Grassland biodiversity can pay

Seth Binder[a,b,1], **Forest Isbell**[c,d], **Stephen Polasky**[d,e], **Jane A. Catford**[f,g,h], **and David Tilman**[d,i]

[a]Department of Economics, St. Olaf College, Northfield, MN 55057; [b]Department of Environmental Studies, St. Olaf College, Northfield, MN 55057; [c]Cedar Creek Ecosystem Science Reserve, East Bethel, MN 55005; [d]Department of Ecology, Evolution & Behavior, University of Minnesota, Saint Paul, MN 55108; [e]Department of Applied Economics, University of Minnesota, Saint Paul, MN 55108; [f]Biological Sciences, University of Southampton, SO17 1BJ Southampton, United Kingdom; [g]School of BioSciences, University of Melbourne, Melbourne, VIC 3010, Australia; [h]Fenner School of Environment & Society, Australian National University, Canberra, ACT 0200, Australia; and [i]Bren School of the Environmental Science & Management, University of California, Santa Barbara, CA 93106

Edited by Scott Barrett, Columbia University, New York, NY, and accepted by Editorial Board Member Ruth S. DeFries February 26, 2018 (received for review July 20, 2017)

The biodiversity–ecosystem functioning (BEF) literature provides strong evidence of the biophysical basis for the potential profitability of greater diversity but does not address questions of optimal management. BEF studies typically focus on the ecosystem outputs produced by randomly assembled communities that only differ in their biodiversity levels, measured by indices such as species richness. Landholders, however, do not randomly select species to plant; they choose particular species that collectively maximize profits. As such, their interest is not in comparing the average performance of randomly assembled communities at each level of biodiversity but rather comparing the best-performing communities at each diversity level. Assessing the best-performing mixture requires detailed accounting of species' identities and relative abundances. It also requires accounting for the financial cost of individual species' seeds, and the economic value of changes in the quality, quantity, and variability of the species' collective output—something that existing multifunctionality indices fail to do. This study presents an assessment approach that integrates the relevant factors into a single, coherent framework. It uses ecological production functions to inform an economic model consistent with the utility-maximizing decisions of a potentially risk-averse private landowner. We demonstrate the salience and applicability of the framework using data from an experimental grassland to estimate production relationships for hay and carbon storage. For that case, our results suggest that even a risk-neutral, profit-maximizing landowner would favor a highly diverse mix of species, with optimal species richness falling between the low levels currently found in commercial grasslands and the high levels found in natural grasslands.

biodiversity | multifunctionality | optimal management | agriculture | ecological production function

Does biodiversity pay? Increasingly, evidence points to the important causative role of species diversity in promoting ecosystem functioning and stability (1, 2). Experimental evidence shows that, on average, as the level of diversity rises so too do measures of ecosystem functioning, such as primary production and carbon storage. The relationship applies not only to single ecosystem functions but to many functions taken together—so-called "ecosystem multifunctionality" (3, 4). Moreover, the temporal stability of ecosystem function increases with greater levels of diversity (5, 6). Qualitatively similar biodiversity–ecosystem function (BEF) relationships have been demonstrated for a variety of ecosystems, including grasslands, crop systems, and even plantation forests (7, 8). The documented ecological benefits of species diversity might seem to suggest a positive economic value to greater diversity in managed ecosystems.

The possibility of unrealized biodiversity payoffs has obvious salience for private land managers, but also for society at large. Productive forests and grasslands make up approximately one-third of the Earth's land surface (9, 10). Even as they are managed for private gain, they produce nonmarket ecosystem services and provide habitat for desirable species. If landowners could simultaneously increase biodiversity and profitability, the societal costs of achieving multiple-use objectives on public land could fall, as could the costs of achieving landscape-scale conservation goals that require the compensation of individual landowners for enhancing biodiversity (as in the US Conservation Reserve Program). The substantial difference in biodiversity between natural and conventionally managed systems implies ample potential for diversification.

However, the biodiversity gap between natural and managed systems is also cause for skepticism that more biodiversity could be profitable. If the benefits of diversity were known, profit-maximizing land managers would have accounted for this already, enhancing diversity to the point where its private marginal value is zero. While there is reason to think that landowners might not be fully informed about the profit potential of more diverse mixtures—the cost of assessing the relative performance of many different species combinations could be prohibitive—the BEF literature itself does not directly speak to the question of profitability or offer guidance for land managers.

Despite demonstrating a positive relationship between biodiversity and ecosystem function, the BEF literature does not address questions of marginal value or optimal management. The disconnect between the ecological evidence and the key economic questions occurs along two dimensions. The first relates to benefits and costs. Greater ecosystem productivity does not necessarily translate into greater benefits to landowners. More biomass may not be better if it belongs to undesirable species or simply comes at the expense of more desirable species. Similarly, ostensibly greater multifunctionality may come at the cost of a particularly valuable function because current multifunctionality

Significance

Ecological research suggests that greater biodiversity could lead to greater economic value, even for private owners of "working" land. However, the studies from which such a conclusion might be inferred do not account for all relevant information in a coherent economic framework. Our paper applies standard economic theory to rigorously account for costs, quality, and risk. Results indicate that higher levels of biodiversity than are typically observed on commercial grasslands would maximize landowner value in the experimental grassland we study. Greater private benefits from biodiversity could encourage private investment in biodiversity and reduce the cost of public conservation efforts.

Author contributions: S. Binder and F.I. designed research; S. Binder performed research; S. Binder analyzed data; D.T. conducted the original experiment; and S. Binder, F.I., S.P., J.A.C., and D.T. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. S. Barrett is a guest editor invited by the Editorial Board.

[1]To whom correspondence should be addressed. Email: binder@stolaf.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1712874115/-/DCSupplemental.

indices equally weight all ecosystem functions. BEF analyses address neither such implicit opportunity costs nor explicit input costs. These costs matter. Even if greater productivity does lead to greater benefits, the explicit costs of achieving or managing more diverse systems could outweigh the benefits.

Second, and perhaps more fundamentally, evidence relating diversity indices to ecosystem function does not align with land managers' discretion in determining the specific mix of species planted. Unlike conservation contexts in which decision makers can influence the likely number but not the particular identities of species that contribute to the value of carbon storage (11) or other ecosystem services, managers of "working" ecosystems actively determine the presence and abundance of target species. A land manager does not receive a randomly drawn combination of, say, grass or tree species at any given level of richness that she might select, but rather chooses a particular combination and relative abundance of species from a feasible set; the richness level follows from this choice. It is the best-performing species mix, not the average species mix, at each level of richness that matters to a land manager.

In economic terms, the privately optimal species mix is that which maximizes the net benefits to the landowner. (The socially optimal mix would additionally account for costs and benefits that accrue to others, maximizing net benefits to society. In this usage, "optimality" corresponds to an objective measure of economic efficiency and is not necessarily meant to convey a choice that is ethically most preferable.) More precisely, the landowner seeks to maximize the expected utility of her planting decision, which can be understood as an optimal portfolio problem (12). In monetary terms, she seeks to maximize the certainty-equivalent (i.e., risk-adjusted) net present value of profits (*Economic Model*). Calculated over an infinite time horizon, this is equal to the certainty-equivalent value of the land. The difference in the (maximum) certainty-equivalent value of the land at adjacent richness levels is the marginal value of richness (*Economic Model*). If marginal value is positive then (more) biodiversity pays.

Favorable species interactions (e.g., niche partitioning, which makes competition weaker between than within species, or facilitation) are a necessary condition for some amount of diversity to pay, but they complicate the analysis. Without interactions, it would not be possible for a multiple-species mixture to outperform the most profitable monoculture. Plus, risk-reduction benefits associated with diversification could be achieved by planting multiple species separately in monoculture, a solution equivalent to standard financial portfolio optimization (13). Species interactions greatly complicate the optimal portfolio problem. Imagine if an investor's selection of equities for her portfolio simultaneously determined the composition and competitive structure of the market in which the firms operate. The landowner must know not only how the productivities of individual species covary when planted in monoculture, but how they covary and perform in the aggregate when planted in particular combinations. Optimizing the species portfolio is an information-intensive proposition.

The method we present relies on experimental data to directly estimate production relationships for grassland species. It draws on the idea of the ecological production function (EPF) (14). An EPF quantifies the relationship between ecological inputs and particular ecosystem outputs. We extend the EPF approach to incorporate biodiversity as an input. Building on the diversity–interaction model (15), our empirical approach accounts for various dimensions of biodiversity—species richness, species identity, and relative abundance—and their influence on the quantity, quality, and variability of hay production. Utilizing data from the longest-running biodiversity experiment in the world, which is at Cedar Creek Ecosystem Science Reserve (*Cedar Creek Long-Term Ecological Research Data*), we estimate EPFs and simulate land values for all possible combinations of up to 16 grassland species. We investigate a base case, in which a risk-neutral landowner maximizes the expected net present value of hay production in 10-y rotations, and we also explore alternative scenarios with internalized carbon values and "insurance" values (16) corresponding to varying degrees of risk aversion (*Economic Data*). This study does not attempt to capture the full social value of diversity. Accounting for the value of other ecosystem services such as habitat provision or the retention of nitrogen and soil might lead the socially optimal level of diversity to diverge from the privately optimal level studied here.

A focus on grasslands is both salient and practical. Managed grasslands represent the most extensive land use worldwide (9). They also offer a simpler production context than do many other multispecies agricultural production problems, making the experimental grassland a relatively strong proxy for a commercially managed system. Land managers seek to plant or retain species that are highly productive in terms of biomass but also protein-rich, balancing quantity and quality. They typically use one-, two-, three-, or four-species mixtures. However, it may be profitable to diversify beyond four-species mixtures.

Results

We find that even a risk-neutral, profit-maximizing landowner would favor a highly, but not maximally, diverse mix of species. In this base case, maximal land values exhibit a pronounced inverse U-shaped relationship with richness, peaking with an optimized 11-species mixture, while average values across all mixtures at each richness level peak at the 16-species extreme (Fig. 1). This pattern holds, with slight differences in optimal richness, for alternative cases that incorporate risk aversion and compensation for carbon storage. Increasing risk aversion leads to slightly greater species evenness but does not generally increase optimal richness. Internalizing even a very high carbon price has little effect on the optimal richness level. (Compensation for below-ground carbon storage could induce changes in other management practices, not modeled here, which might then affect optimal richness. For example, if younger plants sequester more carbon and it is possible to reseed without losing much of the carbon already accumulated below ground, it might be profitable to accelerate reseeding and reduce the life of the stand. Because the yield advantage of more diverse mixes appears to grow over time, reducing the life of the stand might reduce the marginal value of richness.) Despite the large and positive effect of the omitted species (mostly forbs) on root biomass (Table S1), they are not planted due to their very high seed prices (an order of magnitude greater than the price of other seeds).

Across all carbon-price and risk-aversion scenarios, mixes of 9–12 species dominated by *Panicum virgatum*, a warm-season grass, and *Dalea purpurea* (formerly *Petalostemon purpureus*), a legume, making up between 35–40 and 52–56% of planted biomass, respectively, consistently yield the greatest economic value. All other species present in the optimal mix appear at the constrained minimum (1% of planted biomass). Three nonleguminous forbs, *Asclepias tuberosa*, *Liatris aspera*, and *Monarda fistulosa*, are always left out of the optimal mix, primarily due to their prohibitive prices. In comparison, the mixture maximizing an index of multifunctionality based on the geometric mean of normalized function values contains 15 species and is dominated by *P. virgatum* (23%) and *Lespedeza capitata* (64%).

While the economically optimal mixes exhibit high multifunctionality, compositions that maximize multifunctionality have poor economic performance (Fig. 2). With the exception of monocultures, the composition maximizing economic value at each level of richness yields between 87 and 90% of the highest multifunctionality score at the same richness level. The converse is not true: At each level of richness, the composition maximizing the multifunctionality index leads to a large economic loss. This occurs despite some similarities in composition: Both the profit-

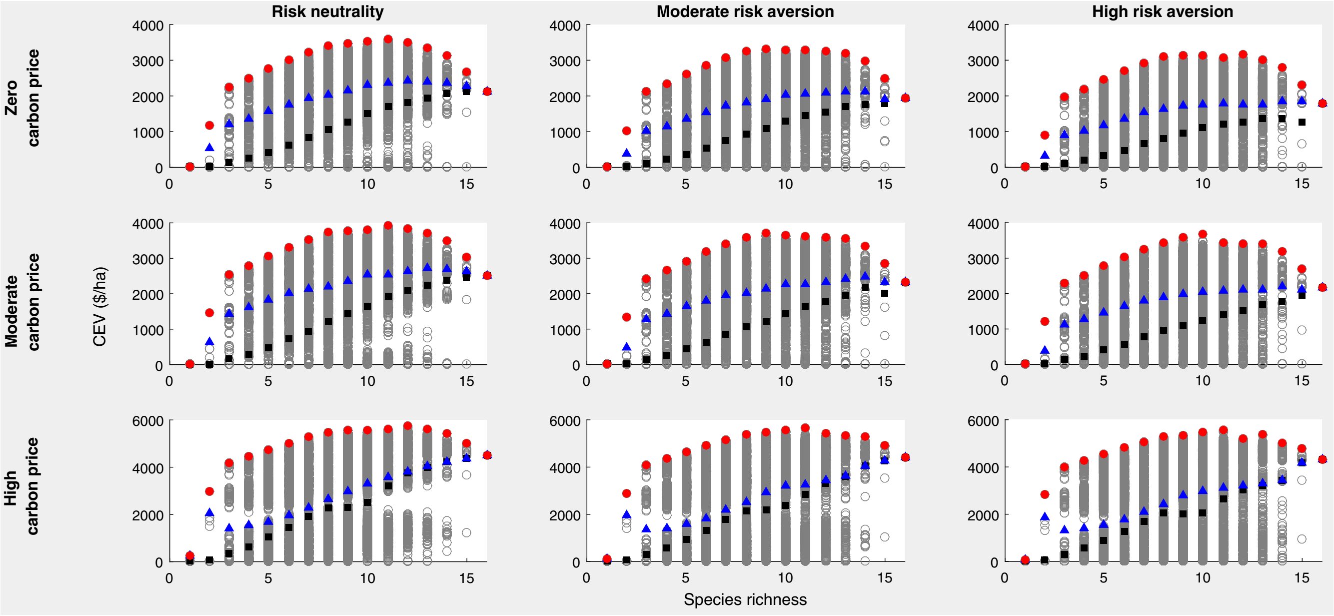

Fig. 1. The figure illustrates the relationship between species richness and economic value for each of nine scenarios representing different combinations of risk aversion and carbon price parameters. Economic value is measured as the certainty-equivalent present value of the future stream of profits from planting a given mixture of species. Potential economic losses are underemphasized here, as negative values have been censored to zero. Each gray, open circle depicts the value of one of the 65,535 possible combinations of species across the 16 levels of richness. The relative abundance of species has been optimized for each combination. Red circles correspond to the species combination that yields the greatest economic value at each level of richness. Blue triangles correspond to the average of compositions yielding strictly positive certainty-equivalent value at each level of richness, while the black squares correspond to the average of all compositions—including those with negative values, censored to zero—at each level of richness.

maximizing and multifunctionality-maximizing mixes are dominated by a legume and *P. virgatum*. The two mixtures, however, differ considerably in cost. Even compositions that maximize an index of cost-effective multifunctionality (index value per dollar of seed cost) perform poorly when it comes to profitability. At best, such compositions deliver one-third of the maximal value; many still lead to losses.

Discussion

While the BEF literature provides strong evidence of the biophysical basis for the potential profitability of greater diversity, such evidence is incomplete for management purposes. Relying only on information about the average relationship between economic value and an index of biodiversity such as richness could lead to over- or underinvestment in diversity. Based on the average values depicted in Fig. 1, a naive land manager might choose the 16-species mix, resulting in excess diversity relative to the economic optimum. She would forego more than 50% additional expected profit. However, a manager currently using, say, the most profitable three-species mix might compare the value of that mixture to the average values of other richness levels and decide to stay with her more profitable, low-diversity mix. For lack of better information she, too, would forego more than 50% in additional expected value.

Similarly, while existing multifunctionality indices provide valuable insight into ecological aspects of agroecosystems, they can also lead to poor management prescriptions. As with average land values, multifunctionality is maximized at peak biodiversity. Also, as with average land values, using multifunctionality as a proxy for the landowner's true decision criterion (risk-adjusted profit) can lead to an inferior choice of species and a loss of profit. Multifunctionality maximization leads not only to an overprescription of biodiversity and some foregone profit; it leads to large economic losses at any level of biodiversity–all for relatively little gain in multifunctionality over the profit-maximizing compositions.

Whereas the trouble with relying only on species richness lies in averaging over different species compositions, the trouble with multifunctionality indices lies in (arbitrarily) averaging over different ecosystem functions and ignoring input costs. Arbitrary averaging is problematic because the marginal benefits of some ecosystem functions are much greater than others; failing to account for differences in cost across compositions is problematic because the marginal explicit costs (i.e., of seeds) of some species are much greater than others. An economically rigorous approach must consider the contributions of ecosystem functions to the quantity, quality, or variability of particular "end products" that people value directly (17). The value of changes in the quantity, quality, or variability of such end products must be assessed with respect to individuals' own subjective preferences to back out the economic value of changes in biodiversity (18). For management and policy purposes, ecosystem service indices (19) can provide a useful complement to multifunctionality indices and may often be more valuable for weighing tradeoffs.

Although inference from purely ecological assessments could lead decision makers to diverse but economically inefficient species mixtures, our empirical analysis and simulation results demonstrate that a biodiverse grassland can be much more economically productive than monocultures. This holds even in the absence of risk aversion or the internalization of carbon-storage benefits. At the same time, the marginal value of richness ultimately falls below zero at high levels of richness. Very high levels of richness are not optimal because even when species interactions enhance ecosystem function they come at a cost by diluting the abundance of particularly valuable species. Marginal species may also have higher seed costs.

Seed cost appears to be an important part of opportunity cost in this case. Seven of the eight different species excluded from at least one optimal mix under the various scenarios have a seed price greater than $100 per pound. The average price of these excluded species is more than 13 times the average price of the

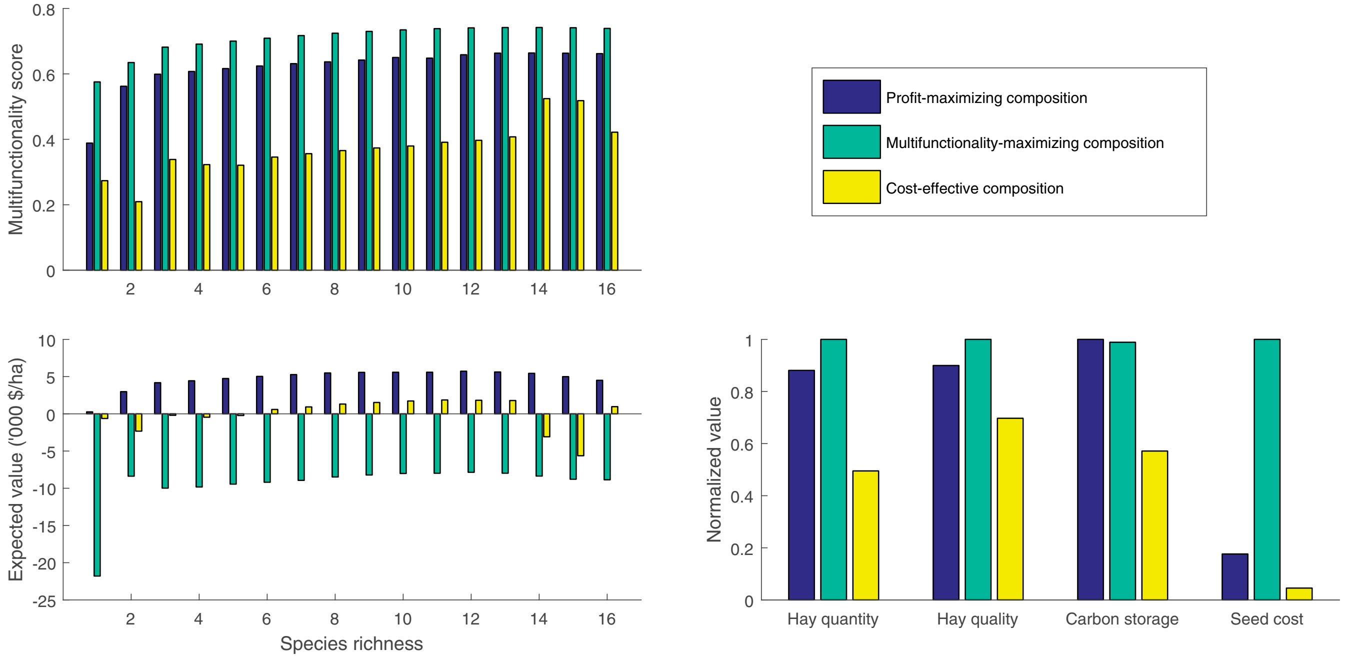

Fig. 2. The figure compares the ecological and economic performance of species compositions optimized for three different objectives: profit-maximization, multifunctionality, and cost-effective multifunctionality (index value per dollar). *Upper Left* shows the multifunctionality index score for the best-performing mixtures for each objective at each level of species richness, while *Lower Left* shows the net present economic value of the best-performing mixtures for each objective at each level of richness. *Lower Right* unpacks the constituents of economic value, revealing how mixtures optimized for the different objectives perform relative to one another in terms of hay quantity, hay quality, carbon storage, and seed cost.

included species. One might argue that, were the seeds of these niche market species produced at commercial scale, their lower prices could lead to an even more diverse optimum. The most commonly excluded species (the nonleguminous forbs), however, have negative interaction effects in the production of nitrogen and are simply not as desirable as the others due to their lower digestibility and lower individual nitrogen content (Table S1). In other words, some species are both costly and of low value. This points to the importance of implicit opportunity costs in addition to explicit input costs.

Results from the application of our model to the Cedar Creek data provide evidence consistent with the hypothesis that biodiversity pays, but they should be interpreted with care. The case we study differs in some important ways from that facing the manager of a hay meadow. We discuss whether and how these differences are likely to affect the results. One important consideration is scale. We simulate per-hectare land values on the basis of EPFs estimated from data collected on 9-m × 9-m plots. Diversity benefits that arise from facilitation and niche partitioning might be affected by spatial scale. For example, if increasing scale brings with it an expansion of the potential niche space, then this could enhance the benefits of the marginal species (20). Furthermore, if there is greater production or accumulation of specialist pathogens or herbivores in larger versus smaller monocultures, dragging down yields, then diversity benefits might have been greater had we considered larger experimental plots or whole fields. Empirically, only one biodiversity experiment has been conducted at multiple spatial scales, finding equivalent strengths of biodiversity effects on plant productivity at small (12 m^2) and large (400 m^2) scales (21). Similarly, in estimating the contributions of biodiversity to agricultural production in the Ethiopian highlands Chavas and DiFalco (22) found no evidence that the value of diversity is affected by scale. While there remains the possibility of bias, the evidence does not seem to preclude scaling the EPF to simulate commercial land values.

The sensitivity of our results to the composition of the set of candidate species is also an important question. The set of species we study is restricted to native grassland species and excludes some important commercial hay species, such as alfalfa. Incorporating such species in the candidate set might raise the opportunity cost of diversification associated with diminishing the proportion of the most desirable species. This would reduce the optimal level of diversity. However, the results here and elsewhere (23, 24) indicate that a substantial portion of the benefits of diversity can be achieved utilizing only small proportions of additional species, mitigating the opportunity cost of diversification. Nevertheless, it is important to explore how the marginal value function might change with the candidate set.

Another important consideration is that plots in the Cedar Creek experiment we utilize (e120) did not receive randomized management treatments, so we are unable to investigate directly the possible interactions or tradeoffs between biodiversity and management intensity. Evidence suggests that the basic positive relationship between grassland diversity and average productivity remains under intensive management (24–26), as does the potential for transgressive overyielding, that is, for higher-diversity mixtures to outperform the highest-yielding monocultures (25). Increasing management intensity might still affect the marginal value and economically optimal level of species richness. The marginal value of richness would rise with intensity if the (presumably positive) effect of intensity positively interacts with richness. The marginal value of richness would fall with intensity if intensity interacts negatively with richness. Even then, the optimal level of diversity might remain unchanged, depending on whether it is actually profitable to increase management intensity.

For hay meadows, two important dimensions of management intensity that could affect optimal diversity are the frequency of mowing and the rate of fertilizer application. Hay meadows are mown anywhere from one to six times per year. Mowing intensity appears to interact positively with the log of species richness in a 2-y experimental study with up to 16 species planted in mixture

(26). This suggests that optimal richness might rise with more frequent mowing, although it may be difficult to maintain diversity at mowing frequencies in excess of three times per year (27). Evidence from ref. 26 on the short-run interaction effect of fertilization is weaker—an index of mowing and fertilization intensity shows statistically significant positive interaction effects while the interaction effect of fertilizer alone is positive but statistically insignificant—and in the long run high levels of realized diversity are difficult to maintain with the application of fertilizer (27). In the case of fertilizer, then, it might be cheaper to produce the same level of output using high-intensity management with relatively little diversity than to rely on a high-diversity mixture. Existing evidence allows a simple thought experiment. In controlled experiments, average yields of unfertilized, high-diversity plots are comparable to those of fertilized low-diversity plots (26). Assume that the best-performing four-species mix could achieve the same yield (and quality) with fertilization as the optimal 11-species mix does without fertilization in our study. The landowner would incur annual fertilizer costs of approximately \$68 per acre (28) in exchange for saving only \$50.35 per acre in seed cost over the life of the stand. Accounting for risk-reduction benefits of the high-diversity mix sets an even higher bar for fertilization to outperform diversification.

The various factors considered above have the potential to alter the optimal level of species richness, but none obviously overturns the prima facie evidence we offer that biodiversity can pay. This raises two important questions. First, if many landowners decided to increase species diversity, could the apparent advantage of biodiversity be sustained in the face of landscape and market effects not considered in our analysis? One such effect is that, as field-scale diversity rises, landscape-scale biodiversity could also rise. Increased landscape diversity might provide additional benefits to landowners at the field scale by further decreasing the risk of pest or disease outbreaks (29, 30). These ecological effects would only enhance the degree to which biodiversity pays, although as positive externalities they would not factor into landowners' private assessment of the optimal level of species richness.

Economically, there are both partial and general equilibrium price effects to consider. First is a (partial equilibrium) change in output prices. Theoretically, an increase in market supply could lead prices to fall proportionally more than quantity sold increases, and the consequent loss in revenues could outweigh producers' cost savings. Whether this would actually occur is an empirical matter, which depends on the price elasticity of demand for hay. From either a normative perspective or a positive perspective, however, the question is moot. The producers' loss is the consumers' gain; overall surplus still increases. Also, producers still face the individual incentive to invest in biodiversity.

A second, more subtle issue is the potential general equilibrium change in input prices. As producers' derived demand for biodiversity increases, this could change the price of seeds. Because demand for the most widely used species would fall as producers diversify, prices of those seeds would drop. Seed prices of less-common species would likely rise—especially in the short run—as demand increases, though prices could drop in the longer run if seed suppliers were able to exploit economies of scale and reduce costs per unit. Changes in input demand and consequent price changes might be slight if the benefits of diversification can be achieved with relatively small proportions of marginal species. In any case, while demand-driven relative price changes for seeds of different species could affect the composition of a producer's optimal species mix and reduce optimal species richness relative to the partial equilibrium analysis, they would not eliminate the advantage of diversification relative to the low-diversity status quo (or else they would not occur).

There still remains the fundamental question: Why would land managers not already have taken advantage of potential gains from greater diversity? Informational constraints are likely an important factor. As we have shown, the BEF literature, which demonstrates the average relationship between richness and ecosystem function, does not provide information sufficient for profit-maximizing planting choices. Landowners are unlikely to have obtained the necessary information on their own, because it is costly. Our study leverages extensive, long-term experimental data and advanced statistical analysis to simulate all 65,535 possible combinations of the 16 candidate species and identify the most profitable. If the optimal seed mixture for a given pasture is a high-diversity combination, a land manager is unlikely to identify it by trial and error or casual experimentation. Given the conventional wisdom in favor of low-diversity mixtures and uncertainty over the potential gains from diversification, land managers might have had little incentive to devote the time, effort, and land necessary to conduct the type of experiment that could yield the insights we have produced here. Our results suggest that such experimentation by large pasture owners or extension services may be warranted. The analytic framework and methodology we present offers a template to be adapted and refined for particular management contexts.

Methods

Our model applies the basic principles of production theory to assess the relationship between biodiversity "inputs" and agricultural output. Much applied work on the microeconomics of agricultural production relies on the theory of the dual (31) to make inferences about the production function based on observed market prices and cost data from a sample of individual producers. Use of such observational data to shed light on the production technology works well when the assumptions of the underlying theory are likely to hold. However, if producers are unaware of potential benefits of biodiversity and restrict themselves to low-diversity production strategies, the costs of their corresponding decisions cannot yield insight on the unexploited region of the production set. Utilizing experimental data, as we do here, allows a direct analysis of the production set space over a greater range of species diversity.

We utilize detailed information on the species planted and repeated measures of ecosystem functions over time to establish the relationship between biodiversity and the temporal mean and variance of the quantity and quality of hay production. Quantity and quality are aggregate, not species-specific, variables—all species in the hay mixture are cut and baled together—captured by measures of above-ground biomass and nitrogen percentage, respectively. The quality of grass hay is primarily determined by its crude protein content, which is itself a function of nitrogen content, and we find that price scales linearly with expected crude protein content (*Economic Data*). In additional analysis, we estimate the relationship between biodiversity and the mean and variance of carbon storage in the root system, valued using the social cost of carbon (*Economic Data*). Taken together, estimated EPFs for above-ground biomass and nitrogen percentage and root biomass and carbon percentage provide the basic inputs to the economic profit and utility functions used to evaluate different species mixtures (*Economic Model*).

EPF Specification and Estimation. Contributions of planted species to ecosystem outputs can be thought of as the result of individual effects associated with particular species plus effects arising from interactions among species, as captured in the "diversity–interaction" (DI) model (15):

$$y = \sum_{i=1}^{n} \beta_i b_i + \sum_{i>j}^{n} \delta_{ij} b_i b_j + \varepsilon,$$

where y is the functional response or output variable of interest, β_i represents the expected contribution of species i to ecosystem function if (or as if) it were planted in isolation, and coefficients δ_{ij} represent the change in output due to the interaction of species i and j. (In our application to hay production, estimation of a single output quantity suffices. In other contexts, in which species represent distinct goods, it would be necessary to estimate separate output quantities.) Positive interaction coefficients imply potential benefits from increasing richness. Such complementarity also implies benefits to evenness.

The DI model as proposed by ref. 15 specifies only pairwise species interactions. If unmodeled higher-order interaction effects exist—for example, one species moderating the competition or facilitation between two others—then the included coefficients represent the statistical average of effects across all observed levels of richness. They do not necessarily represent the expected identity and interaction effects that would be observed in monoculture or two-species mixtures. One must account for higher-order effects to obtain more informative parameter estimates for planting decisions. With a very small set of candidate species, it may be possible to estimate all possible interaction effects. In most cases, however, the data requirements for estimating a full model are prohibitive.

Lacking the statistical power to identify significant differences in the effects of higher-order interactions for different combinations of species, one might instead include an average effect $\bar{\delta}_k$ for each k-way interaction:

$$y=\sum_{i=1}^{n}\beta_i b_i+\sum_{i>j}^{n}\delta_{ij}b_ib_j+\sum_{k=3}^{n}\bar{\delta}_k\Pi_k(b_1,b_2,...,b_n),$$

where the elementary symmetric polynomial $\Pi_k(b_1,b_2,\ldots,b_n)$ is the sum of all $C(n,\ k)$ products of species proportions. The aggregate value of the additional k-way interaction effects is driven by richness and evenness: The greater the richness, the more terms; the greater the evenness, the stronger is each effect. Thus, when $n>5$, it may be possible to estimate a more parsimonious model that includes only $\tilde{R}$, $\tilde{E}$, and their interaction, where

$$\tilde{R}=\begin{cases}R\ if\ R>2\\ 0\ if\ R\le 2\end{cases}$$

$$\tilde{E}=\begin{cases}E\ if\ E>2\\ 0\ if\ E\le 2\end{cases}.$$

This is the strategy we follow. We also estimate functional group interactions rather than individual species interactions to achieve further parsimony.

Because we do not have strong a priori reason to include or exclude particular interaction terms from our model specifications, we employ the Akaike information criteria with finite-sample adjustment for the purpose of model selection (specifically, using a forward selection procedure with -vselect- in Stata 13). In all cases, we retain individual species effects. With the selected ordinary least squares models, we test for random effects, panel-level heteroskedasticity, and serial correlation. Consistent with the notion that biodiversity affects the variability of ecosystem function, we reject the null hypothesis of homoskedasticity for each of the ecosystem functions on the basis of a likelihood ratio test ($P>\chi^2=0.0000$ in each case). Testing for random effects and serial correlation both individually and jointly, we reject the null hypothesis of no random effects for all but root carbon content and reject the null of no serial correlation for root and above-ground biomass. We reestimate each equation accordingly via maximum likelihood using Stata's flexible -mixed- command.

In addition to estimating models for the expected value of each ecosystem output, we utilize information from the variance–covariance structure to account for the role of biodiversity in promoting stability. With T years of observations on plots $k=1,\ldots,N$,

$$\Omega=E(\varepsilon\varepsilon')=diag\ \left[w_k^2\right]\otimes I_T,$$

where w_k^2 is the plot-specific intertemporal variance. For each ecosystem function, we estimate a DI model of the intertemporal variance, using the maximum likelihood estimates of w_k from the original model.

Optimization. Given the estimated EPFs, it is possible to identify the most desirable species mix using the relevant profit and utility functions (*Economic Model*). However, identification of the optimal species mix is complicated by the possible nonconvexity of the EPFs, which arises due to species interactions. Concavity of the production function requires that the matrix of second derivatives (the Hessian) be negative semidefinite. This condition will not generally hold for a production function with species interaction effects. For any given combination of species, there may be multiple locally optimal species proportions. Not only might the optimization problem be nonconvex for a given combination of species, but the production function will exhibit jump discontinuities in richness as species are added to or removed from a combination.

We avoid the problem of jump discontinuities because we solve for the constrained optimum of species proportions—any species planted must make up at least 1% of total planted biomass—for each of the 65,535 possible combinations of species. The optimization algorithm is not required to compare across different combinations, let alone different richness levels. Optimizing the relative abundance of species in a given combination still faces the challenge of nonconvexity. We employ a gradient-based search procedure, MATLAB's fmincon, to identify optimal species proportions. For each combination of n species, the procedure runs from $n+1$ initial points—the maximum constrained proportion of each species, plus full evenness—to guard against the possibility of multiple local optima due to species interaction effects. The gradient-based search appears to perform well. It executes more quickly and reliably than does MATLAB's genetic algorithm. In many cases, the genetic algorithm fails to converge on superior solutions identified by the gradient-based method and does not find any solutions superior to those of the gradient-based method.

ACKNOWLEDGMENTS. We thank an anonymous reviewer for raising the issue of the potential general equilibrium change in input prices. This research was supported by The National Science Foundation (NSF-LTER 1234162) and the Fessler-Lampert Endowment at the University of Minnesota.

1. Balvanera P, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9:1146–1156.
2. Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annu Rev Environ Resour* 45:471–493.
3. Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–190.
4. Lefcheck JS, et al. (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat Commun* 6:6936.
5. Tilman D, Lehman CL, Bristow CE (1998) Diversity-stability relationships: Statistical inevitability or ecological consequence? *Am Nat* 151:277–282.
6. Tilman D, Reich PB, Knops JM (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
7. O'Connor MI, et al. (2017) A general biodiversity–function relationship is mediated by trophic level. *Oikos* 126:18–31.
8. Isbell F, et al. (2017) Benefits of increasing plant diversity in sustainable agroecosystems. *J Ecol* 105:871–879.
9. Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT (2004) Grazing systems, ecosystem responses, and global change. *Annu Rev Environ Resour* 29:261–299.
10. MacDicken K, Jonsson Ö, Piña L (2015) *Global Forest Resources Assessment 2015: How Are the World's Forests Changing?* (Food and Agriculture Organization of the United Nations, Rome).
11. Hungate BA, et al. (2017) The economic value of grassland species for carbon storage. *Sci Adv* 3:e1601880.
12. Koellner T, Schmitz OJ (2006) Biodiversity, ecosystem function, and investment risk. *Bioscience* 56:977–985.
13. Doak DF, et al. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *Am Nat* 151:264–276.
14. Polasky S, Segerson K (2009) Integrating ecology and economics in the study of ecosystem services: Some lessons learned. *Annu Rev Resour Econ* 1:409–434.
15. Kirwan L, et al. (2009) Diversity-interaction modeling: Estimating contributions of species identities and interactions to ecosystem function. *Ecology* 90:2032–2038.
16. Schläpfer F, Tucker M, Seidl I (2002) Returns from hay cultivation in fertilized low diversity and non-fertilized high diversity grassland. *Environ Resour Econ* 21:89–100.
17. Boyd J, Banzhaf S (2007) What are ecosystem services? The need for standardized environmental accounting units. *Ecol Econ* 63:616–626.
18. Brock WA, Xepapadeas A (2003) Valuing biodiversity from an economic perspective: A unified economic, ecological and genetic approach. *Am Econ Rev* 93:1597–1614.
19. Banzhaf HS, Boyd J (2012) The architecture and measurement of an ecosystem services index. *Sustainability* 4:430–461.
20. Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proc Natl Acad Sci USA* 100:12765–12770.
21. Roscher C, et al. (2005) Overyielding in experimental grassland communities–irrespective of species pool or spatial scale. *Ecol Lett* 8:419–429.
22. Chavas JP, DiFalco S (2012) On the productive value of crop biodiversity: Evidence from the highlands of Ethiopia. *Land Econ* 88:58–74.
23. Connolly J, et al. (2013) An improved model to predict the effects of changing biodiversity levels on ecosystem function. *J Ecol* 101:344–355.
24. Finn JA, et al. (2013) Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: A 3-year continental-scale field experiment. *J Appl Ecol* 50:365–375.
25. Lüscher A, et al. (2008) Benefits of sward diversity for agricultural grasslands. *Biodiversity (Nepean)* 9:29–32.
26. Weigelt A, Weisser WW, Buchmann N, Scherer-Lorenzen M (2009) Biodiversity for multifunctional grasslands: Equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences* 6:1695–1706.
27. Plantureux S, Peeters A, McCracken D (2005) Biodiversity in intensive grasslands: Effect of management, improvement and challenges. *Agron Res (Tartu)* 3:153–164.
28. Lazarus WF (2010) Minnesota crop cost & return guide for 2011 (Univ of Minnesota, Minneapolis).
29. Heisey PW, Smale M, Byerlee D, Souza E (1997) Wheat rusts and the costs of genetic diversity in the Punjab of Pakistan. *Am J Agric Econ* 79:726–737.
30. Quaas MF, Baumgärtner S (2008) Natural vs. financial insurance in the management of public-good ecosystems. *Ecol Econ* 65:397–406.
31. Fuss M, McFadden D (1978) *Production Economics: A Dual Approach to Theory and Applications* (Elsevier, Amsterdam).