Ecological Applications, 21(1), 2011, pp. 9–21

Does plant diversity benefit agroecosystems? A synthetic review

Deborah K. Letourneau,[1,2,5] Inge Armbrecht,[2] Beatriz Salguero Rivera,[2] James Montoya Lerma,[2]
Elizabeth Jiménez Carmona,[2] Martha Constanza Daza,[3] Selene Escobar,[2] Víctor Galindo,[2,6]
Catalina Gutiérrez,[2,4] Sebastián Duque López,[2] Jessica López Mejía,[2] Aleyda Maritza Acosta Rangel,[2]
Janine Herrera Rangel,[2] Leonardo Rivera,[2] Carlos Arturo Saavedra,[2,4] Alba Marina Torres,[2]
and Aldemar Reyes Trujillo[3]

[1]*Environmental Studies Department, 1156 High Street, University of California, Santa Cruz, California 95064 USA*
[2]*Department of Biological Sciences, Universidad del Valle, Cali, Colombia*
[3]*Escuela de Ingeniería de Recursos Naturales y del Ambiente, Universidad del Valle, Cali, Colombia*
[4]*Wildlife Conservation Society, Colombia Program, Calle 4A No. 35A-57, Cali, Columbia*

Abstract. Predictive theory on how plant diversity promotes herbivore suppression through movement patterns, host associations, and predation promises a potential alternative to pesticide-intensive monoculture crop production. We used meta-analysis on 552 experiments in 45 articles published over the last 10 years to test if plant diversification schemes reduce herbivores and/or increase the natural enemies of herbivores as predicted by associational resistance hypotheses, the enemies hypothesis, and attraction and repellency model applications in agriculture. We found extensive support for these models with intercropping schemes, inclusion of flowering plants, and use of plants that repel herbivores or attract them away from the crop. Overall, herbivore suppression, enemy enhancement, and crop damage suppression effects were significantly stronger on diversified crops than on crops with none or fewer associated plant species. However, a relatively small, but significantly negative, mean effect size for crop yield indicated that pest-suppressive diversification schemes interfered with production, in part because of reducing densities of the main crop by replacing it with intercrops or non-crop plants. This first use of meta-analysis to evaluate the effects of diversification schemes, a potentially more powerful tool than tallies of significant positive and negative outcomes (vote-counting), revealed stronger overall effects on all parameters measured compared to previous reviews. Our analysis of the same articles used in a recent review facilitates comparisons of vote-counting and meta-analysis, and shows that pronounced results of the meta-analysis are not well explained by a reduction in articles that met its stricter criteria. Rather, compared to outcome counts, effect sizes were rarely neutral (equal to zero), and a mean effect size value for mixed outcomes could be calculated. Problematic statistical properties of vote-counting were avoided with meta-analysis, thus providing a more precise test of the hypotheses. The unambiguous and encouraging results from this meta-analysis of previous research should motivate ecologists to conduct more mechanistic experiments to improve the odds of designing effective crop diversification schemes for improved pest regulation and enhanced crop yield.

Key words: agroecosystems; crop damage; diversification; effect sizes; herbivores; intercropping; meta-analysis; natural enemies; pest regulation; statistical outcome vote-counting; yield.

Introduction

Since the advent of green revolution technologies in the 1960s, agricultural ecologists have explored the application of theory to alleviate unintended negative effects from the loss of biodiversity associated with high-yielding varieties grown in monocultures with fertilizers and pesticides (e.g., Altieri et al. 1983, Wilby and Thomas 2002, Butler et al. 2007, Hendrickx et al. 2007, Attwood et al. 2008). Vegetation management schemes are recommended to restore functional aspects of plant diversity lost through crop intensification (Letourneau 1998, Gurr et al. 2003, Tscharntke et al. 2005, Bianchi et al. 2006, Rey Benayas et al. 2009). Theory generated in the 1960s and 1970s (e.g., Pimentel 1961, Southwood and Way 1970, Root 1973, van Emden and Williams 1974) suggested that vegetation management techniques could serve multiple purposes, including regulating insect pest densities directly or through the action of their natural enemies (Barbosa 1998, Pickett and Bugg 1998). Using data extracted from articles published between 1998 and 2008 in a meta-analysis, we calculated the mean effect of crop diversification schemes on insect herbivores, their natural enemies, crop damage, and

---

Manuscript received 29 October 2009; accepted 11 March 2010; final version received 12 April 2010. Corresponding Editor: E. A. Newell.

[5] E-mail: dletour@ucsc.edu

[6] Present address: Fundación Centro para la Investigación en Sistemas Sostenibles de Producción Agropecuaria, Cra. 25 No. 6-62, Cali, Colombia.

crop yield to determine if pest-suppressive schemes provide overall benefits in agricultural systems.

Direct bottom-up effects of plant diversity involve the disruption of herbivores, particularly specialized feeders, from finding their host plant, causing the tendency for crop-feeding insects to leave the field at greater rates than when suitable hosts are concentrated in monocultures (Root 1973, Vandermeer 1989). Related hypotheses, compiled by Poveda et al. (2008), pose various mechanisms for lower pest densities on mixed vegetation than in monoculture, such as altered plant odor due to physiological changes in the plant (Finch and Collier 2000), repellent properties of associated plants (Uvah and Coaker 1984), masking of host plant odor by other plants (Tahvanainen and Root 1972), or visual masking of host plants by emergent, green non-crop plants (Finch and Collier 2000). Plant diversity may also affect belowground factors, such as microbial community biomass (Zak et al. 2003), which, in turn, may lead to higher levels of plant production (but see Wardle and van der Putten 2002). Associational resistance hypotheses focus on how other plants or crops that are associated with a particular plant or crop might repel or confuse host-seeking phytophagous insects (see Barbosa et al. 2009). The trap crop hypothesis predicts that some herbivores will be "attracted away from" a target plant if a preferred host is in the vicinity (Vandermeer 1989). Root's (1973) enemies hypothesis poses alternative or complementary mechanisms for herbivore suppression in diversified crop habitats. These mechanisms involve indirect, top-down effects of natural enemies enhanced by alternate prey/hosts, pollen, nectar, refugia, and microhabitats that are not available in weed-free crop monocultures (Altieri and Whitcomb 1979) or large-scale cropping operations with little non-crop vegetation (Altieri and Letourneau 1984, Roschewitz et al. 2005). Alternatively, vegetational diversification schemes in agriculture could increase herbivore abundance or neutralize any pest suppression benefits if weeds and other non-crop vegetation in and surrounding cropping areas harbor serious crop pests (Capinera 2005). Also, the searching efficiency of parasitoids and predators could fall to low levels in mixtures of plants that host different herbivore species, vary in structure, and emit different sets of volatiles, thus indirectly disrupting herbivore suppression (Andow and Risch 1985, Sheehan 1986, Perfecto and Vet 2003, Gols et al. 2005).

In a recent review, Poveda et al. (2008) found that vegetational diversification schemes tested in agriculture over the last decade serve to reduce herbivore densities in approximately half of the cases. We reviewed the same 62 papers used by Poveda et al. (2008), and applied meta-analysis, an analytical tool for quantifying general patterns across studies (Gurevitch and Hedges 1999). Hedges and Olkin (1980) have shown that counts of statistical test outcomes, or vote-counting techniques, as conducted by Poveda et al. (2008) and all other reviews of vegetational diversity and herbivore abundance, tend to be overly conservative compared to meta-analysis, which takes into account the relative sizes of the differences among treatments as well as their variance. Tallying the statistical outcomes of individual hypothesis tests as significantly positive, significantly negative, or neutral (no significant effect of the treatment) may underestimate the magnitude of an overall effect if nonsignificant outcomes share the same direction among treatments. In addition, because neutral findings can be expected to outnumber significant positive or negative findings, meta-analysts warn that the resulting reduction in statistical power (Cooper 1998) may reduce detection of real treatment effects (Hunter et al. 1982). For instance, even with a relatively small number of articles analyzed, a recent meta-analysis demonstrated that ecological restoration is likely to increase biodiversity and ecosystem services, including those supporting nutrient cycling and primary production (Rey Benayas et al. 2009).

We used a series of meta-analyses to ask the following questions. Do specific types of diversification schemes designed for associational resistance to herbivores, attraction of natural enemies, or moving herbivores away from crops have the predicted effects? Do more diverse cropping schemes in general have an overall negative effect on herbivores, a positive effect on natural enemies, reduce crop damage and increase crop yield? Does the use of diversification schemes provide an overall benefit in agroecosystems? If more plant diversity creates the desired effects, are there any particularly strong or conflicting results among different types of diversification schemes (intercropping vs. growing flowers around the crop field, for example) or due to other factors such as scale or design of the experiment, type of crop (annual or perennial), or geographic location (tropics vs. temperate zone)? We compared the results of our meta-analyses to those of Poveda et al. (2008) to determine if the two methods agree fundamentally, and we report the level of agreement, article by article, between meta-analysis effect sizes vs. statistical outcome counts of Poveda et al. (2008) to examine the consequences of neutral outcomes on statistical power. Finally, we discuss the advantages and disadvantages of using meta-analysis as an alternative tool to the counting approach used by Poveda et al. (2008) and others (e.g., Andow 1991*a*).

METHODS

Data sources and inclusion criteria

We reviewed the 62 publications (listed in Appendix A) selected by Poveda et al. (2008) from their initial 279 articles published between 1998 and 2008 addressing insect pests, biological control, and plant diversification in agroecosystems. Their criteria for selecting these 62 articles were that the articles were available and reported field experiments on vegetation diversification within or surrounding crop fields, implemented simultaneously with the crop production cycle. Our additional criteria for the meta-analysis were that: (1) plant species richness was quantified, described, or manipulated in a way that could be construed as a relatively species-poor vs. species-rich condition for crop production and (2) researchers reported or were able to provide us with means for arthropod herbivore response variables (abundance of natural enemies, herbivore abundance, herbivore mortality caused by natural enemies, crop damage by herbivores, and/or crop yield), variance around the means, and numbers of replicates. Because most of the articles provided multiple experiments involving different herbivores and/or different natural enemy manipulations at different locations or in different years, our general approach was to include only tests that could not be logically dropped from the analysis. For example, independent tests of monoculture vs. polyculture in 2003 and 2004 would be equally valid for our analysis, as would experiments in two or more locations, or involving different species. However, we excluded experiments that were confounded by differential insecticide applications on plant diversity treatments or that used planting densities that were deemed by the authors to be impractical for effective crop production. Also, in cases where the tests were repeated for all insect stages (e.g., eggs, larvae, pupae, adults), we used only data for the most damaging stage (usually nymphs or larvae). In following these practices, we optimized data collection from these papers while reducing undue representation of often small-scale studies whose numerous repetitions of the test in the same system would otherwise increase nonindependence bias (Gurevitch and Hedges 1999).

Hypotheses tested with meta-analysis

To test different mechanisms by which plant diversity can affect herbivores or natural enemies, we grouped diversification schemes into three categories for the first meta-analysis: (1) interplanting schemes that primarily reduce resource concentration for herbivores and enhance resources for enemies (infield diversification with crops and non-crops); (2) flower addition (for attracting natural enemies); and (3) herbivore movement plantings (trap crops, repellent crops, around crops, push–pull designs which combine repellant and trap crops). The second meta-analysis tested the effects of all diversification schemes on different dependent variables (herbivores, natural enemies, crop damage, and yield). We used a third meta-analysis to test if there was an overall beneficial effect of increased plant diversity when all dependent variables (herbivores, enemies, damage, and yield) were included in the analysis, changing the signs of the effect sizes for herbivores and damage so that all beneficial outcomes had a positive value. In the second and third meta-analyses, we further partitioned the variance to examine possible effects of different types of diversification schemes, scale (small-scale experimental plots of 2–1000 m^2 vs. large-scale plots > 1000 m^2), geographic location (tropical vs. temperate), type of crop (annual vs. perennial), and experimental design (*additive* designs in which crop density is held constant vs. *substitutive* designs in which additional crops or plants replace the main crop).

Data extraction, analysis, and comparison of vote-counting and meta-analysis

Means and measures of variance were estimated from figures using Digi-Matic or Graph-Grabber when these values were not reported in the text. In cases where individual means and their standard errors were plotted for repeated samples over the season, but no overall seasonal mean was provided, we calculated the grand mean for each level of plant diversity. To estimate the standard deviation of the grand mean, we applied Salguero-Rivera's formula (Appendix B):

$$(\mathrm{SD})^2 = \frac{\sum (x_i)^2 - (n_1 + n_2 + \cdots + n_n)\bar{X}^2}{(n_1 + n_2 + \cdots + n_n)}.$$

To calculate separate effect sizes for herbivores, enemies, crop damage, and yield, we used raw effect sizes, with these dependent variables used as categories to partition the variance. That is, a negative effect size resulted if a species-rich cropping scheme had fewer herbivores, fewer natural enemies, lower damage, or lower yield than the control (species-poor cropping scheme). A positive effect size meant the opposite: that herbivores, natural enemies, damage, or yield had a higher value in species-rich cropping schemes compared to controls. To allow for a test of the overall effect of plant diversity in agriculture, we used a column reversal marker for herbivores and crop damage in the meta-analysis spreadsheet (Gurevitch and Hedges 1993) so that a reduction in herbivores or crop damage became a positive value for effect size. In this way, a positive mean effect size would result if, on average, beneficial outcomes of plant diversity prevailed (herbivores less abundant in diverse vegetation, natural enemies more abundant, crop damage lower, and/or greater yield).

To calculate the effect as a proportional change in plant species diversity, we used bias-corrected Hedges' d to calculate the overall treatment effect size (d_+). We did not include the precision of each study's estimates in this analysis (i.e., variance weighting). Instead, mean effect sizes (d_+) were treated equally to remove biases against small sample sizes (e.g., Hedges and Olkin 1985, Halaj and Wise 2001). Hedges' d is appropriate for small sample sizes (n values), and allows for experimental and control group means to have different signs, whereas response ratios do not (Rosenberg et al. 2000). Differences in effect sizes were calculated using mixed-effects models (Gurevitch and Hedges 1993) performed with MetaWin 2.0 statistical software (Rosenberg et al. 2000). Mixed-effects models potentially result in wider (more conservative) confidence intervals around overall effect size estimates as they assume differences in real effect sizes across studies conducted in widely differing systems (Stram 1996, Schmidt et al. 2009). We used the bootstrap confidence intervals because resampling methods are appropriate when data are not normally distributed; our standardized effect sizes on the extreme ends of the distribution did not all fall within a normal distribution (Appendix C). Effect sizes were interpreted as being significantly positive or negative, depending on the value, if the 95% bootstrap confidence intervals excluded zero.

Comparisons of the two methodologies (vote-counting vs. meta-analysis) were done in two ways. First, we considered any difference in the number of articles used in the two methods as part of the methodology. For this comparison, we used the full sample of our Hedges' *d* values to count the raw percentage of directional outcomes (negative values, zero values as neutral effects, and positive values) and compared these percentages with the percentage of positive, negative, and neutral outcomes reported by Poveda et al. (2008). Second, we controlled for article identity, such that we calculated the percentage of mean Hedges' *d* outcomes per species/parameter per article, using only the subset of articles that were included in our meta-analysis. In this comparison, the voting categories of Poveda et al. (2008) for effect sizes of diversification schemes on herbivores, enemies, crop damage, and yields (+,–,0 or a mixed result category in which, for a given parameter, there were both significantly positive and significantly negative outcomes) was compared with our result for the same article, by herbivore, enemy, or crop taxon, using their outcome designations as listed in their review. If individual Hedges' *d* values that made up our mean value for the species and article varied in sign, we did not "disagree" with their mixed-outcome category.

RESULTS

Range of cropping systems, herbivores, and natural enemies, and test for publication bias in the synthetic review

Forty-five of the original 62 articles (Appendix A) yielded 552 "experiments" comparing species-rich vegetational diversification schemes with species-poor cropping systems. These experiments involved ~50 species of herbivores (including various Lepidoptera, herbivorous bugs, beetles, aphids) and over 20 higher taxa of natural enemies (such as spiders, parasitic wasps, and predacious bugs) on ~20 main crops (from apples, bananas, cassava and corn to vineyards and wheat). Low-diversity treatments contained either one or two plant species, and high plant diversity ranged from 2 to 15 species, except for one study on coffee having 200 species of forest trees in the rustic, under-sown treatment. In approximately half (272) of the experiments used in the analysis, a crop species grown alone was compared with the same crop grown in association with one additional plant species (crop or non-crop added to the monoculture). Over 145 697 additional nonsignificant or unpublished studies would need to be added to change the results of the meta-analysis from significance to nonsignificance, as calculated using Rosenthal's method for deriving a fail-safe value. This implies that publication bias was not responsible for the significant outcomes of our meta-analysis, because the publication rate of larger effect sizes in one direction (e.g., positive effects) was not significantly greater than those reporting smaller effect sizes (Rosenthal et al. 2000).

Meta-analysis on categorical diversification schemes to determine if mixed-plant associations met predicted design goals

Interplanting schemes designed to reduce herbivores, possibly through enhancing natural enemies, produced strongly significant effect sizes in the predicted direction for herbivores (negative) and natural enemies (positive) (Hedges' $d_+ = -1.34$, $n = 111$, 95% CI = –1.92 to –0.81 and Hedges' $d_+ = 2.20$, $n = 52$, 95% CI = 1.01 to 3.57, respectively), suggesting that, on average, these diversification schemes achieved the desired results. The addition of flowering plants in or around the crop field also significantly increased natural enemies (Hedges' $d_+ = 1.12$, $n = 31$, 95% CI = 0.45 to 2.01), and diversity schemes designed to influence herbivore movement through repelling herbivores or attracting them away from the main crop were also effective at suppressing herbivores (Hedges' $d_+ = -1.45$, $n = 93$, 95% CI –2.05 to –0.91).

Meta-analysis on all diversification schemes testing effects on herbivores, enemies, damage, and crop yield

Herbivore abundance on crops was strongly suppressed by plant diversification schemes in general, based on the large and negative Hedges' d_+ value for all 221 experiments that measured treatment effects on herbivorous insects (Fig. 1). That is, the mean effect size for herbivores had bootstrap 95% confidence intervals not overlapping zero, with no overlap being the criterion for a significant effect of treatment on the response variable. Overall, herbivores were suppressed by 23%, when comparing the grand mean abundance or, in a few cases, species richness, in cropping systems with higher diversity plantings vs. the grand mean in lower diversity crop systems. In contrast, natural enemies of herbivores were significantly increased (Hedges' d_+ for measures of enemy abundance and percentage mortality inflicted on herbivores, with a few cases of enemy richness), with an equally strong mean effect size (Fig. 1). The average abundance (or rarely richness) of natural enemies was 44% greater and average herbivore mortality was 54% greater in high-diversity than low-diversity cropping systems. The combined effects of direct bottom-up and indirect top-down factors may explain an even stronger negative effect size for crop damage (Fig. 1). The grand mean for crop damage was 23% lower in more diverse plant assemblages than in comparatively lower diversity plantings. A relatively smaller number of studies measured yield of the main crop, which was slightly, but significantly reduced overall, in the diversified cropping schemes compared to lower diversity cropping arrangements (Fig. 1). A mean decrease in yield of 14% accompanied the high-diversity treatments compared to low-diversity crop systems.

A more detailed assessment, calculating separate effect sizes for each of eight diversification schemes, showed that intercrops, nonspecific plants within the field (in-other), and trap crops grown with the main crop but used to attract herbivores away from the crop, had the significant, suppressive effect on herbivores they were designed to have, compared to their low plant diversity controls (Table 1). Intercropping schemes were also effective at increasing natural enemies significantly, as was adding plant diversity around the crop and adding flowers (Table 1). A significantly positive effect size for natural enemies with push–pull schemes was less expected, because these schemes are specifically designed to influence the movement of herbivores (repel herbivores from the crop and attract them elsewhere). Positive effects of diversification schemes on natural enemies were stronger in large-scale than in small-scale experiments (Table 1).

With respect to crop damage levels, all well-replicated types of diversification schemes in our analysis showed a significant reduction in crop damage compared to controls with lower plant diversity (Table 1), although crop damage was only measured on studies with annual crops in the tropics. Although yields were significantly greater in push–pull studies than in their less-diverse counterparts, diversification schemes using intercropping and plantings around the field resulted in significantly lower crop yields than when crop plants were not diversified (Table 1).

Partitioning the heterogeneity for tests on crop yield, we found that when substitutive designs (secondary crop or non-crop plants replacing main crop plants) were used in diversification schemes, the mean effect size for yield was significantly negative (Table 1). In contrast, significantly positive mean effect sizes (increased yield with diversification) were calculated for experimental comparisons using additive designs (secondary crop or non-crop plants were added to the number of main crop plants). Negative effects of diversification on yield were especially pronounced for the small subset of experiments on perennial crops (n = 11, Hedges' $d_+ = -3.0$, 95% bootstrap CI = −4.8 to −1.3), with a broader array of annual crops showing no significant mean effect of plant diversification (n = 76, Hedges' $d_+ = -0.28$, 95% bootstrap CI = −0.87 to 0.30). Also, yield reduction due to plant diversification was a strong outcome in small-scale but not large-scale experiments (Table 1).

In most but not all cases, the direction and size of mean effect sizes were in agreement with the narrative interpretations of Poveda et al. (2008). They observed that repellent plants, intercropping, nonspecific in-crop diversity, and push–pull schemes were most effective at suppressing herbivores. In contrast, the positive effects of repellent plants or nonspecific infield diversification that they observed were not shown in our study. One of the articles that our study did not cover reported the enhancement of herbivores on a crop in the presence of a trap crop. Such a discrepancy would partially explain a disagreement among the two methods if it dampened the overall effects of trap crops on herbivore abundance in the outcome tally used by Poveda et al. (2008).

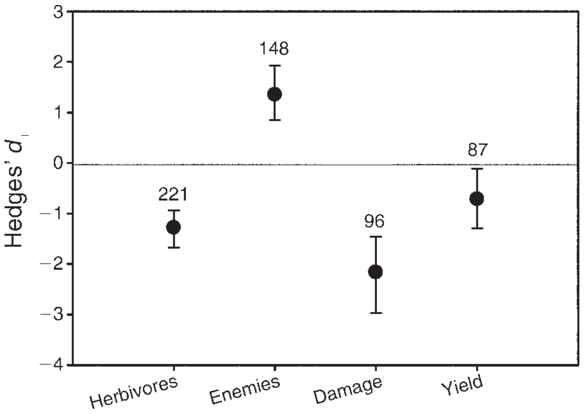

FIG. 1. Results of our meta-analysis of experiments comparing more diverse cropping schemes (polycultures) to less diverse schemes or crop monocultures, showing mean effect size as Hedges' d_+ values (with bootstrap CI calculated from 999 iterations). Pest (herbivores) abundance decreased significantly, natural enemy (predators and parasitoids) abundance increased significantly, and pest damage on crops decreased significantly, but yield was significantly lower when vegetational diversity was increased in agricultural systems. Effect sizes were interpreted as significantly different from zero if the 95% BCI did not overlap zero. Numbers of experiments for each parameter are shown above the CI bars.

Meta-analysis to measure overall effects of diversification schemes on all parameters combined: is plant diversity beneficial for agriculture?

Using the meta-analysis approach to calculate a grand, overall effect of vegetational diversification on agricultural outcomes, we found a large, significant, and positive mean effect size (Hedges' $d_+ = 1.14$; bootstrap 95% CI = 0.88 to 1.41) of increased plant diversity on the combination of measured effects (with a positive overall value for pest suppression, augmentation of natural enemies, reduction of crop damage, and increased yield), indicating an overall beneficial outcome of diversification schemes in agriculture as compared to cropping systems that incorporate fewer species or are simple crop monocultures (Fig. 2). Partitioning the heterogeneity, we found that experiments in our review were mainly conducted with annual crops (475 annual vs. 77 on perennial crops) and more often in tropical regions (413 tropical vs. 139 in the temperate zone). Mean effect size (Hedges' d_+ value) was not significantly different from zero for perennial crops alone (n = 77, Hedges' d_+ =

TABLE 1. Results of meta-analysis showing the mean effect size (Hedges' d_+) on herbivores, enemies, crop damage, and yield caused by different types of vegetational diversification schemes, experimental design, and scale of experiment.

Dependent variable and effect	Diversification scheme							
	Inter-crop	In-other	In-trap	In-repel	Push–pull	Around-crop	In-flower	Around-flower
Herbivore abundance								
No. studies	100	43	23	<2	8	29	17	<2
Effect size	**−1.42**	**−1.30**	**−2.43**		−0.49	−0.86	0.01	
Low BCI bound	−2.09	−1.87	−4.07		−1.16	−2.01	−0.12	
High BCI bound	−0.84	−0.82	−0.99		0.03	0.03	0.13	
Agreement	yes	yes	no		no			
Enemy abundance or % parasitism								
No. studies	49	17	4	<2	30	17	19	12
Effect size	**2.26**	0.04	1.85		**1.30**	**0.43**	**1.23**	**0.95**
Low BCI bound	0.86	−0.19	−0.21		0.93	0.04	0.21	0.52
High BCI bound	3.80	0.31	3.91		1.73	0.82	2.84	1.42
Agreement	yes	no	yes		yes	yes	yes	
Crop damage								
No. studies	48	12	4	9	15	8		
Effect size	**−2.39**	**−0.47**	0.39	**−1.49**	**−3.44**	−3.05		
Low BCI bound	−3.79	−0.80	−0.27	−1.86	−4.20	−7.54		
High BCI bound	−1.30	−0.14	0.99	−1.08	−2.74	0.03		
Agreement	yes	yes	yes	yes	yes	yes		
Yield								
No. studies	42				14	30		
Effect size	**−1.07**				**3.08**	**−1.99**		
Low BCI bound	−1.91				2.68	−2.59		
High BCI bound	−0.29				3.48	−1.43		
Agreement	no				yes	no		

Notes: Comparisons of enemy impact included predator abundance, parasitoid abundance, or the percentage of pests attacked by parasitoids. Crop diversification schemes follow Poveda et al. (2008), with plant diversity altered either within the crop field (in-) or around the margins of the crop field (around-), and according to the motive used to diversify the crop field: increased in-field diversity with other crops (intercrop), flowering plants to provide nectar or pollen (in-flower), pest attractant "trap" plants (in-trap), plants repellent to pests (in-repel), or non-crops that have no specific function (in-other); to increase diversity around the field using other crops (around-crop), flowering plants (around-flower), and other plants (around-other); and "push–pull," designed to move pests out of the crop field by combining an "in-repel" scheme with an "around-trap" scheme. Categories of crop diversification were either additive (density of the main crop remains the same in comparisons of more and less diversified cropping schemes) or substitutive (alternate crops or non-crops replace some of the main crop plants, making density of the main crop lower in more diverse schemes than in less diverse schemes). "Yes" signifies that Poveda et al. (2008) reported trends that agreed with the meta-analysis result, "no" indicates disagreement, and no entry means that a comparison was not possible. Significant effect sizes are indicated with boldface type. BCI is the 95% bootstrap confidence interval, calculated using 999 iterations of resampling.

–0.1, 95% bootstrap CI –0.8 to 0.6) and was relatively small, but significantly positive, for temperate crops ($n = 139$, Hedges' $d_+ = 0.4$, 95% bootstrap CI 0.1 to 0.6), whereas mean effect sizes were large, significant, and positive for annual crops and tropical studies (Hedges' $d_+ > 1.3$, lower 95% bootstrap CI > 1.0). All diversification schemes had significantly positive effects when all measures were combined, except for crop fields surrounded by other crops (around-crop), which had no measurable effect on the overall outcome of crop diversification (Hedges' d_+ not significantly different from zero).

Comparison of vote-counting method with meta-analysis

A basic difference between outcome (or vote-) counting and our meta-analysis was that fewer articles met the stricter criteria for calculating effect sizes (45 articles) than for counting the incidence of particular outcomes (62 articles); see Table 2. However, using original data allowed us to extract 552 individual experiments from which to calculate effect sizes for the effects of crop diversification schemes on herbivore abundance, their natural enemies (abundance, parasitism rate), feeding damage, or crop yield compared to the 171 statistical test outcomes reviewed by Poveda et al. (2008).

The percentages of positive and negative outcome counts were nearly always smaller for counting test results than for counting the precise Hedges' d values in the meta-analysis (Table 2). For instance, the report of 52% cases of herbivore suppression and 53% enemy increase reported in Fig. 1 of Poveda et al. (2008) differs from 72% and 74% incidences, respectively, in our meta-analysis approach. By controlling for the number and identity of articles used by the two methods, the discrepancy between counting percentages of negative and positive outcomes (Poveda et al. 2008) vs. effect sizes became evident. Effect sizes percentages (present study) were nearly the same as when 62 vs. 45 studies were used, if not more pronounced, with 48% of cases reporting herbivore suppression vs. 78%, respectively (Table 2). The largest difference between the two

TABLE 1. Extended.

Design		Scale	
Additive	Substitutive	Small (<225 m^2)	Large (≥225 m^2)
119	102	133	88
−1.50	**−2.20**	**−1.642**	**−0.74**
−0.99	−2.94	−2.22	−1.35
−0.01	−1.60	−1.19	−0.25
112	36	38	110
1.36	**1.31**	−0.04	**1.83**
0.77	0.62	−0.22	1.23
2.08	2.15	0.13	2.59
46	50	62	34
−2.92	**−1.47**	**−1.61**	**−3.19**
−3.93	−2.67	−2.80	−4.03
−2.10	−0.42	−0.67	−2.49
44	43	50	37
0.91	**−2.21**	**−1.51**	0.56
0.16	−2.80	−2.05	−0.51
1.57	−1.67	−1.02	1.57

methods was the effect of diversification practices on crop yield. Whereas Poveda et al. (2008) reported approximately equal percentages of positive and negative effects of diversification on yield (~30%), the meta-analysis found a threefold higher incidence of yield reduction outcomes, with 75% of the individual experiments on yield having at least slightly negative effect sizes. In an article-by-article comparison of individual outcome counts from statistical tests (2008) with mean Hedges' *d* effect sizes calculated in the present study, using only the 45 articles reviewed in common, there was agreement on the outcome in only 41% of the cases (Appendix D).

DISCUSSION

Overall effects of crop diversification schemes

Our quantitative synthesis of studies revealed a dramatic, beneficial effect of the use of vegetational diversification schemes for suppressing herbivores, enhancing natural enemies of herbivores, and reducing crop damage. There were, not surprisingly, some detectable effects in relation to climate (tropical vs. temperate), crop characteristics (perennial vs. annual), vegetational diversification schemes (intercropping, flowers surrounding the crop field, trap crops, and so forth), experimental designs (additive vs. substitutive), and the scale of the experiment (individual plot size less than or greater than 1000 m^2). However, despite these strong positive consequences of plant diversity, crop yield was significantly decreased overall, in part because some of the diversification schemes substituted the alternate plant for a crop plant, reducing crop density in the study. Compared to the large mean effect sizes from our meta-analysis, relatively weaker effects of plant diversity on herbivores, enemies, damage, and yield emerged when a sophisticated vote-counting method was used by Poveda et al. (2008) to review the same collection of studies. Although the fundamental conclusion was in the same direction as ours in the present review, only slightly more than half of the cases in their review showed the predicted result for herbivores, natural enemies, and crop damage, and an overall negative yield effect of plant diversity was less conclusive.

Herbivore suppression and natural enemy abundance

In a review of nonoverlapping, earlier studies of crop diversity effects on pest population densities, Andow's (1991*a*) outcome counts were very similar to those of Poveda et al. (2008), with 56% showing suppression of herbivores, 16% with higher population densities, and 28% with similar or variable densities in polyculture compared to monoculture. Both Poveda et al. (2008), with 53% of the cases showing herbivore suppression, 12% with increased herbivore presence, and 35% with similar or variable herbivore pressure, and Andow

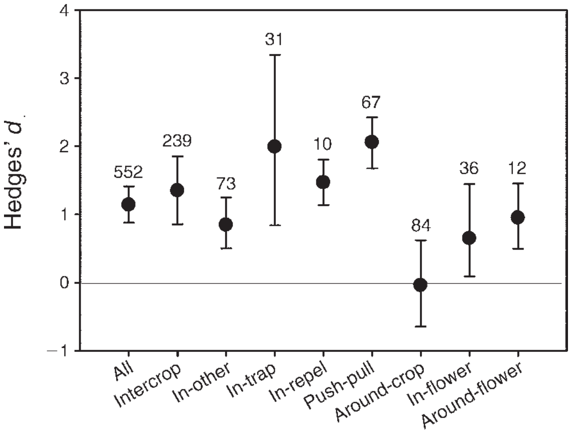

FIG. 2. Results of a meta-analysis of experiments comparing more diverse cropping schemes (polycultures) to less diverse schemes or crop monocultures, showing mean effect size as Hedges' d_+ values (with bootstrap CI calculated from 999 iterations). The overall effect of diversification schemes (pest suppression, natural enemy augmentation, reduction in crop damage, and higher yield all result in positive Hedges' d_+ values) was significantly positive when all diversification schemes were included ("All"), and for individual categories of diversification schemes as defined by Poveda et al. (2008), analyzed separately as intercropping with crops, trap crops, repellent plants, and non-crops, or a combination of repellent and attraction crops for a push–pull effect, as well as for flowers within or outside the field, but not for crops surrounded by other crops, which had a neutral effect overall. Effect sizes were interpreted as significantly different from zero if the 95% BCI did not overlap zero.

TABLE 2. Overall percentages of positive, negative, mixed, and neutral outcomes for the 171 experiments in 62 articles selected by Poveda et al. (2008) (labeled Count) and the 552 meta-analysis effect sizes (Meta) from 45 of those articles.

	Positive outcomes (%)		Neutral (0)/Mixed (+,−) (%)†		Negative outcomes (%)	
Effect type	Count	Meta	Count	Meta	Count	Meta
Herbivore suppression	52 (48)	72 (78)	20 (24)/19 (14)	2 (2)	10 (14)	26 (20)
Enemy increase	53 (50)	74 (75)	22 (26)/13 (18)	3 (4)	12 (5)	24 (21)
Damage suppression	58	72	16/5	0	21	29
Yield increase	32 (33)	39 (25)	26 (22)/13 (11)	0 (0)	29 (33)	61 (75)

Notes: Percentages in parentheses control for sample differences between the present study and that of Poveda et al. (2008) by using the same 45 articles for each method and using counts from Table 1 of Poveda et al. (2008) as shown in Appendix A. Articles 1, 3, 9, 10, 13, 15, 23, 24, 31, 32, 35, 38, 41, 42, 43, 47, and 49 in Poveda et al. (2008: Table 2), listed in our Appendix A, did not meet our additional criteria concerning data reporting or plant richness treatments, so were not used in meta-analysis calculations of effects sizes.

† Note that because Hedges' *d* values from individual tests within articles were calculated as a mean *d* value, the meta-analysis approach had no "mixed" results.

(1991*a*) showed a weaker effect of plant diversification in cropping systems than did our meta-analysis approach. However, Muriel and Vélez (2004) reviewed 350 articles published between 1998 and 2003 and found that 70% of the articles documented improved pest control in diverse agroecosystems. A more decisive outcome using meta-analysis is expected if calculations using original data to estimate the size of individual effects uncover a directional trend, thus accumulating larger values among significant or even nonsignificant test results. In the case of such a directional trend, the actual measurement of effect sizes may lead to a more robust and powerful test of the hypothesis compared to counting the number of results falling into various categories (significantly positive, significantly negative, no significant effect), as has been done in all previous reviews of plant diversification effects in agriculture. Vote-counting reviews of the literature lump nonsignificant outcomes that result from a lack of power with those in which there is a genuine absence of an effect due to treatments, which can lead to the false conclusion that a body of evidence does not support a treatment effect when in fact it does (Cohn and Becker 2003). Cohn and Becker (2003) estimated that relatively low power (less than 0.50) across a review of experimental tests could cause a tabulation of the number of significant outcomes among those experiments to lead to the wrong conclusion. Additionally, in such a case, the chance of arriving at a wrong conclusion increases with the number of outcomes counted (Hedges and Olkin 1985). Therefore, we are confident that meta-analysis, and its support for theoretical predictions about direct and indirect effects on herbivores and natural enemies, is an appropriate approach and can be a more precise test of these hypotheses. We caution, however, that many ecological mechanisms may be responsible for varied effects of diversification on insect pest regulation. These include insect life history, indirect effects, and spatial and temporal scales in the experimental designs, all of which prevent simple extrapolations from general outcomes to any particular case (Muriel and Vélez 2004).

Crop damage and yield

To our knowledge, Poveda et al. (2008) were the first reviewers of the responses of insects to pest-suppressive diversification schemes who evaluated the cumulative extension of pest and natural enemy effects on crop yield across a wide variety of designs, including substitution of crops with other crops or non-crop plants. Andow's (1991*b*) informative review of additive designs for pest suppression in mixed and row intercrops, cover crops, and weedy culture addresses the confounding issue of competition among plants when yield of the main crop is assessed. Whereas the critical link between diversification schemes and crop production is still made in only a handful of studies among the many devoted to insect populations, densities, or even crop damage, two important issues are derived from it: (1) the type of plants used and the design of the diversification scheme can determine whether gains in pest regulation translate to higher or more stable yields, and (2) multifactor cost–benefit measures are needed to assess the net effects of crop diversification schemes for growers. Certainly, the combination of certain crops is not beneficial under strong competition for light, water, or nutrients (e.g., Sastawa et al. 2004). In their case, the addition of two crops to a soybean–millet intercrop reduced the abundance and associated damage by three pest species. However, the reduction in damage did not compensate for yield decreases that were most likely caused by crowding and shading. Also, our meta-analysis results suggest that adding plant diversity rather than substituting other plants such as trap crops or repellent plants for the main crop will have positive yield effects. As suggested by Andow (1991*b*), agronomic considerations concerning crop–crop or crop–noncrop compatibility and spatial arrangement of these plants are important for designing successful pest-suppressive diversification schemes that minimize crop yield loss through plant–plant competition or plant density effects (e.g., Sanchez 1981). Clearly, trade-off effects for reducing herbivores at the expense of yield can vary among crops. For example, Letourneau

(1986) found that the addition of maize intercrops to squash monocultures increased parasitism rates and reduced the abundance of most pest groups, decreased squash yield, maintained maize yield, and increased total production per unit land area. Lower yields in intercropping systems using substitutive designs and measuring yield only of the main crop, however, are expected, because crop density is relatively lower in the diversification scheme than in the control; thus, crop yields in pest-suppressive schemes may be improved simply by using an additive design. Increased crop yield (positive mean effect size) in push–pull systems incorporating repellent and attractive plants needs further investigation because samples for individual practices were relatively small and sometimes contradictory. Even in the worst scenarios for crop yield loss through diversification schemes aimed at reducing herbivore pressure, we expect that environmental benefits and input cost reduction are gained at the expense of crop yield; these are parameters for which speculations were offered, but not measured in most studies. The assessment of ecosystem services resulting from diversification schemes for pest regulation, associated natural enemies, pollinators, crop damage, and yield requires accumulation of quantitative data through diagnostic on-farm assessments, especially with farmer participation.

Sources of error and bias

There are at least three somewhat overlapping primary explanations for a significant decrease in yield with crop diversification in the studies that we reviewed. First, the criteria used for the inclusion of studies in our review limited the collection of articles on yield to those that investigated aspects of herbivore abundance or biological control of pests. Therefore, it is possible that diversification schemes that are first and foremost pest-suppressive designs have not undergone as strict an agronomic analysis as is commonplace for experiments conducted with the aim of increasing crop yield. Whereas these studies are most appropriate for our focus on insects, general reviews on intercropping have found positive effects of plant diversification on yield (e.g., Vandermeer 1989, Fukai and Trenbath 1993, Sileshi et al. 2008), especially when the yields of all crops are included in the analysis. Second, although we excluded some experiments that were deemed by the authors as experimental only, and not appropriate for actual cropping schemes for production purposes, we did not restrict our data to include only the optimal diversity schemes designed for agronomic performance. By including the wider range of ad hoc cropping schemes for the diverse crop comparisons, we certainly biased the results for main crop yields toward the less favorable conclusion (Vandermeer 1998). These first two sources of bias are conceptualized as a trade-off between using vegetation diversity to control pests and taking up space with that vegetation diversity, an issue that needs to be taken into account in future planning (Fig. 3). Assessment of this trade-off is a daunting task using experimental approaches, requiring the development of a theoretical framework (Vandermeer 1986).

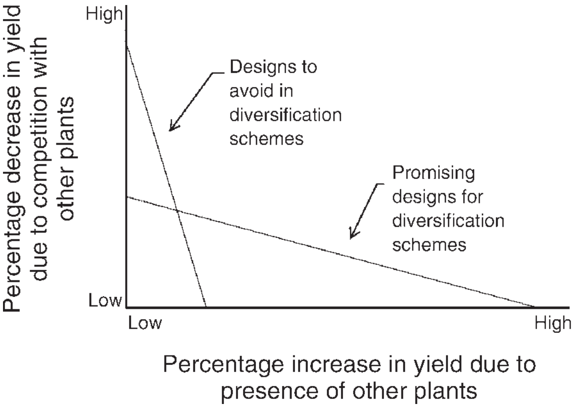

FIG. 3. Conceptual figure of the trade-off between increased crop yield via herbivore suppression caused by vegetational diversity and decreased crop yield because of crop-plant competition with vegetational diversity, showing a negative relationship, where diversification design decisions result in particular points on the graph. The rapidly declining function, which may include substitutive designs that replace the crop itself with another plant or other highly competitive plants, coupled with less effective pest suppression characteristics, is not likely to be a good strategy for controlling pests and increasing net crop yield. However, the slowly declining function shows the types of systems that are more favorable, and worthy of future research: those that minimize crop yield loss through competition and substantially decrease crop damage.

A third source of bias with respect to outcomes on crop yield is that we calculated mean effect sizes based on yields from only the main crop (e.g., Adeniyi 2001). That is, only the main crop yield was accounted for even in intercrop systems, which are known to produce high land-equivalent ratios (LER) or relative yield total (RYT). Because LERs and RYTs take into account all crop production on a unit of land, they often show a total yield advantage (Vandermeer 1981, 1989). Especially for additive designs of intercrops, push–pull crop, or around-crop designs, pooling the yields of all crops to calculate the LER or RYT probably would have resulted in a more positive overall yield for the diversification scheme than for a monoculture crop. In addition to these three explanations, factors outside our analysis include other ecosystem services such as pollination, and compensatory factors such as pesticide costs or land-use options, which have been shown to be ecosystem services that are enhanced with plant diversification through restoration practices (Rey Benayas et al. 2009). Most of the articles in our review reported on experiments conducted outside of the context of working farms with integrative practices supporting polycultures; diversification schemes in isolation of other conservation or sustainability practices may underestimate their potential.

A spin-off of the results indicating an overall slight, but significant, decrease in crop yield within vegetational diversification schemes concerns the potential for unaccounted bias if herbivore response in some of the experiments was confounded by crop quality. Bukovinszky et al. (2004) used the "host-plant quality hypothesis" to explain that plant stress through crowding and direct competition for light and nutrients may cause consequent changes in the developmental rate and nutritional quality of plants, which ultimately influences herbivore population responses to intercropping. They argued that such confounding effects of plant competition in intercropping designs can hamper the evaluation of herbivore responses in pest-suppressive agroecosystems. In some cases, that is, poor crop quality may be associated with reduced herbivore density, but damage to those crops may be greater, owing to more extensive feeding by those herbivores that are utilizing a host plant with lower nutrient content (Bukovinszky et al. 2004). Although our overall result for crop damage was indicative of a beneficial effect of added plant diversity, it is not clear how many of the individual cases could potentially be explained in this way. Because both additive and substitutive designs showed significantly suppressive effects of plant diversity on crop damage, however, with the stronger effect for additive designs, this potentially confounding factor was not operating substantially in the overall results, at least for annual crops tested in tropical agroecosystems.

In addition to the results presented in our review of population processes that take place in and near crop fields, recent research on processes occurring at larger landscape scales highlights critical questions for the conservation of biodiversity and ecological function in agroecosystems (Roland and Taylor 1997, Thies et al. 2003, Tscharntke et al. 2005). Arable crop systems rely on their surroundings more than other types of habitats because they are highly disturbed habitats that depend on recolonization from surrounding perennial habitats (Wissinger 1997, Tscharntke et al. 1999, Roschewitz et al. 2005). However, the results from large-scale studies are equivocal. In a review of studies conducted in the temperate zone, Bianchi et al. (2006) found no significant effect of the complexity of the landscape on pest pressure (in 45% of the articles, complexity reduced pest pressure, but there was no effect in 40%, and enhanced pest pressure in 15% of the articles). They concluded that under certain conditions, and for certain sets of pest species, non-crop habitats in the direct vicinity of crops may attract generalist predators, leading to reduced pest control in arable fields.

Vote-counting vs. meta-analysis

Is it worth the excruciating level of effort it takes to extract data for a meta-analytic synthesis over the simpler, and more intuitive method of outcome counting? The original analysis was a sophisticated "counting" method in which Poveda et al. (2008) derived a categorical value (positive, negative, or mixed when the effect of vegetational schemes were statistically significant, or no effect) for each of 171 statistical tests reported within the 62 papers. This approach is straightforward, intuitive, and extremely common (Rosenberg et al. 2000). Vote-counting reviews of the effects of vegetational diversity on herbivore or pest abundance have found that, in the majority or at least a wide variety of cases, phytophagous insects occurred at lower abundances on plants in mixed vegetation than on plants in monoculture (Altieri and Letourneau 1984, Andow 1991*a*, Muriel and Vélez 2004). However, we found that calculating effect sizes allowed for a stronger, less ambiguous result for each of the hypotheses that we tested as compared to the count-based review of Poveda et al. (2008). A more decisive result is consistent with the inability of counting methods to distinguish between null findings that result from low power and null findings that reflect a true absence of population effects (Cohn and Becker 2003). Hedges and Olkin (1980) showed that the statistical properties of this approach (vote-counting) were problematic, in that more evidence can lead to poorer decisions (Becker 2007). Although Poveda et al. (2008) concluded that diversification practices led to somewhat discouraging results, with only half the cases reporting enhanced natural enemies and reduced herbivores, we found unequivocal evidence supporting the benefits of diversification practices on suppressing herbivores and increasing natural enemies. On the other hand, we also found stronger negative results on crop production from diversification schemes. Thus, rather than coming to wholly different conclusions from the subset of articles we reviewed, we found stronger support for the same proposed relationships discovered by Poveda et al. (2008). The reduction in the number of articles due to added criteria necessary for the meta-analysis was compensated by the much greater number of individual tests that were possible from those articles using the meta-analysis. A larger data set allowed for stronger statistical confidence, and the ability to partition heterogeneity among the studies into explanatory variables is an obvious advantage of meta-analysis. That is, we were able to test more hypotheses with greater confidence, test for publication bias, and examine the structure of the underlying data with the synthetic statistical approach.

Despite the stronger, quite positive conclusions about cropping diversification schemes resulting from our meta-analysis, we agree with the basic conclusions of Poveda et al. (2008) that, on a case-by-case basis, diversification schemes have variable results, even on the parameters that showed the strongest overall effect sizes. On the one hand, our quantitative synthesis showed that plant diversification schemes designed to disrupt or confuse herbivores and those designed to move herbivores away from crops were effective, overall, in achieving their goals. On the other hand, there were many exceptions. For example, intercropping with additional host plants of the pest caused an increase in pest problems (Ngeve 2003); McIntyre et al. (2001) were unable to detect a repellent effect of their intercropped legumes on the banana pest that they had targeted for control. Unlike some of the past reviews, which found weaker effects of plant diversification on natural enemies than on their herbivorous prey (Risch et al. 1983, Andow 1991*a*), the potential for top-down control was strongly enhanced with the provision of pollen and nectar resources in these recent studies. However, experimental field manipulation that provides insight about the underlying mechanisms that lead to the small and large, negative and positive, effect sizes such as found in our analysis are generally lacking in studies of plant diversity, herbivores, and their natural enemies (see Bukovinszky and van Lenteren 2007). The relatively few mechanistic manipulations or predictive modeling approaches that dot the historical literature landscape (e.g., Waage 1983, Letourneau 1990, Hamback et al. 2000, Potting et al. 2005, Frank et al. 2007, Haddad et al. 2009, Winkler et al. 2009) help to move from observational to predictive results in the application of theory.

In conclusion, our analysis depicts strong evidence of the positive impact of plant diversification on agricultural systems, supporting theoretical predictions about pest suppression effects (Tahvanainen and Root 1972, Root 1973, Vandermeer 1989) and substantiating a gap between employing crop-suppressive diversity schemes and improving crop yields (Poveda et al. 2008). Meta-analysis allowed for a stronger level of detection for these effects than previous vote-counting methods (e.g., Andow 1991*a*, Poveda et al. 2008). The strong positive results found in our meta-analysis for using diversification schemes in agroecosystems shows that decades of funding for this scientific research has been useful and encouraging, but our work is not yet completed. The variability in responses discussed by Poveda et al. (2008) indicates that ecologists have an important role to play in discerning which schemes deliver the desired results for herbivore suppression and biological control, and what underlying mechanisms can be used to predict the "right kind of diversity" for providing these ecosystem services for pest regulation while maintaining crop yield.

ACKNOWLEDGMENTS

K. Poveda kindly provided databases and materials, and the Department of Biology of the Universidad del Valle, Cali, Colombia provided logistical resources and facilities for conducting the meta-analysis. Excellent advice on meta-analysis was offered by J. Gurevitch, and advice on calculating cumulative variances was offered by D. Cardona-Salgado. Comments by J. Vandermeer, J. Jedlicka, T. Cornelisse, H. Briggs, and an anonymous reviewer improved earlier drafts. Funding was provided by the Fulbright Commission of Colombia and a U.S. Fulbright Fellowship to D. K. Letourneau, USDA-NRI grant #2005-0288 to D. K. Letourneau, and a University of California–Santa Cruz Faculty Research grant.

LITERATURE CITED

Adeniyi, O. R. 2001. An economic evaluation of intercropping with tomato and okra in a rain forest zone of Nigeria. Journal of Horticultural Science and Biotechnology 76:347–349.

Altieri, M. A., and D. A. Letourneau. 1984. Vegetational diversity and insect pest outbreaks. Critical Reviews in Plant Sciences 2:131–169.

Altieri, M. A., D. K. Letourneau, and J. R. Davis. 1983. Developing sustainable agroecosystems. BioScience 33:45–49.

Altieri, M. A., and W. H. Whitcomb. 1979. Potential use of weeds in the manipulation of beneficial insects. Hortscience 14:12–18.

Andow, D. A. 1991*a*. Vegetational diversity and arthropod population response. Annual Review of Entomology 36:561–586.

Andow, D. A. 1991*b*. Yield loss to arthropods in vegetationally diverse agroecosystems. Environmental Entomology 20:1228–1235.

Andow, D. A., and S. J. Risch. 1985. Predation in diversified agroecosystems: relations between a coccinellid predator *Coleomegilla maculata* and its food. Journal of Applied Ecology 22:357–372.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography 17:585–599.

Barbosa, P. 1998. Conservation biological control. Academic Press, New York, New York, USA.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: Having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40:1–20.

Becker, B. J. 2007. Multivariate meta-analysis: Contributions of Ingram Olkin. Statistical Science 22:401–406.

Bianchi, F., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B 273:1715–1727.

Bukovinszky, T., H. Trefas, J. C. van Lenteren, L. E. M. Vet, and J. Fremont. 2004. Plant competition in pest-suppressive intercropping systems complicates evaluation of herbivore responses. Agriculture Ecosystems and Environment 102:185–196.

Bukovinszky, T., and J. C. van Lenteren. 2007. How to design pest-suppressing intercropping systems? Entomologische Berichten (Amsterdam) 67:231–234.

Butler, S. J., J. A. Vickery, and K. Norris. 2007. Farmland biodiversity and the footprint of agriculture. Science 315:381–384.

Capinera, J. L. 2005. Relationships between insect pests and weeds: an evolutionary perspective. Weed Science 53:892–901.

Cohn, L. D., and B. J. Becker. 2003. How meta-analysis increases statistical power. Psychological Methods 8:243–253.

Cooper, H. 1998. Synthesizing research: a guide for literature reviews. Third edition. Sage, Thousand Oaks, California, USA.

Finch, S., and R. H. Collier. 2000. Host-plant selection by insects: a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomologia Experimentalis et Applicata 96:91–102.

Frank, S. D., S. D. Wratten, H. S. Sandhu, and P. M. Shrewsbury. 2007. Video analysis to determine how habitat strata affects predator diversity and predation of *Epiphyas* *postvittana* (Lepidoptera: Tortricidae) in a vineyard. Biological Control 41:230–236.

Fukai, S., and B. R. Trenbath. 1993. Processes determining intercrop productivity and yields of component crops. Field Crops Research 34:247–271.

Gols, R., T. Bukovinszky, L. Hemerik, J. A. Harvey, J. C. van Lenteren, and L. E. M. Vet. 2005. Reduced foraging efficiency of a parasitoid under habitat complexity: implications for population stability and species coexistence. Journal of Animal Ecology 74:1059–1068.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–398 *in* S. Scheiner and J. Gurevitch, editors. Design and analysis of experiments. Chapman and Hall, New York, New York, USA.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology 80:1142–1149.

Gurr, G. M., S. D. Wratten, and J. M. Luna. 2003. Multifunction agricultural biodiversity: pest management and other benefits. Basic and Applied Ecology 4:107–116.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029–1039.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: How much do they trickle? American Naturalist 157:262–281.

Hamback, P. A., J. Agren, and L. Ericson. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. Ecology 81:1784–1794.

Hedges, L. V., and I. Olkin. 1980. Vote-counting methods in research synthesis. Psychological Bulletin 88:359–369.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, Orlando, Florida, USA.

Hendrickx, F., et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44:340–351.

Hunter, J. E., F. L. Schmidt, and G. B. Jackson. 1982. Meta-analysis: cumulating research findings across studies. Sage, Beverly Hills, California, USA.

Letourneau, D. K. 1986. Associational resistance in squash monocultures and polycultures in tropical Mexico. Environmental Entomology 15:285–292.

Letourneau, D. K. 1990. Abundance patterns of leafhopper enemies in pure and mixed stands. Environmental Entomology 19:505–509.

Letourneau, D. K. 1998. Conservation biology: Lessons for conserving natural enemies. Pages 9–37 *in* P. Barbosa, editor. Conservation biological control. Academic Press, New York, New York, USA.

McIntyre, B. D., C. S. Gold, I. N. Kashaija, H. Ssali, G. Night, and D. P. Bwamiki. 2001. Effects of legume intercrops on soil-borne pests, biomass, nutrients and soil water in banana. Biology and Fertility of Soils 34:342–348.

Muriel, S. B., and L. D. Vélez. 2004. Evaluando la diversidad de plantas en los agroecosistemas como estrategia para el control de plagas. Manejo Integrado de Plagas y Agroecología (Costa Rica) 71:13–20.

Ngeve, J. M. 2003. The cassava root mealybug (*Stictococcus vayssierei* Richard) (Homoptera: Stictococcidae): a threat to cassava production and utilization in Cameroon. International Journal of Pest Management 49:327–333.

Perfecto, I., and L. E. M. Vet. 2003. Effect of a nonhost plant on the location behavior of two parasitoids: the tritrophic system of *Cotesia* spp. (Hymenoptera: Braconidae), *Pieris rapae* (Lepidoptera: Pieridae), and *Brassica oleraceae*. Environmental Entomology 32:163–174.

Pickett, C. H., and R. L. Bugg, editors. 1998. Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, California, USA.

Pimentel, D. 1961. Species diversity and insect population outbreaks. Annals of the Entomological Society of America 54:76–86.

Potting, R. P. J., J. N. Perry, and W. Powell. 2005. Insect behavioural ecology and other factors affecting the control efficacy of agro-ecosystem diversification strategies. Ecological Modelling 182:199–216.

Poveda, K., M. I. Gomez, and E. Martinez. 2008. Diversification practices: their effect on pest regulation and production. Revista Colombiana de Entomologia 34:131–144.

Rey Benayas, J. M., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environmental Entomology 12:625–629.

Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710–713.

Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95–120.

Roschewitz, I., M. Hucker, T. Tscharntke, and C. Thies. 2005. The influence of landscape context and farming practices on parasitism of cereal aphids. Agriculture Ecosystems and Environment 108:218–227.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Rosenthal, R., R. L. Rosnow, and D. B. Rubin. 2000. Contrasts and effect sizes in behavioral research: a correlational approach. Cambridge University Press, New York, New York, USA.

Sanchez, P. A. 1981. Suelos del Trópico, Características y Manejo. Instituto Interamericano de Cooperación para la Agricultura (IICA), San José, Costa Rica.

Sastawa, B. M., M. Lawan, and Y. T. Maina. 2004. Management of insect pests of soybean: effects of sowing date and intercropping on damage and grain yield in the Nigerian Sudan savanna. Crop Protection 23:155–161.

Schmidt, F., I. Oh, and T. Hayes. 2009. Fixed- versus random-effects models in meta-analysis: model properties and an empirical comparison of differences in results. British Journal of Mathematical and Statistical Psychology 62:97–128.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environmental Entomology 15:456–461.

Sileshi, G., F. K. Akinnifesi, O. C. Ajayi, and F. Place. 2008. Meta-analysis of maize yield response to woody and herbaceous legumes in sub-Saharan Africa. Plant and Soil 307:1–19.

Southwood, T. R. E., and M. J. Way. 1970. Ecological background to pest management. Pages 6–29 *in* R. L. Rabb and F. E. Guthrie, editors. Concepts of pest management. North Carolina State University, Raleigh, North Carolina, USA.

Stram, D. O. 1996. Meta-analysis of published data using a linear mixed-effects model. Biometrics 52:536–544.

Tahvanainen, J., and R. B. Root. 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera, Chrysomelidae). Oecologia 10:321–346.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101:18–25.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. Ecology Letters 8:857–874.

Tscharntke, T., A. Kruess, B. A. Hawkins, and H. V. Cornell. 1999. Habitat fragmentation and biological control. Pages 190–205 *in* B. A. Hawkins and H. V. Cornell, editors. Theoretical approaches to biological control. Cambridge University Press, Cambridge, UK.

Uvah, I., and T. H. Coaker. 1984. Effect of mixed cropping on some insect pests of carrots and onions. Entomologia Experimentalis et Applicata 36:159–167.

Vandermeer, J. 1981. The interference production principle: an ecological theory for agriculture. BioScience 31:361–364.

Vandermeer, J. 1986. A computer-based technique for rapidly screening intercropping designs. Experimental Agriculture 22:215–232.

Vandermeer, J. H. 1989. The ecology of intercropping. Cambridge University Press, New York, New York, USA.

Vandermeer, J. 1998. Maximizing crop yield in alley crops. Agroforestry Systems 40:199–206.

van Emden, H. F., and G. F. Williams. 1974. Insect stability and diversity in agroecosystems. Annual Reviews of Entomology 19:455–475.

Waage, J. K. 1983. Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera, Ichneumonidae). Ecological Entomology 8: 447–453.

Wardle, D. A., and W. H. van der Putten. 2002. Biodiversity, ecosystem functioning and above-ground–below-ground linkages. Pages 155–168 *in* M. Loreau, S. Naeem, and P. Inchausti, editors. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK.

Wilby, A., and M. B. Thomas. 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. Ecological Letters 5:353–360.

Winkler, K., F. L. Wackers, L. V. Kaufman, V. Larraz, and J. C. van Lenteren. 2009. Nectar exploitation by herbivores and their parasitoids is a function of flower species and relative humidity. Biological Control 50:299–306.

Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biological Control 10:4–15.

Zak, D. R., W. E. Holmes, D. C. White, A. D. Peacock, and D. Tilman. 2003. Plant diversity, soil microbial communities, and ecosystem function: Are there any links? Ecology 84: 2042–2050.

APPENDIX A

Numbered list of 62 articles used in a previous review (Poveda et al. 2008), including 45 articles used in the present meta-analysis (*Ecological Archives* A021-001-A1).

APPENDIX B

Salquero-Rivera method for calculating a grand standard deviation for a series of measurements each of which has an associated standard error or standard deviation (*Ecological Archives* A021-001-A2).

APPENDIX C

Normal plot of Hedges' *d* values (*Ecological Archives* A021-001-A3).

APPENDIX D

An article-by-article comparison of individual outcome counts from statistical tests (Poveda et al. 2008) with mean or individual Hedges' *d* effect sizes calculated in the present study, using only the 45 articles reviewed in common (*Ecological Archives* A021-001-A4).