Journal of Applied Ecology

Journal of Applied Ecology 2016 doi: 10.1111/1365-2664.12765

Functional diversity in cover crop polycultures increases multifunctionality of an agricultural system

Denise M. Finney[1]* and Jason P. Kaye[2]

[1]*Department of Biology, Ursinus College, 601 E. Main St., Collegeville, PA 19426, USA; and* [2]*Department of Ecosystem Science and Management, Penn State University, 116 ASI, University Park, PA 16802, USA*

Summary

1. Ecological studies identifying a positive relationship between biodiversity and ecosystem services motivate projections that higher plant diversity will increase services from agroecosystems. While this idea is compelling, evidence of generalizable relationships between biodiversity and ecosystem services that could be broadly applied in agricultural systems is lacking.

2. Cover crops grown in rotation with cash crops are a realistic strategy to increase agroecosystem diversity. We evaluated the prediction that further increasing diversity with cover crop polycultures would enhance ecosystem services and multifunctionality in a 2-year study of eighteen cover crop treatments ranging in diversity from one to eight species. Five ecosystem services were measured in each cover crop system and regression analysis used to explore the relationship between multifunctionality and several diversity indices.

3. As expected, there was a positive relationship between species richness and multifunctionality, but it only explained a small fraction of variance in ecosystem services (marginal $R^2 = 0{\cdot}05$). In contrast, indices of functional diversity, particularly the distribution of trait abundances, were stronger predictors of multifunctionality (marginal $R^2 = 0{\cdot}15$–$0{\cdot}38$).

4. *Synthesis and application*. In a corn production system, simply increasing cover crop species richness will have a small impact on agroecosystem services, but designing polycultures that maximize functional diversity may lead to agroecosystems with greater multifunctionality.

Key-words: agriculture, agroecology, biodiversity–ecosystem function relationship, community assembly, cover crops, crop diversity, ecosystem services, functional diversity

Introduction

The positive relationship between biodiversity and ecosystem function (BEF) observed in many ecosystems (Tilman, Wedin & Knops 1996; Balvanera *et al.* 2006; Cadotte, Cardinale & Oakley 2008; Cardinale *et al.* 2012) suggests that intentionally increasing plant diversity in managed ecosystems could enhance multiple ecosystem services simultaneously (hereafter ‘multifunctionality’) (Davis *et al.* 2012; Schipanski *et al.* 2014). For agroecosystems, linking biodiversity to ecosystem services has immediate implications for management practices and policies to promote human well-being (Millennium Ecosystem Assessment 2005). While a few well-developed case studies have made this link (Smith, Gross & Robertson 2008; Kremen & Miles 2012; Wood *et al.* 2015), evidence of generalizable relationships between biodiversity and ecosystem services that could be broadly applied in agricultural systems is lacking (Cardinale *et al.* 2012). Here, we examine the emerging practice of multispecies cover cropping to test the hypothesis that greater plant diversity increases agroecosystem multifunctionality.

Agriculture has a long history of incorporating crop diversity in both time via crop rotation (Smith, Gross & Robertson 2008; Davis *et al.* 2012) and space via intercropping (Finn *et al.* 2013; Brooker *et al.* 2015) to increase harvestable yield. Additional agroecosystem services have also been associated with crop diversity such as enhanced pest and disease control (Letourneau *et al.* 2011; Davis *et al.* 2012), improved nutrient management (Blesh & Drinkwater 2013) and sustained soil quality (McDaniel, Tiemann & Grandy 2014; Tiemann *et al.* 2015). Yet, it has also been noted that some important services are not correlated with biodiversity or decrease with increasing diversity (Cardinale *et al.* 2012), which may lead to trade-offs among services when diversity is intentionally increased in agricultural systems (Iverson *et al.* 2014).

*Correspondence author. E-mail: dfinney@ursinus.edu

Cover crops, unharvested crops planted in rotation between cash crops, are a tractable way to increase agroecosystem diversity because it is possible to enhance diversity without fundamentally changing other aspects of farm management (e.g. cash crop management) (Schipanski *et al.* 2014). The BEF relationship suggests that cover crop polycultures could increase functions critical to the production of agroecosystem services. For instance, services that are positively correlated with cover crop biomass [e.g. weed suppression and nitrogen (N) retention (Finney, White & Kaye 2016)] may increase in polycultures that are more productive than component species grown in monoculture. In addition, many cover crop species are recognized for providing specific services; for example, *Secale cereale* L. provides N retention. Polycultures can utilize combinations of cover crops that excel at different services, potentially sustaining a greater number of services and enhanced multifunctionality (Zavaleta *et al.* 2010; Schipanski *et al.* 2014). For example, bicultures combining legume and non-legume species can both supply inorganic N and retain N (Ranells & Wagger 1997). Yet, N cycling is also an area where trade-offs can occur among services; in our own research, we have found that cover crop polycultures that excel at N retention can decrease N supply to and yield of cash crops (Finney, White & Kaye 2016).

Most BEF research to date is based on studies manipulating species richness, but there is growing evidence that functional diversity (the diversity of species' niches or functions) of a community is often more important to ecosystem functioning than richness (Cadotte, Carscadden & Mirotchnick 2011; Flynn *et al.* 2011; Mouillot *et al.* 2011) and can provide a mechanistic link between diversity and ecosystem function (Petchey & Gaston 2006). Such findings have significant implications for agroecosystems; if the functional diversity of a crop mixture is more important to ecosystem function than species richness, optimizing diversity for ecosystem services may not require maximizing richness. Rather, farmers could design polycultures that provide desired services using species combinations that augment biodiversity while minimizing economic or management constraints.

Presumed increases in ecosystem service provision from cover crop polycultures of more than two species have led to a growing interest in this practice among US farmers (Conservation Technology Information Center 2015). Few scientific studies to date, however, have examined whether polycultures do in fact increase the magnitude of individual services (Teasdale & Abdul-Baki 1998; Wortman, Francis & Lindquist 2012; Smith, Atwood & Warren 2014). And with even fewer tests of the relationship between cover crop diversity and multifunctionality (Storkey *et al.* 2015), two critical questions remain unanswered: (i) Does including more species in a cover cropping system lead to greater multifunctionality? (ii) Are there guiding principles for cover crop polyculture assembly that will lead to increases in net multifunctionality?

To answer these questions, we carried out a 2-year study measuring five ecosystem services in cover crop systems ranging in diversity from one to eight species. Using the BEF heuristic as a framework, we hypothesized that the direction of the relationship between cover crop species richness and ecosystem services would be positive, leading to a net positive relationship between richness and multifunctionality. We also evaluated evidence that trade-offs among services led to relationships contrary to the BEF heuristic. Finally, given growing evidence of the influence of functional diversity on ecosystem function, we expected that components of diversity beyond richness would affect multifunctionality and examined the relationship of ecosystem services to additional diversity indices to test this expectation. The relationships we identified between functional diversity and ecosystem services offer guiding principles for cover crop polycultures with the potential to increase agroecosystem multifunctionality.

Materials and methods

COVER CROP CHARACTERISTICS AND ECOSYSTEM SERVICES

Cover crop and ecosystem service data were collected from a 2-year field study of cover crop diversity conducted in central Pennsylvania, USA, as detailed in Finney, White & Kaye (2016). Briefly, 17 (2011–2012) and 18 (2012–2013) cover crop treatments were planted in late August within a small grain-corn (*Zea mays* L.) cash crop rotation following small grain harvest on neighbouring fields. Current farming convention is to categorize cover crops based on two traits: temporal growth pattern and N-acquisition strategy. These traits were used to derive four functional groups: (i) summer annual N-fixing legumes, (ii) overwintering N-fixing legumes, (iii) summer annual non-fixing non-legumes and (iv) overwintering non-fixing non-legumes. Seven four-species cover crop polycultures and two eight-species polycultures (one of which was only planted in 2012–2013) were assembled to contain one to four functional groups using the selected species. We chose two species to fill each N-fixing legume group and four species to fill each non-fixing non-legume group in order to assemble polycultures across which species richness was constant, but functional composition varied. Eight species were also grown as monocultures, and the control treatment was an unmanaged fallow (Table S1, Supporting Information). Cover crop treatments were drilled in 9·1 × 6·5 m plots in a randomized complete block design replicated four times. Cover crops were sprayed with glyphosate and subsequently flail mowed approximately 2 weeks before corn planting. Residues were incorporated into soil by mouldboard ploughing at least 3 day before planting. Above-ground cover crop and weed biomass and carbon (C) and N content were measured in fall prior to the first killing frost (year 1: 50 days after planting; year 2: 63 days after planting) and spring immediately prior to termination by clipping within quadrats. We measured potential nitrate (NO_3^-) leaching from each cover crop system using anion resin materials buried 30 cm below the soil surface for the length of the cover crop growing season. We monitored soil inorganic N [the sum of ammonium (NH_4^+) and NO_3^-] in the subsequent corn crop fortnightly. Corn grain yield was measured at crop harvest each November (Finney, White & Kaye 2016).

The level of service provision by each cover crop treatment was calculated for five ecosystem services: weed suppression during the cover crop season, N retention during the cover crop season, cover crop above-ground biomass N, inorganic N supply during the subsequent cash crop season, and subsequent corn yield as presented in Finney, White & Kaye (2016) and provided in Appendix S1.

TRAIT DATA

Functional diversity metrics were calculated based on three continuous traits expected to vary among cover crop functional groups: fall growth potential [kg ha^{-1} growing degree day $(gdd)^{-1}$], spring growth potential (kg ha^{-1} gdd^{-1}) and C:N ratio of above-ground plant material (whole shoots; Table S1). Using cover crop and ecosystem service data from this experiment, we had previously found a significant relationship between above-ground biomass and each of the five services measured (Finney, White & Kaye 2016). Provision of several services was also influenced by cover crop C:N ratio. Seasonal growth potential was determined from the maximum growth rate of each species grown in monoculture. For species that were not grown in monoculture, the maximum growth rate (or portion thereof) of a species from the same functional group was used. The C:N ratio was the average ratio of the species in monoculture during its peak growth season.

CALCULATION OF DIVERSITY METRICS

Recent BEF studies in natural and agricultural systems have assessed both species-based and functional diversity metrics (Mouillot *et al.* 2011; Finn *et al.* 2013; Gagic *et al.* 2015). We analysed three species-based diversity measures: species richness (*S*) in the above-ground biomass, which was equal to the number of species planted for all observations; the evenness (*E*) of the species abundance in above-ground biomass calculated using Pielou's index; and Shannon diversity (*H*) (Legendre & Legendre 1998).

Like taxonomic diversity, functional diversity is comprised of several components, namely richness, evenness and divergence (Mason *et al.* 2005). Richness refers to the functional trait space occupied by the species within a community, evenness reflects the regularity with which species are distributed in the trait space, and divergence measures the distance of each species from the centre of the community-level trait space (Villéger *et al.* 2008). Given that there is no single metric that captures all three functional diversity components and the lack of consensus on the most informative metric of functional diversity (Mason *et al.* 2005), we calculated six measures of functional diversity to determine whether representing diversity based on continuous traits of component species informs predictions regarding ecosystem service response to diversity and whether the relative abundance of traits is important to ecosystem services. Three multidimensional indices, functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv), were calculated following Villéger *et al.* (2008). Functional diversity (FD) is a dendrogram-based measure of functional diversity (Petchey & Gaston 2006), and was calculated as both an unweighted (FD) and an abundance-weighted value (wFD). Finally, Rao's quadratic entropy (RaoQ) is a classical distance-based measure of functional diversity that reflects both richness and divergence (Botta-Dukat 2005). This suite of indices, therefore, includes two that reflect the number of functionally distinct species in a polyculture (FD and FRic) and four that reflect the distribution of traits present in above-ground biomass (wFD, FEve, FDiv and RaoQ). Total above-ground biomass (fall plus spring dry matter production) accumulated by each species was used to calculate indices weighted by abundance. All diversity metrics were calculated in FDiversity software (Casanoves *et al.* 2011).

STATISTICAL ANALYSES

Linear mixed-effect models tested whether increasing *S* led to increases in individual ecosystem services and multifunctionality. We constructed a model for each service (the response variable) using *S* as a fixed effect and block nested in year as a random effect. Prior to analysis, service values (derived using eqns 1–5, supplementary materials) were standardized using the z-transformation (Maestre *et al.* 2012; Byrnes *et al.* 2014). Multifunctionality was calculated as the average of standardized service values. We used 95% confidence intervals around the diversity coefficient to determine whether each service was related to *S* (i.e. relationships for which the slope was not zero). Confidence intervals were estimated as the product of the test statistic (assumed to be 1·96) and the Wald standard error of each estimated diversity coefficient. Marginal R^2 is reported as a measure of the explanatory power of *S* (Nakagawa & Schielzeth 2013). The same mixed model structure was used to assess the richness–multifunctionality relationship. Analysis of variance was conducted on the multifunctionality index value to compare the performance of cover cropping systems. Due to a significant treatment*year interaction ($P < 0{\cdot}001$), years were analysed separately in a mixed model using treatment as a fixed effect and block as a random effect. Mean separation of least square means was performed using Tukey's honestly significant difference (HSD) at $\alpha = 0{\cdot}05$. To further understand the ability of each cover crop to provide multiple ecosystem services, we quantified the number of services each species or species combination provided at three multifunctionality thresholds (*T*), which represented the number of services provided at 30%, 50% and 70% of the observed maximum value for each service (Zavaleta *et al.* 2010). To reduce the influence of possible outliers, the observed maximum was the average of the five highest values observed for a service within a given year (Byrnes *et al.* 2014). We also quantified the number of disservices provided by each system, which represent observations in which the cover crop treatment performed worse than the no cover crop control.

To identify attributes of diversity that influence ecosystem services from cover crop polycultures, we again used a linear mixed-effects model for each individual service and the multifunctionality index, substituting *S* with each alternative diversity metric as the predictor variable. We again used 95% confidence intervals around the diversity coefficient to identify services predicted by each diversity metric and marginal R^2 values to indicate explanatory power. We included only polycultures in these analyses. Analyses were carried out in R statistical software (R Development Core Team 2013).

Results

Increasing *S* had a positive effect on weed suppression, N retention, and above-ground biomass N, but negatively

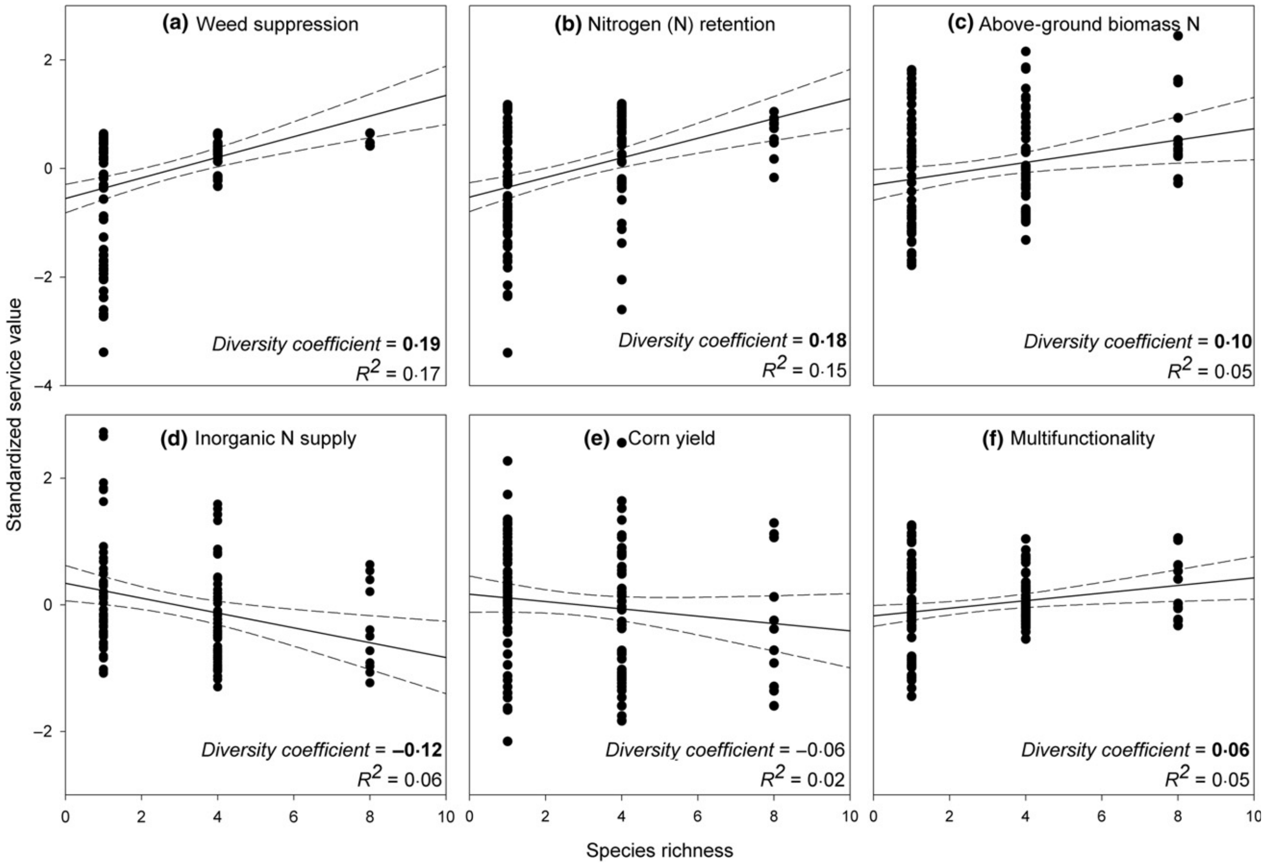

Fig. 1. Regression analysis of species richness as a predictor of five individual ecosystem services; (a) weed suppression during the cover crop season, (b) nitrogen (N) retention during the cover crop season, (c) aboveground biomass N, (d) inorganic N supply during the subsequent cash crop season, and (e) subsequent corn yield; and (f) multifunctionality (the average of the five ecosystem services). Analysis was performed on service values standardized using z-transformation. The solid line is the regression fit and dashed lines represent 95% confidence intervals. Diversity coefficients highlighted in bold are those that are considered significantly different from zero (based on 95% confidence intervals around the estimated slope that do no overlap zero). R^2 is the marginal R^2 (Nakagawa & Schielzeth 2013).

affected inorganic N supply and had no effect on subsequent corn yield (Fig. 1). Increasing *S* also led to increased multifunctionality (Fig. 1). In both years, *Vicia villosa* Roth. grown in monoculture exhibited the highest multifunctionality and led to no disservices (Table 1). In the first year, three polycultures performed as well as *V. villosa* and similarly led to no disservices. In the second year, all but two polycultures experienced a decline in multifunctionality compared to the first year, and no polycultures performed as well as *V. villosa*. Further, all polycultures led to disservices in the second year. For all treatments, the mean number of services provided decreased as the threshold of service provision increased. Among treatments with high multifunctionality in the first year, two polycultures provided more services than *V. villosa* at lower thresholds (30% and 50%), but fewer services at the 70% threshold.

Increasing *E* in the above-ground biomass of cover crop polycultures had no effect on weed suppression, N retention, or above-ground biomass N, but did have a positive effect on inorganic N supply and corn yield (Table 2). There was also a positive relationship between *E* and multifunctionality (Fig. 2a). Increasing *H* had a positive effect on above-ground biomass N, corn yield and multifunctionality associated with polycultures (Table 2, Fig. 2b).

Functional diversity metrics were significantly correlated with one to four of the services measured (Table 2). Functional richness was positively correlated with one service, above-ground biomass N. Increases in unweighted and abundance-weighted FD, also measures of functional richness, were correlated with enhanced weed suppression, N retention and above-ground biomass N. Functional divergence was positively correlated with the same three services. Rao's quadratic entropy demonstrated a positive relationship with four of five services (weed suppression, N retention, above-ground biomass N and corn yield), while three services were positively correlated with FEve (weed suppression, above-ground biomass N and corn yield). All six functional diversity indices were positively related to multifunctionality (Fig. 2).

Discussion

Increasing ecosystem service provision from agroecosystems is an emerging goal of contemporary agriculture. Exploiting biodiversity to meet this goal is a promising

Table 1. Multifunctionality least square means and standard errors of cover crop treatments planted on adjacent fields in Pennsylvania, USA. Multifunctionality is the average of five ecosystem services standardized using z-transformation: weed suppression and nitrogen (N) retention during the cover crop season, inorganic N supply and corn yield in the subsequent cash crop season, and above-ground biomass N. Values with different letters within a column are significantly different based on Tukey's honestly significant difference ($\alpha = 0{\cdot}05$). Threshold values (T) represent the mean number of services provided at the given percentage of maximum service provision, the average of the five highest observed service values in a given year. Disservices (D) indicate the mean number of observations in which the cover crop performed worse than the no cover crop control

	2011					2012				
Cover crop system	Multifunctionality	T = 30%	T = 50%	T = 70%	D	Multifunctionality	T = 30%	T = 50%	T = 70%	D
Crotolaria juncea (CJ)	−1·19 (0·04) g	0·3	0·0	0·0	1·3	−0·94 (0·19) g	0·5	0·3	0·0	2·5
Glycine max (GM)	−0·96 (0·05) g	0·5	0·0	0·0	0·8	−0·85 (0·18) fg	0·5	0·3	0·3	2·5
Trifolium pratense (TP)	0·40 (0·19) bcd	3·8	3·0	2·0	0·0	0·00 (0·22) bcde	3·3	2·8	0·8	1·3
Vicia villosa (VV)	0·94 (0·11) a	4·3	3·8	3·3	0·0	1·12 (0·06) a	5·0	4·8	3·5	0·0
Raphanus sativus (RS)	−0·84 (0·17) g	1·0	0·5	0·0	0·8	0·07 (0·15) bcde	3·0	2·3	1·5	1·3
Avena sativa (AS)	−0·17 (0·02) ef	2·5	1·8	0·8	0·5	−0·03 (0·05) bcde	2·3	1·8	1·5	1·8
Brassica napus (BN)	0·26 (0·07) cde	3·3	2·8	2·0	0·5	0·47 (0·06) b	3·0	3·0	3·0	2·0
Secale cereale (SC)	−0·07 (0·03) ef	3·0	2·0	2·0	1·8	−0·14 (0·08) cde	3·0	3·0	2·5	2·0
RS.AS.SS.SI	−0·22 (0·05) f	2·3	1·8	1·0	0·3	−0·28 (0·12) ef	1·8	1·5	1·3	1·8
BN.SC.HV.LP	−0·08 (0·07) ef	3·0	2·0	2·0	1·8	−0·19 (0·09) e	3·0	2·8	2·3	2·0
BN.SC.RS.AS	0·00 (0·09) def	2·8	2·0	2·0	1·3	−0·16 (0·05) de	3·0	2·8	2·0	2·0
RS.AS.CJ.GM	−0·35 (0·03) f	2·3	1·5	0·5	0·5	0·15 (0·09) bcde	3·3	2·3	1·5	0·5
BN.SC.TP.VV	0·71 (0·08) abc	4·0	3·5	2·5	0·0	0·44 (0·10) bc	3·3	3·0	3·0	1·8
BN.SC.CJ.GM	−0·07 (0·02) ef	3·0	2·0	2·0	2·0	−0·07 (0·04) bcde	3·0	3·0	2·5	2·0
RS.AS.TP.VV	0·81 (0·08) ab	4·5	4·0	2·3	0·0	0·39 (0·12) bcd	4·0	2·8	2·5	0·8
AS.BN.CJ.GM. RS.SC.TP.VV	0·83 (0·12) ab	4·5	4·0	2·8	0·0	0·23 (0·14) bcde	3·0	3·0	2·3	2·0
AS.BN.HV.LP. RS.SC.SI.SS						−0·22 (0·06) e	3·0	2·5	2·0	2·0

HV, *Hordeum vulgare*; LP, *Lolium perenne*; SI, *Setaria italica*; SS, *Sorghum bicolor* × *Sorghum sudanense*.

Table 2. Regression analysis of five ecosystem services provided by cover crop polycultures using eight different diversity indices as predictors. The diversity coefficient is the slope of the index–service relationship, and coefficients highlighted in bold are those that are considered significantly different from zero (based on 95% confidence intervals around the estimated slope that do not overlap zero). The predictive power of each model is indicated by the marginal R^2 (Nakagawa & Schielzeth 2013)

	Weed suppression		Nitrogen retention		Above-ground biomass nitrogen		Inorganic nitrogen supply		Corn yield	
	Diversity coefficient [95% CI]	R^2	Diversity coefficient [95% CI]	R^2	Diversity coefficient [95% CI]	R^2	Diversity coefficient [95% CI]	R^2	Diversity coefficient [95% CI]	R^2
E*	0·24 [−0·10, 0·58]	0·03	−0·29 [−1·38, 0·81]	0·00	0·66 [−0·58, 1·90]	0·02	**1·26 [0·22, 2·30]**	**0·08**	**2·47 [1·06, 3·87]**	**0·15**
H*	0·18 [−0·01, 0·37]	0·05	0·04 [−0·58, 0·66]	0·00	**0·73 [0·05, 1·41]**	**0·06**	0·57 [−0·03, 1·16]	0·05	**1·12 [0·30, 1·94]**	**0·10**
FRic†	0·04 [−0·01, 0·09]	0·03	0·06 [−0·11, 0·23]	0·01	**0·26 [0·07, 0·45]**	**0·10**	0·05 [−0·12, 0·22]	0·00	0·06 [−0·18, 0·30]	0·00
FD†	**0·02 [0·00, 0·04]**	**0·06**	**0·08 [0·02, 0·14]**	**0·08**	**0·13 [0·06, 0·19]**	**0·18**	−0·02 [−0·08, 0·04]	0·00	−0·03 [−0·12, 0·06]	0·01
wFD‡	**0·04 [0·02, 0·06]**	**0·16**	**0·07 [0·00, 0·14]**	**0·05**	**0·19 [0·12, 0·26]**	**0·28**	0·04 [−0·04, 0·11]	0·01	0·07 [−0·04, 0·17]	0·02
Rao‡	**0·10 [0·05, 0·15]**	**0·19**	**0·20 [0·03, 0·37]**	**0·08**	**0·52 [0·36, 0·67]**	**0·39**	0·13 [−0·03, 0·30]	0·03	**0·26 [0·03, 0·50]**	**0·07**
FEve‡	**0·67 [0·42, 0·92]**	**0·29**	0·76 [−0·18, 1·69]	0·04	**2·57 [1·68, 3·46]**	**0·32**	0·82 [−0·09, 1·74]	0·04	**1·41 [0·13, 2·68]**	**0·06**
FDiv‡	**0·69 [0·36, 1·01]**	**0·19**	**2·90 [1·96, 3·85]**	**0·35**	**3·19 [2·09, 4·28]**	**0·33**	−0·70 [−1·85, 0·44]	0·02	−1·10 [−2·71, 0·51]	0·03

E, species evenness; H, Shannon diversity; FRic, functional richness; FD, dendrogram-based functional diversity; wFD, abundance-weighted FD; Rao, Rao's quadratic entropy; FEve, functional evenness; FDiv, functional divergence.
*Species-based diversity metric. †Trait-based diversity metric. ‡Trait-based diversity metric, abundance weighted.

approach, although relationships between diversity and ecosystem services remain largely unexplored for innovative practices such as multispecies cover cropping. Our analyses are the first of their kind to examine the relationship between cover crop diversity and multiple ecosystem services derived from agriculture.

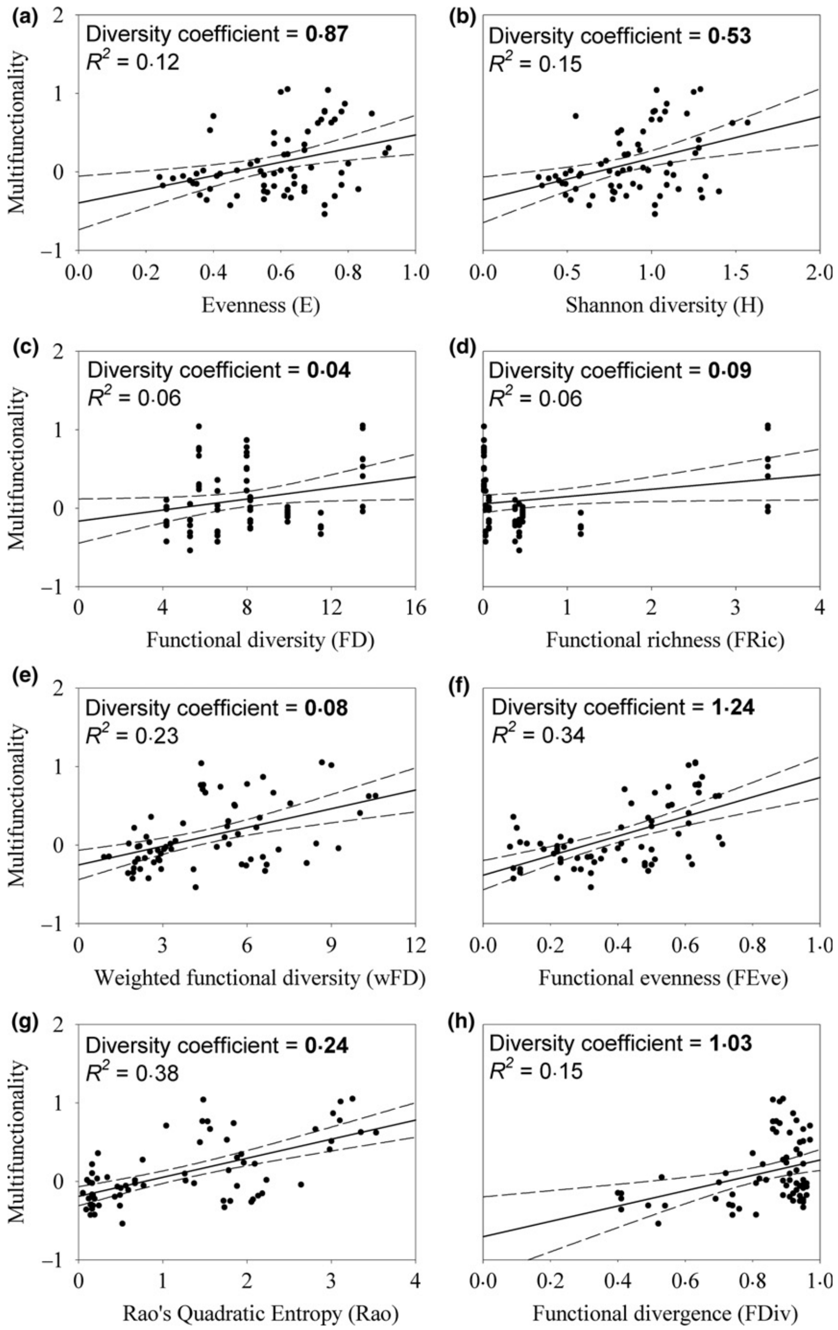

Fig. 2. Regression analysis of agroecosystem multifunctionality using eight different diversity indices as predictors (panels a–h). Multifunctionality is the average of five ecosystem services standardized using z-transformation: weed suppression and nitrogen (N) retention during the cover crop season, inorganic N supply and corn yield in the subsequent cash crop season, and aboveground biomass N. The solid line is the regression fit and dashed lines represent 95% confidence intervals. Diversity coefficients highlighted in bold are those that are considered significantly different from zero (based on 95% confidence intervals around the estimated slope that do no overlap zero). R^2 is the marginal R^2 (Nakagawa & Schielzeth 2013).

COVER CROP RICHNESS AND ECOSYSTEM SERVICES

Applying the traditional metric of biodiversity, *S*, we found that increasing cover crop diversity positively affected three ecosystem services (weed suppression, N retention, and above-ground biomass N), negatively affected one (N supply) and was not related to the yield of a subsequent corn crop (Fig. 1). Yet, the correlations were weak, and polycultures did not necessarily outperform the highest performing monocultures in the provision of individual services (Fig. 1). Still, polycultures may be beneficial if they perform better than monocultures at simultaneously providing multiple ecosystem services (multifunctionality).

This study is the first field-based test of the relationship between cover crop species richness and multifunctionality. Multifunctionality was only weakly correlated with cover crop richness (marginal $R^2 = 0{\cdot}05$), and *V. villosa* monocultures exhibited the highest multifunctionality scores while providing the most services at several threshold levels with the fewest disservices. Thus, as with individual services, our data do not support the hypothesis that increasing cover crop species richness will lead to predictable increases in multifunctionality at levels that are agronomically or ecologically relevant.

Why was species richness a poor predictor of individual ecosystem services and multifunctionality in our study, given that it is considered critical for ecosystem services from natural systems (Hector & Bagchi 2007; Cardinale *et al.* 2012; Maestre *et al.* 2012)? One reason may be the short time-scale of our research; in natural systems, the value of species richness increases over time due to complementarity (Cardinale *et al.* 2007). In perennial cropping systems, a similar effect of time has been observed, although in some cases diversity benefits have manifest relatively quickly (Finn *et al.* 2013). Time may have been a factor for our N supply service, as it is affected by cumulative effects of cover crops on soil organic matter. Yield service could similarly be influenced by cumulative diversity effects over a longer time-scale (Smith, Gross & Robertson 2008). However, for the other services, provisioning was a function of processes that are appropriately measured over the time-scale of our experiment (e.g. N leaching as affected by plant N uptake).

A second reason for the observed weak relationship between ecosystem services and species richness is that in agriculture we do not randomly select species to include in a polyculture – farmers pick species that are known to perform well for the services in which they are interested. Thus, the difference between poor-performing and high-performing species combinations in agriculture should always be lower than in natural systems (Finn *et al.* 2013).

Additionally, richness and multifunctionality were weakly correlated because trade-offs existed among services; increasing S enhanced some services while diminishing others. We expect trade-offs like this to be common among agroecosystem services and suggest that selecting and weighting services with input from stakeholders will improve multifunctionality metrics. In the multifunctionality index we used, all services are weighted equally, and we cannot discern which services are positively, negatively or not influenced by richness (Byrnes *et al.* 2014). Further, in a given system, the average does not reveal information regarding the level at which each contributing service is provided. A metric that allows stakeholders to weight services and define thresholds on an individual basis would be a more realistic tool for evaluating richness–multifunctionality relationships in agriculture.

POLYCULTURE DIVERSITY AND ECOSYSTEM SERVICES

Our analysis of the capacity of eight alternative diversity metrics to predict ecosystem services from cover crop polycultures provides evidence of a link between increasing functional diversity and targeted services. In general, for services that are positively related to cover crop biomass (weed suppression, N retention and above-ground biomass N; Finney, White & Kaye 2016), functional diversity metrics were more strongly correlated with service delivery than species-based metrics (Table 2). Further, among functional diversity metrics, abundance-weighted measures typically provided greater explanatory power (Table 2), suggesting that trait abundances influence these services more so than the simple presence or absence of certain trait values (Gagic *et al.* 2015). We cannot discern, however, whether trait abundances act directly on the target service or indirectly influence service delivery through effects on primary productivity (i.e. the distribution of functional traits influences above-ground biomass production).

There was a different trend for the yield service. For this service, the evenness in abundance of both species (indicated by relationships to E and H) and traits (indicated by relationships with FEve and Rao) influenced service provision (Table 2). Given that this service was negatively related to cover crop C:N ratio in our study ($R^2 = 0{\cdot}55$) (Finney, White & Kaye 2016), we conclude that species and trait evenness influenced yield through effects on N cycling. Specifically, when aggressive grasses (mainly *S. cereale*) with wide C:N ratios dominated polycultures, both evenness and yield declined.

Abundance-weighted functional diversity measures also offered the greatest explanatory power among polyculture multifunctionality models (Fig. 2e–h). Measures of functional evenness explained the highest proportion of variation in multifunctionality (marginal $R^2_{\mathrm{Rao}} = 0{\cdot}38$, marginal $R^2_{\mathrm{FEve}} = 0{\cdot}34$), an indication that greater evenness of trait abundance will lead to greater multifunctionality. The lower explanatory power of species-based indices (Fig. 2a, b) compared to the abundance-weighted functional diversity indices suggests that species abundances alone may not reflect the optimal functional trait distribution, an important consideration for designing multifunctional polycultures.

Across years, there was variability in the magnitude of individual services as well as polyculture multifunctionality. We attribute this variability to differences in species abundances from year to year caused by weather and site conditions (e.g. soil conditions). In the first year of the study, the polyculture *of S. cereale*, *Brassica napus* L., *Trifolium pratense* L. and *V. villosa* was composed of approximately 50% legume biomass and performed as well or better than the highest performing monocultures in all services measured (Finney, White & Kaye 2016). The following year, 80% of biomass in this polyculture was *S. cereale*. While this polyculture excelled in weed suppression, N retention, and above-ground biomass N, corn yield and inorganic N supply were reduced relative to the prior year (Finney, White & Kaye 2016). Year-to-year variability in service provision implies that an understanding of interactions between abiotic factors (e.g. climate, soil) and species-specific cover crop growth will be essential for predicting trait abundances in mixtures. Thus, traits that predict plant responses to abiotic environmental variation should be used to aid species selection.

IMPLICATIONS FOR AGROECOSYSTEM DESIGN

A key finding of this study is that increased cover crop species richness alone does not augment all ecosystem services, nor is it highly correlated with multifunctionality. Functional diversity metrics based on the abundance of plant traits in polycultures were better predictors of multifunctionality. The fact that the traits we used (growth rates in fall and spring and C:N ratio) are the basis of functional categories commonly used by farmers to select cover crops suggests that assembling polycultures by including representatives from a variety of functional groups can lead to enhanced multifunctionality. However, this functional group approach to community assembly suffers several shortcomings. First, while the traits used to quantify functional diversity in this study contribute to a range of services, services such as resource provision for pollinators and beneficial insects are likely influenced by other traits (Storkey *et al.* 2015). Knowledge of traits that mediate specific services (i.e. effect traits) would allow for the quantification of specific functional trait targets to provide desired services and the determination of the species abundances required to achieve these targets (Laughlin 2014).

The functional group approach also has very little power to predict outcomes in novel cover crop assemblages, a hurdle to the development and application of cover crop polycultures optimized for ecosystem service delivery. The importance of trait distribution to multifunctionality is a significant finding of this study, revealing the value of understanding not only the traits that drive ecosystem services, but also traits that mediate species responses to environmental conditions and interspecific competition (i.e. response traits). Knowledge of response traits is essential to predict polyculture stand development across geographic and environmental gradients and within different production contexts. Thus, while research gaps remain, this study offers evidence that a functional trait-based framework, specifically one that incorporates effect and response traits, would enhance diversity management in agroecosystems (Laughlin 2014; Martin & Isaac 2015; Wood *et al.* 2015).

Another area requiring further research is the significance of interdependence among services, functions and traits. Our study emphasized several N-related services, and one of the functions we used to predict these services was above-ground biomass N. Above-ground biomass N was not independent of our other N cycling functions, and is the product of traits we selected (growth and C:N ratio). One could argue that our results are simply a function of the covarying services, functions and traits that we chose, and not a robust test of BEF relationships. Should we strive for BEF tests in which the services, functions and traits vary independently? Statistically, this may be an appealing way forward, but practically speaking it would result in experiments with diminished relevance for critical applied ecological problems. Ecosystem services are value-laden constructs that are not randomly selected, but rather, are identified by stakeholders. Stakeholder-identified services will be derived from a suite of functions that are unlikely to be independent, but are nonetheless essential for providing desired services. The best traits for predicting the level of these functions will be those that are highly correlated with the function. Thus, rather than seeking independence, we expect that the most effective BEF applications will be those that leverage tight interrelationships among traits, functions and services.

The BEF relationship poses the tantalizing prospect that we can use biodiversity to increase ecosystem services from agriculture. In a practical application of this central ecological theory, we found that increasing cover crop diversity can augment specific individual agroecosystem services as well as enhance multifunctionality. But, as in other applied contexts, defining diversity by species richness will not capitalize on the potential of cover crop polycultures to benefit multifunctionality. For the first time, we demonstrated that functional diversity is essential to creating multifunctional cover cropping systems. Considerable research remains to be done to identify the functional traits that shape cover crop community dynamics and in depicting trade-offs among services in multifunctionality metrics. We have shown that applying this knowledge in trait-based models for polyculture assembly will complement practice-based knowledge, enabling farmers to find the right cover crop mix for their fields.

Acknowledgements

We thank the Russell E. Larson Agricultural Research Center staff, Brosi Bradley, Sara Eckert and numerous undergraduate assistants for technical assistance. We also thank Mary Ann Bruns, Debashis Ghosh, Mitchell Hunter and David Mortensen. This project was funded by grants to D.M.F. from the Northeast Sustainable Agriculture Research and Education Graduate Research Programme (#GNE11-017) and to J.P.K. from the USDA National Institute of Food and Agriculture (#2011-51300-30638). D.M.F. also received support from the USDA-NIFA Predoctoral Fellowship Programme (#2012-67011-19662) and the ARCS Foundation, Pittsburgh, Pennsylvania Chapter.

Data accessibility

Data are available on ScholarSphere, Penn State University's institutional repository (https://scholarsphere.psu.edu/files/sj139194f).

References

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.

Blesh, J. & Drinkwater, L.E. (2013) The impact of nitrogen source and crop rotation on nitrogen mass balances in the Mississippi River Basin. *Ecological Applications*, **23**, 1017–1035.

Botta-Dukat, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.

Brooker, R.W., Jones, H.G., Paterson, E., Watson, C., Brooker, R.W., Bennett, A.E. *et al.* (2015) Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytologist*, **206**, 107–117.

Byrnes, J.E., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A. *et al.* (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution*, **5**, 111–124.

Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17012–17017.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. & Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18123–18128.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Casanoves, F., Pla, L., Di Rienzo, J.A. & Díaz, S. (2011) FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution*, **2**, 233–237.

Conservation Technology Information Center (2015) *2014–2015 Annual Report: Cover Crop Survey*. Conservation Technology Information Center, West Lafayette, Indiana.

Davis, A.S., Hill, J.D., Chase, C.A., Johanns, A.M. & Liebman, M. (2012) Increasing cropping system diversity balances productivity, profitability and environmental health. *PLoS ONE*, **7**, e47149.

Finn, J.A., Kirwan, L., Connolly, J., Sebastià, M.T., Helgadottir, A., Baadshaug, O.H. *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 (ed B Wilsey). *Journal of Applied Ecology*, **50**, 365–375.

Finney, D.M., White, C.M. & Kaye, J.P. (2016) Biomass production and carbon/nitrogen ratio influence ecosystem services from cover crop mixtures. *Agronomy Journal*, **108**, 39–52.

Flynn, D., Mirotchnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. *Ecology*, **92**, 1573–1581.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.* (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **282**, 20142620.

Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, **448**, 188–190.

Iverson, A.L., Marin, L.E., Ennis, K.K., Gonthier, D.J., Connor-Barrie, B.T., Remfert, J.L., Cardinale, B.J. & Perfecto, I. (2014) Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *Journal of Applied Ecology*, **51**, 1593–1602.

Kremen, C. & Miles, A. (2012) Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and Society*, **17**, 40.

Laughlin, D.C. (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, **17**, 771–784.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier Science, New York, NY.

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C. *et al.* (2011) Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, **21**, 9–21.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M. *et al.* (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science*, **335**, 214–218.

Martin, A.R. & Isaac, M.E. (2015) Plant functional traits in agroecosystems: a blueprint for research. *Journal of Applied Ecology*, **52**, 1425–1435.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. *Oikos*, **111**, 112–118.

McDaniel, M.D., Tiemann, L.K. & Grandy, A.S. (2014) Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecological Applications*, **24**, 560–570.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N.W.H. (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**, e17476.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ranells, N.N. & Wagger, M.G. (1997) Grass-legume bicultures as winter annual cover crops. *Agronomy Journal*, **89**, 659–665.

Schipanski, M.E., Barbercheck, M.E., Douglas, M.R., Finney, D.M., Haider, K., Kaye, J.P. *et al.* (2014) A framework for evaluating ecosystem services provided by cover crops in agroecosystems. *Agricultural Systems*, **125**, 12–22.

Smith, R.G., Atwood, L.W. & Warren, N.D. (2014) Increased productivity of a cover crop mixture is not associated with enhanced agroecosystem services. *PLoS ONE*, **9**, e97351.

Smith, R.G., Gross, K.L. & Robertson, G.P. (2008) Effects of crop diversity on agroecosystem function: crop yield response. *Ecosystems*, **11**, 355–366.

Storkey, J., Doring, T., Baddeley, J., Collins, R., Roderick, S., Jones, H. & Watson, C. (2015) Engineering a plant community to deliver multiple ecosystem services. *Ecological Applications*, **25**, 1034–1043.

Teasdale, J.R. & Abdul-Baki, A.A. (1998) Comparison of mixtures vs. monocultures of cover crops for fresh-market tomato production with and without herbicide. *HortScience*, **33**, 1163–1166.

Tiemann, L.K., Grandy, A.S., Atkinson, E.E., Marin-Spiotta, E. & McDaniel, M.D. (2015) Crop rotational diversity enhances belowground communities and functions in an agroecosystem (ed D Hooper). *Ecology Letters*, **18**, 761–771.

Tilman, D., Wedin, D. & Knops, J.M.H. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.

Villéger, S., Mason, N.W.H., Mouillot, D. & Mason, H. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S. & Palm, C.A. (2015) Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends in Ecology & Evolution*, **30**, 531–539.

Wortman, S.E., Francis, C.A. & Lindquist, J.L. (2012) Cover crop mixtures for the western Corn Belt: opportunities for increased productivity and stability. *Agronomy Journal*, **104**, 699–705.

Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, D. (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 1443–1446.

Received 22 April 2016; accepted 3 August 2016
Handling Editor: Marc Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Scientific name, common name, phenological niche, nitrogen (N) acquisition strategy, and trait values for cover crop species.

Table S2. Species composition and diversity index values for cover crop polycultures.

Appendix S1. Quantification of ecosystem services.