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Coffee leaf litter decomposition: Short term home-field advantage in shaded coffee agro-ecosystems

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ABSTRACT

Home-field advantage (HFA), when applied to decomposition, predicts that a substrate will decompose more quickly in a home environment compared to away environments, presumably due to specialized decomposer communities. Few empirical tests of HFA have been done in agricultural environments, where manipulated species composition and reduced biodiversity could increase the effects of HFA. We used both a six week tethered line experiment and a yearlong litterbag study as complementary methodologies to assess the decomposition of *Coffea arabica* and *Coffea robusta* leaf litter in three environments: (a) where *C. arabica* is grown, (b) where *C. robusta* is grown and (c) an adjacent forest, where coffee is not cultivated. Using the decay constant (*k*) and carbon to nitrogen ratios, we tested for evidence of accelerated decomposition in home environments, compared to congeneric-away and forested-away environments. We found evidence of HFA with the shorter-term tethered line experiment, where *C. arabica* decayed twice as quickly in its home environment and 50% faster in the congeneric away as it did in the forested-away environment. We found no evidence of HFA in the longer litterbag study, with no difference in decay based on species or environment. The carbon to nitrogen ratios for tethered line samples differed over time and by environments, driven by differences between the coffee environments and the forest. Our results provide some of the first evidence of HFA in an agricultural system, with effects even in a congeneric-away environment. While we found no evidence of HFA in the longer, yearlong litterbag study, a short term HFA could still provide an ecologically important pulse of nutrients if this pulse is synchronized with plant demand.

1. Introduction

Home-field advantage (HFA) is a ubiquitous concept in sports; it posits that a familiar arena and the support of local fans will give the home team an advantage over the visiting team. Ecologists have adopted this framework and applied it to comparison of decomposition dynamics in the environment in which they grew – or where conspecifics are growing – versus environments without conspecifics. This phenomenon has been studied across spatial scales – from individual trees in a watershed (Jackrel and Wootton, 2014) to across-biome comparisons (Heneghan et al., 1999) – and temporal scales – with evidence of HFA acting at the scale of weeks (Jackrel and Wootton, 2014) and persisting for years (Gholz et al., 2000).

HFA is most often evaluated with reciprocal transfer experiments, wherein the litter from each of two environments is observed in its "home" environment and in the "away" environment of the second focal species. Such studies have demonstrated that HFA is a common, though not universal, phenomenon (Vivanco and Austin, 2008; Ayres et al., 2009; Veen et al., 2015). Multiple mechanisms may drive HFA, including plant-herbivore interactions, microbial symbiosis, phyllosphere legacies, and specialization of decomposer communities (Austin et al., 2014). While HFA is not the most important determinant of decomposition rates – approximately 70% of decomposition can be explained by climate and initial litter quality – a meta-analysis of reciprocal decomposition studies, including those specifically looking at HFA, found an 8% average increase in decomposition rates due to HFA across litter types in forests (Ayres et al., 2009). Other studies have reported increases in decomposition as high as 53% when manure was placed in "home-field" pastures (Rashid et al., 2013). Ecosystem characteristics (e.g. total biodiversity and abiotic factors) can play a role in determining the importance of HFA (Heneghan et al., 1999; Gießelmann et al., 2011).

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Leaf chemistry, including secondary metabolites, may also play a key role in mediating HFA. Wallenstein et al. (2013) found that the "home" environment accelerated microbially-derived transformations to a greater extent for the more slowly decomposing lodge-pole pine than for aspen litter, suggesting that HFA may have a greater effect on more recalcitrant species. Secondary metabolites, which may be produced by the plant or associated endophytes, have the potential to impact decomposition through several pathways, operating from the fine scale of organismal inhibition to the broad scale of shaping microbial communities (Chomel et al., 2016). Secondary metabolites, which can act as chemical defenses against herbivory, can also deter detritivores (Asplund et al., 2013). Coq et al. (2010) found that condensed tannins were negatively correlated with decomposer fauna abundance, while fauna abundance correlated positively with mass loss, indicating that secondary metabolites could have a negative indirect effect on decomposition. Decomposer suppression through secondary metabolites (or other mechanisms, including the presence of endophytes [Lemons et al., 2005]) also slows the process of mineralization (Hättenschwiler et al., 2011).

To date, most research on HFA has occurred in natural ecosystems, with very little investigation of HFA in agricultural systems. Agricultural systems are typified by intensive management, which frequently can include moving biomass in and out of systems (i.e. imports in the form of cover crops and fertilizers, exports of cleared or pruned vegetation). Further, crops are often planted outside their naturally occurring ranges, which can lead to mismatches between the arthropod decomposer communities and the crop detritus. Since HFA is expected to increase with environmental dissimilarity, it may be more important in agricultural settings where the crop is non-native. The only study of HFA in agricultural systems, to our knowledge, focused on decomposition of manure (Rashid et al., 2013). The study found an increase in nitrogen recovery of 14–53%, depending on the application rates, which corresponded with the decomposition of the manure (Rashid et al., 2013). While the literature on HFA in crop systems is lacking, it is reasonable to assume management decisions, like crop rotation and input management, could influence the outcome and relative role of HFA in agricultural settings. Micro-arthropods can distinguish between quality differences in detritus that result from farm management choices, as demonstrated through feeding preference tests of isopods in cork-oak agroforestry systems (Reis et al., 2018). Additionally, Barel et al. (2019) found that material characteristics as well as rotational history affected decomposition of cover crop residues underscoring additional pathways by which farm management could influence decomposition.

Here we test for HFA in leaf litter decomposition in a coffee agroforestry system. Coffee agroforestry systems provide a compelling system in which to study HFA. They combine elements of both intensive agricultural systems and forested systems, and as in all agricultural systems, a variety of farm management decisions could influence the magnitude of HFA. For example, a range of management decisions can alter the ways in which plant material enters the detrital pool; clearing can reduce herbaceous cover; canopy cover is managed; coffee plants are pruned and fertilized. Finally, two species of coffee (*Coffea arabica* and *Coffea robusta*), differing in physical and chemical properties, including secondary metabolites like caffeine, are commonly cultivated in proximity, including in our study site.

In the study reported here, we compared the decomposition of *C. arabica* and *C. robusta* with a reciprocal transfer experiment where leaves were placed in their home environment and in two away environments: 1) the environment of the other species (hereafter congeneric-away) and 2) a forested environment, where coffee is not cultivated (hereafter forested-away). We used both tethered lines and litterbags to assess HFA because, in combination, these methods allow us assess decomposition at short and longer timescale, and because each method has different bias, with tethered lines overestimating decomposition and litterbags underestimating decomposition (Robertson and Paul, 2000, Karberg et al., 2008). We hypothesized that:

a) Home-field advantage will allow both species to decompose more quickly in the home environment than the congeneric-away environment, but *C. arabica* will decompose quicker than *C. robusta*, irrespective of HFA.
b) Decomposition will be slower for both species in the forested-away environment than in the congeneric-away environment, due to relative similarity between the agricultural environments.

2. Methods

2.1. Study system and study site

Two species of coffee are cultivated for commercial sale. *Coffea robusta* makes up about 30% of global production and is typically relegated to lower altitudes and lower quality lands (Bunn et al., 2015). *Coffea arabica* is valued more highly than *C. robusta* and requires cooler temperatures, and thus higher elevations. While the two species are similar in many respects, *C. arabica* is smaller in stature, with smaller and thinner leaves. The leaf chemistry of *C. arabica* leaves differs from that of *C. robusta* in two important ways: 1) there is less lignin and other structural compounds, and 2) there are lower levels of the secondary defense compound caffeine. *Coffea arabica* has a higher carbon to nitrogen ratio compared to *C. robusta* (Vega et al., 2020). Caffeine, the primary defensive compound in coffee, is a nitrogenous alkaloid, known to deter generalist herbivores (Nathanson, 1984; Hollingsworth et al., 2002). *Coffea arabica* leaves are approximately 1% caffeine by dry weight, where *C. robusta* leaves are closer to 2% (Ashihara and Suzuki, 2004). This difference in caffeine has potentially important corollaries for nitrogen use and demand since caffeine is approximately 29% N by molecular weight (Vega et al., 2020). The difference in chemistries between *Coffea* species could push decomposition rates in either direction. It could be that higher-caffeine leaves could be preferred by decomposers due to the nitrogen present (caffeine being nitrogen-based), leading to faster decomposition of *C. robusta* compared to the lower caffeine *C. arabica* leaves. Alternatively, defensive compounds that are toxic to herbivores, as caffeine can be, may also negatively affect decomposers, resulting in avoidance of higher caffeine leaves and slower decomposition rates of *C. robusta*. Interspecific differences in nutrient quantity may confound or exacerbate the effects of the defensive compounds, irrespective of HFA.

This study was conducted at Finca Irlanda, a 300 ha organic shaded coffee farm in the Soconusco region of Chiapas, Mexico. The farm ranges from 900 to 1200 m a.s.l. and experiences mean annual rainfall of approximately 4500 mm (Li et al., 2016). The region has a distinct rainy season from May through October and a dry season from November through April.

Finca Irlanda is a certified organic farm. Herbaceous vegetation in the understory is controlled by periodic manual cutting with machetes. The canopy layer includes a diverse range of species, but is dominated by species in the *Inga* genus (Perfecto and Vandermeer, 2002). Canopy trees are pruned periodically and the clippings are generally left in the field. The altitudinal variation at Finca Irlanda permits both *C. arabica* and *C. robusta* to be grown; most of the farm is dedicated to *C. arabica* production, with lower elevations dedicated to *C. robusta* and some cacao. The distribution of the two species within the farm has been approximately static for $\geq$10 years. The adjacent forest reserve has steep topography, which is part of reason why it is not in cultivation. The area is approximately 15 ha and contains some large trees (>25 m) and patches of secondary forest (Moorhead et al., 2010; Briggs et al., 2013).

2.2. Sampling methods

We used two methods to assess decomposition: tethered lines and litterbags. Each method is associated with distinct, opposing methodological issues (Vitousek et al., 1994; Robertson and Paul, 2000; Karberg et al., 2008; Kurz-Besson et al., 2005). Tethered lines are entirely

exposed, so that a piece of leaf material is counted as "lost" or "decomposed" once it is separated from the part of the leaf tied to the fishing line. This approach can therefore greatly overestimate decomposition. On the other hand, estimates of decomposition from litterbags face the opposite issue. Pieces of leaf tissue are retained until they are smaller than the bag mesh size. Additionally, only a partial community of decomposers (species smaller than the litterbag mesh openings) has access to the decomposing material. Thus, relative rates of decay cannot be meaningfully compared between methods, but both are informative in comparing across treatments using the same method.

2.3. Tethered line design

We collected and dried recently senesced *C. arabica* and *C. robusta* leaves. Using four bunches of leaves – two bunches of each species – we created tethered lines. Each line consisted of a 2 meter-long piece of fishing line, with four leaf bunches attached to the line and separated by 40 cm from each other by their petioles. Six lines, arranged like spokes of a wheel, combined to make one experimental unit (Fig. 1). Bunches were weighed so that the starting dry mass was known.

We selected 13 sites: five in plots where *C. arabica* is grown, five in plots where *C. robusta* is grown and three sites in a forested area where coffee is not grown. This design allowed us to assess the decomposition rate of both species in areas where they are typically grown (home environment), in areas where the other species is grown (congeneric-away environment), and in a forested area where neither species of coffee is cultivated (forested-away environment). The forested area was included to provide a non-agricultural point of comparison. Selected sites were relatively flat and away from areas of high human activity. We assessed canopy cover at each site using the iPhone application "CanopyApp" (version 1.0.2, University of New Hampshire).

At each site, one wheel was placed on the existing leaf litter. All wheels were set out within a week of each other in June 2016, during the rainy season. Each week of 6 consecutive weeks, one line was collected from every wheel. Collected lines were dried in at 50 deg. C to a constant weight and weighed. We used mass loss as a proxy for decomposition and saved samples for carbon and nitrogen analysis.

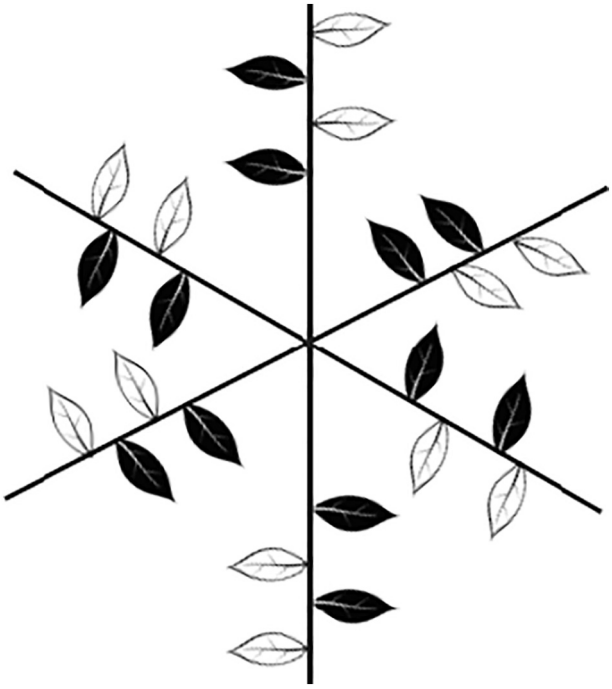

Fig. 1. Overhead schematic of tethered line design. Six lines with two alternating bunches of four *C. arabica* leaves (black) and four *C. robusta* leaves (white) were arranged into a wheel.

2.4. Litterbag design

We repeated the same reciprocal design from the tethered lines with litterbags. We used 5 mm fiberglass mesh for the litterbags to allow micro-arthropods to access the litter. There were a total of 225 litterbags; one third of the litterbags contained *C. arabica* leaves, and another third contained *C. robusta* leaves. The final third of the litterbags had a plastic fabric mimicking the starting density of leaves, to monitor sediment accumulation in the litterbags. As with the tethered line design, we collected and dried recently senesced leaves. We screened leaves for significant blemishes (discoloring, tears in the leaves, heavy herbivory) before homogenizing acceptable leaves into one batch and sewing approximately 50 g of leaves in each of the litterbags.

We selected fifteen sites, with 5 in each of the following environments: *C. arabica* plots, *C. robusta* plots, and forested plots. Litterbags were placed on the litter surface in the field in July 2017, and a set of bags was collected after the following intervals: 1, 3, 6, 9, and 12 months. Upon re-collection, bags were dried to a constant weight in a 50 deg. C oven and re-weighed.

2.5. C:N analysis

We ground dried samples from the tethered line experiment using a Krups brand coffee grinder at its finest setting. We analyzed a subset of samples from each week of collection (thus, 6 time points). From the total ground sample, a representative sub-sample was analyzed for total C and total N using a LECO Trumac CN combustion analyzer (LECO Corporation, St. Joseph, MI). We used the total C and total N data to calculate the carbon to nitrogen ratio (C:N).

2.6. Statistical methods

For the tethered line experiment, the mass loss was averaged for each species, across both leaf bunches in each line. In a few cases where bunches were lost, only one data point was available for a line. We used the exponential decay equation ($N_t = N_0 * e^{-kt}$) to calculate the decay constant, k, as is standard in decomposition literature (Olson, 1963). While many equations have been used to look at the rate of decay, the simple exponential equation is among the most widely used and appropriate for our shorter time frames (Wider and Lang, 1982, though see Cornwell and Weedon, 2014). A higher k is indicative of faster decomposition.

All statistical analysis was done using the software R (version 3.6.2). We made linear mixed models using the "lmer" function in the "*lme4*" package (De Boeck et al., 2011) to further assess the effects of species and environment on the decay constant. With k as the dependent variable, we used species, environment, and the interaction between species and environment as potential predictors. If home-field advantage (HFA) was acting, we would expect an interaction between species and environment. Time is not included in the model because it is incorporated in k. We included wheel as a random variable because wheels were sampled at each sampling point, and thus, decay would be expected to correlate between samples at that site. Wheel was incorporated as a random intercept because, since theoretically no decay would have taken place at day 0, k has a theoretical intercept of 0. The same analysis was repeated for tethered line and litterbag data sets. In the litterbag analysis, days was used as the time variable and for the tethered line data weeks was used. This was done to avoid partial weeks in the litterbag study and to make the values comparable to the published literature.

The assumptions of independence and equal variance were met. However, assumption of normality was not met, even after log-transforming the data. The results of the log-transformed analyses were qualitatively the same as with the untransformed data. Violations

of normality primarily affect the residuals, which are not our focus here, and transformations without justification beyond a lack of normality has come under increasing scrutiny (Changyong et al., 2014; Mena et al., 2017). Given this and our sample size (Schmidt and Finan, 2018), we used un-transformed data for these analyses, despite the violation of the normality assumption.

We used post-hoc tests to generate contrasts that allowed us to make pairwise comparisons between the three environments. We calculated estimated marginal means, or least square means, using the "emmeans" function from the "*emmeans*" package in R (Lenth et al., 2018). With three environments, the linear mixed model output only provides 2 of the potential 3 environment comparisons with any given reference category. The model could be re-parameterized using different reference categories, but using contrasts provides comparisons between all levels of a factor, without the algebra of re-calculating intercepts. For both tethered line and litterbag models we used "emmeans" to calculate pairwise contrasts between environments. For the tethered line data we also calculated pairwise contrasts of environments, by species. This was not done for the litterbag data because it was not warranted based on the model results.

We built a linear mixed model to test for difference in the carbon to nitrogen (C:N) ratio in the tethered line samples. As with the decay constant analysis, we used the "lmer" function from the "*lme4*" package in R (De Boeck et al., 2011). The first run of the model included time, species, environment, and all of the two and three way interactions between the three main effects. We included wheel, nested with time, as a random variable to account for similarity between the repeated samples from each wheel. We used model selection to create a second model with time and environment, both of which were significant in the full model. Again, we used the "emmeans" function from the "*emmeans*" package in R to calculate the estimated marginal means for each of the three pairwise combinations of environments (Lenth et al., 2018).

The data from this study is archived at the Mendeley Digital Repository (DOI: 10.17632/rjmtmkvy6k.1).

3. Results

3.1. Tethered lines

Over six weeks, the decay constant, k, was lower in both the congeneric and forested-away environments, compared to the *C. arabica* environment (Fig. 2A). The decay constant for *C. robusta* varied less, but was also lower in the forested away environment (Fig. 2A). In areas where *C. arabica* is grown, the decay constant, k, was higher for *C. arabica* leaves than *C. robusta* leaves ($k_{CA} = 20.509 \pm 2.01$, $k_{CR} = 12.698 \pm 1.12$, $p < 0.005$, Table 1). In areas where *C. robusta* is grown, k was still higher for *C. arabica* ($k_A = 15.880 \pm 1.64$, $k_R = 13.935 \pm 1.49$), though the difference between the species decay constants was smaller.

In the forest, the rate of litter decay did not differ between species ($k_A = 8.673 \pm 1.99$, $k_R = 8.32 \pm 1.23$). Based on the pairwise

Table 1
Linear mixed model output for decay constant of tethered line samples (A), pairwise estimated marginal means contrasts for the pairwise combinations of locations (B), and contrasts for pairwise combinations of locations, separated by species (C). Pairwise contrasts for all main effects and interactions are provided in Table S1. *Coffea arabica* was the reference species and reference environment for the model (i.e. species estimates for *C. robusta* describe the difference between *C. arabica* and *C. robusta*). Bolded results are significant at the $p < 0.05$ level.

Predictors	Estimates	Std. error	*df*	*t*-Value	*P* value
A. Linear mixed model output					
(Intercept)	20.946	1.787	18.927	11.724	<0.005
Species	**−7.711**	**2.051**	**196.567**	**−3.759**	**0.000225**
Environment					
C. robusta	−5.091	2.624	30.343	−1.94	0.061731
Forest	**−12.273**	**3.067**	**12.642**	**−4.002**	**0.001589**
Species x environment					
C. robusta x *C. robusta*	5.498	3.026	197.91	1.817	0.07077
***C. robusta* x control**	**7.363**	**3.433**	**195.540**	**2.145**	**0.033226**
B. Pairwise contrasts for environments					
***C. arabica* – forest**	**8.59**	**2.54**	**7.08**	**3.389**	**0.0271**
C. arabica – *C. robusta*	2.34	2.07	12.76	1.132	0.512
Forest - *C. robusta*	−6.25	2.56	7.65	−2.441	0.0946
C. Pairwise contrasts for environment, by species					
Species: *C. arabica*					
***C. arabica* – forest**	**12.273**	**3.08**	**15.5**	**3.985**	**0.003**
C. arabica – *C. robusta*	5.091	2.68	36.5	1.902	0.1526
Forest - *C. robusta*	−7.182	3.19	18.4	−2.25	0.089
Species: *C. robusta*					
C. arabica – forest	4.910	3.04	14.7	1.613	0.2715
C. arabica – *C. robusta*	−0.407	2.45	24.5	−0.166	0.9849
Forest - *C. robusta*	−5.317	3.03	15.1	−1.754	0.2183

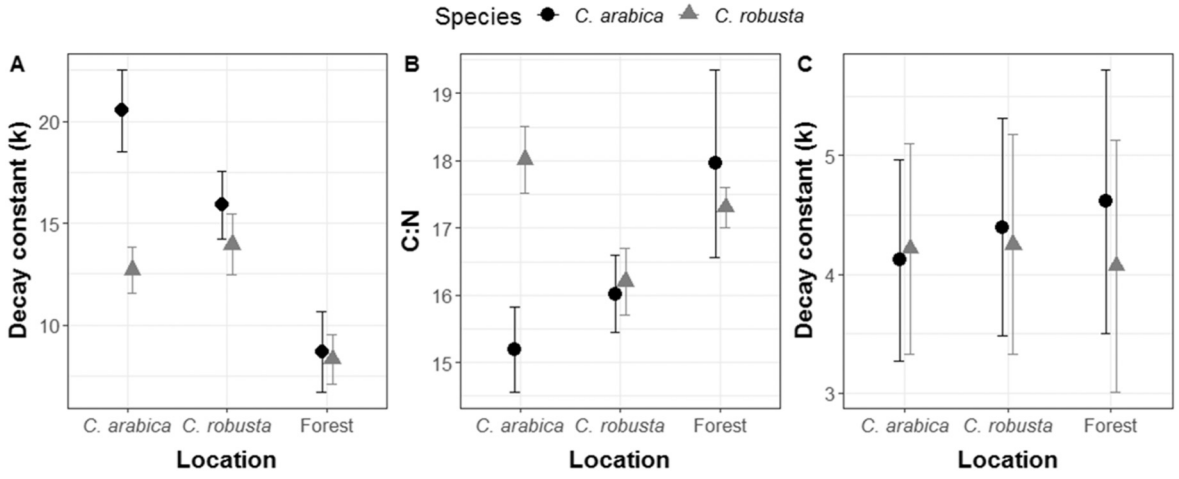

Fig. 2. Decay constant for tethered lines (A), the C:N ratio at week 6 (the end of the experiment) for tethered lines (B), and the decay constant for litterbags (C). Error bars represent standard error.

comparisons, the decay of litter for both species in the forest was significantly slower than in the *C. arabica* environment ($p = 0.0271$, Table 1B) and slower than in the *C. robusta* environment ($p = 0.0946$, Table 1B), though the forest and *C. robusta* environments were not significantly different. The decay of *C. arabica* in coffee environments is driving the difference between the coffee environments (*C. arabica* and *C. robusta*) compared to forest environment (Table 1C).

3.2. Carbon to nitrogen ratio

C:N ratios decreased over time, as would be expected with decay ($p < 0.005$, Table 2, see Table S2 for full model results). Litters decomposing in the forest environment had significantly higher C:N ratio compared to both *Coffea* spp. environments (*C. arabica* – forest, $p = 0.0117$, forest – *C. robusta*, $p = 0.0162$, Table 2B). However, the C:N ratio did not differ significantly between species ($p = 0.307$) or between environments ($p = 0.9821$).

At the end of the 6 week tethered line experiment, C:N ratios were higher for *C. robusta* litter in the *C. arabica* environment than they were for *C. arabica* litter ($C:N_{CR} = 18.0 \pm 0.49$, $C:N_{CA} = 15.2 \pm 0.64$), but did not differ between litter species in the *C. robusta* or forested environments (Fig. 2B).

3.3. Litterbags

Over the one year study period of the litterbag experiment, decomposition rates did not differ between species or between environments (Fig. 2C, Table 3). There was no significant interaction between species and environment (Table 3).

4. Discussion

This study provides one of the first accounts of HFA in agricultural landscapes and highlights the potential role of farm-level management decisions in altering nutrient cycling dynamics. Our study finds support for home-field advantage in litter decomposition over the span of weeks with the tethered line methodology, but these HFA effects did not persist for months in litterbags – nor was there any detectable HFA acting on shorter time scales with the litterbag methodology. Our experimental design provided two away environments for each species – one agricultural or congeneric-away and one non-agricultural forested-away environment. We found evidence for short-term HFA (up to one and a half months) acting between the home and congeneric-away environments, as demonstrated by the interactive effect of the species and environment on the decay constant for the tethered line experiment. Both *C. robusta* and *C. arabica* decomposed more quickly in their home environments compared to the forested away environment and *C. arabica* also decomposed more quickly in the congeneric away environment compared to the forested-away environment, which supports our second hypothesis.

Table 2
Linear mixed model output for carbon to nitrogen ratios from tethered line samples (A), and pairwise estimated marginal means contrasts for the pairwise combinations of locations (B). The full model, before variable selection, is provided in Table S2. *Coffea arabica* was the reference species and reference environment for the model (i.e. species estimates for *C. robusta* describe the difference between *C. arabica* and *C. robusta*). Bolded results are significant at the $p < 0.05$ level.

Predictors	Estimates	Std. error	*df*	*t*-Value	*P* value
A. Linear mixed model output					
(Intercept)	20.0102	0.40084	85.2111	49.920	<0.005
Time	−0.08585	0.01301	64.0475	−6.599	<0.005
Environment					
C. robusta	0.07957	0.41541	19.9047	0.192	0.85004
Forest	**1.55847**	**0.42893**	**14.7035**	**3.633**	**0.00252**
B. Pairwise contrasts for environments					
***C. arabica* – forest**	**−1.5585**	**0.456**	**13.2**	**−3.418**	**0.0117**
C. arabica – *C. robusta*	−0.0796	0.439	17.9	−0.181	0.9821
Forest - *C. robusta*	**1.4789**	**0.469**	**15.8**	**3.153**	**0.0162**

Table 3
Linear mixed model output for decay constant of litterbag material (A) and pairwise estimated marginal means contrasts for the pairwise combinations of locations (B). Pairwise contrasts for all main effects and interactions are provided in Table S3. *Coffea arabica* was the reference species and reference environment for the model (i.e. species estimates for *C. robusta* describe the difference between *C. arabica* and *C. robusta*).

Predictors	Estimates	Std. error	*df*	*t*-Value	*P* value
A. Linear mixed model output					
(Intercept)	4.12115	0.91886	134	4.485	<0.005
Species	0.09197	1.29947	134	0.071	0.944
Environment					
C. robusta	0.27724	1.31294	134	0.211	0.833
Forest	0.49054	1.35994	134	0.361	0.719
Species x environment					
C. robusta x *C. robusta*	−0.23990	1.85677	134	−0.129	0.897
C. robusta x control	−0.656	1.92325	134	−0.330	0.742
B. Pairwise contrasts for environments					
C. arabica – forest	−0.1728	0.963	12.4	−0.179	0.9824
C. arabica – *C. robusta*	−0.1573	0.929	10.9	−0.169	0.9843
Forest - *C. robusta*	0.0155	0.972	12.8	0.016	0.9999

The slower decomposition that we found in the forested-away environment could be partially due to the abiotic conditions of a forest e.g. increased canopy cover leads to less light and lower temperatures which may outweigh a possible increase in humidity. Similarly, the species initial differences in leaf nutrients and secondary chemistry (which we did not measure, but has been established in previous studies) likely contribute to the faster decomposition of *C. arabica* relative to *C. robusta* that we saw across environments. However, we found an interaction between species and environment for the tethered line, when looking at *k*, and a higher *k* for both species in their home environments, which is indicative of HFA.

The difference between environments in the tethered line study is driven primarily by differences in the *C. arabica* leaves between home and congeneric-away environments and the forest, as indicated by the pairwise contrasts, when environments are separated by species. While both species are decomposing more quickly in coffee environments, the magnitude of change between rates of decay in agricultural and forest environments is greater for *C. arabica*. There was no difference in the decay rate of C:N ratio for *C. robusta* between coffee environments. *Coffea arabica* has smaller, thinner leaves with less caffeine, than *C. robusta*, so the higher decay constants are not altogether surprising, particularly with the tethered line methodology where there is greater exposure to abiotic factors. However, if caffeine is an impediment to decomposers, we should expect *C. robusta* to benefit most from a specialized home community of decomposers. It may also be that less biodiversity and more disturbances in the agricultural environments prevent the expected development of specialized decomposer communities (Jangid et al., 2008). Our results suggest that the decomposer community in the forest may be highly specialized or less able (or perhaps less inclined, given the other litter types that may be available) to break down any quantity of caffeine, but we cannot disentangle the potential effects of the physical and chemical differences between the two *Coffea* spp., the magnitude of environmental differences, or the role of decomposer communities.

In the tethered line experiment, variation in C:N ratios supported the findings from the decay constant in that there was a significant difference between the two coffee environments and the forest environment. However, C:N ratios did not differ between home and congeneric-away

environments for either species. Ratios of carbon and nitrogen are traditionally used as a proxy for litter quality and an indicator of the decomposition stage of litter. Our C:N ratio results reflect the decomposition stage of the litter, though we know there are also initial species differences (Vega et al., 2020). Thus, the high *k* for *C. arabica* in the *C. arabica* environment is reflected in a low C:N ratio for *C. arabica* in a *C. arabica* environment. The C:N ratio could be lower for our treatments with highest decay rates if more stable or inaccessible forms of N are left behind over time as relative labile C is lost. Most studies of HFA have used *k* as a response variable, not C:N ratio. C:N ratios describe the quality of undecomposed litter, not the quantity of already decomposed materials (Bonanomi et al., 2013).

Our results suggest that HFA occurs on the scale of weeks, but does not play a significant role over a longer period of time. In the yearlong litterbag study we found no differences in the rate of decay between the home environment and congeneric-away or forested-away environments for either species. Other yearlong tropical litterbag studies have also failed to find evidence of HFA (Bachega et al., 2016); it might be harder to detect HFA on longer time scales in our study system, given the rapid rate of decay in tropical systems. However, we did not find evidence of HFA, even at the one-month collection of litterbags (see Table S4).

Our ability to detect HFA at the four-week time point in the tethered line experiment, but not the one-month collection of litterbag samples, may be due to the inherent biases in the respective methodologies. We know of few studies that use both tethered line and litterbag examples (for exceptions see Woods and Raison, 1983, Lawrence and Wise, 2004). In contrast to our results, one such study in a sub-alpine forest reported similar decay rates between tethered lines and litterbags (Woods and Raison, 1983). At first glance, it is perplexing to have a higher proportion mass loss (and, thus, higher *k*) in a six-week experiment, compared to a yearlong experiment, but it is congruent with the respective methodological biases. We did not survey the decomposer community, so while we suspect the biotic community was important in driving different rates of decomposition between treatments, further study would be needed to see how both microbial and invertebrate decomposer communities differ between environments and on different species. We hypothesize that microbes are more likely to be highly specialized than larger decomposers, but perhaps specialized decomposers with larger body sizes were excluded from the litterbags. Our study used 5 mm mesh, which allows access to most micro- and mesofauna. We know of one decomposer larger than 5 mm at our field site, a common millipede species, but small soil biota, which would have access to the litter in our bags, have been implicated as the drivers of HFA in grassland systems (Li et al., 2020), not larger decomposers. The two methods used offer different exposures to the largest decomposers, but also lead to disparities in abiotic conditions. The litter on the tethered lines is far more exposed to abiotic conditions compared to the litter in the litterbags, which may experience a different micro-climate than litter adjacent to the bags. The micro-climate in the litterbags is unlikely to have had a directional effect (that is, a reverse HFA effect), but could also have impeded our ability to detect HFA if HFA is happening in the early stages of decomposition and those early stages are elongated due to the litterbag design.

Our study did not seek to identify the mechanism behind the HFA operating in this system, and many potential mechanisms could be responsible for the observed patterns. Differences in vegetation quality and soil quality, and disparity in environments are often cited in the literature as determinants in predicting the strength of HFA (Veen et al., 2015; Palozzi and Lindo, 2018), but here we see evidence of HFA despite using two species of the same genus and similar, adjacent environments. This suggests high levels of decomposer specialization may be responsible, which is congruent with other research (Austin et al., 2014; Lin et al., 2019), though we did not explicitly examine the soil biota. Our study also lacks data on soil chemistry. We assume that soil parameters did not differ, except in differences that might result from different plants, because the environments were adjacent to one another, but future studies should incorporate chemical parameters into their analysis as well. While we do find evidence of HFA between home and congeneric-away environments, in some cases, decay rates were more similar in congeneric-away environments than in the forested-away environment, which highlights the role that environmental disparity, and potentially, microbial communities, play in driving HFA.

HFA could be important in agro-ecosystems, even though it appears to operate only on short time scales in this coffee agro-ecosystem. Given the rapid pace of decomposition in the tropics, differences in decomposition rates in the initial weeks could have a relatively large impact on plants if the pulse is synchronized with plant demand (Lodge et al., 1994). Moreover, work with agricultural cover crops finds that even a short-term pulse of nutrient availability can increase yields in temperate agricultural systems (Blesh, 2018). Our results also suggest that farm-level management decisions could play a role in determining the magnitude of HFA. Increasing homogeneity in agro-ecosystems could lead to accelerated decomposition and potentially increased nutrient availability or tighter cycling if the nutrients are bioavailable and stay in the agro-ecosystem. However, there are many other, often negative, consequences of homogenization that could reduce yields and decrease the resiliency of agro-ecosystems (Jha et al., 2014). These negative consequences of homogenization are unlikely to be outweighed by the accelerated decomposition possible with stronger HFA.

Additional research into HFA in agricultural systems is warranted to ascertain how exactly management decisions could drive HFA and if and how HFA is meaningful in terms of nutrient availability to crops in an agricultural context. This is among the first reports of home-field advantage in agricultural systems and could have important implications for nutrient cycling in tropical agricultural settings, even if HFA could not be detected over a longer time frame.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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