines, C Gratton, KL Gross, H Liere, CM Malmstrom, TD Meehan, L Ruan, BA Robertson, GP Robertson, TM Schmidt, AC Schrotenboer, TK Teal, JK Wilson, DA Landis.
 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. Proceedings of the National Academy of Sciences USA 111:1652-1657

1.5 Results of Supplemental Support

Since 2010 we have received six supplements to our base award. In 2011 we received \$30,000 to enhance KBS participation in Network Information System (NIS) activities: programming support for data submissions and participation in sensor and spatial activities. We additionally received \$20,000 in ROA support to fund an investigator from UW-Oshkosh to conduct mycorrhizal research, and \$16,000 to support a high school intern (RAHSS) and teacher (RET). A \$25,000 equipment award helped to meet sample archiving plus information management (IM) and lab hardware needs. In 2012 a \$90,000 supplement included IM support for aerial imagery and database programming, and support for an ROA investigator and an RET teacher to study rapid evolution in plant-microbial interactions. In 2015 we received a major supplement (\$50,000) to replace a field truck and meet other field needs. Also in 2015 we received a major supplement (\$386,000) to expand our watershed hydrology efforts as part of the SEES: Food-Water-Energy Nexus program, bringing to KBS LTER expertise in landscape hydrology and new research on the long-term implications of rapidly expanding irrigation in the region using remote sensing and landscape-level modeling. In 2016 we received supplements to support two RET teachers and ROA support for an early career investigator to conduct work on evolutionary biology at the site.

1.6 Broader Impacts of Prior Research

KBS LTER research bears directly on agricultural management and policies from local (e.g., soil and water conservation) to global scales (e.g., IPCC assumptions about the relationship between fertilization and N₂O emissions: Hoben et al. 2011, Shcherbak et al. 2014). We disseminate our research broadly in national and international scientific venues, engage in opportunities to inform policymaking, and communicate our science to students, teachers, journalists, farmers, and the general public. To broaden our reach we have partnered with MSU's Knight Center for Environmental Journalism and the Society of Environmental Journalists to host two climate change communication workshops at KBS for journalists and scientists from around the Great Lakes (2012) and the US (2013), including scientists from other LTER sites. We also publish blogs written by student researchers, partner teachers, and research scientists on social media. Since 2010, over 5,800 individuals have toured KBS LTER research sites, aided by the establishment of two LTER walking trails at KBS, one for the public and the other (described below) for K-5 students. Since 2010, 108 graduate students and 43 REUs and other interns have conducted research at KBS LTER; as noted in Section 8.3, many have been members of underrepresented groups. Two of our REUs presented at the first World Congress on Undergraduate Research in Oatar in November 2016, and several have presented research at national scientific meetings (e.g., ESA, AGU, and the Society for Freshwater Science). Below we describe two of our impacts in more detail.

K-12 Educators. The KBS K-12 Partnership for Science Literacy, supported since 1996 with Schoolyard LTER (sLTER) funds, annually provides ~130 science teachers from 16 school districts around KBS indepth exposure to ecological science, including two full-day school-year workshops plus a 3-day summer science institute. The KBS K-12 Partnership has created an array of web-based resources, which we have compiled into a searchable database to make our research more accessible to educators. Since 2010 we offered (with mostly non-LTER funds) RET experiences to 16 K-12 Partnership teachers to participate in research on site. During this period, we leveraged sLTER funds for a cross-site NSF Math and Science Partnership (2008-2013, with LTER sites SBC, SGS, and BES) and GK-12 (2010-2015), DRK-12 (2010-2015), and STEM+C (2014-2019) awards led by LTER scientists and teacher educators. A highlight of the GK-12 award is the Data Nuggets project developed by GK-12 fellows with LTER and other data. Data Nuggets help K-12 and undergraduate students learn quantitative skills and promote evidence-based science discussions (Schultheis & Kjelvik 2015). The Data Nuggets mailing list reaches over 2,000 educators, and from January 2017-18, the website had 23,000 unique visitors. Data Nuggets have been used by teachers in 50 US states and 135 countries and have been featured in data workshops across the country. We have also partnered with elementary students and teachers to engage with KBS science via two projects: 1) Teaching Science Outdoors is a professional development program specifically for elementary teachers, offered in partnership with MSU's College of Teacher Education and funded by a US EPA Environmental Education grant. Since 2014, 68 elementary teachers from 19 urban and rural districts across Michigan have participated. 2) The Agriculture and Ecology Student Activity Trail had 1330 visitors (grades K-5) since 2014. In summer 2017, an RET-funded teacher updated the trail and aligned it with the recently adopted Michigan Science Standards. On the trail, students learn about topics such as the water cycle, seed germination, and beneficial insects in the context of where food comes from and how LTER research informs sustainable agricultural practices.

Agricultural Professionals and Industry. We have partnered with agricultural professionals and industry to develop a C credit protocol for agricultural N management to allow farmers to participate in voluntary C credit markets. This protocol, the first for N, compensates farmers for precise application of N fertilizer to reduce N₂O emissions (Millar et al. 2010, 2013). Development was supported by 7 electric utilities coordinated by the Electric Power Research Institute, and protocols are now registered with the American Carbon Registry and the Verified Carbon Standard and under development for California's Climate Action Reserve; in 2014 a Michigan farmer sold the first ever nitrogen C credits to The Climate Trust, who then retired them. We also developed climate change and agriculture programming for Extension educators in Michigan in partnership with MSU Extension, and in the upper Midwest in

partnership with USDA-SARE, EPA, and NOAA. Finally, we have initiated a series of <u>Roundtable</u> <u>Discussions</u> with agricultural professionals, bringing together scientists, farmers, Extension, agency staff, and private sector farm advisors to discuss topics including N management (June 2016; Reimer et al. 2017, Doll & Reimer 2017), adoption of sustainable agricultural practices (December 2017), and the use of bioinoculants (February 2018). These roundtable discussions are the foundation for making our future research more translational and informed by dialogue with stakeholders (see Section 2.6).

1.7 Response to Previous Reviewers

The previous review raised three main concerns regarding the future directions of our project: 1) our central question was too similar to past work and was considered to have "already been answered," 2) the conceptual framework was considered insufficient in detail and integration, and 3) the choice of structural equation modeling as a single integrated modeling approach was criticized. On the positive side, review scores were very high, and the panel praised the novelty and impact of our accomplishments to date and noted that our team was capable and strong.

We have revised our proposed research in several important ways in response to these concerns and subsequent discussions. We now make the resilience of ecosystem services to changing climate and land use a primary research focus, and have completely revised our conceptual framework to be more integrated, mechanistic, and testable with long-term data combined with new experiments. Specifically, we now focus on three classes of stabilizing mechanisms (resources, diversity, and adaptation). This mechanistic approach expands our research to new areas of ecology and evolution, and also provides opportunity for integration between the ecological/biophysical and social factors influencing resilience. We have bolstered the work on evolutionary ecology by co-PIs Jen Lau and Sarah Evans, and gained new expertise in landscape ecology and diversity-ecosystem function relationships with the addition of co-PI Nick Haddad. To address the modeling critique we now embrace a variety of modeling approaches, ranging from dynamic process-based crop simulation models to statistically based models suited to particular questions, and we are no longer exclusively focused on structural equation modeling. We have also engaged an external advisory committee who has provided feedback on these new directions; its members include Elena Bennett, John Blair, Lars Brudvig, Debra Peters, Douglas Jackson-Smith, Matt Liebman, and Katherine Suding.

2.0 Proposed Research

Our prior long-term research documented multiple ecosystem services that can be provided by agricultural landscapes (e.g., yield, GHG mitigation and C sequestration, clean water, and pest suppression), how management influences these services, and the tradeoffs entailed (Hamilton et al. 2015b). This rich knowledge base now allows us to investigate the mechanisms underlying the resilience of a diverse set of ecosystem functions to one of the most important global change factors in the US Midwest: climate change (specifically growing-season drought) coupled with expected changes in land use (Fig. 1). We use prior data to motivate hypotheses about when and how resilience mechanisms work across the spatial domain of the KBS LTER, specifically the three land use classes that will likely dominate future agricultural landscapes of the US Midwest: annual grain crops, perennial bioenergy crops, and conservation lands. We ask how and why different mechanisms influence the resilience of different ecosystem functions in each land use, and we seek to answer the overarching question: What mechanisms contribute to the resilience of key ecosystem functions and services in agricultural landscapes?

Classic theory and our prior results point to three major classes of mechanisms contributing to resilience in our landscapes, elaborated below: 1) resource availability, 2) diversity, and 3) adaptation. We are uniquely poised to understand the mechanisms that promote the resilience of ecosystem functions across diverse land uses because we have up to three decades of data on numerous ecosystem functions in treatments that have intentionally or unintentionally manipulated different resilience mechanisms. In this phase, we will test the resilience of major ecosystem functions to a major disturbance (growing-season drought) across annual crop, perennial crop, and conservation lands and will more explicitly investigate land use change by integrating a native perennial crop (switchgrass) and diverse native perennial conservation strips into the MCSE (see Section 2.2). Additionally, we pair our experiments with longitudinal surveys of farmer attitudes to better understand how social and ecological factors interact to affect ecosystem resilience, especially in annual cropping systems.

2.1 Theoretical Foundation for Resilience Mechanisms

Resource availability: The relative performance of cropping systems at a given location is strongly affected by biophysical attributes of soils (biophysical resources) in concert with the technologies, equipment, and information available to farmers (social resources). We expect that the resilience of cropping systems will likewise be strongly affected by local soil attributes and the availability of social resources. Soils with higher C content, for example, appear to allow ecosystem functions such as productivity to withstand environmental disturbances, or recover from them more rapidly (Robertson & Grandy 2006). Thus it is crucial to understand how soil C stocks will affect microbial taxa and activity and the resilience of GHG fluxes, nutrient cycling, and productivity in the face of environmental disturbances such as drought. That soil C sequestration is increasingly promoted as a negative C emissions strategy (Field & Mach 2017) adds motivation to understand the resilience of this resource itself (Paustian et al. 2016). Social resources can be equally important. Information and income can particularly influence farmers' abilities to adapt and innovate in response to new challenges including environmental change. We propose below new lines of KBS LTER research that simultaneously examine both the biophysical and social resources that, in concert with diversity and adaptation, are hypothesized to be key mechanisms that interact to determine cropping system resilience.

Diversity: Classic theory predicting that diversity should increase the resilience of communities and the functions they provide (MacArthur 1955) has engendered much research and debate (Woodwell & Smith 1969, May 1974, Pimm 1991, McCann 2000). As a result, diversity-stability relationships have been quantified in many experimental settings (e.g., Tilman & Downing 1994, Isbell et al. 2009, Hector et al. 2010, Haddad et al. 2011). Positive diversity-stability relationships are often observed and result from several processes, including species identity effects (increased likelihood of including a particularly stable dominant species), portfolio effects (the statistical averaging of large numbers of species that produces decreased variation in community properties), and compensatory dynamics (negative covariances among species abundances resulting from differential responses to environments or competition) (Tilman 1996, Huston 1999, Grman et al. 2010). Although many empirical studies have investigated the relationship between diversity (most commonly species richness) and the resilience (usually temporal stability) of primary productivity, advances are needed in understanding how diversity influences the resilience of other ecosystem functions, or the relevance of diversity to resilience in agronomic systems (cf. Davis et al. 2012, Tiemann et al. 2015, Isbell et al. 2017). Likewise, functional and genetic diversity may be as or more important to many ecosystem functions than species diversity per se (Tilman 2001, Hughes et al. 2008, Hersch-Green et al. 2011, Des Roches et al. 2018). For instance, functional diversity plays a greater role than species richness in determining the stability of productivity and control of agricultural pests (Tilman et al. 1997, McCann 2000), and intraspecific (genetic) diversity increases the resilience of seagrass productivity to abiotic stress (Evans et al. 2017). Our proposed research considers the role of species, genetic, and functional diversity in driving diversity-resilience relationships across land uses and ecosystem functions.

In agricultural landscapes, where annual crop fields receive frequent and intense disturbance, dispersal of organisms from stable habitats into crop fields is a primary mechanism maintaining diverse food webs and resilient ecosystem functions (Tscharntke et al. 2012, Winfree et al. 2018). However, mechanization and other technological advances have led to increasingly simplified cropping systems, with landscapes increasingly dominated by monocultures that reduce biodiversity and degrade ecosystem functions (Landis 2017). Targeted programs that compensate farmers to adopt conservation practices and to set aside conservation lands counter the negative impacts of landscape simplification, potentially increasing

the resilience of ecosystem services and farming income. Accordingly, we propose to test how such areas may influence dispersal as well as how to best incentivize such strategically conserved areas, thereby increasing diversity and potentially the resilience of ecosystem services in agricultural landscapes.

Adaptation: Adaptation, both through biological evolution by natural selection and through technological innovation, may buffer agronomic landscapes from environmental change. Rapid biological adaptation has the potential to stabilize ecosystem functions through two mechanisms. First, rapid adaptation can lead to evolutionary rescue, which occurs when a declining population adapts rapidly enough to return to positive population growth rates before reaching a so-called "extinction threshold" (Gomulkiewicz & Holt 1995, Gonzalez et al. 2013). For populations contributing key functions that cannot be provided by other species, evolutionary rescue may be the only mechanism to maintain those functions. Second, rapid evolution can lead to eco-evolutionary feedbacks, where the evolutionary changes in plant, animal, or microbe traits alter ecological adaptations increase resilience when farmers decide to change management practices or adopt new technologies to proactively respond to changing environmental conditions. Farmers can respond to drought, for instance, by changing crops, controlling water via irrigation or drainage, or selecting drought tolerant crop varieties (Hoeft et al. 2000). New technologies and products continually change the options available, offering farmers evolving tools for new challenges.

Both biological and technological adaptation may be more likely in certain situations (i.e., the strength of this mechanism, like other mechanisms, may be context dependent). Biological adaptation is most likely when populations are large, when the degree of maladaptation is low, and when populations have previously experienced low levels of similar stress (e.g., as occurs when the environment changes slowly) (Lynch & Lande 1993, Bell & Gonzalez 2009, Gomulkiewicz & Shaw 2013). Biological adaptation also may be constrained by the conflicting selection pressures that occur in complex communities (Wise & Rausher 2013, Strauss 2014). Thus the strength of adaptation as a stabilizing mechanism may be more likely in simple systems, where the populations contributing key functions are large and capable of evolving in response to stressors that have been experienced in the past (e.g., drought). In parallel fashion, technological adaptation is most likely when the challenges are broad enough to affect input and crop prices (Hayami & Ruttan 1985) and to influence farmer awareness and attitudes (Prokopy et al. 2008). We propose to simultaneously evaluate the potential for rapid biological adaptation of microbial populations and communities to growing-season drought and to explore farmer perceptions of changing climate and preferences for ecological versus technological adaptation strategies.

2.2 Major experiments and related research projects

KBS LTER is the only LTER site focused on understanding ecological processes in agricultural cropping systems and landscapes. To date we have focused primarily on row crops (mainly corn, soybean, and wheat) and perennial systems (successional fields, prairie, and poplar) to test hypotheses about the effects of agricultural management on ecosystem services, and the potential for ecological processes to replace synthetic inputs. *Here we expand our work in new directions by testing:* 1) the resilience (temporal stability) of ecosystem functions (productivity, nutrient conservation, GHG mitigation and C sequestration, and pest suppression) to interannual variation in climate in each of the three land uses that may dominate future agricultural landscapes (annual crops, perennial bioenergy crops, and conservation lands), and 2) the mechanisms hypothesized to contribute to resistance and recovery of ecosystem functions to simulated growing-season drought in a subset of our core treatments. Our research thus strives to identify the importance of these resilience mechanisms for different ecosystem functions across different land uses.

Our proposed research builds on our previous work quantifying selected ecosystem services in row-crop systems by expanding to include harvested perennial grasslands and unharvested conservation lands, extending our core sampling to include a wider diversity of taxa, and by simulating disturbance (growing-season drought) and manipulating underlying drivers of resilience to examine causal mechanisms. Below we describe the core experiments and observations that form the basis of our proposal, as well as

proposed modifications to existing treatments and additional experimental manipulations, surveys, and analyses that will allow us to disentangle and quantify the important mechanisms underpinning the resilience of agricultural systems and landscapes. While we will devote resources to these new initiatives, we will continue to maintain and sample key variables in all MCSE treatments. In the next three pages, we describe our four main long-term experiments and our new Rainfall Manipulation Experiment that will enable us to test mechanisms of resilience, and later we describe in detail the hypotheses, methods, and predictions for each mechanism.

Main Cropping System Experiment (MCSE): The MCSE (Fig. 11) is the core focus of KBS LTER, and treatments within this experiment will be used to address all proposed hypotheses. As noted earlier, the MCSE (established in 1988) includes treatments spanning a gradient of agricultural intensities that include four annual cropping systems (corn-soybean-wheat rotations under Conventional, No-till, Reduced Input, and Biologically Based/organic managements), two perennial cropping systems {Alfalfa (to become Switchgrass, see below) and Hybrid Poplar}, unmanaged Early Successional grasslands, and mid- and late-successional forests (Robertson & Hamilton 2015). This experiment thus represents a gradient of ecological complexity (along with gradients of disturbance frequency, resource subsidization, and perenniality), and we have monitored numerous ecosystem functions continuously since its establishment. In the next phase of KBS LTER research, we will work in a subset of treatments to induce growing-season drought while manipulating mechanisms of resilience (e.g., microbial diversity and soil resources; see Rainfall Manipulation Experiment below) and thereby empirically test the importance of different resilience mechanisms in representative land uses.

In addition to rainfall manipulations, we propose two changes to the MCSE that will help reveal how resilience mechanisms vary across land use types, and lay groundwork for studying dispersal, a potentially important driver of diversity in our system. First, we propose to replace Alfalfa, our current herbaceous perennial crop, with switchgrass (*Panicum virgatum*), a native C₄ perennial grass now planted for conservation purposes and a leading bioenergy crop candidate (Robertson et al. 2017). This will incorporate a perennial bioenergy crop into the MCSE, bringing all of our focal land use types into the experiment. Because legacy effects of alfalfa will affect

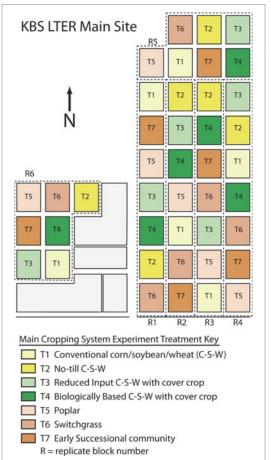


Fig. 11. Layout of the Main Cropping System Experiment (MCSE). Treatments include four annual cropping systems (corn-soybean-wheat rotations under Conventional, No-till, Reduced Input, and Biologically Based managements), two perennial cropping systems (Switchgrass and Poplar), an Early-Successional plant community, and mid- and late-successional ecosystems (not shown). All three focal land use types are reflected in the MCSE (annual crops, perennial bioenergy crops, and conservation lands), and these treatments are broadly representative of the spatial domain of the KBS LTER. Productivity, crop yield, GHG emissions, soil carbon, and predator abundance have been measured in each treatment since 1988, and new long-term experiments will manipulate growing-season drought, soil C, and microbial diversity in Conventional, Notill, Switchgrass, and Early Successional treatments to test how hypothesized resilience mechanisms (resources and diversity) influence ecosystem function responses to a major disturbance (drought). 1-ha plots are arranged in 6 blocks.

switchgrass yields, soil properties, and even microbial populations (e.g., Liang et al. 2011) for several years, for the coming grant period we will restrict use of the new Switchgrass treatment to withintreatment rather than crosstreatment comparisons (as described in H1.1.1 below).

Second, we propose to incorporate perennial grassland habitats (hereafter "conservation strips"), designed to enhance diversity, into our Reduced Input and **Biologically Based treatments** at the MCSE (see H2.3.1 below). Conservation strips are widely used to enhance ecosystem services in Europe (Batáry et al. 2015) and increasingly proposed for the US (Schulte et al. 2017). They will allow us to investigate whether perennial habitat within annual crops influences dispersal, community assembly, diversity, and, therefore, resilience of ecosystem functions in crops exposed to frequent disturbance. Specifically, we will install 4.6 m wide strips consisting of perennial grasses and forbs in the center of 1 ha plots, replacing approximately 5% of the existing crop area. Plant species chosen for inclusion will be those commonly included in restorations (Grman et al. 2013, 2015), represented in the **Conservation Lands** Experiment (see below), and most attractive to pollinators and natural enemies (Fiedler & Landis 2007a.b) and beneficial microorganisms (Bauer et al.

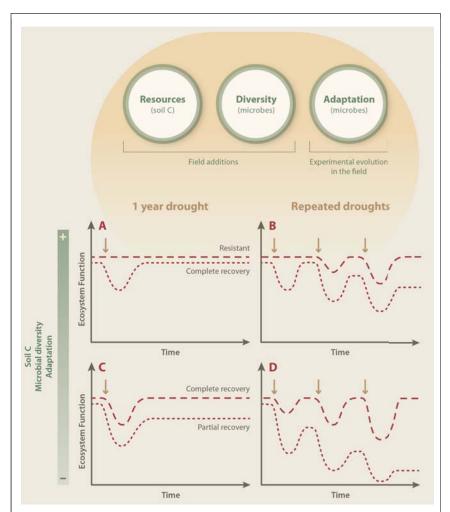
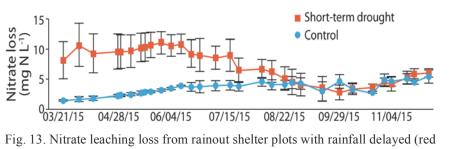


Fig. 12. The Rainfall Manipulation Experiment includes two drought treatments (Pulse and Press) and a control. The experiment will be installed in 4 MCSE treatments representing our three focal land uses: Conventional corn-soybean-wheat rotation, No-till corn-soybean-wheat rotation, Switchgrass, and Early Successional grassland. Hypothesized resilience mechanisms will be experimentally tested with field additions of resources (soil C) and microbial diversity (soil inocula) in subplots within each rainfall manipulation. The contributions of microbial adaptation to resilience will be tested by allowing microbial populations to evolve *in situ* within field treatments and comparing plots inoculated with soil microbial communities that evolved under drought to those inoculated with control communities. The power of this approach is that: 1) the factorial design allows for tests of direct and interactive effects of the major resilience mechanisms; we predict that ecosystem functions will be most resilient (measured as resistance and recovery) to drought in plots where soil C and microbial diversity have been added and microbial populations have evolved (panels A and B vs. C and D), and 2) the combination of single year and multi-year drought treatments allows for tests of legacy effects of drought; for example, resistance and recovery may decline with each successive drought event (panels B and D).

2012). Due to legacy effects, only within-treatment experiments are proposed (H2.3.1). We intend to

maintain both the Switchgrass treatment and the conservation strips indefinitely and to eventually implement conservation strips in fullsize fields at KBS to broaden the taxa affected and study effects of landscape context.

<u>Rainfall Manipulation</u> Experiment: Testing our



squares) was greater than from control plots with normal rainfall (blue circles) in the Conventional system, showing that the rainfall manipulation using rainout shelters strongly affected soil processes. From Hess (2017).

proposed resilience mechanisms and their context dependence requires imposing a disturbance within different land use types in combination with explicit manipulations of hypothesized mechanisms (see H1.1.1, H2.2.2, H3.1.1). We propose to install a Rainfall Manipulation Experiment in the MCSE that will induce growing-season droughts by altering rainfall timing. In subplots of these treatments, we will manipulate soil resources and microbial diversity (proposed resilience mechanisms), and perform additional follow-on experiments that will allow for tests of adaptation as a resilience mechanism (Fig. 12, see also Section 2.3). We will include three precipitation treatments: long-term mean growing-season precipitation applied at 3-4 day intervals (~ mean rainfall interval observed at our site), and two long-term growing-season drought manipulations (a press and a pulse). In both drought manipulations precipitation will be eliminated for 6 weeks during the growing season, simulating drought conditions of agronomic importance like those observed in 2012, and that are predicted to increase in frequency (Pryor et al. 2013, Tomasek et al. 2017). In the press drought treatment, precipitation will be withheld from the same plot repeatedly for 4 consecutive years; in the pulse treatment, precipitation will be withheld for a single year by moving the shelter to a different area within the full MCSE treatment plot each year, for a sequence of 3 years. Including the pulse experiment allows for tests of lag effects of drought. Our conceptual model illustrates resilience in response to a single disturbance event, but climate change is projected to make such events more frequent, and sequential drought years may yield different and unexpected responses (Fig. 12). Precipitation manipulations will be crossed with subplot treatments that manipulate hypothesized resilience factors (e.g., soil C and microbial diversity). This design allows for explicit tests of resilience mechanisms that are both experimentally imposed and/or naturally vary across MCSE treatments, and also allows for testing interactions among mechanisms.

We will model rainout shelter design after existing shelters erected in the MCSE in 2015 (Hess 2017). Three 8 x 8 m rainout shelters (each containing four 4 x 4 m subplots) will exclude all rainfall. Rainfall will then be reapplied to one shelter at 3-4 day intervals and to the other shelters after 6 weeks. The water applied will be collected from rainout shelters and supplemented as necessary with rainwater collected nearby. Beginning with the 2020 corn crop, rainfall manipulations will be applied to 4 replicates of Conventional, No-till, Switchgrass, and Early Succession MCSE treatments. All shelters will be installed in each plot's northern 10 m, reserved for such manipulations. In total, this experiment will include 16 blocks for a total of 48 rainout shelters deployed each year (n=4 MSCE treatments x 4 replicates). Similar rainout shelters in the MCSE (Hess 2017) demonstrate that our shelter design and scale are feasible and that 4 replicates are adequate for many response variables (Fig. 13).

Bioenergy Cropping System Experiment (BCSE): The BCSE expands our work to perennial croplands and also provides a broader plant diversity gradient for testing relationships between plant species and functional diversity and resilience. This experiment will be used to test hypothesis H2.1.3. Established in 2008, the BCSE includes 10 different bioenergy cropping systems ranging from monoculture corn to monoculture switchgrass to restored prairie. Now that measurements are available over a decade that included considerable interannual climate variability, we have the opportunity to test how resilience

(measured as temporal stability) varies across an even greater distribution of ecological complexity and diversity than that represented within the MCSE.

<u>Conservation Lands Experiment (CLE)</u>: The CLE expands our experimental work to grasslands on abandoned agricultural lands and examines processes underlying restoration. It will be used to test hypothesis H2.2.1. In 2015 we established a prairie restoration experiment in which we manipulated plant species and genetic diversity in 12 restored grasslands. We manipulated plant genetic diversity at the whole field scale by sowing each site with either one or three populations of each of 12 focal species commonly used in prairie restorations. Source populations originated from geographically distant locations (~1000 km apart) and differ in key traits (Zirbel, Lau, and Brudvig, *unpub. data*). Plant species diversity also is manipulated in a split plot design (12 vs. 75 species). With time, this experiment will provide the long-term data needed to assess resilience of restored prairie ecosystems, and specifically how both intraspecific diversity and species diversity influence the temporal stability of ecosystem functions (e.g., productivity) in the face of interannual variation in climate.

<u>Crop Management and Stewardship Practices (CMSP) Survey:</u> The CMSP will provide a long-term social dataset to complement our long-term ecological datasets and investigate the social factors influencing resilience (see hypotheses H1.2.1, H2.3.2, and H3.1.2). In 2016 we initiated a regional farmer survey of social factors affecting farmer decision-making in the face of environmental and technological change. The 2016 survey yielded ~3,000 valid responses from corn-soybean farmers in Michigan, Ohio, Indiana, and Illinois, providing a foundation for future surveys to monitor change in information and practice adoption, and incorporate modules to test specific hypotheses tied to changing environmental conditions and existing or planned ecological research (e.g., conservation strips). We will use focus groups and in-person interviews to engage with farmers about how resources, diversity, and adaptation factor into the long-term viability of their operations. We will follow this survey with repeated surveys of the same farmers in order to understand the long-term resilience of farm operations to environmental changes through management decisions affecting resources, diversity, and technological adaptation.

2.3 Major Focal Areas

Resource Availability (Robertson, Basso, Hamilton,

Marquart-Pyatt)--Resources provide foundational assets that may allow ecosystem functions and farm profitability to withstand or recover from environmental disturbances quickly. Biophysical resources at the landscape scale include habitat and genetic resources described in the Diversity Section that follows. We focus here on the soil resources that promote interactions among plants, invertebrates, and microbes to maximize ecosystem service delivery, often by alleviating plant stress (increasing primary productivity) or mitigating environmental harms (reducing GHG emissions). We propose to examine the resource-based mechanisms that give different land uses and systems different capacities to resist or recover from disturbances by combining observations from our long-term MCSE treatments (systems that vary in slowly changing soil attributes) with additional smaller-scale manipulations of a key soil resource, soil C. Because in many cases the potential for soil resources to increase resilience can only be realized via intentional management change, we will also ask questions about factors that lead to farmer adoption of technologies that improve soil resources and confer

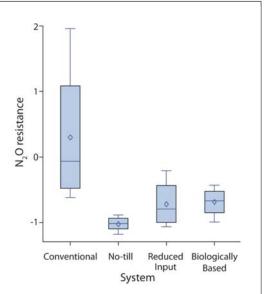


Fig.14. N₂O fluxes during the 2012 drought were most resilient (resistant) in the Conventional system. In this case, resilience is actually a disservice as the reduced resistance in No-till, Reduced Input, and Biologically Based systems arises because N₂O fluxes were reduced during the 2012 drought.

favorable resilience (see also *Adaptation* section). Our overarching question is **How might key soil** resource stocks be managed to contribute to the long-term resilience of ecosystem functions and services?

Q1.1 To what extent can soil attributes stabilize ecosystem function? Soil resources that help to confer favorable stability in managed ecosystems can be broadly characterized as soil sustainability traits. Perhaps the most important manageable resource conferring stability in agricultural systems is soil organic C, an LTER core area foundational to soil fertility (Allison 1973, Robertson & Grandy 2006). Soil C now differs among MCSE treatments (Syswerda et al. 2011), and stocks appear to have been reduced already by climate change (Senthilkumar et al. 2009). Soil C differences among MCSE treatments also appear to contribute to the resilience (temporal stability and resistance) of aboveground net primary productivity (ANPP): the No-till treatment with its higher soil C content is also the treatment with yields best buffered against growing-season drought and perhaps other stresses (Fig 3; Robertson et al. 2014). Soil C also provides microbial habitat, perhaps facilitating the persistence of a favorable microbiome or other taxa that confer plant drought tolerance (Marasco et al. 2012) or better maintain mineralization or other functions otherwise diminished by drought (e.g., Evans & Wallenstein 2012, 2014).

There is also evidence suggesting that the resilience of other ecosystem functions, such as denitrification (as indicated by long-term N₂O flux measurements) and leaching losses of nitrate (lysimeter measurements), differ among MCSE treatments. For example N₂O emissions, unlike yield, were most resilient in Conventional treatments when 2012 drought-year fluxes were compared to long-term means (Fig. 14). In this case, resilience is a disservice as it indicates little reduction in emissions during drought vears. Furthermore, higher nitrate leaching and N₂O emissions following drought appear buffered by treatments with higher soil C. In a two year experiment in which intervals between rainfalls (but not total amounts of rainfall) were increased by three weeks across the growing-season, Hess (2016, 2017) found substantially more nitrate leached from the rainfall-delayed treatment than from the control (normal rainfall interval) treatment, but only in the Conventional system (Fig. 13); in the No-till system the effect was reversed such that less nitrate leached from the rainfall-delayed treatment. Likewise, Glanville and Robertson (2017) found almost four times more cumulative N₂O emitted from a BCSE corn treatment with rainfall delayed four weeks than from a control treatment, but no effect of rainfall deprivation in a switchgrass system with a larger stock of active-fraction soil C (Sprunger et al. 2017). Although these associations point to a key role of soil C in resilience to drought, it is unclear how much of these effects are due to soil C per se vs. an associated indirect effect on soil structure, microbial community, or other soil attributes, motivating our proposed experiment that explicitly manipulates soil C.

H1.1.1. Soil C, in combination with related soil sustainability traits, will increase the resilience of ANPP and reduce nutrient exports and GHG emissions during growing-season drought.

We will install two long-term soil C addition experiments. First, we will measure the resilience of ANPP in the face of long-term interannual variation in climate (temporal stability) with and without augmented soil C stocks. Second, additional soil C manipulations in our Rainfall Manipulation Experiment will directly test the potential for soil C to increase the resistance or recovery of select functions (ANPP, N conservation, and GHG mitigation) to growing-season drought (Fig. 12). To increase soil C, we will annually add pyrogenic C (biochar) sufficient to increase stabilized soil C 50% over a decade. We will use pyrogenic C (produced from switchgrass biomass at a nearby site) rather than crop residue or litter to enhance soil C because litter additions can decrease as often as increase soil C (e.g., Lajtha 2013, Pisani et al. 2015), with decreases likely due to priming effects. Pyrogenic C additions contribute mainly to passive and slow soil C pools in soil (Wang et al. 2016), and thus represent the most certain way to increase long-term soil C stocks without adding additional nutrients or creating a significant N immobilization sink.

In addition to ANPP, we will monitor major N transformations (denitrification potentials, mineralization, and immobilization), N leaching, GHG (N₂O, CH₄, CO₂) exchanges, water availability, changes in soil physical structure (e.g., aggregate stability) and soil chemical attributes (e.g., soil C pools) in response to

soil C manipulations using methodologies well-established at KBS (Paul et al. 2015). Changes in soil microbial communities, with a specific focus on those taxa thought to confer drought tolerance (e.g., Calvo et al. 2014), will be assessed by methods described in H2.1.1 To provide a more robust picture of overall soil biotic responses, we will also test for potential changes in carabid beetle and ant communities by sampling in soil C addition plots as we do in main treatments (see H2.1.2). These microbial and arthropod surveys help to investigate connections between resilience mechanisms (*Resources* and *Diversity*) and also will provide a more mechanistic understanding of how soil C might increase resilience through both direct and indirect (e.g., provision of favorable microbial habitats) pathways (see Fig. 2).

H1.1.2. At landscape to regional scales, soil C increases resilience of yield, which is a primary predictor of regional nitrogen conservation including nitrate loss and N_2O emissions.

At field and larger scales, resilience is expressed spatially as well as temporally because different portions of landscapes would be expected to be differentially resilient based on the distribution of stabilizing soil resources. In a recent analysis (Basso et al., in review), we showed that temporal stability of yield at within-field scales is an excellent predictor of nitrogen conservation at large scales. Using high-resolution satellite imagery for 2010-2015, we assessed the temporal stability of corn and soybean yields on 10⁸ Midwest fields (representing 30 million ha) and found that ~50% of subfield areas can be characterized as stable high productivity areas, ~25% stable low productivity, and the remainder unstable (Fig. 15). N conservation varied concomitantly: inferred rates of N fertilizer loss, based on N fertilizer inputs less export in grain, ranged from 11 kg ha⁻¹ in the stable high productivity areas to 59 kg ha⁻¹ in stable low productivity areas to 24 kg ha⁻¹ in unstable areas where yields (and N fertilizer use efficiencies) were high some years and low in others. These losses translate to average N fertilizer efficiencies of 94% in stable high productivity areas, 67% in stable low productivity areas, and 87% in unstable areas.

We hypothesize that these differences are related to soil C stocks as affected by topographic position. Where soil C is highest we expect stable high productivity, and where soil C is lowest we expect stable low productivity. However, we predict an interaction with topographic position such that high soil C soils in depressions will be lower productivity in wetter years, while low soil C soils in top slope positions will be lower productivity in drier years. Thus the effects of soil C on resilience at the landscape scale are context dependent and a function of an interaction between soil C and topographic position.

We will test this hypothesis at two scales, farm and region. For the farm-scale test we will assess vield resilience (measured as temporal stability) across ~40 commercially-managed fields at KBS. Since 1996 grain crops have been harvested with yield monitoring combines that provide within-field measures of yield. By combining spatially explicit yields with known topographic positions (slopes calculated from digital elevation maps) and measured soil C contents, we can test at high resolution for a 22-year period the associations hypothesized above. We will also test this hypothesis for 10^8 subfield areas at the regional scale using existing databases of topographic position (calculated as for KBS fields), and yields inferred from satellite imagery. Soil C contents will be estimated with the SALUS model (Basso & Ritchie 2015), which contains the same multi-pool soil C algorithm as CENTURY and SOCRATES, which we used earlier to estimate historical versus contemporary soil C stocks for the US Midwest (Grace et al. 2006a, 2006b). We will also evaluate the impact of increased climate variability on spatial and temporal variation and resilience of crop yield across a broadly distributed set of of commercial fields by quantifying historically the effects of early season increased rainfall (pre-planting and emergence stages) followed by drought and vice versa. We will monitor changes in harvest index and vield across spatial scales, along with fluxes of water and nutrients through a combination of measurements in the field, analysis of remotely sensed imagery (visible, NIR, thermal and SAR), and process based modeling.

Q1.2 What influences farmer decisions to manage lands in ways that improve soil resource stocks?

Social resources - economic, technological and knowledge-based - can be as important as biophysical

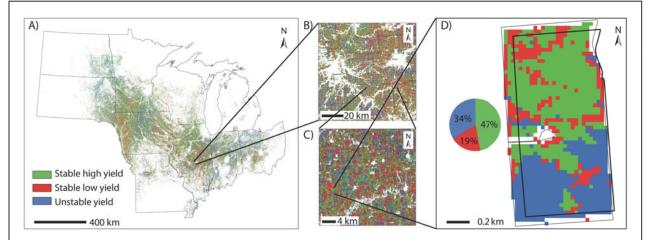


Fig. 15. Crop yield temporal stability maps for ten U.S. Midwest states (A) and subregions of 10,000 km² (B), 196 km² (C), and 118 ha (D). Colors represent yield stability zones for 0.1 ha portions of fields planted to corn or cornsoybean for at least three years during 2010-2015 (\sim 30 Mha total). We hypothesize that this spatial variation in temporal stability is driven by variation in soil C content (Basso et al., in review).

resources in determining the resilience of cropping systems. Separately and in combination, biophysical and social resources both enable and constrain farmer management decisions regarding tillage, crop rotation, and nutrient and pesticide use (Blesh & Drinkwater 2013, Stuart et al. 2015, King & Blesh 2018, Weber & McCann 2015). Farmers' decisions about tillage depend on farm and farmer characteristics, are influenced by previous management decisions, and respond to climate and weather variability (Baumgart-Getz et al. 2012, Mase & Prokopy 2014, Ulrich-Schad et al. 2017). For instance, although a farmer may have tillage as part of the typical management regime, the timing or number of events may vary due to precipitation extremes. Here we investigate how adoption of conservation management practices (e.g., no-till, cover crops) informs future farmer decisions, what primary information sources farmers use to improve their ecological knowledge, and their likelihood of embracing novel ecologically-based management practices to improve soil resources and, potentially, resilience of their farming operations.

H1.2.1. Use of conservation practices increases farmers' knowledge of soil resources and influences the information they access and their likelihood to adopt novel ecologically-based practices intended to further build soil resources.

When farmers witness the yield benefits of soil composition and soil C, they may increase adoption of ecologically informed practices, including reduced fertilizer application (Robertson et al. 2014), no-till and reduced or conservation tillage (Robertson & Vitousek 2009), and use of cover crops (Arbuckle & Roesch-McNally 2015). Although personal observation can be the source of knowledge of these benefits, farmers can also acquire information from other sources, some of which they interact with and trust more than others (Stuart et al. 2018; Houser et al. in review). We hypothesize that farmers using certain combinations of practices, like cover crops and no-till, are likely to be early adopters of ecologically-based management approaches, have improved ecological knowledge, and use diverse information sources. To test this, we will conduct interviews with farmers to determine their experience with and knowledge of biophysical resources and investigate how this knowledge shapes their decision-making. From these interviews, we will develop questions to be included on the CMSP survey to gauge how pervasive these knowledge and information gains are across watershed, landscape, and regional scales.

Diversity (Evans, Haddad, Landis, Lau, Swinton)— Despite the long history of biodiversity-ecosystem function and diversity-stability studies, when and how diversity is most likely to increase key ecosystem functions such as C and nutrient fluxes and their resilience is not well understood (Cardinale et al. 2012, Isbell et al. 2017). Our proposed research takes advantage of observational and manipulative experiments

in three land uses to better understand diversity as a mechanism promoting resilience by: 1) testing whether diversity-resilience relationships commonly observed in unmanaged grasslands are also prevalent in annual row crops or harvested perennial crops (i.e., testing the context-dependence of diversityresilience relationships), and 2) investigating how diversity-resilience relationships vary across ecosystem functions.

Our overarching question is **When does diversity, and management that promotes it, increase resilience to growing-season drought?** We address this question using a range of approaches: 1) analyzing long-term data across treatments that intentionally or unintentionally differ in their microbial, arthropod, and plant diversity and composition to examine resilience (temporal stability, resistance, and recovery) of productivity and GHG mitigation to natural climate variation, 2) using the new Rainfall Manipulation Experiment, to test how natural variation in plant and microbial diversity influences resistance and recovery of productivity and GHG emissions to drought, and 3) experimentally manipulating microbial diversity and drought to examine how microbial diversity alone (and in

combination with resource availability and adaptation) affects resistance and recovery to drought. Given that dispersal is a key driver of biodiversity, especially in heavily disturbed annual crops, we also test how conservation strips influence arthropod diversity and the resilience of ecosystem services provided by arthropods, and evaluate farmer willingness to install such habitats. Finally, recent findings suggest that consideration of multiple taxonomic groups is necessary to predict the multitude of ecosystem functions in a landscape (Mitchell et al. 2014) and that studies focusing on a single trophic level underestimate biodiversity effects (Lefcheck & Duffy 2015, Soliveres et al. 2016). Because we consider a wide variety of microorganisms, arthropods, and plants, we will obtain a more complete understanding of biodiversity effects on both function and resilience than most previous studies (Fig. 16).

Table 1. Bacterial and fungal isolates from KBS differ dramatically in drought tolerance, measured as the inverse of the proportional reduction in growth under drought-simulated conditions in the lab (Evans & Boot, *unpub. data*). Darker shading indicates higher drought tolerance.

Domain	Species	Drought tolerance	
Bacteria	Lysinibacillus xylanilyticus	0.00%	
Bacteria	Pseudomonas stutzeri	0.17%	
Bacteria	Lysinibacillus fusiformis	0.59%	
Bacteria	Stenotrophomonas sp.	3.25%	
Bacteria	Brevibacterium sp.	8.53%	
Bacteria	Bacillus mycoides	24.22%	
Bacteria	Bacillus megaterium	29.46%	
Bacteria	Bacillus stratosphericus	39.18%	
Fungi	Mortierella alpina	0.00%	
Fungi	Fusarium sp.	13.99%	
Fungi	Talaromyces sp.	25.63%	
Fungi	Trichoderma sp.	60.13%	
Fungi	Penicillium griseofulvum	69.70%	
Fungi	Penicillium brasilianum	78.95%	
Fungi	Mucor fragilis	98.28%	

Q2.1 How do taxonomic, functional, and intraspecific diversity affect resilience of ecosystem functions, and how do these effects vary across land use?

H2.1.1 Microbial diversity will be positively associated with resilience of functions carried out by specific groups (N_2O and CH_4 flux), but not more cosmopolitan processes (CO_2 flux).

Relationships between microbial diversity and the resilience of microbially-mediated functions are unresolved (Wertz et al. 2007). Most functions mediated by microorganisms are expected to be resilient to environmental perturbations due to high functional redundancy, including redundancy of dormant taxa acting as seed banks (Allison & Martiny 2008). For example, because many diverse taxa can metabolize soil C to produce CO₂, resilience of CO₂ flux might not be sensitive to microbial taxonomic diversity.

However, some functions are performed by a limited set of taxa (e.g., methanotrophic bacteria), limiting the chances for functional redundancy (Allison & Martiny 2008). Although there has been some evidence that this "broad vs. narrow" hypothesis (*sensu* Schimel et al. 2005) can predict whether a function is sensitive to changes in microbial diversity (e.g., Graham et al. 2016), tests are scarce because few studies quantify the resilience of multiple ecosystem processes as well as the groups that mediate them in a single study.

We will examine how microbial diversity affects ecosystem resilience in both an exploratory and targeted approach. In our exploratory approach, we will expand existing diversity sampling at MCSE plots to include microbial diversity (using 16S and ITS rRNA amplicon sequencing) and abundance (assessed by qPCR). These measurements will be used to test whether microbial diversity and composition influence the resilience of broad and narrow ecosystem functions to both natural (temporal stability, resistance, and recovery) and manipulated rainfall regimes (resistance, recovery, duration). As microbial response traits are not easily obtained from microbial taxonomies, we will monitor changes in species isolated from KBS with known drought sensitivities (Table 1; Evans & Boot, *unpub. data*). Data generated in this effort will serve as a baseline for a valuable long-term dataset on effects of cropping systems and climate variation on microbial composition. Additional experiments that manipulate microbial diversity (see H.2.2.2) will help determine whether any diversity-resilience relationships observed across MCSE treatments are driven by diversity per se, or other co-occurring resilience mechanisms, like soil C.

We will test the effects of microbial diversity on resilience by targeting denitrifiers, a subset of microorganisms whose genes directly mediate a specific and important ecosystem function, N_2O emission. At KBS, denitrification is the primary origin of N_2O (Ostrom et al. 2010) through nitric oxide (*nor*) and nitrite (*nir*) reductase genes. N_2O can also be consumed by nitrous oxide reductase (*nos*), producing radiatively-inert N_2 . For this reason, some studies have found that the ratio between *nir:nos*

(i.e., N₂O producer:consumer) is a good predictor of N₂O flux (Morales et al. 2010). Nir and nos genes can be highly diverse, and diversity can be impacted by cropping system (Stres et al. 2004), but how denitrifier diversity influences resilience to drought is unknown. We will complement measurements of N₂O flux (see Resources, H1.1.1) after rainfall rewetting in drought treatments with measurements of denitrifier diversity (*nir*, *nor*, and *nos* genes) and abundance using a high-throughput quantitative PCR system recently acquired by MSU's Genomics Core Facility. We will be able to examine short-term changes in diversity after a single extended drought to examine how changes in diversity affect N₂O pulses following drought. We will also examine long-term diversity changes, which may emerge after multiple years of drought.

H2.1.2 Arthropod species richness and functional trait diversity will be associated with increased efficacy and resilience of pest suppression.

Arthropods are important drivers of ecosystem processes in both natural and agroecosystems (Yang & Gratton 2014), contributing to a wide range of ecosystem services (Noriega et al. 2017). In previous research we focused on the role of

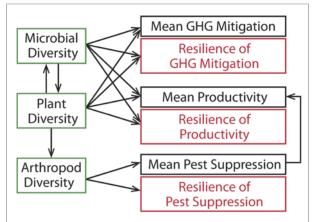


Fig. 16. Microbial, plant, and arthropod functional, taxonomic, and genetic diversity contribute to ecosystem functions, including productivity, GHG mitigation, and pest suppression, and also may contribute to the resilience of those functions. We will investigate associations between diversity and the resilience of ecosystem functions in annual crops, perennial crops, and conservation lands. Specifically, we will: 1) test how diversity-ecosystem function and diversity-resilience relationships vary across land use types, 2) test how diversity effects on resilience vary across ecosystem functions, and 3) determine which functions require consideration of multiple taxa to predict resilience.

coccinelid communities in suppressing insect pests. Here, we build on that long term data using traitbased approaches that can provide a more mechanistic understanding of how diversity influences resilience of pest suppression (Standish et al. 2014). In addition, because ants (Hymenoptera: Formicidae) and ground beetles (Coleoptera: Carabidae) have been studied in the MCSE and affect every trophic level and several ecosystem processes (Wills & Landis 2018), we will initiate long-term sampling of these taxa to assess their contributions to the resilience (temporal stability in the face of interannual climate variability) of pest suppression and impacts on soil resources.

A recent review suggests that pest suppression services in agriculture could be enhanced by better understanding multi-trophic (plant, herbivore, predator) trait interactions (Perovic et al. 2018). Previously we showed how a single trait (adult predator voracity) can be used to understand the impact of species invasions on the resilience of pest suppression (Bahlai et al. 2013). Here we extend that analysis using a multi-trait approach to test the effects of agricultural production practices and invasive species introductions on the functional diversity of predator communities and pest suppression services. We will enhance our long-term database of predatory Coccinellidae (currently 29 years, 74,235 records) by addition of functional traits including body size, activity period, diet breadth, reproductive capacity, voracity, floral resource use, and habitat preferences (overwintering and summer). We predict that treatments with lower management intensity (corresponding to higher plant diversity) will have higher trait diversity, resulting in increased pest suppression and higher resilience (temporal stability) of pest suppression (Fig. 16).

The intensity of agricultural practices influences arthropod diversity and their impact on ecosystem services (Lichtenberg et al. 2017). To investigate effects of the wider arthropod community on the resilience of ecosystem functions, we will sample ground-dwelling arthropods with pitfall traps in all MCSE treatment plots (Bestelmeyer et al. 2000). Carabid communities have been periodically sampled at the MSCE in the past, and they show clear responses to management intensity (Clark et al. 1997), which cascades to influence post-dispersal weed seed predation (Menalled et al. 2007). Ant abundance and diversity at KBS vary with crop identity and perenniality (Wills & Landis 2017). We will test the effects of carabids and ants on pest suppression by use of sentinel weed seed and pest insect egg card exposures (Werling et al. 2011, Meehan et al. 2012). Over time, we will examine relationships between soil arthropod diversity and resilience (temporal stability) of pest suppression and other core ecosystem functions (soil C sequestration, GHG emissions) in response to interannual climatic variation.

H2.1.3 Plant species and functional diversity increase resilience of productivity and reduce GHG emissions in response to drought

Like insects, plant species diversity and plant functional or trait diversity can stabilize ecosystem functions functions, such as productivity (e.g., Tilman et al. 2006). Less is known about other ecosystem functions and services provided by plant diversity in agronomic landscapes (Soliveres et al. 2016, Isbell et al. 2017). We have long-term plant community composition data from the MCSE Early Successional treatment and the BCSE perennial treatments, and we are accumulating community composition data from the new CLE. The MCSE and BCSE treatments include long-term N-addition treatments that have altered the diversity and composition of plant communities (Dickson & Gross 2013). These responses, with additional spatial variation across replicates, create a gradient of plant species richness and functional diversity. We will combine these community composition datasets with existing LTER network trait databases (e.g., Suding et al. 2005), recent trait databases of KBS prairie species (Zirbel, *unpub. data*), and long-term ecosystem function measures to test the hypothesis that plant species and trait diversity alter resilience (temporal stability, resistance, and recovery) of productivity, GHG mitigation, and pest suppression services.

Interactions among microbes, arthropods, and plants—The methods described for each of the above hypotheses result in diversity metrics (species richness and evenness, and often functional diversity) for each taxonomic group in MCSE treatment plots. We will test the combined and interactive effects of arthropod, microbial, and plant diversity on resilience of ecosystem functions (Fig. 16). Given that recent

studies find that a diversity of trophic levels are required to produce the multitude of ecosystem services provided by a landscape (Lefcheck & Duffy 2015, Soliveres et al. 2016), we would expect that multiple taxonomic groups (plants, microbes, and arthropods) also may be required to maintain the resilience of multiple ecosystem functions and services.

Q2.2 Can higher diversity created by restoration or management produce more resilient ecosystems?

H2.2.1 Restoring plant species and genetic diversity will increase resilience to drought.

Intraspecific diversity may affect population resilience (Abbott et al. 2017, Evans et al. 2017) and ecosystem function (Hughes et al. 2008; Hersch-Green et al. 2011, Forsman & Wennersten 2016), yet the relative strength of intraspecific diversity compared to interspecific diversity as a resilience mechanism remains unknown. The CLE prairie restoration includes manipulations of both species (number of prairie species sown) and genetic diversity (seeds originating from 1-3 populations per species) over large spatial and, eventually, long temporal scales. This provides a unique opportunity to assess the relative role of intraspecific and interspecific diversity as mechanisms promoting resilience. Beginning in 2019, we will quantify productivity and GHG emissions in the CLE, allowing us to build the long-term dataset necessary to examine the resilience (temporal stability, resistance, and recovery) of these functions to natural climate variability. Our findings will inform both basic and applied ecology. First, few studies have manipulated genetic diversity over large spatial scales and for multiple generations. As a result, because several key mechanisms underlying genetic diversity effects on ecosystem functions and the resilience of these functions may only be apparent over multiple generations and over large spatial scales, intraspecific diversity effects may be underestimated (Kettenring et al. 2014, Crutsinger 2016). Second, the "local is best" paradigm dominates restoration ecology. This hypothesis assumes that seeds obtained from local sources will be better adapted to site conditions and yield better restoration outcomes; however, such assumptions may be invalid under climate change (Havens et al. 2015). In a changing environment, a more genetically diverse seed mix, including both local and non-local seed sources, may increase the resilience of restored ecosystems to climatic variability and climate change.

H2.2.2 Bioinoculants (microbial diversity) will increase the resilience of agronomic yields to drought, especially when accompanied by enhanced soil resources.

Tests of microbial diversity-stability relationships are often confounded by changes in other ecosystem properties (e.g. soil chemistry) that result from a disturbance or stress (Allison & Martiny 2008), and these changes in ecosystem properties can enhance microbial function (Ezawa et al. 2002). Thus, it is unclear how much microbial diversity contributes to resilience, compared to factors like soil C, and how these factors interact with soil resources. In agronomic studies, microbial bioinocula (the additions of specific microbial taxa) have received increased attention (and industrial production) because they can enhance agricultural services (e.g., Ortas 2015). There is now a need for studies that examine the ecological determinants of inoculant establishment, or bioinoculants' ability to confer resilience under environmental stress. Using the Rainfall Manipulation Experiment, we will test whether and how microbial establishment and diversity affect resistance and recovery of plant productivity and other ecosystem functions to drought in annual crops, perennial crops, and unmanaged grasslands.

Specifically, in subplots within rainout shelters, we will independently manipulate soil C (see *Resources* Section above) and microbial diversity by inoculating plants with prairie soil liquid extracts. We will use prairie soil inocula collected from two 12 year old restored prairies so that we can standardize the inocula composition across land use type and maximize chances for increasing diversity. Microbial inoculation does not always result in communities similar to the inocula (but see Wubs et al. 2016), likely because environment is often a stronger determinant of microbial composition than dispersal limitation (Delgado-Baquerizo et al. 2018). However, many other studies have successfully manipulated microbial communities (e.g. Carbajo et al. 2011, Ortas 2015, Wubs et al. 2016), and we will draw from previous and planned preliminary studies that identify specific inoculation concentrations and environmental

conditions that enhance colonizer survival in these systems (e.g. inoculating on warm, wet, days; Steinke, *unpub. data*). An advantage of this design is that it will also allow us to study controls on microbial establishment across varied soil types and resident communities, informing future studies on microorganism dispersal that synergize with proposed research on insects (see H2.3.1). We expect that bioinocula will most strongly increase microbial diversity and composition in high soil C environments (either natural variation in soil C across treatments in the MCSE, or through the soil C treatment described above) and that resilience will be improved when bioinoculation successfully increases microbial diversity. As with other resilience mechanisms, we also acknowledge the possibility for inoculations to have negative effects on the resilience or absolute magnitude of ecosystem functions (cf Johnson et al. 1992; Box 1).

Q2.3 Does the presence of diverse perennial species in annual crops modify dispersal and, therefore, community composition and diversity, and increase resilience of ecosystem functions?

H2.3.1: Conservation strips create habitats that increase arthropod diversity of annual croplands and increase the resilience of ecosystem functions.

In landscapes dominated by annual crops, lack of perennial habitats limits dispersal of key organisms, reducing beneficial interactions and the resilience of ecosystem functions such as pollination and pest suppression (Rand et al. 2006, Kremen et al. 2007, Winfree et al. 2018). In one study in the Midwest US, establishment of perennial prairie strips comprising 10% of cropland provided disproportionate benefits, independently increasing species richness of birds and insects, and water quality (Liebman & Schulte 2015, Schulte et al. 2017). However, little is known about the mechanisms by which conservation lands alter dispersal and community assembly at local or landscape scales, and the extent these propagate to resilience of ecosystem functions. Conservation strips will be planted in the spring of 2019 into Reduced Input and Biologically-Based MCSE treatments (see Section 2.2) and will be fully established by 2021. We will create four sampling transects perpendicular to the strips to assess selected insect communities within and at increasing distances from the strips, and our long-term data will allow for pre-strip vs. poststrip comparisons of a variety of ecosystem functions. We focus on both "transient" arthropod taxa, species that may not permanently colonize conservation strips but rather use them as temporal or spatial stepping stones as they move through the landscape (e.g., aphid pests of field crops and their natural enemies, principally lady beetles and Hymenopteran parasitoids), and taxa that establish persistent populations, from which individuals can move into adjacent crops (carabids, ants, and in future work microbes).

In the MCSE, both Reduced Input and Biologically-Based treatments contain winter cover crops that are tilled into the soil in early spring prior to planting the main crop. This is a major annual disturbance creating temporally unfavorable conditions for many taxa in the main crop area. We predict that following this initial disturbance, more transient taxa such as mobile predators and parasitoids will preferentially move to conservation strips that can harbor aphid prey and provide pollen (Woltz et al. 2012, Woltz and Landis 2013), a protein resource used by some aphid natural enemies. We will assess the degree of pest suppression provided by natural enemies by placing potted sentinel plants (crop plant infested with relevant aphids) in the crop area at varying distances from strips. One plant per location will be caged to prevent predators and parasitoids from accessing aphids, providing data needed to calculate an index of pest suppression (see Gardiner et al. 2009). Similarly, pest suppression functions provided by ants and carabids, including herbivore suppression and weed seed removal, will be assessed by use of sentinel prev (egg cards, tethered herbivores, and seed trays) paired with appropriate controls at increasing distances from the conservation strips (Werling et al. 2011, Meehan et al. 2012). By tracking these indices over multiple years, we can determine the temporal stability (and potentially resistance and recovery in response to natural growing season-drought events) of this ecosystem function over time, and how conservation strips have altered the resilience of pest suppression.

H2.3.2 Farmers of cropland with below-average agronomic yields will be open to adding conservation strips for less than proportional monetary compensation.

Farm income resilience hinges upon crop yield stability as well as cropped land area and management costs. Many farmers require little or no compensation to adopt environmental stewardship practices that are either low-cost or else privately beneficial (Baumgart-Getz et al. 2012, Swinton et al. 2015b). However, conservation strips fall in the category of land retirement practices that have high direct or opportunity costs coupled with indirect benefits that may take years to be fully realized. Such practices tend not to be adopted without compensating lost income (Rollins et al. 2018). However, farmers who value environmental stewardship are often willing to adopt stewardship practices for less than the financial cost of providing them (Ma et al. 2012, Palm-Forster et al. 2017).

Using a contingent valuation-based choice experiment in the CMSP mail survey, we propose to investigate the factors contributing to farmer willingness to install and maintain conservation strips on corn-soybean cropland. We will present respondents with hypothetical contracts for conservation strip installation and maintenance at a specified payment offer that they may accept or reject. A binary probit analysis on contract acceptance will draw on a set of individual and factor variables describing farmer objectives, resources, attitudes, knowledge, and market conditions. We predict that probability of acceptance will increase with compensation offered, perceived beneficial ecosystem services, and environmental stewardship values, while acceptance will decrease with expected agronomic yield loss, perceived costs, and perceived ecosystem disservices (e.g., weed and pest diffusion). Building on results from the MCSE conservation strips experiment, we anticipate a future, follow-up choice experiment in 2021 or 2022 that incorporates ecological research findings that may affect farmer adoption decisions.

<u>Adaptation (Lau, Evans, Marquart-Pyatt, Swinton)</u>—The potential for adaptation (through both natural selection and technological innovation) to be a viable mechanism of resilience depends on whether adaptation: 1) is rapid enough, and 2) influences ecosystem function. We aim to identify when biological and technological adaptation to growing-season drought are likely to occur and to quantify the effects of observed adaptation on ecological functions. We predict that biological and technological adaptation adaptations. We predict that biological and technological adaptation will increase the resilience of different ecosystem functions (e.g., GHG mitigation, yield) and

will vary in importance across land uses (e.g., highly managed annual crops vs. restored grasslands).

Long-standing quantitative genetic theory predicts that rapid adaptation (adaptive evolution occurring on ecological timescales) is most likely in large populations with short generation times and ample genetic variation, in response to relatively slow environmental change (Lynch & Lande 1993, Bell & Gonzalez 2009, Gomulkiewicz & Shaw 2013). Recent theory predicts that ecological community complexity might slow adaptation because of increased ecological constraints that occur when a trait simultaneously influences interactions with multiple community members (Strauss 2014). Although some of these hypotheses have been tested in lab systems, we still do not fully understand how and when adaptation may occur rapidly enough to stabilize ecosystem functions in nature. Moreover, rapid biological adaptation rarely has been linked to the resilience of ecosystem services, but such linkages are likely through both evolutionary rescue and eco-evolutionary feedbacks (see Section 2.1).

Like biological adaptation, technological adaptation is also more likely under some scenarios than others. Humans face many individual and institutional constraints

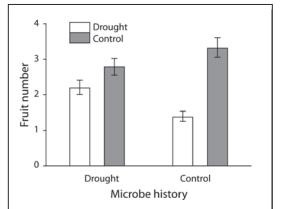


Fig. 17. In a greenhouse experiment with soil from an early successional plant community, multi-generation soil moisture treatments resulted in changes to microbial communities that protected *Brassica rapa* plants from the negative fitness effects of drought. Drought reduced plant fitness by ~60% when plants were grown in association with microbes from control conditions, but only reduced plant fitness by 20% when plants were grown in association with microbes that had adapted to drought (from Lau & Lennon 2012).

when making decisions about technological adoption. How they do so in the face of changing ecological or environmental contexts is less well understood. People adopt new technologies in response to new opportunities and to socioeconomic and environmental change (Lenski 1966, Boserup 1990, Crenshaw et al. 2000). The production technologies that farmers choose to adopt are based on their objectives, awareness, attitudes, business resources, and incentives (prices and policies) (Swinton et al. 2015b). Changing precipitation patterns could reduce a farm's profitability; farmers' interest in adopting stabilizing technology will depend on the degree of income risk they perceive and the availability of non-technologies, implementing that choice will depend on the ability to overcome constraints on resources such as knowledge, capital, and labor (Nowak 1992, Baumgart-Getz et al. 2012, Swinton et al. 2015b). These studies have shown that new technologies that are inexpensive and require little change in the farming system (e.g., genetically improved seed, bioinoculants) are much more readily adopted than technologies that require significant investment or change in the farming system (e.g., installing irrigation or setting aside cropland for conservation).

Q3.1: When are adaptive evolutionary and technological responses likely, and how do they increase resilience?

H3.1.1 Rapid microbial adaptation will commonly increase resilience in annual cropping systems.

Using experimental evolution approaches in the greenhouse, our previous research showed that rapid changes to microbial communities in response to drought strongly reduced the negative effects of drought stress for plants (Fig. 17; Lau & Lennon 2012). The responses of diverse soil microbial communities may occur through shifts in community composition or the evolution of key species; we refer to both as "adaptation." If similar patterns are observed in the field, changes in microbial community composition or the evolution of specific microbial taxa may increase the resistance and recovery of productivity, GHG emissions, and nutrient fluxes to drought.

In our proposed research, we take experimental evolution approaches from the lab (e.g., Gonzalez & Bell 2013. Lenski 2017) into the field. We use our Rainfall Manipulation Experiment to allow whole soil microbial communities and key species that can be readily cultured in the lab (rhizobia) to evolve *in situ* for one or three growing seasons in the pulse and press rainfall treatments respectively, plus the controls. We focus on rhizobia because they can be easily cultured, are responsible for key ecosystem functions (N-fixation), and mediate plant responses to drought in other habitats (Suwa 2016). To test the effects of microbial adaptation on ecosystem function, we will conduct reciprocal transplant experiments where microbes (diverse microbial communities or isolated rhizobium strains) from each treatment are inoculated back into the same or different field Rainfall Manipulation Experiment treatments. Because resident field microbial populations could dilute the effects of the evolved microbial communities, parallel experiments will be conducted in the greenhouse using mesocosms to simulate plant populations/communities and rainfall treatments. During the transplant phase, we will measure ecosystem functions including productivity, GHG emissions, and soil N. If microbial adaptation confers resilience, ecosystem functions should change less in response to drought (resistance) or recover more completely once drought ceases (recovery) in plots inoculated with microbial populations/communities that have evolved under drought conditions. Our approach allows us to test predictions that adaptation, and the resilience conferred by adaptation, will be most likely in agronomic row crop systems (Conventional and No-till) where microbial population densities and diversity are higher and where association with less complex plant and arthropod communities may result in fewer ecological constraints. Furthermore, we hypothesize that adaptation will be more rapid and, therefore, will have greater effects on resilience in subplots where microbial diversity has been increased with inoculation and soil C additions.

H.3.1.2: Farmers who perceive a need to adapt to changing precipitation regimes will seek to increase the resilience of their income to drought either by adopting suitable technologies and ecological stewardship practices or by changing crops.

Climate change will affect crop yields and other ecosystem services. For farmers to choose to adapt first requires that they perceive a need to do so. Farmers are especially sensitive to income risk, which is affected by crop yield and price (Hardaker et al. 2004). Through focus groups and in-person interviews, we will measure how farmers perceive the links between changes in precipitation and expected changes in crop yield and net income. We hypothesize that the perception of changing precipitation regimes and their impacts on individual farm operations will depend on recent personal experience with crop yields, trusted information sources (including detailed yield maps), local biophysical conditions, personal attitude toward risk, and other conditioning factors, such as education, knowledge, and experience in farming. Building on standard behavioral models of agricultural technology adoption as a function of farmer objectives, resources, knowledge, and attitudes (Baumgart-Getz et al. 2012, Swinton et al. 2015b), we will investigate what shapes farmers' decisions to adapt. We hypothesize that recent drought will influence the likelihood of farmers to install water management technology (controlling for capital constraints), and that successive years of drought will intensify this effect on adoption likelihood in a nonlinear fashion. Given heterogeneity of farming conditions, we expect that the type of water management technology adopted will depend upon soil and landscape conditions. We further hypothesize that capital constraints will affect the adoption of water management technologies that entail land improvement. Hence, capital availability would be expected to influence costly investment decisions in irrigation, whereas the opposite would be true of relatively inexpensive adaptive technologies like purchasing bio-inoculated seed.

We will also examine how better resource knowledge (See H1.2.1) and more detailed information, separately and in combination, lead to farmers' novel adaptations including new combinations of practices and altered timing of existing practices. Concurrent adoption of multiple practices may be important for the resilience of agroecological systems (Denny et al. in review). This, in turn, is determined by social capital accumulation, knowledge, and information.

Q3.2 How does technological adaptation influence the potential for biological adaptation to increase long-term resilience?

We propose to investigate how technological and biological adaptation interact. They do not act independently, and how these two forms of adaptation combine to influence resilience of yields and other ecosystem functions over both short and longer time-scales is unknown. Technological change could reduce the adaptive potential of biological systems. For example, if farmers respond to increased frequency of drought with increased use of irrigation, increased soil moisture may result in microbial communities that are much less resilient to even mild drought stress. In other cases, however, new technological or biological adaptation alone. For example, farmers are increasing use of bioinoculants, believed to increase yields. Increasing microbial diversity through bioinoculants may facilitate biological adaptation by increasing genetic variation. In short, adoption of new technologies likely influences biological evolution and reciprocally, rapid biological adaptation may reduce the need for technological adaptation (or increase it in the case of the evolution of pesticide resistance).

H3.2.1 Irrigation will disrupt the potential for biological adaptation to provide drought resilience.

Changes in water law (Lautenberger & Norris 2016), combined with high crop farm revenues during 2008-13 and a severe drought in 2012, led to increased investment in irrigation infrastructure in southwestern Michigan. Given that microbes likely respond similarly regardless of whether soil moisture is influenced by natural precipitation or irrigation, increased irrigation will probably change microbial communities, potentially in ways that reduce resilience of yields to future droughts. Thus, increased technological adaptation may reduce the effectiveness of biological adaptation (see H3.1.1) and make row crop systems more dependent on technological adaptation. We will test this hypothesis by combining a field irrigation experiment installed in 2005 with greenhouse experiments and small-scale field

manipulations. The irrigation treatment provides enough water to meet plant growth needs as estimated from a crop growth model and is applied to large (4.6m x 27.4m plots) receiving 9 different rates of fertilizer (N=4 blocks of irrigated plots + 4 blocks of non-irrigated control plots). We will collect soil samples from irrigated and non-irrigated plots and use those soils to inoculate potted soybean plants in the greenhouse and in adjacent field plots. Based on previous research on a model system (Lau & Lennon 2012), we hypothesize that microbes from non-irrigated fields will buffer yields from the negative effects of drought more so than microbes from irrigated fields (i.e., increased resistance). Simultaneously, we will use the long term CMSP survey 1) to assess farmer awareness of the potential of microbial communities to buffer crop yields, and 2) to assess farmer willingness and ability to rely on natural microbial selection over water management technologies, like irrigation and drainage.

2.4 Data Analyses & Modeling

We will use multiple analytical techniques for our ecological, social, and social-ecological models. Tests of individual ecological hypotheses will commonly use generalized linear mixed models (GLMM), where the temporal stability, resistance, or recovery of the measured ecosystem function is the response variable, and cropping treatment (MCSE, BCSE, or CLE treatment) is included as a categorical predictor variable, often along with other treatments (e.g., soil C or microbial diversity treatments) or continuous (e.g., plot level soil C or species richness) predictor variables. Plot will be included as a random factor. Given possible autocorrelation in our stability metrics, we will use first-order autoregressive models (Crawley 2007) and detrend (Tilman et al. 2006) as appropriate. We will employ GLMM and hierarchical statistical models (Cressie et al. 2009) to test for some of the potential interactions among resilience mechanisms, particularly those manipulated in the Rainfall Manipulation Experiment (soil resources, microbial diversity, and biological adaptation), and to estimate effect sizes to compare the relative strengths of different resilience mechanisms across different functions (response variables) or land uses.

Social hypothesis tests will be evaluated based on CMSP survey data with analytical techniques including categorical regression (Wooldridge 2010, Long & Freese 2014), multilevel/hierarchical regression (Gelman & Hill 2007, Snijders & Bosker 2012), and structural equation modeling with latent variables (SEM) (Bollen 1989, Hoyle 2012). For models where the outcome variable is the choice of agricultural practice(s) (e.g., irrigation, bioinoculated seed, or conservation strips), explanatory variables will include farmer characteristics, attitudes, perceptions, knowledge, and information; farm resources; relevant prices; and any experimental treatment variables (e.g., conservation strip contract specifications). For models with multiple outcome variables and with latent (unobserved) variables, we will use MSEM, a multi-equation regression technique accommodating complex relations between multiple exogenous and endogenous variables

Our integrated model (Fig. 2) allows us to empirically assess interactions and feedbacks between the ecological and social resilience mechanisms using multilevel and longitudinal structural equation modeling (Curran 2003, Pearl 2009, 2014, Bollen & Pearl 2013, Preacher et al. 2010, Rabe-Hesketh & Skrondal 2012). MSEMs and latent growth curve (LGC) models are increasingly employed in multidisciplinary research projects to provide statistical and visual expressions of complex hypotheses that cross scales and time (Bollen & Curran 2006, Grace 2006, Shipley 2009, Grace et al. 2010, 2015, Little 2013, Eisenhauer et al. 2015). Each has advantages for modeling such systems because they incorporate both measured (manifest) and inferred (latent) variables, and they reveal direct, indirect, and total effects, reciprocal relations, and feedback loops, as well as processes that are time-varying and take place across differing levels of granularity. Similar approaches will also be used to model the combined effects of microbial, plant, and arthropod diversity on the resilience of ecosystem function (e.g., Fig 16). These approaches will allow us to develop predictions about the relative strengths of different biotic components (microbes, arthropods, plants) and mechanisms (resources, diversity, or adaptation) determining the resilience of ecosystem functions responding to both intense growing-season drought and interannual variation in climate.

2.5 Intellectual Merit

KBS-LTER is uniquely positioned to advance understanding of the resilience of agricultural ecosystems and landscapes in response to projected long-term changes in rainfall regimes and land use. Our treatments represent land uses that are dominated by human decisions and crucial to human welfare, yet vulnerable to the degradation of productivity and other ecosystem services. Our 30-year dataset has allowed us to show differences in resilience of treatments of variable agricultural intensity in response to growing-season droughts. A challenge faced by us—and by the broader ecological community—is to understand the mechanisms of resilience, both ecological and socioecological. We will maintain our long-term data collection while initiating new long-term experiments to advance understanding of three key classes of mechanisms conferring resilience of ecological functions in agricultural ecosystems and landscapes: resource availability (soil resources and social resources), diversity, and adaptation (biological and technological).

Our combination of observational and experimental approaches will yield a more definitive understanding of the mechanisms underlying resilience. Our treatments varying in intensity of land use and subjected to interannual fluctuations in growing-season water availability enable tests that are not possible with short-term studies, and our integrated ecological and socioecological investigations provide a complete picture of the mechanisms driving the resilience of human-dominated landscapes.

We supplement our long-term datasets with new experiments to test the importance of specific mechanisms of resilience. We propose to impose new manipulations of growing-season drought as a model test for resilience across different land use types. We propose to create treatments within rainfall manipulations to test the roles of resource availability, diversity, and adaptation in conferring resilience. We will capitalize on recently initiated experiments (CLE) and will add new manipulations (conservation strips) to test the effects of land conservation on maintenance of services across agricultural landscapes.

A powerful aspect of our proposed research is that we test for possible interactive effects of resilience mechanisms, including both ecological and social mechanisms (Fig. 2). In ecological systems, for example, microbial diversity might be most likely to show effects at higher levels of soil C, leading to synergistic effects of microbial diversity and soil C in conferring resilience. We will test this hypothesis with the new Rainfall Manipulation Experiment. In socioecological systems, interactive effects result because the ability of humans to manipulate one resilience mechanism depends on environmental conditions and/or technological resources, and may produce undesirable side effects. We will test this through our Crop Management and Stewardship Practices Survey, which together with our outreach will lead to co-production of scientific understanding. Our integrated ecological experiments and social observational studies will build the broad understanding of mechanisms of resilience that is essential for the future sustainability of human dominated landscapes.

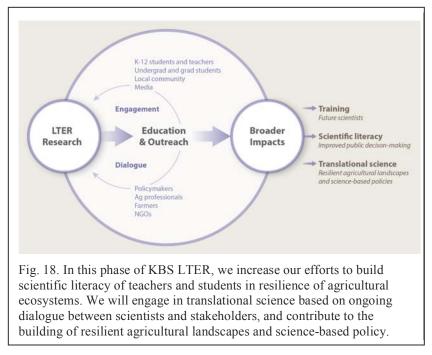
2.6 Broader Impacts

Our broader impact goals are to increase scientific literacy and the understanding of the ecology of agricultural systems to inform management, public decision-making, and policy. Education and Outreach Coordinator Doll will work closely with LTER scientists and K-12 Partnership Coordinator Kara Haas. Doll's membership on the LTER Network Education Working Group, the LTER Communication Committee, the LTER Diversity Committee, MSU Extension field crop and climate teams, and the USDA North Central Region SARE (Sustainable Ag Research & Education) Administrative Council will help connect and expand our efforts to the Network and regional levels.

Dialogue with stakeholders is at the core of our program (Fig. 18), helping us be responsive to emerging opportunities where LTER data can contribute to scientific literacy, training future scientists, and translational science.

Scientific Literacy. In this next phase, we will focus our <u>K-12 Partnership</u> on the resilience of agroecosystems, inviting teachers and students to two science field days, and each year we will hold 2 school-year and 1 summer workshop for \sim 75 teachers, offer RET positions as funding opportunities

allow, and invite our scientists to participate in teacher workshops. Each RET will create two LTER Data Nuggets (short datasets to improve quantitative skills in K-12 students: Section 1.6) related to resilience that will be archived on the Data Nuggets and K-12 Partnership websites, presented at work-shops, and made available to teachers nationwide. In addition, we have recently secured funds to develop digital versions of Data Nuggets to increase use of LTER datasets. We will reach learners of all ages through informal education programs, including 4H and



nature centers such as our successful 2017 <u>Field Day for Informal Educators</u>. 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. Doll will recruit graduate students and summer REUs to pitch stories to MSU's Knight Center for Environmental Journalism, helping us to reach broader audiences.

Training Future Scientists. REU evaluations, including blog posts on our website, illustrate the transformative and educational values of LTER internship experiences. We will support two REUs each year via core funding, and our KBS REU site award will fund 10 undergraduates each summer, many of whom will work at the LTER site. KBS-based LTER REUs and interns participate in professional development programming and are part of an interactive, diverse group of summer undergraduates. Graduate students and postdoctoral mentors of these students receive mentorship training (including diversity and inclusion training). All LTER REUs (off-site and on-site) present their research in a final symposium to ~150 KBS researchers, students, staff, and local community members.

Translational Science. We will expand our successful <u>Roundtable Discussion</u> series by bringing together intellectual, thought, and moral leaders to explore how long-term research can help inform the design, management, and sustainability of resilient agricultural landscapes and how we can effectively inform policy and management. This <u>Resilient Ag Coalition (RAC)</u> will include scientists, agencies (USDA-NRCS), NGOs (Environmental Defense Fund, The Nature Conservancy), farm organizations (Farm Bureau), farmer advisors (Extension, crop consultants), and farmers. In addition, we will invite civic (Citizens' Climate Lobby) and faith groups (Interfaith Power and Light) who are engaged in environmental and sustainability initiatives. Doll and co-PIs have current contacts within each of these groups. RAC will create a vision for resilient, sustainable Midwestern agriculture and will serve as a sounding board for new LTER scientific endeavors, policy initiatives, and educational/outreach efforts. We will host a RAC Roundtable Discussion each year (2019-2021), leading to a capstone symposium—including a field tour of our LTER—in 2022, coinciding with our 35th anniversary. Additional outputs will include white and peer-reviewed papers, national press, and webinars sharing highlights to broad audiences.

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