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AGROECOSYSTEMS

Who gives a flux? Synchronous flowering of *Coffea arabica* accelerates leaf litter decomposition

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Abstract. Coffee (*Coffea arabica*) flowers synchronously and flowers are only open for a few days before senescing. Flower petals often decompose easily, containing higher concentrations of nutrients relative to other plant tissues. Thus, a pulse of petals into the detrital pool could be beneficial for the decomposer community and accelerate decomposition processes. Our research assessed the magnitude of the pulse of petals within a shaded coffee farm, and the impact of petals on the litter arthropod community and on the rate of leaf litter decomposition. Three plots of 12 coffee plants were monitored throughout the flowering period to estimate the magnitude of the bloom. Pitfall traps were used to assess the litter arthropod community before and after flowering. Finally, litterbags with *C. arabica* leaves alone and *C. arabica* leaves with flower petals were used to compare the effect of petals on decomposition rates. The average number of flowers open per plant at the peak of the bloom was 792 flowers. When scaling to obtain an estimate per hectare in a year, our results indicate flower petals could contribute 26.27 kg of nitrogen, 2.03 kg of phosphorus, and 26.7 kg of potassium. The leaf litter community did not change during our sampling, suggesting that any community effects may be acting on a longer time scale or smaller spatial scale. Leaf litter decomposed nearly three times as quickly in litterbags that included flower petals, relative to litterbags with only *C. arabica* leaf litter in the first month and twice as fast in the second month. The rate of decomposition with petals exceeded the rate of decomposition without petals and was highest after one month, though the benefit continued after two months. Our results demonstrate that the presence of flower petals can accelerate short-term decomposition processes.

Key words: coffee agroecosystems; decomposer community; flower petals; leaf litter decomposition; litterbags; mass bloom.

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INTRODUCTION

Nutrient limitations constrain plant growth in all managed and unmanaged ecosystems. Annual and seasonal oscillations in availability can provide essential contributions to nutrient pools where natural cycles are not overshadowed by anthropogenic inputs (Pastor and Durkee Walker 2006, Galloway et al. 2008). Some seasonal or intra-annual inputs are dramatic and well-studied, such as oceanic upwellings or periodical insect outbreaks (Falkowski et al. 1998, Yang 2004). In other cases, low volume but synchronous inputs could have the potential to temporarily alleviate nutrient limitations, but have received little attention from researchers. Coffee flowering provides one such example, where blooms across fields occur synchronously with thousands of flowers open for just one or two days. Typical nutrient budgets are unlikely to include such inputs, given the brief residence times of the flowers in the ecosystem (Glover and Beer 1986, Dossa et al. 2008, Tully and Lawrence 2011). We propose that, despite their transient nature, mass coffee blooms could be an important source of nutrients in coffee agroecosystems, with the potential to affect both ecosystem function and the decomposer community.

Input pulses have the potential to alter ecosystem function through their contribution to the detrital pool. Increased quantity or quality of inputs to the detrital pool can influence decomposition rates and the pace of nutrient cycling. A pulse of relatively labile material, meaning material with easily available carbon and other nutrients, can act to prime decomposition of soil organic matter, temporarily accelerating decomposition processes (Kuzyakov et al. 2000). Altered activity and relative abundances of decomposer microbes may explain this priming effect (Kuzyakov et al. 2000, De Graaff et al. 2010).

Nutrient pulses can also have cascading effects across trophic levels, with consequences for ecosystem function. Some of the most well-known and well-studied examples in ecology come from aquatic systems, including upwellings and turnover that can stimulate organismal growth across trophic levels (Tilman et al. 1982, Falkowski et al. 1998), but there are examples from plant ecology as well. For example, the nitrogen contribution of seed masting in nitrogen-limited boreal forests has been linked to tree regeneration (Zackrisson et al. 1999). Events like seed masting or inter-annual spikes in abundance of arthropods can drive consumer community dynamics, too (Ostfeld and Keesing 2000). A pot experiment with a grass found that larger individuals benefit disproportionately from pulses, highlighting the importance of pre-pulse conditions (Lamb et al. 2012). These examples emphasize the potential of nutrient pulses to influence both primary producers and upper trophic levels in a range of contexts.

Flowering events have rarely been considered within the lens of periodic pulses, though many species, especially domesticated crop species (Jung and Müller 2009), flower synchronously, and profusely (e.g., almonds, blueberries, canola, and sunflower). Bamboo, which reproduces with a single mass flowering event at the end of a life span that can range 3–120 yr, has been well studied and provides an exception (Janzen 1976). However, studies of the ecosystem consequences of bamboo flowering have focused on the input of the bamboo plant into the detrital pool, rather than the flowers themselves (Austin and Marchesini 2012), and there are key differences between bamboo, a monocotyledon, and other plant species that may make it harder to draw parallels to other plant systems.

Even annual flowering events, especially when conspecifics are abundant and the bloom is short-lived, have the potential to provide an important pulse of resources. This is particularly true given that floral tissue is likely to have an outsized influence on decomposition dynamics, relative to its biomass (Whigham et al. 2013). Flowers generally have higher concentrations of nutrients compared to leaves and other plant tissue (Belkhodja et al. 1998, Martinez et al. 2003). Additionally, petals have fewer structural compounds, for example, lignin, which can constrain decomposer access to nutrients and increase the longevity of a tissue in an ecosystem. Further, detritivores have been shown to select flowers over leaves in preference experiments and grow faster when fed a diet of floral tissue (Smallegange et al. 2007, Whigham et al. 2013). Detritivores, including protozoa, nematodes, Collembola, mites, millipedes, isopods, earthworms, and others, can influence decomposition in several ways including by regulating bacterial and fungal populations and by fragmenting and consuming litter (Hättenschwiler et al. 2005, Wickings et al. 2011). Collembola (commonly known as springtails) can be especially important meso-fauna due to their ability to directly consume and alter organic material and regulate the fungal communities (Rusek 1998). Further, Collembola can increase microbial biomass, accelerating decomposition rates, linking their abundance to microbial biomass, and making them an important indicator group within the detritivore community (Hanlon and Anderson 1979, Seastedt 1984, A'Bear et al. 2012, Yang et al. 2012).

In agricultural systems, naturally occurring nutrient levels are often augmented by the addition of inorganic or organic fertilizers (Potter et al. 2010). This is especially true in tropical agriculture, where soils are known for being highly weathered and, subsequently, nutrient poor (Palm et al. 2007). Organic fertilizers, which are derived from plant and animal matter, are less available to plants than inorganic fertilizers, but avoid the externalities (notably, water pollution) and costs of inorganic fertilizers and have long been used in agriculture to increase nutrient cycling (Drinkwater and Snapp 2007, Kremen and Miles 2012). Use of plant matter as nutrient supplements (e.g., cover crops, mulch, and compost) is a widespread and ancient practice. The mass coffee bloom represents an endogenous source of plant matter, so the ecosystem level nutrient budget is unchanged. Thus, flower petals would be unlikely to replace the need for fertilizer, but the nutrients provided could supplement nutrient budgets and alter the seasonal timing of fertilizer needs.

Here, we describe the magnitude of the nutrient flux of a coffee mass bloom and its consequences for decomposition and detritivore community composition in a shaded organic coffee farm in southern Mexico. We focused on Collembola as part of the detritivore community because of their important role in decomposition (Yang et al. 2012) and their abundance in our study system (Schmitt et al. 2020). Our study addressed these three main objectives with the following hypotheses:

H 1: Coffee flower petals will have higher nutrient concentrations than coffee leaf tissue and represent an important pool of nutrients on a farm scale. We used the nutrient concentrations in petal tissues to scale the density of the bloom on a plant basis to estimates of farm-level nutrient inputs for nitrogen (N), phosphorus (P), and potassium (K).

H 2: Senesced flower petals will positively influence coffee leaf litter decomposition rates.

We predicted that leaf litter decomposition would be accelerated with the addition of relatively labile flower petals.

H 3: Finally, we assessed the impact of the bloom on the leaf litter invertebrate community.

We expected that the decomposers, namely Collembola, would increase in abundance where more flowers were present, if the petal biomass alleviates nutrient limitations.

METHODS

Study system and site

Coffee is grown in the tropics and usually in areas that experience distinct dry and rainy seasons. Coffee blooms occur in the dry season (Drinnan and Menzel 1995). At our field site, coffee will have a mass bloom 2–4 times in a season, over the span of 1–2 months. We conducted this study in 2018, when flowering occurred from late January through early March, though in other years the bloom as occurred as late as mid-March through the end of April (Philpott et al. 2006). Blooms are cued by a period of dryness, followed by 7–10 mm of precipitation (Crisosto et al. 1992, DaMatta et al. 2007, Schroth et al. 2009). Flowers are open for approximately 48 h before senescence (Cannell 1983), though they are most attractive to pollinators in the first 24 h (Free 1993). *Coffea arabica*, the most common commercially grown species of coffee and the focus of this study, is self-compatible, but fruit set increases with outcrossing (Klein et al. 2003). Many varietals of *C. arabica* are grown commercially and are present at our study site. The most common varietals at our site include Catimor, Java, and Carchimor, with lesser quantities of Arabe, Bourbon, Caturra, Costa Rica, Colombiano, Marceleza, and Tupic varietals.

Field work was carried out at *Finca* Irlanda, a 300-ha, shaded, organic coffee farm in the Soconusco region of Chiapas, Mexico. *Finca* Irlanda is located ~950–1150 m above sea level and receives 4500 mm of rainfall each year (Philpott and Bichier 2012). Precipitation is concentrated in the rainy season, which extends from May through October (Lin 2010). Few external inputs are added, with the exception of compost and compost tea (stewed compost) which is made onsite from chicken manure, calcium carbonate, and worm vermiculture of coffee parchment (Gonthier et al. 2013). One kilogram of compost is applied to each plant in March and September, and 200 mL of compost tea is applied to each plant in February and August.

Density of the bloom and nutrient content of tissues

Three plots with 12 coffee bushes in each were setup mid-February 2018 and monitored nine times between 21 February 2018 and 10 March

2018. Upon setup, the height and total number of branches were recorded, as well as the spatial arrangement of the plants. Plots ranged in size from 20 to 30 m^2; plot size varied because coffee plants were not planted with perfectly even spacing. The number of branches with flowers and the total number of flowers on each plant were recorded at each observation. Plots were located 200–1000 m apart. The sites were chosen where planted rows were intact and plants were of a similar size.

Recently senesced flower petals were collected from the ground and dried at 50°C to a constant weight. Samples were homogenized and ground, and nutrient concentrations (N, P, K, S, Mg, Ca, Na, B, Zn, Mn, Fe, Cu, Al) were analyzed using inductively coupled argon plasma mass spectrometry, run on a Thermo iCap 6500 at A&L Great Lakes Laboratory (Fort Wayne, Indiana, USA). Nutrient data were used, with the mass of flowers, to scale the nutrient pulse to a farm-relevant scale ($kg \cdot ha^{-1} \cdot yr^{-1}$). We focused on nitrogen, phosphorus, and potassium, the three nutrients that most commonly limit plant growth. The same analysis was run on recently senesced *C. arabica* leaf samples collected from the same farm, to provide a relative comparison of flower and petal nutrient content.

Leaf litter decomposition

Litterbags made of 2-mm fiberglass mesh were placed at 15 sites around the farm. Mesh size was chosen to allow micro- and meso-fauna access to the litter, which includes collembolans (Bradford et al. 2002). Sites were a minimum of 75 m apart. Four litterbags were placed at each site on a 0.5 m diameter ring. Half the litterbags were filled with *C. arabica* leaf litter and half with a combination of *C. arabica* leaf litter and *C. arabica* flowers. Approximately 20 g of leaves was placed in each bag with approximately 6 g of petals in half the bags. This ratio is higher than would occur throughout the farm, but it could represent litter immediately beneath a plant or under a clump of petals. All plant tissue was collected when recently senesced, and dried to a constant weight before being sewn into the bags. The treatments were affixed to opposite sides of the ring to prevent direct contact. Precise masses were recorded for each bag and used to calculate mass lost upon collection. Metal identification tags with a unique number were used to track individual bags. Litterbags were put in the field in March 2018.

One bag of each treatment (leaves and leaves with petals) was collected from each site after one month, in April 2018, and after two months, in May 2018. Collected bags were dried, and the leaf tissue was re-weighed. Petal and leaf tissue were distinguished upon collection at one month. No petal tissue remained in any bag after two months. Mass loss (the difference in mass between time points) was used as a proxy for decomposition.

Community effects

Twelve pitfall sites were set up throughout the farm, a minimum of 75 m from one other. Sites were approximately 4 m^2 and contained five pitfall traps (Fig. 1). One trap was collected before the bloom (time A), after which the remaining four traps were manipulated through the physical removal and exclusion of flowers or addition of 15 g of dried flower petals. To attract decomposers, petals were added around the edge of the pitfall trap in a ring approximately 3 inches in diameter. One addition and one exclusion trap were sampled after three days (time B), and the remaining two (one addition and one exclusion trap) were sampled 7 d after the manipulation (time C). These times were chosen with the aim of assessing short-term response of the litter arthropod and would denote recruitment rather than reproduction.

Plastic 16-oz. deli containers were used as a traps. Containers were buried, flush with the soil surface, and allowed to sit for a minimum of 24 h before lids were removed. Each was covered with a plate, propped up with wooden dowels, to allow organisms to walk beneath the plate and fall into the trap, but to prevent falling detritus or larger organisms from accessing the trap. Traps were filled with water with a drop of dish soap to break surface tension and facilitate the capture of organisms in the traps. They were collected 24 h after opening and organisms were transferred to alcohol and identified to order, and then morpho-species.

Statistical methods

Nutrient content was measured in five homogenized floral samples and scaled to hectare-level estimates using the following equation:

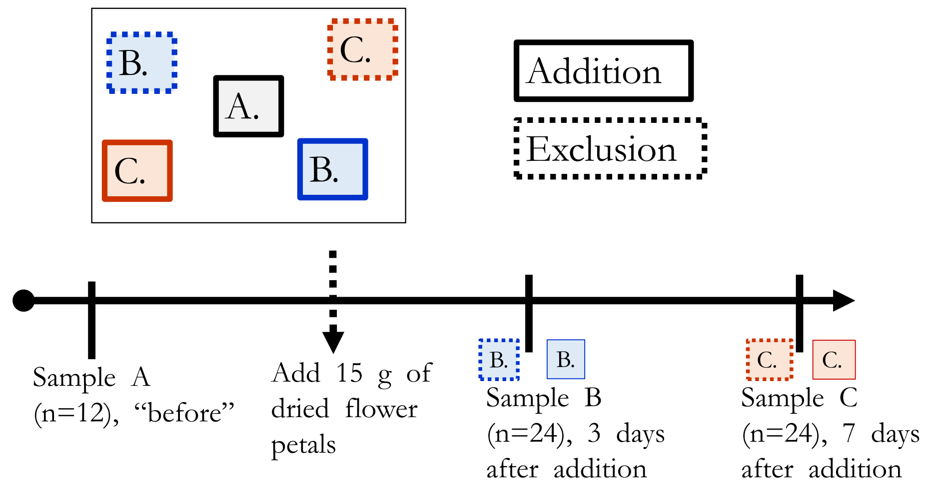

Fig. 1. Conceptual figure of the pitfall trap study design. Five pitfall traps were placed within each site. Sampling took place at three time points: before manipulation and 3 and 7 d after manipulation. For the additional manipulation, 15 g of dried flower petals was added around the edge of the pitfall trap; for the exclusion, all flower petals in the area were cleared.

$$\%\,\text{nutrient} \times \frac{0.1848\,\text{g}}{\text{flower}} \times \frac{792\,\text{flowers}}{\text{plant}} \times \frac{2400\,\text{plants}}{\text{hectare}} \times \frac{3\,\text{mass}\,\text{blooms}}{\text{year}} = \text{X}\text{g} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}. \quad (1)$$

The values in Eq. 1 are estimated from the field site in this study. Because *Finca* Irlanda is relatively un-intensified, some of the parameter estimates (especially plants/ha) are on the low end of the range seen in coffee farms. Thus, this calculation, which resulted in an estimate of grams of nutrient per hectare per year, provides a conservative estimate of the nutrient flux affected by the mass coffee bloom. We did not scale the leaf nutrient data to $\text{g}{\cdot}\text{ha}^{-1}{\cdot}\text{yr}^{-1}$ because leaves senescence continually throughout the year and, to our knowledge, there are no reliable estimates of leaves lost per year.

To test for differences across time or treatments in proportion of mass lost in the litterbags—a proxy for decomposition—we used a two-way ANOVA, implemented with the aov function in the dplyr package from R (Wickham et al. 2015). Assumptions of normality and homogeneity of variances were met. Looking at the proportion of mass lost allows us to assess the decay linearly.

The decay constant k, as derived from the exponential decay equation ($N_t = N_0 \times e^{-kt}$), was also used to compare rates of decomposition. The exponential decay equation is commonly used in decomposition analyses (Olson 1963, Aerts 1997, Bärlocher 2005). We used a linear mixed-effects model using the lmer function with lmerTest package in R (R Core Team 2009, Kuznetsova et al. 2017) to test for differences between treatments and across time points. Site was included as a random effect. The decay constant, k, was log-transformed to meet assumptions of normality and heterogeneity of variance.

Change in the litter arthropod community, as a function of time and treatment, was visualized using non-metric dimensional scaling plots (NMDS) and assessed with analysis of similarity (ANOSIM). The NMDS plots were made using the metaMDS function from vegan in R (Oksanen et al. 2007). Analysis of similarity was calculated using the anosim function from vegan in R (Oksanen et al. 2007). We calculated distances based on Bray–Curtis, since our data were count data, and ran 1000 permutations. We used two dimensions when calculating the Bray–Curtis distances, as our stress values were relatively low. R is the output of the ANOSIM analysis and, like R^2, indicates the amount of the variation that can be explained by the explanatory variable being tested. NMDS and ANOSIM were repeated with the full community pitfall data at the order level and morpho-species level. At the order level, groups included Diptera, Arachnida, Coleoptera, Orthopteran, Hemipteran, Collembola, Hymenoptera, and other. Ants were excluded from ANOSIM analysis because, due to the eusocial nature of ants, their counts in pitfall traps conflate activity level and abundance.

To test for differences in the abundance of Collembola across treatments and times, we used a two-way ANOVA, run with the aov function in the dplyr function (Wickham et al. 2015). To meet the assumption of normality, one outlier was removed and data were log-transformed. A Tukey honestly significant difference post-hoc test was used to look at pair-wise comparisons of time points.

RESULTS

Density of the bloom and nutrient content of tissues

Two of the three plots we monitored experienced mass blooms during the observation period (Fig. 2). Within those two plots, plants produced an average of 792 flowers at peak bloom. The maximum number of flowers recorded on a single plant on a single day was 1540 flowers, but there was considerable variability between plants in a given plot. In the two plots that had a mass bloom during the monitoring period, the peak number of flowers per plant ranged from 292 to 1540, with an average peak of 818.9 ± 77.9 flowers per plant.

Nutrient concentrations per sample and on a per hectare basis are given in Table 1. The petals averaged 2.49% nitrogen, 0.22% phosphorus, and 2.53% potassium per sample. When scaling to an estimate per hectare and per season, our results indicate flower petals could contribute approximately 26.27 kg of nitrogen, 2.03 kg of phosphorus, and 26.7 kg of potassium.

The same nutrient analyses were conducted on leaves from the same farm site. The leaves averaged 2.51% nitrogen, 0.13% phosphorus, and 1.83% potassium per sample.

Leaf litter decomposition

Leaves decomposed faster in the presence than in the absence of flowers ($F = 736.067$, $P < 0.00$), and a greater proportion of mass was lost in two months compared to one month ($F = 247.788$, $P < 0.005$). There was a significant interaction between time and treatment on proportion mass lost in the litterbags ($F_{1,52} = 5.391$, $P = 0.0242$); the difference in decay rates with and without petals is greater in month 2 compared to month 1 (Fig. 3), leading to this ordinal interaction. Assumptions for homogeneity of variances (Levene's test, $F = 0.8505$, $P = 0.4726$) and normality (Shapiro–Wilk normality test, $W = 0.96583$, $P = 0.113$) were met.

Comparing the decay constant (k) confirms that the rate of decomposition is higher after one month and with petals (Fig. 3). The linear mixed-effects model indicated that treatment ($\beta = 0.917$, df = 39, $P < 0.0005$) and month ($\beta = -0.250$, df = 39, $P < 0.0005$) were both significant predictors of k, and there was an interaction between treatment and month ($\beta = -0.163$, df = 39, $P = 0.0051$).

Community effects

Flower availability had no impact on the abundance of collembolan ($F = 0.077$, $P = 0.7827$), though there were fewer collembolan over time ($F_{1,52} = 4.692$, $P = 0.0134$). There was also no significant interaction between time and treatment ($F = 1.232$, $P = 0.2721$). A post-hoc Tukey test showed that collembolan abundances were lower across sites before the manipulation as compared to the samples taken 3 d after manipulation ($P = 0.0114$) or 7 d after manipulation ($P = 0.0376$). There were no significant differences in collembolan abundance between the two sampling times after manipulation ($P = 0.8075$).

The NMDS plot illustrated the lack of separation of arthropod communities based on treatments or time points, regardless of the level of taxonomic resolution (for order-level resolution, see Fig. 4). Analysis of similarity, at the level of orders, indicated significant separation between treatments ($R = 0.066$, $P = 0.02$), but there was no separation between treatments at the level of morpho-species ($R = -0.001$, $P = 0.64$). An R statistic of 0 indicates no separation and a negative R value indicates greater dissimilarity among replicates than between samples.

DISCUSSION

Our study provides the first estimates of the nutrient flux associated with mass coffee flowering, and its effects on leaf litter arthropod

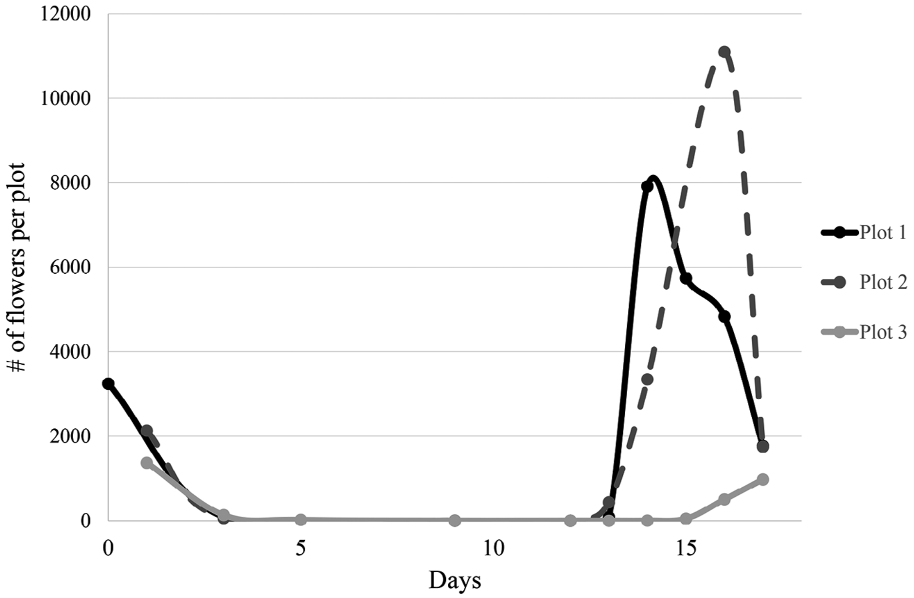

Fig. 2. Flowers per plot across the monitoring period. Flowers from all 12 plants in each plot were summed. Plot 3 did not have a mass bloom during the monitoring period.

Table 1. Flower petal nutrient data for nitrogen, phosphorus, and potassium at multiple scales.

Calculation	Nitrogen (N)	Phosphorus (P)	Potassium (K)
Average %/sample	2.492	0.218	2.532
Standard deviation	0.09471	0.016432	0.119875
Standard error	0.042356	0.007348	0.05361
Grams/flower†	0.04605	0.000403	0.004679
Grams/plant‡	3.647331	0.319068	3.705876
Grams/ha§	8753.595	765.7639	8894.102
Grams·ha^{-1}·season^{-1}¶	26260.78	2297.292	26682.31
Kilograms·ha^{-1}·season^{-1}	26.26078	2.0297292	26.68231

† Average mass of a single flower is approximated at 0.1848 g.
‡ Assuming average of 792 flowers per plant, per bloom.
§ Assuming 2400 plants per hectare.
¶ Assuming three major blooms per year.

communities. We report limited changes to the litter arthropod community but evidence of accelerated leaf litter decomposition as a result of petal inputs.

Nutrient fluxes and decomposition

We estimate that approximately 26 kg N·ha^{-1}·yr^{-1}, 2 kg P·ha^{-1}·yr^{-1}, and 27 kg K·ha^{-1}·yr^{-1} are cycled from flower petals to the detrital pool during the flowering season at our field site. Senesced leaves from *C. arabica* have 2.51% N, 0.13% P, and 1.83% K, whereas the petals had 2.49% N, 0.22% P, and 2.53% K. While the percentage of nitrogen is nearly identical between tissues, the phosphorus and, in particular, potassium are substantially higher in the petals than in the leaves. Further, given the structural tissue in leaves, each of the nutrients is less accessible for microbes and micro-invertebrates. This finding is consistent with other research showing high nutrient levels in floral tissue compared to leaves (Belkhodja et al. 1998, Martinez et al. 2003).

While coffee flowers have relatively high concentrations of nutrients, the impact of these nutrients in the agroecosystem will be dependent on

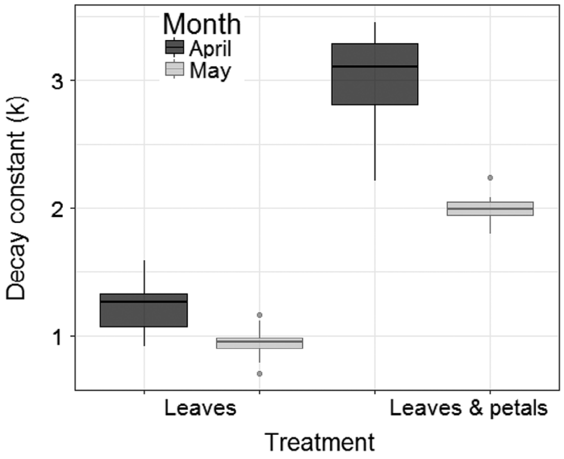

Fig. 3. Box plot of decay constant (*k*) by treatment (leaves, leaves, and petals) and by time (April [one month], May [two months]).

the timing of the inputs, mineralization dynamics, and the fate of mineralized N. Our study does not allow us to speak to the form of the nutrients or their retention in the system. However, it is clear that nutrient form greatly affects the accessibility of nutrients to plants and other organisms and the form of the nutrients will influence their likelihood of leaching out of a system. For example, phosphorus is often the limiting nutrient for plant growth in tropical systems, in part because much of the total phosphorus in the soils is bound up in iron oxides (Turner et al. 2018). Nitrogen, on the other hand, can be problematically mobile, particularly when present as nitrate (Fowler et al. 2013). Therefore, it is crucial to determine whether the nitrogen from flower petals is retained in the system and if phosphorus is bioavailable. The mobility of nutrients can stem from both management decisions and inherent ecosystem properties. In a study of Costa Rican coffee farms, nitrogen leaching was negatively related to shade tree biomass, a management decision, whereas phosphorus leaching was correlated with soil iron pools, an inherent property (Tully et al. 2012). Overall, abiotic and management conditions will interact to drive the

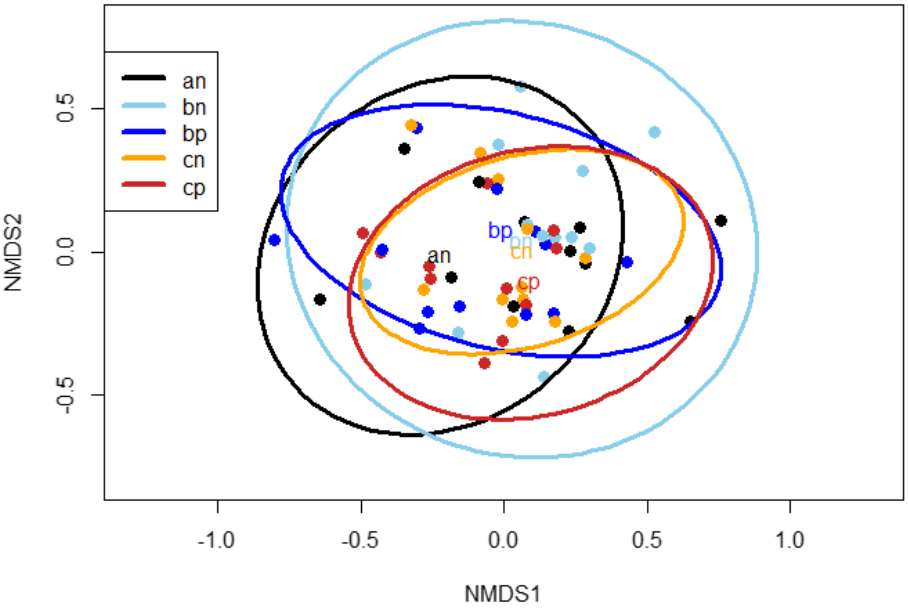

Fig. 4. Non-metric dimensional scaling (NMDS) plot that includes order-level data from pitfall traps. Analysis of similarity, at the level of orders, indicated significant separation between treatments ($R = 0.066$, $P = 0.02$). The stress value was 0.186, indicating a good representation. Each color represents a different treatment (an, before manipulation; bn, 3 d after, no petals added; bp, 3 d after, petals added; cn, 7 d after, no petals added; cp, 7 d after, petals added), and the letters indicate the centroid of each treatment. Ellipses represent 95% confidence intervals; the overlap of ellipses indicates a lack of separation between treatments.

fate of floral-derived nutrients in coffee agroecosystems.

The timing, duration, and intensity of the blooms also mediate the potential effects of the bloom on nutrient cycling. The timing of the bloom is dependent on each year's climate, with blooms having the potential to occur over a two-month period. In years when mass blooms occur in short succession and are highly synchronous at a local scale, we suspect that their nutrient impact is likely to be greater than in years when blooms are less synchronous or are spaced across a longer period of time. The response of decomposer communities to pulses will depend on their life history strategy (Treseder et al. 2011), as well as the size of the pulse.

The timing of the bloom also has implications for nutrient availability for developing coffee fruit and, thus, for coffee yields. We scaled our nutrient estimates to an annual basis, but the blooms occurred on the scale of weeks and all petal tissue had decomposed within months. Flowering necessarily precedes the start of fruit development, a stage during which coffee plants have elevated nitrogen demands (Bruno et al. 2011). One study found that up to 20% of total plant nitrogen was found in flowers during the bloom (Malavolta et al. 2002). Thus, if flowers contain a significant portion of a plant's nitrogen and the demand for nitrogen is greatest immediately following a bloom during early fruit formation, the nutrient input from petals into the soil nutrient pool may reduce the need for external inputs at a time when crop nutrient demand is high. The nutrient demands of coffee plants in early fruit formation have been established in previous research, and it is likely the decomposition of petal tissue contributes to these nutrient needs. Further research is needed to determine the fate of decomposed nutrients from petal tissue.

The rate of leaf litter decomposition in litter bags, as measured by the proportion of leaf biomass lost and the decay constant *k*, increased over time and when petals were present in the litterbags with the leaves. No recognizable petal tissue was found in the litterbags at the end of two months, suggesting that the petal tissue decomposes quickly, but the effect of petals may alter decomposition even after the petals have gone. The presence of petals at the start of decomposition could have priority effects on microbial communities, altering the community and abundance of bacterial and fungal species (Strickland et al. 2009). In changing the composition and trajectory of decomposer communities, the impact of petals could continue after the petal tissue has been entirely broken down.

The observed increase in decomposition rates with the addition of petals to the detrital pool indicates that petals represent a biologically accessible source of nutrients.

Litter community effects

We found little evidence of changes within the leaf litter invertebrate community on the whole, or collembolans, in response to the addition or exclusion of petals. The abundance of Collembola did decrease over our sampling times, but there were no differences between treatments. Our experiment was carried out during the bloom and at sites that measured approximately 4 m squared. The farm, as a whole, was relatively saturated with flowers during this time, minimizing the potential impact of our smaller scale manipulations. We suggest that future experiments be executed in the dry season, outside of the bloom, when abiotic conditions are similar but the environment is less saturated with petal tissue, or during the bloom season outside of a coffee farm. We do not expect the decrease in Collembola to be biologically important, but still, the direction of change is counterintuitive given the increase in labile detritus across the farm during the mass blooms. An overall increase in Collembola would be expected as the result of migration of Collembola from soil to the leaf litter or from Collembola reproduction.

We did find some evidence of a shift in leaf litter invertebrate community composition at the level of orders, but the *R* value was less than 0.07, indicating the shift was relatively unimportant in explaining the community. Further, there was no indication of separation between treatments at the level of morpho-species in the ordination plots. Thus, while there was a statistical effect at the level of orders, we do not expect the shift was biologically important. The duration of our study also likely limited our ability to detect shifts in the community. The time frame of our pitfall study, with the latest sample 7 d after manipulation, is insufficient for the majority of invertebrate life cycles, meaning our samples after manipulation measured recruitment rather than reproduction. Further studies should assess micro-invertebrate response on a longer time scale to determine whether there is a signal of increased reproduction or recruitment in response to this floral nutrient pulse. While we find no evidence of a response by micro-invertebrate decomposers, it may be that microbial decomposers were responding. We did not assess the microbial community, but previous studies on the mechanisms behind priming underscore the importance of bacteria and fungi in priming dynamics (Kuzyakov 2002, Kuzyakov 2010). Microbes can respond to labile material much more rapidly than invertebrates. A shift in the dominant microbial groups (e.g., via priority effects, where early arrival of a species or group impacts the resultant community; Hiscox et al. 2015, Lin et al. 2015, Tláskal et al. 2016) could also explain the increased decomposition rates seen after the flower petals had fully decomposed.

The nutrients we measured in petals and scaled to a farm level were not inputs from outside the system, unlike most fertilizer additions. Fertilizer additions are relatively small at our study site, but at more intensified farms where fertilizer is used, suggested fertilizer application rates would result in nutrient inputs far greater than those obtained from the mass bloom. For reference, the annual recommended fertilization rates for coffee in Mexico, as per the Food and Agriculture Organization of the United Nations, are $60\ \mathrm{kg\ N{\cdot}ha^{-1}{\cdot}yr^{-1}}$, $40\ \mathrm{kg\ P{\cdot}ha^{-1}{\cdot}yr^{-1}}$, and $15\ \mathrm{kg\ K{\cdot}ha^{-1}{\cdot}yr^{-1}}$ (FAO 2006). Our estimates of the contribution from petals are much lower, except in the case of potassium, where we estimate the petals could represent more than the yearly budget of potassium, provided the potassium is in an available form. While the overall nutrient pools within the agroecosystem are not increasing with the addition of petals to the detrital pool, our results do provide evidence of accelerated cycling of nutrients cued by floral senescence.

Considering a mass bloom for its impacts beyond pollination is important in agroecosystems where yield is influenced by many factors, including nutrient availability. Here, we provide evidence that an annual pulse of senescent floral tissue is altering and increasing decomposition dynamics in a coffee agroecosystem. Our results suggest that, after a year of gradually reduced amounts of nutrients in the soils (due to uptake by coffee plants), the mass bloom could function to release those sequestered nutrients, potentially increasing relative nutrient availability if not relative nutrient totals, and allowing these nutrients to cycle within other pools. Isotopic methods could resolve the specific fate of petal nitrogen inputs. However, increasing management intensity of coffee systems is resulting in more exogenous fertilization (Lin et al. 2008), while climate change is reducing the synchronization of coffee blooms (Drinnan and Menzel 1995). In intensified coffee systems, and especially under climate change, the impacts of the coffee bloom may be reduced.

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