REVIEW

Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis

Aaron L. Iverson[1]*, Linda E. Marín[2], Katherine K. Ennis[3], David J. Gonthier[2], Benjamin T. Connor-Barrie[2], Jane L. Remfert[2], Bradley J. Cardinale[1,2] and Ivette Perfecto[2]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, MI 48109, USA;* [2]*School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, MI 48109, USA; and* [3]*Department of Environmental Studies, University of California-Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA*

Summary

1. Agriculture comprises the largest global land use, makes it a leading cause of habitat loss. It is therefore critical to identify how to best construct agricultural systems that can simultaneously provide food and other ecosystem services. This challenge requires that we determine how to maximize win-win relationships and minimize trade-offs between services.

2. Through meta-analysis, we tested whether within-field crop diversification (polyculture) can lead to win-win relationships between two ecosystem services: yield of a focal crop species and biocontrol of crop pests. We selected only studies that recorded both services ($N = 26$ studies; 301 observations), allowing us to better determine the underlying mechanisms of our principal findings. We calculated log-response ratios for both ecosystem services in mono- and polycultures.

3. We found win-win relationships between per-plant yield of the primary crop and biocontrol in polyculture systems that minimized intraspecific competition via substitutive planting. Additionally, we found beneficial effects on biocontrol with no difference in per-unit area yield of the primary crop in polyculture fields at high cropping densities (additive planting) where legumes were used as the secondary crop. These results suggest that there is a strong potential for win-win relationships between biocontrol and per-unit area yield under certain scenarios. Our findings were consistent across geographical regions and by type of primary crop. We did not find evidence that biocontrol had an effect on yield, but rather, both were independently affected by polycultural cropping.

4. *Synthesis and applications.* We show that well-designed polycultures can produce win-win outcomes between per-plant, and potentially per-unit area, primary crop yield and biocontrol. Biocontrol services are consistently enhanced in polycultures, so polyculture management that focuses on yield optimization is likely to be the best strategy for maximizing both services. In doing so, we suggest that practitioners utilize polycultures that decrease plant–plant competition through a substitution of relatively large quantities of the primary crop for compatibly harvestable secondary crops. Additionally, if planting at high cropping densities, it is important that legumes be the secondary crop.

Key-words: additive design, agroecosystems, biological control, ecosystem services, multifunctionality, polyculture, substitutive design, trade-off, win-win, yield

Introduction

The green revolution was very successful at producing food on a scale that the world had never before seen.

However, it also contributed significantly to the degradation of many of the other services that ecosystems provide to humanity – services such as soil formation, nutrient cycling, water supply, climate regulation, pollination and biological control of crop pests (Costanza *et al.* 1997; Tilman 1999; Millenium Ecosystem Assessment 2005;

*Correspondence author. E-mail: iverson@umich.edu

Losey & Vaughan 2006; Foley *et al.* 2011). Now that ca. 40% of the Earth's terrestrial surface is covered by agricultural habitats, these represent the single largest land use globally (Foley *et al.* 2005; Ramankutty *et al.* 2008) and are arguably one of the most important focal areas for conservation of biodiversity and ecosystem services (Clay 2004; Perfecto, Vandermeer & Wright 2009). There is considerable evidence that agricultural practices differ in their impacts on ecosystem services, and therefore, there is growing interest in how agroecosystems might be managed as a source not only of a provisioning service (food, fuel or fibre), but of other ecosystem services as well (Perfecto & Vandermeer 2008; Perfecto, Vandermeer & Wright 2009; Power 2010; Kremen & Miles 2012).

Increasing crop diversity through the use of polycultures has often been proposed as a means to achieve win-win scenarios among ecosystem services in agroecosystems (Power 2010). Yet, the vast majority of empirical studies performed to date have examined how crop diversity influences ecosystem services individually. For example, although there is evidence that increasing crop diversity can enhance pollination (Holzschuh *et al.* 2006; Kennedy *et al.* 2013), soil fertility (Mäder *et al.* 2002), disease regulation (Power & Flecker 1996) and biological control (Andow 1991; Simon *et al.* 2010; Letourneau *et al.* 2011), there is little work showing how these ecosystem services covary in response to crop diversity, especially with respect to crop yield (Steffan-Dewenter *et al.* 2007). With an improved understanding of how these services covary, we will better be able to optimize agroecosystems for both food production and other important services by maximizing synergies and minimizing trade-offs (Power 2010).

Using meta-analysis, we examine the effect of polycultural cropping on two agricultural ecosystem services: biocontrol of herbivorous pests (reduction in pest abundance or plant damage, increase in natural enemy abundance) and yield of a focal crop (grams of consumable product per plant). In so doing, we explore whether polycultural cropping promotes a trade-off or a win-win relationship between these two ecosystem services. We also separately examine the individual components of primary crop yield and biocontrol (e.g. separating by focal crop type, secondary vegetation type, biocontrol response metric) and analyse results according to the broad geographical region of the study (temperate vs. tropical). All studies included in this meta-analysis report the levels of both biocontrol of herbivorous pests and yield of focal crop in the same experiment (same location and same seasons), allowing us to ascertain more directly the relationship between polycultural cropping and these ecosystem services. With these analyses, we not only determine whether trade-offs or win-wins result between biocontrol and yield, but shed light on the mechanisms by which these relationships may result. Building upon the work of others (Poveda, Gomez & Martinez 2008; Power 2010; Letourneau *et al.* 2011; Cardinale *et al.* 2012; Kremen & Miles 2012), this is the first synthesis study, to the best of our knowledge, to directly assess how biocontrol and yield are simultaneously affected by polycultural cropping.

Materials and methods

DATA COLLECTION

We conducted a literature search on 18 December 2011 in ISI Web of Science, returning 1479 publications (for keywords, see Appendix S1 in Supporting Information). To augment this search, we reviewed the bibliographies of two key reviews of intercropping and pest control (Andow 1991; Letourneau *et al.* 2011). We also surveyed co-authors for additional known papers. We selected papers from these searches using the following criteria:

1. The study was an empirical investigation that directly measured yield and at least one biocontrol variable in agricultural fields with at least two levels of plant species richness (e.g. monoculture and polyculture). We considered fields as polycultures only if the multiple species were grown in the same field. Species richness included both harvested crops and non-harvested plants (e.g. cover crops). Yield was defined as total biomass of the plant tissue for which the crop is grown (e.g. fruit, seed, fibre or leaf weight), not overall plant biomass. Metrics of biocontrol were as follows: (i) abundance of arthropod herbivores, (ii) abundance of natural enemies of pests, (iii) degree of pest parasitism or (iv) amount of plant damage.
2. Crop species richness differed between treatments at a single point in time (i.e. crop rotations not included).
3. Experimental treatments varied based on plant species richness, rather than on other forms of diversity (e.g. genetic diversity).
4. The treatment (i.e. monoculture or polyculture) had more than one replicate.

Papers rarely included estimates of yield of the secondary crop(s); therefore, we could only consider primary crop yield in the analysis (see 'Experimental design' below). Weeds were not included as a secondary species with the exception of the studies ($N = 2$) that explicitly included associated plants as a diversity treatment and, therefore, excluded them from monocultures (Schellhorn & Sork 1997; Showler & Greenberg 2003). Although most of the secondary species were crops, not all were. Therefore, we refer to them collectively as 'secondary vegetation'. In the rare cases where similar data on a biocontrol metric were reported using two or more different methods, we used only the data from the method that, in our expert opinion, would most likely have a direct impact on yield. For example, Belay, Schulthess & Omwega (2009) reported internode damage, exit holes, tunnelling and cob damage on maize. In this case, we chose cob damage as the category that most likely directly affected the yield of the commercially important part of the crop. If the author reported damage on the above- and below-ground parts of the plant that reflected activity from different arthropod guilds (e.g. Sekamatte, Ogenga-Latigo & Russell-smith 2003), we included both damage metrics as separate observations. If a study reported multiple biocontrol variables (e.g. natural enemy diversity and plant damage), each was considered as a separate observation. Percentage parasitism was pooled into the natural enemy abundance category because there were not enough observations to consider it individually ($N = 4$). If a study investigated the effects of different

combinations of crop ratios in polyculture (e.g. Weiss *et al.* 1994), each ratio treatment was compared to the monoculture values and included as a separate observation.

A total of 26 studies (Villamajor 1976; Nordlund, Chalfant & Lewis 1984; Letourneau 1986; Rodenhouse *et al.* 1992; Weiss *et al.* 1994; Williams *et al.* 1995; Schellhorn & Sork 1997; Hooks, Valenzuela & Defrank 1998; Ogol, Spence & Keddie 1999; Nabirye *et al.* 2003; Sekamatte, Ogenga-Latigo & Russell-smith 2003; Showler & Greenberg 2003; Hooks & Johnson 2004; Maluleke, Addo-Bediako & Ayisi 2005; Schader, Zaller & Köpke 2005; Skelton & Barrett 2005; Arim *et al.* 2006; Gianoli *et al.* 2006; Matama-Kauma *et al.* 2006; Chabi-Olaye *et al.* 2007; Rao 2007; Belay, Schulthess & Omwega 2009; Hummel, Dosdall & Clayton 2009; Lenardis *et al.* 2011; Nyasani *et al.* 2012; Ramalho *et al.* 2012) yielded 301 comparisons between monocultures and polycultures (see Table S1, Supporting information). Of these, 16 resulted from our ISI search, an additional six from two key review papers (Andow 1991; Letourneau *et al.* 2011) and a further three studies from surveying co-authors (Maluleke, Addo-Bediako & Ayisi 2005; Belay, Schulthess & Omwega 2009; Ramalho *et al.* 2012). From these studies, we extracted data from tables or text or used the program DataThief (Tummers 2006) to obtain data points from figures. If the data that were needed to calculate effect sizes were not available, we contacted the authors and requested the original data sets. Three data sets were contributed in this manner, whereas one could not be included due to lack of response.

EXPERIMENTAL DESIGNS

Of the 26 studies, 12 were designed as substitutive experiments, and 14 were designed as additive. Substitutive designs hold overall plant density constant in mono- and polycultures, whereas in additive designs, the primary crop density does not change and secondary species are added so that total crop density increases (see Vandermeer 1989). In the additive design, intraspecific interactions are held constant at a fixed density, even as interspecific interactions are added in polyculture. In the substitutive design, the addition of interspecific interactions in polyculture is coupled with the potential of reduced intraspecific interactions. Polycultural cropping systems can best be viewed in the framework of a continuous response surface, where the response (e.g. yield) is projected as a function of various combinations of densities of each crop (Law & Watkinson 1987), where optimal scenarios can be developed through modelling approaches (García-Barrios *et al.* 2001). Therefore, dividing cropping systems into a binary designation as additive or substitutive is not ideal, yet we did not see practical alternatives given the type of data our analysed studies included.

As it was not possible to include secondary crop yield in the analysis, we calculated yield as the mass of consumable product per individual plant of primary crop rather than per unit area for substitutive studies, as the former allowed us to better ascertain ecological mechanisms underlying yield increases or decreases. Any decrease in yield per unit area in a substitutive design can result from (a) a decrease in the per-plant yield that results from the treatment and/or (b) a decrease in plant density, which is imposed by and inherent to the substitutive design. Per-unit area calculations with these designs thus confound the explanation of observed relationships. By comparison, calculating yield on a per-plant or per-unit area basis makes no difference for studies performed using an additive design because the constant density of the primary crop from mono- to polyculture ensures that one achieves the same yield ratio (see 'Meta-analysis' below).

META-ANALYSIS

Calculating overall trade-off or win-win relationships

To standardize results between studies and allow for meaningful comparisons, we calculated dimensionless effect sizes for the impact of polycultural cropping (as compared to monocultural cropping) on yield per plant of the primary crop and for biocontrol, measured as a decrease in herbivorous pests or plant damage, or an increase in natural enemies. We calculated log-response ratios for yield and biocontrol variables by taking the natural log of the mean value for polyculture over the mean value for monoculture for each observation (Hedges, Gurevitch & Curtis 1999). Because a beneficial effect of polycultural cropping on biocontrol differs for herbivore abundance and plant damage (negative log-response ratio is beneficial) as opposed to natural enemy abundance (positive log-response ratio is beneficial), we changed the sign of log-response ratios for herbivore abundance and plant damage so that all beneficial biocontrol effects were reflected in positive values.

When a biocontrol variable was zero in monoculture (e.g. no herbivores found), we used the lowest value found in the rest of that particular study's data set for that variable (i.e. the lowest non-zero value). We chose this method as opposed to adding a constant, as there was a large variation in the magnitude of biocontrol values between studies, and a constant would have considerably (and arbitrarily) changed the effect sizes for small values. In cases where biocontrol data were reported as a time series (e.g. biweekly measures of pest abundance) within a growing season, the mean of the individual ratios of an entire time series was used as an estimate of each biocontrol variable that was measured. We determined whether time had a significant effect on the log-response ratios by calculating the statistical significance ($P < 0.05$) of the linear and quadratic regressions of the log-response ratios of each time series. For time series that showed a significant trend ($N = 4$ observations), data were plotted separately as a series in order to visualize the time effect (Fig. S1, Supporting information), but were still included in the other analyses.

We used the effect sizes to determine whether polycultural cropping leads to a negative or positive relationship between biocontrol and yield. To do so, we calculated the mean and 95% confidence intervals of the effect sizes using the estimated means generated from generalized linear mixed models (GLMMs), using study as a random factor. We plotted these data on a Cartesian plane with the primary crop yield and biocontrol response ratios on the x- and y-axis, respectively. This plot allows an easy visualization of trade-off, win-win and lose-lose relationships (Fig. 1).

Mechanisms 1: Role of plant competition and biocontrol

In order to determine the influence of inter- and intraspecific plant competition on per-plant yield, we calculated the proportional change in density of the primary crop relative to the secondary vegetation for substitutive studies as:

$$\text{Proportional Density Change} = \frac{\text{Density}_{mono} - \text{Density}_{poly}}{\text{Density}_{mono}}$$

where Density_{mono} and Density_{poly} refer to the planting densities (per-unit area) of the primary crop in monoculture and polyculture, respectively. This analysis was facilitated by the fact that
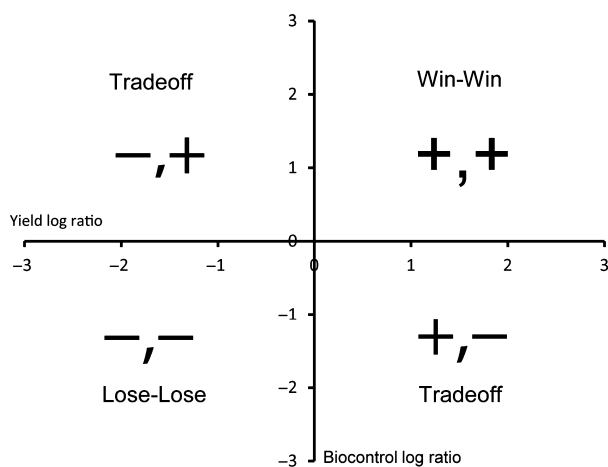
Fig. 1. Graphical display of outcome scenarios for log-response ratios of yield and biocontrol.

studies varied in the ratio of primary crop to secondary vegetation when planted in polyculture (i.e. planting mixes in polyculture were not always 50:50). If we found a more positive effect on yield as the secondary vegetation's relative density increased, it would suggest that improvements in yield may have resulted from decreased intraspecific competition despite increased interspecific competition, or alternatively, because of facilitation. Note that a similar analysis could not be performed for additive studies where the focal crop density did not change from monoculture to polyculture.

To test whether biocontrol influences yield through indirect effects of suppression of pests and decreased plant damage, we calculated the Spearman rank correlation between the effect sizes for biocontrol and primary crop yield, where a significant correlation would indicate covariance between the two services.

Mechanisms 2: Examining variation in yield and biocontrol

To understand what might drive variation in biocontrol or yield, we dissected each into the following categories: (i) biocontrol metric (e.g. herbivore abundance, predator abundance and plant damage), (ii) type of primary crop, (iii) type of secondary vegetation and (iv) geographical region. Primary crops were categorized in a manner that allowed sufficient sample size for meaningful analysis according to the following groups: maize, legumes and all others. For the secondary vegetation, we performed two separate analyses, first grouping as legumes or non-legumes and secondly as a harvested crop (e.g. produced for food or fibre) or a non-harvested plant (e.g. cover crops, weeds or grass strips). For geographical region, we divided the experiments by temperate (>23·5° N and S) and tropical (<23·5° N and S) latitudes. All analyses were separated by substitutive and additive designs.

Unless otherwise noted, all statistical analyses were conducted using R, version 2.13.1 (R Development Core Team 2011). Studies were weighted by sample size according to the 'weights' element within the glmer function (for GLMMs, lme4 package) and compared to the non-weighted values. As conclusions did not differ when values were weighted, here we present only non-weighted results. Because there can be a tendency not to publish non-significant or small-negative-result studies, we tested our

results for this publication bias by calculating Rosenthal's fail-safe value (Rosenthal 1979) using the Fail-safe Number Calculator (Rosenberg 2005).

Results

YIELD AND BIOCONTROL: TRADE-OFF OR WIN-WIN?

Our first goal was to understand how polycultural cropping impacts biocontrol and primary crop yield simultaneously. Plotting log-response ratios for both services on a Cartesian plane allowed for easy visualizations of win-win or trade-off relationships (Fig. 1). We found a significant win-win scenario for biocontrol and per-plant primary crop yield in substitutive design experiments, which showed a 40% and 31% increase for yield and biocontrol, respectively, in poly- over monocultures (Table 1, Fig. 2a). In additive studies, on the other hand, we found a significant trade-off between biocontrol and per-plant (*ergo* per-unit area, see 'Materials and methods') primary crop yield, where the biocontrol effect was higher in polycultures compared to monocultures (36% increase), but yield of the primary crop was lower (24% decrease) (Table 1). When additive studies were split into those with legumes vs. without legumes as secondary vegetation, polycultures with legumes retained their biocontrol advantage and did not show reduced yields (Fig. 2b). These results are robust to publication bias, according to Rosenthal's method for deriving a fail-safe value (Rosenthal 1979) (Table S2, Supporting information).

Mechanisms 1: Role of plant competition and biocontrol

When we analysed how primary crop yield effect sizes varied as a function of the relative density of the primary (in relation to secondary) crop in substitutive polycultures, we found a significant positive relationship ($P < 0.001$; Fig. 3). This result indicates that as individuals of the primary crop are replaced with individuals of the secondary plant(s), the per-plant yield of the primary crop increases. This trend appeared to be driven primarily by the presence of legumes; when we repeated the analysis separating studies into legume or non-legume polycultures, those with legumes remained highly significant ($P < 0.001$), whereas those without legumes showed no trend ($P = 0.320$). However, all regressions became non-significant when a single large study (Nordlund, Chalfant & Lewis 1984) ($N = 46$ observations) was eliminated. When the biocontrol response was plotted in the same way against the proportion of the polyculture field in primary crop, the linear regression was non-significant ($P = 0.756$), indicating that having relatively more secondary crop did not influence the degree of biocontrol.

To determine whether primary crop yield covaries with biocontrol, we performed a Spearman rank correlation between the effect sizes of the two variables. This analysis resulted in a non-significant trend for additive designs and

Table 1. Log-response ratios for primary crop yield and biocontrol

	Yield			Biocontrol			
	Mean	%Δ*	$P^†$	Mean	%Δ*	$P^†$	N
Overall							
Additive	−0·279	−24·3	**0·038**	0·306	35·7	**0·016**	184
Substitutive	0·339	40·4	**0·000**	0·273	31·4	**0·017**	117
Biocontrol variable‡							
Herbivore	−0·075	−7·2	0·438	0·390	47·6	**0·002**	149
Damage	0·016	1·6	0·783	0·230	25·8	**0·032**	98
Predator	0·001	0·1	0·853	0·256	29·2	0·075	54
Primary crop							
Maize (sub)	0·516	67·5	**0·001**	0·212	23·7	0·178	39
Legume (sub)	0·343	40·9	**0·007**	0·192	21·2	0·132	30
Other (sub)	0·453	57·3	**0·000**	0·336	40·0	**0·013**	48
Maize (add)	−0·235	−20·9	**0·046**	0·403	49·6	**0·011**	109
Legume (add)	−0·152	−14·1	0·061	−0·020	−2·0	0·880	40
Other (add)	−0·489	−38·7	0·055	0·445	56·0	**0·045**	35
Secondary crop: Legume or non-legume							
Non-legume (sub)	0·399	49·0	**0·000**	0·246	27·9	0·054	61
Legume (sub)	0·415	51·5	**0·026**	0·308	36·1	0·103	50
Non-legume (add)	−0·371	−31·0	**0·012**	0·064	6·6	0·344	73
Legume (add)	−0·166	−15·3	0·214	0·555	74·1	0·052	102
Secondary crop: Harvested or not							
Harvested (sub)	0·367	44·3	**0·000**	0·304	35·5	**0·032**	97
Not harvested (sub)	0·273	31·4	**0·034**	0·169	18·4	0·074	20
Harvested (add)	−0·190	−17·3	**0·002**	0·126	13·5	0·322	82
Not harvested (add)	−0·396	−32·7	0·075	0·398	48·8	**0·023**	101
Region							
Tropical (sub)	0·373	45·2	**0·000**	0·288	33·3	0·056	51
Temperate (sub)	0·301	35·1	**0·013**	0·257	29·3	0·155	66
Tropical (add)	−0·181	−16·6	0·081	0·282	32·5	0·082	124
Temperate (add)	−0·623	−46·4	0·054	0·389	47·6	0·113	60
All tropical				0·279	32·2	**0·022**	175
All temperate				0·360	43·3	**0·012**	126

*Bold indicates significance at $P < 0.05$ level.
†Refers to the percentage difference in log-response ratios between the monoculture and polyculture values.
‡Sign for plant damage and herbivore abundance values has been switched, such that a positive value for each of these reflects a beneficial biocontrol effect. Additive and substitutive studies were combined.

a marginally significant negative trend for substitutive designs (Fig. 2a,b, grey dots), showing that yield does not covary consistently with biocontrol. When we performed a Spearman rank correlation for effect sizes of each biocontrol metric separately (herbivore abundance, predator abundance, plant damage) with primary crop yield, results varied between negative, positive and non-significant relationships, further suggesting that biocontrol does not consistently covary with primary crop yield (Table S3, Supporting information).

Mechanisms 2: Examining variation in yield and biocontrol

The studies used in this meta-analysis included 12 primary crops and 42 secondary crops (Table S1, Supporting information). We examined how the type of secondary crop influenced biocontrol and primary crop yield by calculating separate effect size means for two groupings of secondary crops: 1) legume vs. non-legume and 2) harvested vs. non-harvested (e.g. cover crop, grass corridor).

In additive designs, polyculture yields did not differ from monocultures when the secondary crop was a legume but were significantly lower in polycultures when the secondary crop was a non-legume (Table 1, Fig. 2b, Fig. S2, Supporting information). In substitutive designs, primary crop yields were improved regardless of whether the secondary crop was a legume or a non-legume (Table 1, Fig. S2, Supporting information). Whether a secondary crop was a harvested crop or not did not affect the primary crop yield in substitutive studies. However, if a secondary crop was a non-harvested crop in additive studies, the negative effect on primary crop yield was not significant (Table 1). Biocontrol values did not vary substantially between secondary crop categories, although in additive studies the biocontrol benefit in polycultures was not significant with non-legumes or harvested crops as secondary crops (Table 1, Fig 2b).

When the primary crop was grouped according to crop type (maize, legumes or all others), we found that the yield effect sizes for each of the groups followed the same trends as the corresponding overall values (overall
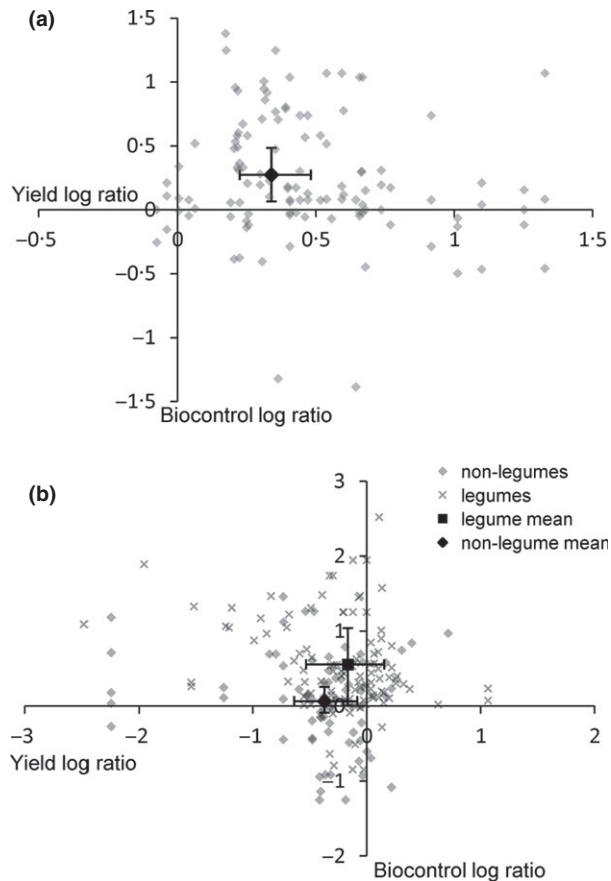
(a)

(b)

Fig. 2. Log-response ratios of yield and biocontrol for (a) substitutive and (b) additive design experiments. In (a), large diamond = model mean estimate for all studies $\pm 95\%$CI. In (b), large square = model mean for observations with a legume as secondary crop; large diamond = model mean for observations with a non-legume as secondary crop. Spearman rank correlation: (a) all substitutive observations: $\rho = -0.178$ ($N = 117$, $P = 0.055$), (b) all additive observations: $\rho = -0.085$ ($N = 184$, $P = 0.252$).

Fig. 3. Proportion of primary crop substituted for secondary crop (legume, non-legume and combined) vs. primary crop yield response ratio. Trendline for legume and non-legume combined: $R^2 = 0.1456$ ($P < 0.001$, $N = 117$); trendline for legume only: $R^2 = 0.310$ ($P < 0.001$, $N = 50$); trendline for non-legume only $R^2 = 0.0004$ ($P = 0.31$, $N = 61$). Sample size of combined values is larger than sum of subsets as some studies included a mix of both legumes and non-legumes as secondary crops.

Fig. 4. Yield log-response ratios (model mean estimate $\pm$ 95% CI) for different primary crop groups. 'Other' crops include wheat, cotton, tomato, zucchini, collards, broccoli and oilseed rape. Numbers above points indicate sample size.

Discussion

Our study shows that while no universal relationship is apparent between biocontrol and primary crop yield, win-win outcomes may be achieved under certain scenarios. We found that win-win relationships between per-plant yield and biocontrol can be attained by reducing intraspecific competition through replacing the primary crop with a secondary crop. Furthermore, by observing additive studies, we show that per-unit area (= per-plant) primary crop yields are enhanced most with legumes as a secondary crop, where they produce the same as their monoculture counterparts, even without including secondary crop yields. This polycultural scenario thus shows strong potential for overall win-win outcomes considering per-unit area yields.

Biocontrol services were consistently enhanced by polycultural cropping in both additive and substitutive designs, and this effect was attained even at low densities

additive or substitutive) (Fig. 4, Table 1). When we observed effect sizes for biocontrol when separated by primary crop type, we found that maize crops in additive studies and 'other' crops (non-maize/non-legume) in both additive and substitutive studies had the largest biocontrol benefit when in polyculture (Table 1). When we separated the biocontrol effect according to each of the three metrics (plant damage, predator abundance and pest abundance), each metric was greater (more beneficial to farmers) in polycultures relative to monocultures (all significant ($P < 0.05$), except for the predator category ($P = 0.075$; Fig. 5).

Finally, we separated studies into tropical ($<23.5°$ N and S latitudes) and temperate ($>23.5°$ N and S) regions. Effects of polycultural cropping on biocontrol and yield had a similar pattern in both temperate and tropical regions, although some outcomes were not significant (Fig. S3, Supporting information). These results mirrored the trend observed in the overall results of additive or substitutive studies (Fig. 2a,b).
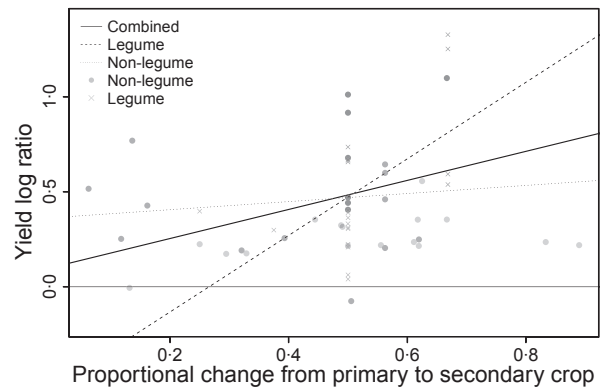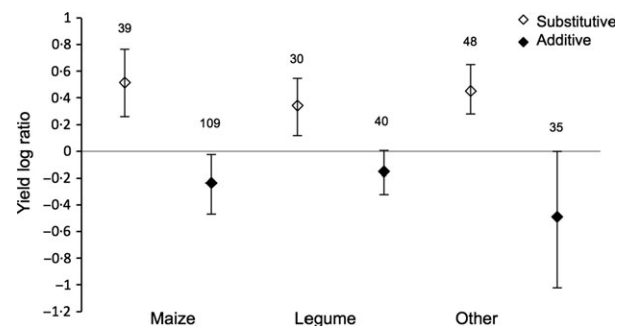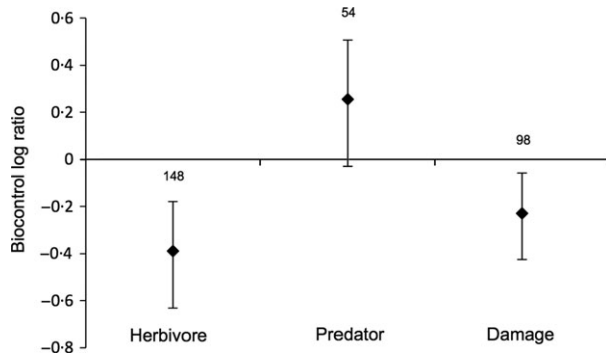
Fig. 5. Biocontrol response ratios (model mean estimate ± 95% CI) for each metric of biocontrol. Numbers above points indicate sample size.

of secondary crop relative to primary crop (Fig. 3). These results support the findings of other studies showing the benefits of biocontrol services provided by diverse cropping systems (Andow 1991; Simon *et al.* 2010; Letourneau *et al.* 2011). Biocontrol benefits may result from associational resistance, such as a decrease in food concentration for specialized pests (i.e. resource concentration hypothesis) or an increase in their natural enemies (i.e. enemies hypothesis) (Root 1973; Beizhou *et al.* 2012; Hamback, Agren & Ericson 2013).

Given the strong biocontrol effect found in diverse cropping systems, the overall outcome of a win-win or trade-off relationship was largely determined by the yield response. Our analysis suggests that the yield response is highly influenced by plant–plant competition as mediated by planting density. When total crop density was held constant (substitutive designs), more diverse cropping systems had higher per-plant primary crop yield, thus resulting in a significant win-win relationship between biocontrol and per-plant yield. When overall crop density increased in polycultures relative to monocultures (additive designs), more diverse cropping systems had a lower per-plant (or per-unit area, see 'Materials and methods') primary crop yield, leading to a trade-off between the two services. These results were relatively consistent by region, type of primary crop and biological control metric, suggesting that the patterns observed in this meta-analysis are broadly applicable, despite variations in species and climate.

Our results provide important insights into the ecological mechanisms that may contribute to crop production in agroecosystems. In additive studies, the decrease in primary crop yield in polycultures probably reflects increased interspecific competition in these mixtures. However, notably, this loss in yield disappeared when the secondary crop was a legume, suggesting that legume facilitation minimized the negative effects of increased competition (Table 1, Fig. 2b, Fig. S1, Supporting information). Letourneau *et al.* (2011), in a meta-analysis sharing nine studies in common with ours, found a beneficial effect of polycultural cropping on primary crop yield in additive studies (also without including secondary crop yield), sug-

gesting that win-win scenarios may not be uncommon with additive designs. For studies using substitutive designs, the beneficial effects of polycultural cropping on per-plant yield suggest that interspecific competition is less costly than intraspecific competition and/or that positive interactions, such as facilitation, enhance per-plant yield. Further supporting this evidence, we found a significantly positive relationship between primary crop yield and the proportion of a plot made up of secondary crop (Fig. 3). However, the influence of one particular study (Nordlund, Chalfant & Lewis 1984) limits our confidence in the generality of this finding.

Our analysis suggests that the beneficial effects of polycultural cropping on yield may not result primarily from increased biocontrol effects of lower plant damage, suppression of pests or augmented natural enemy populations. However, due to the diversity of herbivores and natural enemies recorded in these studies, it is possible that biocontrol could sometimes be influential on yield despite the lack of a significant correlation between the two services. For example, a small change in the biocontrol value could have a considerable benefit to yield in one study, whereas in another it could make no difference. This particular outcome could occur if the herbivore species in one study, but not another, were particularly damaging or if natural enemies in one study were more effective predators of relevant herbivores. As a result, we may not see a positive correlation between the biocontrol metric (e.g. number of herbivores) and yield, even if generally there is a biocontrol effect.

LIMITATIONS

We were unable to include overall yield data in our analyses due to the lack of secondary crop yield information reported in the majority of studies. It was therefore most logical to calculate yield on a per-plant basis for substitutive studies. Additive studies were equivalent in log-response ratios irrespective of calculating by area or by plant. Focusing on per-plant yield was, in the end, most useful for understanding the ecological interactions that underlie the relationships between yield and biocontrol, as these occur at the scale of an individual plant. However, per-plant primary crop yield calculations may lead to over-estimations and underestimations compared to total yields in substitutive and additive studies, respectively. Our results for additive studies are thus conservative. For substitutive studies, we believe that per-plant yield is indicative of overall yield for two reasons. First, the great majority of the substitutive observations ($N = 97$ out of 117) had a harvestable secondary crop that would have contributed to total yield. Second, of all secondary crop observations, 56% ($N = 65$ out of 117) were species that were also primary crops in other studies and therefore also showed an average benefit from polycultural cropping.

Undoubtedly, in some cases yield (or profit) per-unit area will be lower under substitutive polycultural systems

due to the combination of a lower density of primary crop and a less productive or non-saleable (or lesser value) secondary crop. There are thus some concerns that more land area would be required to produce the same amount of food, resulting in a net loss of ecosystem services, such as biodiversity conservation, across the landscape (Green *et al.* 2005; Phalan *et al.* 2011). However, others contest that this viewpoint relies on various assumptions that are not always met, such as countries being able to protect land (which relies on a complex social and political interplay), and that ecosystem service provision and high yield are not compatible (Fischer *et al.* 2011; Tscharntke *et al.* 2012). Although we cannot assess this question directly in our study, our results support the notion that crop production and ecosystem service provision need not be inversely related. Indeed, many studies show that polyculture overyielding can be predominant when considering total yield, especially with monocot/non-monocot crop combinations (Trenbath 1974; Vandermeer 1989; Picasso *et al.* 2011), and that polycultures often benefit biodiversity (Kremen & Miles 2012).

IMPLICATIONS FOR MANAGEMENT AND POLICY

Our findings have important implications for scientists, farmers, policy-makers and society at large. A critical issue facing our world today is how we can produce and justly distribute sufficient food for a growing population while simultaneously minimizing adverse impacts on other important ecosystem services (Foley *et al.* 2011). Current global levels of agricultural intensification reflect a trend of simplifying agricultural systems for increasing production and have resulted in monocultures dominating the agricultural landscape in many regions of the world (Glaeser 2011). This intensification, which is expected to continue given projections of food demands to double by 2050 (Tilman *et al.* 2011), has had several negative effects on the health of ecosystems and the life that depends on them (Tilman 1999). Our study shows that polycultures consistently enhance biocontrol services and, depending on the context, may provide yield benefits. Our results show that win-win relationships between per-plant yield and biocontrol may be achieved by reducing intraspecific competition through partial substitution of primary crops for secondary crops. For per-unit area yield, our results suggest that fields incorporating harvestable legumes as a secondary crop have the best potential for win-win relationships when fields are at high cropping densities (i.e. within an additive framework). However, several other considerations, including crop value, crop–crop compatibility and farmer preference, will be important in determining the crops to plant and the proportions in which to plant them. Finally, we urge for a greater investment in researching the underlying relationships between multiple agroecosystem services so we can better achieve agroecosystem multifunctionality.

Data accessibility

Datasheet of all observations included in meta-analysis is available in Dryad Digital Repository: http://doi:10.5061/dryad.m1m50. Iverson *et al.* (2014).

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Supporting Information

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

Appendix S1. Search terms for article selection.

Fig. S1. Observations with time series having a significant linear or quadratic trend.

Fig. S2. Log-response ratios by type of secondary crop (legume vs. non-legume).

Fig. S3. Log-response ratios by geographical region.

Table S1. Annotated list of all studies included in the meta-analysis.

Table S2. Rosenthal's fail-safe numbers.

Table S3. Spearman rank correlations.