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**Spatial and temporal variability of forest floor duff characteristics in long-unburned *Pinus palustris* forests**

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**Abstract**

Duff fires (smoldering in fermentation and humus forest floor horizons) and their consequences have been documented in fire-excluded ecosystems but with little attention to their underlying drivers. Duff characteristics influence the ignition and spread of smoldering fires and their spatial patterns on the forest floor may be an important link to the heterogeneity of consumption observed following fires. We evaluated fuel bed characteristics (depths, bulk densities, and moisture) of duff in a long-unburned longleaf pine (*Pinus palustris* Mill.) forest and corresponding spatial variation across  $10^0$  to  $10^3$  scales. Fermentation and humus horizon depths both varied with moderate to strong spatial autocorrelation at fine scales, however fermentation bulk density varied less than humus bulk density, which varied considerably at fine scales. Fermentation horizons retained more moisture and were much more variable than humus following rainfall. Humus moisture was moderately autocorrelated at fine scales, but fermentation was highly variable, showing no evidence of spatial autocorrelation under dry, intermediate, or wet conditions. Laboratory drying revealed substantial variation in adsorption and desorption that highlight the fine-scale complexity of these fuels. Our field and laboratory observations highlight the underlying spatial variability in duff, informing future sampling and fire management efforts in these long-unburned coniferous forests.

**Keywords:**

fire exclusion, fuel heterogeneity, longleaf pine, spatial autocorrelation, wildland fuels

## Introduction

Forest floor fuels are dominant drivers of fire behavior and ecological effects of burning. The surface litter (Oi horizon), composed of recently cast foliage, is an important driver of flaming combustion, while the partially decomposed fermentation (Oe horizon) and humus (Oa horizon), collectively “duff” (Van Wagner 1972), tend to smolder when ignited beneath the litter and can cause significant overstory tree mortality when burned (Ryan and Frandsen 1991; Swezy and Agee 1991; Varner et al. 2005, 2007). Duff consumption varies tremendously within and among burns: even when surficial litter burns, the underlying duff horizons may not ignite (Kreye et al. 2013a), and when duff does ignite, duff consumption can be quite variable (Van Wagner 1972; Miyanishi 2001; Miyanishi and Johnson 2002). The spatial heterogeneity of duff consumption is poorly understood and the underlying processes of smoldering combustion in these dense organic horizons are still unclear (Miyanishi 2001).

Duff accumulates in forests where the rate of organic litter input exceeds decomposition. In fire-prone ecosystems, duff development is usually interrupted via consumption of surface litter during recurrent fires (Varner et al. 2005). When fire is excluded from these ecosystems, however, litter decomposes and duff accumulates over time (Agee et al. 1977). Duff accumulations pose substantial challenges to managers via consequent tree mortality, erosion, understory plant mortality, and emissions when these dense organic horizons smolder for extended periods (Ryan and Frandsen 1991; Swezy and Agee 1991; O’Brien et al. 2010).

Little work has evaluated the spatial patterning of duff consumption or elucidated the mechanisms that may be involved (Miyanishi 2001; Miyanishi and Johnson 2002; Hille and den Ouden 2005). Forest floor properties (depth, bulk density, mineral content, and moisture content) have been linked to their ignition and consumption (Frandsen 1997; Miyanishi and Johnson

2002; Varner et al. 2005; Garlough and Keyes 2011). In addition, surface debris such as pine cones and other woody fuels may act as vectors for duff ignition when these horizons are beyond presumed moisture or bulk density thresholds (Brown et al. 1991; Kreye et al. 2013a). While these forest floor properties are important drivers of duff combustion, few studies have examined the spatial or temporal variability of these characteristics (Schaap et al. 1997; Smit 1999; Banwell et al. 2013). Understanding the variability of duff across spatial scales may provide some insight into the heterogeneous patterns of duff consumption observed following fires.

Of duff characteristics important to smoldering combustion, moisture content is most temporally variable and overwhelmingly determines ignition and the extent of consumption (Frandsen 1987; 1997; Robichaud and Miller 1999). Moisture content varies in time as wetting and drying occurs (Ferguson et al. 2002; Keith et al. 2010), however little work has addressed how duff moisture varies in space (Robichaud and Miller 1999; Miyanishi and Johnson 2002; Banwell et al. 2013), the spatial scale of variability (e.g. autocorrelation) (Robichaud and Miller 1999), or how spatial variability differs under varying moisture conditions. And while drying rates of forest floor fuels can vary greatly (Anderson 1990; Nelson and Hiers et al. 2008; Kreye et al. 2012), little work has been conducted to calculate drying rates of forest floor duff (Hille and den Ouden 2005). Differential wetting or drying of duff, both in time and space, may be a primary factor in understanding or predicting duff consumption during fires.

Duff depth and bulk density are important drivers of duff consumption (Frandsen 1987, 1997, Garlough and Keyes 2011), which may vary in space (Smit 1999, Banwell and Varner 2014), but are unlikely to change over short time periods. Spatial variability of these attributes may contribute to the heterogeneity of consumption patterns observed following fires. Depth

and bulk density may also indirectly influence combustion through direct control over the ability of duff to absorb or retain moisture (Garlough and Keyes 2011).

Predicting smoldering combustion during prescribed fires is difficult; the ignitability of duff and the extent of its consumption are influenced by duff characteristics (Frandsen 1987, 1997), each of which may vary within a single burn unit. Duff sampling procedures commonly used for prescribed burns assume homogeneous bulk density (Brown 1974). Due to the inability to rapidly assess duff moisture with accuracy (Ferguson et al. 2002, Engber et al. 2013), a single estimate of duff moisture is often applied to a wide area based on precipitation, with little attention given to variability. Understanding spatial variation in duff is needed to effectively and more efficiently sample forest floor fuels, but may also lend important insight into why observed patterns of duff consumption are often heterogeneous following fires and what ecological consequences or benefits may result from such variability.

The goal of this study was to quantify the spatial and temporal variability of duff properties in a long-unburned longleaf pine (*Pinus palustris* Mill.) forest. Historically a frequently burned ecosystem (Frost 1993), longleaf pine uplands develop substantial accumulations of duff when fire is excluded (Varner et al. 2005). Our objectives were to 1) examine differences in depth, bulk density, and moisture content between the fermentation and humus horizons of duff in a long-unburned longleaf pine ecosystem; 2) evaluate the spatial variability in these duff properties across different scales; 3) examine the spatial variability of duff moisture content within and across three moisture conditions (dry, intermediate, wet); and 4) calculate moisture desorption rates of duff through laboratory experiments. Evaluating the spatial variability of duff properties and moisture dynamics will clarify forest floor fuel dynamics, inform the scale of importance for duff sampling, and potentially clarify our more

general understanding of the patchy consumption patterns observed in duff fuels in long-unburned longleaf pine forests and other ecosystems where forest floor fuels are important.

## Methods

### *Study Sites*

Forest floor duff was sampled in long-unburned longleaf pine forests at the Ordway-Swisher Biological Station (N29° 40' W81° 74') in northern Florida, USA. The temperate climate of the region consists of warm humid summers and short winters, a mean annual temperature of 20 °C, and 1430 mm of annual precipitation (Readle 1990). Three stands with similar structure and composition, soils, and fire history were selected from within a 1 km<sup>2</sup> portion of the site. Although stands went unburned for >20 years, a prescribed burn was conducted in one stand seven years prior to this study. Deep duff accumulations, however, were still prevalent in the more recently burned stand, suggesting little duff consumption during the burn, an objective of the burn to limit overstory mortality (Varner et al. 2007). The overstory in each stand was dominated by mature longleaf pines with a patchy midstory of oaks (*Quercus laevis* Walt., *Q. geminata* Small., and *Q. hemisphaerica* Bartr. Ex Willd.) with an average basal area of 17±6 m<sup>2</sup> ha<sup>-1</sup> across stands. As is typical of long-unburned longleaf pine forests, herbaceous understories were absent and the forest floor in each stand consisted of deep litter (Oi) overlying the duff (Oe and Oa) horizons (Varner et al. 2005). Soils across all stands were deep, excessively drained Quartzipsamments (Readle 1990) and topography was generally flat (<5% slopes).

### *Field Sampling*

Within each stand, three parallel transects (10 m apart) were established with three sub-transects nested along each main transect. Along each nested sub-transect, we extracted duff

samples at the origin (0 cm) and at 10, 40, 100, 300, 700, and 1500 cm beyond, in parallel with the primary transect. All three sub-transects were oriented along the primary transect and the distance between the origins of the first two sub-transects was 30 m, while the distance between the origins of the second and third sub-transects was 90 m. Therefore, the distances between individual samples ranged from 10 cm to 1500 cm within each sub-transects, and up to 105 m across the main transect. The three stands were constrained to a 1 km<sup>2</sup> area with sampling locations (transects), approximately 400 m between the two stands nearest each other and 800 m between the two stands farthest apart. Therefore, the scale of sampling in this study ranged across several orders of magnitude, from 10<sup>-1</sup> to ~10<sup>3</sup> m, but included a nested sampling scheme consisting of 10<sup>1</sup> m (sub-transects), 10<sup>2</sup> m (transects or stands), and 10<sup>3</sup> m (forest level) scales from which to evaluate variation in duff properties.

To examine the spatial variability of duff moisture across a gradient of relevant fuel moisture conditions, sampling occurred under three different meteorological conditions: 1) following a prolonged drying period (11 March 2013, 13 days since rain, 31 mm in the preceding 30 days); 2) following an intermediate moisture period (30 April 2013, 1 day since rain (23 mm), 24 mm in the preceding 7 days, 129 mm in the preceding 30 days); and 3) following heavy precipitation (04 May 2013, 1 day since rain (190 mm), 291 mm in the preceding 7 days, 400 mm in the preceding 30 days) (see Fig. 2). Moisture content of duff horizons are slow to change in response to daily environmental fluctuations (Ferguson et al. 2002; Hille and den Ouden 2005), however sampling was constrained to midday (1100 to 1600 h) to ensure consistency across sampling periods. During each of the sampling periods, one of the three primary transects per stand was randomly selected and duff was destructively sampled. One transect was randomly selected during the initial (dry) sampling period, one of the remaining transects was randomly



selected and sampled during the second (intermediate) sampling period, and the final transect was sampled during the third (wet) sampling period.

At each location, we removed the litter and extracted the underlying duff with a 7.4 cm diameter cylindrical soil corer. Prior to extraction, duff was incised with a serrated knife so that depths of the fermentation and humus horizons could be measured without compaction. The extracted fermentation and humus horizons were separated and bagged in sealed polyethylene bags, and transported for laboratory analysis.

In addition to spatial sampling, we also randomly extracted 15 duff samples from a nearby stand with similar characteristics and fire history to conduct laboratory drying experiments. At each sampling location, litter was removed and an intact 15×45 cm duff sample was carefully extracted by cutting the duff to dimensions with a serrated knife, pulling away the adjacent material, and removing the sample with a flat metal baking sheet. Samples were then placed into boxes with the same dimensions to maintain their integrity and then transported to a laboratory for drying experiments.

#### *Laboratory Analyses*

Following each of the three sampling periods, all spatial samples were weighed in the laboratory to the nearest 0.01 g and subsequently oven-dried at 70 °C until sample weights no longer changed. Oven-dried samples were weighed and gravimetric moisture content was determined from initial “wet” weights and oven-dry weights of each sample. Bulk density was calculated as the dry mass divided by the field sample volume, as determined from corer geometry and measured horizon depth.

Duff samples for laboratory drying experiments were allowed to dry under lab conditions to reach equilibrium moisture content. Samples were subsequently split into three 15×15 cm

177 subsamples, placed into aluminum pans (18.5×18.5×3.5 cm), perforated with 36 holes (1-2 mm  
178 diameter) on the bottom for drainage (as in Kreye et al. 2013b), and their depths measured.  
179 Samples were then wrapped laterally in aluminum foil, to constraint moisture exchange to the  
180 upper surface, and placed under an overhead water sprinkler for 3 days, then subsequently  
181 allowed to dry under laboratory conditions ( $24\pm1$  °C and  $30\pm7$  % RH) for 30 days. For each of  
182 the 15 sampling locations, one of the three subsamples was randomly selected and a layer of  
183 plastic crafting grass (25 g), that we refer as “pseudo-litter”, was added to the duff surface to  
184 simulate the physical barrier of needle litter. While actual foliar litter would absorb and desorb  
185 moisture (Nelson and Hiers et al. 2008), this method was intended to evaluate if the role of duff  
186 depth or bulk density on duff moisture dynamics is consistent with or without the physical  
187 barrier of litter. Samples were weighed every 12 h during the first 300 h of drying, and then  
188 every 24 h thereafter. Following lab drying, duff samples were oven-dried at 70° C for 72 h to  
189 back-calculate moisture contents during the drying experiments.

#### 190 *Data Analysis*

191 To evaluate the variation of duff characteristics, we first tested whether sample  
192 distributions of depths and bulk densities, by horizon, followed a normal distribution using the  
193 Shapiro-Wilk Test. We then compared the magnitude of variation between fermentation and  
194 humus, for both depth and bulk density, using the Modified-Levene Equal Variance Test. To  
195 determine differences between horizons, we compared depth and bulk density, separately,  
196 between the fermentation and humus using the Wilcoxon Rank-Sum Test. Gravimetric moisture  
197 content was also tested for normality using the Shapiro-Wilk Test for each horizon within each  
198 of the three moisture periods (dry, intermediate, and wet). The Modified-Levene Test was used  
199 to test whether variances of moisture content were equal across horizon and moisture period. We

first compared variances between the two horizons, but for each moisture sampling period separately. Then we compared variances between each of the three moisture periods for each horizon separately. Mean moisture content was compared between duff horizons and across moisture periods using a 2-way general linear model analysis of variance (ANOVA) with horizon (fermentation vs. humus) and moisture period (dry, intermediate, wet) as main factors. The interaction between horizon and moisture period was also tested to determine if differences in moisture content between horizons changed under different moisture conditions. Gravimetric moisture contents were transformed using the natural logarithm to meet model assumptions.

To evaluate spatial variation in duff characteristics, we first compared the level of variation in each duff characteristic across three different spatial scales (sub-transect,  $10^1$  m; transect,  $10^2$  m; and forest,  $10^3$  m). Means and standard deviations (SD) of each duff characteristic (depth, bulk density, and gravimetric moisture content of each horizon) were calculated at each scale, but using the average values at the next smaller scale. For each of the twenty-seven 15 m sub-transects, the seven  $43\text{ cm}^2$  samples for each horizon were averaged and SD calculated. Therefore, 27 SDs were calculated at this  $10^1$  m scale, one for each sub-transect. For the transect-scale ( $10^2$  m), the mean from each of the three sub-transects, within each 105 m transect, was used to calculate a mean and SD for each of the nine 105 m transects in the study. Therefore, the level of variation at the  $10^2$  m scale was based on the average value of a scale of  $10^1$  m. Because transects were 105 m long, this  $10^2$  m scale also represents the stand scale in our study since the three parallel transects in each stand were only 10 m apart, to each be allocated to a different moisture sampling period. Nine SDs were calculated at the  $10^2$  m scale across the three stands in this study. Finally, for the  $10^3$  m (forest) scale, mean values were calculated from the  $10^2$  m scale averages and one SD was calculated for the  $10^3$  m scale of the forest. For

223 somewhat static depths and bulk densities, data were pooled across the three sampling periods  
 224 (wet, dry, and intermediate), whereas means and SDs of dynamic moisture contents were  
 225 calculated and evaluated within each of the sampling periods. Coefficients of variation (CV) for  
 226 each duff characteristic were then calculated from the means and SDs at each spatial scale  
 227 (within plots, within stands, across the forest). SD and CV were then compared across scales for  
 228 each duff characteristic.

229 Our second approach to evaluating spatial variability of duff was to examine spatial  
 230 autocorrelation of each duff characteristics using Moran's *I* statistic (Moran 1950; Legendre and  
 231 Legendre 1998). For each duff characteristic measured (depth, bulk density, and moisture  
 232 content within sampling periods), Moran's *I* was calculated within 10 m distance classes, and  
 233 tested for positive correlations up to a maximum of distance of two-thirds of transect lengths (as  
 234 in Fortin and Dale 2005) or 70 m. The Moran's *I* test statistic extends the Pearson correlation  
 235 statistic over a spatial context and is defined as Equation 1.

$$I(d) = \left[ \frac{1}{W(d)} \right] \frac{\sum_{i=1}^n \sum_{j=1, j \neq i}^n w_{ij}(d)(x_i - \bar{x})(x_j - \bar{x})}{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2} \quad \text{Eq. 1}$$

236 where  $I(d)$  estimates the spatial autocorrelation at a distance class  $d$ ,  $w_{ij}(d)$  form the distance  
 237 class weighting matrix,  $x_i$  and  $x_j$  are sample values at locations  $i$  and  $j$ , and  $W(d)$  is the sum of the  
 238 weighting matrix ( $\sum w_{ij}(d)$ ). Similar to the Pearson's correlation coefficient, Moran's *I* values  
 239 range from -1 to 1. Correlograms were then prepared presenting Moran's *I* as a function of  
 240 distance classes evaluated and significant positive correlations (at  $\alpha=0.05$ ) for distance classes  
 241 indicated. Therefore, where positive correlations exist, spatial autocorrelation occurs within that  
 242 distance class. All three stands were analyzed together when testing for spatial autocorrelation  
 243 of each duff characteristic.

For drying experiments, gravimetric moisture contents were calculated for each duff sample at each weighing period throughout the drying process. Moisture contents were then converted to relative moisture content ( $E$ ) (Fosberg 1970) and initial timelag response times ( $\tau$ ) were calculated for each duff sample using the methods of (Kreye et al. 2013b). Longer response times (larger  $\tau$ ) indicate slower fuel drying rates. Our goal was to compare variation in duff drying rates, but also to evaluate the role that duff depth and bulk density have on response time ( $\tau$ ). We used a general linear modeling approach to test the random effect of sample location, with bulk density and depth as covariates, to determine whether variability between subsamples within a sample location was smaller than across all locations. We used step-wise methods to determine whether bulk density, depth, or both should be included in the model to determine the random effect of sample location. We then used multiple linear regression to determine how much of the variation in response time ( $\tau$ ) was explained by bulk density, depth, or both. We included the random factor of subsample, that included those with pseudo-litter, to determine if the relationships between response time ( $\tau$ ) and duff characteristics (bulk density or depth) was similar with or without the physical barrier of litter.

## Results

In the long-unburned longleaf pine forests in this study, duff physical characteristics were spatially variable. Depths and bulk densities of both the fermentation and humus horizons of the duff were not normally distributed, but skewed, and variances of both depths and bulk densities were unequal when compared between horizons (Fig. 3). Humus was deeper (2.86 cm) on average than the overlying fermentation (1.90 cm) ( $p < 0.001$ ) and substantially (400%) more dense ( $p < 0.001$ ). Gravimetric moisture content of fermentation horizons were normally distributed during intermediate and wet sampling periods, however during the dry period

fermentation moisture was not normally distributed, nor was humus moisture during any of the dry, intermediate, or wet sampling periods (Fig. 4). Moisture contents were more variable in fermentation horizons compared to humus during the wet and intermediate sampling periods, however differences in variances were marginal under dry conditions ( $p = 0.062$ , Modified Levene Test). Moisture content variation also differed across sampling periods in both the fermentation and the humus horizons, with variation increasing as moisture conditions became wetter (Fig. 4). Moisture contents of both fermentation and humus differed across sampling periods ( $p < 0.001$ , ANOVA), as expected, with higher moisture contents during the wetter sampling periods. Moisture content also differed between duff horizons ( $p < 0.001$ ), with a significant interaction between horizon and sampling period ( $p < 0.001$ ). Fermentation was consistently more moist than the underlying humus and these differences became more pronounced as conditions became more wet (Fig. 4).

#### *Spatial Analysis*

Although we don't statistically compare SD or CV across the three scales of study we evaluated ( $10^1$  m, subtransect;  $10^2$  m, transect;  $10^3$  m, forest), differences were apparent across these scales for many of the duff characteristics. Variation (both SD and CV) in fermentation depths are similar at both the subtransect ( $10^1$  m) and transect ( $10^2$  m) scales, but when averaged within each of the three stands, forest ( $10^3$  m) level variation was quite low in comparison (Fig. 5 a,b). In contrast, humus depths varied less when successively evaluated at larger scales where mean values at the next smaller scale were used to determine SD and CV. Bulk densities of both duff horizons also varied less when evaluated at larger scales (Fig. 5 c,d). Standard deviations of bulk density were higher in humus compared to fermentation horizons (Fig. 5c), but were a function of the much higher bulk densities (ca. four times greater) of humus horizons.

Coefficients of variation in bulk density appeared similar between the two horizons (Fig. 5d). During and intermediate moisture sampling periods SDs and CVs of fermentation moisture were highest at the subtransect ( $10^1$  m) scale with variation being smaller at the larger transect ( $10^2$  m) and forest ( $10^3$  m) scales, but with little evidence of difference between these two higher scales (Fig. 6 a,b). During the wettest sampling period, variation (SD and CV) was highest at the subtransect ( $10^1$  m) scale, moderate at the transect ( $10^2$  m) scale, and lowest at the forest ( $10^3$  m) scale. During dry and intermediate moisture sampling, humus moisture content varied similarly at the subtransect ( $10^1$  m) and transect ( $10^2$  m) scale, but varied less across the forest ( $10^3$  m) scale (Fig. 6 c,d). During the wettest sampling period, however, humus moisture varied more at the smaller subtransect ( $10^1$  m) scale in comparison to the transect ( $10^2$  m) scale, with slight evidence of humus moisture varying more than at the transect ( $10^2$  m) scale, but somewhat less than at the subtransect ( $10^1$  m) scale.

Using Moran's  $I$  to evaluate spatial autocorrelation, positive correlations of duff depths and bulk densities occurred at short distances for both horizons, but varied in the strength of correlations. Both fermentation and humus depths showed moderately strong spatial autocorrelation within 1 m and moderate autocorrelation within 10 m (Fig. 7). Fermentation depths were weakly autocorrelated between 10 and 20 m. Fermentation bulk densities were moderately autocorrelated within 1 m and weakly autocorrelated within 10 m, but very weakly autocorrelated between 40 and 50 m. Humus bulk densities were not autocorrelated within 1 m distances, however weak autocorrelation was detected within 10 m. Moisture contents of the fermentation horizon were not spatially autocorrelated during any of the sampling periods (Fig. 8), however humus moisture contents were moderately autocorrelated within 1 m and 10 m distances during dry and intermediate moisture sampling. Humus moisture was moderately

autocorrelated within 10 and 20 m during the intermediate moisture sampling period and weakly autocorrelated within up to 20 m during the wettest sampling period.

Our laboratory moisture experiments resulted in variable water adsorption by 15×15 cm duff samples, with moisture contents ranging from 64 to 200% ( $\bar{x}$  121%, SD 32%) . Response times ( $\tau$ ) of duff samples, without pseudo-litter, drying under controlled laboratory conditions averaged 120 h but ranged widely (54 to 209 h; SD 43 h). Although moisture adsorption and desorption both varied widely across our samples, they were not related ( $p = 0.636$ ,  $r = 0.09$ ). Response times ( $\tau$ ) of samples with pseudo-litter were 77% longer ( $p < 0.001$ ), averaging 212 h (SD 57 h), and also ranged widely from 126 to 329 h. Using a GLM approach, without samples with pseudo-litter, bulk density was the only significant covariate ( $p = 0.013$ ), and the random effect of sampling location (variance across locations  $> 0$ ) was marginally significant ( $p = 0.058$ ), suggesting slight evidence that variation across sampling locations was greater than within (i.e. between subsamples). Using multiple linear regression with all subsamples (included those with pseudo-litter), duff depth, which ranged from 5.7 to 11.3 cm, was not significant ( $p = 0.316$ ), however bulk density, ranging from 0.06 to 0.16 g cm<sup>-3</sup>, significantly influenced moisture response time ( $p = 0.001$ ). Including pseudo-litter slowed moisture response ( $p < 0.001$ ) but as expected, there was no difference in response time between subsamples that did not include pseudo-litter. There was no significant interaction between bulk density and pseudo-litter treatment, indicating the effect of bulk density on moisture response time ( $\tau$ ) was similar with or without the physical barrier litter provides (Fig. 9). The resulting model (Eq. 2) explained 57% of the variation in response time ( $R^2 = 0.57$ )

$$\tau = 38 + 795 * \rho + 88 * L \tag{Eq. 2}$$



where  $\tau$  is response time (h),  $\rho$  is duff bulk density ( $\text{g cm}^{-3}$ ), and  $L$  is the presence of pseudo-litter.

## Discussion

Duff characteristics in the long-unburned longleaf pine forest in this study varied considerably, even at small spatial scales. Given the long-durations of fire exclusion, humus horizons were deeper and more compact than fermentation horizons. Decomposition of pine needles in this region, including longleaf pine, can be slow due to low litter quality (Gholz et al. 1985; Hendricks et al. 2002), and long periods of fire exclusion can result in substantial accumulations of organic material on the forest floor (Heyward 1939; Varner et al. 2005). The less decomposed fermentation horizons varied less in bulk density compared to the underlying humus, however fermentation horizons were considerably more variable in moisture contents, especially under wet conditions. Fermentation horizons were wetter than humus following precipitation, contrary to western US studies where humus horizons have held more moisture (e.g., Banwell et al. 2013), but similar to observations in other longleaf pine forests (Ferguson et al. 2002). Duff depths were more variable than many of the other characteristics measured, but were also moderate to strongly autocorrelated at short distances. The stark differences in both bulk density and moisture content observed between upper and lower duff horizons in this study and the extent of their spatial variability highlight the importance of understanding the heterogeneity of forest floor fuels.

Variability of duff moisture content has been observed in coniferous forests in the western US (Hille and Stephens 2005; Banwell et al. 2013), Canada (Chrosiewicz 1989; Miyanishi and Johnson 2001), and Europe (Schapp et al. 1997, Hille and den Ouden 2005). While studies have looked at spatial variation relative to position to trees (Hille and Stephens

2005; Banwell et al. 2013), we examined spatial variability of duff properties across scales, from fine scales up to the forest level, and evaluated spatial autocorrelation. While duff smoldering at the base of trees is important for tree mortality, prescribed burns are planned on a larger scale. Burn-prioritization for landscape-scale management can be difficult with limited resources, yet fire-excluded sites need to be prioritized to meet conservation needs (Hiers et al. 2003; Engber et al. 2013). Duff consumption during prescribed fires, however, may be difficult to predict due to fine-scale variability of important duff characteristics even within stand-scale burn units. Although duff horizon depths varied widely, they also showed the strongest spatial autocorrelation at small scales. Bulk densities also varied considerably, with fermentation densities having the highest coefficient of variation of all measurements, however, while bulk densities of fermentation horizons showed moderate spatial autocorrelation, humus bulk density showed little to no spatial autocorrelation, highlighting the fine-scale variability of the compactness of lower duff. Bulk density may be an important factor more generally for fuel moisture dynamics (Kreye et al. 2012), as observed here in drying experiments, and both the moisture content and bulk density of compact fuels may interact to influence fire behavior (Miyanishi and Johnson 2002; Garlough and Keyes 2011).

There are likely mechanisms that account for the spatial variation of duff characteristics we observed. Spatial variation of duff depths and bulk densities is not surprising given that these horizons are a reflection of the foliar litter fallen from patchily distributed overstory trees. Litter dynamics vary by species in regard to their relative decomposition rates (e.g., Melillo et al. 1982; Baker et al. 2001). Canopy structure directly affects the spatial input of litter onto the forest floor, but may also indirectly influence localized decomposition rates through shading, rain interception, stemflow, and effects on surface winds, all of which may influence forest floor

temperatures and moisture conditions that are important for decomposition (Prescott et al. 2004). Forest floor moisture may additionally vary due to the variability in how duff absorbs water and then dries, beyond the influence of forest structure, as evidenced by our laboratory experiments.

Variation in duff characteristics within stands was higher than across stands, highlighting fine-scale heterogeneity in moisture conditions in this study. Patchy forest floor moisture is not uncommon. Banwell et al. (2013) observed spatial variation in moisture conditions of forest floor fermentation layers in the Sierra Nevada when surface litter and woody fuels were homogeneous. In those sites, humus horizons were consistently wetter than fermentation horizons, however, opposite of our findings. In dry forests of the western USA and Mediterranean ecosystems, humus layers beneath the surface may be slow to lose moisture as upper surface fuels dry in response to prolonged annual dry periods (Trouet et al. 2009). In seasonally wet southeastern USA forests, sporadic heavy, but short-duration rain events (Chen and Gerber 1990) may wet upper horizons with lower humus remaining drier. In these contrasting fire weather climates, the gain or loss of humus moisture may be subdued given its insolation from the overlying fermentation and litter, but as a response to different environmental conditions; slow response to drying in the west and resistance to wetting in the southeast. Another hypothesis may be that coarse sandy soils in xeric southeastern USA pine forests (so-called “sandhills”) may enhance water movement downward from lower humus horizons, whereas more loamy or clayey soils may dampen infiltration rates, enhancing moisture retention. Nonetheless, high fine-scale variation of fermentation moisture was most prominent following precipitation in this study when prescribed burning is likely to occur in long-unburned forests in the region (Wade and Lunsford 1989; Varner et al. 2007).

Beyond environmental controls on duff moisture, the influence of duff horizon characteristics (depth, bulk density) may indirectly influence moisture dynamics via greater depths or bulk densities (Miyanishi 2001; Miyanishi and Johnson 2002). Total duff depth did not influence drying response in lab experiments in this study, however increases in bulk density consistently slowed moisture loss regardless of the influence of a litter barrier. Our laboratory experiments could not differentiate moisture loss between horizons, however, but they do reveal that variation in duff moisture is not likely to be exclusive to overstory conditions: as duff varies tremendously in its ability to hold moisture following precipitation. A better understanding of the hydrological processes in forest floor organic soil horizons may elucidate the differences observed across sites or regions and help inform fire management in other ecosystems with substantial forest floor accumulation.

The level of spatial variability in duff characteristics observed in this study may provide some insight into the spatial variability of duff consumption during wild or prescribed fires. Duff depth, bulk density, and moisture content are all drivers of duff combustion (Frandsen 1987, 1997; Garlough and Keyes 2011) and their spatial variability may allude to heterogeneous consumption. Spatial autocorrelation was evident for some duff characteristics measured in this study, but not all. All measurements were quite variable at fine scales even where autocorrelation existed. Duff consumption, and the potential ecological consequences associated with duff consumption (Ryan and Frandsen 1991; Varner et al. 2005, 2007), may be difficult to predict from coarse scale measurements, especially under most prescribed burn scenarios. It is difficult to rapidly assess duff moisture with accuracy (Ferguson et al. 2002; Engber et al. 2013) and managers often rely on indirect methods such as days since rain or drought indices to predict moisture levels over a large area, without any estimation of the variability that may exist at

scales relevant for predicting ecological effects. Variation in moisture conditions, as well as depths and bulk densities, highlight the difficulties in understanding and predicting smoldering fire behavior in long-unburned forests.

Our results reveal that moisture was most variable in fermentation horizons where duff ignition is likely to occur. Humus moisture may be below critical values for duff combustion (60% observed in duff from these sites; Kreye et al. 2013a) while the upper fermentation is wet enough to resist ignition. If drier patches of upper duff ignite, however, smoldering might propagate horizontally through dry humus even where the upper fermentation is above ignition thresholds. Ignition vectors such as large wood or cones may also be important given their ignition capability of duff that would otherwise be too moist to burn (Kreye et al. 2013a). Such vectors are also likely to vary spatially on the forest floor (Keane et al. 2001; Gabrielson et al. 2012; Banwell and Varner 2014). Even when ignited, it is still unclear how smoldering combustion proceeds spatially in these compact organic fuels (Miyanishi 2001; Watts and Kobziar 2013). Several factors, including duff characteristics, may contribute to the ignition of duff. A better understanding of the process of smoldering in these stratified forest floor fuels is clearly needed.

Sampling of duff characteristics for other research purposes will need to take into consideration the spatial autocorrelation we document. While autocorrelation was observed for duff depths, fermentation bulk densities, and humus moisture, moderate to strong correlations generally occurred at small scales ( $\leq 10$  m), indicating the importance of the scale used for characterizing variation (Dungan et al. 2002). Sampling schemes that maintain 10 m distances between sample locations will likely suffice for most purposes. Studies aimed at evaluating factors that drive spatial variability, however, may need to use sampling schemes that include a

fine-scale sampling approach to obtain the variability necessary to evaluate how such factors may contribute to variability (Fortin et al. 1989). When considering certain research questions, autocorrelation may not be a 'nuisance' factor to be ruled out or simply accounted for in a study or modeling scheme and instead capitalized on for research questions and management solutions.

In addition to the importance of duff variability for fire behavior and consumption, such heterogeneity may be important for other ecological reasons. Spatial patterns of duff may contribute to patterns of duff consumption during fires, which is important for post-fire seedling recruitment and the ultimate regeneration of herbaceous plants and subsequent generations of the overstory (Flinn and Wein 1977; Thomas and Wein 1985; Kembell et al. 2006). Duff consumption may be critical for groundcover restoration in long-unburned longleaf pine forests where grass and forb establishment is desired and a more frequent fire regime is a goal for ecological restoration (Van Lear et al. 2005, Hiers et al. 2007). In other ecosystems where fire is less frequent, and duff naturally accumulates, heterogeneous forest floor conditions may be important for the establishment of younger cohorts within patches of consumed duff following infrequent fires (Miyanishi and Johnson 2001, 2002). The ensuing variation in fire severity that is linked to this high variation in fuels fits within the larger body of research that touts the importance of variation for vegetation dynamics and the maintenance of biodiversity.

### **Acknowledgments**

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597 scale significance. *Fire Ecol.* **9**: 124-132.

598 **Table 1.** Variation in forest floor duff characteristics in a long-unburned longleaf pine (*Pinus palustris*) forest in northern Florida.

	Range	Mean	Median	Standard Deviation	Coefficient of Variation
Depth (cm)					
Fermentation	0.0-13.0	1.90 <sup>a</sup>	1.4	1.86	1.0
Humus	0.0-12.0	2.86 <sup>b</sup>	2.4	2.23	0.78
Bulk Density (g cm <sup>-3</sup> )					
Fermentation	0.01-1.49	0.12 <sup>a</sup>	0.08	0.14	1.23
Humus	0.08-2.02	0.46 <sup>b</sup>	0.39	0.30	0.65
Moisture Content (%) <sup>□</sup>					
Fermentation					
Dry	0.06-2.32	0.49	0.46	0.34	0.69
Intermediate	0.32-1.80	0.93	0.93	0.33	0.36
Wet	0.45-2.78	1.72	1.79	0.62	0.36
Humus					
Dry	0.09-0.81	0.28	0.24	0.16	0.58
Intermediate	0.12-0.90	0.42	0.38	0.20	0.48
Wet	0.20-1.37	0.62	0.55	0.26	0.42

599 <sup>□</sup> Dry: thirteen days since rain, 31 mm in preceding 30 days; Intermediate: one day since rain (23 mm), 24 mm in the preceding 7  
600 days, 129 mm in the preceding 30 days; Wet: one day since rain (190mm), 291 mm in the preceding 7 days, 400 mm in the preceding  
601 30 days.

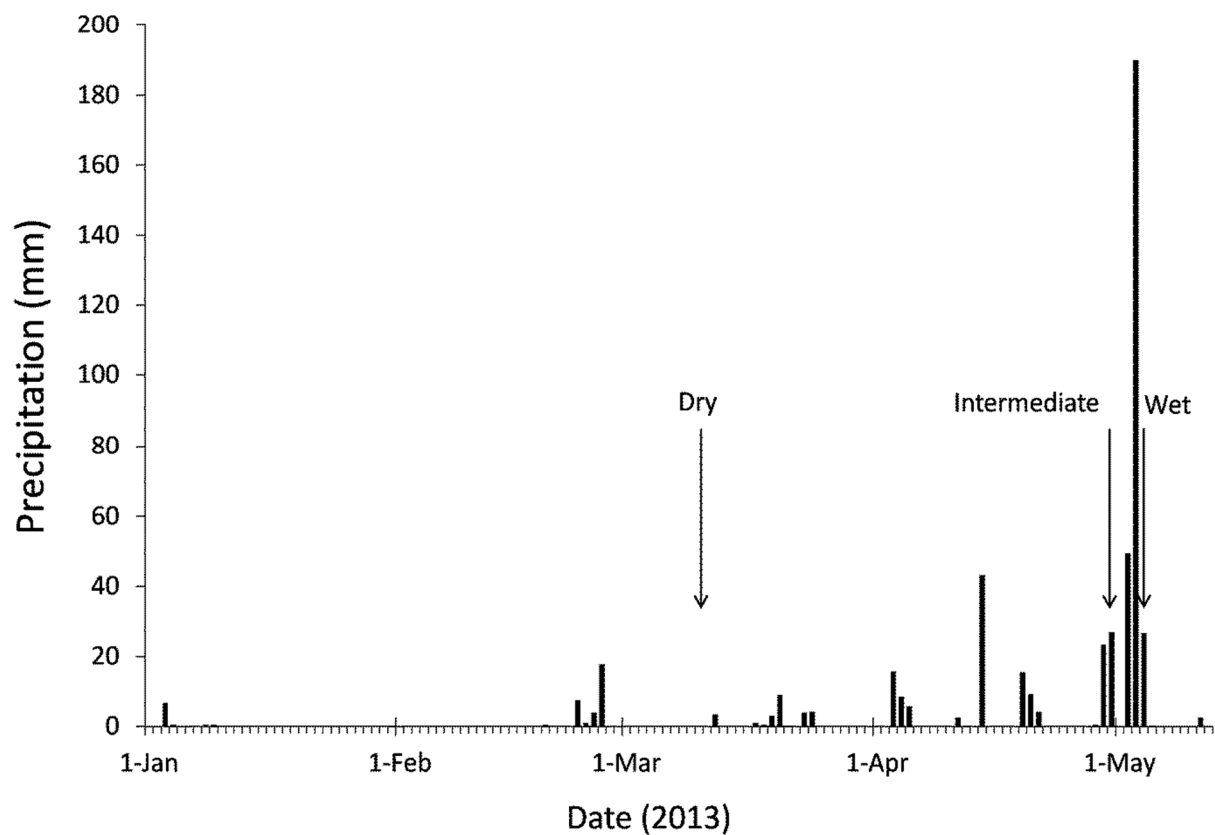




603 **Fig. 1.** Forest floor of a long-unburned longleaf pine (*Pinus palustris*) forest at Ordway-Swisher  
604 Biological Station in Florida, USA. Depths of fermentation and humus duff horizons were  
605 measured and samples were extracted to quantify bulk density and moisture contents.

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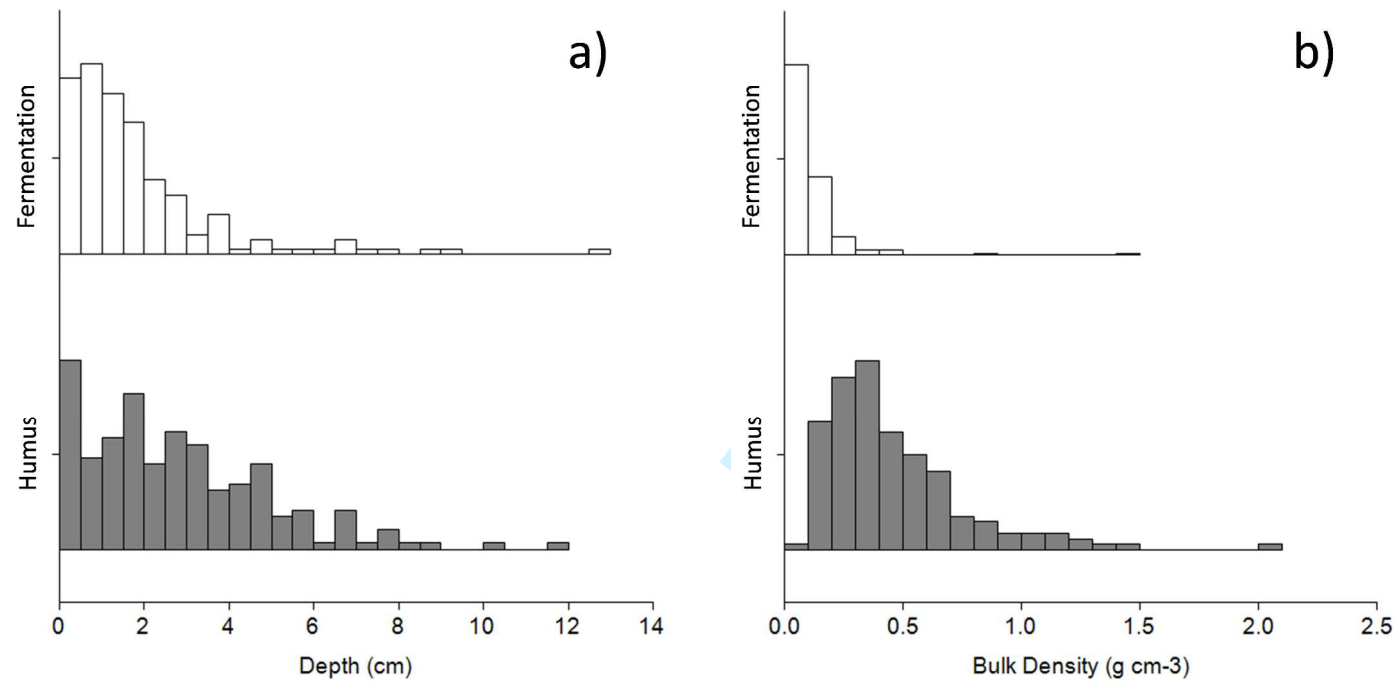
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**Fig. 2.** Daily rainfall at the Ordway-Swisher Biological Station (Florida, USA) during spring 2013 when duff sampling occurred to evaluate spatial variability under 3 moisture conditions (Dry, Intermediate, Wet). Sampling dates (indicated by arrows) were 11 March 2013 (Dry), 30 April 2013 (Intermediate), and 04 May 2013 (Wet).

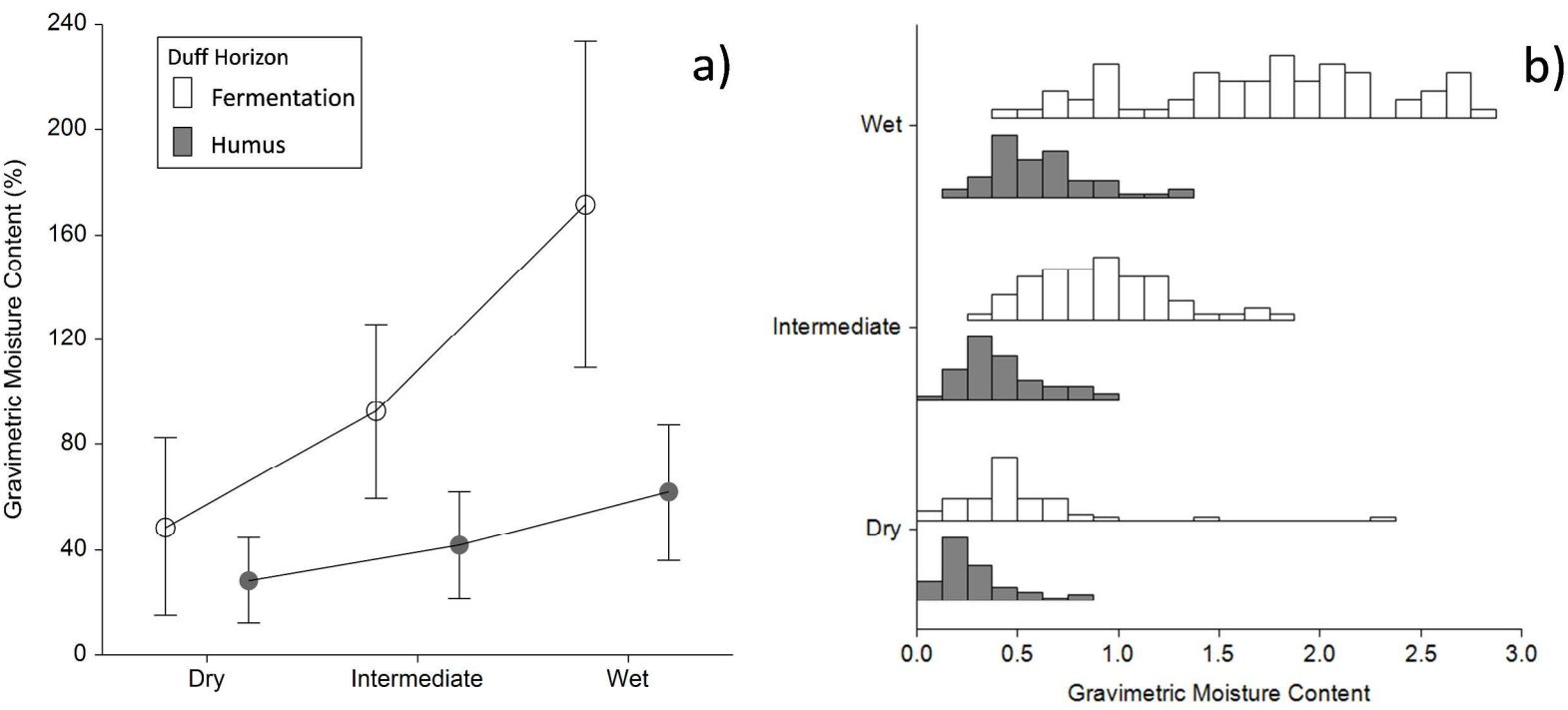


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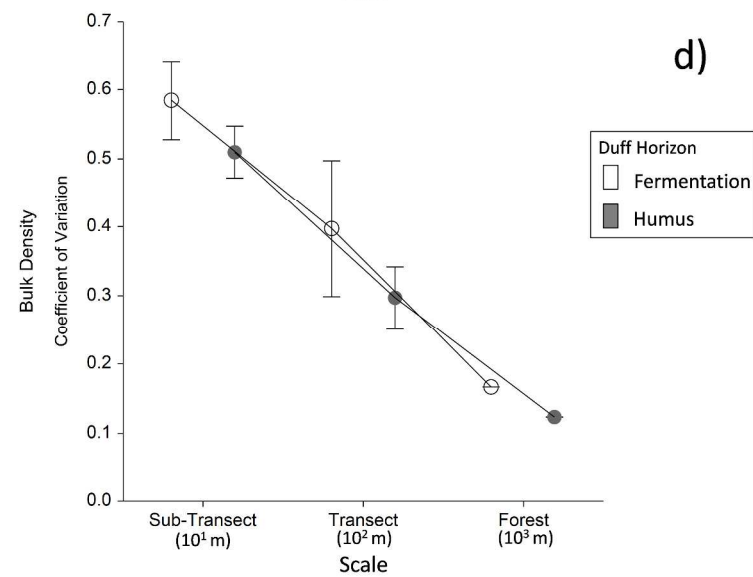
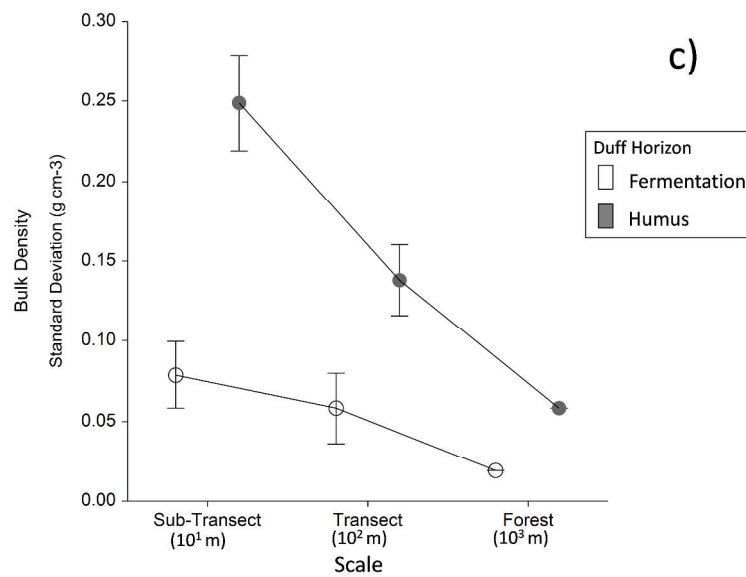
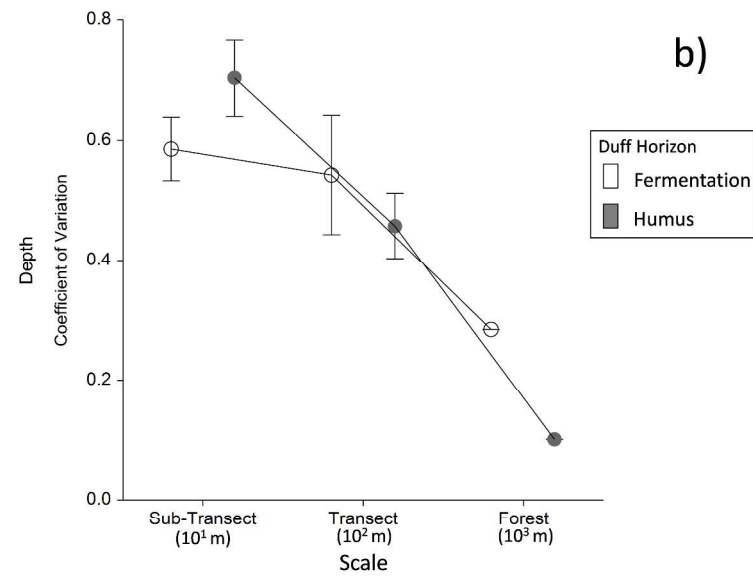
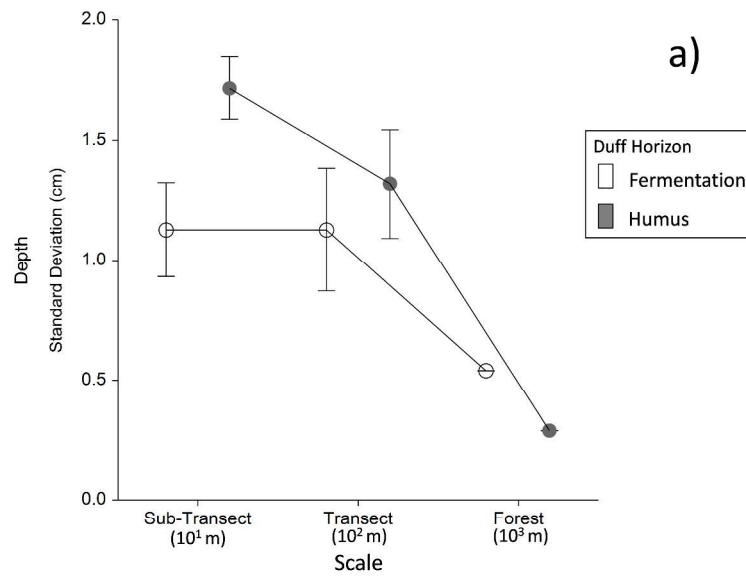
613 **Fig. 3.** Variation of depths (a) and bulk densities (b) of the fermentation and humus duff horizons in a long-unburned longleaf pine  
 614 forest of northern Florida, USA.

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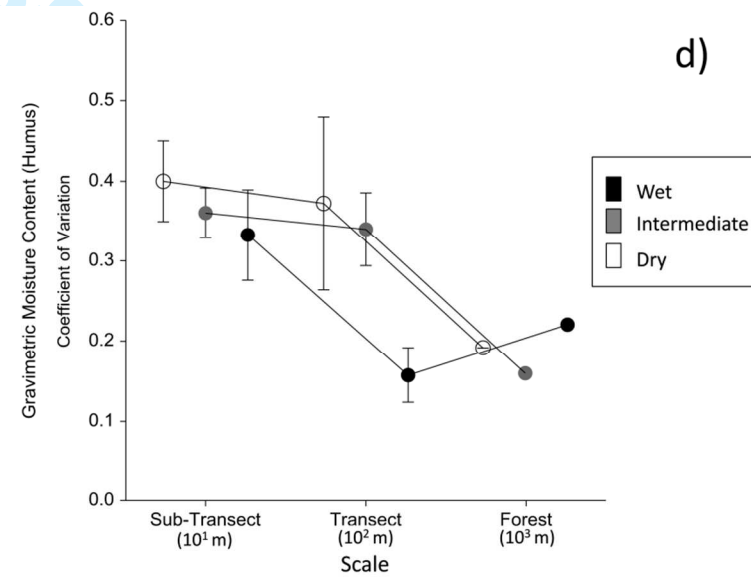
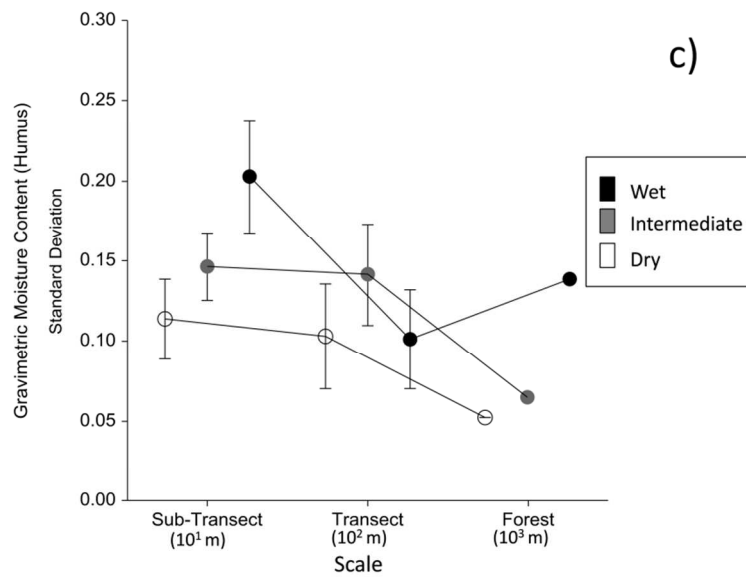
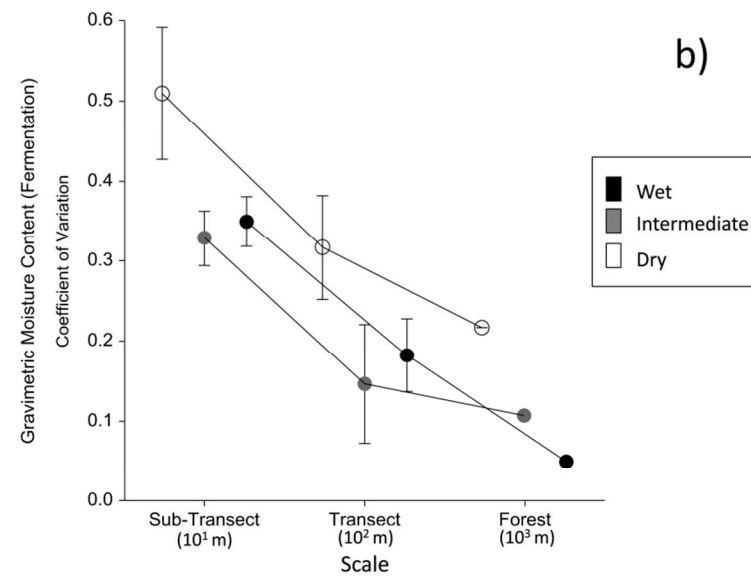
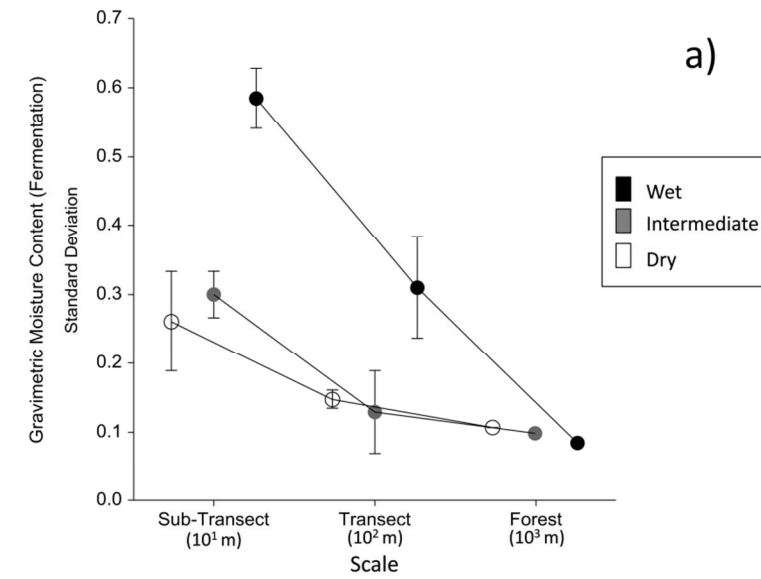
616 **Fig. 4.** Variation in moisture contents (water mass/dry duff mass) of the fermentation and humus duff horizons in a long-unburned  
617 longleaf pine forest of northern Florida, USA under three different moisture conditions (dry, intermediate, wet). Error bars (a)  
618 indicate standard deviations; histograms are shown (b) for both fermentation (white) and humus (dark) horizons.

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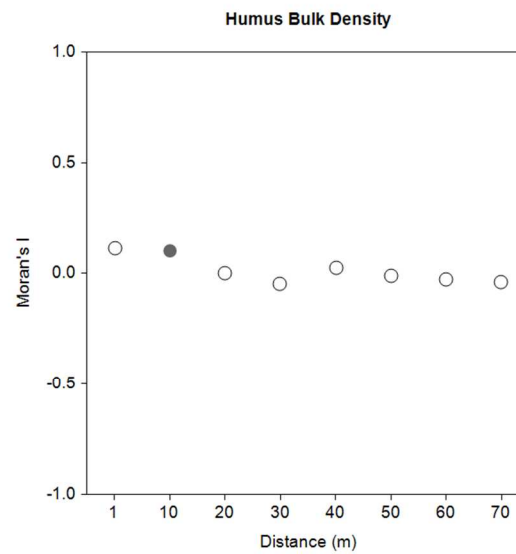
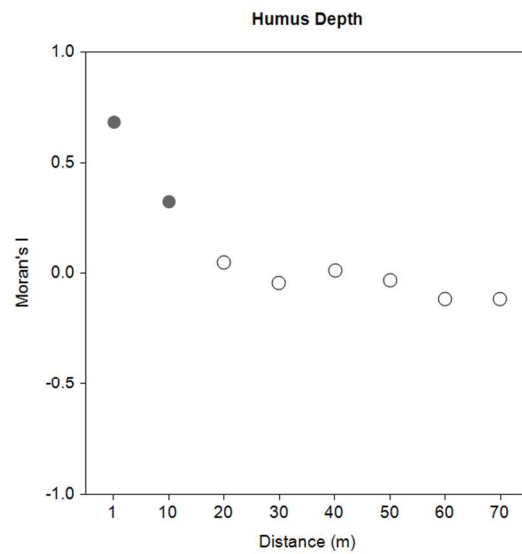
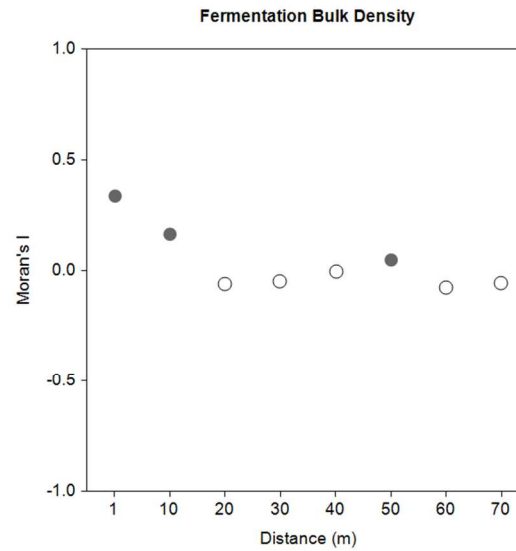
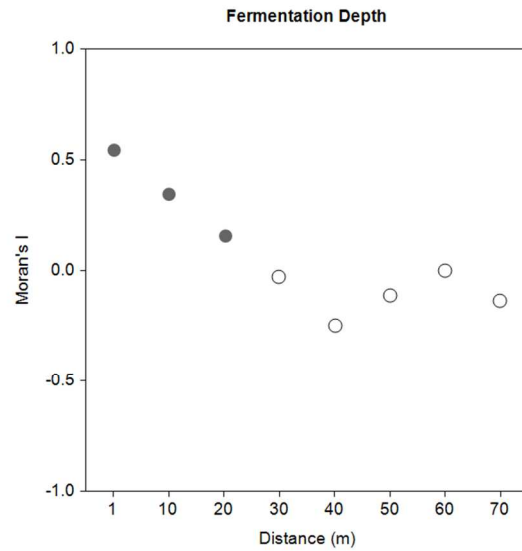
620 **Fig. 5.** Standard deviations (a,c) and coefficients of variation (b,d) of duff depth (a,b) and bulk density (c,d) as measured across three  
621 spatial scales (Sub-Transect,  $10^1$  m; Transect,  $10^2$  m, Forest,  $10^3$  m). The error bars indicate standard error about the mean of the  
622 variation metric (standard deviation or coefficient of variation).  
623

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624 **Fig. 6.** Standard deviations (a,c) and coefficients of variation (b,d) of gravimetric moisture content of fermentation (a,b) and humus  
625 (c,d) horizons of duff as measured across three spatial scales (Sub-Transect,  $10^1$  m; Transect,  $10^2$  m, Forest,  $10^3$  m). The error bars  
626 indicate standard error about the mean of the variation metric (standard deviation or coefficient of variation).

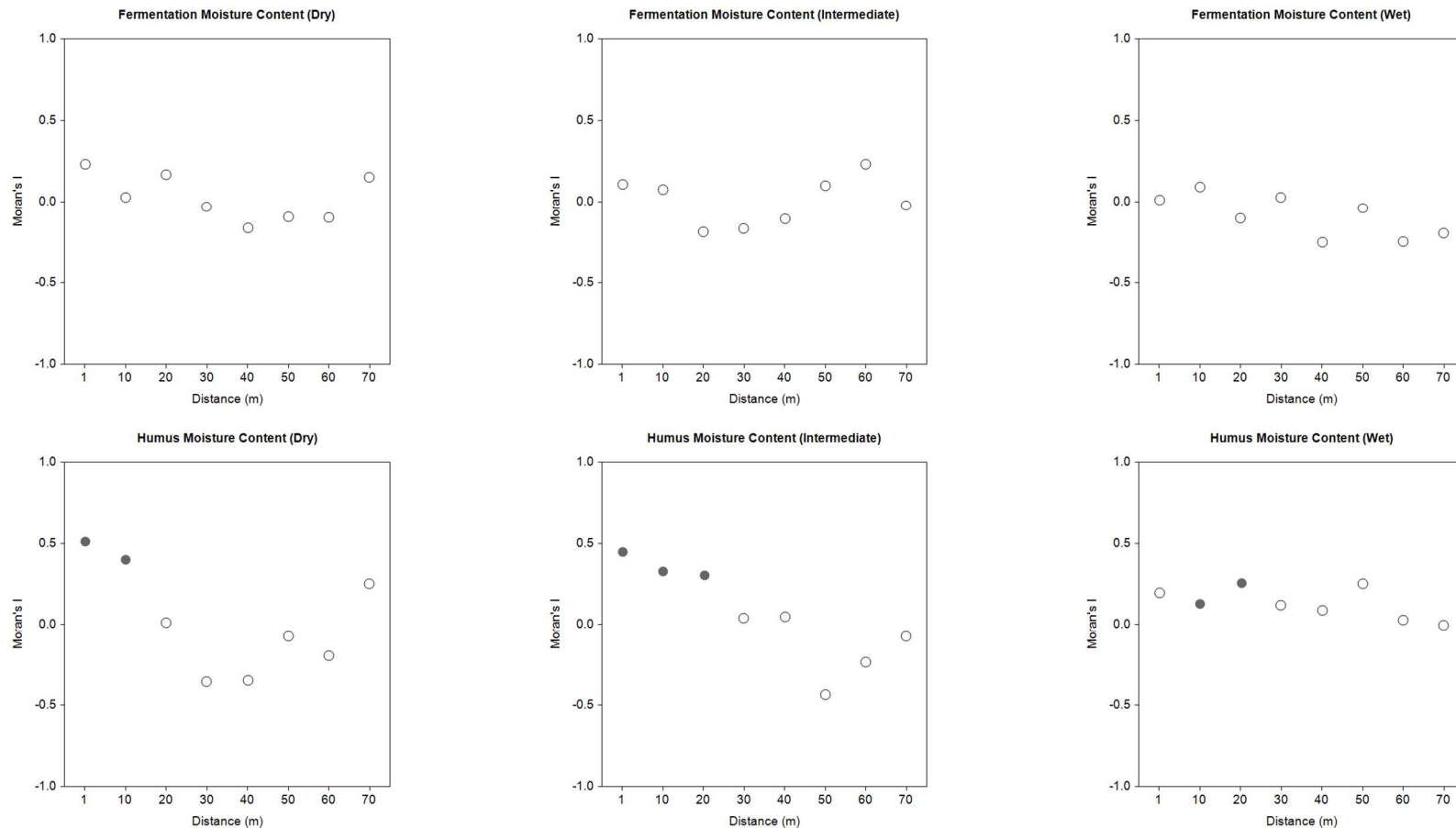
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627 **Fig. 7.** Spatial correlograms of depth (left) and bulk density (right) of duff horizons (fermentation above, humus below) in a long-  
628 unburned longleaf pine (*Pinus palustris*) forest in northern Florida. Solid circles indicate significant positive spatial autocorrelation  
629 (significant Moran's *I* statistic).  
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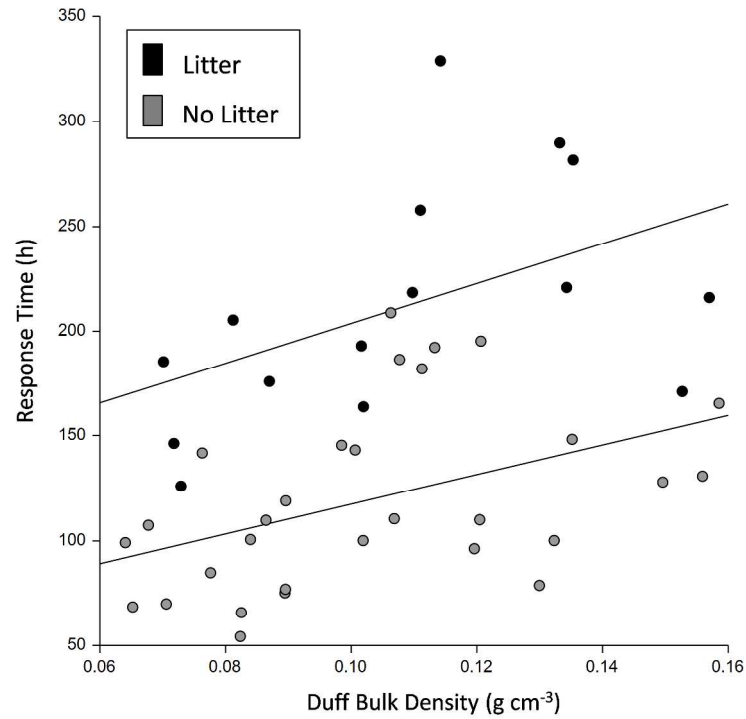




631 **Fig. 8.** Spatial correlograms of moisture content in duff horizons (fermentation above, humus below) during three sampling periods  
 632 (dry, intermediate, wet) in a long-unburned longleaf pine (*Pinus palustris*) forest in northern Florida. Solid circles indicate significant  
 633 positive spatial autocorrelation (significant Moran's *I* statistic).

634 Sampling periods- Dry: thirteen days since rain, 31 mm in preceding 30 days; Intermediate: one day since rain (23 mm), 24 mm in the  
635 preceding 7 days, 129 mm in the preceding 30 days; Wet: one day since rain (190mm), 291 mm in the preceding 7 days, 400 mm in  
636 the preceding 30 days.

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637

638 **Fig. 9.** Drying response time (h) as a function of duff bulk density (g cm<sup>-3</sup>) and the presence or  
 639 absence of litter (pseudo-litter made of plastic). Model  $R^2 = 0.57$ .