**Intercropping increases soil extracellular enzyme activity: A meta-analysis**

Andrew J. Curtright\*; Lisa K. Tiemann

Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing MI, United States

\* Corresponding author, curtrig1@msu.edu

**Abstract**

Intercropping has been shown to increase the productivity of agroecosystems, but the belowground mechanisms for this have not been well elucidated. The soil microbial community produces extracellular enzymes that are responsible for degrading plant residues and maintaining nutrient cycles in the soil. While the effects of plant diversity on enzyme activities have been studied, the results are often highly variable, both within and between studies. Therefore, to determine whether intercropping enhances nutrient cycling by increasing extracellular enzyme activity and to identify sources of variation in enzyme rates, we performed a meta-analysis drawing on 969 observations across 100 studies from around the world. We find that intercropping significantly increases enzyme activities by an average of 13% (P < 0.001) and that the intercropping effect varies by enzyme category, the type of plant used as the main crop or intercrop, and other experimental and environmental factors. Increased quantity and quality of plant residue inputs is a likely driver of the intercropping effect. The larger intercropping effect on increasing enzyme activity in nutrient-poor soils, together with differences between plant types, supports the view that soil nutrient status mediates patterns of microbial nutrient acquisition strategies. Future research should be aimed towards capturing regional variation within North American and Europe and towards identifying the specific drivers of the microbial response to increased plant diversity.

**Keywords**: Plant diversity, agriculture, belowground microbial community, nutrient cycling

**1. Introduction**

Intercropping is the practice of growing two or more crops at the same time in the same area and has been used around the world, typically in small-acreage systems, to increase yield and reduce inputs (Brooker et al., 2015). Intercropping draws on the biodiversity-ecosystem functioning (BEF) relationship, wherein increased biodiversity is correlated with greater plant primary productivity (Finney and Kaye, 2017; Smith et al., 2008; Tilman et al., 1996). While this relationship has been well-studied in natural ecosystems, only limited work has thus far been performed in agroecosystems. Available studies suggest that a BEF relationship does exist within agriculture, with increased spatial diversity (e.g. through mixed cropping or intercropping) being positively correlated with increased biomass production and yield. Studies have observed a wide range in yield increases, with one review finding a mean increase of 40% compared to monoculture (Brooker et al., 2015; Chen et al., 2018; Dai et al., 2013; Rao and Willey, 1980). The mechanisms underlying the BEF relationship in agriculture and how spatial diversity affects belowground microbial communities have not been investigated.

The BEF relationship in agriculture may be related to plant-diversity effects on the soil microbial community, which is responsible for a host of ecosystem services that support agriculture (Swinton et al., 2007). These range from direct effects, such as plant-growth promotion, pathogen suppression, and the formation of symbiotic relationships involving mycorrhizal fungi and rhizobial bacteria (Hayat et al., 2010; Van Der Heijden et al., 2008). Indirect benefits provided by the soil microbial community include the maintenance of soil fertility by increasing nutrient provisioning, aggregate stability, and soil carbon (C) formation (Balestrini et al., 2015; Fierer, 2017). When properly exploited, the soil microbial community can augment or replace synthetic pesticides and fertilizers. Indeed, legumes have been used in rotations for centuries to provide nitrogen (N) to crops by exploiting the microbial N-fixation reaction (Hayat et al., 2010). However, without proper management, the soil microbial community can also be a source of complementary ecosystem disservices, causing disease, contributing to the loss of soil organic matter, and producing greenhouse gas emissions (Robertson and Tiedje 1987; Zhang et al. 2007). For example, agriculture is responsible for 50% of global N2O emissions, which are primarily due to nitrifying and denitrifying soil microbes (IPCC, 2014). It is therefore essential to identify the effects that various management practices have on the soil microbial community and to determine how best to enhance the ecosystem services the microbial community provides while minimizing potential negative impacts.

Plant community diversity in both managed and unmanaged systems has an impact on belowground community composition and activity. One meta-analysis of rotational diversity effects showed significant, large increases in microbial biomass compared to monoculture (McDaniel et al., 2014b), while another found significant effects of temporal diversity (i.e. rotations) on the richness and diversity of the soil microbial community compared to continuous monocultures (Venter et al., 2016). While these meta-analyses and several other studies (e.g. King and Hofmockel 2017; Tiemann et al. 2015) have indicated that management practices that increase plant diversity tend to also impact soil microbial communities, the effect this has on agroecosystem functioning remains unclear.

Nutrient cycling is a particularly important ecosystem service performed by the soil microbial community (Bardgett and Van Der Putten, 2014; Toju et al., 2018). Soil microorganisms produce extracellular enzymes to decompose organic residues and litter inputs in order to obtain the materials required for energy production and growth (Dick, 1994; German et al., 2011; Sinsabaugh, 1994). These enzymes can become stabilized to soil particles and colloids, accruing over time (Burns, 1982). By releasing enzymes to the soil solution, microorganisms have the potential to either mineralize or immobilize essential nutrients and increase or decrease, respectively, their availability to crops. Plant diversity affects extracellular enzyme activity. For instance, enzyme activity associated with N- and phosphorous (P) acquisition was greater when cropping system diversity was increased through longer rotations compared to continuous monoculture (Tiemann et al., 2015). However, this study was focused on temporal diversity (i.e. crop rotation) rather than spatial diversity (i.e. intercropping). In studies where enzyme activities have been measured in monoculture compared to intercropping, results are highly variable, with the intercropping treatment showing greater (Kuang et al., 2010; Santos et al., 2018), similar (Wang et al., 2014), or reduced (Dai et al., 2013; Solanki et al., 2017) enzyme activity.

One of the principal difficulties associated with comparing enzyme data is the variety of methods used to assess enzyme activity. In addition, studies often range across a variety of cropping systems and a spectrum of climates and soil types, adding further to the heterogeneity between studies. A meta-analytical approach can therefore help to synthesize such wide-ranging data on enzyme activity. Meta-analysis provides a systematic and statistically rigorous way of integrating data and comparing studies, even in the face of methodological and experimental differences (Hedges and Olkin, 1985; Rosenberg et al., 2013). Meta-analysis has been widely used to synthesize soil enzyme data and assess the effects of various management practices, including fertilization, organic amendments, and tillage (Geisseler and Scow, 2014; Kallenbach and Grandy, 2011; Luo et al., 2018; Zhou and Staver, 2019; Zuber and Villamil, 2016).

In our study, to determine the global effect of increasing spatial diversity on the functional potential of microbial communities in agroecosystems and to help us understand why results between studies are so variable we used a meta-analytical approach to combine and evaluate enzyme data. We hypothesized that (i) by increasing the plant diversity in an agriculture system, microbially-mediated nutrient cycling in the soil will be increased as indicated by elevated rates of extracellular enzyme activities, and that (ii) the effect of intercropping on enzyme activities will be affected by crop productivity, cropping system diversity, and the plant functional group of either the main crop or intercrop. We also examined other potentially moderating variables, such as climate factors, soil texture, pH and fertilizer application rates that may help account for the variation in the intercropping effect on enzyme activities.

2. Methods

2.1 Construction of database

In total, our data set is comprised of 969 observations across 100 studies. Most studies were conducted in China and Asia, with a few studies located in South America and Africa. Only three field studies were identified from North America or Europe.

Studies were located using ISI Web of Knowledge using the following search terms: (intercrop\* OR interseed\*) AND (enzyme OR urease OR \*sidase OR protease OR \*terase OR \*genase OR sucrase OR \*olase OR \*ulase OR \*idase OR \*terase). Abstracts were screened to find papers that met the following criteria: 1) had an intercropping treatment with a paired monoculture control, 2) was an agricultural system, which included agroforestry, and 3) measured the activity of at least one soil extracellular enzyme.

Enzyme activities as well as associated metadata were extracted from the studies. If data were only reported on graphs, the values were extracted using WebPlotDigitizer (Rohatgi, 2019). Within studies, independent observations were considered as unique combinations of an enzyme rate and an intercropping pair. If enzyme activity for the same intercropping pair was reported multiple times within a study (i.e. multiple times across the growing season), an averaged value was used as a single observation.

Metadata associated with each study were also extracted and these included: latitude and longitude, type of experiment (greenhouse or field), mean annual precipitation (precip.), mean annual temperature (MAT), soil type, soil texture (% clay, % silt, % sand), pH, soil organic matter (SOM), soil organic carbon (SOC), total N and P, available N and P (i.e. extractable inorganic N or P), N fertilizer amount, N fertilizer type, P fertilizer amount, plant biomass or yield, length of study, sample type (rhizosphere or bulk soil), sampling depth, main crop, intercrop, and microbial biomass. Methodological information was also extracted, including general information on the assay protocol and whether fresh or air-dried soil was used.

If only mean separations were reported, standard deviations were back calculated from the smallest significant difference, using the indicated mean group size, significance level, and multiple-comparisons correction method. If no multiple-comparisons correction was specified, means were assumed to have been separated by Fisher’s LSD (which would result in the most conservative back-calculated estimate of the standard deviation). If studies were missing key information, authors were contacted. If authors did not respond, soil textural data was imputed from other studies reported from the same field site or from the Harmonized World Soil Database v1.2 (Fischer et al., 2008). If authors did not provide standard errors or standard deviations, either in the paper or upon contact, standard deviations were imputed based on the average CV for the provided values (Zuber and Villamil, 2016).

2.2 Meta-analysis

Statistical analyses were performed using OpenMEE (Wallace et al., 2017). Response ratios were calculated for each observation by taking the natural log of the average extracellular enzyme activity ( of the monocrop (control) and intercrop treatments, as described in Formula 1. The variance for the response ratio was calculated according to Formula 2. Formula 1 was also used to calculate an unweighted response ratio for plant biomass yield and microbial biomass C.

(1)

(2)

To calculate the intercropping effect overall and by sub-group, a random effects model was used, which accounts for both within- and between-study variability, using τ2 estimated via the DerSimonian-Laird method. Accordingly, the response ratio was weighted using a variance term that accounted for between-study heterogeneity.

Analyses of various moderators were performed to identify drivers for the intercropping effect. The moderators examined included enzyme type, main crop (monocrop) type, intercrop type, sampling type (rhizosphere or bulk soil), experiment type (greenhouse or field), latitudinal zone (temperate or tropical), and fertilizer amount. We categorized enzymes based on the type of substrate they react with or the nutrient that is released with activity. Hydrolytic C enzymes are those that target relatively easy to access forms of C with a regularly repeating polymeric structure (invertase, cellulase, cellobiohydrolase, β-glucosidase, and β-xylosidase); oxidative C enzymes included peroxidase, phenoloxidase, and polyphenoloxidase; N enzymes included N-acetyl-glucosaminidase, proteases, peptidases, and urease; P enzymes included both alkaline and acid phosphatases as well as phytase (Table S1). A “general” category of enzymes was also included for enzymes routinely used as indicators of overall microbial activity but not associated with the acquisition of particular nutrients (Alef, 1995; Prosser et al., 2015; Tabatabai, 1994). This category included dehydrogenase and catalase as well as fluorescein diacetate (FDA) degradation activities.

To determine the role of plant type on the intercropping effect, we grouped observations according to the type of plant used as the main crop and the intercrop. In our analysis, each observation consisted of a treatment (i.e. a main crop grown with an intercrop) compared to a control (i.e. the main crop grown in monoculture). Accordingly, the main crop was defined as the crop that was grown in monoculture in the control group. Any particular species of plant could therefore be considered as the main crop or intercrop depending on how it was used in the study. For example, if the intercrop treatment included maize grown with soybean and the control group was only maize, then maize would be considered the main crop and soybean the intercrop. On the other hand, if the intercropped treatment was compared to a control group consisting of soybean by itself, then maize would be considered the intercrop and soybean the monocrop. These treatment designations were defined according to the crops grown during the growing season(s) reported by the study. Additional elements of diversity, such as the use of rotations, were not specifically included in our analysis.

Plants were grouped according to the following categories: the grasses category included grains as well as forage grasses; legumes included pulses, oilseeds, and forages; woody species included shrubs and trees; the forbs category included non-woody plants that did not fall into the grasses or legumes categories. The same categories were used to group main crops and intercrops.

Sub-group means were determined within the categories of enzyme type, intercrop type, main crop type, sampling type, experiment type, latitudinal zone, and fertilizer amount. Differences within categories (between sub-groups) were considered to be significant if the two groups’ 95% confidence intervals were non-overlapping.

We used the meta-regression tool in OpenMEE to assess relationships between the intercropping effect and the continuous experimental, edaphic, and environmental factors. For meta-regressions, τ2 was estimated via maximum likelihood.

3. Results

We found that, overall, intercropping increases enzyme activity by an average of 13%, a significant increase with a P-value less than 0.001 (Fig. 1). This effect was significant for all enzyme classes except oxidative enzymes (Fig. 1). The magnitude of the intercropping effect differs slightly between enzyme classes: the effect was significantly greater for N, P, and S enzymes than oxidative enzymes. S-acquisition enzymes were also significantly higher than N- and P-acquisition enzymes as well as general enzymes.

Differences between plant types were pronounced with significant differences between the categories of plants used as intercrops and main crops (Fig. 1). The intercropping effect is apparent across all main crop types and all intercropping types, and these differences vary between enzyme types (Fig. 2). At an overall level, there is no significant difference between bulk soils and rhizosphere samples (Fig. 1). Likewise, there is no significant difference between greenhouse and field studies, or between studies in temperate or tropical environments.

Overall, the intercropping effect on microbial biomass C (MBC) explained a significant amount of variation in the intercropping effect on enzyme activity (Fig. 3). The intercropping effect on yield explained relatively less, but a still significant amount of variation in the intercropping effect on enzyme activity (Fig. 4). In addition, total N, total P, annual precipitation, sampling depth, and length of study are also suggested to be significant drivers of the overall intercropping effect (Table 1). Other environmental and experimental factors—such as, soil texture, pH, soil C, fertilization, and available nutrients—do not explain a significant amount of variation. However, some of these drivers are significant regressors when examined within different enzyme types. Interestingly, there is no clear linear relationship between amount of N fertilizer and the size of the intercropping effect but there are significant differences when fertilizer amount is combined into groups (Fig. 1). Moderate N-fertilizer applications have a significantly higher intercropping effect than low N-fertilizer applications, suggesting a possible unimodal response.

3.1 Carbon enzymes

To determine how intercropping affected the nutrient cycling of specific elements, we analyzed the response ratio separately by enzyme class. Intercropping has a positive effect on the activity of C enzymes, increasing their rate of activity by an average of 14% (Fig. 1). While similar to the overall rate of increase, the increase in activity of C enzymes is subject to greater variability.

There is some variation in effect between plant types. The intercropping effect is significantly positive when grasses and woody plants are introduced as intercrops (Fig. 2A). The effect with grasses here is significantly higher than the effect with forbs.

Between main crop types, the effect on C enzymes is only significantly positive with legumes (Fig. 2B). That is, introducing an intercrop to a legume main crop significantly increases C-enzyme activities compared to when the legume is grown in monoculture. This effect with legume main crops is significantly higher than the effect with grasses or forbs.

Neither MBC nor yield were significantly related to the intercropping effect on hydrolytic C enzymes (Figs. 3 & 4). Of the other examined covariates, total N and length of study explained a significant amount of variation (Table 1).

3.2 Nitrogen enzymes

The activity of N enzymes increases by 16% due to intercropping (Fig. 1). Across studies, there is relatively less variation than in C enzymes. However, there is some variation in this effect between plant types (Fig. 2). All plant types used as intercrop significantly increase enzyme activities (Fig. 2A). However, this effect does not differ significantly between intercropping plant types.

Between main crops, all plant types demonstrate a significant increase in N-acquisition enzyme activity when receiving an intercrop (Fig. 2B). This effect is significantly higher for woody plants as main crops than it is for legumes or grasses.

A large portion of the variation in the intercropping effect is accounted for by the response of MBC and yield to intercropping (Figs. 3 & 4). Total N and P account for a significant amount of the variation between studies, while length of study and sampling depth are also significant sources of variation (Table 1). Further, there is a significant inverse relationship between amount of N fertilizer and the intercropping effect within N enzymes (slope values not presented).

3.3 Phosphorous enzymes

Intercropping increases P-enzyme activities by an average of 12% (Fig. 1). When added to a system as intercrops, all plant types except forbs result in a significant intercropping effect on P-enzyme activity (Fig. 2A). The effect with woody plants and legume intercrops is significantly higher than the effect with forbs. Moreover, the effect with woody plants is also significantly greater than with grasses.

Compared to growing as monoculture, intercropping into woody plants and grasses, but not into legumes or forbs, results in a significant increase in P-enzyme activity (Fig. 2B). The effect is greatest with woody plants, but is also significantly higher with grasses than with forbs or legumes.

Soil available N, annual precipitation, and study length were significantly related with the intercropping effect on P enzymes (Table 1). MBC explained the most variation within P enzymes (Fig. 3). Yield was not a significant covariate (Fig. 4).

3.4 Oxidative enzymes

Intercropping elicits an overall 3% decrease in oxidative enzyme activity across all studies (Fig. 1), but low sample size makes it difficult to examine the sources of variation. There are no significant differences between intercrop or main crop plant types (Fig. 2). Intercropping with legumes and forbs shows a non-significant decrease in oxidative enzyme activity (Fig. 2A), while legume and grass main crops tends to have lower oxidative enzyme activities after intercropping (Fig. 2B).

Soil sand % and total P are significantly related with the intercropping effect on oxidative enzymes (Table 1).

3.5 General enzymes

Similar to hydrolytic C-, N-, and P-acquisition enzymes, there is a significant 12% increase in general enzyme activity associated with intercropping (Fig. 1). The use of legumes and woody plants as intercrops results in a significantly positive intercropping effect, which is higher than that associated with intercropping grasses (Fig. 2A). Between main crops, all crop types except legumes demonstrate a significantly positive intercropping effect (Fig. 2B). Interestingly, intercropping into legumes is associated with a significant reduction in general microbial enzyme activity.

Significant sources of variation in the intercropping effect on general enzymes include pH, soil C, total N and P, annual precipitation, sampling depth, and length of study (Table 1). In addition, MBC and yield possessed significant positive relationships with the intercropping effect on general enzyme activity (Figs. 3 & 4).

3.6 Enzyme assay protocol

To ensure that differences in assay methodology or protocol did not introduce any systematic bias in the intercropping effect, in an early phase of database construction we compared effect sizes between different types of protocols. Almost every study used a bench-scale method to assess enzyme activities, with only two studies reporting the use of a microplate-scale assay. Urease and phosphatase were the only enzymes that were assayed using more than one type of method with at least ten observations, and methodology had no impact on the intercropping effect in either of these cases (Table S2). Moreover, within each enzyme type, there were no differences in effect size between procedures using fresh or air-dried soil (Table S3). Of course, studies varied further in terms of their exact assay procedures, but such variation is accounted for in our meta-analysis through the use of a random-effects model (Hedges and Olkin, 1985).

4. Discussion

The studies in our analysis tend to represent the areas where intercropping is most commonly utilized (Brooker et al., 2015). The majority of these studies are in China, with many in Latin America and Africa. We found only a handful of reports on intercropping in North America and Europe, and only three of these included data on enzyme activity that met our criteria for inclusion in this analysis. This likely reflects the rarity of intercropping in North America and Europe; a USDA report found that as of 2012, just 2% of crop land in the United States utilized a “double cropping” system—which mostly refers to single-year rotations rather than intercropping—and only 1–2% of crop land utilized cover crops (Borchers et al., 2014). By contrast, intercropping in China occurs on about one-quarter of arable land (Knörzer et al., 2009), and it is likewise common in Latin America and Africa (Brooker et al., 2015; Knörzer et al., 2009; Vandermeer, 1992).

Overall, we find that intercropping increases enzyme activities by an average of 13%, providing support for our hypothesis that increasing plant diversity through intercropping increases the functional potential of the belowground microbial community. This is consistent with others’ findings that enzyme activities are impacted by plant species (Kourtev et al., 2002), management practice (Bandick and Dick, 1999; Tiemann et al., 2015), and land use (Waldrop et al., 2000).

4.1 Crop productivity and residue quality

We hypothesized that the magnitude of the intercropping effect on enzyme activities would be determined by the productivity, diversity, and plant functional groups in the intercropping system. Intercropping increases C inputs through greater plant density when the space between rows of the main crop is utilized for the intercrop. Indeed, greater residue input is reported with intercropping in many of the studies included here (e.g. Chander et al., 1998; Santos et al., 2018; Zhou et al., 2011). In our analysis, of the studies that included yield or biomass data, we find a highly significant relationship between the intercropping-induced increase in plant biomass and the corresponding increase in enzyme activity; however, this relationship appears to be driven primarily by N- and general enzymes (Fig. 4). Increased plant productivity leads to increased C inputs to soils, which in turn stimulates the soil microbial community and promotes greater microbial biomass (Kallenbach and Grandy, 2011) and higher activity levels (Mancinelli et al., 2013; Nyberg et al., 2000; Yang and Wu, 2011). This combination of increased inputs and increased enzyme activities results in a more active nutrient cycle that often leads to greater N and P availability for plants and a positive feedback to productivity (Piotrowska and Wilczewski, 2012; Randhawa et al., 2005).

Overall, enzyme activities in both bulk soil samples and the rhizosphere were significantly increased by intercropping with no difference in intercropping effect between the two sample types (Fig. 1). Bulk soil is relatively nutrient poor, and additional residue inputs are more likely to reach the bulk soil than the rhizosphere. The large intercropping effect in the bulk soil demonstrates the potential for microbes to synthesize and release hydrolytic enzymes in response to increased C and nutrient inputs from intercropping. Although average microbial activity is lower in the bulk soil, the volume of bulk soil far outweighs the volume of rhizosphere in most soils (Kuzyakov and Blagodatskaya, 2015; Young et al., 2008). Therefore, a similar increase in bulk soil enzyme activities will go a long way towards increasing overall nutrient cycling in the field. This points to intercropping as a potential avenue for improving the nutrient cycling of many annual systems, where most of the soil over a significant portion of the year is not in contact with plant roots.

The significant intercropping effect on enzyme activity in the rhizosphere suggests that intercropping elicits a systemic response that extends to the roots of individual plants. Many of the studies in this analysis focus on the rhizosphere, which is a microbial hotspot where the number of active microbes can be as much as twenty times greater than the bulk soil due to an increase in plant-derived C around the roots (Kuzyakov and Blagodatskaya, 2015; Ma et al., 2018). Belowground C inputs, such as root exudation and deposition, can increase with intercropping for the same reasons as identified for aboveground residues, but these inputs may have a larger impact because they are already in close association with microbes and their enzymes.

Root exudates appear to play a large role in the intercropping effect. We noticed that the amount and composition of root exudates were reported to be affected by intercropping: in a field study Dai et al., (2013) described how different phenolic compounds were excreted by the same plants depending on whether they were in a monoculture or intercropping system, and B. Li et al., (2016) found that intercropping of maize and faba bean influenced the root exudation profile of maize as well as the N fixation activity of faba-bean-associated rhizobia. Further, in many of the greenhouse studies we identified, a complete or partial root-separation design was used; in both designs roots were prevented from direct physical contact but exudates could mix in the partial-separation treatments. The majority of these rhizosphere experiments report significantly less enzyme activity with complete barriers between intercrop roots, but no difference between partial- and non-separated treatments, suggesting that exudates rather than the roots themselves promoted enzyme activities (Hu et al., 2013; Khan et al., 2014; Q. Li et al., 2016; Li et al., 2018; Xu et al., 2007). Similar to how increases in the amount and diversity of aboveground C could accelerate nutrient cycling, differences in the quantity and composition of belowground root exudates could also stimulate the production of soil enzymes.

4.2 Plant species and type

In addition to increasing total C inputs, intercropping increases the diversity of C inputs to the soil, which has the potential to support greater biodiversity in soil communities (Eisenhauer, 2016; Tiemann et al., 2015; Venter et al., 2016) and increase microbial biomass and soil C (McDaniel et al., 2014b). We were unable to test the response of enzyme activities to intercropping-system diversity *per se* due to a lack of studies at higher levels of diversity (i.e. > 2 species). However, we know that another important impact of increasing diversity via intercropping on microbial activity is the potential for increasing overall crop residue quality, especially when transitioning from systems like monoculture maize or other crops with low-quality litters.

Residue quality, which can be roughly defined as the ease with which a residue can be decomposed, has been shown to have a strong effect on enzyme activities (Tiemann et al., 2011; McDaniel et al. 2014). Quality can be considered in terms of C:N ratio as well as the chemical composition of the residues. Residue N content has been suggested to be a stronger driver of microbial activity than soil nutrient status (Bini et al., 2013; Chander et al., 1998), and lignin content has been shown to be inversely related to mineralization rates and can be a better indicator of potential mineralization rates than N content alone (Fanin and Bertrand, 2016; Kumar and Goh, 2003). The exact C:N content of residues was rarely reported in the studies included in our meta-analysis; therefore, we used plant type as a broad-scale indicator of residue quality. Quality effects are suggested by the significant difference between systems that introduce a legume as an intercrop, which has narrow C:N residues, versus those that introduce a grass or forb that tend to have wider C:N residues (Fig. 1). Beyond N effects, overall nutrient balance and P content also appear to influence the degradation of crop residues. In one study included here, it was thought that greater microbial demand for P than N caused high-N litters to be decomposed more slowly than residues with a wider C:N ratio but higher P content (Santos et al., 2018).

We see further support for residue quality effects in the difference in the response of hydrolytic and oxidative C enzymes. Enzymes in these categories work on C from different types of plant tissues that differ in bioaccessibility. Oxidative enzyme activities generally increase only when systems are C limited, have high amounts of poor quality (wide C:N) residue inputs, or are experiencing high levels of stress or disturbance (Sinsabaugh, 2010; Xiao et al., 2018). On the other hand, hydrolytic C enzymes appear to be driven by different factors, and it is suggested that the ratio of hydrolytic-to-oxidative enzyme activities is positively related to C quality (Sinsabaugh and Shah, 2011). In our analysis, hydrolytic C enzyme activity significantly increases by 14%, while oxidative enzymes are not significantly different from zero and even display a trend towards decreasing activity with intercropping (Fig. 1). This suggests that across a variety of systems, intercropping increases the availability of higher quality litter to microbial communities and decreases nutrient stress in the soil environment.

Given the importance of residue type and quality as discussed above, it is not surprising that we also find that the magnitude of the microbial response to intercropping is sensitive to the plant type of both the intercrop and the main crop. Intercropping systems that introduce woody crops and legumes tend to elicit stronger effects on enzyme activities than other crop types (Fig. 1). It should be noted that some of the tree species used in the agroforestry systems examined here are leguminous and as such could provide a net input of N through fixation and the subsequent production of high-quality, narrow-C:N litter.

Insight toward the contributions of each plant species can be obtained by comparing plant-type differences within each enzyme class (Fig.2). Intercropping with grasses had the most significant increase in C enzyme activities, while the effect of using a legume intercrop on C enzyme activities was highly variable, which may be due to differences in overall residue quality with different main crop types. Unfortunately, there were not enough data points to test for differences between each main crop type paired with a legume intercrop. The molecular composition of legume and grass residues differs markedly. Grass residues have a higher composition of cellulose and structural components compared to legume residues and would require a greater investment in hydrolytic C degradation enzymes to decompose. On the other hand, legumes generally have greater protein (N) and P content, thus an increase in N- and P-mineralization activity would be expected, as increased availability of nutrient-containing substrate can stimulate production of extracellular enzymes (Allison and Vitousek, 2005; Kumar and Goh, 2003; Sinsabaugh et al., 2008). Legumes can also increase inorganic-P mobility (Li et al., 2007), causing P from inorganic pools to be transferred into plant biomass, which can then be mineralized by microbial phosphatases. In addition, alleviation of N limitation through the introduction of an intercropped legume could stimulate the production of phosphatases in systems that are co-limited by N and P. The introduction of N would supply the nutrients required for production of phosphatases.

We also considered how the effect of intercropping varies between the plant types used as the main crop. Overall, between main crop types, woody crops had the largest overall intercropping effect and legumes the smallest, albeit still significantly positive, and forbs and grasses were in between (Fig. 1). We find additional significant differences between the main crop types within enzyme categories (Fig. 2B). For hydrolytic C enzymes, we see a significant increase after intercrops are introduced to a legume monocrop system, while no other main crop type had a significant response in C-enzyme activities. In systems with a legume, or those with narrow-C:N residue inputs, N is assumed to be relatively more available while overall C inputs may be a more limiting factor for enzyme production and microbial activity (McDaniel et al., 2014a; Tiemann and Billings, 2011). Therefore, C- or energy-limited microbes in legume systems that receive an intercrop would respond positively to additional biomass inputs, producing more enzymes that target C substrates.

We also report that N- and P enzymes have a significantly greater response when woody monocrops receive an intercrop relative to when legume or grass monocrops receive an intercrop (Fig. 2B). Tree litter is typically of poor quality, and trees often translocate N and P from leaves before senescence and litterfall (Zechmeister-Boltenstern et al., 2015). This results in a C-rich but nutrient-poor residue input. Intercropping into woody species such as trees would therefore have a greater impact on the average quality of residue inputs to the soil and lead to larger increases in enzyme activities, as discussed above.

4.3 Effects on the microbial community

By far, changes in microbial biomass explained the greatest amount of variation in the overall intercropping effect (Fig. 3; Table 1). While the degradation of plant and animal tissues can release enzymes to the environment, the soil microbial community is the primary producer of the enzymes responsible for nutrient cycling in the soil (Skujiņš and Burns, 1976). The strong and significant relationship between the response ratios of MBC and enzyme activity after intercropping provides compelling evidence that the increase in enzyme rates we observe after intercropping is mainly due to microbial activity. Further, the category of enzymes that indicate general microbial activity consists of enzymes thought to be mostly intracellular. The increase in this general category therefore indicates an increase in microbial activity on a similar magnitude to the increase in most other nutrient-cycling extracellular enzymes (Fig. 1).

Given the role of the microbial community in the production of nutrient-cycling enzymes, it is interesting to consider how changes to the microbial community in terms of abundance and composition can affect enzyme production and nutrient cycling (Waldrop et al., 2000). For instance, saprotrophic fungi are relatively more prolific producers of cellulases than mycorrhizal fungi or bacteria (Taylor and Sinsabaugh, 2015; Wallenstein and Burns, 2015), while protease production is more widely distributed amongst members of the microbial community (Bardgett et al., 2006; Geisseler et al., 2010; Geisseler and Horwath, 2008). Therefore, intercropping effects on enzyme activities could be mediated by changes to the soil microbial community, especially over the long term.

Intercropping has been demonstrated to alter the composition of the soil microbial community (Dai et al., 2013; Hernandez et al., 2015; Khan et al., 2014; Zheng et al., 2018; Zhou et al., 2011). For example, within our analysis, microbial communities from the rhizospheres of some intercropped plants are more closely related to each other than to their monocultured counterparts (Bini et al., 2018; Q. Li et al., 2016). In some of these studies, the effect of intercropping is stronger than that of N fertilization (Chen et al., 2018; Dai et al., 2013). One study lasting multiple growing seasons shows this effect to persist over three years (Zhou et al., 2011). Bacteria tend to respond faster to intercropping treatments than fungi in some studies (Khan et al., 2014; Zhou et al., 2011); in others, intercropping increases total AMF colonization (Bini et al., 2018; Hernandez et al., 2015).

Plant-mediated effects on community composition can range from being general to specific. For example, some plants exert directional control over their associated microbial communities (Hartmann et al., 2009), while at the same time microbial communities associated with one plant are able to inoculate the other plant in an intercropping system (Bini et al., 2018; Hernandez et al., 2015; Sun et al., 2009). However, such effects may depend on both the host plant and the presence or abundance of particular members of the microbial community. Sun et al. (2009) describe that intercropped alfalfa affected rye-associated microbial communities only when the alfalfa is first treated with a rhizobial inoculant. Other outcomes include a mixing of microbial communities, with both initial communities being represented about equally (Q. Li et al., 2016; Rachid et al., 2015), and synergistic increases during intercropping in the abundance of certain taxa that are less abundant when either crop is in monoculture (Rachid et al., 2015; Sun et al., 2009).

Functional differences may reflect changes in the composition of the microbial community in addition to, or instead of, changes to the functionality of the existing microbial community. From an observational perspective, ideally, functional shifts would occur alongside changes in the abundance of key genes involved in nutrient cycling, allowing for changes in functional potential to be detected through quantitative gene sequencing. For example, differences in N-cycling processes following intercropping with legumes have been accounted for by increases in the abundance of N-fixing microbes and ammonia-oxidizing bacteria (Sun et al., 2009; Wang et al., 2015). However, such links between function rates and the abundance of functional genes or key taxa are, more often than not, quite difficult to establish. With regard to extracellular enzyme production in particular, the relative abundance of enzyme-coding genes does not tend to have a consistent relationship to enzyme activity (Burns et al., 2013). One study included in our analysis was able to correlate cellobiohydrolase activity with greater expression of the cellobiohydrolase gene, but within the same study the researchers did not find similar correlations between gene abundance and activity of β-glucosidase or β-xylosidase (Zheng et al., 2018). Nevertheless, since extracellular enzymes are the products of soil microbes, the membership of the microbial community and its genetic potential must exert a certain degree of control over the intercropping effect. Future work should utilize genomic tools in concert with manipulative experiments, as well as observational studies, to elucidate how environmental factors together with the abundance and expression of enzyme-coding genes interact to determine the functional potential of the soil microbial community.

4.4 Edaphic, environmental, and experimental factors

4.4.1 Environmental and edaphic properties

Soil nutrient concentrations explained significant amounts of variation within the intercropping effect within various enzyme classes (Table 1). These relationships were particularly consistent within general enzymes, with significant inverse relationships with soil C, total N, and total P. Total N was also inversely related to the overall intercropping effect as well as that within C- and N-acquisition enzymes. That the intercropping effect is greater when there are fewer available nutrients suggests that intercropping tends to have the largest stimulatory effects on microbial activity in relatively more depleted soils. Such a relationship is predicted for the productivity of intercropped plants themselves by the stress gradient hypothesis, which posits that facilitative interactions between differing species become more likely as ecological conditions become more stressful (e.g. nutrient or water limitation), resulting in greater primary productivity or nutrient complementarity (Brooker et al., 2015). The additional plant residues from intercropping would have a relatively greater effect in resource poor soil, alleviating substrate limitation that may have been preventing enzyme synthesis. These results could indicate that the greater effects of intercropping in stressful environments extend beyond plant productivity itself and go on to increase nutrient cycling activity in the soil and stimulate the microbial community.

Only within general enzymes was the relationship between pH and the intercropping effect statistically significant (Table 1). The intercropping effect was greater for general enzymes at lower pH. Differences in pH can affect cation exchange with clays, impacting the availability of enzyme substrates as well as important enzyme co-factors, such as Fe, Mg, and Mn ions, which tend to be depleted in many acidic soils. Therefore, intercropping could have a greater effect in mobilizing and distributing nutrients in lower pH soils. Enzyme activity is also directly affected by pH, with most soil enzymes exhibiting maximum activity at slightly acidic pH, although this varies by enzyme and between soils (German et al., 2011; Turner, 2010). At a lower pH, activity of enzymes with more acidic optima could therefore be more responsive to increases in substrate and nutrient availability.

Water availability, retention and distribution can also impact the intercropping effect (Brooker et al., 2015; Hernandez et al., 2015; Morris and Garrity, 1993). Here we found that overall, mean annual precipitation was positively related to the intercropping effect, with the amount of variation explained by precipitation in the intercropping effect of P-acquisition and general enzymes being particularly high (Table 1). C- and nutrient mineralization are consistently linked to soil moisture (Crowther et al., 2019). Increasing plant density and diversity through intercropping can improve water infiltration by creating a more widely distributed network of soil pores formed by roots. By limiting the exposure of bare soil to the physical impact of precipitation, greater plant densities can also reduce soil crusting and surface run-off, providing a more favorable environment for microbial activity. On the other hand, there is also the potential for intercropping to improve microbial activity in drier systems as well. Differential rooting zones between intercropped plants (especially if one is a tree or shrub) can exploit water resources from different parts of the soil profile and redistribute moisture to drier areas, stimulating microbial activity (Brooker et al., 2015; Hernandez et al., 2015). In this connection, one study demonstrates how intercropping with indigenous shrubs increases water retention during times of water stress in an arid environment; it is suggested that this promotes microbial activity (Hernandez et al. 2015; Bogie et al. 2018).

Other environmental factors not quantified here may also play a role in increasing or decreasing enzyme activity. Variables such as weather and season can be difficult to control, casting uncertainty on perceived trends within a single study. For example, studies that took multiple time points throughout the season often found widely varying data (for the purpose of our analyses, we averaged measurements taken multiple times over a season; e.g. Bini et al., 2013; Liu et al., 2014; Ma et al., 2017; Wang et al., 2014; Xiao et al., 2012). Much of this variation comes from the timing of plant development and associated differences in plant nutrient uptake, root exudation, and litter inputs (Bini et al., 2013; Zhou et al., 2011). Regardless, while the wide variation throughout the growing season makes it difficult to draw conclusions from the data presented by one study, in our meta-analysis a decided trend has emerged—across a number of sites and experimental conditions—that intercropping increases enzyme activities.

In addition, we found there were no significant differences in the intercropping effect between greenhouse and field studies, suggesting that while environmental factors could contribute to the variation in the intercropping effect, it may not negate it. It is also worth noting in this connection that the greenhouse studies included in our analysis were, for the most part, pot experiments and were not meant to model or evaluate commercial greenhouse systems.

Interestingly, we found no significant differences in the intercropping effect between latitudinal zones (Fig. 1, Fig. S1), even though differences may be expected given that the edaphic properties and environmental conditions between temperate and tropical soils differ widely. Tropical soils are highly weathered and are typically poor in nutrients, particularly P. That the effect of intercropping is no different between tropical and temperate environments suggests that, from a microbial perspective, the effects of increased plant diversity and nutrient inputs are similar across a wide range of locations where row-crop agriculture is practiced. Together with other studies that have found consistent microbial responses to environmental drivers at global scales (Fierer et al., 2009; Leff et al., 2015), our results support the generalizability of environmental controls on microbial function across a broad spectrum of geographic locations.

4.4.2 Fertilizer application rate

We examined the effect of N fertilizer by regressing enzyme activity response ratio with fertilization rate and by binning studies into N-application categories. There is no significant linear relationship between the overall intercropping effect and application rate (Table 1), but studies that that applied a moderate amount (between 100-250 kg N ha-1) have a significantly larger intercropping effect than those with low rates of fertilizer application (less than 100 kg N ha-1; Fig. 1). The opposing influences of residue quantity and nutrient availability could account for this unimodal pattern. Compared to no fertilization, low to moderate rates of application stimulate plant growth without exceeding plant demand. As a result, excess fertilizer nutrients are not available to the microbial community but increased residue inputs stimulate enzyme activity. On the other hand, applying fertilizer at higher rates, in excess of plant demand, could increase nutrient concentrations for the microbial community and reduce the need for microorganisms to invest in nutrient-acquisition enzymes.

While there is no relationship between fertilization and overall enzyme activity, there is a significant inverse relationship between fertilization and N-enzyme activities, as may be expected. Intercropping produces a smaller effect on stimulating N enzymes with greater fertilization (Table 1). In addition, total soil N also possesses a negative relationship with the intercropping effect on N-mineralization enzymes. This suggests that greater N availability moderates intercropping-induced increases in N-mineralization activity. Extracellular enzymes are expressed in response to a combination of microbial demand and substrate availability (Allison and Vitousek, 2005; Sinsabaugh et al., 2008). Economic theories of microbial metabolism suggest that certain induced enzymes, particularly those for N mineralization, are expressed only when labile sources of the target nutrient are limiting and there is a potential supply of the nutrient in complex forms (Allison and Vitousek, 2005; Chen et al., 2014). The presence of labile N provided as fertilizer could alleviate N demand and prevent the induction of enzymes for the acquisition of this already available nutrient. Nevertheless, another meta-analysis that investigated the long-term effects of fertilizers on enzyme activities found that fertilization had no effect on N-mineralization activity and significantly increased C-cycling enzymes and acid phosphatase (Geisseler and Scow, 2014). The lack of a consistent relationship of N-fertilization on enzyme activities could be due to the manifold effects that fertilization has on the cropping system, including increases in primary production, soil pH, and overall nutrient balance.

4.4.3 Length of study

One of the strongest covariates with the overall intercropping effect is length of study, with the longest studies having the largest effects (Table 1). Temporal dynamics of increased plant diversity have been well-studied in natural ecosystems, where the benefits of diversity—including improved biomass production and soil nutrient status—accrue over time (Cardinale et al., 2007; Reich et al., 2012). The significant length-of-study effect here demonstrates that it may also take time in agricultural systems for the effects of plant diversity to be reflected in the functioning of soil microbial communities.

In addition, previous work in agroecosystems has shown that microbial communities from more diverse rotational histories process organic residues faster than monocultured counterparts independent of plant diversity at the time of soil collection, suggesting that long-term diversity can produce persistent legacy effects in the activity of the soil microbial community (Crème et al., 2018; McDaniel et al., 2014a; Schipanski et al., 2014). This could be due in part to the fact that soil enzymes can become stabilized in the soil long after release from the cell where they were originally synthesized (Burns, 1982). Certain management practices can stimulate the production of nutrient cycling enzymes, and as extracellular enzymes become stabilized, such increases can accumulate over the course of the practice, with potential nutrient cycling activity increasing year-to-year.

5. Conclusion

Sustainable intensification of agricultural production will require relying more on ecosystem services and less on synthetic chemical inputs. As described by the BEF hypothesis, the provisioning of ecosystem services is enhanced through greater plant diversity. Therefore, intercropping can support agricultural production by increasing plant diversity and ecosystem functioning. Here, we argue for nutrient cycling as a possible mechanism by which intercropping improves crop productivity by increasing enzyme activity in the soil.

Extracellular enzymes play a key role in nutrient cycling, and we find that intercropping significantly increases enzyme activity across most enzyme classes and plant types. We suggest that this intercropping effect is mediated by responses of the soil microbial community to increases in the quantity and quality of residue inputs. We see support for this in the specific effects that intercropping has on the activity of different classes of enzymes across various plant-type combinations. In addition, much of the variation in the intercropping effect is accounted for by intercropping-induced increases in microbial biomass and general microbial activity. Given the role of the soil microbial community in producing extracellular enzymes, the effect of intercropping on microbial community structure and function remains an important question requiring further investigation.

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**Table 1**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Overall | | |  | Carbon Enzymes | | |  | Nitrogen Enzymes | | |  | Phosphorous Enzymes | | |  | Oxidative Enzymes | | |  | General Enzymes | | |  |
|  | R2 | P | *n* |  | R2 | P | *n* |  | R2 | P | *n* |  | R2 | P | *n* |  | R2 | P | *n* |  | R2 | P | *n* |  |
| Environmental and  Edaphic Factors |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| % Clay | 0.15% | 0.152 | 592 |  | 0.17% | 0.268 | 79 |  | 0.61% | 0.206 | 163 |  | 1.22% | 0.024 | 215 |  | 0.00% | 0.902 | 19 |  | 0.00% | 0.877 | 96 |  |
| % Sand | 0.23% | 0.171 | 557 |  | 0.00% | 0.552 | 78 |  | 0.00% | 0.389 | 162 |  | 0.00% | 0.996 | 182 |  | **15.87%** | **0.042** | **19** |  | 1.61% | 0.103 | 96 |  |
| pH | 0.22% | 0.177 | 882 |  | 2.01% | 0.132 | 115 |  | 1.97% | 0.091 | 226 |  | 0.01% | 0.367 | 298 |  | 0.00% | 0.116 | 52 |  | **3.84%** | **0.012** | **170** |  |
| Soil C | 0.00% | 0.516 | 775 |  | 0.00% | 0.852 | 104 |  | 0.00% | 0.407 | 221 |  | 0.00% | 0.884 | 243 |  | 0.00% | 0.587 | 40 |  | **2.44%** | **0.041** | **147** |  |
| Total N | **1.67%** | **0.003** | **555** |  | **10.38%** | **0.004** | **78** |  | **5.40%** | **0.004** | **160** |  | 1.29% | 0.080 | 172 |  | 3.33% | 0.093 | 38 |  | **6.75%** | **0.006** | **101** |  |
| Available N | 0.25% | 0.173 | 604 |  | 0.00% | 0.932 | 93 |  | 0.00% | 0.315 | 165 |  | **10.79%** | **<0.001** | **175** |  | 1.69% | 0.147 | 43 |  | 0.00% | 0.897 | 126 |  |
| Total P | **2.35%** | **0.002** | **400** |  | 0.00% | 0.398 | 67 |  | **5.33%** | **0.007** | **121** |  | 0.65% | 0.193 | 100 |  | **34.82%** | **<0.001** | **38** |  | **7.49%** | **0.019** | **72** |  |
| Available P | 0.00% | 0.447 | 814 |  | 2.22% | 0.054 | 104 |  | 0.00% | 0.823 | 217 |  | 0.00% | 0.610 | 282 |  | 2.22% | 0.078 | 49 |  | 0.00% | 0.762 | 144 |  |
| Annual Precipitation | **2.95%** | **<0.001** | **478** |  | 3.33% | 0.298 | 48 |  | 0.00% | 0.787 | 145 |  | **12.72%** | **<0.001** | **168** |  | 1.15% | 0.279 | 12 |  | **9.44%** | **0.004** | **84** |  |
| Experimental Factors |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| N Fertilizer | 0.00% | 0.692 | 563 |  | 0.00% | 0.913 | 70 |  | **2.92%** | **0.024** | **153** |  | 0.86% | 0.176 | 215 |  | 0.00% | 0.683 | 29 |  | 0.62% | 0.214 | 93 |  |
| Length of Study | **8.36%** | **<0.001** | **885** |  | **3.03%** | **0.045** | **125** |  | **6.41%** | **<0.001** | **226** |  | **8.02%** | **<0.001** | **294** |  | 8.31% | 0.063 | 48 |  | **9.18%** | **<0.001** | **171** |  |
| Sampling Depth | **0.23%** | **0.029** | **432** |  | 3.70% | 0.089 | 64 |  | **1.71%** | **0.016** | **117** |  | 1.13% | 0.218 | 133 |  | 0.00% | 0.842 | 6 |  | **4.59%** | **0.040** | **91** |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

Table 1: Strength of correlations between continuous moderators and the intercropping effect, given as R2 and associated P-value, with *n* number of observations. Values are reported for the overall intercropping effect and for the intercropping effect within each enzyme type.

**Appendix: Studies included in meta-analysis**

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