



RESEARCH

Open Access



Forest floor properties in pine forests of the southeastern and western United States

Susan J. Prichard^{1*}, Deborah G. Nemens¹, Maureen C. Kennedy², Jessie Thoreson¹, Lauren C. Satterfield¹, Paige C. Eagle¹, Eric M. Rowell¹, Andrew T. Hudak³ and Nuria Sánchez-López⁴

Abstract

Background Wildland fuels are fundamental variables in modeled predictions of fire behavior and effects. In forest ecosystems, accumulated forest floor layers, including recently fallen litter and highly decomposed organic material (i.e., duff), often constitute most surface fuel—biomass and stored carbon. Associated error in estimated litter and duff biomass can thus propagate to major sources of uncertainty in predicted fire effects, including tree mortality and smoke production. Distributions of forest floor biomass are difficult to measure, and estimates of litter and duff biomass typically involve high uncertainty. In this study, we evaluated relationships between forest floor characteristics (i.e., depth, biomass, and bulk density) and how forest floor layers vary between locations against the boles of trees, inside tree crown drip lines, and outside tree crown drip lines. Our study focused on pine-dominated systems with open forest canopies including southeastern (SE) pine mesic flatwoods, SE loblolly pine plantations with sweetgum understories, and western (W) ponderosa pine and mixed conifer forests.

Results Across the three forest types, litter depths were highest in SE flatwood sites and lowest in W pine sites, but W pine litter generally had higher bulk density and thus greater biomass than SE pine sites. Duff depth and biomass were greater in W sites, likely related to less frequent burning and slower rates of decomposition than SE forests. Linear regression models were constructed to predict litter and duff biomass from sampled depth and transect positions for each forest type. Even with high variance among samples, there were significant differences in litter and especially duff characteristics across transect positions. Across all forest types, litter and duff accumulations generally were significantly greater inside than outside tree crowns, particularly when bole and outside positions were compared.

Conclusions Modeled relationships revealed significant trends that could inform process models of forest floor development and decomposition over time. With increased availability of stem and crown mapping based on lidar metrics, estimates of forest floor accumulations can be made through mapping of tree crown positions and predictive modeling of litter and duff biomass in relation to tree crowns.

Keywords Forest floor, Litter, Duff, Carbon, Wildland fuels, Ponderosa pine, Longleaf pine, Loblolly pine, Slash pine

Resumen

Antecedentes Los combustibles vegetales son una variable fundamental en la predicción del modelado del comportamiento y efectos del fuego. En ecosistemas forestales, la acumulación de capas en la superficie del suelo, incluyendo la hojarasca recién caída (i. e. hojarasca, broza, o litter) y también el material altamente descompuesto (i.e. mantillo en descomposición, o duff), constituyen la mayoría del combustible superficial, de la biomasa y el carbono en él

*Correspondence:

Susan J. Prichard
sprich@uw.edu

Full list of author information is available at the end of the article

acumulado. El error asociado en la estimación de biomasa contenida en el litter y duff, pueden entonces transmitir las mayores fuentes de incertidumbre en la predicción de los efectos del fuego, incluyendo la mortalidad de árboles y la producción de humo. La distribución de la biomasa en la superficie del suelo forestal es difícil de medir y las estimaciones de hojarasca (litter) y mantillo en descomposición (duff) implican típicamente una gran incertidumbre. En este estudio, evaluamos las relaciones entre las características de la superficie del suelo forestal (i. e. profundidad, biomasa y densidad aparente) y cómo las distintas capas u horizontes superficiales varían entre diferentes ubicaciones; contra los troncos de los árboles, dentro de la línea de proyección del dosel arbóreo (superficie por debajo del dosel), y por fuera del perímetro de esa superficie. Nuestro estudio se enfocó en sistemas dominados por pinos con doseles abiertos, incluyendo sabanas planas de bosques de pinos del sudeste de los EEUU (SE), plantaciones de pino taeda en el SE con sotobosques de liquidámbar, y pinos ponderosa del oeste (W) y bosques mixtos de coníferas.

Resultados A través de los tres tipos forestales, la profundidad de la hojarasca (litter) fue mayor en los sitios de bosques del SE, y menor en los bosques del oeste (W), aunque la hojarasca del oeste (W) presentó una densidad aparente más alta y por lo tanto mayor biomasa que los sitios de pinos de SE. La profundidad del mantillo en descomposición (duff) y la biomasa fue mayor en los sitios W, probablemente debido a quemas menos frecuentes y menores tasas de descomposición que en los bosques del SE. Los modelos de regresión lineal fueron construidos para predecir la hojarasca (litter) y el mantillo basados en muestreos sobre su profundidad en transectas posicionadas en cada tipo forestal. Aun con una gran variación entre muestras, hubo diferencias significativas en las características de la hojarasca y especialmente en el duff entre las transectas posicionadas en cada tipo forestal. A lo largo de todos los tipos forestales, la acumulación tanto de la hojarasca (litter) como del mantillo (duff) fueron mayores debajo del dosel arbóreo que fuera de él, principalmente cuando las comparaciones fueron hechas contra los troncos de los árboles, y por fuera del perímetro de la proyección del dosel.

Conclusiones Las relaciones modeladas revelaron tendencias significativas que pueden informar sobre modelos de procesos del desarrollo y descomposición del suelo forestal en el tiempo. Con la creciente disponibilidad de mapeos de troncos y doseles con modelos métricos de LIDAR, la estimación de las acumulaciones en la superficie de los suelos forestales pueden ser hechos a través del mapeo de la posición de los doseles de los árboles y modelos predictivos de la hojarasca y del mantillo en relación con los doseles de los árboles.

Background

Improved characterization of forest floor biomass distributions is critical to refining predictions of wildland fire behavior and smoke emissions (Keane 2015; Prichard et al. 2022). Leaf and needle litter layers contribute to high fuel continuity under forest canopies and are often key drivers of wildland fire spread (Varner et al. 2015). In many temperate and boreal forests, partially or highly decomposed litter, termed duff, accumulates over time as dense organic soil layers that can burn in long-duration smoldering fires (Reardon et al. 2007) or in large wildfire events following persistent drought conditions (Zhao et al. 2019).

Contemporary decision support models on wildland fuel consumption and smoke rely on two-dimensional (i.e., biomass per unit area or fuel density; e.g., Mg ha^{-1}) inputs of forest litter and duff accumulations (Reinhardt et al. 1997; Prichard et al. 2014), but these area-based estimates fail to represent the inherent heterogeneity of forest floor layers and can lead to high uncertainty in model predictions. For example, in a study of accumulated duff in long-unburned pine forests of the southeastern (SE) US, Kreye et al. (2014) reported high spatial variability in measured depth and biomass across a range of sampled

spatial scales from fine scale (submeter) to coarse scale (100–1000 m) heterogeneity. Studies conducted in pine and mixed conifer forests of California similarly reported high variance between samples and significant relationships between forest floor accumulations and tree crown position (Banwell and Varner 2014; DiMario et al. 2018).

With mounting concerns about greenhouse gas emissions and smoke impacts from wildland fires, there is a critical need to improve the characterization and mapping of fuels that contribute to wildland fire behavior, pollutant emissions, and other fire effects (Urbanski 2014; Prichard et al. 2022). In particular, duff consumption in wildland fire events can lead to substantial emissions of fine particulate matter (PM_{2.5}) and long-duration smoke impacts to communities (Ottmar 2014; D'Evelyn et al. 2022). Because accumulated duff layers are densely packed, they are often slowly consumed by long-duration smoldering fires (Frandsen 1987; Reardon et al. 2007) with low combustion efficiencies that not only produce high amounts of PM_{2.5} but also result in long-duration soil heating that damages the living tissue of trees and other plants (Ryan and Frandsen 1991; Varner et al. 2007). In long-unburned forests, litter and duff layers often comprise a substantial portion of forest biomass

available to burn (Ryan and Frandsen 1991; Varner et al. 2005).

When fire is reintroduced to fire-excluded forests, older trees can be particularly susceptible to damage from long-duration burning of forest floor layers, with high rates of tree mortality even among fire-resistant species that are adapted to low-intensity surface fires of the past (Swezy and Agee 1991; Stephens and Finney 2002; Varner et al. 2007). In fire-excluded ecosystems, old trees often contain accumulated forest floor materials at their base, termed duff mounds (Garlough and Keyes 2011) or basal accumulations (Ottmar et al. 2007). Following a long absence of fire in older forests, individual trees can build extensive fine root systems within these deep organic soils that are vulnerable to long-duration consumption of duff layers (Varner et al. 2005, 2007). Efforts to protect old trees from future fire events sometimes include raking or clearing materials away from tree stems, but where fine root systems are extensive, raking can also contribute to tree injury or mortality (Dalrymple and Safford 2013). Reliable estimates of where basal accumulations exist are therefore important for estimating smoke production and informing strategies to reintroduce fire in such a way that forest floor materials can be burned incrementally over time to protect old trees.

Because of the inherent variability of forest floor layers and the time-intensive nature of field sampling, improved estimation of forest floor distributions is exceedingly difficult. To date, field-based approaches to measuring litter and duff are the most common and reliable methods to characterize forest floor biomass and bulk density (Keane 2015). Remote-sensing methods such as terrestrial laser scanning or photogrammetry can be used to estimate the cover of forest floor layers but not depth or bulk density (Prichard et al. 2022). Ground-penetrating radar may offer a way to estimate litter and duff depths synoptically across sites but is still under evaluation (André et al. 2016).

A promising approach to refining estimates of site litter and duff biomass is through modeling relationships between overstory tree crowns and the cover, depth, and biomass of understory forest floor material (Sánchez-López et al. 2023). By incorporating litter decomposition rates, predictive equations and ecosystem process models may be able to estimate litter and duff depth and biomass as a function of tree crown inputs (McDanold et al. 2023). In support of future models, field datasets are needed to provide site estimates of litter and duff layers by forest type and to quantify relationships of depth, biomass, and bulk density in relation to tree crowns.

In this study, we evaluated the influence of overstory tree crowns on litter and duff cover, depth, and bulk density in open pine forests. This research is part of a larger effort to characterize the three-dimensional structure

and biomass of forest types common to prescribed burning programs in the SE and western (W) US, including SE pine flatwoods, SE loblolly sweetgum plantations, and W ponderosa pine and mixed conifer forests (Prichard et al., this issue). The main objective of this study was to evaluate if overstory tree crowns, in combination with other site variables such as forest type and time since disturbance, can be used to inform local predictions of forest floor cover, depth, and biomass.

Methods

Study areas

Seven SE pine sites were sampled in this study, including four mesic pine flatwood sites and three loblolly pine-sweetgum forest sites in Florida and Georgia (Table 1). Sites were selected to represent open pine-dominated forests that are broadly representative of forests that are common to prescribed burning programs in the SE US. The climate of the SE US is humid subtropical with warm to hot humid summers and a relatively dry dormant season between November and February (Ingram et al. 2013). Sites in each forest type were selected to represent a range of burn histories from 1-year post-fire to over 5-years post-fire. Overstory tree species in the pine flatwood sites included longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), and slash pine (*Pinus elliottii*). Understories included some sites with high wiregrass (*Aristida stricta*) cover to shrub understories dominated by saw palmetto (*Serenoa repens*) and gallberry (*Ilex glabra*).

Four sites were sampled in the western (W) US, including open-grown pine forests that are dominated either by ponderosa pine (*Pinus ponderosa*) or ponderosa pine with codominant Douglas-fir (*Pseudotsuga menziesii*) (Table 1). Sites have a wide geographic range but were selected based on their comparable overstory characteristics. The precise burn histories are unknown, although the apparent encroachment of Douglas-fir in some sites is indicative of a longer period of fire exclusion than at the sites without codominant Douglas-fir. Ponderosa pine is adapted to and tolerant of low-intensity surface fires, whereas young Douglas-fir is much more sensitive to fire and vulnerable to fire-induced mortality (Fitzgerald 2005). Because prescribed burning is not as common or frequent in the western (W) US, sites were visually selected to represent a range of understory biomass from sparse understories with low biomass to relatively higher shrub cover and understory biomass. Shrub species varied across sites but included bitterbrush (*Purshia tridentata*), kinnikinnick and pinemat manzanita (*Arctostaphylos uva-ursi* and *Arctostaphylos nevadensis*), and Gambel oak (*Quercus gambelii*).

Table 1 Study sites, including site name, location, time since fire (TSF), ranking of understory biomass (low, moderate, or high), vegetation type description, and sampling date

Site name	Location	TSF/biomass range	Vegetation type	Sampling date
<i>Southeast flatwood</i>				
Tate's Hell A	Tate's Hell State Forest, FL, USA	1–2 yrs	Slash pine plantation/palmetto-gallberry	Jan 2020
Tate's Hell B	Tate's Hell State Forest, FL, USA	2–3 yrs	Slash pine plantation/palmetto-gallberry	Jan 2020
Ft Stewart A	US DOD Ft Stewart, GA, USA	2–3 yrs	Longleaf and loblolly pine/palmetto-gallberry	Jan 2021
Aucilla	Suwannee River Water Management District, FL, USA	> 5 yrs	Longleaf pine forest/palmetto-gallberry	Apr 2021
<i>Southeast loblolly sweetgum</i>				
Hitchiti B	Hitchiti Experimental Forest, GA, USA	1 yr	Loblolly pine plantation/sweetgum	Feb 2022
Hannah Hammock	Tall Timbers Research Station, FL, USA	1–2 yrs	Loblolly pine plantation/sweetgum	Jul 2022
Hitchiti A	Hitchiti Experimental Forest, GA, USA	2–3 yrs	Loblolly pine plantation/sweetgum	Feb 2022
<i>Western pine</i>				
LANL Forest	Los Alamos National Laboratory, NM, USA	Low	Ponderosa pine/Gambel oak timber-litter	Jun 2021
Sycan Forest I	Sycan Marsh Preserve, OR, USA	Low	Ponderosa pine/bitterbrush and timber-litter	Sep 2019
Methow	Methow Wildlife Area, WA, USA	Moderate	Ponderosa pine/bitterbrush	Oct 2020
Lubrecht	Lubrecht Experimental Forest, MT, USA	High	Ponderosa pine and Douglas-fir/timber litter-low shrub	Jul 2019

Field methods

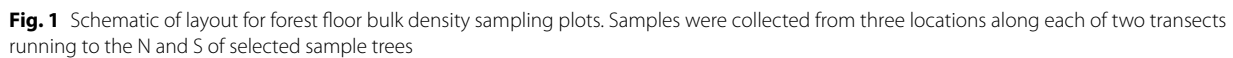
This study was part of a larger study design to characterize surface and overstory fuels that are common to prescribed burns in the southeastern and western US. We used a hierarchical sampling design employing multiple methods to characterize the 3D structure and composition of overstory and understory fuels in open-canopied pine forests, including airborne laser scanning, terrestrial laser scanning, close-range photogrammetry, and destructive field sampling (Prichard et al., this issue). This study is intended to inform how litter and duff accumulations may be modeled based on relative position under dominant tree crowns. For each site, we selected a minimum of nine overstory trees to evaluate how forest floor characteristics such as depth and bulk density relate to position under tree crowns. The Lubrecht study site had 11 focal trees, and the Sycan site had 12 focal trees. To select the focus trees, we used a randomly chosen azimuth at the northwest corner of each 5×5 m sampling plot within the 3D fuels project area (Prichard et al., this issue) to locate a tree that met our criteria (i.e., living, diameter at breast height > 15 cm, and positioned 15–30 m from the 5×5 m plot). Each sample tree was photographed, and GPS coordinates were collected from the base of the tree along with tree DBH (cm), height (m), height to live crown (m), and species.

Forest floor samples were measured and collected along two transects originating from the bole of the tree and extending in both north and south directions to

outside of its crown radius (drip line). Following a similar method to Banwell et al. (2014), samples were positioned at three locations along each transect: 10 cm from the base of the tree bole (bole), half the distance between the bole and the outer edge of the crown (inside), and 2 m outside of the drip line of the tree being sampled (outside, Figs. 1 and 2). The distance from the bole to the drip line of each tree was recorded along both transects. If the outside sampling position still had a relatively closed canopy because of adjacent tree crowns, we moved the outside sample to a position along the transect that was both outside the drip lines of the focus tree and any nearby trees with overlapping crowns.

Prior to destructive sampling of forest floor layers, each destructive plot was cleared of live and standing dead vegetation, pine cones, and downed wood, leaving litter and duff layers undisturbed. Downed wood and cones were considered part of the litter layer if the central axis of the particle was embedded in the litter. Needles, leaves, or other material that was suspended in grass or other vegetation was not considered part of the litter layer and excluded from the bulk density sample. A 25×25×10-cm sampling frame was placed on the top of the litter layer, and material along the edges of the frame was clipped to allow the frame to be inserted to the base of the organic soil layer (duff).

Once the sampling frame was in place, six nails (termed duff pins) were equally spaced on a systematic grid and pushed into the surface such that the top of the pin was



Distinguishing between litter and duff layers can be challenging in the field (Keane 2015). Duff is defined as partially to highly decomposed litter (Oe and Oa soil horizons), and depending on how dry and friable duff is during sampling, delineating boundaries between litter and duff can be difficult. Field crew members carefully calibrated definitions across sites and classified material as duff where forest litter became highly fragmented with evidence of decay such as the presence of fungal hyphae,

Through initial processing, we determined that duff samples were contaminated with sand and other mineral soil particles and required further processing. Following sieving, each duff sample was dried, weighed, and then sent to the University of Washington Soil Analytics Lab. A homogenous subsample was finely ground and then processed through an elemental analyzer (2400 Series II



Fig. 2 Example of a focus tree and beginning of a sampling transect in Fort Stewart, GA, USA

CHNS/O, PerkinElmer, Waltham, MA, USA), to determine the proportion of each sample that was carbon. This value was then multiplied by 2 to approximate the proportion of organic matter, because dry weight carbon is approximately half of biomass (Nelson and Sommers 1996). The proportion of organic matter was then multiplied by the original dry weight of the sample for a final estimate of organic matter biomass contained in the sample (Supp. Table S1). This value was then added to the dry weight of the “pure duff” sample to calculate a total duff sample biomass.

Statistical analysis

Litter and duff depths, sampled at the six pin locations at each sampling position, were averaged and multiplied by the area of the sampling frame for an estimate of the sampled volume for each litter and duff layer. The bulk density of litter and duff layers was then calculated as dry weight biomass per unit volume (kg m^{-3}). Forest floor characteristics (i.e., depth, biomass in kg m^{-2} , and bulk density in kg m^{-3}) were summarized by forest floor type. Relationships between forest

floor characteristics and transect position were evaluated using analysis of variance tests for significant mean differences between the depth, biomass, and bulk density of litter and duff layers and transect position (bole, inside, and outside tree drip lines). Given the potential for dependence of transects associated with individual trees and plots associated with individual transects, we considered mixed-effects models with either individual tree or individual transect (given a tree) as random effects, where the Akaike information criterion (AIC) was used to choose random effects. Mixed-effects models and associated post hoc multiple comparisons were estimated using the lme4 (Bates et al. 2015) and multcomp (Hothorn et al. 2008) packages in the R statistical program. For each forest type, linear regression models were constructed to predict litter and duff biomass from sampled depth, dependent on transect location.

Results

Measured forest floor characteristics were highly variable across all study sites. Within-site variability was notable, represented by the wide reported standard deviations for summarized depth (cm), biomass (kg m^{-2}), and bulk density (kg m^{-3}) for both litter and duff (Tables 3, 4, and 5). Overall, SE flatwood sites had significantly greater litter depth than the loblolly sweetgum and W pine sites, and litter bulk density was significantly greater in the W pine sites than SE sites (Table 3, Fig. 4). Duff depth, biomass, and bulk density were significantly greater in W pine sites than SE sites. Of the two SE forest types, loblolly sweetgum sites had greater duff accumulations than SE flatwoods.

Even with high variance among samples, litter and duff characteristics significantly varied as a function of position in relation to tree crowns and among the forest types. In general, including tree as a random effect resulted in a lower AIC, but no further improvement was found when including individual transect as a random effect. All inferences were therefore made with mixed-effects models with tree as the random effect. Sample tree measurements are reported in Table 6. Although tree species composition differed among the three forest types, crown characteristics were comparable among sites.

Forest litter

Across SE flatwood sites, litter depths ranged from 1.89 (± 1.36 standard deviation) to 7.36 (± 1.51) cm. Biomass values ranged from 0.16 (± 0.06) to 1.28 (± 0.34) kg m^{-2} (Table 4). Litter depths were significantly greater underneath tree crowns than the outside transect position



Fig. 3 Photo of the 25 × 25-cm sampling square (left) and nail placement in a forest floor sampling plot (right). Once the litter layer was removed and protruding nail lengths measured, nails were placed flush with the top of the duff layer for duff layer measurement and sampling

(Fig. 4, Table 7). Although litter biomass also tended to be greater at bole positions than inside the drip line, there was high variance among samples and no significant difference between those positions. Litter depth and biomass generally increased with time since fire across the four SE flatwood sites (Table 4). Litter bulk density ranged from 9.47 (± 6.86) to 21.33 (± 9.51) kg m^{-3} and was significantly higher at the bole position than inside and outside positions. Unlike depth and biomass, there was no observable trend in litter bulk density with time since fire.

Loblolly sweetgum sites had lower overall litter depths than SE flatwood sites (Fig. 4); mean litter depth ranged from 2.45 (± 0.84) to 4.97 (± 1.60) cm. Litter biomass ranged from 0.36 (± 0.18) to 1.11 (± 0.53) kg m^{-2} . Litter depth was not significantly different across

transect positions, but biomass was significantly greater at the bole position relative to inside and outside positions (Table 7). Across the three sites, litter bulk density ranged from 8.89 (± 2.55) to 28.76 (± 17.90) kg m^{-3} . Litter bulk density was significantly higher at the bole position relative to inside and outside positions.

Across the W pine sites, litter depths were generally lower than SE forests (Table 4), ranging from 1.25 (± 0.68) to 3.68 (± 1.32) cm. Mean biomass values ranged from 0.20 (± 0.12) to 1.79 (± 1.49) kg m^{-2} . Litter depth and biomass were significantly higher at the bole and inside positions compared to outside tree drip lines. Overall, W pine sites had higher litter bulk density than SE flatwood and loblolly sweetgum sites, ranging from 15.78 (± 11.63) to 55.02 (± 27.6) kg m^{-3} . Litter bulk density was significantly higher at the bole position relative to inside and outside

Table 2 Definitions used for classification of litter types of samples collected during forest floor sampling

Litter code	Definition	Litter code	Definition
BS	Bark slough	LP/LH	Long needle pine/loose hardwood
CS	Cone scales	M	Moss
DH	Deciduous hardwood	MH	Matted hardwood
EH	Evergreen hardwood	MS	Mineral soil
EL	Evergreen litter	NS	No surface material
F	Forb	OC	Other conifer
FHL	Fir/hardwood	PA	Palmetto
FL	Fir litter	PF	Palm frond
GL	Ground lichen	PL	Pine litter
GR	Grass	PN	Pine needles
LH	Loose hardwood	ROCK	Rock
LOG	Log	SF	Spruce-fir-hemlock
LP	Long needle pine (open)	SP	Short needle pine
LP/EL	Long needle pine/evergreen litter	UK	Unknown

Table 3 Summary of litter and duff characteristics by forest type and transect position, including sample counts (n), mean depth (cm), mean biomass (kg m⁻²), and mean bulk density (kg m⁻³) and associated standard deviations (SD). Significant differences in mixed models between forest types (*p* < 0.01) are indicated by superscripts next to forest type means (a, b, c). Transect positions include bole (next to tree bole), inside (inside crown dripline), and outside (outside crown dripline)

Forest type and transect position	Litter			Duff			Depth (cm)	SD	Biomass (kg m ⁻²)	SD	Bulk density (kg m ⁻³)	SD	Bulk density (kg m ⁻³)	SD
	n	Depth (cm)	SD	n	Depth (cm)	SD								
<i>SE flatwood</i>	215	4.88a	2.68	215	0.95a	1.02	0.95a	1.02	0.48a	0.62	38.72a	39.1	38.72a	39.1
Bole	72	5.04	2.74	71	0.88	1.09	0.88	1.09	0.38	0.58	31.05	33.97	31.05	33.97
Inside	71	5.51	2.72	72	1.13	1.02	1.13	1.02	0.58	0.67	44.26	42.65	44.26	42.65
Outside	72	4.11	2.4	72	0.85	0.93	0.85	0.93	0.46	0.61	40.75	39.45	40.75	39.45
<i>SE loblolly sweetgum</i>	162	3.58b	1.43	161	1.3a	0.89	1.3a	0.89	0.71a	0.72	55.97b	31.37	55.97b	31.37
Bole	54	3.31	1.1	53	1.61	1.17	1.61	1.17	1.03	1.02	68.03	38.57	68.03	38.57
Inside	54	3.52	1.57	54	1.3	0.74	1.3	0.74	0.62	0.45	49.58	23.52	49.58	23.52
Outside	54	3.9	1.53	54	1	0.57	1	0.57	0.5	0.42	50.52	27.22	50.52	27.22
<i>Western pine</i>	246	2.23c	1.36	222	2.17b	1.82	2.17b	1.82	2.01b	1.98	88.66c	65.69	88.66c	65.69
Bole	82	2.5	1.45	76	2.83	2.06	2.83	2.06	2.81	2.31	92.73	53.99	92.73	53.99
Inside	84	2.45	1.31	70	2.42	1.55	2.42	1.55	2.36	1.84	95.1	41.8	95.1	41.8
Outside	80	1.72	1.17	76	1.27	1.4	1.27	1.4	0.88	1.03	78.66	89.65	78.66	89.65

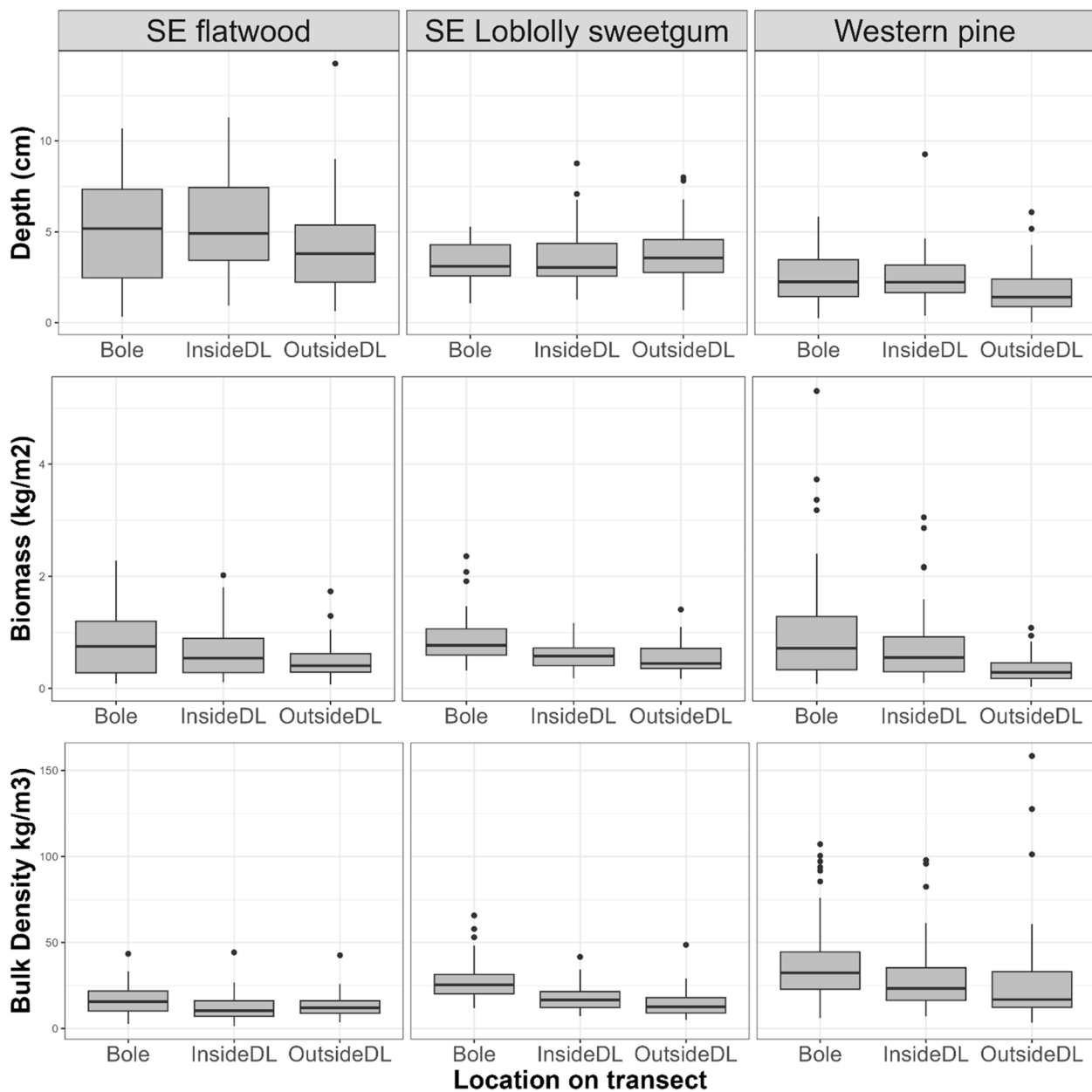


Fig. 4 Litter depth (cm), biomass (kg m^{-2}), and bulk density (kg m^{-3}) distributions across the three transect positions (next to bole, inside drip line, and outside drip line) and three sampled forest types

positions. Across all sites, predictive linear regression models relating litter biomass to depth and transect position were significant but had low coefficients of determination (Table 8, Supp. Fig. S1). Modeled relationships between litter biomass and depth at specific transect positions (i.e., bole, inside, and outside) were generally stronger under tree crowns than outside tree crowns.

Forest duff

Overall, SE flatwood sites had lower duff depth and biomass than loblolly sweetgum and W pine sites (Fig. 5).

Mean duff depths ranged from 0.11 (± 0.18) to 1.37 (± 1.14) cm, and duff biomass values ranged from 0.05 (0.08) to 0.81 (± 1.09) kg m^{-2} (Table 5). Duff depth and biomass were not significantly different between transect positions (Table 6) and did not increase with time since fire. Duff biomass was markedly lowest at Aucilla, which had not been burned in over 5 years. Bulk density ranged from 1 (3.91 ± 10.87) to 71.97 (± 39.44) kg m^{-3} . There were no significant differences in duff bulk density values across transect position.

Table 4 Litter depth (cm), biomass (kg m^{-2}), and bulk density (kg m^{-3}) of southeast flatwood forest (SE flatwood), southeast loblolly pine-sweetgum forests (loblolly sweetgum), and western pine forests by site. SE sites are ordered by time since fire (TSF). Transect positions include bole (next to tree bole), inside (inside crown dripline), and outside (outside crown dripline)

Site name	Transect position	n	Depth (cm)				Biomass (kg m ⁻²)				Bulk density (kg m ⁻³)			
			Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
SE flatwood														
Tate's Hell A	All	54	2.37	0.33	10.15	1.7	0.2	0.07	0.62	0.1	11.73	1.49	42.58	8.37
	Bole	18	1.89	0.33	5.87	1.36	0.16	0.09	0.3	0.06	12.73	2.69	30.74	8.81
	Inside	18	3.03	0.95	10.15	2.11	0.21	0.11	0.62	0.11	9.47	1.49	26.34	6.86
	Outside	18	2.18	0.65	6.13	1.41	0.22	0.07	0.42	0.1	12.99	3.78	42.58	9.25
Tate's Hell B	All	53	4.55	1.53	10.98	2.39	0.46	0.23	1.07	0.17	12.43	4.1	30.01	6.59
	Bole	18	4.56	1.58	10.65	2.48	0.54	0.23	1.07	0.21	14.73	4.1	30.01	8.11
	Inside	17	5.62	2.3	10.98	2.66	0.44	0.26	0.69	0.14	9.85	4.18	23.69	6.12
	Outside	18	3.53	1.53	7.15	1.55	0.39	0.26	0.57	0.1	12.56	5.46	21.64	4.42
Fort Stewart	All	54	6.18	1.3	14.25	2.44	0.97	0.13	2.28	0.46	17	5.2	44.27	8.67
	Bole	18	6.35	3.2	9.13	1.71	1.24	0.55	2.28	0.42	21.33	7.71	43.47	9.51
	Inside	18	6.44	3.03	11.3	2.48	0.95	0.33	2.02	0.45	16.17	7.13	44.27	9.05
	Outside	18	5.76	1.3	14.25	3.02	0.71	0.13	1.73	0.35	13.51	5.2	22.32	5.36
Aucilla	All	54	6.42	2.13	10.68	1.96	0.94	0.27	1.87	0.43	14.8	4.42	32.01	5.68
	Bole	18	7.36	5.17	10.68	1.51	1.28	0.62	1.87	0.34	17.95	9.05	32.01	5.68
	Inside	18	6.95	4.5	10.48	1.91	0.93	0.39	1.67	0.38	13.55	8.04	24.73	4.61
	Outside	18	4.96	2.13	7.7	1.6	0.6	0.27	1.3	0.27	12.9	4.42	25.91	5.57
Loblolly sweetgum														
Hitchiti B	All	54	2.68	0.7	4.57	0.85	0.52	0.18	1.12	0.18	21.2	9.14	57.88	10.16
	Bole	18	2.45	1.08	4.43	0.84	0.57	0.32	0.79	0.12	26.71	11.92	57.88	12.72
	Inside	18	2.73	1.57	4.57	0.75	0.49	0.18	1.12	0.21	18.04	10.98	29.44	5.17
	Outside	18	2.85	0.7	4.48	0.93	0.5	0.2	1.07	0.21	18.86	9.14	48.64	9.22
Hannah Hammock	All	54	3.45	1.28	7.82	1.3	0.6	0.17	1.37	0.32	18.99	5.15	53.05	11.08
	Bole	18	3.36	1.62	4.87	0.94	0.93	0.47	1.37	0.25	28.77	17.91	53.05	8.41
	Inside	18	2.87	1.28	5.8	1.12	0.5	0.18	0.93	0.21	19.31	7.22	41.66	9.78
	Outside	18	4.11	2.2	7.82	1.51	0.36	0.17	0.93	0.18	8.89	5.15	14.45	2.55
Hitchiti A	All	54	4.62	2.65	8.77	1.37	0.87	0.37	2.36	0.4	19.87	7.29	65.74	10.01
	Bole	18	4.13	2.65	5.28	0.81	1.11	0.6	2.36	0.53	26.95	12.94	65.74	12.23
	Inside	18	4.97	2.68	8.77	1.6	0.77	0.41	1.17	0.2	16.98	8.1	34.31	6.87
	Outside	18	4.75	2.75	8	1.49	0.71	0.37	1.41	0.27	15.7	7.29	28.55	5.95
Western pine														
LANL Forest	All	51	2.47	0.03	9.27	1.69	1.1	0.03	5.31	1.09	45.09	12.26	127.63	28.51
	Bole	15	2.94	0.27	5.2	1.73	1.79	0.08	5.31	1.49	55.02	27.28	107.19	27.6
	Inside	18	2.97	1.08	9.27	1.8	1.24	0.33	3.05	0.8	44.25	16.05	97.93	25.16
	Outside	18	1.59	0.03	4.28	1.18	0.39	0.03	0.94	0.24	37.66	12.26	127.63	31.38
Sycan Forest I	All	67	1.83	0.25	3.93	0.94	0.52	0.07	2.16	0.38	30.27	6.5	158.44	22.77
	Bole	23	2	0.25	3.68	0.89	0.64	0.15	1.41	0.37	34.85	12.3	97.17	20.3
	Inside	23	2.2	0.72	3.93	0.97	0.58	0.14	2.16	0.45	25.15	11.6	61.4	11.08
	Outside	21	1.25	0.32	2.5	0.68	0.3	0.07	0.84	0.21	30.85	6.5	158.44	32.67
Methow Wildlife Area	All	54	3.17	1.28	6.08	1.21	0.93	0.2	3.18	0.6	29.55	8.33	63.26	14.12
	Bole	18	3.68	1.83	5.83	1.32	1.49	0.63	3.18	0.69	40.97	21.52	63.26	13.72
	Inside	18	3.17	2	4.63	0.93	0.8	0.29	1.21	0.27	26.67	14.25	49.56	10.59
	Outside	18	2.65	1.28	6.08	1.18	0.51	0.2	1.08	0.23	21	8.33	40.88	9.82
Lubrecht	All	70	1.84	0.38	5.38	1.08	0.37	0.03	2.35	0.37	22.22	3.43	100.44	16.63
	Bole	24	2.04	0.43	5.38	1.12	0.56	0.1	2.35	0.55	28.32	6.13	100.44	20.99
	Inside	24	1.86	0.38	3.9	0.97	0.33	0.1	0.69	0.16	22.01	7.08	55.51	13.67
	Outside	22	1.6	0.43	5.17	1.14	0.2	0.03	0.47	0.12	15.78	3.43	51.82	11.63

Duff depth and biomass values were similar between SE flatwood and loblolly sweetgum sites (Fig. 5). Within SE loblolly sweetgum sites, duff depths ranged from 1.00 (± 0.70) to 1.93 (± 1.25) cm. Biomass values ranged from 0.33 (± 0.28) to 1.41 (± 1.48) kg m⁻². Duff depth was significantly higher at bole positions than outside positions, and duff biomass was significantly higher at the bole position compared to inside and outside positions (Table 4). Duff bulk density values ranged from 41.33 (± 29.57) to 72.61 (± 42.77) kg m⁻³. Bulk density was significantly higher at bole and inside positions than outside tree crowns.

Western pine sites generally had greater duff depths, biomass, and bulk density than SE sites (Fig. 5). Duff depths ranged from 0.59 (± 0.69) to 3.61 (± 1.28) cm, and duff biomass values ranged from 0.32 (± 0.43) to 3.96 (± 1.72) kg m⁻². Duff depth and biomass were significantly higher at bole and inside versus outside positions (Table 7). Duff bulk density values ranged from 35.97 (± 31.33) to 124.41 (± 49.39) kg m⁻³. Bulk density was significantly higher at bole and inside versus outside positions. Across all sites, modeled relationships of biomass to depth were stronger in duff models than litter models (Table 8) but exhibited high variance (Supp. Fig. S2).

Discussion

Reliable estimates of forest floor characteristics are critically important for predicting fire effects, particularly in fire-excluded forests with substantial organic soil accumulations. In pine and oak forests, litter layers and pine cones are often major drivers of fire spread and intensity (Gabrielson et al. 2012; Kreye et al. 2013; Varner et al. 2015), whereas accumulated duff can contribute to major fire effects including postfire tree mortality and smoke impacts. In long unburned forests, deep duff accumulations present challenges not only for smoke management but also in their negative impacts on understory diversity (Hiers et al. 2007) and their contribution to postfire tree mortality.

A small number of studies have been conducted to measure relationships of forest floor depth, biomass, and bulk density to tree crowns. Of these, Banwell and Varner (2014) have one of the most robust samples of accumulated duff in four long-unburned Jeffrey—white fir (*Pinus jeffreyi* and *Abies concolor*) forest sites of Lake Tahoe Basin, CA, USA. A similar study was conducted to characterize accumulated litter and duff mounds around old sugar pine (*Pinus lambertiana*) trees in the western Klamath Mountains of California (DiMario et al. 2018). In an earlier study, Hille and Stephens (2005) sampled pre-burn duff depth and postburn consumption along systematic transects from focus pine trees in young,

mixed conifer forests also within the Sierra Nevada range, CA, USA. All studies reported significant differences between forest floor accumulations and distance from tree crown. The inherent variability in forest floor depth, biomass, and bulk density poses substantial challenges to field study designs and necessary investments in collecting field datasets with large enough sample sizes to inform robust statistical models (Keane 2015).

We conducted this study to inform statistical models that relate overstory tree crown cover to forest floor characteristics, including litter and duff depth, biomass, and bulk density, in pine forests that are common to prescribed burning programs in the US. Existing literature demonstrates how variable litter and duff depth, and biomass can be across all scales of inference—from high reported variability at submeter scales to high variability within forest patches (Hille and Stephens 2005; Kreye et al. 2014). Obtaining accurate forest floor estimates requires a large investment in time and effort. Destructive sampling is time intensive due to the time required to clear existing vegetation, systematically measure litter and duff depths and extract forest floor layers. Laboratory analysis is also required, involving not only drying samples to obtain a dry weight biomass but also analyzing contaminated duff material to determine mineral content (i.e., mineral soil content was present in duff samples across all sites in this study). As such, we view this study as an incremental step towards more comprehensive datasets on forest floor characteristics related to tree crown position. Additional studies are needed to inform robust statistical inferences across forest types commonly represented in wildland fire management and smoke planning. With larger datasets, relationships between tree crown dimensions, diameter, and species could be developed to inform larger-scale forest floor characterization based on forest composition and structure.

Differences in litter and duff accumulations between W and SE sites were anticipated. Western sites were located at more northern latitudes and within a semiarid climate that has cold winters and extended summer drought periods. The combination of colder climate and drier soils both likely contributed to lower rates of decomposition and thus greater duff accumulations in W sites. Western sites also had longer fire return intervals because they are not prescribed burned regularly, as is the practice on the SE forest sites. Even with key differences in site climate and less frequent burning, litter depths were much lower overall on W pine than SE pine sites, likely reflecting differences in overstory tree composition and related litter composition. Western sites contained a mix of species including Douglas-fir and ponderosa pine. Even though ponderosa pine is a three-needled pine, individual needles are typically much shorter than loblolly, longleaf, and

Table 5 Duff depth (cm), biomass (kg m^{-2}), and bulk density (kg m^{-3}) of southeast flatwood forest (SE flatwood), southeast loblolly pine-sweetgum forests (loblolly sweetgum), and western pine forests by site. SE sites are ordered by time since fire (TSF). Transect positions include bole (next to tree bole), inside (inside crown dripline), and outside (outside crown dripline)

Site name	Transect position	n	Depth (cm)				Biomass (kg m ⁻²)				Bulk density (kg m ⁻³)			
			Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
SE flatwood														
Tate's Hell A	All	54	0.78	0	2.62	0.82	0.5	0	2.5	0.56	52.21	0	179.95	40.93
	Bole	18	0.11	0	0.62	0.18	0.05	0	0.28	0.08	17.46	0	86.95	28
	Inside	18	1.13	0	2.57	0.76	0.76	0	1.86	0.51	71.97	0	179.95	39.44
	Outside	18	1.1	0	2.62	0.88	0.69	0	2.5	0.62	67.21	0	115.01	30.86
Tate's Hell B	All	53	1.24	0.08	4.97	0.92	0.67	0.03	2.64	0.55	56.82	9.93	177.16	30.49
	Bole	17	1.23	0.08	4.97	1.2	0.67	0.03	2.49	0.67	54.09	14.72	89.65	24.53
	Inside	18	1.3	0.45	2.83	0.65	0.62	0.06	1.37	0.36	50.31	9.93	151.93	30.48
	Outside	18	1.2	0.17	3.05	0.91	0.71	0.16	2.64	0.62	65.9	31.16	177.16	34.77
Aucilla	All	54	0.89	0	3.67	1.08	0.14	0	0.72	0.2	8.06	0	45.43	11.05
	Bole	18	1.37	0	3.5	1.14	0.24	0	0.72	0.25	12.05	0	34.84	12.05
	Inside	18	1.04	0	3.67	1.18	0.14	0	0.47	0.16	8.21	0	31.77	9.06
	Outside	18	0.27	0	1.4	0.52	0.04	0	0.49	0.12	3.91	0	45.43	10.87
Fort Stewart	All	54	0.91	0	4.78	1.18	0.6	0	3.54	0.87	38.14	0	172.55	44.62
	Bole	18	0.83	0	3.77	1.1	0.59	0	2.51	0.79	41.89	0	133.23	44.97
	Inside	18	1.06	0	4.78	1.39	0.81	0	3.54	1.09	46.56	0	172.55	52.89
	Outside	18	0.84	0	3.95	1.08	0.41	0	2.21	0.68	25.98	0	126.44	33.77
SE loblolly sweetgum														
Hitchiti B	All	54	1.45	0.22	5.22	1.03	0.84	0.06	6.89	1	56.33	12.93	216.64	32.5
	Bole	18	1.93	0.73	5.22	1.25	1.41	0.34	6.89	1.48	72.61	34.74	216.64	42.77
	Inside	18	1.4	0.3	3.65	0.83	0.57	0.17	1.77	0.37	43.74	18.28	87.92	18.24
	Outside	18	1.02	0.22	2.95	0.78	0.54	0.06	1.85	0.52	52.64	12.93	98.48	25.85
Hannah Hammock	All	54	1.06	0	5	0.91	0.54	0	2.93	0.56	53.19	0	145.81	30.39
	Bole	18	1.31	0	5	1.34	0.77	0	2.93	0.74	64.35	0	145.81	31.37
	Inside	18	1	0.17	2.45	0.7	0.52	0.08	2.11	0.5	53.88	13.38	112.92	27.2
	Outside	18	0.87	0.2	1.83	0.46	0.33	0.03	0.95	0.28	41.33	4.85	129.07	29.57
Hitchiti A	All	53	1.4	0.33	3.17	0.66	0.76	0.14	2.11	0.45	58.43	15.91	197.88	31.57
	Bole	17	1.58	0.35	3.17	0.82	0.89	0.3	2.11	0.46	67.08	18.85	197.88	42.51
	Inside	18	1.51	0.52	2.77	0.62	0.76	0.14	1.83	0.47	51.13	15.91	97.91	24.38
	Outside	18	1.12	0.33	2.07	0.43	0.62	0.2	1.96	0.39	57.57	29.04	106.88	24.92
Western pine														
LANL Forest	All	54	1.66	0	12.03	2.19	1.25	0	10.13	1.82	56.47	0	203.65	43.99
	Bole	18	2.24	0	12.03	3.19	1.77	0	10.13	2.61	65.02	0	203.65	51.82
	Inside	18	2.15	0	5.88	1.57	1.67	0	4.77	1.39	68.42	0	121.76	36.82
	Outside	18	0.59	0	2.52	0.69	0.32	0	1.38	0.43	35.97	0	124.83	36.33
Sycan Forest I	All	59	2.44	0	9.39	2.07	2.38	0.02	10.18	2.4	101.95	0	477.6	84
	Bole	21	3.27	0.07	5.62	1.65	3.38	0.03	6.61	2.23	100.08	20.58	245.79	49.67
	Inside	17	2.83	0.87	7.92	1.97	3.48	1.09	10.18	2.64	124.41	70.66	264.98	49.39
	Outside	21	1.29	0	9.39	2.07	0.5	0.02	2.41	0.56	85.63	0	477.6	123.83
Methow Wildlife Area	All	49	2.67	0.32	5.77	1.5	2.8	0.34	7.98	1.72	116.42	36.31	434.01	70.74
	Bole	16	3.61	1.53	5.28	1.28	3.96	1.87	7.98	1.72	119.62	41.93	304.59	60.53
	Inside	16	2.96	0.62	5.77	1.46	2.91	1.15	5.65	1.35	104.94	56.13	186.6	27.6
	Outside	17	1.52	0.32	3.32	0.91	1.62	0.34	4.47	1.25	124.22	36.31	434.01	103.23
Lubrecht	All	60	1.95	0.15	5.4	1.22	1.67	0.02	8.83	1.55	81.89	12.91	211.89	40.09
	Bole	21	2.3	0.15	5.4	1.41	2.27	0.02	8.83	2.09	88.62	12.91	211.89	45.72
	Inside	19	1.88	0.4	4.23	0.94	1.57	0.42	3.58	0.94	85.85	29.14	140.89	30.23
	Outside	20	1.64	0.2	4.33	1.21	1.15	0.1	5.02	1.17	71.05	26.88	179.37	41.66

pitch pine needles (i.e., ponderosa pine needles typically range between 10 and 17 cm versus 20–43 cm in longleaf pine) (Landers 1991; Fonda 2001). Tree species also differ in their frequency of needle turnover. Needle retention for longleaf and loblolly pine can be less than 2 years (Sheffield et al. 2003) compared to 3–5 years for ponderosa pine (Berner and Law 2016). True fir and Douglas-fir trees have even longer needle retention rates (6–8 years) with much lower annual deposition rates (Balster and Marshall 2000).

Within the three forest types sampled in this study, we evaluated how forest floor layers vary across bole, inside tree crown drip line, and outside drip line positions. As anticipated, we found that forest floor characteristics were highly variable within and between sites, with high reported standard deviations. Even with high within-site variability, there were significant patterns in litter and especially duff characteristics across transect positions.

The SE flatwood and W pine sites both contained much greater accumulations of litter and duff next to tree boles than the inside drip line and outside drip line positions. In contrast, litter depth and biomass were not significantly different across transect positions in SE loblolly sweetgum sites. The presence of the broadleaf deciduous tree, sweetgum, throughout loblolly pine understories likely created more uniform leaf litter across the sites and contributed to more even distributions of litter depth and biomass than SE flatwood sites. However, accumulated duff layers were significantly greater next to tree boles than inside and outside transect positions in loblolly sweetgum forests. This could be due to incremental differences in accumulated litter, including pine needles and bark scales near tree boles, that over time contribute to greater duff accumulations than in positions farther from boles. Bole positions may also support higher fuel moisture and reduce the availability of forest floor fuels for burning under some circumstances (Garlough and Keyes 2011; Banwell et al. 2013).

Although our study design did not support statistical models of forest floor characteristics with time since fire on SE flatwood and SE loblolly sweetgum sites, litter depths tended to be higher on sites with greater time since fire. However, there were no trends in duff accumulations on these sites (Table 4). This may be due to generally greater consumption rates of litter than duff in prescribed burns (Varner et al. 2007). Because SE sites are all part of active prescribed burning programs, the only site that represents a long-unburned forest is the SE flatwood Aucilla site. Even though litter depths and biomass at Aucilla were on the higher end of SE flatwood sites, duff biomass and bulk density were markedly lower than other sites (Table 5). Compared to other SE sites, Aucilla has smaller and likely younger trees than other

sites, which may be related to less accumulated duff than other sites. Tree basal area was not accounted for in this study, but smaller trees would likely be associated with lower accumulations of litter and duff layers.

Across the four W sites, litter and duff accumulations were significantly greater under tree crowns (bole and inside positions) compared to outside of tree crowns (outside positions) (Table 3). Litter and duff accumulations were highly variable on W sites, partly reflecting the patchy distribution of forest floor layers associated with tree cover. All W sites represent a long time since fire (> 20 years). As such, there was a strong pattern of highest accumulation of duff next to tree boles with intermediate duff depth and biomass on the inside dripline position and lowest values outside of tree crowns. Given significant patterns in forest floor accumulations relative to tree crowns, our study suggests that it may be possible to refine estimated forest floor distributions and inform future smoke management decisions with more investments in field sampling and development of robust, predictive models.

Management applications

To better predict the impacts of smoke on adjacent communities and infrastructure, fire and fuel planners need to estimate the amount of forest floor material available to burn in prescribed burn operations. To date, unit-level estimates are often made through the use of photo series datasets (e.g., Ottmar and Vihnanek 2000), maps of wildland fuels (Prichard et al. 2019), and through field-based depth measurements that are converted to estimated biomass using published bulk density values. This study provides summarized depth, biomass, and bulk density values for frequently burned SE pine flatwoods and SE loblolly pine plantations. Because Aucilla was the only site in which more than 5 years had passed since fire, all estimates for SE sites are representative of forest floors under frequent prescribed burning. In contrast, the W pine sites represent ponderosa pine forests that have greater duff accumulations, in part due to a lack of regular prescribed burning and slower decomposition rates than the SE pine sites.

Because the depth of litter and duff layers is by far the most efficient and cost-effective measurement compared to dry weight biomass or bulk density to take prior to prescribed burning, we evaluated predictive models that use depth to estimate biomass for each forest type. The low sample size and high variance among forest floor samples contributed to high root-mean-squared errors and low confidence in predictive models (Table 7). Although models are not necessarily suitable for predicting litter and duff biomass in similar

Table 6 Characteristics of focal trees that formed the center point of forest floor transect measurements, including mean and standard deviation (SD) of diameter at breast height (DBH, cm), tree height (m), height to live crown (HLC, m), crown radius — along the north transect (N, m), and crown radius along the south transect (S, m) of sampled trees by site

Site	Species	<i>n</i>	DBH		Height		HLC		Crown radius N		Crown radius S	
<i>SE flatwood</i>												
Tate's Hell A	All	9	29.8	(2.81)	20.57	(1.23)	14.29	(1.63)	3.53	(0.55)	3.16	(0.50)
Tate's Hell B	Slash pine	9	29.8	(2.81)	20.57	(1.23)	14.29	(1.63)	3.53	(0.55)	3.16	(0.50)
	All	9	29.9	(5.45)	20.47	(2.53)	14.06	(1.17)	3.08	(0.55)	3.12	(0.88)
Fort Stewart	Slash pine	9	29.9	(5.45)	20.47	(2.53)	14.06	(1.17)	3.08	(0.55)	3.12	(0.88)
	All	9	32.7	(6.87)	23.79	(2.84)	14.97	(2.81)	2.61	(1.07)	4	(1.15)
Aucilla	Longleaf pine	8	32.7	(7.34)	23.77	(3.04)	14.91	(2.99)	2.29	(0.49)	4.03	(1.22)
	Slash pine	1	33.5	(—)	23.9	(—)	15.4	(—)	5.2	(—)	3.8	(—)
	All	9	18.7	(3.22)	14.83	(2.98)	8.61	(1.50)	2.55	(1.17)	2.06	(1.01)
	Longleaf pine	9	18.7	(3.22)	14.83	(2.98)	8.61	(1.50)	2.55	(1.17)	2.06	(1.01)
<i>SE loblolly sweetgum</i>												
Hitchiti B	All	9	54	(10.85)	21.09	(4.67)	10.92	(5.61)	3.67	(2.02)	6.59	(3.37)
	Loblolly pine	9	54	(10.85)	21.09	(4.67)	10.92	(5.61)	3.67	(2.02)	6.59	(3.37)
Hannah Hammock	All	9	48	(7.92)	21.93	(1.43)	12.13	(2.17)	5.78	(2.02)	4.91	(1.41)
	Loblolly pine	9	48	(7.92)	21.93	(1.43)	12.13	(2.17)	5.78	(2.02)	4.91	(1.41)
Hitchiti A	All	9	40.2	(12.41)	22.9	(4.23)	13.14	(3.19)	3.64	(1.00)	5.11	(1.89)
	Loblolly pine	7	44.5	(10.24)	23.86	(4.11)	13.43	(2.66)	3.81	(0.94)	5.84	(1.38)
	Slash pine	2	25	(2.76)	19.55	(3.61)	12.15	(6.01)	3.05	(1.34)	2.55	(0.35)
<i>Western pine</i>												
LANL	All	8	44.1	(14.48)	12.41	(2.61)	3.56	(2.31)	2.84	(1.31)	3.05	(0.91)
	Ponderosa pine	7	43.9	(15.63)	12.31	(2.80)	3.93	(2.23)	2.79	(1.41)	3.03	(0.98)
	White fir	1	45.5	(—)	13.1	(—)	1	(—)	3.2	(—)	3.2	(—)
Methow	All	9	43.1	(5.75)	22.21	(1.93)	7.47	(1.90)	3.17	(0.62)	3.5	(0.89)
	Ponderosa pine	9	43.1	(5.75)	22.21	(1.93)	7.47	(1.90)	3.17	(0.62)	3.5	(0.89)
Lubrecht	All	11	39.3	(14.76)	21.76	(4.20)	7.8	(3.92)	2.42	(1.37)	3.43	(1.75)
	Douglas-fir	1	43.4	(—)	22.2	(—)	1.3	(—)	3.2	(—)	3.8	(—)
	Lodgepole pine	1	19.5	(—)	16	(—)	2	(—)	1.7	(—)	1.5	(—)
	Ponderosa pine	9	41	(14.76)	22.35	(4.18)	9.17	(2.76)	2.41	(1.48)	3.6	(1.82)
Sycan	All	12	37.5	(10.45)	15.68	(5.44)	3.88	(1.87)	2.32	(0.92)	2.75	(1.03)
	Ponderosa pine	12	37.5	(10.45)	15.68	(5.44)	3.88	(1.87)	2.32	(0.92)	2.75	(1.03)

Table 7 Reported *p*-values for mixed models including tree as a random variable of litter and duff depth (cm), biomass (kg m⁻²), and bulk density (kg m⁻³) across transect position (next to tree bole—bole, inside crown drip line—inside, and outside crown dripline—outside) by forest type

Forest type	Comparison	Litter			Duff		
		Depth	Biomass	Bulk density	Depth	Biomass	Bulk density
SE flatwood	Inside vs. bole	0.336	0.002	0	0.179	0.036	0.032
	Outside vs. bole	0.01	0	0.004	0.977	0.588	0.158
	Outside vs. inside	0	0.006	0.828	0.116	0.293	0.78
SE loblolly sweetgum	Inside vs. bole	0.628	0	0	0.12	0.003	0.004
	Outside vs. bole	0.024	0	0	0	0	0.006
	Outside vs. inside	0.206	0.424	0.086	0.137	0.609	0.985
Western pine	Inside vs. bole	0.925	0	0.008	0.175	0.145	0.874
	Outside vs. bole	0	0	0	0	0	0.392
	Outside vs. inside	0	0	0.609	0	0	0.178

Table 8 Modeled relationships between depth, transect position and biomass of litter and duff layers in southeastern flatwood forests, loblolly sweetgum forests, and western pine forests

Position	Model	Litter models				Duff models				RMSE	p-value		
		B0	B1	B2	r ²	B0	B1	B2	r ²				
SE flatwood													
All	Biomass = B0 + B1 × depth + B2 × location	0.313	0.098	−0.217	0.39	0.36	< 0.001	0.313	0.098	−0.217	0.39	0.36	< 0.001
Bole	Biomass = B0 + B1 × depth	0.131	0.134	−	0.436	0.416	< 0.001	0.012	0.423	−	0.637	0.346	< 0.001
Inside	Biomass = B0 + B1 × depth	0.207	0.078	−	0.23	0.386	< 0.001	0.057	0.465	−	0.5	0.473	< 0.001
Outside	Biomass = B0 + B1 × depth	0.169	0.076	−	0.383	0.23	< 0.001	−0.002	0.547	−	0.693	0.335	< 0.001
Loblolly sweetgum													
All	Biomass = B0 + B1 × depth + B2 × location	0.497	0.112	−0.303	0.397	0.268	< 0.001	0.497	0.112	−0.303	0.397	0.268	< 0.001
Bole	Biomass = B0 + B1 × depth	0.18	0.208	−	0.313	0.335	< 0.001	−0.067	0.679	−	0.61	0.63	< 0.001
Inside	Biomass = B0 + B1 × depth	0.288	0.086	−	0.306	0.201	< 0.001	0.038	0.445	−	0.532	0.307	< 0.001
Outside	Biomass = B0 + B1 × depth	0.169	0.091	−	0.283	0.221	< 0.001	−0.013	0.512	−	0.493	0.296	< 0.001
Western pine													
All	Biomass = B0 + B1 × depth + B2 × location	0.236	0.305	−0.291	0.471	0.509	< 0.001	0.236	0.305	−0.291	0.471	0.509	< 0.001
Bole	Biomass = B0 + B1 × depth	−0.192	0.476	−	0.533	0.641	< 0.001	0.193	0.925	−	0.679	1.303	< 0.001
Inside	Biomass = B0 + B1 × depth	0.068	0.255	−	0.347	0.454	< 0.001	−0.003	0.976	−	0.676	1.043	< 0.001
Outside	Biomass = B0 + B1 × depth	0.162	0.102	−	0.269	0.196	< 0.001	0.383	0.393	−	0.284	0.869	< 0.001

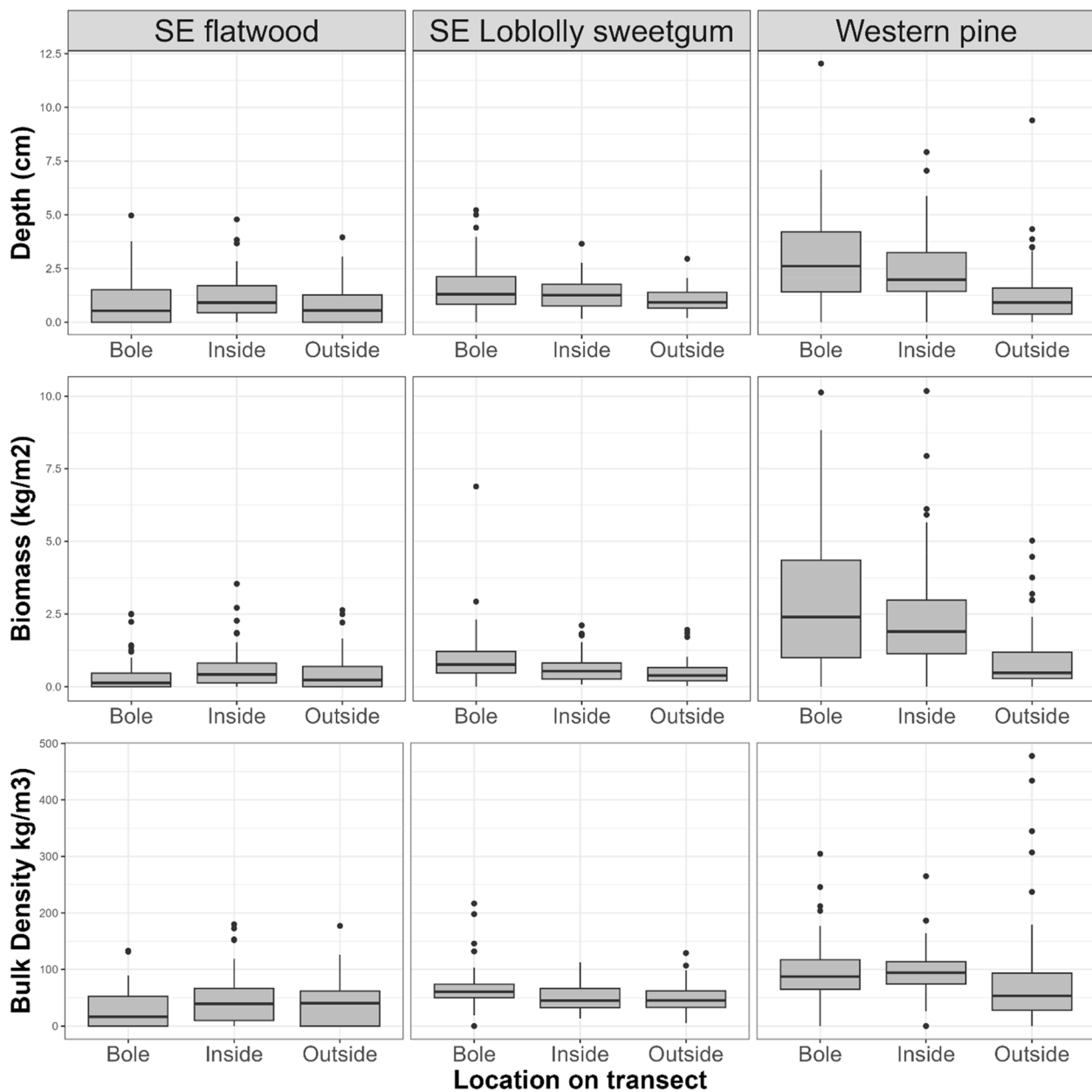


Fig. 5 Duff depth (cm), biomass (kg m^{-2}), and bulk density (kg m^{-3}) distributions across the three transect positions (next to bole, inside drip line, and outside drip line) and three sampled forest types

forest types based on measured depth and position relative to tree crowns, they reflect significant trends that could inform process models of forest floor development and decomposition over time. Additional work would be needed to develop predictive models of litter and biomass that can incorporate disturbance history, including past harvests, time since fire, and fire return intervals.

With increased availability of stem and crown mapping based on lidar metrics from airborne and

terrestrial laser scanning, estimates of forest floor accumulations may increasingly be made through mapping of tree crown positions and predictive modeling of litter biomass in relationship to tree crowns. Our study found particularly strong statistical differences in duff depth and biomass when comparing bole, inside mid-points beneath tree crowns, and outside tree crowns measurements. Predictive models to inform how litter accumulates beneath tree crowns are currently under development (Sánchez-López et al. 2023). Our findings,

along with other related studies (i.e., Banwell and Varner 2014; DiMario et al. 2018), suggest that similar models can be created to predict accumulated duff layers as well. However, given how heterogeneous litter and duff layers are within forest ecosystems, greater investment would be required in future field campaigns to obtain reliable measurements and calibrate and/or validate predictive models that can be used in wildland fuel mapping and modeling applications.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00429-5>.

Additional file 1.

Acknowledgements

Two anonymous reviewers provided constructive comments, which greatly improved the manuscript. We thank the many host agencies for supporting our research sites, including the Florida Forest Service (Blackwater and Tates Hell State Forests), Hitchiti Experimental Forest, Los Alamos National Laboratory, University of Montana (Lubrecht Forest), Suwannee River Water Management District (Aucilla), US Department of Defense (Ft Stewart), and Washington Department of Fish and Wildlife (Methow Wildlife Area). Last but not least, we thank our field and laboratory crew members for their hard work and dedication, including Nick Tripodi, Lindsay Lascheck, Maddy Hallet, Teagan Darmody, Mason Patterson, Henry Gould, Kate Patronik, Grace Swan-Streepy, Jordan Hilton, Sophia Boyd, Jane Wynne, and Caitlyn Bell.

Authors' contributions

SJP, ER, JC, and JT contributed to study design. PE contributed to database development and design, DN, MCK, and LS led statistical analysis and figure development. SJP, DN, AH, NSL, MCK, and JT contributed to manuscript writing. All authors read and approved the final manuscript.

Funding

This study was funded by the US Department of Defense Strategic and Environmental Research and Development Program (SERDP Project nos. RC19-1064 and RC20-1346). This research was supported (in part) by the US Department of Agriculture, Forest Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Data availability

The datasets and analysis scripts for this study are open source and are being archived with the Wildland Fire Science Initiative data repository ([<https://wfsi-data.org>] (<https://wfsi-data.org>)), including project metadata, methods documentation and data libraries.

Declarations

Ethics approval and consent to participate

N/A.

Consent for publication

NA.

Competing interests

The authors declare no competing interests.

Author details

¹School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA. ²Department of School of Interdisciplinary Arts and Sciences, Sciences and Mathematics, University of Washington, Tacoma, WA, USA. ³US

Department of Agriculture Forest Service, Moscow Forestry Laboratory, Rocky Mountain Research Station, Moscow, ID, USA. ⁴Institute of Natural Resources and Spatial Planning (INDUROT), University of Oviedo, Mieres, Asturias 33600, Spain.

Received: 2 April 2025 Accepted: 20 October 2025

Published online: 23 December 2025

References

- André, F., F. Jonard, M. Jonard, and S. Lambot. 2016. *In situ* characterization of forest litter using ground-penetrating radar. *Journal of Geophysical Research: Biogeosciences* 121: 879–894.
- Balster, N.J., and J.D. Marshall. 2000. Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. *Tree Physiology* 20: 1191–1197.
- Banwell, E.M., and J.M. Varner. 2014. Structure and composition of forest floor fuels in long-unburned Jeffrey pine-white fir forests of the Lake Tahoe Basin, USA. *International Journal of Wildland Fire* 23 (3): 363–372.
- Banwell, E.M., J.M. Varner, E.E. Knapp, and R.W. Van Kirk. 2013. Spatial, seasonal, and diel forest floor moisture dynamics in Jeffrey pine-white fir forests of the Lake Tahoe Basin, USA. *Forest Ecology and Management* 305: 11–20.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Berner, L.T., and B.E. Law. 2016. Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999–2014. *Scientific Data*. <https://doi.org/10.1038/sdata.2016.2>.
- D'Evelyn, S.M., J. Jung, E. Alvarado, J. Baumgartner, P. Caligiuri, R.K. Hagmann, S.B. Henderson, P.F. Hessburg, S. Hopkins, E.J. Kasner, M.A. Krawchuk, J.E. Krenz, J.M. Lydersen, M.E. Marlier, Y.J. Masuda, K. Metlen, G. Mittelstaedt, S.J. Prichard, C.L. Schollaert, E.B. Smith, J.T. Stevens, C.W. Tessum, C. Reeb-Whitaker, J.L. Wilkins, N.H. Wolff, L.M. Wood, R.D. Haugo, and J.T. Spector. 2022. Wildfire, smoke exposure, human health, and environmental justice need to be integrated into forest restoration and management. *Current Environmental Health Reports* 9: 366–385.
- Dalrymple, S.E., and H.D. Safford. 2013. Natural forest floor clearings around trees in Jeffrey pine forests reduce tree damage and mortality following wildfire. *Forest Ecology and Management* 310: 847–856.
- DiMario, A.A., J.M. Kane, and E.S. Jules. 2018. Characterizing forest floor fuels surrounding large sugar pine (*Pinus lambertiana*) in the Klamath Mountains, California. *Northwest Science* 92: 181–190.
- Fitzgerald, S.A. 2005. Fire ecology of ponderosa pine and the rebuilding of fire-resilient ponderosa pine ecosystems. in: PSW-GTR-198, General Technical Report. Klamath Falls, OR: Pacific Southwest Research Station, U.S. Department of Agriculture, Forest Service. p. 197–225.
- Fonda, R.W. 2001. Burning characteristics of needles from eight pine species. *Forest Science* 47: 390–396.
- Frandsen, W.H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. *Canadian Journal of Forest Research* 17: 1540–1544.
- Gabrielson, A.T., A.J. Larson, J.A. Lutz, and J.J. Reardon. 2012. Biomass and burning characteristics of sugar pine cones. *Fire Ecology* 8: 58–70.
- Garlough, E.C., and C.R. Keyes. 2011. Influences of moisture content, mineral content and bulk density on smoldering combustion of ponderosa pine duff mounds. *International Journal of Wildland Fire* 20: 589.
- Hiers, J.K., J.J. O'Brien, R.E. Will, and R.J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric (*Pinus palustris*) ecosystems. *Ecological Applications* 17: 806–814.
- Hille, M.G., and S.L. Stephens. 2005. Mixed conifer forest duff consumption during prescribed fires: Tree crown impacts. *Forest Science* 51: 417–424.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346–363.
- Ingram, K., L.C. Dow, and J. Anderson. 2013. *Climate of the southeast United States: variability, change, impacts, and vulnerability*. Washington, DC: Island Press.
- Keane, R. E. 2015. *Wildland Fuel Fundamentals and Applications*. Springer.
- Kreye, J.K., J.M. Varner, C.J. Dugaw, J. Cao, J. Szecsei, and E.A. Engber. 2013. Pine cones facilitate ignition of forest floor duff. *Canadian Journal of Forest Research* 43: 512–516.

- Kreye, J.K., J.M. Varner, and C.J. Dugaw. 2014. Spatial and temporal variability of forest floor duff characteristics in long-unburned *Pinus palustris* forests. *Canadian Journal of Forest Research* 44: 1477–1486.
- Landers, J. L. 1991. Disturbance influences on pine traits in the southeastern United States. In: *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida.
- McDanold, J. S., R. R. Linn, A. K. Jonko, A. L. Atchley, S. L. Goodrick, J. K. Hiers, C. M. Hoffman, E. L. Loudermilk, J. J. O'Brien, R. A. Parsons, C. H. Sieg, and J. A. Oliveto. 2023. DUET - distribution of understory using elliptical transport: a mechanistic model of leaf litter and herbaceous spatial distribution based on tree canopy structure. *Ecological Modelling* 483: 110425.
- Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. In D.L. Sparks, A. Page, P. A. Helmke, et al. *Methods of Soil Analysis: Part 3 Chemical Methods*. Soil Science Society of America and American Society of Agronomy, Madison, WI.
- Ottmar, R.D. 2014. Wildland fire emissions, carbon, and climate: Modeling fuel consumption. *Forest Ecology and Management* 317: 41–50.
- Ottmar, R. D., and R. E. Vihnanek. 2000. Stereo photo series for quantifying natural fuels. Volume I: Mixed-conifer with mortality, western juniper, sagebrush, and grassland types in the interior Pacific Northwest. PMS 830. National Wildfire Coordinating Group, National Interagency Fire Center, Boise, ID.
- Ottmar, R.D., D.V. Sandberg, C.L. Riccardi, and S.J. Prichard. 2007. An overview of the fuel characteristic classification system — Quantifying, classifying, and creating fuelbeds for resource planning. *Canadian Journal of Forest Research* 37: 2383–2393.
- Prichard, S.J., E.C. Karau, R.D. Ottmar, M.C. Kennedy, J.B. Cronan, C.S. Wright, and R.E. Keane. 2014. Evaluation of the CONSUME and FOFEM fuel consumption models in pine and mixed hardwood forests of the eastern United States. *Canadian Journal of Forest Research* 44: 784–795.
- Prichard, S. J., E. M. Rowell, A. T. Hudak, R. E. Keane, E. L. Loudermilk, D. C. Lutes, R. D. Ottmar, L. M. Chappell, J. A. Hall, and B. S. Hornsby. 2022. Fuels and Consumption. Pages 11–49 in D. L. Peterson, S. M. McCaffrey, and T. Patel-Weyand, editors. *Wildland Fire Smoke in the United States*. Springer International Publishing.
- Prichard, S.J., M.C. Kennedy, A.G. Andreu, P.C. Eagle, N.H. French, and M. Billmire. 2019. Next-generation biomass mapping for regional emissions and carbon inventories: Incorporating uncertainty in wildland fuel characterization. *Journal of Geophysical Research: Biogeosciences* 124: 3699–3716.
- Reardon, J., R. Hungerford, and K. Ryan. 2007. Factors affecting sustained smoldering in organic soils from pocosin and pond pine woodland wetlands. *International Journal of Wildland Fire* 16: 107.
- Reinhardt, E. D., R. E. Keane, and J. K. Brown. 1997. First Order Fire Effects Model: FOFEM 4.0, user's guide. *Gen. Tech. Rep. INT-GTR-344*. USDA Forest Service, Intermountain Research Station, Ogden, UT.
- Ryan, K., and W.H. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa*. *International Journal of Wildland Fire* 1: 107–118.
- Sánchez-López, N., A.T. Hudak, L. Boschetti, C.A. Silva, K. Robertson, E.L. Loudermilk, B.C. Bright, M.A. Callahan, and M.K. Taylor. 2023. A spatially explicit model of tree leaf litter accumulation in fire maintained longleaf pine forests of the southeastern US. *Ecological Modelling* 481: 110369.
- Sheffield, M.C.P., J.L. Gagnon, S.B. Jack, and D.J. McConville. 2003. Phenological patterns of mature longleaf pine (*Pinus palustris* Miller) under two different soil moisture regimes. *Forest Ecology and Management* 179: 157–167.
- Stephens, S.L., and M.A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: Effects of crown damage and forest floor combustion. *Forest Ecology and Management* 162: 261–271.
- Swezy, D.M., and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21: 626–634.
- Urbanski, S. 2014. Wildland fire emissions, carbon, and climate: Emission factors. *Forest Ecology and Management* 317: 51–60.
- Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: Novel fire effects and consequences for long-unburned ecosystems. *Restoration Ecology* 13: 536–544.
- Varner, J.M., J.K. Hiers, R.D. Ottmar, D.R. Gordon, F.E. Putz, and D.D. Wade. 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: The importance of duff moisture. *Canadian Journal of Forest Research* 37: 1349–1358.
- Varner, J.M., J.M. Kane, J.K. Kreye, and E. Engber. 2015. The flammability of forest and woodland litter: A synthesis. *Current Forestry Reports* 1: 91–99.
- Zhao, F., Y. Liu, S. Goodrick, B. Hornsby, and J. Schardt. 2019. The contribution of duff consumption to fire emissions and air pollution of the Rough Ridge Fire. *International Journal of Wildland Fire* 28: 993.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.