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REGULAR ARTICLE

Landscape context mediates the relationship between plant functional traits and decomposition

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Abstract
Aims It has been well demonstrated that several interacting endogenous and exogenous factors influence decomposition. However, teasing apart the direct and indirect effects of these factors to predict decomposition patterns in heterogenous landscapes remains a key challenge.
Methods At 157 locations in a temperate forest, we measured decomposition of a standard substrate (filter paper) over two years, the landscape context in which decomposition took place, and the functional composition of the woody species that contributed leaf litter to the forest floor where litter bags were placed. We tested for direct and indirect effects of landscape context and direct effects of forest functional composition on decay using structural equation modelling.
Results We found that landscape context had direct effects on decay and indirect effects on decay via its influence on the functional composition of the surrounding forest. Forest functional composition also had direct effects on decay, but these effects decreased or disappeared completely over time. Moreover, community weighted mean trait values were better predictors of decay than functional dispersion of leaf traits, and leaf nitrogen content and carbon content were better predictors of decay than leaf dry matter content or leaf toughness.
Conclusions Our results highlight the importance of an integrative approach that examines the direct and indirect effects of multiple factors for understanding and predicting decomposition patterns across heterogenous landscapes.

Keywords Decomposition · Functional diversity · Plant functional traits · Litter bags · Mass loss · Ozark oak-Hickory forest · Tyson research center plot

Introduction

Decomposition is a key ecosystem function that influences nutrient cycling and soil organic matter formation (Bardgett and Shine 1999; Meier and Bowman 2008a; Wardle et al. 2004) and it is clear that a host of interacting endogenous and exogenous factors influence decomposition (i.e., Bardgett and Shine 1999; Cornwell et al. 2008; Gessner et al. 2010; Hattenschwiler et al. 2005; Hobbie 2005; Melillo et al. 1982; Vitousek 1998; Zanne et al. 2015). For example, litter decomposition is influenced by endogenous factors such as the diversity of chemical (Meier and Bowman 2008a; Stoler et al. 2016; Talbot and Treseder 2012) and morphological

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traits in the litter (Cornwell et al. 2008; Santiago 2007) as well as exogenous factors such as broad-scale climate (Aerts 1997; Fierer et al. 2005; Hobbie 1996) and local-scale topographic position and landscape context (Dwyer and Merriam 1981; Olear and Seastedt 1994; Zanne et al. 2015). For all the progress enumerating the many exogenous and endogenous factors that influence decomposition, predicting litter decomposition across heterogeneous landscapes has still proven challenging (Zanne et al. 2015).

Part of the challenging in predicting decomposition, is that it is increasingly being demonstrated that multiple direct and indirect drivers interact to influence decomposition (Bradford et al. 2014; Cornwell and Ackerly 2009; Zanne et al. 2015). For example, soil fertility may have direct effects on decomposition, where decomposition is accelerated in more fertile soils (Bardgett and Wardle 2010; Hobbie 2005). Concurrently, soil fertility may also have indirect effects on decomposition where more fertile soils result in plants with higher tissue nitrogen content or lower leaf dry mater content (LDMC) (Cornwell and Ackerly 2009; Reich et al. 1997; Spasojevic and Suding 2012; Westoby et al. 2002), which decompose more rapidly due to variation in these chemical and morphological traits (Cornwell et al. 2008; Santiago 2007). While some experimental studies are beginning to jointly test the relative importance of exogenous and endogenous factors (i.e., Midgley et al. 2015; Szefer et al. 2017; Zanne et al. 2015), these studies generally do not address indirect effects.

Here, we examined landscape scale variation in decomposition of a standard substrate (filter paper) in a temperate deciduous Oak-Hickory forest to better understand the multiple direct and indirect drivers of decomposition. Specifically, we asked how landscape context (soil fertility and topographic position) directly influenced decomposition, and how landscape context indirectly influenced decomposition via its effect on forest functional composition. We focus on forest functional composition (the functional traits of the living trees in the forest) rather than the functional traits of the leaf litter on the forest floor as a secondary objective to test how well plant functional traits predict decomposition. While decomposition experiments are often logistically challenging – as deploying, monitoring and harvesting litterbags can be resource intensive – there has been a proliferation of available leaf trait data (Kattge et al. 2011; Maitner et al. 2018) and plant functional traits associated with the leaf economics spectrum have been found to be correlated with leaf litter decomposition at local (Bakker et al. 2011; Jackrel and Wootton 2015; Santiago 2007) and global scales (Cornwell et al. 2008; Pietsch et al. 2014), suggesting that these functional traits have "after-life" effects on decomposition (Freschet et al. 2012; Jackrel and Wootton 2015; Zukswert and Prescott 2017).

Importantly, functional composition has the potential to influence decomposition via two processes: niche complementarity and mass-ratio effects (Grime 1998; Hooper et al. 2005; Tilman 1997; Tilman et al. 2014). The niche-complementarity hypothesis suggests that increasing species richness increases resource-use efficiency due to niche differentiation, which consequently enhances ecosystem function (Tilman 1997; Tilman et al. 2014). Numerous studies have now established that functional diversity metrics outperform taxonomic indices in predicting ecosystem function (Diaz et al. 2004; Garnier et al. 2004; Lavorel and Garnier 2002; Suding and Goldstein 2008), and thus, under niche-complementarity, communities with higher functional diversity should have greater decomposition as compared to communities with low functional diversity (Garcia-Palacios et al. 2017; Handa et al. 2014; Kuebbing et al. 2018). In contrast, the mass-ratio hypothesis posits that ecosystem function is controlled by the dominant species in a community (Grime 1998) and thus, the functional identity of the dominant species will have the largest effect on decomposition (i.e., Garcia-Palacios et al. 2017; Lin and Zeng 2018; Tardif et al. 2014). Importantly, these two processes are not mutually exclusive (Chiang et al. 2016; Garcia-Palacios et al. 2017; Mokany et al. 2008) and are likely influenced by the landscape context in which they occur (Brose and Hillebrand 2016; Mori et al. 2018; Tylianakis et al. 2008).

To address our questions, we used structural equation modeling to examine how decay was influenced by the direct and indirect effects of landscape context and by the direct effects of the forest functional composition. To describe the landscape context, we quantified 14 soil and 5 topographic variables over an area of 12 ha – this spatial scale includes a representative range of habitat types found in typical oak-hickory forests (e.g., east-facing slopes, north-facing slopes, ridges, southwest-facing slopes, west-facing slopes, valleys). We quantified the functional composition of the forest where each litter bag was placed using functional dispersion (FDis) and community weighted mean trait values (CWM) of leaf dry matter content (LDMC), leaf toughness, leaf N content, and leaf carbon (C).

Methods

Study site This study was conducted at Washington University in St. Louis' Tyson Research Center, located 25 miles (40 km) southwest of Saint Louis, Missouri (38° 31' N, 90°33'W; mean annual temperature 13.5°C; mean annual precipitation 957 mm). The research center is situated on the northeastern edge of the Ozark ecoregion in a temperate deciduous forest dominated by oak and hickory species. This site has been relatively undisturbed for 80+ years, with tree cores indicating 120–160 year old trees in the early 1980's (Hampe 1984). The soil at this site includes silty loams and silty clays that develop from shale limestone, limestone, cherty limestone and chert formations (Zimmerman and Wagner 1979).

Our study site was located within a 25-ha (500 × 500 m), stem-mapped, forest-dynamics plot (the Tyson Research Center Plot), that is part of a global network of forest-ecology plots coordinated through the Smithsonian Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) (Anderson-Teixeira et al. 2015). This site includes strong edaphic and topographic gradients characteristic of oak-hickory forests in the Ozark region. Elevation at our study site ranges from 172 to 233 m (mean = 206 m) and slope ranges from 0.8–26.9° (mean = 13.8°) at the 20 × 20 m scale.

Litter bags In this ecosystem, decomposition is relatively slow (Kucera 1959; Li et al. 2009) and leaf litter accumulates on the forest floor (Rochow 1974). Since litter on the forest floor can influence the decomposition of litter bags through mixing effects (e.g., Chadwick et al. 1998; Gartner and Cardon 2004; Nilsson et al. 1999), we used a standard substrate (filter paper) to examine landscape-level variation in mass loss and decay among habitat types while minimizing the impact of litter mixing effects. To determine how decomposition rates varied across this landscape, we placed litterbags at 157 locations within a 12-ha subsection of the TRCP (Figure S1) which included each of the key habitat types found in typical oak-hickory forests. Locations were chosen based on their proximity to established seedling plots and seed traps where soil resources and plant functional traits have been previously measured (Spasojevic et al. 2016; Spasojevic et al. 2014). Each litter bag location was in a separate 10x10m quadrat of the forest plot.

Litter bags were constructed from 1-mm nylon mesh and filled with four pieces (~ 4 g) of Qualitative Grade Plain Filter Paper Circles (Fisher Scientific), sealed with rustproof staples and weighed prior to deployment. We deployed 10 replicate litter bags at each of the 157 locations for a total of 1570 litter bags. Prior to deployment pairs of bags were attached together with a ~0 .5m string of fishing line, resulting in 5 pairs of bags. Each group was attached to a stake in the field 1 m apart from each other and placed on the surface. All bags were deployed on 09 November 2013 at the end of the growing season. At each location, one pair of samples (two litter bags) were collected after 0 days to account for any mass loss due to transport to the field. Subsequent collections were conducted after 154 days (12 April 2014) at the beginning of the next growing season, after 350 days (25 October 2014) at the end of that growing season, after 532 days (24 April 2015) at the beginning of the second growing season, and finally after 706 days (15 October 2015) at the end of the second growing season. Upon collection all litter bags were oven dried at 60 °C for four days and weighed to ±0. 01 g to determine mass loss. Observed mass loss was determined by subtracting the fill weight at each collection time from the initial fill mass, corrected for loss from transport (mass loss on the 09 November 2013 collection). Some litter bags were lost in the field resulting in variable samples sizes at the four-time points: 154 days, $n = 281$; 350 days, $n = 305$; 532 days, $n = 269$; and 706 days, $n = 298$.

Landscape context To describe variation in environmental conditions that may influence decomposition, we conducted a principal components analysis (PCA) of 14 soil and 5 topographic variables measured in the TRCP including: available nitrogen (N), N mineralization rates, base saturation, effective cation exchange capacity (ECEC), exchangeable cations (Al, Ca, Fe, K, Mg, Mn, Na), pH, plant-available phosphorous (P), total exchangeable bases (TEB), aspect, convexity, mean elevation, and slope (see Spasojevic et al. 2014 for details). Since aspect is a circular variable, we used sin(aspect) and cosine(aspect) in our analyses (Legendre et al. 2009). All variables were scaled prior to PCA. Since our primary focus was to test the landscape-scale drivers of decomposition, rather than to compare the importance of different environmental variables, we focus on the first three axes of the PCA to describe variation in soil-resource availability (Figure S2). The first three PC axes together explained 71.7% of the variation in soil and topographic variables. PC1 (50.1% of the explained variation) characterizes a gradient ranging from low soil-resource availability (e.g., higher Al, Fe, and lower Ca, K, Mg, Mn, P, K, pH) and higher elevation, south-facing aspects to high soil-resource availability (e.g., lower Al, Fe, and higher Ca, K, Mg, Mn, P, K, pH) and lower elevation north-facing aspects. PC2 (11.1%) characterizes gradients in NO_3, Total N, and convexity. PC3 (10.4%) characterizes gradients in slope and NH_4. Together, these PCA axes provide a continuous measure of habitat type in this forest.

Functional composition To describe variation in forest functional composition that may be related to decomposition, we calculated community weighted mean (CWM) trait values and community functional dispersion (FDis) for each 10x10m quadrat (local forest community) in which litter bags were placed. Here we focus on four putatively important traits with the potential to influence decomposition (Cornwell et al. 2008; Garcia-Palacios et al. 2016; Santiago 2007) – two associated with leaf morphology (leaf dry matter content (LDMC) and leaf toughness), two associated with leaf chemical composition (leaf nitrogen (N) content, and leaf carbon (C) content). While other traits (e.g., lignin, Ca, Mg) are often better predictors of decay, our goal here was to assess the predictive power of these four commonly measured plant functional traits (Cornwell et al. 2008; Freschet et al. 2012; Jackrel and Wootton 2015; Santiago 2007; Zukswert and Prescott 2017).

Trait data were collected previously (see Spasojevic et al. (2014) and Spasojevic et al. (2016) for details) on 795 individuals of the 40 forest tree and shrub species located across the 12 ha plot. In brief we collected 3 leaves from the upper-crowns of each individual and the number of individuals sampled per species ranged from1–57 individuals based on the relative abundances of each species within the 12 ha forest plot (i.e., the species with only 1 individual sampled had only 1 individual tree in the 12 ha plot). We then calculated community-weighted mean (CWM) trait values for each quadrat as the abundance-weighted trait averages (Garnier et al. 2004) of each trait. We calculated FDis for each trait individually, as the mean distance of each species in trait space to the centroid of all species using the dbFD function in the FD package in R (Laliberte and Legendre 2010). FDis is statistically independent of species richness (Laliberte and Legendre 2010). In both cases we used trait values for these quadrat level calculations that came from individuals measures within the habitat type in which that quadrat is located. Here, we focus on individual trait analyses because ecological processes may be masked by multivariate trait indices that integrate traits with potentially opposing influences on our response variables (Spasojevic and Suding 2012). We additionally conducted the below described structural equation model using all four traits together in one model, but our data did not fit the proposed model.

Statistical analysis

To assess how decomposition varies across space and time in this landscape, we first examined patterns of mass loss across habitat types within each time point. While not the primary focus of our analysis, we include this analysis to show general pattern in mass loss to provide a more complete picture of landscape scale variation in decomposition (See Appendix 1). We examined differences in mean mass loss across habitat types using general linear models and used Tukey post-hoc comparisons to evaluate differences in means among habitat types using JMP version 10 (SAS Institute Inc., Cary, N.C.).

Next, we estimated exponential decay constants from mass loss data for each time point as $k = -\ln(\text{dry mass at time } t \text{ per initial dry mass})$ following (Olson 1963). Replicates of litter bags at a given location and time point ($n = 2$) were averaged. We then analysed the univariate relationships among k, FDis, CWM trait values, and landscape context (the first three principal components of the above PCA) to test for non-linear relationships among our variables and to aid in the interpretation of our results. We tested for linear and quadratic relationships for each response measure and selected the best fit using Akaike Information Criteria (Burnham and Anderson 2004). Prior to analysis, k was log-transformed. We then used structural equation models to investigate links among landscape context, FDis, CWM trait values, and k.

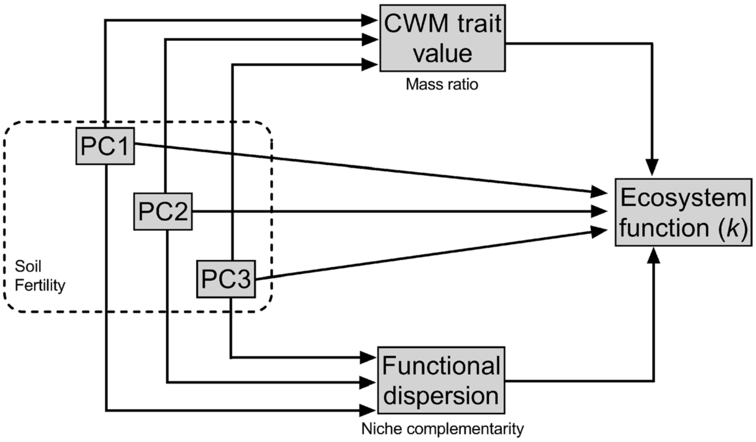


Fig. 1 General form of the structural equation model used to evaluate how landscape context (PC1–3: the first three axes from a principal components analysis), community weighted mean (CWM) trait values, and functional dispersion (FDis) of tree communities is related to decomposition. k is the exponential decay constant from mass loss data for each time point calculated as $k = -\ln(\text{dry mass at time } t \text{ per initial dry mass})$ following Olson (1963)

To test the relative influence of landscape context, FDis, and CWM trait values on decay (k) we then built an initial model (Fig. 1) that included the direct effects of the landscape context, FDis, and CWM trait values on k and the indirect effect of the landscape context via its influence on FDis, and CWM trait values. In our model, we only considered the bottom-up effect of soil resources on FDis and CWM trait values even though forest functional composition likely also influence the soil resource availability. However, such an analysis is beyond the scope of our study and would necessitate more dynamic measurements of soil resource availability.

For each of our models, we first assessed model fit with three indices: chi-square (χ^2) tests, root mean square error of approximation (RMSEA) and goodness-of-fit index (GFI); χ^2 values associated with a P value >0.05 (suggesting that observed and expected covariance matrices are not different), RMSEA <0.05, and GFI > 0.95 indicate a good model fit (Kline 2010). After our initial model runs, we then used the "modindices" function to find paths whose elimination from the model would result in the greatest improvement in the overall chi-square value until we found the best fitting model (the model with the lowest Akaike information criterion (AIC) score). Path analysis was conducted using the Lavaan package (Rosseel 2012) implemented in R (R Core Team 2017). In Figs. 3 and 4, non-significant pathways (arrows) have been removed (as compared to the initial model; Fig. 1) and marginally significant pathways ($0.10 < p < 0.05$) are represented by a dashed line. It is important to note that when interpreting path analyses, consistency between our statistical model and data does not mean that our interpretations are correct, only that the data are consistent with our interpretations (McCune and Grace 2002).

Results

Mass loss Considerable variation in mass loss occurred over time and across habitat types (Fig. 2; Appendix 1). Mass loss significantly differed among habitat types at all time points, but was generally found to be greater in

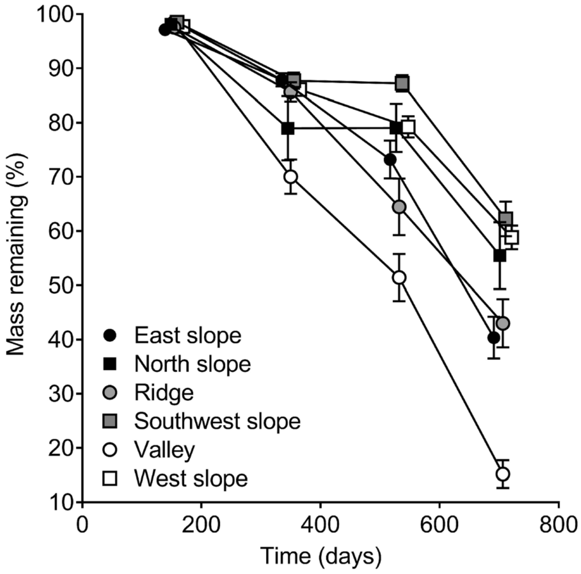


Fig. 2 Mean (± SE) values for % mass loss across six habitat types in an Ozark Oak-Hickory forest after 154 ($n = 281$ litter bags), 350 ($n = 305$ litter bags), 532 ($n = 269$ litter bags), and 706 ($n = 298$ litter bags) days in the field. Data points have been nudged around each time point to increase visibility

Table 1 Goodness of fit measures - chi-square (χ^2) tests, root mean square error of approximation (RMSEA) and goodness of fit index (GFI) - for each of the 16 models

Trait	Time period	$\chi 2$	df	P value	RMSEA	GFI	k R^2
LDMC	1	0.400	2	0.819	0.000	0.999	0.409
	2	0.858	3	0.836	0.000	0.998	0.157
	3	0.251	1	0.616	0.000	0.999	0.233
	4	0.123	1	0.726	0.000	1.000	0.309
Leaf Toughness	1	0.914	1	0.339	0.000	0.998	0.441
	2	1.352	1	0.245	0.048	0.997	0.147
	3	1.154	1	0.219	0.060	0.997	0.245
	4	3.760	2	0.153	0.076	0.992	0.294
Leaf N	1	0.896	2	0.639	0.000	0.998	0.439
	2	1.141	2	0.565	0.000	0.998	0.191
	3	0.983	2	0.612	0.000	0.998	0.229
	4	0.125	1	0.680	0.000	0.999	0.333
Leaf C	1	2.785	2	0.249	0.050	0.994	0.450
	2	0.198	1	0.656	0.000	0.999	0.166
	3	0.196	1	0.658	0.000	0.999	0.243
	4	0.119	1	0.730	0.000	1.000	0.310

χ^2 values associated with a P value >0.05 (suggesting that observed and expected covariance matrices are not different), a RMSEA <0.05, and a GFI > 0.95 indicate a good model fit (Kline 2010). Traits include leaf dry matter content (LDMC), leaf toughness, leaf nitrogen content (Leaf N), leaf carbon content (Leaf C). Time periods T1–4 indicate decay after 154, 350, 532, and 706 days in the field respectively. k R^2 = r-squared value for each model for decay (k)

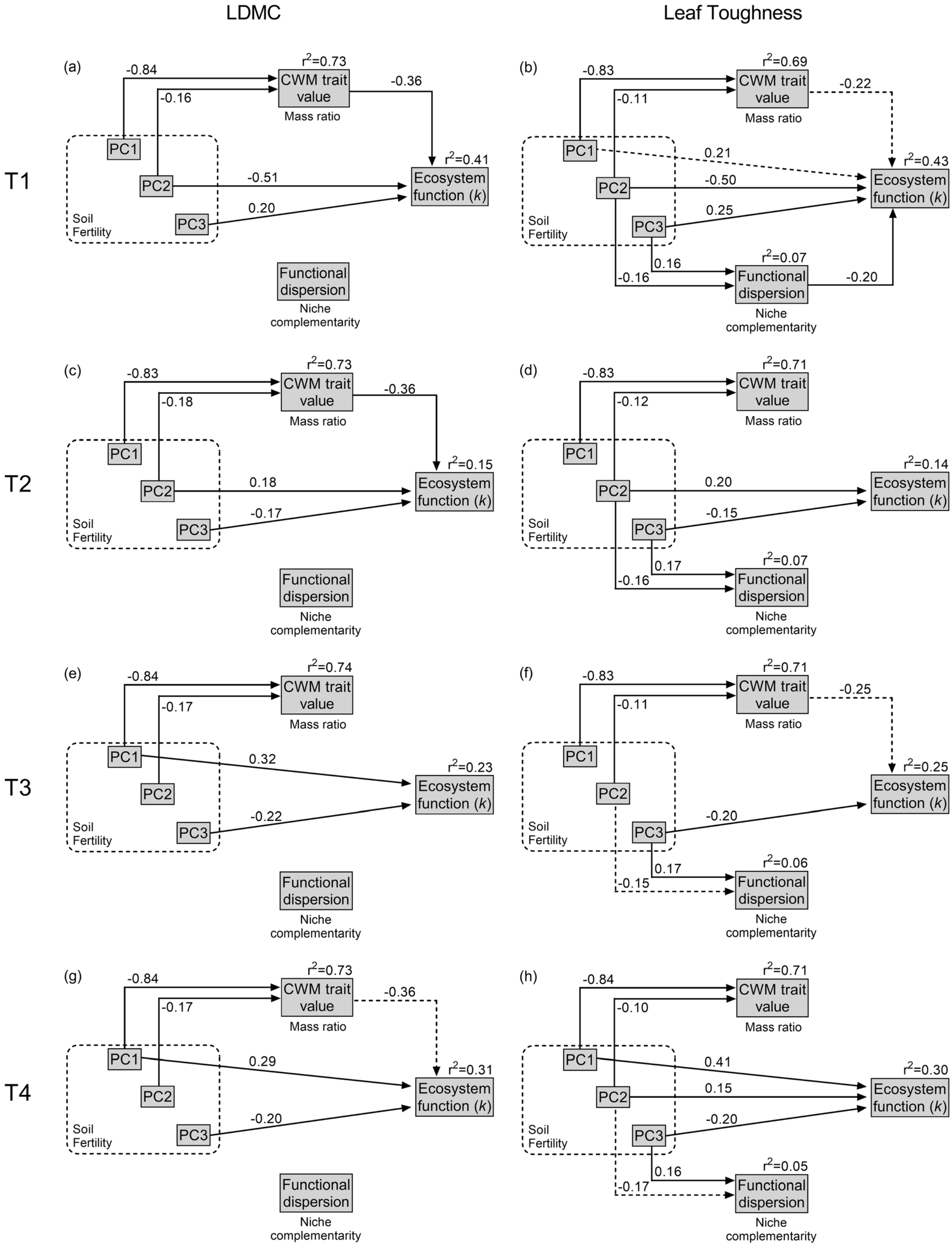
Valleys, East slopes, and Ridges and lowest on Southwest slopes and West slopes (see Appendix 1 for details). While these categorical habitat classifications are useful for understanding broad scale patterns of decompositions, in the below analysis we use the first three axes of the above described PCA, which better describe the variation among habitat types.

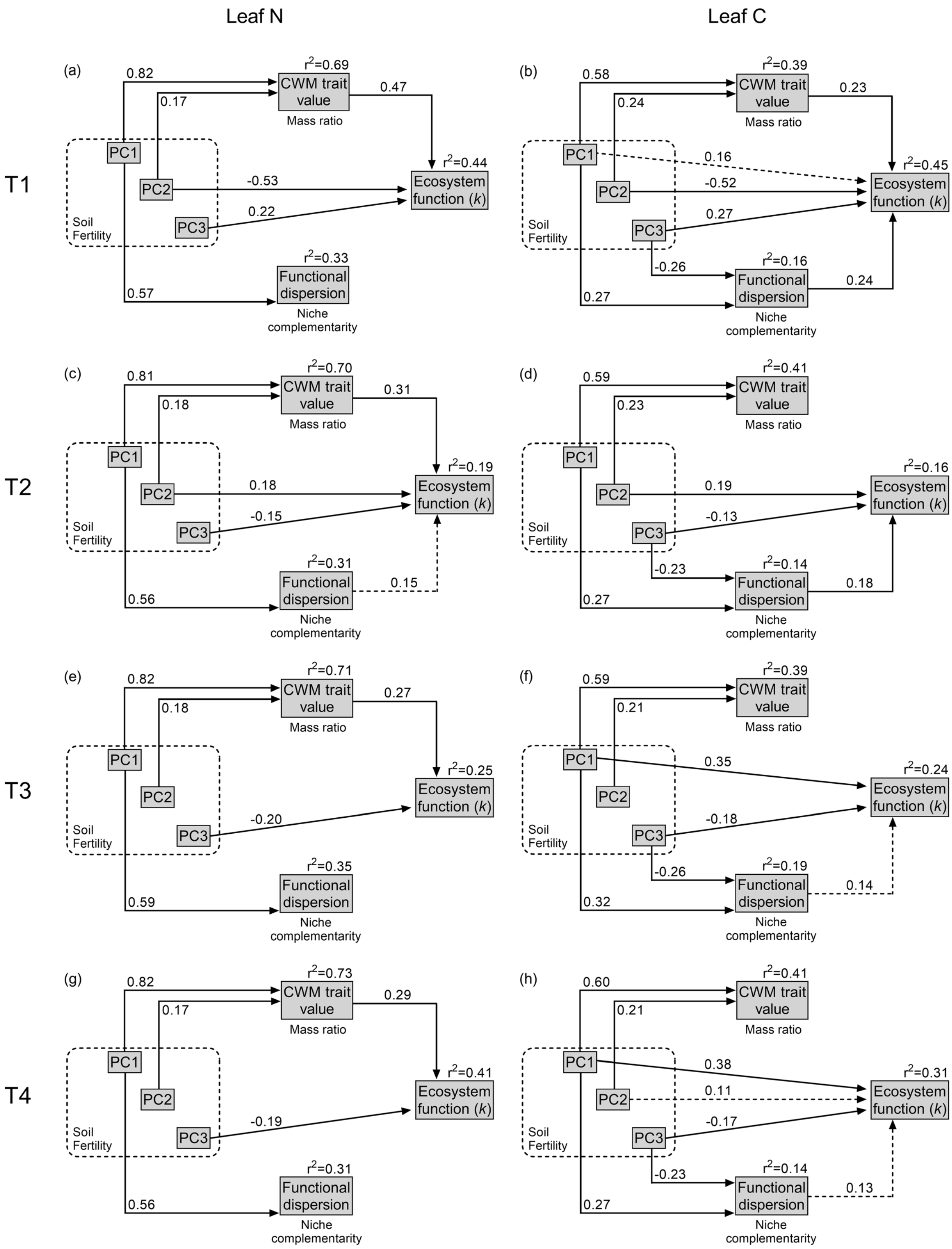
Decay (k) In general, we found that the effects of leaf traits on decomposition were stronger in the initial time periods and decreased or disappeared completely over time while the effects of environmental conditions were more stable and consistent over time. All models were found to generally have a good fit to the data (Table 1), but the amount of variation in decay (k) and the drivers of decay varied both over time and among leaf traits (Figs. 3 and 4, Tables 2 and 3).

We found that FDis of LDMC had no influence on decay, but we found a significant effect of CWM LDMC on decay in times 1 and 2 (Fig. 3, Table 2) where decay was higher in communities where leaves had lower LDMC. However, this effect of CWM was absent at time 3 and only marginally significant by time 4 (Fig. 3, Table 2). In contrast we found that PC3 (slope and NH_4 concentrations) directly influenced decay at all four-time points, PC2 (NO_3, Total N, and convexity) directly influenced decay at time 1 and 2 and had significant indirect effects at time 1 and 2 via its effect on CWM LDMC. PC1 (Al, Fe, Ca, K, Mg, Mn, P, K, pH) directly influenced decay at times 3 and 4 and had a marginally significant indirect effect at time 4 via its effect on CWM LDMC. In general, PC1 and PC2 explained between 73 and 74% of the variation in CWM LDMC. The relative strength and directionality of the environmental variables varied over time (Fig. 3, Table 2).

For leaf toughness, we found a significant negative effect of FDis on decay at time 1 only, and marginally

Fig. 3 Structural equation model testing the relative importance of CWM traits values, FDis, and landscape context on decomposition (k) for morphological leaf traits (leaf dry matter content (LDMC) and leaf toughness) across four time periods (T1-T4). CWM = community weighted mean trait values. PC1–3 = landscape context based on the first three axes of a principal components analysis of 14 soil and 5 topographic variables. Path coefficients are standardized prediction coefficients (Grace and Bollen 2005). Pathways not found to be influential (non-significant $P > 0.1$) are removed and marginally significant pathways ($P < 0.1$ and $P > 0.05$) are represented by dashed lines ▶


LDMC
Leaf Toughness
T1
T2
T3
T4
(a)
-0.84
-0.16
r^2=0.73
CWM trait value
Mass ratio
-0.36
PC1
PC2
PC3
Soil Fertility
-0.51
0.20
r^2=0.41
Ecosystem function (k)
Functional dispersion
Niche complementarity
(b)
-0.83
-0.11
r^2=0.69
CWM trait value
Mass ratio
-0.22
PC1
0.21
PC2
-0.50
PC3
0.25
r^2=0.43
Ecosystem function (k)
Soil Fertility
0.16
-0.16
r^2=0.07
Functional dispersion
-0.20
Niche complementarity
(c)
-0.83
-0.18
r^2=0.73
CWM trait value
Mass ratio
-0.36
PC1
PC2
0.18
PC3
-0.17
r^2=0.15
Ecosystem function (k)
Soil Fertility
Functional dispersion
Niche complementarity
(d)
-0.83
-0.12
r^2=0.71
CWM trait value
Mass ratio
PC1
PC2
0.20
PC3
-0.15
r^2=0.14
Ecosystem function (k)
Soil Fertility
0.17
-0.16
r^2=0.07
Functional dispersion
Niche complementarity
(e)
-0.84
-0.17
r^2=0.74
CWM trait value
Mass ratio
PC1
0.32
PC2
PC3
-0.22
r^2=0.23
Ecosystem function (k)
Soil Fertility
Functional dispersion
Niche complementarity
(f)
-0.83
-0.11
r^2=0.71
CWM trait value
Mass ratio
-0.25
PC1
PC2
PC3
-0.20
r^2=0.25
Ecosystem function (k)
Soil Fertility
0.17
-0.15
r^2=0.06
Functional dispersion
Niche complementarity
(g)
-0.84
-0.17
r^2=0.73
CWM trait value
Mass ratio
-0.36
PC1
0.29
PC2
PC3
-0.20
r^2=0.31
Ecosystem function (k)
Soil Fertility
Functional dispersion
Niche complementarity
(h)
-0.84
-0.10
r^2=0.71
CWM trait value
Mass ratio
PC1
0.41
PC2
0.15
PC3
-0.20
r^2=0.30
Ecosystem function (k)
Soil Fertility
0.16
-0.17
r^2=0.05
Functional dispersion
Niche complementarity


Leaf N
Leaf C
T1
T2
T3
T4
(a)
0.82
0.17
r^2=0.69
CWM trait value
Mass ratio
0.47
PC1
PC2
PC3
Soil Fertility
-0.53
0.22
r^2=0.44
Ecosystem function (k)
r^2=0.33
Functional dispersion
Niche complementarity
0.57
(b)
0.58
0.24
r^2=0.39
CWM trait value
Mass ratio
0.23
0.16
-0.52
0.27
r^2=0.45
Ecosystem function (k)
-0.26
r^2=0.16
Functional dispersion
0.24
0.27
Niche complementarity
(c)
0.81
0.18
r^2=0.70
CWM trait value
0.31
Mass ratio
r^2=0.19
0.18
-0.15
Ecosystem function (k)
r^2=0.31
Functional dispersion
0.15
0.56
Niche complementarity
(d)
0.59
0.23
r^2=0.41
CWM trait value
Mass ratio
r^2=0.16
0.19
-0.13
Ecosystem function (k)
-0.23
r^2=0.14
Functional dispersion
0.18
0.27
Niche complementarity
(e)
0.82
0.18
r^2=0.71
CWM trait value
0.27
Mass ratio
r^2=0.25
Ecosystem function (k)
-0.20
r^2=0.35
Functional dispersion
0.59
Niche complementarity
(f)
0.59
0.21
r^2=0.39
CWM trait value
Mass ratio
0.35
r^2=0.24
Ecosystem function (k)
-0.18
-0.26
r^2=0.19
Functional dispersion
0.14
0.32
Niche complementarity
(g)
0.82
0.17
r^2=0.73
CWM trait value
0.29
Mass ratio
r^2=0.41
Ecosystem function (k)
-0.19
r^2=0.31
Functional dispersion
0.56
Niche complementarity
(h)
0.60
0.21
r^2=0.41
CWM trait value
Mass ratio
0.38
0.11
-0.17
r^2=0.31
Ecosystem function (k)
-0.23
r^2=0.14
Functional dispersion
0.13
0.27
Niche complementarity

◀ **Fig. 4** Structural equation model testing the relative importance of CWM traits values, FDis, and landscape context on decomposition (*k*) for chemical leaf traits: Leaf N and Leaf C) across four time periods (T1-T4). CWM = community weighted mean trait values. PC1–3 = landscape context based on the first three axes of a principal components analysis of 14 soil and 5 topographic variables. Path coefficients are standardized prediction coefficients (Grace and Bollen 2005). Pathways not found to be influential (non-significant P > 0.1) are removed and marginally significant pathways (P < 0.1 and P > 0.05) are represented by dashed lines. Chemical leaf traits: Leaf N and Leaf C

significant effects of CWM trait values at times 1 and 3, suggesting overall week effects of leaf toughness on decay. In the leaf toughness models, we found again that PC3 (slopes and NH_4 concentrations) significantly influenced decay at all four time points (Fig. 3, Table 2). The influence of PC1 and PC2 was more variable than in the LDMC models and we found that PC2 influenced decay at times 1, 2, and 4, while PC1 had a marginally significant effect at time 1 and a significant effect at time 4 (Fig. 3, Table 2).PC1 and PC2 explained between 69 and 71% of the variation in CWM leaf toughness and PC2 and PC3 explained between 5 and 7% of the variation in FDis of LDMC.

Leaf chemical traits had more consistent effects on ecosystem functioning than leaf morphological traits. We found that CWM leaf N concentrations had a significant effect on decay in all four-time periods, but that the strength of that effect (path coefficients) generally decreased over time (T1 = 0.47; T2 = 0.31; T3 = 0.27; T4 = 0.29). PC1 and PC2 explained between 69 and 73% of the variation in CWM Leaf N. FDis of leaf N only had a marginally significant effect at time 2 and PC1 explained between 31 and 35% of the variation in FDis of Leaf N. Environmental variables were less variable in this model with PC3 (slopes and NH_4 concentrations) significantly influencing decay at all four-time points, PC2 having direct effects at times 1 and 2, and both PC1 and PC2 having indirect effects at all four times (Fig. 4, Table 3).

Lastly, leaf carbon content was unique in that it was the only trait where FDis had a greater influence than CWM trait values. We found a positive effect of FDis on decay at all four times, though only marginally

Table 2 Direct, indirect and total standardized effects (based on structural equation modelling) of the five predictor variables on decomposition for morphological leaf traits: leaf dry matter content (LDMC) and leaf toughness

		Effect (pathway coefficient)							
		LDMC				Leaf Toughness			
Predictor	Pathway to decomposition (*k*)	T1	T2	T3	T4	T1	T2	T3	T4
FDis	Direct	NS	NS	NS	NS	**−0.20**	NS	NS	NS
CWM trait value	Direct	**−0.36**	**−0.36**	NS	*−0.36*	*−0.22*	NS	*−0.25*	NS
PC1	Direct	NS	NS	**0.32**	0.29	*0.21*	NS	NS	**0.41**
	Indirect through FDis	NS	NS	NS	NS	NS	NS	NS	NS
	Indirect through CWM trait value	**0.30**	**0.30**	NS	**0.30**	*0.18*	NS	*0.21*	NS
	Total effect	**0.30**	**0.30**	**0.32**	***0.59***	*0.39*	NS	*0.21*	**0.41**
PC2	Direct	**−0.51**	0.18	NS	NS	**−0.50**	**0.20**	NS	**0.15**
	Indirect through FDis	NS	NS	NS	NS	**0.03**	NS	NS	NS
	Indirect through CWM trait value	**0.06**	**0.06**	NS	*0.06*	*0.02*	NS	*0.03*	NS
	Total effect	**−0.45**	**0.24**	NS	*0.06*	***−0.44***	**0.20**	*0.03*	**0.15**
PC3	Direct	**0.20**	**−0.17**	**−0.22**	**−0.20**	**0.25**	**−0.15**	**−0.20**	**−0.20**
	Indirect through FDis	NS	NS	NS	NS	**−0.03**	NS	NS	NS
	Indirect through CWM trait value	NS	NS	NS	NS	NS	NS	NS	NS
	Total effect	**0.20**	**−0.17**	**−0.22**	**−0.20**	**0.22**	**−0.15**	**−0.20**	**−0.20**

Effects (pathway coefficients) describe the relative strength of the relationship between a given predictor variable and ecosystem function. Positive values indicate a positive relationship while negative values indicate a negative relationship and bold values indicated significant pathways (P < 0.05) while italics represents marginally significant pathways ($P < 0.10$). FDis = functional dispersion. CWM = community weighted mean trait values. PC1–3 = environmental conditions based on the first three axes of a principal components analysis of 14 soil and 5 topographic variables. NS = non-significant relationships. See Table 1 for trait abbreviations

Table 3 Direct, indirect and total standardized effects (based on structural equation modelling) of the five predictor variables on decomposition for chemical leaf traits: leaf nitrogen content (Leaf N) and leaf carbon content (Leaf C)

		Effect (pathway coefficient)							
		Leaf N				Leaf C			
Predictor	Pathway to decomposition (*k*)	T1	T2	T3	T4	T1	T2	T3	T4
FDis	Direct	NS	*0.15*	NS	NS	**0.24**	**0.18**	*0.14*	*0.13*
CWM trait value	Direct	**0.47**	**0.31**	**0.27**	**0.29**	**0.23**	NS	NS	NS
PC1	Direct	NS	NS	NS	NS	*0.16*	NS	**0.35**	**0.38**
	Indirect through FDis	NS	*0.08*	NS	NS	**0.13**	**0.05**	*0.04*	0.04
	Indirect through CWM trait value	**0.39**	**0.25**	**0.22**	**0.24**	**0.06**	NS	NS	NS
	Total effect	**0.39**	***0.34***	**0.22**	**0.24**	***0.36***	**0.05**	***0.39***	***0.42***
PC2	Direct	**−0.53**	**0.18**	NS	NS	**−0.52**	**0.19**	NS	*0.11*
	Indirect through FDis	NS	NS	NS	NS	NS	NS	NS	NS
	Indirect through CWM trait value	**0.08**	**0.06**	**0.05**	**0.05**	**0.06**	NS	NS	NS
	Total effect	**−0.45**	**0.24**	**0.05**	**0.05**	**−0.46**	**0.19**	NS	*0.11*
PC3	Direct	**0.22**	**−0.15**	**−0.20**	**−0.19**	**0.27**	**−0.13**	**−0.18**	**−0.17**
	Indirect through FDis	NS	NS	NS	NS	**−0.06**	**−0.04**	*−0.04*	*−0.03*
	Indirect through CWM trait value	NS	NS	NS	NS	NS	NS	NS	NS
	Total effect	**0.22**	**−0.15**	**−0.20**	**−0.19**	**0.21**	**−0.1714**	***−0.2164***	***−0.20***

Effects (pathway coefficients) describe the relative strength of the relationship between a given predictor variable and ecosystem function. Positive values indicate a positive relationship while negative values indicate a negative relationship and bold values indicated significant pathways ($P < 0.05$) while italics represents marginally significant pathways ($P < 0.10$). FDis = functional dispersion. CWM = community weighted mean trait values. PC1–3 = environmental conditions based on the first three axes of a principal components analysis of 14 soil and 5 topographic variables. NS = non-significant relationships. See Table 1 for trait abbreviations

significant at times 3 and 4 (Fig. 4, Table 3). PC1 and PC3 explained between 14 and 19% of the variation in FDis of Leaf C. In contrast CWM leaf C content was only significant at time 1. PC1 and PC2 explained between 39 and 41% of the variation in CWM leaf C. Again, PC3 (slope and NH_4 concentrations) significantly influenced decay at all four-time points, PC2 had direct effects at times 1 and 2 (and marginally at time 4) and PC1 influenced decay at times 3 and 4 (and marginally at time 1) (Fig. 4, Table 3). PC1 and PC2 had indirect effects via their influence on FDis at all four times, and PC2 had an indirect effect via its influence on CWM leaf C at time 1.

Discussion

While a growing number of studies are demonstrating that multiple processes simultaneously drive decomposition (e.g., Zanne et al. 2015), we still lack a clear picture of the importance of indirect effects in influencing decomposition. This is particularly important for studies using live plant functional traits to study decomposition (e.g., Cornwell et al. 2008; Santiago 2007; Zukswert and Prescott 2017) as numerous studies have demonstrated a clear link between landscape context (soils, topography) and plant functional traits (e.g., Cornwell and Ackerly 2009; Reich et al. 1997; Spasojevic and Suding 2012; Westoby et al. 2002). Here we found that while both landscape context (soils, topography) and functional composition directly influence decomposition of a standard substrate (filter paper), landscape context also indirectly influenced decomposition via its influence on plant functional traits. Importantly, this suggest that the “after life” effect of plant functional traits on decomposition (Freschet et al. 2012; Jackrel and Wootton 2015; Zukswert and Prescott 2017) is mediated by landscape context, and that we should be careful when using live plant functional traits to predict decomposition without considering the landscape context in which these traits were measured.

We found landscape context to be an important determinant of decomposition. Previous work at this site has shown that landscape position (ridge top vs. valley bottom) only explained a modest amount of variation (4 to 6%) in wood decay where decomposition was slower on Ridges than in Valleys (Zanne et al. 2015). In contrast, by incorporating more detail of this heterogenous landscape we found that landscape position highly influenced mass loss (Fig. 2) of a standard substrate (filter paper). Interestingly, the relative importance of different components of the landscape changed over time. Total N, NO_3 and convexity (PC2) were important in earlier stages of decomposition, generally having a negative effect on decay in time 1 and a positive effect in time 2. On the other hand, micronutrients (PC1; Al, Fe, Ca, K, Mg, Mn, P, K, pH) were more important in the later stages of decomposition, times 3 and 4. Micronutrients have been found to be important determinants of decomposition in several cases (e.g., Kaspari et al. 2008; Powers and Salute 2011) and the shift in the importance of N and micronutrients over time points to an importance of dynamics beyond Liebig's Law of the Minimum, which postulates the existence of a single primary limiting nutrient underlying population and ecosystem processes (Chapin et al. 2002). PC3 (slope and NH_4) was the only landscape variable that influenced decay across all four-time periods. Interestingly we found that PC3 had a positive effect in time 1 and a negative effect during the other time periods (for all models), suggesting that increased NH_4 availability and slope may have initially stimulated mass loss and then reduced mass loss later. The variable influence of N availability on mass loss was not surprising as a meta-analysis found that litter decay responses to N additions ranged from a 38% inhibition to 64% stimulation (Knorr et al. 2005).

In addition to these direct effects of landscape context, we also found direct effects of forest functional composition on decay. Generally, we found a significant relationship between CWM and FDis of live leaf traits and decomposition, supporting the idea that two processes by which functional diversity influences ecosystem functioning (niche complementarity and mass-ratio effects) are not mutually exclusive (e.g., Chiang et al. 2016; Mokany et al. 2008). In this Ozark Oak-Hickory forest, we found that mass ratio effects (CWM trait values) were more strongly related to decomposition for three traits (LDMC, Leaf Toughness, and Leaf N) and occurred over all four-time periods for one trait (Leaf N). These results support several lines of research suggesting that mass ratio effects may be key drivers of decomposition (i.e., Garcia-Palacios et al. 2017; Lin and Zeng 2018; Tardif et al. 2014) particularly for C loss (we used filter paper derived of C). While many hypotheses have been proposed for why mass ratio effects may be important for diverse mixtures of litter (i.e., the idiosyncratic annulment hypothesis (Tardif and Shipley 2013)) our results suggest that multiple mechanisms may operate simultaneously. Specifically, we found evidence for niche complementarity for leaf C and in the first two-time periods (Fig. 4). Carbon quality and quantity are key determinants of decomposition (Aerts 1997; Meier and Bowman 2008a; Talbot and Treseder 2012; Vitousek 1998) and chemical traits have been previously found to be strong predictors of decay at this site (Zanne et al. 2015). While we did not quantify variation in the quality of C in the litter (i.e., lignin concentrations), our results do suggest that there is a relationship between the C content in the community in which decomposition occurs that that "after life" effect of live leaves can predict decay rates. Future research, examining more details of C (i.e., lignin) or other leaf chemical components (i.e., Ca, P, pH) may provide a better understanding of decay as nutrient concentrations can be strong predictors of decay (Aerts 1997; Cornwell et al. 2008; Garcia-Palacios et al. 2017) and different decomposers specialize on different chemicals or fractions (Meier and Bowman 2008b; Talbot and Treseder 2012).

Interestingly, we found that forest functional composition (both CWM trait values and FDis) was related to decay at early time periods and that this relationship weakened (as indicated by lower path coefficients) or was no longer significant at later time points. Similarly, Zukswert and Prescott (2017) found that early mass loss (first 3 months) was correlated with plant functional traits, but litter traits were better predictors after 3 months due to changes in the physical and chemical composition of the leaves. Additionally, this temporal variation in decay may also be a result of temporal variation in the decomposer community where the litter bags were placed. For example, Voriskova and Baldrian (2013) found that although cellulose was available in litter during all stages of decomposition, the community of cellulolytic fungi changed substantially over time. Similarly, Matulich et al. (2015) found that temporal variation largely exceeded the response of leaf-litter microbial communities to simulated global change in a California annual grassland, suggesting that temporal variation may play a stronger role in decomposition than exogenous factors. While we were not able to test for these mechanism in our study, future research addressing temporal variation in the "after life" effect of live plant traits may help resolve the specific mechanisms.

Lastly, we found that environmental conditions indirectly influenced decay via their effect on functional composition (Table 2). In previous studies at this site (Spasojevic et al. 2016; Spasojevic et al. 2014) we found that the environment is a strong driver of variation in functional trait diversity. Since leaf functional traits have been demonstrated to influence decomposition (Cornwell et al. 2008; Santiago 2007), it is not surprising that we find these indirect effects of the environment on decay. Interestingly though, we find that the indirect effects are somewhat context specific (Table 2). For example, in our models for LDMC and Leaf N (Fig. 3) the only effect of PC1 (at time points 1 and 2) is via its indirect effect on LDMC or Leaf N – a results that only emerged from using structural equation modeling (Fig. 1). Since functional traits are tightly correlated with species' *responses to*, and *effects on*, the environment and ecosystem functioning (Cadotte et al. 2011; Lavorel and Grigulis 2012; Suding et al. 2008) an integrative approach that examines the direct and indirect effects of multiple factors is critical for understanding decomposition (i.e., Gessner et al. 2010; Grace et al. 2016; Zanne et al. 2015), especially for approaches that seek to link plant functional traits with decomposition.

Conclusions The joint evaluation of direct and indirect effects is rare in the decomposition literature (Garcia-Palacios et al. 2017). Our results highlight the importance of an integrative approach that examines the direct and indirect effects of multiple factors for understanding and predicting decomposition patterns across heterogenous landscapes. Our results highlight that different mechanisms operate simultaneously, and that different processes (mass-ratio vs. niche complementarity) may be contingent on the functional-traits and landscape context examined.

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