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Tansley insight

Home-field advantage of litter decomposition: from the phyllosphere to the soil

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Summary

Plants often associate with specialized decomposer communities that increase plant litter breakdown, a phenomenon that is known as the 'home-field advantage' (HFA). Although the concept of HFA has long considered only the role of the soil microbial community, explicit consideration of the role of the microbial community on the foliage before litter fall (i.e. the phyllosphere community) may help us to better understand HFA. We investigated the occurrence of HFA in the presence vs absence of phyllosphere communities and found that HFA effects were smaller when phyllosphere communities were removed. We propose that priority effects and interactions between phyllosphere and soil organisms can help explain the positive effects of the phyllosphere at home, and suggest a path forward for further investigation.

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I. An ecological theory derived from a sports concept

Athletes often prefer to play games at their home venue because of the support from their home crowd and the familiarity of the stadium, rather than playing away in front of a hostile audience. This preference corresponds to an advantage, in that '*home teams in sport competitions win over 50% of the games under a balanced home and away schedule*' (Courneya & Carron, 1992). In ecological

studies, the concept of 'home-field advantage' (HFA) emerged in the early 2000s (Gholz *et al.*, 2000), though earlier studies had noted the phenomenon (e.g. Hunt *et al.*, 1988). Home-field advantage in soil ecology refers specifically to the idea that decomposer communities are specialized in colonizing and utilizing the substrates that they most frequently encounter, leading to the prediction that litter decomposition is accelerated in the close vicinity of the plant from which it originates (Ayres *et al.*, 2009).

Although an increasing number of studies provide evidence for a HFA (e.g. Vivanco & Austin, 2008; Milcu & Manning, 2011; Asplund *et al.*, 2018; Lin *et al.*, 2019), many other studies find no effect (e.g. Ayres *et al.*, 2006; Gießelmann *et al.*, 2011; Veen *et al.*, 2015a; Bachecha *et al.*, 2016) or even a home-field disadvantage (e.g. St John *et al.*, 2011; Luai *et al.*, 2019). This inconsistency has led to the conclusion that HFA effects are not universal, and that a finer understanding of the context of litter decomposition is necessary to understand the underlying mechanisms underpinning HFA (Austin *et al.*, 2014; Veen *et al.*, 2015b; Palozzi & Lindo, 2018).

II. Home sweet home: the underestimated role of the phyllosphere community

Past litter decomposition studies which calculate HFA using differences in decomposition between 'home' and 'away' sites identify the litter species as the 'team' and the soil as the 'stadium', with the litter being moved among locations (Keiser *et al.*, 2014). The advantage of decomposing at home is therefore due to the composition and the functional ability of the soil decomposer community at the site from which the litter originated. However, the litter is moved from one site to another with its phyllosphere, and sometimes also with recently colonized soil organisms, when freshly fallen litter is collected directly from the ground surface. The phyllosphere community comprises diverse communities of organisms, present on most surfaces of the leaves as well as within their internal spaces, whose composition can vary strongly in both space and time (Vacher *et al.*, 2016). Bacteria are by far the most numerous living organisms on leaves, but phyllosphere organisms also include fungi, algae, mosses, lichens, viruses, protozoa and nematodes (Lindow & Brandl, 2003). The phyllosphere communities perform many functions for their host plants, such as protecting them against pathogens and air pollutants, or providing them with nitrogen fixed from the air (Lindow & Brandl, 2003). In the same way that plant roots sustain unique rhizosphere communities that benefit both the soil community and the plant (Walker *et al.*, 2003), the phyllosphere communities may be specific to their leaf host because of their affinity for the exudates shed by leaf cuticles when alive and their chemical makeup once senesced.

Although Austin *et al.* (2014) have previously discussed a possibly important role of foliage microbes, the contribution of the phyllosphere to explaining HFA effects has rarely been evaluated (Veen *et al.*, 2019). In this light, our goal was to understand the role of phyllosphere vs soil microbial communities in driving HFA effects. We hypothesized that the presence of phyllosphere microorganisms at both sites (i.e. at 'home' and 'away') would reduce HFA effects due to their significant impacts on litter decomposition rates, which potentially decreases the relative importance of soil decomposer communities. To test this hypothesis, we can make use of the fact that some HFA studies have kept litter intact, while others have oven dried it at 60–65°C for several d (therefore considerably reducing the phyllosphere communities), or sterilized it (by gamma radiation or autoclaving) before transplanting litter without its 'home' phyllosphere community (e.g. Ayres *et al.*, 2006; Fanin *et al.*, 2016; Veen *et al.*, 2018; Li *et al.*, 2020). This sterilization procedure is often implemented to control

for the effect of the phyllosphere microbiome, and for soil organisms already present when freshly fallen leaf litter is collected from the ground, so as to eliminate their effects when testing the local adaptation of the soil community. However, because phyllosphere organisms are ubiquitous and can be important contributors to litter decomposition once the leaves fall on the ground (Voříšková & Baldrian, 2013; Vacher *et al.*, 2016), their presence must somehow be taken into account to quantify the occurrence and magnitude of HFA effects.

By updating the dataset from the HFA synthesis published by Veen *et al.*, (2015b) with some more recent studies, we assessed the effect of phyllosphere removal on the magnitude and direction of HFA effects (Supporting Information Notes S1). We calculated the decomposition constant k (using a negative exponential function % mass loss = $100 - 100 \times e^{-kt}$) to compare decomposition rates between studies of different duration. We calculated the home-field advantage index (HFA_{*i*}) for each pair of reciprocal litter transplants to correct for inherent differences in the rates of decomposition between habitats and litter types (Ayres *et al.*, 2009):

$$\text{HFA}_i = \left[\left(\frac{A_{Rka} + B_{Rkb}}{2} \right) / \left(\frac{A_{Rkb} + B_{Rka}}{2} \right) \right] \times 100 - 100$$

where i_{Rkj} represents the relative decomposition constant k of species i in environment j . We then employed mixed models to assess the effect of phyllosphere removal through sterilization before litter transplantation (done by oven drying, autoclaving or gamma radiation, vs not done) on HFA_{*i*}, with 'study' as a random factor. The models were weighted based on the inverse variance of the number of HFA_{*i*} observations per study.

Overall, the majority of studies using a procedure affecting the phyllosphere communities had lower HFA_{*i*} than those that kept the litter intact (Notes S1). We found that sterilizing the litter had a negative effect on HFA_{*i*}, with values ranging from +8.2% in the presence of a phyllosphere to -0.5% in the absence of a phyllosphere ($P = 0.009$, Fig. 1). The different phyllosphere removal procedures (i.e. oven drying, autoclave or gamma radiation) did not differ between each other and had relatively similar negative effects on HFA_{*i*} ($P = 0.55$, data not shown). These results highlight that the presence of the phyllosphere community is needed to increase decomposition rates at home relative to away.

III. Hypothesized effects of phyllosphere communities on litter decomposition

Contrary to the idea that exporting the phyllosphere with the litter would decrease HFA effects due to the effects of the phyllosphere microbiome on litter decomposition at both 'home' and 'away' sites, our analysis showed that the removal of the phyllosphere community significantly reduced the HFA. This result highlights that the phyllosphere community present at the time of litter collection is an important factor in explaining HFA effects across various studies. Two questions that emerge from this are as follows: How can we explain the effects of the phyllosphere community at home? And what kind of factors could be important to consider for

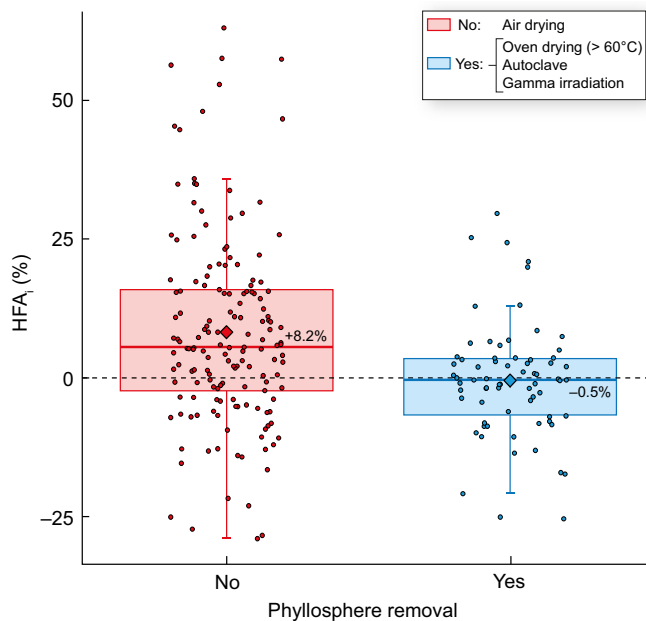


Fig. 1 Influence of phyllosphere removal procedure on home-field advantage index (HFA). Using published data on litter mass loss from 227 reciprocal litter transplants from 43 studies (Supporting Information Notes S1), we assessed the effect of sterilizing the litter to remove the resident phyllosphere community before using it in transplantation experiments (i.e. by oven drying, autoclaving or gamma radiation; in blue) compared to nonremoval of this community (air drying; in red). The boxplots characterize the lower quartile, median, upper quartile and interquartile range (upper quartile – lower quartile), which covers the central 50% of the data; the whiskers represent 95% of the data. The diamond within each boxplot represents the mean and each small circle represents one individual observation. We found that HFA_i was higher for unmanipulated litter ($P = 0.009$; mean = 8.2%, $n = 157$) compared with sterilized litter (mean = -0.5%, $n = 70$). Sensitivity analysis did not show disproportionate effects of specific studies on these results (Notes S1).

predicting HFA effects on litter decomposition? We first briefly discuss the potential role of phyllosphere organisms in leaf decomposition and suggest two potential mechanisms at play that may explain the role of the phyllosphere in driving the HFA effects (Fig. 2).

Phyllosphere organisms

Upon the death of leaves, the initial phase of decomposition generally involves the release of substantial amounts of easily degradable and nutrient-rich compounds (Ibrahima *et al.*, 1995). In this context, the loss of these critical resources by leaching may be largely pre-empted through their consumption and retention by phyllosphere microorganisms, which could in turn lead to rapid development of the phyllosphere community within and on the leaf litter material (Osono, 2006). As such, the early colonizers in the phyllosphere may act as accelerators of the decomposition process, independent of any particular ability to degrade their own host substrate. Additionally, the phyllosphere may also select for microorganisms that are specialized for utilizing at least some of its specific constituents (for a review, see Wolfe & Ballhorn, 2020).

For instance, it has been shown that Xylariaceous endophytes increase decomposition rates due to their ability to break down lignin (Osono & Takeda, 1999; Osono, 2002) a process which may require very specific enzymes. Although early colonizers and specialized endophytes may therefore contribute to increased decomposition rates of their host leaves both at home and away, their overall impact on litter decomposition rates could be either positive or negative because of their effects on determining the soil microbial species that subsequently colonize during the decomposition process. As discussed in the following sections, such priority effects, including aspects of niche modification and niche pre-emption, may further explain HFA effects.

Niche modification

The composition of the phyllosphere community drives the subsequent succession of microbial communities (Voříšková & Baldrian, 2013), which is in turn likely to impact the decomposition process over time (van der Wal *et al.*, 2013). For instance, several studies have observed that the ability of late-successional fungal species to colonize wood is highly dependent on the identity of the fungal species that were previously present (Heilmann-Clausen & Boddy, 2005; Hiscox *et al.*, 2015). Because the degradation of hemicellulose and pectin regulates the access of enzymes to more complex carbon forms such as lignin (Fanin & Bertrand, 2016), partial attack of these polysaccharides by phyllosphere organisms may promote increased decay rates of other structural compounds via soil species which arrive later (i.e. niche modification; Fukami, 2015). More generally, most decomposer meso- and macro-fauna, as well as many microorganisms, have a greater capability to degrade litter material after the conditioning of the litter has started (Gessner *et al.*, 1999). By accelerating the conditioning phase, as well as helping retain nutrients during the earlier leaching phase, the early colonizers in the phyllosphere may play a critical role in stimulating the HFA effect brought about by a range of 'home' soil decomposers.

Niche pre-emption

By living on the leaf surface close to stomatal openings and even inside leaf parenchyma, phyllosphere microbial communities are able to gain rapid access to internal and external surfaces of the leaf after its death, and can thereby rapidly colonize it (Saikkonen *et al.*, 2015). The reduction in available resources, such as space, energy or nutrients, brought about by the resident phyllosphere community may impair colonization by soil bacteria and fungi (i.e. niche pre-emption; Fukami, 2015). This niche pre-emption by the phyllosphere community may explain the greater HFA relative to when this community is absent, if it impairs colonization by generalist soil microbes that utilize labile litter compounds, and instead favors the persistence of endophytes that specialize in the breakdown of recalcitrant carbon forms and thus accelerate leaf litter decomposition. An efficient phyllosphere community operating in a favorable home environment may further contribute to HFA. For example, microbial communities are influenced by their past climatic histories, and decomposition rates can slow dramatically in

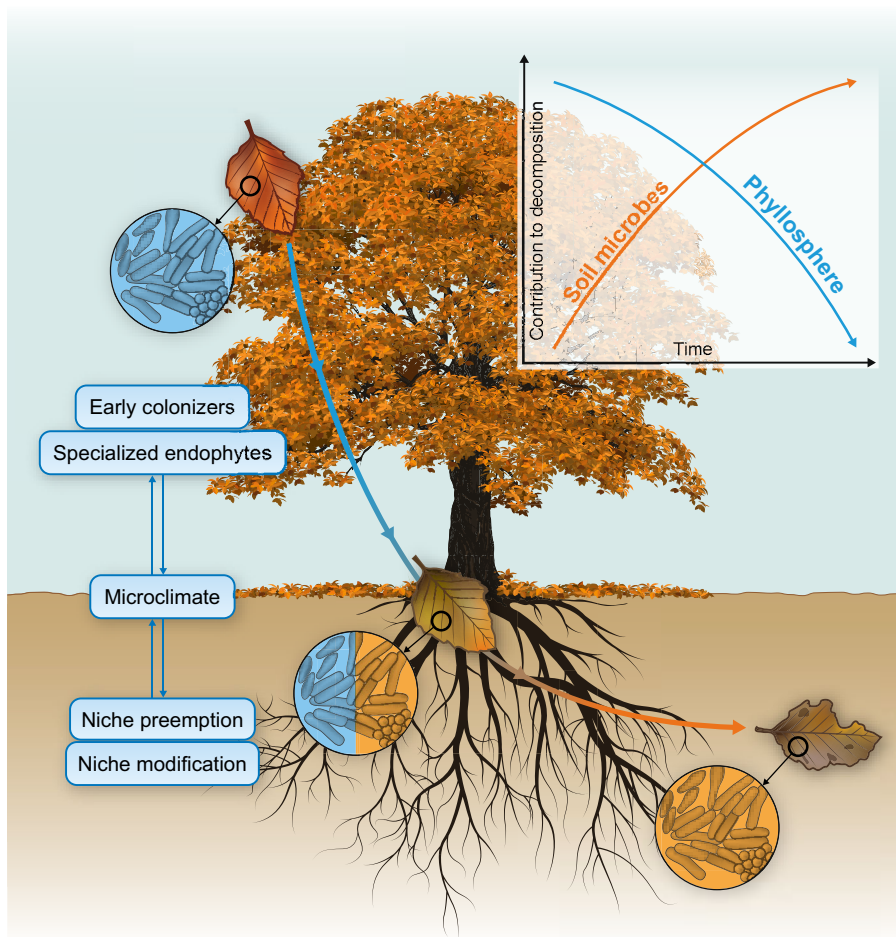


Fig. 2 Schematic diagram of the effects of phyllosphere vs soil communities during litter decomposition. Upon the death of leaves, the phyllosphere communities contribute to the degradation of leaf litter and generate a 'home-field advantage' (HFA), through either fast-growing early colonizers or specialized endophytes. Phyllosphere organisms may then either prevent the colonization by soil microorganisms due to their occupation of the available space (niche pre-emption), or facilitate the arrival of specific species due to the conditioning of leaf tissues (niche modification). The role of phyllosphere organisms and priority effects may further be impacted by the microclimate at the local scale: changes in temperature, humidity or light radiation may influence the abundance and colonization capabilities of phyllosphere and soil organisms on the litter. As decomposition proceeds, the influence of phyllosphere communities on HFA effects may decrease as soil communities take over.

an away environment depending on the microbial community's ability to sustain function under new conditions of temperature and humidity (Strickland *et al.*, 2015). Furthermore, microclimatic differences between 'home' and 'away' sites influence the ability of new decomposer species to establish (Hiscox *et al.*, 2015), which influences microbial community succession and assembly history (Nemergut *et al.*, 2013). Temperature, moisture, wind and exposure to radiation may all affect the composition, structure and diversity of phyllosphere organisms (Leveau, 2019). As a consequence, different climate conditions compared to home may induce fast succession rates and rapid colonization by away generalist soil microbes, decreasing decomposition rates in away environments, and contributing to HFA effects.

IV. Interactions between phyllosphere and soil organisms: implications and a way forward

Our data synthesis and analysis revealed that phyllosphere organisms increase litter decomposition rates at home. We attribute this to early colonizers and specialized endophytes influencing the subsequent recruitment of soil microorganisms over the course of the decomposition process. Therefore, priority effects may be important in helping us understand the decomposition process in

natural conditions, beyond simply better understanding HFA effects. In particular, this finding suggests that the successional dynamics of microbial communities are driven by deterministic processes (i.e. through ecological interactions), either due to the creation of new favorable niches or through competitive exclusion, although stochastic effects may play a larger role before the litter fall (Koskella, 2020). If this theory is true, it indicates that microbial succession depends mainly on litter quality (i.e. along a spectrum of labile to recalcitrant), the phyllosphere organisms present on the leaves at the time of litter fall, and the interaction between the pool of soil species adjacent to the decomposing litter and microclimate (Fig. 2).

Such implications are likely to hold not just for decaying leaf litter but also for decaying roots, and perhaps even more so for roots because after senescence they generally remain in place in their growing medium (i.e. the rhizospheric soil) and do not move. However, one notable difference between decaying roots and leaves is that the living root rhizosphere microbiome tends to be recruited from previous decaying roots in the soil (Zhou *et al.*, 2020), which increases the opportunity for the rhizosphere microbiome to be specialized in decomposing its own root hosts. A second fundamental difference regarding mycorrhizal-associated roots is that fungal symbionts may further interact with the dying roots, with a

range of largely unknown effects on the decomposing tissues (Freschet *et al.*, 2021). For both leaf and root litter, because an increasing number of studies have demonstrated that the assembly order of microbial species can affect not only microbial community structure but also ecosystem functioning (Fukami *et al.*, 2010; Veen *et al.*, 2019), assessing whether microbial succession during litter decomposition follows predictable patterns over time can help us to better predict nutrient dynamics and carbon cycling at the ecosystem level (Wolfe & Ballhorn, 2020).

V. Conclusions and future outlook

Our objective was to highlight the potential role of aboveground phyllosphere communities on HFA for litter decomposition. Although the concept of HFA has long been considered to be restricted to soil communities (Ayres *et al.*, 2009), our data synthesis showed that explicit recognition of the role of the phyllosphere community may contribute to a better understanding of HFA effects (Austin *et al.*, 2014). Because even subtle differences in species arrival history can cause large differences in the subsequent structure and function of microbial communities (Fukami *et al.*, 2010; Dickie *et al.*, 2012), we propose that a better understanding of biotic interactions between phyllosphere and soil organisms and priority effects (i.e. through either niche pre-emption or niche modification) would help us to identify the mechanisms driving litter decomposition and HFA in terrestrial ecosystems (Fig. 2).

This synthesis suggests a need for new studies. First, we argue that manipulating phyllosphere communities (i.e. experimental removal, transplants and inoculation) should be a priority objective in future HFA studies, to confirm its role and better understand the context-dependency of HFA effects. In particular, future studies should also consider other factors that can potentially interact with phyllosphere communities. Microclimate (St John *et al.*, 2011), the match between litter chemical composition and its new incubation environment (Freschet *et al.*, 2012), and the presence of saprophytic and microbivorous fauna (Milcu & Manning, 2011), may all directly or indirectly affect phyllosphere communities, and thereby change the course of decomposition processes and HFA effects. Second, our results highlight the fact that assessing the succession of microbial communities on leaves as they die and decompose (i.e. the shift from phyllosphere to soil communities) in relation to their functioning can shed a new light on 'if, who, when and how' decomposers accelerate decomposition rates at home (Voříšková & Baldrian, 2013). Finally, our preliminary analysis emphasizes the importance of phyllosphere communities, and we suggest a path forward for further investigation.

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collaborative projects. We also invite those conducting reciprocal litter experiments to contact the lead authors and to submit their data to our synthetic HFA project, which aims to assess the main drivers of HFA in aquatic and terrestrial ecosystems. This project is free to join and open to researchers at all career stages.

Author contributions

NF and GFV planned and designed the research, collected the data and performed analyses. NF wrote the first draft of the manuscript in close consultation with GFV and DL. GTF, ADK, LA and DAW contributed substantially to the improvement of the initial idea. All authors contributed to manuscript completion and revision.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Plot showing the effects of the litter handling procedure on the home-field advantage index (HFA_i).

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