

FORUM

Disentangling the mechanisms underlying functional differences among decomposer communities

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Summary

1. Home-field advantage (HFA) is a commonly used sports analogy, which has seen recent growth within the ecosystem ecology literature. It is most often invoked in litter transplant studies, where local adaptation (HFA) explains higher decomposition rates of leaf litter on ‘home’ soil communities.

2. In exploring the mechanisms driving functional differences among soil decomposer communities, a consistent quantitative framework is lacking.

3. We review methods for calculating HFA, propose a consolidated regression approach and demonstrate why HFA must be calculated along with a new ‘ability’ metric if we are to test definitively the competing hypotheses that soil decomposer communities are functionally equivalent versus dissimilar. We demonstrate that qualitative interpretations of HFA differ when the ability of a decomposer community is calculated simultaneously with HFA. For example, communities may differ in their ability to degrade litter in the absence of HFA, or apparent HFA may instead be caused by differing abilities, changing our ecological interpretation of the factors generating functional differences among decomposer communities.

4. *Synthesis:* We propose a single, statistical approach to help evaluate how and why soil decomposer communities differ in functional abilities. Our approach should help formalize mechanistic interpretations of why soil community composition commonly influences litter decomposition rates.

Key-words: functional equivalence, functional redundancy, functional similarity, home-field advantage, litter decomposition, local adaptation, plant–soil (below-ground) interactions

How a sports analogy became ecological theory

If the Boston Red Sox were playing the Baltimore Orioles at Fenway Park, they would have a greater chance of winning simply because the game is played at their home stadium as opposed to a neutral location. This ‘home-field advantage’ (HFA) derives from the familiarity of a home venue and crowd, providing an advantage for the home team (Vergin & Sosik 1999) independent of other factors such as talent and injuries (Courneya & Carron 1992). Those teams perform better at home than away is documented for American baseball and for many other sports (Snyder & Purdy 1985; Clarke & Norman 1995). The concept of performing better at ‘home’ than ‘away’ is also well-established within local adaptation literature (Clausen, Keck & Hiesey 1941; Kawecki & Ebert 2004; Blanquart *et al.* 2013) whereby local adaptation is

present if a local population has greater fitness in its own habitat (‘home’) than in other habitats (‘away’).

Gholz *et al.* (2000) were the first to apply the term HFA in ecosystem ecology, suggesting that local adaptation of decomposer communities explained the more rapid decomposition of a broadleaf litter in broadleaf forests than in coniferous forests. It is now well documented that leaf litter may decompose faster in its local environment than would be predicted from the two primary controls of decomposition rates: litter quality and climate (e.g. Hunt *et al.* 1988; Castanho & de Oliveira 2008; Vivanco & Austin 2008; Strickland *et al.* 2009a; Wallenstein *et al.* 2010; Schimel & Schaeffer 2012). Since HFA is suggestive of local adaptation, it indicates that soil decomposer communities differ functionally. Therefore, finding HFA identifies local adaptation as a potential mechanism driving functional differences among soil communities. Yet, finding faster decomposition rates at home than away does not discount the possibility that the functional differences among soil communities are explained not by HFA, but

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rather by differences in the overall ‘ability’ of soil communities to decompose litter. That is, a community may be adapted to decompose a ‘home’ litter or it may just simply be more able to decompose all litters (or a combination of both factors).

One way by which the ability of communities to degrade a litter might differ arises through the functional breadth hypothesis (FBH). This hypothesis suggests that decomposer communities from recalcitrant litter environments have a wider functional capacity, meaning they degrade litter species that vary widely in their chemical and physical properties at more similar rates than functionally narrow communities (Keiser *et al.* 2011). Functionally narrow communities arise in higher nutrient environments and degrade recalcitrant litters at much slower rates than more labile litters (van der Heijden, Bardgett & van Straalen 2008; Keiser *et al.* 2011). Differences in ability to degrade varying litter types are expected to be maintained under common garden environments (i.e. neutral grounds) and perhaps result from the proportion of microbial generalists versus specialists (Gravel *et al.* 2011). Ability is then separate from HFA because functional differences between soil decomposer communities through HFA rely on functional differences arising from the matching of a community with its home environment. Differences in ability might arise through mechanisms other than the FBH; for example, dispersal limitation might generate communities that differ functionally because of the taxa that happen to be present. What is clear, however, is that ability and HFA are two mechanisms that together can generate functional differences among soil decomposer communities. To date, their contributions to generating functional differences in soil communities have not been separately quantified. By quantifying both metrics, we can determine whether soil decomposer communities are functionally different and attribute a mechanism to those differences.

Identifying HFA and ability

Multiple experimental approaches are required to disentangle the contributions of the HFA and ability mechanisms and also more generally to identify whether soil decomposer communities differ functionally. Reciprocal litter transplants in the field are often used to examine how decomposition rates are affected by different soil communities. These transplant studies test for HFA, with higher litter mass loss at ‘home’ than ‘away’ indicative of local adaptation of the soil decomposer community to its ‘home’ litter species (Blanquart *et al.* 2013). Transplants also provide an indication of the ability of the soil communities, but environmental heterogeneity (e.g. in local moisture or temperature) might also explain some of the difference in decomposition rates attributed to ability. Heterogeneity in the field may even obscure differences in functioning, leading to the erroneous conclusion that soil communities are functionally equivalent. In contrast, abiotically controlled experiments may dampen the magnitude of differences among decomposer communities if adapted to local climatic conditions. However, these controlled experiments under common

abiotic conditions [e.g. common garden field or laboratory experiments using locally sourced soil for each decomposer community (sensu Keiser, Knoepp & Bradford 2013)] are still necessary to quantify unambiguously functional differences among soil communities (Reed & Martiny 2007; Allison & Martiny 2008).

Until recently, we did not have a metric by which to quantify HFA in litter decomposition studies. Ability still seems unquantified, and HFA is commonly inferred from a statistical interaction term in a two-way ANOVA or simply through visual assessments of litter decomposition rates (Gholz *et al.* 2000; Castanho & de Oliveira 2008; Vivanco & Austin 2008; Strickland *et al.* 2009a; Wallenstein *et al.* 2010; Wang, Zhong & He 2012). There are exceptions where HFA has been quantified through an analytical solution (Ayres *et al.* 2009a; Milcu & Manning 2011). This quantification is important because the soil \times litter interaction term in ANOVA, combined with a visual assessment, can fail to identify HFA of individual home pairs (Figs 1 and 2). For example, faster rates could result not from HFA but rather a greater ability of the community to decompose all litters, whether home or foreign (Freschet, Aerts & Cornelissen 2012).

The formal quantification of HFA in litter decomposition used to date was adapted by Ayres *et al.* (2009a) from the model presented by Clarke and Norman (1995), which calculates HFA for English soccer clubs. Clarke and Norman (1995) also developed a method for calculating ability, distinguishing a team’s ability from HFA, but this ability metric has not been used in quantifying the function of decomposer communities. By calculating ability, we can, however, unambiguously identify if soil communities differ in functioning and parse out the contributions of HFA and ability to these differences. We demonstrate this here and start with a brief review of the existing quantitative framework and ecological assumptions made when evaluating HFA in litter decomposition studies. We then present a novel quantitative method for calculating HFA that builds on prior models in the sports and ecological literature, by estimating HFA, ability and the statistical significance of both metrics. Our aim was to provide a consistent, quantitative estimate of HFA and ability of ecological communities that can be used to test for functional differences among soil decomposer communities. We focus on litter decomposition because reference to HFA is growing within the ecosystem ecology literature but seems best developed for litter studies (Prescott 2010) and also because the community composition of decomposer microbes commonly affects litter decomposition rates (Schimel & Schaeffer 2012). Within this context, the traditional view that soil decomposer communities are functionally equivalent is repeatedly being challenged and found wanting (e.g. Allison & Martiny 2008; Bradford & Fierer 2012; Schimel & Schaeffer 2012). The need for a formal, standardized metric for comparing litter decomposition rates between sites – that separates out different mechanisms (i.e. HFA from ability) contributing to contrasting decomposition rates – is an essential requirement for efficiently advancing theory relating soil community composition to function.

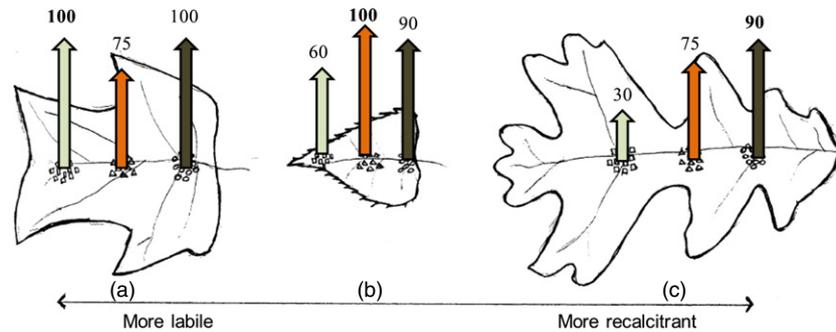


Fig. 1. An illustrated example depicting potential functional differences between soil decomposer communities generated by the mechanisms of home-field advantage (HFA) and/or functional breadth hypothesis (FBH). The arrows represent litter mass loss, with larger arrows representing faster rates. Arrow shading designates the soil decomposer community (light = a, medium = b and dark = c). The environment is the litter material they are decomposing. Litter chemical recalcitrance ranges from (a), the most labile, to (c), the most recalcitrant. Matching letters designate soil \times litter 'home' pairings, which is also designated with a bold numerical value. The HFA and ability rankings were determined using our regression approach (see Appendix S3 for SAS code and data file). Community (a) always does worse away from home. Consequently, community (a) has a high HFA, but low ability. Coming from a labile environment, it does not have the functional breadth to decompose the more recalcitrant litters at a rate equal to its home litter. Community (b) performs the best on its home litter environment and degrades the more labile and more recalcitrant litter environments at lesser, but equal rates. Community (b) has an intermediate HFA and ability. Community (c) comes from the most recalcitrant environment and perceives little difference between litter types giving it low HFA but high ability. On all three environments, the ability metric (FBH estimate) allows for understanding of the soil decomposer community that goes beyond HFA.

Existing metrics

In 1995, Clarke and Norman published a model that calculates HFA for an individual soccer club from the difference in goals scored at 'home' and 'away' (i.e. home- and away-goal differences: HGD and AGD) by that team, expressed relative to the number of teams in the league and their collective HFA. Then, knowing the HGD and HFA, one can calculate an individual team's ability, which is essentially its expected performance on neutral ground (explained in detail below). Ayres *et al.* (2009a) modified the analytical solution found in Clarke and Norman's sports model to derive HFA for litter decomposition in a 3-L species, reciprocal transplant study. We refer to the Clarke and Norman (1995) approach as the 'sports model' and the Ayres *et al.* (2009a) approach as the 'decomposition model'. The decomposition model by Ayres *et al.* (2009a) takes the difference, in mass loss, between litter 'teams' both home and away to estimate HFA. In this model, HFA is defined for a single litter as additional decomposition at home over that observed away. In the context of investigating what causes soil microbial communities to differ, the decomposition model by Ayres *et al.* (2009a) does not estimate ability and so does not disentangle HFA from other factors that might generate differences in functional ability (e.g. the presence of a decomposer species that degrades litter substrates rapidly regardless of the environment).

What constitutes a team?

We returned to the sports model by Clarke and Norman to incorporate ability into our analysis. Adapting this model to investigate litter decomposition creates conceptual issues about whether the leaf litter or the decomposer community should be treated as the team. In this section, we demonstrate that the HFA value is independent of whether the litter or decomposers are chosen, but ability is dependent on this

choice, and hence, so is our interpretation of the role that local adaptation plays in regulating ecosystem process rates.

Published, full data sets on reciprocal litter transplant studies with three or more litters and sites are not readily available. To evaluate the approaches of the sports model and the decomposition model, we therefore used data from one of our own studies (Strickland *et al.* 2009a). The experiment had three litters and soils, replicated eight times with a blocked design, and so for the purposes of this paper we considered that we had 3 'teams', but 24 independent observations for analysis. Using this Strickland *et al.* (2009a) data set, we calculated HFA using both the sports and decomposition models. As expected, all values were equivalent between the two methods. The analysis did, however, reveal conceptual issues with adapting the sports model to investigate litter decomposition, especially regarding what constitutes a team.

In both the sports and decomposition models, 'teams' play each other, and HFA results from the difference in goals or mass loss, respectively. Investigations of HFA in litter decomposition studies identify the litter species as the 'team' and site as the 'field'. This role assignment seems non-intuitive because the active players in litter decomposition are soil microbes and fauna, and they are associated with the site. Yet reciprocal litter transplant designs move litter, not decomposer communities, from a home site to the sites of all other litter species. One might argue that the designation of the litter as the team therefore appears logical because the litter travels to 'away grounds'; but regardless, the HFA metric is robust whether it is the decomposer community or litter that are considered the team (Table 1B vs. C, respectively). In contrast, for the ability metric, our understanding of ecological processes is influenced by whether we assign the team to the decomposer community or the litter (compare Table 1B vs. C and see next paragraph).

If we treat the litter as the team, then ability scores the relative quality of a litter species across all sites, where quality relates to how rapidly a litter is decomposed. Henceforth, we

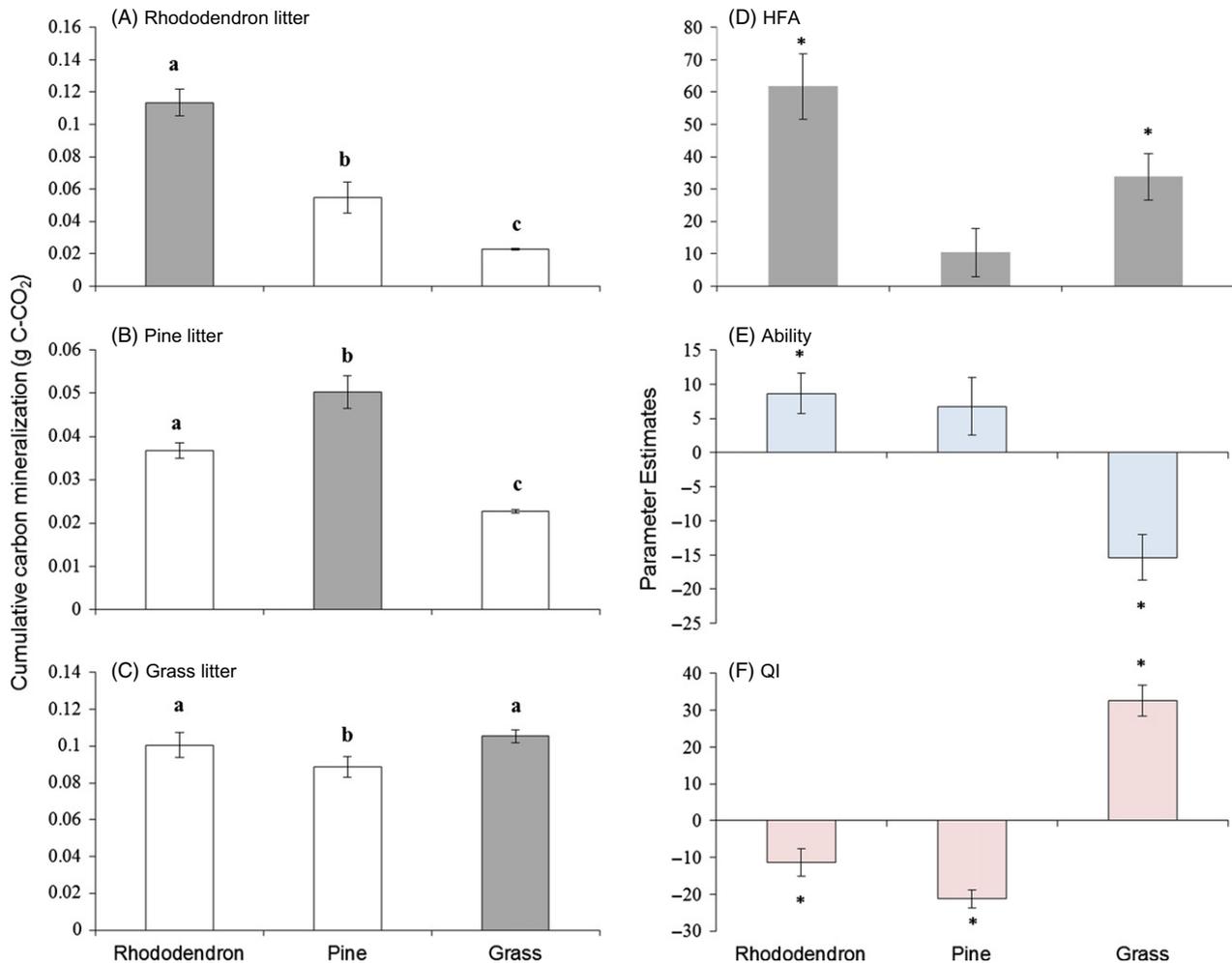


Fig. 2. Left panels (A–C) recreated from Strickland *et al.* (2009a) [Republished from Strickland *et al.* (2009a) with permission from the Ecological Society of America]. The average cumulative carbon mineralized (mean \pm SE) after 300 days for (A) rhododendron litter, (B) pine litter and (C) grass litter incubated with three different decomposer communities. The decomposer communities were sourced from soils under the three litter types. The grey bars indicate the ‘home’ litter \times decomposer community pairing. Letters indicate significant differences between community treatments within a litter type. Parameter estimates (mean \pm SE) calculated using the new approach for (D) HFA, (E) ability and (F) the quality index (QI). Stars (*) indicate significance ($P \leq 0.05$). QI relates both the chemical/physical quality of the litter and how all decomposer communities perceive the relative quality of a litter species. Ability quantifies the overall functional capacity of a decomposer community across environments, relative to one another. Strickland *et al.* (2009a) assessed HFA visually through panels (A–C) after finding a significant soil \times litter interaction effect (using ANOVA). HFA estimates produced through the approach we present (i.e. plate D) provide a different interpretation of HFA. That is, Strickland *et al.* (2009a) concluded that the pine soil community had a strong HFA and the grass community a weaker HFA. Under the quantitative model we propose, the grass community has a much stronger HFA than the pine community. And our proposed model also calculates ability, emphasizing that despite a high HFA, the grass decomposer community has low functional ability compared to the much greater abilities of the pine and rhododendron communities. Apparent functional equivalence between the grass and rhododendron soil communities in (C) therefore masks pronounced differences in HFA and functional ability (D and E).

therefore refer to ‘litter ability’ as the quality index (QI). A litter with a higher QI will degrade more rapidly than a litter with a lower QI. The rate of degradation (i.e. QI) is presumably related to the physical and chemical properties of litters, such as the initial nitrogen content (Aber, Melillo & McLaugherty 1990; Jacob *et al.* 2010), and also to how the decomposer communities collectively ‘perceive’ these properties (see: Strickland *et al.* 2009b). For our test data set, the grass litter has the highest QI (i.e. degrades fastest across all litter by soil community combinations) and the pine litter the lowest QI, as demonstrated by the degradation rates of the grass vs. pine litter (compare Fig. 2B,C) and reflected in the QI scores (Table 1C).

If the decomposer community is treated as the team, then ability scores the relative functional capacity of the community across all litter species (i.e. environments). A difference in ability means that decomposer communities differ in functional capacity; that is, they are not functionally redundant in relation to the overall rate at which they decompose the litter species investigated. Ability therefore provides a quantitative metric by which the functioning of different decomposer and other communities can be compared when evaluating hypotheses that go beyond HFA to explore phenomena such as redundancy, similarity and equivalence (Allison & Martiny 2008; van der Heijden, Bardgett & van Straalen 2008; Bradford & Fierer

Table 1. Example regression output applying data from Strickland *et al.* (2009a) using (A) the approach presented in this paper, (B) Soil as the 'team' under the sports model by Clarke & Norman (1995), and (C) Litter as the 'team' under the sports model

Variable	Parameter estimates (A)	P-value	Parameter estimates (B)	P-value	Parameter estimates (C)	P-value
Intercept	54.35 ± 2.17	<0.0001				
ability: Grass	-15.37 ± 3.32	<0.0001	-15.37 ± 2.47	<0.0001		
ability: Pine	6.74 ± 4.23	0.1159	6.74 ± 2.52	0.0096		
ability: Rhodo	8.63 ± 2.99	0.0053	8.63 ± 1.50	<0.0001		
QI: Grass	32.60 ± 4.26	<0.0001			32.60 ± 2.22	<0.0001
QI: Pine	-21.27 ± 2.46	<0.0001			-21.27 ± 1.79	<0.0001
QI: Rhodo	-11.34 ± 3.69	0.0031			-11.34 ± 1.87	<0.0001
HFA: Grass	33.78 ± 7.29	<0.0001	33.78 ± 4.40	<0.0001	33.78 ± 4.09	<0.0001
HFA: Pine	10.40 ± 7.43	0.1666	10.40 ± 4.44	0.0223	10.40 ± 4.62	0.0276
HFA: Rhodo	61.8 ± 10.15	<0.0001	61.80 ± 4.61	<0.0001	61.80 ± 4.48	<0.0001

Parameter estimates present the expected decomposition ± SE*. *White robust standard errors provide a more conservative estimate for significance testing. Variables 2–4 indicate the overall functional ability of the soil decomposer community (across all litter environments), and variables 5–7 show the ability (QI – litter quality index) of the litter species. The three litters and associated decomposer communities were Grass (mouse barley), Pine (loblolly pine) and Rhodo (great laurel). The home-field advantage (HFA) represents the home litter × decomposer community pairing. When varying the 'team' designation under the sports model (B vs. C), HFA is independent of the designation and matches the new model (A). Our approach produces identical parameter estimates to the sports model assessments, but in a single regression framework (A vs. B/C). Although these estimates remain the same, the standard errors in our model appear greater than when using the sports model. In fact, the standard errors in the sports model are sensitive to which soil and litter replicates are paired to calculate the difference term. Obviously, if standard errors depend on which samples are paired to calculate differences, then they should be deemed unreliable. Our model returns consistent standard errors and *P*-values regardless of how comparisons are ordered. Most importantly, it builds on other ecological approaches (e.g. Ayres *et al.* 2009a) by introducing the metrics of QI and ability, the latter of which permits assessments of functional differences between ecological communities that arise through mechanisms other than HFA.

2012). For example, it has traditionally been assumed that soil decomposer communities are functionally redundant because, across the hundreds to many thousands of taxa of which they are composed, there is likely to be many species that perform a specific function at equivalent rates under the same conditions (Allison & Martiny 2008). Our test data estimating ability for different soil communities reinforce the emerging perspective that litter decomposer communities are not functionally redundant (Schimel & Schaeffer 2012), with the community in the rhododendron soil being associated with much faster degradation rates than the community in the grass soil (Fig. 2 and Table 1B) across all litter environments.

A NEW APPROACH

Our analyses reveal that the ability metric provides a useful quantitative estimate for comparing the functioning of communities across environments to their functional capacity in their home environment. For example, a community (or species) might have high ability but exhibit no HFA, or high HFA and low ability. As such, we propose a regression approach that explicitly models ability and HFA simultaneously. Our statistical approach is based on a least squares regression that provides the following advantages compared to previous HFA and ability models: (i) creates a single, empirical model that explicitly accounts for and estimates the influence of relative litter and soil community abilities on decomposition, as well as the HFA of each home combination; (ii) provides a statistical test for differences in relative abilities and the presence of HFA; and (iii) permits calculation of the expected decomposition rate of a single litter × soil combination using the parameter estimates. We discuss each advantage in turn.

To calculate HFA and ability, we propose the following model:

$$Y_i = \alpha + \sum_{l=1}^N \beta_l \text{Litter}_l + \sum_{s=1}^M \gamma_s \text{Soil}_s + \sum_{h=1}^k \eta_h \text{Home}_h + \varepsilon_i \quad \text{eqn1}$$

where Y_i is the decomposition for observation i , β_l is the ability of litter species l (from species 1 to N), γ_s is the ability of the soil community s (from community 1 to M), and η_h is the HFA of h (from home combinations 1 to K). $\text{Home}_h = \text{Litter}_l * \text{Soil}_s$ when l and s are home-field pairings. Litter_l , Soil_s and Home_h are dummy variables that equal 1 or 0 depending on the presence or absence of the litter species, soil community or home combination, respectively. The parameters to be estimated are β_l , γ_s and η_h . The model states that decomposition is equal to litter ability (β_l) plus soil ability (γ_s) plus a home interaction (η_h). The intercept term is defined by α and represents the average decomposition for all observations in the data set after controlling for litter, soil and home-field pairings. The error term is defined by ε . Since perfect collinearity would otherwise arise, we restrict $\sum_{l=1}^N \beta_l = 0$ and $\sum_{s=1}^M \gamma_s = 0$. To demonstrate an example of this model, we use data from Strickland *et al.* (2009a) for decomposition for an individual observation i with pine litter (*Pinus taeda*) on the pine soil community:

$$Y_i = \alpha + \beta_{\text{pine}_i}(1) + \beta_{\text{Grass}_i}(0) + \beta_{\text{Laurel}_i}(0) + \gamma_{\text{pine}_i}(1) + \gamma_{\text{Grass}_i}(0) + \gamma_{\text{Laurel}_i}(0) + \eta_{\text{pine}_i}(1) + \eta_{\text{Grass}_i}(0) + \eta_{\text{Laurel}_i}(0) + \varepsilon_i \quad \text{eqn2}$$

Consistent with the sports model, the equation returns relative differences in HFA and ability within a specified data set. In our model, however, we approximate ability for litter

and soil simultaneously since no one group is defined as a 'team' (see Appendix S1 in Supporting Information). Note that the restrictions on the litter and soil parameters allow us to test parameter estimates against group averages. Similar results can be achieved when estimating parameters relative to a baseline litter, soil (i.e. dropping the restrictions, 1 L, and 1 field from our regression). Similarly, we could drop the intercept and 1 restriction. Our restrictions, however, provide an estimate for each litter, soil and home combination explicitly. Although ANOVA could be used to accomplish similar goals, estimating the model parameters within a single regression framework allows for easier interpretation and builds upon prior work (Clarke & Norman 1995; Ayres *et al.* 2009a).

The model could first be run with a general HFA term [$Home_{hi}$] to test whether there is an overall presence of HFA derived from the coefficients of all home combinations (see Appendix S2). However, if a majority of combinations are not significant, the general HFA term will likely show non-significance. It is our opinion that the parameter estimates associated with each home pairing are more applicable to ecological theory than a general home statistic.

Advantages of the new model

Our approach estimates the relative HFA and abilities of each litter species and decomposer community in a single regression. Using our sample data set, the QI estimates demonstrate that the grass litter, *Hordeum murinum* (mouse barley), decomposes faster across all soil communities than the rhododendron litter, *Rhododendron maximum* (great laurel), which decomposes faster than the pine litter, *P. taeda* (loblolly pine) (Table 1A). The QI estimates rank in order of highest to lowest in chemical recalcitrance (defined as lignin:N) of the three species, which reinforces the usefulness of litter ability in describing not only chemical/physical quality, but also how soil communities perceive different litter types. The most important parameter obtained from our new model, however, is the ability of the soil decomposer community because we can use this to explore questions beyond HFA related to functional equivalence vs. dissimilarity. Estimated soil abilities rank in order of the total decomposition of all litter types on a single soil decomposer community. The grass soil community has the lowest ability estimate, followed by the pine soil and then the rhododendron community (Table 1A). This range in soil abilities quantifies functional differences among soil communities regarding the rate at which they decompose litters of different species and chemical quality, providing a quantitative estimate of overall community functioning across all study environments (Allison & Martiny 2008; van der Heijden, Bardgett & van Straalen 2008; Keiser *et al.* 2011). The ability values for the soil communities demonstrate that the pine and rhododendron soil communities should have greater ability to decompose all litter types than the soil community sourced from the chemically labile grass litter environment (Table 1A), a result consistent with the FBH (Keiser *et al.* 2011).

Parameter estimates and statistical significance are provided by our model for each home pairing (Table 1A). The significance (P -value) reported for each home-field combination signals a statistical advantage for a specific litter decomposing on its 'home' soil. Within the Strickland *et al.* (2009a) data (Table 1A), the parameter estimates indicate that the rhododendron soil community has the greatest HFA, with the grass soil community's HFA intermediate. Conversely, the pine soil community has the lowest HFA, and this is not statistically significant ($P = 0.25$). These conclusions contrast with those of Strickland *et al.* (2009a); based on ANOVA and plotting of the decomposition data, they concluded that the rhododendron and pine soil communities demonstrated strong HFA and concluded that the grass soil community had a weak HFA. Our quantitative parameter estimates for HFA therefore demonstrate that the general interaction effect (soil \times litter) within ANOVA combined with qualitative HFA determinations can be misleading (Fig. 2), highlighting the need for the formal framework that we suggest to estimate both HFA and ability.

Using the parameter estimates provided in our linear regression, one can back-calculate to the expected decomposition (e.g. $\mu\text{g C per g dry weight litter}$) for all replicates within a specific litter \times soil combination. This is an advance over the sports model where the same parameter values can only back-calculate to the decomposition difference between the 'home' and 'away' teams. Our new approach therefore moves away from the sports analogy of HFA that calculates the relative difference in performance of teams playing against each other and instead focuses on the absolute rates at which individual litter species decompose with specific soil communities. The capacity to calculate expected decomposition across multiple studies facilitates meta-analyses to compare HFA across studies and, more broadly, the functional role of ecological communities.

Ayres *et al.* (2009b) also performed a meta-analysis of HFA using a novel set of equations only applicable to the more common litter transplant experiment design using two species and sites (Jacob *et al.* 2010; Perez *et al.* 2013). Novel equations were required because the divisor term $[(N-2)]$ in the analytical solution of both the sports and decomposition models necessitates that at least three litter species are investigated. The meta-analysis created an HFA index (HFAI), which produces a single value for both litter species involved in the transplant. This work was important for building the evidence base for the hypothesis that soil decomposer communities differ in function. The degree of adaptation of a decomposer community to a litter type does, however, differ (Keiser *et al.* 2011) and so it seems necessary to quantify these differences in future work to disentangle how HFA and ability differ across communities.

Conclusions

HFA is a concept now commonly tested and invoked when investigating relationships between plant litter decomposition rates and soil decomposer community composition (Wang, Zhong & He 2012), and is being extended to the decomposition of other organic inputs to soils (e.g. Throckmorton *et al.* 2012). HFA has also been invoked within the local adaptation

(Ortegon-Campos *et al.* 2012; Sherrard & Maherali 2012) and aquatic ecology (Olden, Larson & Mims 2009) literature. A quantitative metric for HFA is, however, rarely determined. We provide a statistical framework for calculating HFA and with it ability, which scores the perceived quality of litter and also the overall functioning of a decomposer community. Our approach thus provides a quantitative framework to test definitively the competing hypotheses that ecological communities are functionally equivalent versus dissimilar. For the process of litter decomposition, such a framework is essential to advance our understanding of the mechanisms underlying when and how decomposer community composition will influence function.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Limitations of the sports model.

Appendix S2. General HFA term.

Appendix S3. SAS code plus data frame.