

Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes

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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.

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

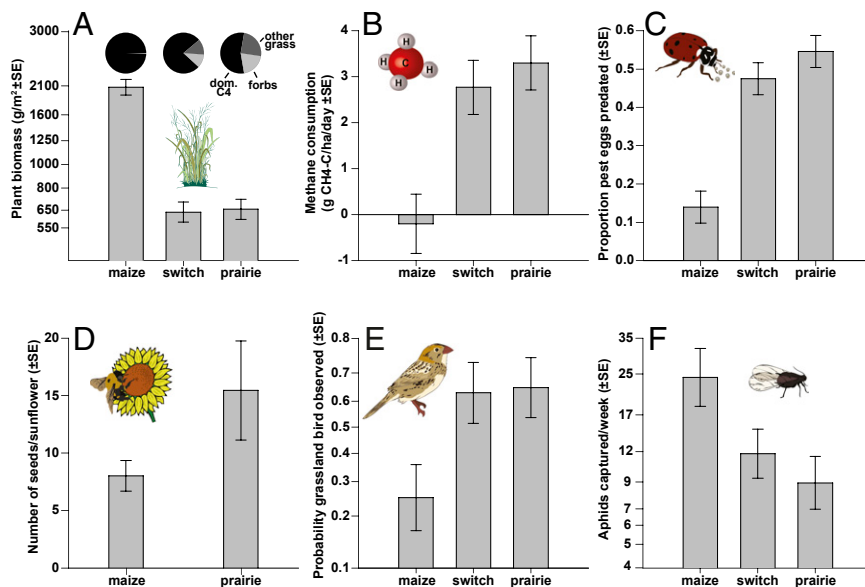


Fig. 2. Key ecological processes varied between maize and perennial grasslands. Variation between maize, switchgrass, and prairie in production of aboveground plant biomass (A), methane consumption by soil methanotrophs (B), predation of pest eggs by beneficial insects (C), pollination of sentinel sunflower 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

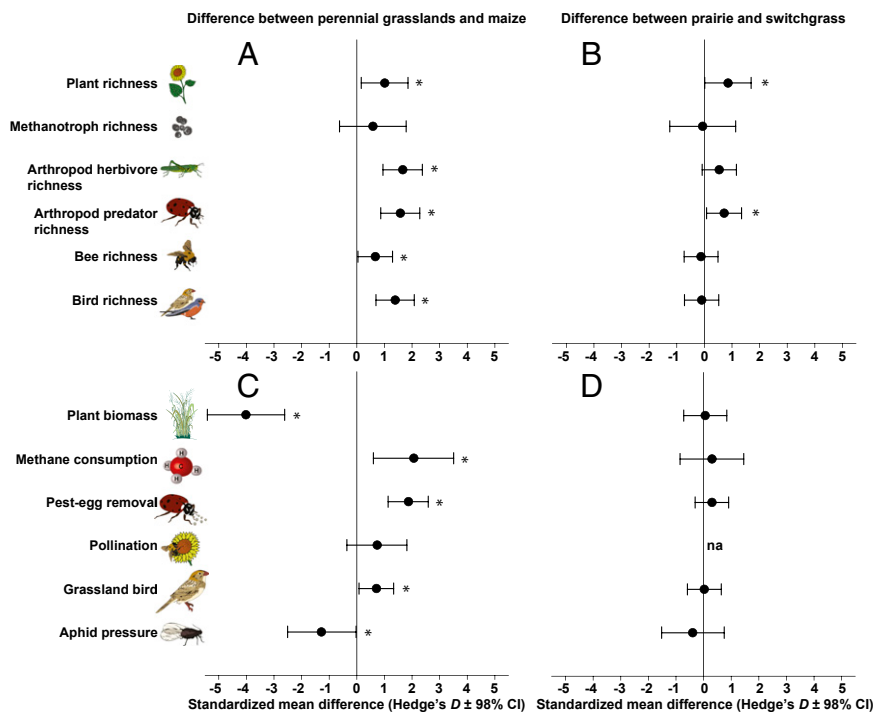


Fig. 3. Differences in richness and ecological processes were larger between the two perennial grasslands and maize than between prairie and switchgrass. Standardized effect sizes (Hedge's *D*) are shown for differences in richness and key ecological processes between grasslands and maize (A and C) (effect 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 $\alpha = 0.02$.

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 \times 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.

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