

Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes

Ben P. Werling^{a,b}, Timothy L. Dickson^{b,c}, Rufus Isaacs^{a,b}, Hannah Gaines^{d,e}, Claudio Gratton^{d,e}, Katherine L. Gross^{b,f,g}, Heidi Liere^{d,e}, Carolyn M. Malmstrom^{b,g}, Timothy D. Meehan^{d,e}, Leilei Ruan^{b,f,h}, Bruce A. Robertson^{b,i}, G. Philip Robertson^{b,f,h}, Thomas M. Schmidt^{b,j}, Abbie C. Schrotenboer^{b,k}, Tracy K. Teal^{b,l}, Julianna K. Wilson^{a,b}, and Douglas A. Landis^{a,b,1}

^aDepartment of Entomology, Michigan State University, East Lansing, MI 48824; ^bGreat Lakes Bioenergy Research Center, US Department of Energy, Michigan State University, East Lansing, MI 48824; ^cDepartment of Biology, University of Nebraska at Omaha, Omaha, NE 68182; ^dGreat Lakes Bioenergy Research Center, US Department of Energy, University of Wisconsin–Madison, Madison, WI 53706; ^eDepartment of Entomology, University of Wisconsin–Madison, Madison, WI 53706; ^fW. K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060; ^gDepartment of Plant Biology, Michigan State University, East Lansing, MI 48824; ^hDepartment of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI 48824; ⁱDivision of Science, Mathematics and Computing, Bard College, Annandale-on-Hudson, NY 12504; ^jDepartment of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109; ^kDepartment of Biology, Trinity Christian College, Palos Heights, IL 60463; and ^lDepartment of Microbiology and Microbial Genetics, Michigan State University, East Lansing, MI 48824

Edited by Peter M. Kareiva, The Nature Conservancy, Seattle, WA, and approved December 11, 2013 (received for review May 23, 2013)

Agriculture is being challenged to provide food, and increasingly fuel, for an expanding global population. Producing bioenergy crops on marginal lands—farmland suboptimal for food crops—could help meet energy goals while minimizing competition with food production. However, the ecological costs and benefits of growing bioenergy feedstocks—primarily annual grain crops—on marginal lands have been questioned. Here we show that perennial bioenergy crops provide an alternative to annual grains that increases biodiversity of multiple taxa and sustain a variety of ecosystem functions, promoting the creation of multifunctional agricultural landscapes. We found that switchgrass and prairie plantings harbored significantly greater plant, methanotrophic bacteria, arthropod, and bird diversity than maize. Although biomass production was greater in maize, all other ecosystem services, including methane consumption, pest suppression, pollination, and conservation of grassland birds, were higher in perennial grasslands. Moreover, we found that the linkage between biodiversity and ecosystem services is dependent not only on the choice of bioenergy crop but also on its location relative to other habitats, with local landscape context as important as crop choice in determining provision of some services. Our study suggests that bioenergy policy that supports coordinated land use can diversify agricultural landscapes and sustain multiple critical ecosystem services.

energy policy | greenhouse gas mitigation

In agricultural landscapes, balancing the provisioning of food and energy with maintenance of biodiversity and ecosystem functions is a global challenge. To avoid impacts on food production, attention is increasingly being focused on the potential for marginal lands to support bioenergy production (1). Marginal lands, those suboptimal for food production, may consist of relatively small areas within generally productive landscapes or larger regions where conditions generally limit crop productivity. However, there is increasing recognition that these lands are already performing a variety of useful functions, and their conversion to bioenergy cropping could reduce these services. For example, in the north central United States, rising commodity prices are predicted to bring marginal croplands—including Conservation Reserve Program lands—into annual crop production with negative impacts on wildlife habitat and water quality (2, 3). With 2013 corn plantings at recent record highs (4) and new reports of grassland and wetland conversion to cropland (5, 6), this may be occurring already.

An alternative to annual cropping is conversion of marginal croplands to perennial, cellulosic crops for bioenergy. Although current US biofuel production centers on grain ethanol derived from annual monocultures of maize (*Zea mays*), this situation

could change with full implementation of the 2007 US Energy Independence and Security Act (7), which calls for increased production of cellulosic biofuels. In the Midwest United States, perennial grasses and forbs grown on marginal lands could provide up to 25% of national targets for cellulosic biofuel, with substantial greenhouse gas (GHG) benefits (8). Moreover, increasing the area of perennial cover on the landscape is predicted to positively affect a diverse array of organisms and ecological functions (9–11), leading to important synergies that have not yet informed the ongoing bioenergy debate. Here we provide the most comprehensive empirical evaluation of this hypothesis to date, reporting data that elucidate the impacts of different bioenergy cropping systems on a wide variety of organisms and the ecosystem functions they perform.

Previous studies have examined the ability of select bioenergy crops to support specific taxa (12) or individual services such as energy production (13) or GHG mitigation (14), without consideration of the tradeoffs or synergies that can arise when considering entire suites of organisms and ecosystem functions. We report on a unique multidisciplinary study of matched sets of organisms and ecosystem services and show that perennial grass energy crops (switchgrass, *Panicum virgatum*, and mixed prairie plantings) synergistically enhance diversity of a variety of

Significance

Science-based policies are needed to inform sustainable bioenergy landscape design. Our key finding is that the linkage between biodiversity and ecosystem services is dependent not only on the choice of bioenergy crop but also on its location relative to other habitats. The implication is that careful design of bioenergy landscapes has the potential to enhance multiple services in food and energy crops, leading to important synergies that have not yet informed the ongoing bioenergy debate. This study is especially timely as high commodity prices are driving conversion of marginal lands to annual crop production, reducing future flexibility.

Author contributions: B.P.W., R.I., C.G., K.L.G., C.M.M., T.D.M., B.A.R., G.P.R., T.M.S., and D.A.L. designed research; B.P.W., H.G., C.G., T.D.M., L.R., B.A.R., A.C.S., T.K.T., and J.K.W. performed research; B.P.W., T.L.D., C.M.M., L.R., B.A.R., and T.K.T. analyzed data; and B.P.W., T.L.D., R.I., H.G., C.G., K.L.G., H.L., C.M.M., T.D.M., L.R., B.A.R., G.P.R., T.M.S., T.K.T., J.K.W., and D.A.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹To whom correspondence should be addressed. E-mail: landisd@msu.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1309492111/-DCSupplemental.

organisms and levels of the services they provide. We further quantify the importance of landscape context on service provisioning, suggesting that policy supporting intentional design of bioenergy landscapes could increase sustainability of both food and energy production.

Results

We compared biodiversity and key ecological processes among maize, switchgrass, and prairie, three plant communities representing distinct alternatives for use of marginal lands that vary in management intensity, perenniality, and sown diversity (Fig. S1). To accomplish this, we identified and sampled 115 maize, switchgrass, and prairie fields across the major agricultural production regions of Michigan and Wisconsin (Fig. S1 and Tables S1–S3). Maize was grown as an annual monoculture and managed for high yields using herbicides and fertilizers (Table S2). Switchgrass and prairie sites were planted as perennial monocultures and polycultures, respectively, and managed using prescribed burns or mowing on 2–5 y cycles. Supplemental analyses found no evidence that recent burning or mowing negatively affected response variables (Text S2, Figs. S2 and S3, and Table S4).

Biodiversity was quantified by measuring the taxonomic richness of plants, methane-consuming soil bacteria (methanotrophs), predatory and herbivorous arthropods, bees, and breeding birds using sampling methods and measures of richness appropriate for each group. As expected, maize fields contained a low-diversity plant community dominated by the crop itself (99% of biomass; Figs. 1A and 2A). Although planted as monocultures, switchgrass stands were more diverse, with biomass typically composed of 20% opportunistic forbs and grasses. Prairies were most diverse in both plant species and biomass composition. Diversity of herbivorous and predatory arthropods showed a stairstep increase from maize to prairie that mirrored trends in plant diversity (Fig. 1C and D), whereas methanotroph, bee, and breeding-bird diversity was equally high in the two perennial grasslands compared with maize (Fig. 1B, E, and F). Effect statistics (Hedge's *D*) were used to standardize differences and test for statistical significance (15). Compared with maize, perennial grass plantings had positive effects on diversity of all taxa, which were statistically significant for all but methanotrophs (Fig. 3A). Differences in richness between the two perennial grass systems were either smaller (plant

and predatory arthropod richness) or near zero (all other organisms; Fig. 3B).

We also quantified ecological processes involving each focal group, including plant primary productivity, consumption of methane by soil bacteria, consumption of insect pest eggs by arthropod natural enemies, pollination, colonization by pest aphids, and habitat use of grassland birds. Although maize fields produced an order of magnitude more aboveground biomass than the two perennial grass systems, all other beneficial processes measured were greater in grasslands (Fig. 2). In grasslands, rates of methane consumption were an order of magnitude higher, predation of pest eggs by beneficial insects increased by a factor of two, and grassland birds—a nationally imperiled group (16)—were observed twice as frequently (Fig. 2A–D). In addition, pollination of sentinel sunflowers almost doubled adjacent to prairie, and pressure of pest aphids was ~50% lower in prairie compared with maize (Fig. 2E and F). Effect statistics likewise identified substantial differences between maize and perennial grass plantings, which were statistically significant for all processes except pollination (Fig. 3C). In contrast, differences between prairie and switchgrass were near zero (Fig. 3D).

Multiple regression models that incorporated landscape influences on pest suppression (17) and bird prevalence (16) showed that landscape composition—the identity and extent of nearby vegetation types—can have as strong an impact on service provisioning as the nature of the planting itself (Fig. 4). After accounting for differences in crop types, our model predicted that rates of predation of pest eggs by beneficial insects increased by 30% as the extent of grassland within 1.5 km of a focal field increased to maximum observed values (Fig. 4A). This was comparable in size to the difference in within-field service provisioning between maize and perennial grass plantings. Likewise, our model of landscape influence on grassland birds predicted a 60% increase in occupancy of patches as surrounding landscapes became less forested at the 1.5-km scale (Fig. 4B), an increase that was again comparable to differences between planting types. Land use patterns at these scales are typically influenced by multiple landowners, suggesting a role for regional planning to maximize provisioning of ecosystem services in agricultural landscapes.

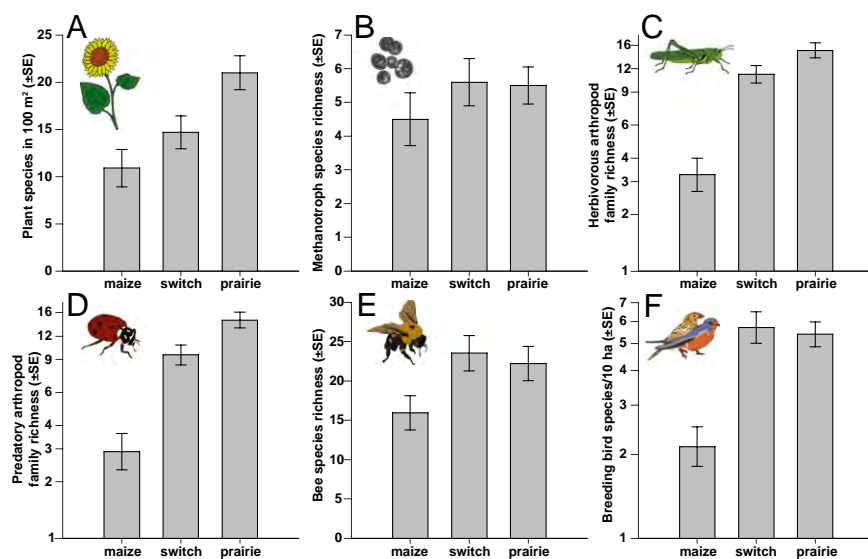


Fig. 1. Compared with maize, perennial grasslands supported a greater diversity of organisms ranging from plants to vertebrates. Graphs show variation between maize, switchgrass, and prairie in richness of plants (A), methanotrophic soil bacteria (B), herbivorous arthropods (C), predatory and parasitic arthropods (D), bees (E), and breeding birds (F). Error bars are ± 1 SE. Note logarithmic axes in C, D, and F.

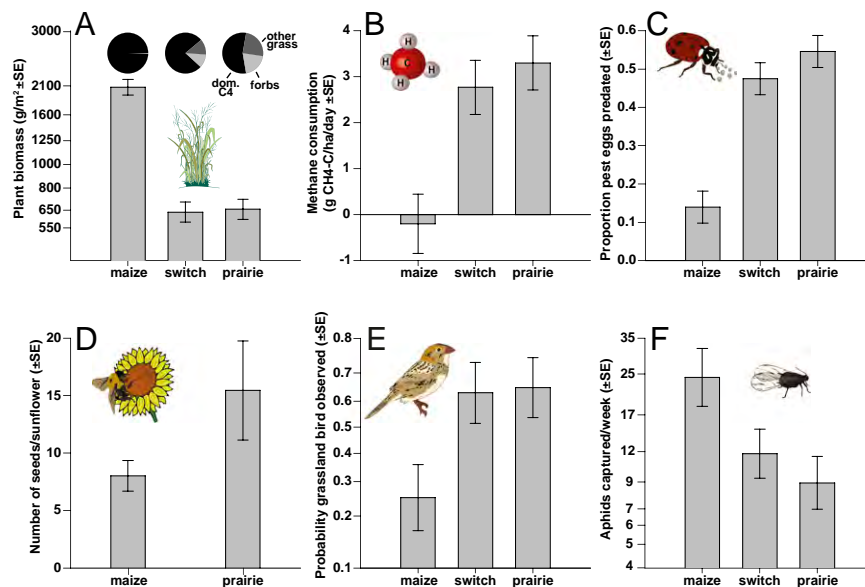


Fig. 2. Key ecological processes varied between maize and perennial grasslands. Variation between maize, switchgrass, and prairie in production of aboveground plant biomass (A), methane consumption by soil methanotrophs (B), predation of pest eggs by beneficial insects (C), pollination of sentinel sunflower plants (maize and prairie only) (D), occurrence of obligate grassland birds (E), and pest aphid pressure (F). Pie graphs in A show the percentage of biomass composed of the dominant C4 grass species (*Z. mays* in maize, *P. virgatum* in switchgrass, and *A. gerardii* in prairie), other grasses, and forbs. Error bars are ± 1 SE. Note logarithmic (A and F) and logit-scale axes (E).

Discussion

Considering a broad suite of ecosystem services could alter conclusions about the relative value of different bioenergy crops. Relatively high aboveground productivity (Fig. 2A) along with current price and policy incentives cause maize to outcompete

switchgrass and prairie when farmer income is the only consideration (18). However, our data show that perennial grasses support greater biodiversity and higher rates of a variety of other ecosystem services (e.g., pest suppression and pollination) valuable to society as a whole (Fig. 3). Planting perennial energy

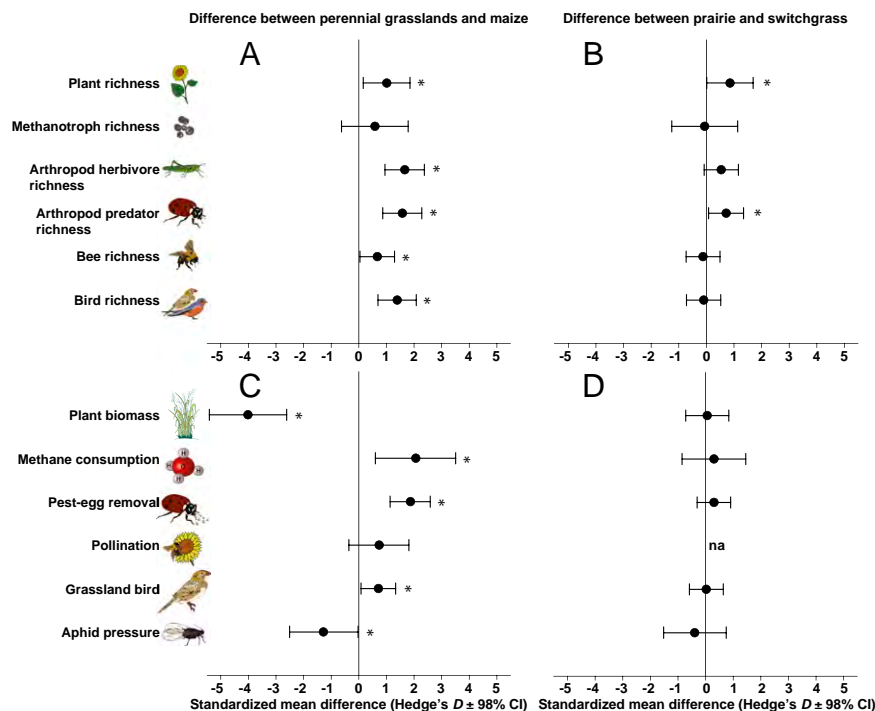


Fig. 3. Differences in richness and ecological processes were larger between the two perennial grasslands and maize than between prairie and switchgrass. Standardized effect sizes (Hedge's *D*) are shown for differences in richness and key ecological processes between grasslands and maize (A and C) (effect is difference between average of the two grasslands and maize) and prairie compared with switchgrass (B and D). Error bars show 98% confidence intervals. Asterisks indicate statistical significance at $\alpha = 0.02$.

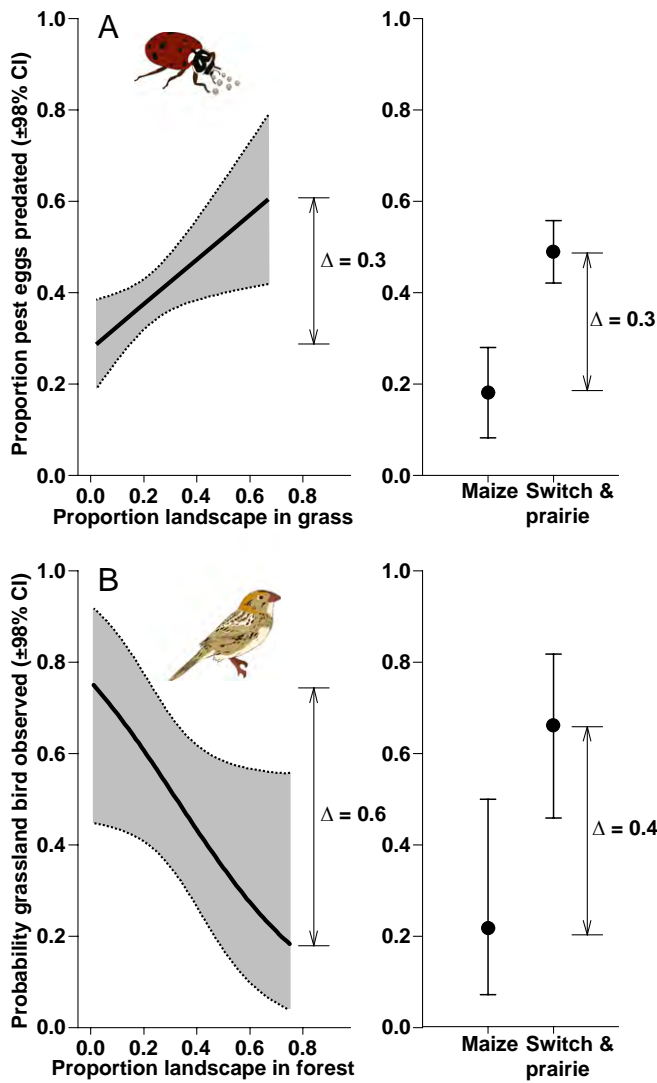


Fig. 4. Multiple-regression models indicated that habitats surrounding bioenergy crops can have as large an effect on ecosystem services as the crop itself. Predation of pest eggs (A) increased by 30% as the proportional area of grasslands within 1.5 km of sites increased, an effect as large as differences between maize and the two grasslands. The probability of observing a grassland-dependent bird species (B) declined by 60% as forest land cover increased within 1.5 km of sites, an effect larger than differences between maize and grasslands.

crops on marginal lands could maintain or enhance these functions, complementing and even feeding back to benefit commodity production on prime agricultural land (10). In this respect, these perennial systems provide a means to support bioenergy goals, broaden the portfolio of services supported by agricultural landscapes, and support their long-term functioning (19).

Site-level management decisions are likely to alter ecosystem services provided by bioenergy crops. For example, incorporating features of perennial systems into maize, through practices like cover cropping, could enhance services such as greenhouse gas mitigation (20). Alternatively, intensifying grassland management by fertilization may increase biomass production but reduce other services. For example, fertilization will likely reduce plant diversity (21), particularly of forbs, and so likely also reduce pollination and pest suppression services (17). Our landscape analyses—in which grasslands were broadly defined to include lands such as pastures and hayfields which are managed for agricultural production—have

detected positive effects of grasslands on services (Fig. 4A) (9, 10). This suggests that it is possible to actively manage grasslands for biomass while maintaining their positive contribution to other ecosystem services.

For agricultural landscapes to be sustainable, production of food, energy, and biodiversity need to coexist (22). Using policy to encourage thoughtful placement of energy crops in the landscape could allow agriculture to take advantage of ecosystem service synergies (23). Highly intensified annual crop landscapes might be strategically diversified with perennial grassland bioenergy crops, increasing biodiversity (9) and pest suppression in annual crops (10) while reducing water pollution (11), GHG fluxes (14), and reliance on pesticides (24, 25). Our ability to design sustainable agroenergy landscapes that producers will implement requires additional understanding of the costs of potential ecosystem service tradeoffs (25), elucidation of “bundles” of ecosystem services that could be jointly produced (26), and understanding society’s perception of the value of these services (27). Finally, realizing the benefits of such landscape design will require policies that encourage landowners to make informed and coordinated decisions at the landscape scale. Prior work on biodiversity conservation at landscape scales suggests that the benefits of such coordinated land use decisions are substantial (28) and that spatially explicit incentives show promise as a voluntary tool for achieving desired landscape configurations (29, 30). Applying such lessons to the development of agricultural landscapes for sustainable bioenergy production is a logical next step.

Materials and Methods

Sample Sites. We collaborated with farmers, private landowners, and state land managers to locate 115 maize, switchgrass, and prairie plantings across the major crop production regions of Michigan and Wisconsin (Fig. S1 and Table S3). Management of these plantings is described in Table S2. Sampling at each site was conducted in four plots spaced 50 m apart at the corners of a 50 × 50 m square, with two plots located 50 m from the habitat edge and two located 100 m away. For more narrow sites, plots were arranged in a linear transect down the center of each patch with the first plot 50 m from the edge and remaining stations spaced 50 m apart. Departures from this design are noted below.

Taxonomic Richness. We measured the taxonomic richness of plants, microbes, and animals present in each habitat, sampling different subsets of our total pool of sites for each experiment (Text S1 and Table S3). Plant species richness was measured by recording all species (planted and naturally colonizing) present in four 100-m² circular plots at 10 maize, 13 switchgrass, and 12 prairie sites between 2008 and 2010. Methanotroph richness was measured by taking soil samples (10 cm deep × 2.5 cm diameter) from four maize, five switchgrass, and eight prairie plantings during 2009–2011 and quantifying the total number of genetically distinct strains [operational taxonomic units (OTUs)] present at each site. Two cores were taken at each of the four plots and aggregated at the site level and transported to the laboratory on ice, where they were sieved to 4 mm and then stored at –80 °C for genetic analysis (Text S1). For insects and spiders (“arthropods”), we separately measured richness of herbivores, predators, and bees. Richness of herbivorous and predatory arthropods was measured by taking 100 sweeps with a sweep net at 19 maize, 20 switchgrass, and 20 prairie sites in June and July of 2008 and 2009 and determining the number of families in each of these two groups; methods are detailed elsewhere (31). Bee species richness was measured by trapping bees in arrays of white, yellow, and blue 29-mL soufflé cups filled with soapy water. Traps were deployed for 48 h in June, July, and August on platforms (Text S1) at four plots in 20 maize, 20 switchgrass, and 20 prairie sites in 2009. Before analysis, one observation was removed from both the predatory arthropod and bee richness datasets; these observations were sixfold and fivefold greater than median values of predatory arthropod and bee richness, respectively, and were the largest outliers across all datasets. Finally, breeding bird richness was measured by visually or aurally identifying all species perching, feeding, or singing during whole-field searches at 20 sites of each habitat during 2008 and 2009; see published methods (16). All data are available in Dataset S1.

Ecological Processes. We measured key ecological processes supported by the plant, microbe, and animal communities inhabiting maize, switchgrass, and prairie plantings (Table S1). For plants, we measured the current year's production of aboveground biomass by collecting, drying (65 °C for ≥72 h), and weighing standing vegetation from four 0.5 × 2 m quadrats at 16 maize, 10 switchgrass, and 10 prairie sites during 2008–2010 (Text S1). We sorted vegetation into the dominant C4 grasses (*Andropogon gerardii*, *Sorghastrum nutans*, and *P. virgatum*), other grasses, and forbs to estimate functional group composition. We measured consumption of methane by soil microbes by sinking seven cylindrical chambers (28 cm diameter and 26 cm height) 5 cm into the ground at five maize, six switchgrass, and six prairie sites in 2011. Chambers were equipped with a removable lid and septum, allowing multiple samples to be taken on July 15, August 18, and October 5, 2011 (Text S1). For arthropods, we measured the attractiveness of habitats to aphids (Hemiptera: Aphididae), which is related to the incidence of plant viruses that these insect herbivores vector. We sampled aphids using yellow bowl traps (horizontal surface area ~145 cm²) filled with 25% (vol/vol) propylene glycol and water. Four traps spaced 40 m apart were deployed at five maize, seven switchgrass, and six prairie sites. Traps were 0.5 m above vegetation and were raised as canopies grew taller. Samples were taken weekly between June 8 and 29, 2009. We also quantified the ability of predatory arthropods to suppress pests by measuring predation of pest eggs placed out at four plots in 20 maize, 20 switchgrass, and 20 prairie sites in June and July 2009. This technique, detailed in published work (17), provides information on the activity of a wide range of invertebrate predators important in suppressing crop pests. For bees, we measured pollination of sentinel dwarf sunflowers (*Helianthus annuus* L., "Sunspot") placed out at 10 maize and 10 prairie sites in 2010; switchgrass sites were not sampled for pollination. Sunflowers were grown in the greenhouse; after developing two to eight florets, two sets of four plants were placed in the grassy margins adjacent to each maize and prairie field and exposed to pollination for 1 wk. Cages were used to exclude or allow pollinator access to flowers to estimate the effect of bee pollination on seed set (Text S1). Finally, we recorded the presence or absence of obligate grassland birds during area searches at 20 maize, 19 switchgrass, and 20 prairie sites in 2008 and 2009 using published methods (16). All data are available in Dataset S1.

Data Analysis. Either samples were lumped for each site (richness of methanotrophic bacteria) or data were averaged across subsamples to obtain a single site average. Datasets used for plant richness and biomass, herbivorous and predatory arthropods, methanotrophs, and birds contained a mixture of single-year and multiyear observations (Text S1). Preliminary analyses suggested that there was no systematic variation in these variables between years (Text S1) (16). Consequently, data from sites visited in multiple seasons were averaged across years to obtain a single observation for analysis.

We estimated taxonomic richness using approaches appropriate for each organism. For plants, we used the mean number of species per 100 m² as a measure of species density that was directly comparable among sites. For methanotroph bacteria, we used raw data on richness of OTUs because past work indicated that the level of sampling conducted here was sufficient to sample the majority of species in the community. However, for arthropods, it was unlikely that all taxa were detected. In this case, raw values of richness would have been affected by the total number of individuals captured. This could confound differences in richness with differences in abundance or sampling efficiency between habitats. To account for this, a Chao1 estimator was used to estimate asymptotic richness for families of herbivorous and predatory arthropods and bee species at each site (32).

We applied a common set of statistical analyses to compare richness and rates of key ecological processes between maize, switchgrass, and prairie (Dataset S1). Generalized linear models were used to calculate means and confidence intervals by specifying habitat type (maize, switchgrass, or prairie) as a categorical variable. For birds, we also included log₁₀(x)-transformed patch area as a covariate because grassland bird richness is known to increase with patch area (16). Models were fit using Gaussian (plant, methanotroph and bee richness, methane consumption, and log₁₀(x)-transformed captures of aphids), Poisson (breeding bird richness), quasi-Poisson (arthropod predators and herbivores), gamma (plant biomass), or binomial distributions (occurrence of grassland birds) as indicated by residual diagnostic plots (33). For pollination, we fit a generalized least squares model with separate variances for maize and prairie because neither data transformation nor use of nonnormal distributions accounted for overdispersion. Models were implemented using the "glm" and "gls" functions

of R version 2.15.1 (34); means and SEs were calculated using the "effects" package of R. For birds, mean richness was calculated for each habitat at a common area of 10 ha.

We next used preplanned contrasts in combination with standardized effect statistics to test hypotheses and display differences on a common scale. A first group of contrasts was used to compare response variables between maize vs. switchgrass and prairie, to test the hypothesis that taxonomic richness and rates of key processes differ between lightly managed perennial grasslands compared with a highly managed annual crop. A second group of contrasts was used to compare variables between switchgrass and prairie and test the hypothesis that within lightly managed grasslands, communities differ between habitats with low and high levels of planted diversity. We then calculated Hedge's *D* and 98% confidence intervals using the approach of Nakagawa and Cuthill (15) and R code therein. Setting $\alpha = 0.02$ for each contrast maintained an overall error rate of $\alpha = 0.04$ for the full set of two contrasts calculated for each variable. Contrasts were calculated using the "contrast" package of R version 2.15.1 (34). For pollination we were able to estimate differences between only maize and prairie because pollination was not measured in switchgrass. Statistical code is available in Dataset S2.

Highlighting Landscape Dependencies. Earlier work has shown that rates of ecological processes in maize, switchgrass, and prairie depend not only on local plant communities but also on the composition of surrounding landscapes (16, 17). Specifically, predation of pests (17) and the occurrence of grassland birds (16) varied with the extent of grassland and forest cover in landscapes. Here we combine multiple regression models with effect displays (35) to directly compare the magnitude of these landscape effects to differences between plant communities. To focus on the major differences documented between maize and grassland habitats (Figs. 1 and 2), we first changed the three-level habitat variable (maize, switchgrass, or prairie) used in initial analyses into a binary one that indicated whether a patch was maize vs. one of the two perennial grasslands. Likelihood ratio tests suggested that reducing habitat type to a binary variable did not result in a significant loss of explanatory power (predation: $\chi^2 = 1.5$, $df = 1$, $P = 0.2$; bird occurrence: $\chi^2 = 0.01$, $df = 1$, $P = 0.9$).

To directly compare habitat and landscape effects, we next incorporated landscape covariates identified as important in earlier work. For predation of pest eggs, we included variables describing the areal extent of grasslands and forests within 1.5 km of sites (17). The effect of forest cover was only modeled to ensure accurate estimation of the effect of grassland extent; forest effects were weak and are not reported here (17). For grassland birds, earlier analyses used principal component analysis (PCA) to describe a gradient ranging from crop- to forest-dominated landscapes. Here we described this gradient using the proportion of forest in the landscape within 1.5 km of sites, which was strongly correlated with the original PCA variable (Pearson's $r = 0.96$) and is more interpretable. Calculation of landscape variables is described in refs. 16 and 17. As expected, likelihood ratio tests showed that incorporating landscape variables significantly improved model fit for predation of pest eggs ($\chi^2 = 10.4$, $df = 2$, $P = 0.006$) and birds ($\chi^2 = 5.6$, $df = 1$, $P = 0.02$).

Effect displays (35) were constructed from these regression models to isolate and compare landscape effects to differences between plant communities. Briefly, landscape effects were visualized by plotting variation in the across-habitat mean of responses as a function of landscape composition, whereas differences between plant communities were isolated by calculating means for maize and grasslands at average levels of landscape covariates. Further details of this approach are described in ref. 35. Regression lines, means, and confidence intervals were calculated using the "effects" package of R version 2.15.1 (34).

ACKNOWLEDGMENTS. We thank C. Baker, N. Batora, and numerous undergraduate students for help with data collection; S. Nakagawa for advice on effect statistics; D. Schemske and J. Tiedje for critical reviews; cooperating landowners; and Brett Blaauw and the US Department of Energy (DOE) Genomic Science program (<http://genomicscience.energy.gov>) for illustrations. This work was funded in part by the DOE Great Lakes Bioenergy Research Center DOE Biological and Environmental Research Office of Science (Grant DE-FC02-07ER64494), the DOE Office of the Biomass Program Office of Energy Efficiency and Renewable Energy (Grant DE-AC0576RL01830), the US National Science Foundation Long-Term Ecological Research program Division of Environmental Biology (Grant 1027253), US Department of Agriculture National Institute of Food and Agriculture (Grant 2011-67009-30137), and Michigan State University AgBioResearch.

1. Dauber J, et al. (2012) Bioenergy from “surplus” land: Environmental and socio-economic implications. *BioRisk* 7:5–50.
2. Langpap C, Wu J (2011) Potential environmental impacts of increased reliance on corn-based bioenergy. *Environ Resour Econ* 49(2):147–171.
3. Secchi S, Gassman PW, Williams JR, Babcock BA (2009) Corn-based ethanol production and environmental quality: A case of Iowa and the conservation reserve program. *Environ Manage* 44(4):732–744.
4. USDA-NASS (2012) *Acreage* (USDA-NASS, Washington, DC). Available at www.usda.gov/nass/PUBS/TODAYRPT/acrg0613.pdf. Accessed October 30, 2013.
5. Faber S, Rundquist S, Male T (2012) *Plowed Under: How Crop Subsidies Contribute to Massive Habitat Losses* (Environmental Working Group, Washington, DC). Available at http://static.ewg.org/pdf/plowed_under.pdf. Accessed April 21, 2013.
6. Wright CK, Wimberly MC (2013) Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proc Natl Acad Sci USA* 110(10):4134–4139.
7. Energy Independence and Security Act of 2007 (2007) H.R.6. 110th Congress of the United States of America, 1st Session.
8. Gelfand I, et al. (2013) Sustainable bioenergy production from marginal lands in the US Midwest. *Nature* 493(7433):514–517.
9. Meehan TD, Hurlbert AH, Gratton C (2010) Bird communities in future bioenergy landscapes of the Upper Midwest. *Proc Natl Acad Sci USA* 107(43):18533–18538.
10. Meehan TD, Werling BP, Landis DA, Gratton C (2012) Pest-suppression potential of midwestern landscapes under contrasting bioenergy scenarios. *PLoS ONE* 7(7):e41728.
11. Parish ES, et al. (2012) Multimetric spatial optimization of switchgrass plantings across a watershed. *Biofuels Bioprod Biorefin* 6(1):58–72.
12. Dauber J, Jones MB, Stout JC (2010) The impact of biomass crop cultivation on temperate biodiversity. *GCB Bioenergy* 2(6):289–309.
13. Gelfand I, Snapp SS, Robertson GP (2010) Energy efficiency of conventional, organic, and alternative cropping systems for food and fuel at a site in the U.S. Midwest. *Environ Sci Technol* 44(10):4006–4011.
14. Robertson GP, Hamilton SK, Del Grosso SJ, Parton WJ (2011) The biogeochemistry of bioenergy landscapes: Carbon, nitrogen, and water considerations. *Ecol Appl* 21(4):1055–1067.
15. Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biol Rev Camb Philos Soc* 82(4):591–605.
16. Robertson BA, Doran PJ, Loomis LR, Robertson JR, Schemske DW (2011) Perennial biomass feedstocks enhance avian diversity. *GCB Bioenergy* 3(3):235–246.
17. Werling BP, Meehan TD, Robertson BA, Gratton C, Landis DA (2011) Biocontrol potential varies with changes in biofuel-crop plant communities and landscape perenniality. *GCB Bioenergy* 3(5):347–359.
18. James LK, Swinton SM, Thelen KD (2010) Profitability analysis of cellulosic energy crops compared with corn. *Agron J* 102(2):675–687.
19. Atwell RC, Schulte LA, Westphal LM (2010) How to build multifunctional agricultural landscapes in the US Corn Belt: Add perennials and partnerships. *Land Use Policy* 27(4):1082–1090.
20. Robertson GP, Paul EA, Harwood RR (2000) Greenhouse gases in intensive agriculture: Contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289(5486):1922–1925.
21. DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: A review. *Plant Ecol* 84(1):9–29.
22. Tilman D, et al. (2009) Energy. Beneficial biofuels—The food, energy, and environment trilemma. *Science* 325(5938):270–271.
23. Power AG (2010) Ecosystem services and agriculture: Tradeoffs and synergies. *Philos Trans R Soc Lond B Biol Sci* 365(1554):2959–2971.
24. Meehan TD, Werling BP, Landis DA, Gratton C (2011) Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc Natl Acad Sci USA* 108(28):11500–11505.
25. Zhang W, Ricketts TH, Kremen C, Carney K, Swinton SM (2007) Ecosystem services and dis-services to agriculture. *Ecol Econ* 64(2):253–260.
26. Raudsepp-Hearne C, Peterson GD, Bennett EM (2010) Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proc Natl Acad Sci USA* 107(11):5242–5247.
27. Martín-López B, et al. (2012) Uncovering ecosystem service bundles through social preferences. *PLoS ONE* 7(6):e38970.
28. Polasky S, et al. (2008) Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol Conserv* 141(6):1505–1524.
29. Parkhurst GM, Shogren JF (2007) Spatial incentives to coordinate contiguous habitat. *Ecol Econ* 64(2):344–355.
30. Parkhurst GM, et al. (2002) Agglomeration bonus: An incentive mechanism to reunite fragmented habitat for biodiversity conservation. *Ecol Econ* 41(2):305–328.
31. Robertson BA, Porter C, Landis DA, Schemske DW (2012) Agroenergy crops influence the diversity, biomass, and guild structure of terrestrial arthropod communities. *BioEnergy Res* 5(1):179–188.
32. Chao A (1984) Non-parametric estimation of the number of classes in a population. *Scand J Stat* 11(4):265–270.
33. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York).
34. R Core Development Team (2006) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna). Available at www.R-project.org. Accessed April 21, 2013.
35. Fox J (2003) Effect displays in R for generalised linear models. *J Stat Software* 8(15):1–27.

Supporting Information

Werling et al. 10.1073/pnas.1309492111

SI Text

Text S1. Datasets with mixtures of single-year and multiyear observations. Datasets for plant species richness and composition, methanotrophic bacterial diversity, and plant biomass contained a mixture of single-year and multiyear observations. Multiyear observations were averaged across years and pooled with single-year observations into single datasets because there was no evidence for systematic differences across years (see below). Data on plant species composition and richness were collected in Michigan during August of 2008 (9 switchgrass and 10 prairie sites), 2009 (10 maize, 4 switchgrass, and 2 prairie sites), and 2010 (6 prairie and 2 switchgrass sites). Six prairie and two switchgrass sites were sampled in multiple years. A paired t test comparing 2008 and 2010 estimates of species richness provided no evidence for systematic differences in species richness across years ($t = -0.93$, $df = 6$, $P = 0.39$; mean difference: $\bar{X} = -2.6$, 95% confidence interval (CI) for difference: -9.3 , 4.2).

Diversity of methanotroph soil bacteria was measured in Michigan during 2009 (three maize, two switchgrass, and four prairie sites), 2010 (one maize, three switchgrass, and six prairie), and 2011 (one switchgrass and one prairie). A paired t test did not reveal detectable differences in estimates of methanotroph richness taken at the same sites in 2009 and 2010 ($t = 0.76$, $df = 2$, $P = 0.53$; mean difference: $\bar{X} = 0.67$, 95% CI for difference: -3.12 , 4.46), although sample sizes ($n = 3$ sites sampled in both years) were extremely small. Because the estimated difference was small and only a handful of sites were sampled in 2 y, richness estimates were averaged across years for sites visited twice and combined with single-year observations for analysis.

Plant biomass was measured in August or September of 2008 (3 prairie and 3 switchgrass sites), 2009 (10 maize, 10 switchgrass, and 10 prairie sites), and 2010 (8 maize, 2 switchgrass, and 6 prairie sites). Some sites were sampled only once (14 maize, 5 switchgrass, and 5 prairie sites), whereas others were sampled in multiple years (4 maize, 15 switchgrass, and 15 prairie sites). Paired t tests did not reveal detectable differences in above-ground peak biomass measurements taken at the same sites in 2008 and 2009 ($t = 1.00$, $df = 2$, $P = 0.42$; mean difference: $\bar{X} = 135.11$, 95% CI for difference: -443.5 , 713.7) or in 2009 compared with 2010 ($t = 0.82$, $df = 9$, $P = 0.43$; mean difference: $\bar{X} = 48.0$, 95% CI for difference: -84.5 , 180.6).

Methanotrophic bacteria genetic analysis. DNA was extracted from soil samples using the MoBio PowerSoil DNA Extraction kit according to the manufacturer's instructions with two modifications: we added a second 500- μ L wash with C5 and C6 solution warmed to 65 °C. Final elution volume was 150 μ L. Methanotroph diversity was then assessed by sequencing the gene that encodes the alpha-subunit of the particulate methane monooxygenase protein (this gene is hereafter abbreviated as *pmoA*) from the template DNA, as previously described (1). Briefly, *pmoA* was amplified using the primers A189 (5'-GGNGACTGGGACTTCTGG-3') and A682 (5'-GAASGCN-GAGAAGAASGC-3') and a touchdown PCR. To minimize the sequencing of *amoA*, a gene that encodes a portion of the ammonia monooxygenase protein and often amplifies with *pmoA* primers, the PCR product was digested using PfiFI, which cuts *amoA* but not *pmoA*. The digestion was run on a gel, and the undigested DNA (at 500 bp) was extracted using the Promega Gel Extraction kit according to the manufacturer's instructions. Adenine was added to the gel extraction product, and clone libraries were created using the Invitrogen TOPO TA cloning kit with the pCR4 vector and sequenced using Sanger sequencing at

the Michigan State University Research Technology Support Facility. *pmoA* sequences were aligned, and any sequences that were not *pmoA* (either because of nonspecific amplification or because they were *amoAs*) were excluded from further analysis. Operational taxonomic units (OTUs) at 94% sequence similarity, approximating species level (2), were determined using mothur v 1.21.0 (3). The number of OTUs was used to estimate methanotroph species richness.

Bee bowl platform design. At each site, an array of white, yellow, and blue 29-mL soufflé cups (Solo Cup Company) were placed out at each of four sampling stations and filled with soapy water to collect bees (4). At each station, one cup of each color was fastened atop a 30 \times 30 cm platform consisting of either 30 \times 30 cm pieces of 4-mm-thick green plastic board (in Michigan; N. Glantz and Sons) or a 30 \times 30 cm piece of plywood painted a similar shade of green (in Wisconsin). Platforms were initially elevated atop a 50-cm length of 2-cm-diameter PVC placed over a 61-cm length of metal rebar pounded halfway into the ground. In July, an additional 50- and 150-cm piece of PVC was added to raise traps 1 and 1.5 m off the ground in grasslands and maize, respectively, to keep traps level with the plant canopy.

Methane sampling. Methane consumption was estimated using static chamber methods (5). On each of the three sample dates (*Materials and Methods*), gas samples were collected using a 10-mL syringe four times from each chamber at intervals of roughly 15 min. Samples were stored in 5.6-mL glass vials (Labco Ltd.) and were analyzed by gas chromatography (Agilent 7890a) in the laboratory. Methane was separated on a Porapak Q column (3 m, 80/100 mesh, 2 mm ID) at 85 °C and analyzed with a flame ionization detector at 300 °C. Cumulative flux values were calculated by linearly interpolating CH₄ fluxes between sampling days. Mean daily methane fluxes (g CH₄-C ha⁻¹ d⁻¹) were then determined by dividing cumulative fluxes by the duration of the sampling period. These values were calculated such that a positive sign indicates net removal (i.e., consumption) of methane from the atmosphere by soil microbes, whereas negative values indicate a net release.

Measuring effect of bee pollination on seed set. Two sets of four plants were placed in grassy margins adjacent to sampled maize and prairie field. Each sunflower was covered with a 1-gallon mesh paint strainer (The Cary Company) to exclude pollinators; upon deployment to field sites, three sunflowers within each set were uncovered and exposed to potential pollinators. After 1 wk, plants were removed from the field and uniformly maintained under greenhouse conditions until maturity, after which seeds were harvested and counted. Seed set was then averaged across all bagged and exposed plants at a site. Increases in seed set due to pollination were then calculated by subtracting mean seed of plants not exposed to pollinators from those exposed to pollinators for each site.

Text S2. Removal of aboveground plant biomass for harvest will be an inherent component of managing bioenergy grasslands, raising the following questions: (i) How will biomass harvest affect diversity and ecological processes documented in the grass plantings studied here? (ii) Is the effect of biomass harvest large enough to negate benefits of grasslands relative to maize? Most grass plantings included in this study were managed for conservation purposes and not biomass harvest, reflecting the current dominant human motivation for planting warm-season grasses in existing landscapes. To explore the short-term impacts of plant biomass removal on biodiversity and ecosystem services, we compared data from (i) grassland sites where biomass had been

removed via burning or mowing within a year of data collection to (ii) data from sites where plant biomass had not been removed for 2 or more y (Table S4). We used data from these sites in two ways. First, we parameterized generalized linear models to calculate means and confidence intervals for select diversity and service variables in (i) corn, (ii) perennial grasses where biomass was removed via burning or mowing in the spring of the sampling year or during the prior year, and (iii) grasses where biomass had not been removed in 2 or more y. Second, we conducted contrasts using these models to compare differences between grasslands managed in different ways to the overall difference between grasslands and corn estimated in the main manuscript (Fig. 3). To accomplish this, we drew from datasets on plant species richness ($n = 21$), bee species richness ($n = 50$), plant biomass production ($n = 28$), removal of pest eggs ($n = 59$), and pressure of pest aphids ($n = 17$); subsets of the larger datasets from the

paper were used to focus on sites where we had obtained complete information on all facets of management. We used an additional dataset on richness of blooming flowers, described but not analyzed as a response variable in published work, which was available for a large number of sites (6). We used these datasets because sampling overlapped with collection of management data in 2009. Overall, differences between grasslands where biomass was recently removed or not removed were smaller than the overall difference between grasslands and corn (Figs. S2 and S3). The only difference between “biomass removed” and “not removed” sites was for floral richness, which was lower in sites not recently burned or mowed (Figs. S2 and S3). These results suggest that the short-term effects of biomass harvest are unlikely to negate the biodiversity and ecosystem service benefits of grasslands compared with maize; however, studies to directly test that hypothesis are warranted.

1. Levine UY, Teal TK, Robertson GP, Schmidt TM (2011) Agriculture's impact on microbial diversity and associated fluxes of carbon dioxide and methane. *ISME J* 5(10):1683–1691.
2. Konstantinidis KT, Ramette A, Tiedje JM (2006) The bacterial species definition in the genomic era. *Philos Trans R Soc Lond B Biol Sci* 361(1475):1929–1940.
3. Schloss PD, et al. (2009) Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microbiol* 75(23):7537–7541.
4. Droege S, et al. (2010) Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conserv Diversity* 3(1):15–23.
5. Ruan L, Robertson GP (2013) Initial nitrous oxide, carbon dioxide, and methane costs of converting conservation reserve program grassland to row crops under no-till vs. conventional tillage. *Global Change Biology* 19(8):2478–2489.
6. Werling BP, Meehan TD, Robertson BA, Gratton C, Landis DA (2011) Biocontrol potential varies with changes in biofuel-crop plant communities and landscape perenniality. *GCB Bioenergy* 3(5):347–359.

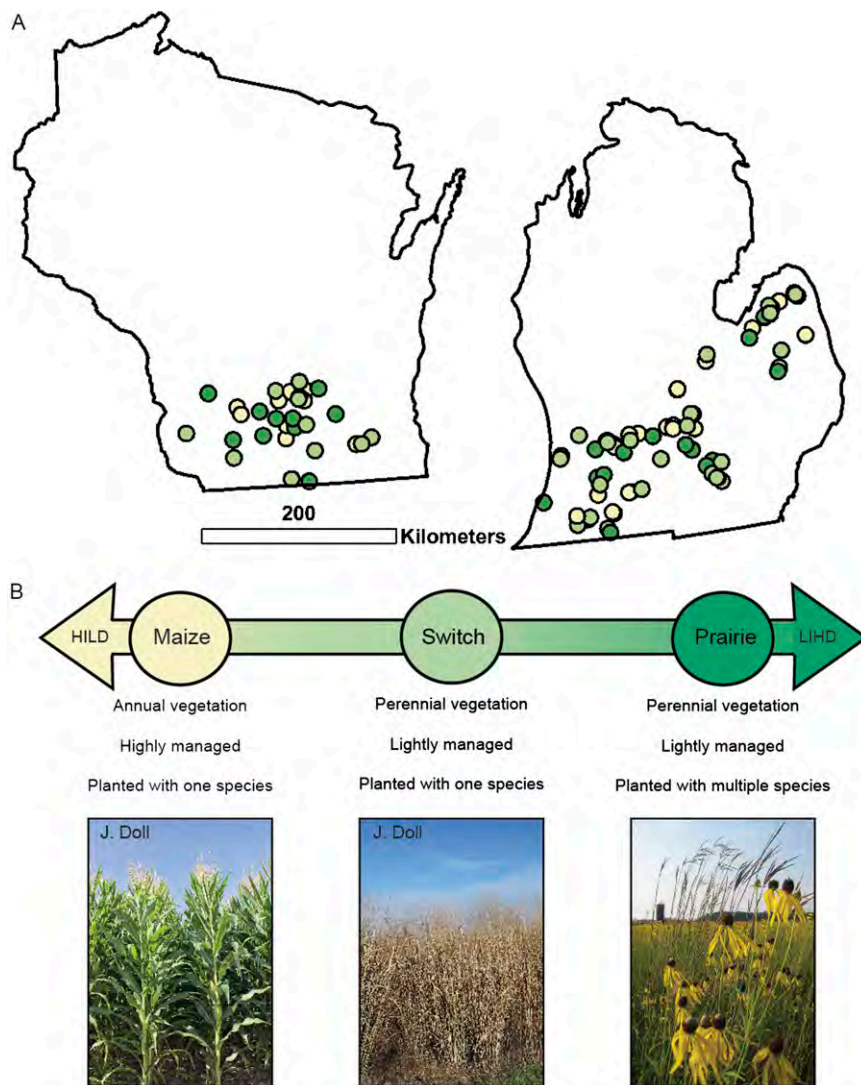


Fig. S1. (A) Location of maize, switchgrass, and prairie sites in Michigan and Wisconsin. (B) Sampled communities represent a gradient of management intensity and sown diversity spanning from high-input, low-diversity (HILD) annual crops to low-input, high-diversity (LIHD) perennial grasslands.

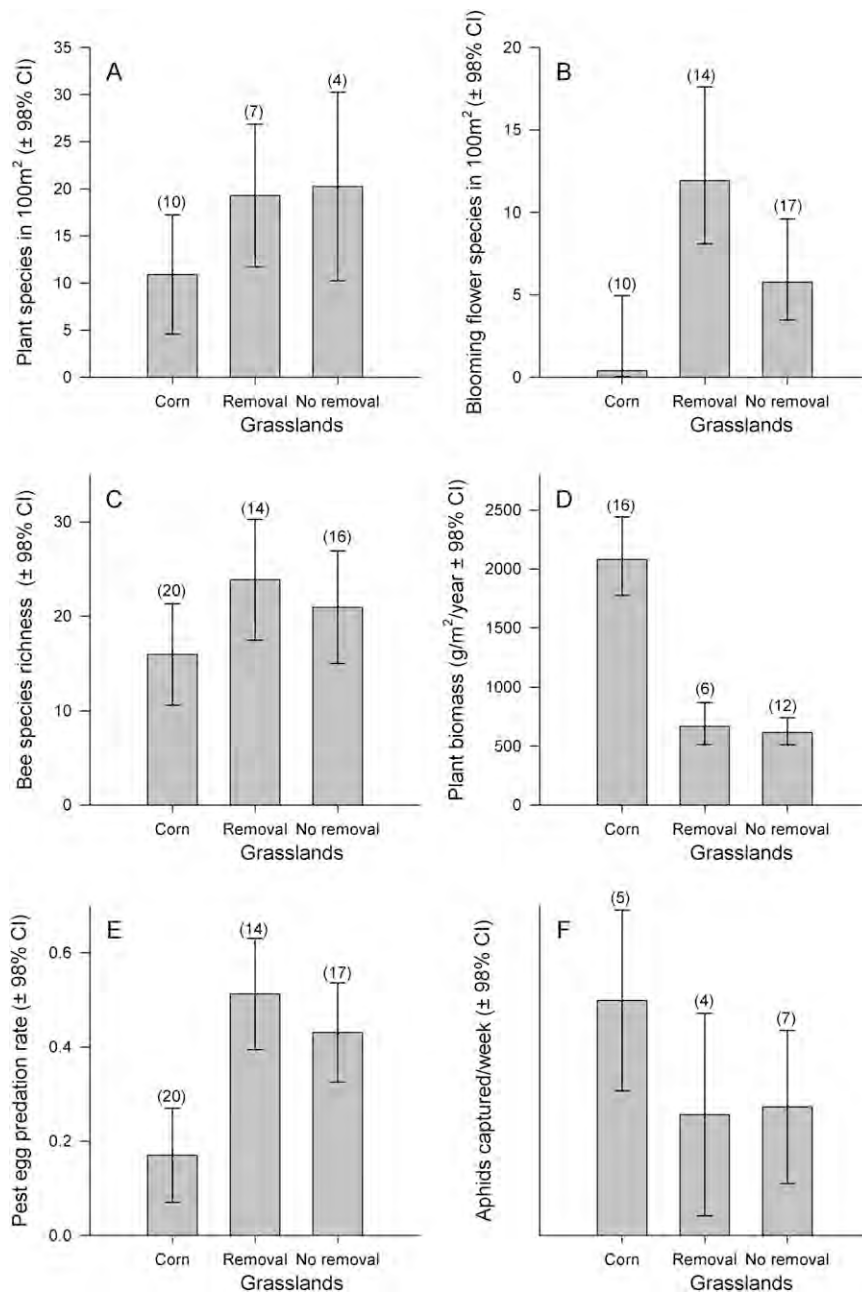


Fig. S2. Graphs show variation in response variables between maize, grasslands where aboveground plant biomass was removed via burning or mowing within the year before sampling, and grasslands which were not burned or mowed in the year before sampling. Diversity variables include richness of (A) all plants, (B) blooming flower species, and (C) bees. Measures of ecological processes include (D) production of aboveground plant biomass, (E) predation of pest eggs by beneficial insects, and (F) pest aphid pressure. Samples sizes are in parentheses.

Table S2. Results of a survey distributed to managers of 20 maize, 20 switchgrass, and 20 prairie plantings in Michigan and Wisconsin during fall 2009

Variable	Maize*	Switchgrass	Prairie
% sites tilled [†]	90% (10)	0% (16)	0% (16)
% sites with whole-field herbicide application	100% (10)	23% (13)	6% (16)
% sites with fertilizer application [‡]	100% (10)	na	na
% sites with vegetation harvested, burned, or mowed in study year	100% (20)	17% (18)	19% (16)
Median number of grass species sown [§]	1 (20)	1 (19)	4 (13)
Median number of forb species sown [§]	0 (20)	0 (19)	8 (10)

n = 60 plantings. The number of landowners responding to a given question is given in parentheses.

*Only 10 maize farmers in Michigan returned responses to detailed survey questions.

[†]Six out of 10 Michigan farmers practiced reduced tillage.

[‡]We did not ask managers of switchgrass and prairie if they applied fertilizer because it is not a typical practice (na, not applicable); one landowner volunteered that they did fertilize their switchgrass, which was the only stand used for biomass production during this study.

[§]At 4 of 19 switchgrass sites a mix of species were originally sown, although stands are currently dominated by *Panicum virgatum*.

Table S3. Biodiversity of multiple taxa and associated ecosystem services were measured at 115 maize, switchgrass, and prairie plantings in Michigan and Wisconsin

Site ID	State	Plant comm	Plant rich	Meth rich	Herb arth rich	Pred arth rich	Bee rich	Bird rich	Plant bmass	Methane cons	Aphid pressure	Pest pred	Pollination	Bird occupancy
1	MI	maize			X	X		X						X
2	MI	maize	X		X	X	X	X	X			X		X
3	MI	maize	X		X	X	X	X	X	X	X	X		X
4	MI	maize	X		X	X	X	X	X			X		X
5	MI	maize			X	X		X						X
6	MI	maize			X	X		X						X
7	MI	maize			X	X		X						X
8	MI	maize	X		X	X	X	X	X		X	X		X
9	MI	maize	X	X	X	X	X	X	X	X		X		X
10	MI	maize	X		X	X	X	X	X			X		X
11	MI	maize	X	X	X	X	X	X	X		X	X		X
12	MI	maize	X		X	X	X	X	X		X	X	X	X
13	MI	maize	X	X	X	X	X	X	X	X	X	X	X	X
14	MI	maize	X				X		X			X		
15	MI	maize							X				X	
16	MI	maize		X					X				X	
17	MI	maize							X					
18	MI	maize							X					
19	MI	maize							X				X	
20	MI	maize							X				X	
21	MI	maize			X	X		X						X
22	MI	maize			X	X		X						X
23	MI	maize			X	X		X						X
24	MI	maize			X	X		X						X
25	MI	maize			X	X		X						X
26	MI	maize			X	X		X						X
27	MI	maize								X				
28	MI	maize								X				
29	MI	maize						X						X
30	MI	prairie	X		X	X		X						X
31	MI	prairie	X		X	X	X	X	X			X	X	X
32	MI	prairie	X	X			X	X	X		X	X	X	X
33	MI	prairie	X		X	X	X	X	X		X	X	X	X
34	MI	prairie	X		X	X		X						X
35	MI	prairie	X	X			X	X	X	X	X	X	X	X
36	MI	prairie	X	X	X	X	X	X	X	X		X	X	X
37	MI	prairie	X	X	X	X	X	X	X	X		X	X	X
38	MI	prairie	X				X	X	X		X	X		
39	MI	prairie	X	X	X	X	X	X	X	X	X	X		X
40	MI	prairie	X	X	X	X	X	X	X	X		X		X
41	MI	prairie	X		X	X	X	X	X		X	X		X
42	MI	prairie			X	X		X						X
43	MI	prairie			X	X		X						X
44	MI	prairie			X	X		X						X
45	MI	prairie			X	X		X						X
46	MI	prairie			X	X		X						X
47	MI	prairie			X	X								
48	MI	prairie			X	X		X						X
49	MI	prairie			X	X		X						X
50	MI	prairie			X	X		X						X
51	MI	prairie		X										
52	MI	prairie						X		X				X
53	MI	prairie			X	X		X						X
54	MI	prairie			X	X								
55	MI	prairie						X						X
56	MI	switch						X						X
57	MI	switch	X	X	X	X	X	X	X	X	X	X		X
58	MI	switch	X		X	X	X	X	X	X	X	X		X
59	MI	switch	X											
60	MI	switch	X		X	X								
61	MI	switch	X											

Table S3. Cont.

Site ID	State	Plant comm	Plant rich	Meth rich	Herb arth rich	Pred arth rich	Bee rich	Bird rich	Plant bmass	Methane cons	Aphid pressure	Pest pred	Pollination	Bird occupancy
62	MI	switch	X		X	X	X	X	X	X	X	X		X
63	MI	switch	X	X	X	X	X	X	X		X	X		X
64	MI	switch	X		X	X	X	X	X		X	X		X
65	MI	switch	X	X	X	X	X	X	X		X	X		X
66	MI	switch	X		X	X	X	X	X			X		X
67	MI	switch	X				X		X		X	X		
68	MI	switch	X	X	X	X	X		X			X		
69	MI	switch	X	X	X	X	X	X	X			X		X
70	MI	switch			X	X		X						X
71	MI	switch			X	X		X						X
72	MI	switch			X	X		X						X
73	MI	switch			X	X		X						X
74	MI	switch			X	X		X						X
75	MI	switch			X	X		X						X
76	MI	switch			X	X		X						X
77	MI	switch			X	X		X						X
78	MI	switch			X	X		X						X
79	MI	switch								X				
80	MI	switch								X				
81	MI	switch								X				
82	MI	switch			X	X								
83	MI	switch						X						X
84	MI	switch						X						X
85	WI	maize					X					X	X	
86	WI	maize					X					X		
87	WI	maize					X					X	X	
88	WI	maize					X					X		
89	WI	maize					X					X		
90	WI	maize					X					X		
91	WI	maize					X					X	X	
92	WI	maize					X					X	X	
93	WI	maize					X					X		
94	WI	maize					X					X		
95	WI	prairie					X					X		
96	WI	prairie											X	
97	WI	prairie					X					X		
98	WI	prairie					X					X	X	
99	WI	prairie					X					X		
100	WI	prairie					X					X		
101	WI	prairie					X					X	X	

Plant species richness (Plant rich), richness of methanotrophic soil bacteria (Meth rich), herbivorous (Herb arth rich) and predatory arthropods (Pred arth rich), bees, birds, aboveground production of plant biomass (Plant bmass), methane consumption (Meth cons), pressure of aphid pests, predation of pest eggs (Pest pred), pollination of sunflowers, and occupancy of sites by grassland-dependent bird species dependent on grasslands for breeding were measured in maize, switchgrass, and prairie communities in Michigan and Wisconsin.

Table S4. Complete survey data on management were available from $n = 31$ sites, which were used to estimate the effect of management on select response variables

Site ID	State	Plant comm	Plant rich	Floral rich	Bee rich	Plant bmass	Aphid pressure	Pest pred	Burned	Mowed	Harvested	Fertilized
31	MI	prairie		X	X	X		X				
32	MI	prairie		X	X	X	X	X	X			
33	MI	prairie	X	X	X	X	X	X		X		
35	MI	prairie	X	X	X	X	X	X	X			
36	MI	prairie	X	X	X	X		X	X			
37	MI	prairie		X	X	X		X				
38	MI	prairie		X	X	X	X	X				
39	MI	prairie	X	X	X	X	X	X				
40	MI	prairie	X	X	X	X		X				
41	MI	prairie	X	X	X	X	X	X		X		
58	MI	switch		X	X	X	X	X				
62	MI	switch		X	X	X	X	X				
63	MI	switch		X	X	X	X	X				
65	MI	switch	X	X	X	X	X	X				
66	MI	switch	X	X	X	X		X				
67	MI	switch	X	X	X	X	X	X				
68	MI	switch	X	X	X	X		X	X			
69	MI	switch	X	X	X	X		X				
98	WI	prairie		X	X			X	X			
99	WI	prairie		X	X			X	X			
101	WI	prairie		X	X			X	X			
104	WI	prairie		X	X			X				
105	WI	prairie		X	X			X	X			
106	WI	switch		X				X				
107	WI	switch		X	X			X	X			
108	WI	switch		X	X			X			X	X
109	WI	switch		X	X			X				
110	WI	switch		X	X			X				
112	WI	switch		X	X			X				
113	WI	switch		X	X			X	X			
115	WI	switch		X	X			X	X			

Switchgrass and prairie sites for which data on both management and plant species richness (Plant rich), richness of blooming flower species (Floral rich), bees, birds, aboveground production of plant biomass (Plant bmass), pressure of aphid pests, and predation of pest eggs (Pest pred) were available. Some sites had not been managed in the year leading up to the study, whereas others had biomass removed via burning, mowing (biomass left in field), or harvesting; one switchgrass site was fertilized and used for biomass production. Site ID values match those in Table S3.

Other Supporting Information Files

[Dataset S1 \(CSV\)](#)

[Dataset S2 \(TXT\)](#)