Variation in home-field advantage and ability in leaf litter decomposition across successional gradients

G. F. (Ciska) Veen1,2 | Ashley D. Keiser3,4 | Wim H. van der Putten2,5 | David A. Wardle1,6

1Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden; 2Department of Terrestrial Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands; 3Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa; 4Institute on the Environment, University of Minnesota, St. Paul, Minnesota; 5Laboratory of Nematology, Wageningen University, Wageningen, The Netherlands and 6Asian School of the Environment, Nanyang Technological University, Singapore City, Singapore

Abstract

1. It is increasingly recognized that interactions between plants and soil (a)biotic conditions can influence local decomposition processes. For example, decomposer communities may become specialized in breaking down litter of plant species that they are associated with, resulting in accelerated decomposition, known as “home-field advantage” (HFA). Also, soils can vary inherently in their capacity to degrade organic compounds, known as "ability." However, we have a poor understanding how environmental conditions drive the occurrence of HFA and ability.

2. Here, we studied how HFA and ability change across three types of successional gradients: coastal sand dunes (primary succession), inland drift sands (primary succession) and ex-arable fields (secondary succession). Across these gradients, litter quality (i.e. nutrient, carbon and lignin contents) increases with successional time for coastal dunes and decreases for the other two gradients.

3. We performed a 12-months reciprocal litter transplant experiment under greenhouse conditions using soils and litters collected from early-, mid- and late-successional stages of each gradient.

4. We found that HFA and ability did not consistently shift with successional stage for all gradients, but were instead specific for each type of successional gradient. In coastal dunes, HFA was positive for early-successional litter, in drift, sands it was negative for mid-successional litter, and for ex-arable fields, HFA increased with successional time. Ability of decomposer communities was highest in mid-successional stages for coastal dunes and drift sands, but for ex-arable fields, ability decreased throughout with successional time. High HFA was related to high litter C content and soil and organic matter content in soils and to low litter and soil nutrient concentrations. Ability did not consistently occur in successional stages with high or low litter quality.
1 | INTRODUCTION

Decomposition is a key driver of carbon and nutrient cycling in ecosystems world-wide. At broad geographic scales, climate and litter quality appear to consistently drive litter decomposition (Berg et al., 1993; Cornwell et al., 2008). However, a growing body of evidence suggests that the impact of small-scale variation in decomposer communities and their activities, as well as abiotic soil properties, may be much more important for driving decomposition than previously assumed (Bradford, Berg, Maynard, Wieder, & Wood, 2016; Bradford et al., 2017; Fanin, Hättenschwiler, & Fromin, 2014). For example, decomposer communities may be specialized in the breakdown of localized litter which can lead to accelerated decomposition of this litter, a phenomenon known as “home-field advantage” (HFA) (Ayres et al., 2009; Gholz, Wedin, Smitherman, Harmon, & Parton, 2000). Moreover, inherent differences in decomposition rates of the same litter between soil decomposer communities, referred to as “ability” (Keiser, Keiser, Strickland, & Bradford, 2014; Keiser, Strickland, Fierer, & Bradford, 2011), may drive variation in litter mass loss. This can be due to differences in the functional capacity among decomposer communities (Keiser et al., 2014). Several studies have tested HFA and ability using reciprocal litter transplant approaches, and these reveal strong variation in their occurrence and magnitude (e.g. Fanin, Fromin, & Bertrand, 2016; Giesselmann et al., 2011; Hunt, Ingham, Coleman, Elliott, & Reid, 1988; Keiser & Bradford, 2017; Veen, Sundqvist, & Wardle, 2015; Vivanco & Austin, 2008). The divergent results of these studies indicate that home-field effects and ability can depend strongly on environmental context (Freschet, Aerts, & Cornelissen, 2012; Keiser et al., 2014); however, we still have a limited understanding of what environmental drivers are important and how they influence HFA (Veen, Freschet, Ordonez, & Wardle, 2015). To better understand the role of context in determining HFA and ability, we tested how home-field effects and ability vary across successional stages of vegetation development across which litter quality changes.

Across successional gradients, variation in decomposition processes may be driven by shifts in the functioning of decomposer communities with successional time. With increasing successional age there is more time for intimate litter-decomposer interactions to develop (Morriën et al., 2017) through adaptation or dispersal. Moreover, later-successional plants are often longer-lived which gives them more time to select for litter-specific decomposer communities. In addition, soil communities from later-successional stages have experienced a wider range of litter qualities over time and therefore may have a broader functional capacity, resulting in an increased ability of decomposer communities to degrade different litter types (Keiser et al., 2014). For these reasons, as succession proceeds both HFA and ability may increase.

Alternatively, variation in litter quality (a key driver of litter decomposition rates; Cornwell et al., 2008) may explain the magnitude of HFA and ability (Keiser et al., 2014; Veen, Freschet, et al., 2015). Litter quality is known to change markedly along successional gradients (Wardle, Bardgett, Walker, & Bonner, 2009). During vegetation succession, temporal changes in the functioning of soil food webs (which regulate plant-litter decomposition) and soil nutrient cycling go hand in hand with shifts in traits of the dominant plant species and hence shifts in litter chemical composition (Wardle, 2002). In addition, reduced disturbance and changes in the intensity of competition for light along gradients can impact on litter quality. In primary successional gradients that start with soils with little or no organic matter, litter production by slow-growing, pioneer plant species and accumulation of nutrients in the system can gradually increase soil nutrient mineralization. This favours the establishment of faster-growing, later-successional plant species that can produce litter of higher quality, for example, with higher nutrient and lower structural content (Berendse, 1998). In contrast, in secondary successions, early-successional stages have relatively high soil nutrient availability (Holtkamp et al., 2011; van der Wal et al., 2006) and are colonized by fast-growing pioneer plant species with high litter quality (Cortez, Garnier, Pérez-Harguindeguy, Debussche, & Gillon, 2007; Milcu & Manning, 2011), while later-successional species produce poorer-quality litter.

These changes in plant-litter quality across successional stages can affect patterns in home-field advantage in three alternative ways. First, HFA could become stronger with decreasing litter quality, because specialized organisms may be required to decompose litter of poor nutritional value, whereas generalist decomposers may be better suited for breaking down higher-quality litter (Milcu & Manning, 2011; Wallenstein et al., 2013). Second, easily accessible nutrients in higher-quality litter may intensify...
competition between decomposer organisms, which could lead to specialization and hence stronger HFA with increasing chemically labile litter environments (Fanin et al., 2014; Perez, Aubert, Decaens, Trap, & Chauvat, 2013). Third, each litter type may have its own specialized decomposer community (Freschet et al., 2012), leading to HFA being potentially equally strong for low- and high-quality litters, and thus independent of litter quality. Ability may also be tied to litter chemical quality through the idea of functional breadth whereby decomposer communities from habitats with a low litter quality may be best equipped to decompose a broad range of organic compounds (van der Heijden, Bardgett, & van Straalen, 2008). Hence, decomposer communities from low litter quality environments have a high functional capacity to degrade all litter types (Keiser & Bradford, 2017; Keiser et al., 2014). The extent to which HFA and ability vary with successional time, or the extent to which changes in HFA and ability along successional gradients match changes in litter quality, is poorly understood (Fanin et al., 2016).

The aim of this study was to determine whether patterns in HFA and ability vary along successional gradients for which litter quality changes between successional stages. We examined three successional gradients on sandy soils, that is two primary successional gradients (one on coastal dunes and the other on inland drift sands), and one secondary successional gradient (on ex-arable fields). We tested the hypothesis that HFA and ability effects on litter mass loss would increase with successional age for each of our three gradients. We expected an increase in the magnitude of HFA because increasing successional age increases the time for intimate litter–decomposer interactions to develop (Morriën et al., 2017). We expected an increase in the magnitude of ability effects with successional age because soil communities have experienced a wider range of litter qualities over time for later-successional stages and therefore have a broader functional capacity. In addition, we tested how HFA and ability vary with changes in litter quality. HFA can be high in sites with high litter quality when competition for nutrients stimulates specialization in the decomposer community (Perez et al., 2013). Alternatively, HFA could be high in sites with low litter quality where a specialized decomposer community is needed to degrade complex compounds (Milcu & Manning, 2011; Perez et al., 2013). Ability is expected to be high for decomposer communities from sites with low-quality litter (Keiser et al., 2014), because these communities could be better equipped to decompose a broad range of organic compounds (van der Heijden et al., 2008).

To test our hypothesis, we performed a 12-months reciprocal litter transplant experiment in a greenhouse using soils and litters from three different types of successional gradients, hereafter referred to as “gradients.” All three gradients were from the Netherlands; two are primary successional gradients (one in coastal dunes and one in inland drift sands) while one is a secondary successional gradient (on ex-arable fields) (Table 1). All successional gradients were situated on nutrient-poor sandy soils (see Table 2 for soil abiotic characteristics). Mean annual temperature was 10.5–10.7°C and mean annual precipitation 837–881 mm in the 10 years prior to our study, that is 2003–2012 (Royal Netherlands Meteorological Institute (KNMI)). Within each gradient, we selected early-, mid- and late-successional stages. Coastal dune gradients were situated along the North Sea coast in the south-west of the Netherlands between Oostvoorne (51°54′28″N, 4°03′20″) and Renesse (51°44′23″N, 3°49′20″). Drift sand gradients were situated in the central part of the Netherlands, in the nature area “De Veluwe” between Nunspeet (52°21′13″N, 5°45′09″) and National Park “De Hoge Veluwe” (52°04′47″N, 5°50′30″). The gradients of ex-arable fields were also situated on the same parent soil material as the drift sands, in the central part of the Netherlands, in the nature area “De Veluwe” between Ede (52°04′20″N, 5°44′12″) and Wolfheze (52°00′77″ N, 5°48′58″). The ex-arable fields were part of a well-established gradient of old-field succession (e.g. Kardol, Bezemer, & van der Putten, 2006; Morriën et al., 2017; van de Voorde, van der Putten, & Bezemer, 2011).

2 | MATERIALS AND METHODS

2.1 | Study sites

We set up a reciprocal litter transplant experiment in a greenhouse using soils and litters from three different types of successional gradients, hereafter referred to as “gradients.” All three gradients were from the Netherlands; two are primary successional gradients (one in coastal dunes and one in inland drift sands) while one is a second-ary successional gradient (on ex-arable fields) (Table 1). All successional gradients were situated on nutrient-poor sandy soils (see Table 2 for soil abiotic characteristics). Mean annual temperature was 10.5–10.7°C and mean annual precipitation 837–881 mm in the 10 years prior to our study, that is 2003–2012 (Royal Netherlands Meteorological Institute (KNMI)). Within each gradient, we selected early-, mid- and late-successional stages. Coastal dune gradients were situated along the North Sea coast in the south-west of the Netherlands between Oostvoorne (51°54′28″N, 4°03′20″) and Renesse (51°44′23″N, 3°49′20″). Drift sand gradients were situated in the central part of the Netherlands, in the nature area “De Veluwe” between Nunspeet (52°21′13″N, 5°45′09″) and National Park “De Hoge Veluwe” (52°04′47″N, 5°50′30″). The gradients of ex-arable fields were also situated on the same parent soil material as the drift sands, in the central part of the Netherlands, in the nature area “De Veluwe” between Ede (52°04′20″N, 5°44′12″) and Wolfheze (52°00′77″ N, 5°48′58″). The ex-arable fields were part of a well-established gradient of old-field succession (e.g. Kardol, Bezemer, & van der Putten, 2006; Morriën et al., 2017; van de Voorde, van der Putten, & Bezemer, 2011).

2.2 | Experimental design

For each of the three gradients, we laid out six replicate transects that included early-, mid- and late-successional stages, resulting in three gradient types (dunes, drift sands and ex-arable fields) × 3 successional stages per gradient (early, mid, late) × 6 transects = 54 locations from which litter and soil were collected. For each gradient, successional stages within any given transect were always within a distance of between 300 m and 3 km from each other, and transects were always between 100 m and 30 km apart. Between 25 October and 9 November 2012, we collected ~10 g of freshly senesced leaf litter from the soil surface within each location using four to eight randomly placed quadrats of 10 × 10 cm from an area of 2 × 2 m. Soils in each location were sampled underneath each of the litter-collection quadrats with a shovel to a depth of 10 cm and bulked within locations.

For each location, we gently homogenized all the collected soil samples and removed stones and large roots by hand. A subsample
of the soil from each of the 54 locations was used for analysing soil abiotic properties, and the rest of it was used to fill three 1-L pots. Each of the three 1-L pots received litter from early-, mid- or late-successional stages respectively. The litter collected from each location was bulked and air-dried for at least 48 hr until constant weight and cut into 5-mm fragments. For each location, we filled six nylon mesh bags of 5 × 10 cm and mesh size 0.9 × 1 mm with 1 g of litter from that location. This mesh size allowed entrance of litter bags by micro-organisms and micro- and mesofauna. Mesh bags were buried in the pots (to ensure close contact between litter and soil) according to a reciprocal transplant approach: within every transect litter originating from each successional stage (early, mid or late) was incubated in soils from all three successional stages (early, mid and late). This resulted in a total of three gradient types (coastal dunes/drift sands/ex-arable fields) × 6 replicate transects × 3 soil sources (early/mid/late-successional stage) × 3 litter sources (early-/mid-/late-successional stage) = 162 pots. As every pot received two mesh bags, one for each of two harvest dates, there were 324 mesh bags in total. Although we expect that decomposer communities play an important role in driving HFA and ability effects (Keiser et al., 2014; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009), our experimental set-up did not allow us to assess the independent influence of soil decomposer communities. Instead we examined how both biotic and abiotic soil properties impact on decomposition processes across successional stages and gradients.

The use of unsterilized litter may have resulted in the introduction of microbes with the litter, which could influence the litter × soil decomposer community effect on mass loss. Therefore, for the 12-months litter decomposition period, we incubated a set of gamma-irradiated litter (25 KGray), using the same experimental design and level of replication as for the nonsterilized litter. Litter sterilization weakly enhanced litter mass loss in gradients of ex-arable fields (F_{2,85} = 5.15, p = .026). However, there were no interactive effects between sterilization and the source of litter (i.e. early-, mid- or late-successional stage) (coastal dunes: F_{2,85} = 0.99, p = .376; ex-arable fields: F_{2,85} = 0.75, p = .477) or between sterilization and the source of the soil (i.e. early, mid- or late-successional stage) (coastal dunes: F_{2,85} < 0.01, p = .993; drift sands: F_{2,85} = 0.38, p = .683; ex-arable fields: F_{2,85} = 0.45, p = .641), except for drift sands where there was a weak interactive effect of litter source and sterilization (F_{2,78} = 3.50, p = .035). This interaction occurred because unsterilized, late-successional litter decomposed slower than unsterilized, early-successional litter, while there was no difference for sterilized litter. As the impact of sterilization was minor, we use the mass loss values of unsterilized litter to test our hypotheses, which ensures that the structural and chemical properties of the litter have not been altered in the manner that may occur through the sterilization process (Howard & Frankland, 1974).

Pots were placed in a greenhouse with day/night temperatures of 21°C/16°C, relative humidity of 60% and a day length of 16 hr, which is a typical of average growing season conditions in all three study areas (Royal Netherlands Meteorological Institute (KNMI)). Pots were covered with perforated tin foil to reduce moisture loss and watered to weight every 2 weeks to maintain the mean field soil moisture content, which was representative for soil moisture

<table>
<thead>
<tr>
<th>Coastal dunes</th>
<th>Habitat type</th>
<th>Successional age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>Ammophila arenaria</td>
<td>Grass</td>
</tr>
<tr>
<td>Mid</td>
<td>Betula pendula</td>
<td>Developing forest</td>
</tr>
<tr>
<td>Late</td>
<td>Quercus robur, Fraxinus excelsior</td>
<td>Closed forest</td>
</tr>
<tr>
<td>Drift sands</td>
<td>Corynephorus canescens, Carex arenaria</td>
<td>Bare sand with grass patches</td>
</tr>
<tr>
<td>Early</td>
<td>Festuca rubra</td>
<td>Grassland</td>
</tr>
<tr>
<td>Late</td>
<td>Pinus sylvestris</td>
<td>Closed forest</td>
</tr>
<tr>
<td>Ex-arable fields</td>
<td>Elytrigia repens, Lolium perenne, Senecio jacobaea, Myosotis arvensis</td>
<td>Grassland</td>
</tr>
<tr>
<td>Mid</td>
<td>Anthoxanthum odoratum, Agrastis capillaris, Leucanthemum vulgare, Plantago lanceolata</td>
<td>Grassland</td>
</tr>
<tr>
<td>Late</td>
<td>Betula pendula, Pinus sylvestris, Quercus robur</td>
<td>Closed forest</td>
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</tbody>
</table>

For each successional stage, we list up to four abundant species as examples of common species in these stages.

Values based on Kardol et al. (2006), Neutel et al. (2007), van de Voorde et al., 2011) and personal observations.
### Data analysis

We used a general linear model with mass loss as the response variable. We used soil source (early-, mid-, late-successional stage), litter source (early-, mid-, late-successional stage), gradient type (coastal dunes, drift sands, ex-arable fields), harvest time, and the interactions among these factors as fixed factors and transect and harvest time as random factors. To test how litter and soil properties varied between successional stages and gradient types, we used a general linear mixed model with soil source (i.e., the successional stage where litter and soil were collected), gradient type, and the interactions among these factors as fixed factors and transect as a random factor. To test how HFA varied with successional stage for the different gradients, we ran the Decomposer Ability Regression Test (DART) (Keiser & Bradford, 2017) proposed by Keiser et al. (2014) using SAS 9.4 (SAS Institute, Cary, NC) for all three gradient types together. This approach separates effects of litter quality (i.e., differences in litter decomposition rates due to differences in chemical lability), ability (i.e., effects of inherent impacts of soil source as for example driven by soil abiotic conditions and the functional.

### Table 2

<table>
<thead>
<tr>
<th>Coarse sediments</th>
<th>Early</th>
<th>Mid</th>
<th>Late</th>
</tr>
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<tbody>
<tr>
<td>Moisture (%)</td>
<td>8.17 ± 1.17</td>
<td>2.23 ± 0.49</td>
<td>22.3 ± 6.38</td>
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<tr>
<td>pH</td>
<td>6.27 ± 0.71</td>
<td>6.04 ± 0.50</td>
<td>6.95 ± 1.00</td>
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<td>Soil NH₄-N (μg/g)</td>
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<td>114.62 ± 16.7</td>
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### Table 3

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capacity of decomposer communities), and HFA (i.e. acceleration of decomposition in some soils relative to others, for example due to specialization of the decomposer community in its local environment) on litter mass loss. The regression model (eqn 1) defines the rate of decomposition ($Y_i$) by the following parameters: the litter quality index (QI) or a ranking of the chemical quality of litters within a gradient ($\beta_i$), the inherent functional capacity of soils (the ability metric) ($\gamma_s$), and HFA or the advantage of litter decomposing in its home soil ($\eta_h$). Litter, Soil, and Home 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 $\beta_i$, $\gamma_s$ and $\eta_h$ (Keiser et al., 2014). The average decomposition across all data ($i$) in a dataset, after controlling for litter, soil and home combinations, is represented by the intercept ($a$), and the error term is defined by $\epsilon$. The $\beta_i$ and $\gamma_s$ are restricted to prevent perfect collinearity.

$$Y_i = a + \sum_{i=1}^{N} \beta_i \text{Litter}_i + \sum_{i=1}^{M} \gamma_s \text{Soil}_s + \sum_{h=1}^{K} \eta_h \text{Home}_h + \epsilon_i$$ (1)

Under a single model (3 gradients × 3 successional stages × 2 time points × 6 replicates), litter mass loss was a function of litter source, soil source and the “home” combinations. Each model had 12 restriction terms: one for the soils and one for the litters of each of the three gradients at each time point. Because the DART model is a regression, the results provide one parameter estimate for each response variable (i.e. HFA, ability and litter quality) for each successional stage and not for each replicate within that stage. The DART model provides statistical evaluation of differences between successional stages within a gradient for each of the response variables. Using t-tests, we evaluated how in HFA, ability and litter quality differed between successional stages within each gradient. In addition, we also calculated HFA as the percentage of additional decomposition at home (ADH; modified from Ayres et al. (2009) and as used by Giesselmann et al. (2011)) to calculate an individual ADH value for each replicate. We used ADH as a response variable in stepwise (both forward and backward steps) multiple regression analyses with litter chemical (i.e. litter C, N, P and lignin content and their ratios) or soil abiotic properties (i.e. pH, soil organic matter content, soil C, N and P and their ratios, NO3-N and NH4-N concentrations) as predictor variables. In this way, we explored whether and which litter chemical and soil abiotic properties are important for explaining HFA. All models also included gradient type as a predictor variable. Model fit was determined based on AIC, where a difference of more than two AIC points was considered an improvement of the model fit.

Data analysis was performed in R version 3.2 (Team, R.D.C. 2013). For general linear models, we used the `lmertest` package (Kuznetsova, Brockhoff, & Christensen, 2013). Data were tested for normality with a Shapiro test and for homogeneity of variances with a Levene’s test. For stepwise regression analyses, we used `stepaic`. DART regression analysis was performed in SAS.

### 3 | RESULTS

#### 3.1 | Soil abiotic properties and litter chemical composition

Soil abiotic properties were affected by interactions between successional stage and gradient type (Table 2 and Table S1). Generally, soil organic matter content, soil N content, soil C:P ratios and soil N:P ratios increased and pH decreased during succession, but this trend was not significant for SOM and soil C:P ratios in ex-arable fields and for soil N content in both ex-arable fields and drift sands. For the two primary successional gradients (i.e. coastal dunes and drift sands), soil moisture was lowest in early-successional stages, but it was not different among successional stages in ex-arable fields. Soil nitrate availability was lowest and soil C:N ratio highest in early-successional stages for coastal dunes but did not differ with stage for the other two gradients.

Litter chemical composition was affected by interactions between successional stage and gradient type (Table 3 and Table S2). For coastal dunes, early-successional stage litter had the highest C:N, C:P, lignin:N and lignin:P ratios, indicating that this litter was the most chemically recalcitrant. In contrast, for drift sands and ex-arable fields, these ratios were highest in late-successional stages, indicating a transition from labile to recalcitrant litter with successional age. Litter N:P ratios did not change with succession in coastal dunes, but were, or tended to be, highest in the late-successional stages for the other two gradients.

#### 3.2 | Litter mass loss

Litter mass loss was affected by two- and three-way interactions between litter source, soil source and gradient type (Table 4, Figure 1), indicating that the effect of soil and litter source on mass loss differed between the three gradient types. For drift sands and ex-arable fields, mass loss of late-successional litter was less than that of early- and mid-successional litter, while mass loss was not significantly different between litter sources in the case of coastal dunes (Figure 1). For ex-arable fields, mass loss was less for litter incubated in late-successional soils than for litter incubated in mid- or early-successional soils, while this was not different for the other two gradients (Figure 1). Litter mass loss was also affected by a two-way interaction between harvesting time and gradient type, because after 4 months, mass loss was highest in ex-arable fields and lowest in drift sands, while after 12 months mass loss was highest in dunes and lowest in drift sands.

#### 3.3 | DART: Home-field advantage, ability and litter quality

The DART regression analysis revealed that across all gradients, successional stage did not drive differences in home-field effects ($F_{2,9} = 0.28, p = .765$) and there were no interactive effects of successional stage and gradient type on home-field effects.
TABLE 3  Mean values (± SE) for litter chemical properties of each successional stage (early, mid, late) in each type of successional gradient

<table>
<thead>
<tr>
<th></th>
<th>Coastal dunes</th>
<th>Drift sands</th>
<th>Ex-arable fields</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Mid</td>
<td>Late</td>
</tr>
<tr>
<td>Litter C (%)</td>
<td>47.0 ± 0.63&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>49.6 ± 0.69&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>46.4 ± 0.53&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Litter N (%)</td>
<td>0.57 ± 0.04&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.32 ± 0.12&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.38 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Litter P (%)</td>
<td>0.07 ± 0.01&lt;sup&gt;cde&lt;/sup&gt;</td>
<td>0.12 ± 0.01&lt;sup&gt;bcd&lt;/sup&gt;</td>
<td>0.14 ± 0.02&lt;sup&gt;abc&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lignin (%)</td>
<td>16.9 ± 0.43&lt;sup&gt;c&lt;/sup&gt;</td>
<td>21.7 ± 1.30&lt;sup&gt;c&lt;/sup&gt;</td>
<td>16.6 ± 0.81&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lignin:N (%)</td>
<td>30.6 ± 2.29&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>17.3 ± 2.14&lt;sup&gt;de&lt;/sup&gt;</td>
<td>12.1 ± 0.58&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lignin:P (%)</td>
<td>269.3 ± 31.8&lt;sup&gt;bcd&lt;/sup&gt;</td>
<td>212 ± 42.5&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>133 ± 27.5&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Differences between successional stages were tested using a general linear model (Table S2) followed by Tukey’s HSD test. Within each type of gradient, numbers within rows followed by different letters are significantly different at p < .05.
gradient-specific effects of successional stage on ability. For coastal dunes, ability was higher in mid- than early- successional stages at 4 and 12 months ($t = 2.44, p = .026, t = 3.53; p = .003$) and late-successional stages at 4 months ($t = 2.56, p = .020$). For drift sands, ability was positive in mid-successional stages and higher than in early ($t = 2.82, p = .012$) and late-successional soils ($t = 4.24, p < .001$) at 12 months. For ex-arable fields, ability was positive in early-successional soils and negative in late-successional soils (Figure 2a,p), and differed significantly between these two stages ($t = 8.091, p < .001$) and between mid- and late-successional stages ($t = 6.63, p < .001$) at 4 months and between early- and mid- ($t = 2.52, p = .022$) and early and late stages ($t = 4.19, p < .001$) at 12 months. For ex-arable fields, ability was high in stages with a high litter quality index, that is in stages with chemically labile litter types (Figure 2, Table 3).

The litter quality index from the DART model, an estimate for the decomposability of a litter type, was affected by an interaction between successional stage and gradient type ($F_{2,9} = 33.66, p < .001$), indicating gradient-specific effects of successional stage on litter quality. For coastal dunes, the litter quality index was lower for early- than for late-successional litter at 4 months ($t = −2.62, p = .018$). In contrast, for early-successional litter from both drift sands and ex-arable fields, where succession progresses from early-successional grasses to pine- and birch forest, the litter quality index changed from positive to negative with successional time (Figure 2k,l,q,r) at both 4 and 12 months. Across both time points, the drift sands litter quality index was lowest in the late-successional stage (compared to early: $t = 5.91, p < .001$; early-mid: $t = 2.39, p = .029$; and late-mid: $t = 5.85, p < .001$ at 4 and 12 months, respectively). For ex-arable fields, the litter quality index differed between all successional stages at 4 months (early-mid: $t = 3.71, p = .002$, early-late: $t = 24.84, p < .001$, mid-late: $t = 8.10, p < .001$) and was lower for late-successional stages than for early- ($t = −6.46, p < .001$) and mid-successional stages ($t = −5.92, p < .001$) at 12 months. The litter quality index extracted from the DART model was generally consistent with changes in litter chemical quality within each of the successional gradients (Table 3). The lowest litter quality index occurred in
stages with the most chemically recalcitrant litter (i.e. high C:N, C:P, lignin:N and lignin:P ratios) and the highest index estimate occurred for stages with the most labile litter (i.e. low C:N, C:P, lignin:N and lignin:P ratios) (Figure 2e,f,k,l,q,r).

4 | DISCUSSION

In this study, we tested how litter mass loss was impacted by home-field advantage (i.e. the specific affinity between litter and soil), and by ability (i.e. inherent differences between soil sources) along successional gradients. In contrast to our hypothesis, the effects on litter mass loss of neither HFA nor ability varied consistently with successional stage; instead, shifts in HFA and ability with successional stage were specific to each of the gradient types. For the primary successional gradients (i.e. coastal dunes and drift sands), ability was highest in mid-successional soils and there was no pattern for HFA. However, in the secondary successional gradient (i.e. ex-arable fields) HFA increased and ability decreased towards later-successional stages. Across all gradients, home-field effects tended to increase with increasing C content in litter and organic matter content in soil, and decreased with higher P content in litter and N content in soil. This points at the role of external environmental factors in explaining the occurrence and magnitude of HFA. Below we discuss our findings and highlight the implications for how soil decomposer communities may drive nutrient cycling and plant-soil feedback across successional gradients.

Overall, HFA and ability did not vary consistently along the successional gradients. This contrasts with our hypothesis predicting that HFA should become stronger at later-successional stages because decomposer communities may become more specialized as intimate relationships between litter and decomposer communities
have more time to develop (Morriën et al., 2017). Also, our finding is inconsistent with our hypothesis that ability would increase with successional stage as a result of soil communities becoming increasingly familiar with a greater variety of litter types (Keiser et al., 2014) during the course of succession. Regardless, we found gradient-specific shifts in home-field effects and ability between successional stages. Home-field effects increased and ability decreased with successional time in ex-arable fields, while for coastal dunes and drift sands, we found only few home-field effects. In contrast, ability decreased over successional time in ex-arable fields and was generally highest in mid-successional stages. This suggests that even though successional stage in itself was not an important predictor of shifts in HFA and ability effects, other environmental conditions that vary between successional stages may be driving the occurrence and magnitude of HFA and ability effects for litter mass loss (Austin, Vivanco, González-Arzac, & Pérez, 2014).

Litter quality has often been identified as a key environmental variable that explains variation in HFA and ability between sites (Fanin et al., 2016; Keiser et al., 2014; Veen, Freschet, et al., 2015). Across all gradients, we showed that high HFA was related to high litter carbon and low litter phosphorous content (Table S3) and often occurred in sites with a low litter quality index (Figure 2). This finding contrasts from those studies that found increased HFA for high-quality litters (Li et al., 2017; Perez et al., 2013), but supports the idea that recalcitrant plant litter may require specialized decomposers for its breakdown (Milcu & Manning, 2011). In addition to litter quality, our results show that edaphic characteristics, such as high soil carbon and low soil nutrient content, can also contribute to explain high HFA (Table S3). Meanwhile, we did not find consistently high or low ability in sites with a high or low litter quality index (Figure 2), suggesting that the capacity of soils to degrade litter was not directly linked to the chemical composition of the litter. This contrasts with the idea that soil communities from lower-quality environments are better equipped to degrade a broad range of organic compounds (van der Heijden et al., 2008) and therefore have a higher ability (Fanin et al., 2016; Keiser & Bradford, 2017; Keiser et al., 2014).

The relationships we found between litter and soil characteristics and HFA were neither very strong nor consistent. For example, HFA increased with increasing litter carbon content, but decreased with increasing litter C:N ratios, making it hard to predict whether HFA increases or decreases for more recalcitrant litters. This finding indicates that environmental factors other than those that we have measured also play a role determining HFA and ability (Veen, Sundqvist, et al., 2015), for example current soil enzymatic activity. Moreover, in our study we have used naturally occurring litter mixes and a full soil matrix, which enables interactions between litter types and soil biotic and abiotic properties. In litter mixes, individual litter types can each develop their own specialized decomposer community (Freschet et al., 2012; Perez et al., 2013) leading to neutral HFA on average (Chomel, Guittionny-Larchevêque, DesRochers, & Baldy, 2015; Jewell, Shipley, Paquette, Messier, & Reich, 2015; Veen, Sundqvist, et al., 2015). Moreover, high-quality carbon sources in some litter types may prime the breakdown of recalcitrant compounds (Gartner & Cardon, 2004; Klotzbucher, Kaiser, Guggenberger, Gatzek, & Kalbitz, 2011) regardless of specialization by the decomposer community. Finally, in a soil matrix, abiotic conditions can interact with soil communities to drive decomposition processes. This could potentially mask or modify the effect of specific interactions (due to specialized decomposer communities or specific soil abiotic conditions) between litter and soil sources (Austin et al., 2014). The finding that early-successional stages in ex-arable fields experienced negative home-field effects also suggests that home-field effects are unable to be explained solely by specialization by decomposer communities and that other factors such as accumulation of toxins (Mazzoleni et al., 2015) and of other microbes (Kardol et al., 2006) that impair decomposer microbes could also play a role.

5 CONCLUSIONS

We show that the magnitude and direction of HFA and ability effects on litter mass loss vary along successional gradients. Variation in HFA does not consistently change with successional stage among the three gradient types, but is partly contingent on specific variation in litter chemical properties and soil abiotic conditions that occurs along each of the three gradients. Our results highlight that the impact of HFA and ability on decomposition varies greatly between sites, suggesting that the consequences of specific interactions between plant litter and soil conditions for litter mass strongly depend on site-specific environmental conditions. How these interactions play out will determine the rate and timing of nutrients released from plant litter and thereby the feedback of decomposition processes to plant growth and performance (Wardle et al., 2004). Studies focusing on plant-soil feedback effects have mostly considered direct interactions between plants and soil communities (i.e. via pathogens and mutualists), while only a few focused on indirect interactions between litter and decomposer communities (e.g. Berendse, 1998; Kardol, Veen, Teste, & Perring, 2015; Zhang, Van der Putten, & Veen, 2016). Therefore, to fully understand plant-soil feedback effects and their role in the functioning of terrestrial ecosystems including feedbacks between plants, plant litter and decomposer communities are necessary.

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DATA ACCESSIBILITY

Litter mass loss and environmental data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.07hc0m4 (Veen, Keiser, Van der Putten, & Wardle, 2018).

ORCID

G. F. (Ciska) Veen http://orcid.org/0000-0001-7736-9998

REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.