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RESEARCH ARTICLE

Evaluating the roles of microbial functional breadth and home-field advantage in leaf litter decomposition

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Abstract

1. Soil biota are increasingly recognized as a primary control on litter decomposition at both local and regional scales, but the precise mechanisms by which biota influence litter decomposition have yet to be identified.
2. There are multiple hypothesized mechanisms by which biotic communities may influence litter decomposition—for example, decomposer communities may be specially adapted to local litter inputs and therefore decompose litter from their home ecosystem at elevated rates. This mechanism is known as the home-field advantage (HFA) hypothesis. Alternatively, litter decomposition rates may simply depend upon the range of metabolic functions present within a decomposer community. This mechanism is known as the functional breadth (FB) hypothesis. However, the relative importance of HFA and FB in litter decomposition is unknown, as are the microbial community drivers of HFA and FB. Potential relationships/trade-offs between microbial HFA and FB are also unknown.
3. To investigate the roles of HFA and FB in litter decomposition, we collected litter and soil from six different ecosystems across the continental US and conducted a full factorial litter × soil inoculum experiment. We measured litter decomposition (i.e. cumulative CO_2-C respired) over 150 days and used an analytical model to calculate the HFA and FB of each microbial decomposer community.
4. Our results indicated clear functional differences among decomposer communities, that is, litter sources were decomposed differently by different decomposer communities. These differences were primarily due to differences in FB between different communities, while HFA effects were less evident.
5. We observed a positive relationship between HFA and the disturbance-sensitive bacterial phylum Verruomicrobia, suggesting that HFA may be an important mechanism in undisturbed environments. We also observed a negative relationship between bacterial r versus K strategists and FB, suggesting an important link between microbial life-history strategies and litter decomposition functions.
6. Microbial FB and HFA exhibited a strong unimodal relationship, where high HFA was observed at intermediate FB values, while low HFA was associated with

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both low and high FB. This suggests that adaptation of decomposers to local plant inputs (i.e. high HFA) constrains FB, which requires broad rather than specialized functionality. Furthermore, this relationship suggests that HFA effects will not be apparent when communities exhibit high FB and therefore decompose all litters well and also when FB is low and communities decompose all litters poorly. Overall, our study provides new insights into the mechanisms by which microbial communities influence the decomposition of leaf litter.

KEYWORDS
carbon, decomposition, ecosystem, microbial community, soil, soil organic matter

1 | INTRODUCTION

Leaf litter decomposition is a fundamental ecosystem process that influences carbon (C), nutrient and energy cycling worldwide. The dominant conceptual model of litter decomposition includes three primary controls on decomposition rates: climate, litter quality and decomposer organisms (Bradford et al., 2016). Historically, these controls have been thought to act hierarchically, with climate and litter quality dominating decomposition at broader spatial scales, and decomposer organisms having smaller, strictly local-scale influences (Berg et al., 1993; Cornwell et al., 2008; Meentemeyer, 1978). However, recent work has cast doubt on this traditional hierarchical model, showing that biota are the primary controls on decomposition at both local and regional scales when data are disaggregated and local-scale variation is explicitly considered (Bradford et al., 2014, 2017). Indeed, explicitly considering biotic (e.g. microbial) processes has been shown to improve projections of global C dynamics by earth system models (Wieder et al., 2013). Overall, these findings highlight the need for improved understanding of the mechanisms by which decomposer organisms exert influence on leaf litter decomposition.

The biotic agents of decomposition include animals (e.g. soil invertebrates) and micro-organisms (e.g. prokaryotes and fungi), which break down non-living organic matter into simpler constituents to obtain energy and build/maintain their own biomass (Swift et al., 1979). Several aspects of these decomposer communities can influence decomposition rates, including diversity and species composition of decomposer organisms (Bardgett & van der Putten, 2014; Handa et al., 2014). A commonly invoked mechanism by which biota influence litter decomposition rates is adaptation of decomposer communities to local plant litter inputs, that is, the 'home-field advantage' (HFA) hypothesis. The HFA hypothesis is most commonly applied to litter transplant studies, where leaf litter is often decomposed more rapidly by soil communities with a historical association with that litter (i.e. 'home' communities) than by communities without a historical association with that litter (i.e. 'away' communities) (Keiser et al., 2014). HFA, therefore, may represent a promising framework that links decomposer communities to the key decomposition processes that they facilitate.

HFA effects have been identified across multiple ecosystem types in both faunal and microbial communities (e.g. Ayres et al., 2009; Gholz et al., 2000; Milcu & Manning, 2011; Strickland et al., 2009). A recent meta-analysis identified a positive global HFA effect on litter decomposition, with 7.5% faster decomposition of litters on their 'home' soils (Veen et al., 2015). HFA effects are often particularly apparent with recalcitrant litter sources, as specialized metabolic processes are necessary for the breakdown of lignin and other complex compounds (e.g. Ayres et al., 2009; Milcu & Manning, 2011; Wang, Gossart, et al., 2020). However, in many cases, no HFA or even negative HFA effects are observed (e.g. Bachega et al., 2016; Gießelmann et al., 2011; Luai et al., 2019; St. John et al., 2011; Wang, Li, et al., 2020). This variation in the presence and/or strength of HFA effects has been attributed to several factors, including the degree of dissimilarity in 'home' and 'away' plant communities (Veen et al., 2015), litter lability versus recalcitrance (Ayres et al., 2009), substrate–matrix interactions (Freschet et al., 2012), plant phenology (Pearse et al., 2014) and plant–decomposer interactions (Austin et al., 2014). Regardless, it has become clear that HFA alone cannot account for the full range of biotic controls over leaf litter decomposition.

An alternative mechanism by which biota may influence decomposition rates is through decomposer community functional breadth (FB). The FB hypothesis states that the ability of a community to decompose litters with varying chemical and physical properties will depend upon the range of metabolic functions present within the organisms that make up that community (Keiser et al., 2011, 2014). Like HFA, FB has been associated with recalcitrant litter sources, which require a broad suite of metabolic functions to decompose (van der Heijden et al., 2008). In contrast, communities from copiotrophic environments (i.e. high nutrients and/or labile litter) are hypothesized to be functionally narrow and should therefore decompose recalcitrant litters much more slowly. Because of the associations of HFA and FB with litter quality, some studies have considered high FB to be an indicator of communities with high HFA (e.g. Palozzi & Lindo, 2018). However, other studies have provided evidence that HFA and FB are distinct mechanisms by which communities influence litter decomposition

(Fanin et al., 2016; Keiser et al., 2014). Furthermore, while HFA arises through specific litter species–decomposer community pairings, FB may arise through more general mechanisms, such as overall litter recalcitrance or diversity of plant inputs. Therefore, FB may represent a more broadly applicable framework for investigating biotic controls on decomposition. However, few studies have simultaneously evaluated the roles of both HFA and FB in litter decomposition and no studies to our knowledge have explicitly examined relationships between FB and HFA in decomposer communities.

The goal of this study was to evaluate the relationship between soil microbial HFA and FB and to explore potential microbial community drivers of HFA and FB. To accomplish this goal, we collected soil and litter samples from six different ecosystems across the continental United States and conducted a full factorial litter × soil inoculum microcosm experiment. We then measured CO_2 production by each microcosm over the course of 150 days and used an analytical model (Keiser et al., 2014) to simultaneously calculate microbial HFA and FB based on cumulative CO_2 respired. We hypothesized that local adaptation of microbial communities (i.e. high HFA) would constrain the development of high FB, which requires wide rather than specialized metabolic capacity. This constraint of HFA on FB, in turn, would result in a distinct nonlinear relationship between decomposer community HFA and FB.

2 | MATERIALS AND METHODS

2.1 | Site description and sampling methods

We collected soil and litter samples from six locations across the continental United States. The species include blue bunch wheatgrass (BW, *Pseudoroegneria spicata*) collected from the Hudson Biological Reserve at Smoot Hill, WA (46°49′N, 117°14′W), trembling aspen (TA, *Populus tremuloides*) from the University of Idaho's Arboretum, ID (46°43′N, 117°1′W), ponderosa pine (PP, *Pinus ponderosa*) from the University of Idaho's Agricultural Experiment Station, ID (46°55′N,116°49′W), rosebay rhododendron (RM, *Rhododendron maximum*) collected from Pandapas pond, Montgomery County, VA (37°17′N, 80°28′W), and tulip poplar (TP, *Liriodendron tulipifera*) and white pine (WP, *Pinus strobus*), both collected from Kentland farm, Montgomery County, VA (37°11′N, 80°34′W). All samples were collected from sites where the named plant species created the dominant leaf litter substrate, although the tulip poplar site was also a mixed hardwood forest stand. Trembling aspen, ponderosa pine, rhododendron, tulip poplar and white pine litters were collected as recent litterfall and blue bunch wheatgrass litter was collected as standing-dead material. In the laboratory, litter samples were sorted to remove unwanted additions (seed, fruits, etc.), air-dried and milled (4 mm). Litter was sterilized in an autoclave (121°C, 30 min). Based on C:N and lignin:N ratios, the selected litter species vary in chemical complexity from relatively labile to more recalcitrant (see Appendix S1, Table S1).

Soils to serve as microbial inocula were collected as 5–6 soil cores (5 cm depth) at each site with a soil auger 8 cm in diameter. Soil samples were passed through a 4-mm sieve, homogenized and then stored at 4°C. Each microbial inoculum derived from each soil is named after the dominant plant species present at the site of collection, the same as the litter substrates. All samples were collected under USDA permit number P330-20-00092.

2.2 | Initial litter and soil properties

Prior to our microcosm experiment, we determined initial litter quality (i.e. chemical properties) for all litter types. We analysed total C and N of each litter using an ECS 4010 Nitrogen/Protein Analyzer (Costech). Lignin content was determined by DairyOne Laboratories through their forage laboratory (Ithaca, NY, USA) using standard wet chemistry procedures (Ibáñez & Bauer, 2014). These data are provided in Table S1. For all soil samples serving as microbial inocula, we determined gravimetric water content (GVM) and water-holding capacity (WHC). Both GVM and WHC (after wetting to field capacity) were determined by drying soil at 105°C for 24 hr.

2.3 | Initial microbial inoculum characteristics

Bacterial and fungal community composition of the initial soil inocula was determined via amplicon sequencing of the 16S rDNA region (bacteria) and the ITS1/ITS2 region (fungi; see Appendix S1 for additional details). We then used the resulting sequence data to determine several bacterial and fungal community metrics, including Shannon diversity, community composition (i.e. PCoA axis 1) and phylum- and class-level taxonomy for bacteria and fungi, respectively (see Appendix S1). We also used the bacterial phylum-level taxonomy to calculate putative r:K ratios of bacterial taxa for each sample, where r:K is the ratio of the relative abundances of putative r-selected bacterial phyla (Proteobacteria + Bacteroidetes) to the relative abundances of putative K-selected bacterial phyla (Acidobacteria + Verrucomicrobia) (e.g. Osburn et al., 2021; Zhou et al., 2018). To determine active microbial biomass, we measured substrate-induced respiration (SIR) using a static incubation technique (Bradford et al., 2008). Then, to determine community metabolic function, we measured catabolic responses to five different C substrates (glucose, oxalic acid, glycine, cellulose and chitin) using a modified substrate-induced respiration method (Degens & Harris, 1997). As an index of microbial functional diversity, we used the microbial catabolic responses to calculate catabolic evenness for each inoculum using the Simpson index (Degens et al., 2001).

2.4 | Microcosm experiment

To determine the role of microbial HFA and FB in leaf litter decomposition, we conducted a full factorial litter × inoculum microcosm

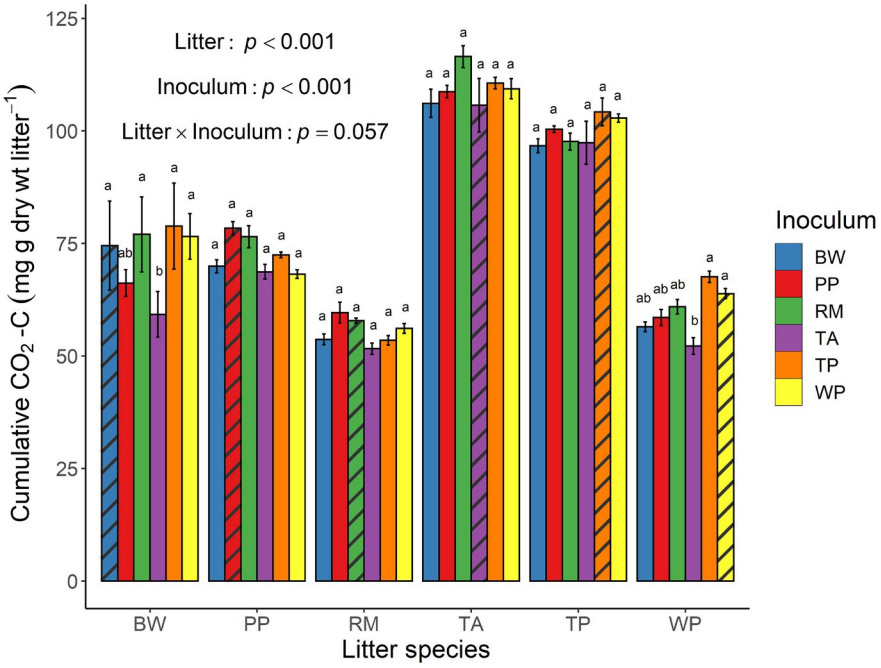

FIGURE 1 Cumulative CO_2 production from the full factorial microcosm experiment. Each bar represents a different inoculum as it decomposes each type of litter as shown in groups along the *x*-axis (blue bunch wheatgrass (BW), trembling aspen (TA), ponderosa pine (PP), rhododendron (RM), tulip poplar (TP) and white pine (WP)). Values are means while error bars represent 1 *SE*. *p* values for each factor are from a generalized linear model. Different letters represent significantly different cumulative respiration between inocula within each litter (Tukey's HSD, $p < 0.05$). Bars displaying an inoculum that share a historical association with the litter are patterned

experiment and measured each litter's decomposition in the presence of each microbial inoculum for 150 days. Six litter species were crossed with six microbial inocula with five replicates each, a total of 180 experimental units. We placed the experimental units in 50 ml centrifuge tubes, where 1g of sterilized litter substrate was inoculated with 0.25 g of dry mass equivalent soil for the inoculum source. Litter and soil were mixed by vortexing. We maintained the mixture at 65% WHC and 20°C to facilitate microbial activity during the 150-day incubation. We measured respiration in all microcosms on days 2, 3, 7, 10, 14, 17, 22, 24, 28, 35, 46, 51, 57, 64, 72, 80, 86, 93, 101, 107, 122, 136 and 150, using a static incubation technique. First, all microcosms were capped and flushed with CO_2-free air. Then, after a 24-hr incubation period, headspace CO_2 of each microcosm was measured using an infrared gas analyzer (IRGA; Model LI-7000, Li-Cor Biosciences). Total litter decomposition, that is, cumulative CO_2-C respired, was calculated by integrating under CO_2 evolution time-series curves.

2.5 | Data analyses

All statistical analyses were performed in R (R Core Development Team, 2019). We determined effects of litter, inoculum source and litter × inoculum interactions on cumulative CO_2 production using a generalized linear model ('glm' function, gamma distribution, log-link function), as the residuals of our initial linear model were not normally distributed (Shapiro–Wilk $p < 0.05$). The cumulative CO_2 data were then used as the input for the model described by Keiser et al. (2014) to calculate microbial HFA and FB. This model uses a least-squares regression approach to simultaneously model both HFA and FB, which are represented by parameter estimates in the model. The model is based on differences in CO_2 production by an inoculum (compared with the other inocula) on its 'home' litter versus 'away' litters, expressed relative to the number of different inocula and their collective HFA. The model also calculates the overall decomposition 'ability' of each soil microbial inoculum (i.e. FB), as well as the 'ability' of each litter to be decomposed. This 'litter ability' is known as the quality index (QI) for each litter, that is, the quality of each litter as perceived by an 'average' microbial community. The model states that carbon mineralization (Y_i) is equal to QI (i.e. 'litter ability', β_l) plus FB (i.e. 'soil inoculum ability', γ_s) plus HFA (η_h):

$$Y_i = \alpha + \sum_{l=1}^{N} \beta_l \, \text{Litter}_{l_i} + \sum_{s=1}^{M} \gamma_s \, \text{Soil}_{s_i} + \sum_{h=1}^{k} \eta_h \, \text{Home}_{h_i} + \varepsilon_i,$$

Y_i is the carbon mineralization for observation *i*, β_l is the QI of litter species *l* (from species 1 to *N*), γ_s is the FB of the soil inoculum community *s* (from community 1 to *M*), η_h is the HFA of *h* (from home combinations 1 to *K*) and $\text{Home}_h = \text{Litter}_l \times \text{Soil}_s$ when *l* and *s* are home-field pairings. The parameters to be estimated are β_l, γ_s and η_h, which represent QI, FB and HFA, respectively. The intercept term is defined by α and represents the average carbon mineralization rate for all observations in the dataset after controlling for litter, soil inoculum and home-field pairings. Negative parameter estimates indicate lower litter decomposition than the average rate observed across all samples. The error term is defined by ε. The model not only provides estimates of HFA, FB and QI for each litter/inoculum, but also provides a statistical test for the presence/absence of HFA, FB and QI for each litter/inoculum.

We determined overall effects of litter/inoculum on HFA, FB and QI using linear models and verified normality of residuals of each model using Shapiro–Wilk tests. Pairwise comparisons were performed using Tukey's HSD. We analysed the relationship between HFA and FB using a polynomial regression model: HFA ~ FB + FB^2,

due to the observed nonlinear relationship between HFA and FB. Finally, we used Pearson correlation to identify relationships between microbial community characteristics of each initial inoculum with the average HFA and FB values for each inoculum. For all statistical analyses, $p < 0.05$ was considered significant while $p < 0.1$ was considered marginally significant.

3 | RESULTS

3.1 | Litter decomposition dynamics

Cumulative CO_2 production was significantly affected by both litter source and inoculum source (both $p < 0.001$, Figure 1). The overall inoculum effect was driven by the trembling aspen (TA) inoculum having lower respiration than all other inocula except for blue bunch wheatgrass (BW) when averaged across all litters (Figure S1), and by the rhododendron (RM) and tulip poplar (TP) inocula having generally greater cumulative respiration than the other inocula when averaged across all litters (Figure S1). The overall litter effect was driven by generally greater decomposition of TA and TP litter when averaged across all inocula and by generally lower decomposition of RM and white pine (WP) litter when averaged across all inocula (Figure S2). We also identified a marginal litter × inoculum interaction ($p = 0.057$, Figure 1), indicating that litters were decomposed at different rates by different inoculum communities. Therefore, we performed pairwise comparisons between inocula within each litter. Pairwise comparisons revealed that the TA inoculum generally decomposed BW and WP litters at lower rates compared with other inocula while no differences were detected between inocula for the other litters (Figure 1).

3.2 | Microbial HFA and FB

The analytical model identified a marginal positive HFA for only one inoculum community, the PP inoculum ($p = 0.08$, Table S2). Furthermore, there was no significant overall effect of inoculum on HFA (Figure 2a), indicating no significant differences in the HFA of different inoculum communities in our study. In contrast, the analytical model identified two inocula as having significant positive FB (RM, TP) (Table S2), indicating significantly greater decomposition of an 'average' litter by these communities than expected by chance. The TA inoculum, on the other hand, had significant negative FB, indicating significantly lower decomposition of an average litter (Table S2). Furthermore, there was a significant overall effect of inoculum on FB (Figure 2b), indicating significant differences in the FB of different inoculum communities. Microbial HFA and FB exhibited a strong unimodal relationship, where FB explained ~90% of the variation in HFA (Figure 3). In general, low HFA was associated with both low and high FB, while high HFA was associated with intermediate values of FB (Figure 3). All litters exhibited significant positive or negative QI (Table S2), indicating significantly higher or

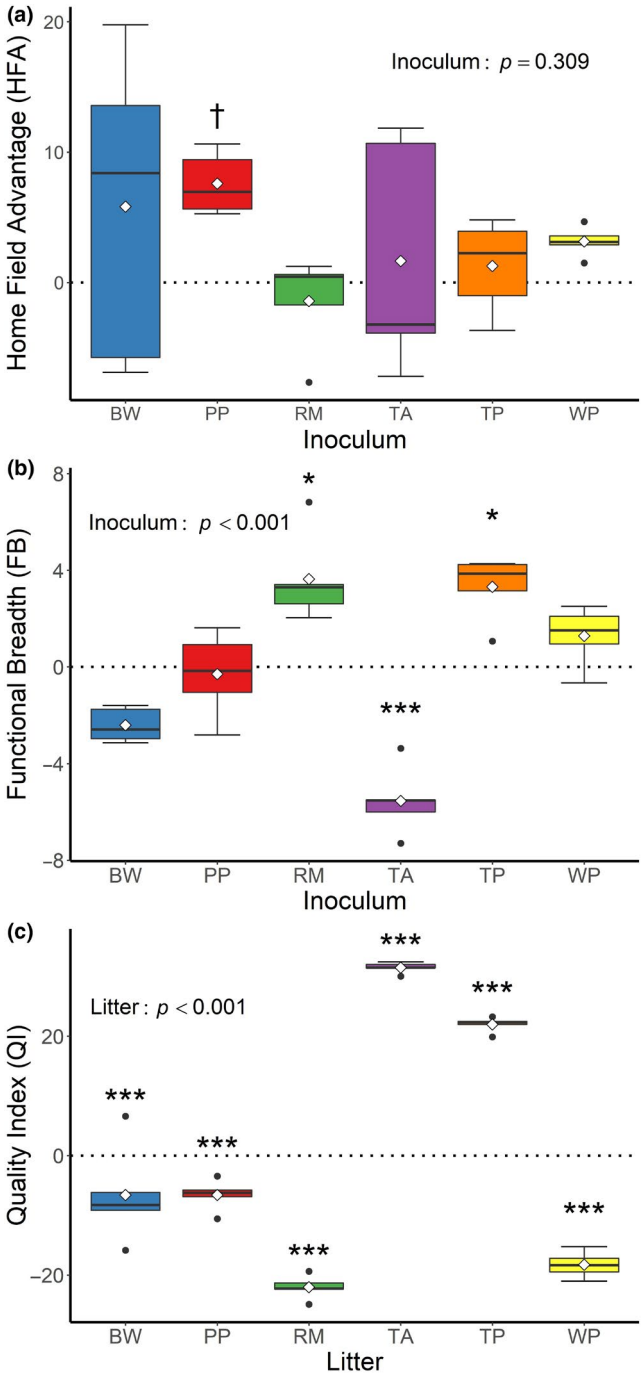

FIGURE 2 Boxplots show home-field advantage (a) and functional breadth (b) of each inoculum source: blue bunch wheatgrass (BW), trembling aspen (TA), ponderosa pine (PP), rhododendron (RM), tulip poplar (TP) and white pine (WP). (c) shows the quality index of each litter as perceived by an 'average' microbial community. Values are parameter estimates calculated using the quantitative model approach from Keiser et al. (2014). White diamonds represent means of each inoculum/litter. *p* values for the effect of inoculum are from linear models. Symbols indicate significant parameter estimates at the following significance levels: $^{\dagger}p < 0.1$, $^{*}p < 0.05$, $^{***}p < 0.001$

lower decomposition when exposed to an 'average' inoculum than expected by chance. There was a significant overall effect of litter on QI, indicating significant differences in QI among litters (Figure 2c).

3.3 | Relationships of HFA and FB to microbial community characteristics

Pearson correlation analysis revealed several relationships between microbial community characteristics of the starting inocula and the average FB/HFA of each inoculum. A full correlation matrix showing all relationships is provided in Figure S3. Notably, HFA was positively associated with active microbial biomass (i.e. SIR, Figure 4a) and the relative abundance of the bacterial phylum Verrucomicrobia (Figure 4c). FB, on the other hand, was positively associated with microbial catabolic diversity (i.e. catabolic evenness, Figure 4b). Finally, FB was negatively associated with r:K ratios of bacterial phyla, where putative r-selected (i.e. copiotrophic) phyla are represented by Proteobacteria and Bacteroidetes while putative K-selected (i.e. oligotrophic) phyla are represented by Acidobacteria and Verrucomicrobia (Figure 4d). HFA and FB were not correlated with bacterial diversity, overall bacterial community composition or any fungal community metrics (Figure S3).

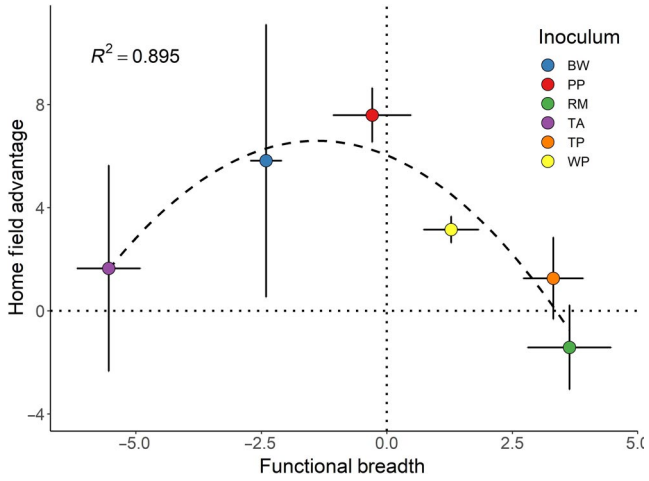

FIGURE 3 Relationship between the parameter estimates of home-field advantage (HFA) and functional breadth (FB). Each point represents the means of HFA and FB of each inoculum. Error bars are standard errors. BW is blue bunch wheatgrass, TA is trembling aspen, PP is ponderosa pine, RM is rhododendron, TP is tulip poplar and WP is white pine. The unimodal line of best fit and R^2 value shown are from a polynomial regression equation relating FB to HFA: HFA ~ $-0.81 \times FB + -0.29 \times FB^2 + 6.03$

4 | DISCUSSION

In our study, litter decomposition rates varied among litter sources and also among microbial decomposer communities. This finding illustrates clear differences in the decomposition functions of different microbial communities and adds to the growing body of literature recognizing biota as a primary control on decomposition rates (Bradford et al., 2014, 2017; Wieder et al., 2013). These differences in litter decomposition rates among different communities, that is, litter × inoculum interactions, have often been treated as evidence of the presence of an HFA effect (Keiser et al., 2014). However, we observed clear functional differences among communities even though HFA effects were essentially absent. Instead, the functional differences we observed in this study were primarily attributed to differences in FB among communities. In general, our results suggest that HFA may be an important mechanism in some contexts,

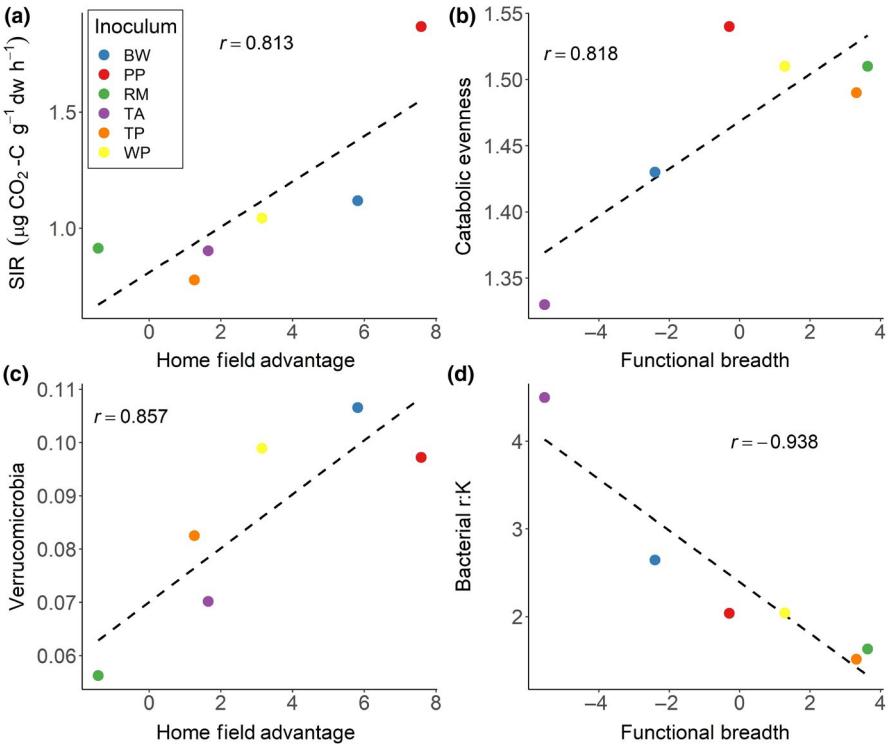

FIGURE 4 Scatterplots showing relationships between initial inoculum microbial community characteristics and the average HFA/FB of each inoculum: HFA and substrate-induced respiration (SIR; a), HFA and the relative abundances of Verrucomicrobia (c), FB and Catabolic Evenness (b) and FB and putative bacterial r:K ratios (d). Bacterial r:K represents a ratio of the relative abundances of putative r-selected bacterial phyla (Proteobacteria + Bacteroidetes) to the relative abundances of putative K-selected bacterial phyla (Acidobacteria + Verrucomicrobia). Values shown are Pearson correlation coefficients and all correlations are statistically significant at $p < 0.05$

but that FB is likely to be a more generally important mechanism by which communities influence litter decomposition.

Some prior studies have suggested that communities with high HFA will also exhibit high FB (e.g. Palozzi & Lindo, 2018). However, similar to other studies (Fanin et al., 2016; Keiser et al., 2014), we provide evidence that HFA and FB are independent or semi-independent mechanisms by which communities influence litter decomposition. Indeed, in our study, FB and HFA did not have a 1:1 relationship, but instead exhibited a strong unimodal relationship. High HFA was found at intermediate levels of FB, while low HFA was found at both low and high levels of FB. This low HFA at high levels of FB does not, however, imply that communities with high FB will decompose their 'home' litter poorly—it simply implies that communities with high FB will decompose all litters at high rates due to the high functional capacity of these communities, and therefore no HFA effect will be evident. Furthermore, the unimodal FB-HFA relationship is consistent with our hypothesis that local adaptation of decomposer communities to specific litter sources (i.e. high HFA) may constrain FB, as FB requires broad rather than specialized functionality. Finally, our results suggest a re-formulation of the traditional FB hypothesis, which states that copiotrophic communities with low FB will decompose recalcitrant litters poorly but implies that these low FB communities will still effectively decompose labile litters (Keiser et al., 2014). In contrast, our results show that low FB communities will also decompose labile litters poorly when compared with high FB communities, evidenced by the reduced decomposition of relatively labile litter sources (e.g. BW, TA) by our lowest FB community (TA) compared with other inoculum communities.

Multiple prior studies have associated both high HFA and high FB with recalcitrant litter sources (Ayres et al., 2009; Heijden et al., 2008; Milcu & Manning, 2011; Wang, Gossart, et al., 2020). These associations are based upon the notion that recalcitrant litter sources will require a wide range (i.e. high FB) of specialized metabolic functions (i.e. high HFA) compared with labile litters. However, we found little evidence of HFA in any of the inocula, including the inocula with a historical association with the most recalcitrant, lowest quality litters (i.e. lowest QI, *Rhododendron maximum* and *Pinus strobus*). Indeed, the only community with marginally positive HFA was associated with *Pinus ponderosa* litter, which had intermediate QI. In some cases, low HFA in communities associated with recalcitrant litters might be explained by those communities having high FB. For example, the *Rhododendron maximum* (RM) inoculum exhibited high FB and also developed in association with highly recalcitrant RM litter, potentially supporting the commonly invoked link between FB and litter recalcitrance. However, the *Liriodendron tulipifera* (TP) inoculum also exhibited significant positive FB even though TP litter was the second highest in quality. Overall, it is clear that litter quality alone does not fully account for differences in HFA and FB among decomposer communities. Other potential drivers of these functional metrics include specific soil properties that control decomposer diversity and community composition (e.g. soil pH) or diversity of plant litter inputs found at a particular site. Indeed, our TP community was sourced from a mixed forest stand, and this greater diversity of litter inputs may have promoted a greater range of metabolic functions and therefore greater FB in that community despite the high quality of TP litter.

Our results also cast light on potential microbial community drivers of HFA and FB. For example, microbial catabolic diversity was positively associated with high FB, which is expected given that a broad range of metabolic functions should be present in communities with high FB. In addition, putative bacterial r:K ratios were negatively associated with FB, that is, decreasing FB was associated with increased relative abundance of r-selected bacterial phyla. Bacterial life-history strategies have been previously linked to soil C dynamics (Fierer et al., 2007; Osburn et al., 2021) and it is not surprising that resource-acquiring K-selected (i.e. oligotrophic) taxa would be associated with high FB, as these taxa are known to invest in resources (e.g. extracellular enzymes) that allow them to degrade a broader range of chemically complex litter sources (Malik et al., 2020; Shao et al., 2021). It is also not surprising that high-yield r-selected (i.e. copiotrophic) taxa are associated with low FB, as these taxa are typically found in high-nutrient environments and typically maximize growth rates at the expense of resource acquisition strategies (Shao et al., 2021). Furthermore, we found that microbial HFA was positively associated with the relative abundance of the bacterial phylum Verrucomicrobia, a taxon that is often associated with undisturbed environments (Fierer et al., 2013; Osburn et al., 2019; Strickland et al., 2017). Indeed, undisturbed environments are precisely the context in which adaptation of decomposer communities to local litter inputs (i.e. high HFA) would be expected. These relationships between microbial communities and HFA/FB are suggestive of specific mechanisms that underlie differences in decomposer community functioning. Surprisingly, our analyses did not reveal relationships between fungal communities and decomposer functions. This may have been due to the relatively small number of starting inocula in our study ($n = 6$) and therefore these relationships should be more thoroughly investigated in future work.

The relationships between microbial communities and HFA/FB we observed also suggest important influences of ecosystem disturbance regime on the litter decomposition functions of soil communities. Specifically, the association of high HFA with disturbance-sensitive Verrucomicrobia suggests that HFA will be maximized in late stages of ecosystem succession, when plant communities are relatively stable (i.e. 'climax communities') and microbial adaptations to specific leaf litter inputs have had sufficient time to develop. In contrast, recently disturbed environments host disrupted decomposer communities that exhibit reduced diversity and altered species composition (Allison & Martiny, 2008; Fountain-Jones et al., 2017). These disrupted communities, in turn, may exhibit reduced functionality (i.e. low FB) and have had insufficient time to adapt to local plant inputs (i.e. low HFA). This could account for the co-occurrence of low FB and low HFA we observed. High FB, therefore, may develop in intermediate successional stages, which often feature the highest diversity of plant inputs (e.g. Fox, 1981) that support a diverse set of metabolic functions in decomposers. Indeed, the disturbance regimes of the specific sites we sampled

qualitatively support these conclusions. For example, the highest HFA community (PP) is from a relatively undisturbed site that has been forested for at least the past several decades, while the lowest FB community (TA) is from a highly disturbed, heavily visited site. The highest FB sites (TP and RM), on the other hand, are relatively young secondary forest sites established within the last few decades. Most of our sites are characterized by relatively recent disturbances, which might account for the general lack of HFA observed in our study. Regardless, these results suggest a generally increasing relationship of HFA with time since disturbance, and a more complex, potentially unimodal pattern for FB over time. Such temporal dynamics are poorly understood with regards to microbial ecosystem functions (Guerra et al., 2020), thus representing a key area for future research.

Similar to many previous studies (e.g. Berg et al., 1993; Cornwell et al., 2008; Meentemeyer, 1978), we also observed influences of litter quality on decomposition rates. QI varied among litter sources, indicating clear influences of litter chemistry on decomposition. Indeed, even the lowest FB decomposer community (TA) decomposed the highest QI TA and TP litters at much greater rates than it did the lowest QI litters (RM, WP), illustrating the importance of litter characteristics on decomposition rates. However, we also identified microbial decomposer functionality as an additional key control over decomposition rates. Specifically, we found that microbial FB, and not HFA, was the primary mechanism by which communities influenced decomposition rates, though HFA may be important in some environments and may act to constrain FB in some cases. Regardless, we show that biota represent a critical control over decomposition, possibly equal in importance to climate and litter quality, which have historically received precedence in conceptual models (Bradford et al., 2014, 2017). Indeed, decomposer organisms are not simply beholden to the effects of litter quality and climate—they exert independent influence over ecosystem processes such as litter decomposition, which must be considered when seeking to understand and predict changes in ecosystem function over space and time.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

P.J.H. and M.S.S. designed the study; P.J.H. conducted the study; J.M.L. prepared the samples for sequencing and performed sequence analyses; P.J.H. and S.G.M. collected soils and conducted soil analyses; P.J.H., M.S.S. and J.M.L. conducted the statistical analyses; E.D.O. performed the additional statistical analyses and wrote the manuscript. All authors contributed to editing the manuscript.

DATA AVAILABILITY STATEMENT

All data analysed in this manuscript can be found at the following Dryad Digital Repository https://doi.org/10.5061/dryad.7pvmcvdvm (Osburn et al., 2022).

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