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Modeling spatial patterns of longleaf pine needle dispersal using long-term data

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Abstract

Background Predicting patterns of fire behavior and effects in frequent fire forests relies on an understanding of fine-scale spatial patterns of available fuels. Leaf litter is a significant canopy-derived fine fuel in fire-maintained forests. Litter dispersal is dependent on foliage production, stand structure, and wind direction, but the relative importance of these factors is unknown.

Results Using a 10-year litterfall dataset collected within eighteen 4-ha longleaf pine (*Pinus palustris* Mill.) plots varying in canopy spatial pattern, we compared four spatially explicit models of annual needle litter dispersal: a model based only on basal area, an overstory abundance index (OAI) model, both isotropic and anisotropic litter kernel models, and a null model that assumed no spatial relationship. The best model was the anisotropic model ($R^2 = 0.656$) that incorporated tree size, location, and prevailing wind direction, followed by the isotropic model ($R^2 = 0.612$), basal area model ($R^2 = 0.488$), OAI model ($R^2 = 0.416$), and the null model ($R^2 = 0.08$).

Conclusions As with previous studies, the predictive capability of the litter models was robust when internally validated with a subset of the original dataset ($R^2 = 0.196$ – 0.549); however, the models were less robust when challenged with an independent dataset ($R^2 = 0.122$ – 0.319) from novel forest stands. Our model validation underscores the need for rigorous tests with independent, external datasets to confirm the validity of litter dispersal models. These models can be used in the application of prescribed fire to estimate fuel distribution and loading, as well as aid in the fine tuning of fire behavior models to better understand fire outcomes across a range of forest canopy structures.

Keywords Fine fuels, Leaf litter dispersal, Longleaf pine, *Pinus palustris*, Spatially explicit models

Resumen

Antecedentes Predecir los patrones de comportamiento del fuego y sus efectos en incendios frecuentes de bosques se basa en el entendimiento de los patrones espaciales a escala fina de los combustibles disponibles. La broza de hojas (hojarasca) es un combustible fino significativo derivado del dosel arbóreo en bosques mantenidos por el fuego. La dispersión de esta hojarasca es dependiente de la producción de follaje, de la estructura del rodal, y de la dirección del viento, aunque la importancia relativa de estos factores es desconocida.

Resultados Usando un conjunto de 10 años de datos de hojarasca coleccionada dentro de dieciocho parcelas de Pino de hoja larga (*Pinus palustris* Mill.) de 4 ha cada una, y que variaban en el patrón espacial de sus doseles, comparamos cuatro modelos explícitos de dispersión anual de hojarasca de acículas: un modelo basado solamente en el área basal, un modelo de índice de abundancia del dosel (OAI), tanto isotrópicos como anisotrópicos -modelo kernel de hojarasca-, y un modelo nulo que asumía ninguna relación espacial. El mejor modelo fue el anisotrópico ($R^2 = 0.656$)

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que incorporó el tamaño del árbol, ubicación, y dirección del viento predominante, seguido por el del área basal ($R^2 = 0,488$), el modelo OAI ($R^2 = 0,416$), y el modelo nulo ($R^2 = 0,08$).

Conclusiones Como en estudios previos, la capacidad de predicción de los modelos de hojarasca fue robusto cuando fue validado internamente con un subconjunto de la base de datos original ($R^2 = 0,196$ – $0,549$); sin embargo, los modelos fueron menos robustos cuando fueron cotejados con un conjunto de datos independientes ($R^2 = 0,122$ – $0,319$) derivados de doseles nuevos. Nuestra validación del modelo subestima la necesidad de pruebas rigurosas con conjuntos de datos independientes y externos, para poder validar los modelos de dispersión de hojarasca. Estos modelos pueden ser usados en la aplicación de quemas prescriptas para estimar la distribución y carga del combustible, como también pueden ayudar en la calibración fina de modelos de comportamiento para entender mejor los efectos del fuego a través de un amplio rango de estructuras de doseles.

Background

Leaf litter dynamics shape multiple ecosystem processes including nutrient cycling, plant competition, heat and water transfer between the soil and the atmosphere, and fire characteristics (Facelli & Pickett 1991). The annual input of litterfall at any point on the forest floor is influenced by the species, size, and location of surrounding trees, timing of peak litterfall, and wind speed and direction (Staelens et al. 2003; Jonard et al. 2006). Spatial patterns of litter accrual and retention through time are also affected by decomposition, fire, and other agents of litter removal (Facelli & Pickett 1991). Leaf litter dispersal modeling is one approach to predicting the influence that leaf litter spatial patterns have on forest ecosystem processes.

Previous studies have developed spatially explicit models of leaf litter dispersal to predict the influence of forest composition and structure on litterfall patterns (Ferrari and Sugita 1996, Staelens et al. 2004, Jonard et al. 2006, Bigelow and Canham 2015, Nickmans et al. 2019, Sánchez-Lopez et al. 2023). These studies use measurements of tree size and location to predict litter input from individual trees. Species-specific factors influence the dispersal patterns of leaf litter such as leaf morphology, surface area, weight, and other physical characteristics. Thus, models of leaf litter dispersal vary among individual tree species (Ferrari and Sugita 1996). Ferrari and Sugita (1996) developed a spatially explicit isotropic model for leaf litterfall that combined an allometric equation for litter production and a negative exponential decay function for dispersal distance to characterize spatial patterns of leaf litter in hemlock-hardwood forests. Staelens et al. (2003) extended litter dispersal functions by including an anisotropic model that accounted for wind influence. Jonard et al. (2006) and Nickmans et al. (2019) used a ballistic leaf litter dispersal model that included leaf release height and leaf fall velocity to predict litterfall patterns. These previous studies on litterfall modeling have focused on mixed hardwood forests and their role in nutrient cycling, but similar studies on leaf

litter dispersal are lacking in pine-dominated forests, despite the role of pine needles as the primary fuel for maintaining fire in many pine forests (Hiers et al. 2009; Loudermilk et al. 2011).

The role of vegetation as fuel is a major topic of research and management concern within fire-dependent ecosystems (Hiers et al. 2020). The ecology of fuels is a concept that emphasizes feedbacks among fuels, fire behavior, and vegetation response (Mitchell et al. 2009). Vegetation serves as fuel and modifies fire behavior, and in turn, fire behavior affects plant response. A key component of this feedback cycle is the availability and distribution of fine fuels supplied by the forest canopy. Overstory conditions affect spatial patterns of fire behavior and subsequent fire effects impact the composition and structure of ground-layer vegetation (Platt et al. 2016), impacting processes such as plant mortality and germination (Wiggers et al. 2013). Management activities and disturbances routinely alter the density and configuration of overstory trees (Rutledge et al. 2021; Cannon et al. 2022), and thereby alter the availability and distribution of canopy-derived fuels such as leaf litter. It is important to know what level of canopy density is recommended for achieving restoration and prescribed burning goals depending on the pre-existing site conditions and forest type.

In longleaf pine (*Pinus palustris* Mill.) ecosystems, pine needles provide an important source of fine fuels from the canopy that influence fire behavior and effects (Mitchell et al. 2006; Hiers et al. 2009; O'Brien et al. 2016). Although it is known that proximity to adult tree crowns can affect fuel loading and subsequent fire behavior in longleaf forests (Williamson and Black 1981; Rebertus et al. 1989; Grace and Platt 1995; O'Brien et al. 2008; Whelan et al. 2018), much less is known about how litter patterns vary at fine scales in spatially complex forest stands. Thus, an improved understanding of fuel availability and continuity across a range of overstory conditions can improve prescribed fire application through forest management that maintains adequate litter fuel across the landscape.

In addition, pine needle litter accumulation from the canopy and decomposition in the litter layer occurs between fires (Sánchez-López et al. 2023), and understanding the temporal as well as the spatial heterogeneity of litter patterns is salient to the management of fire dependent ecosystems.

In this study, our objectives were to parameterize and validate spatially explicit models of litterfall in longleaf pine-dominated forests. Specifically, we sought to understand how leaf litter varies spatially with tree diameter, local tree neighborhood (i.e., tree location), and prevailing wind direction. We expected individual-tree-based models to predict litterfall patterns better than area-based models. In addition, we expected prevailing wind direction to influence leaf dispersal patterns. To evaluate the predictive power of the models across a range of novel site conditions, we used an independently collected dataset that included litterfall from sites that varied by edaphic gradient and performed a second validation using a subset of the original dataset to compare model performance to the independently collected dataset.

Methods

Study approach

To predict the distribution of pine needle fuels, we used a 10-year litterfall dataset (2011–2020) collected from stem mapped plots that varied in spatial pattern. We predicted annual litterfall by fitting four neighborhood models using data from plots with mapped trees of known diameter. We also included a null model (hereafter referred to as the interannual null model) which allowed litter amounts to vary annually but assumed no spatial relationship of trees as well as a simplified version of this model that excluded annual variability (hereafter referred to as the intercept-only null model). This allowed us to understand the relative contribution of spatial variability and interannual variability to litter production. Maximum likelihood estimates of model parameters were generated by simulated annealing, a global optimization approach (Canham and Uriarte 2006). This approach allowed for spatially explicit prediction of needle fuel distribution based on overstory structure, using measurements of local stand density and the influence of individual tree characteristics. We used three independent datasets (hereafter referred to as external validation) collected from a separate study to evaluate the predictive power of the models. Previous studies validated models using only a subset of the original dataset without challenging it against an independently collected dataset. Thus, we also used this method, in addition to the external validation, to allow comparison across studies (hereafter referred to as internal validation).

Study site

The study was conducted at the Jones Center at Ichauway in southwestern Georgia, an 11,000-ha research center located in the Gulf Coastal Plain physiographic province. Second-growth longleaf pine forests at this site occur primarily on upland, well-drained soils and have been actively managed since the 1930s with prescribed fire on 1–3 year fire return interval and selective harvesting mainly by individual-tree selection silviculture (McIntyre et al. 2008). Frequent, low-intensity fire supports a savanna-like vegetation structure with a longleaf pine-dominated overstory and an understory dominated by grasses and a diverse array of woody and herbaceous species (Walker and Peet 1983; Drew et al. 1998; Kirkman et al. 2001). Summer daily average temperatures range between 21–34 °C and winter temperatures range between 5–17 °C. Annual precipitation averages about 1310 mm (Goebel et al. 1997). The region is subject to tropical air masses that originate in the Gulf of Mexico and cause frequent thunderstorms, high winds, and occasional tropical depressions such as hurricanes that can create significant canopy disturbance (Rutledge et al. 2021).

Study design and data collection

For model parameterization, we used a litterfall dataset collected from 108 traps distributed among eighteen 4-hectare plots where overstory tree locations were known (Cannon et al. 2022). Litter traps consisted of a 0.25 m² conical plastic mesh bag attached to a plastic ring elevated 0.75 m from the ground. Overstory composition in the study plots was dominated by longleaf pine (~95%) with a minor component of oak species (e.g., *Quercus virginiana* Mill. and *Quercus falcata* Michx.). Tree density ranged from 102 to 152 trees ha⁻¹ and mean basal area ranged from 13.3 to 16.2 m² ha⁻¹. Tree locations within plots also varied in spatial pattern as they were part of a silvicultural experiment that employed three spatially distinct harvest methods, including individual-tree selection, group-selection, group-selection with reserves, and control treatments (Cannon et al. 2022). Selective harvest occurred within these plots in 2009 using the Stoddard-Neel approach of individual-tree selection (McIntyre et al. 2008) and group-selection treatments aimed to have the same residual basal area as the individual-tree treatment which varied based on site conditions. In both group-selection treatments three openings were installed that were ~0.20 ha in size. Stand surveys were conducted in 2009, 2014, and 2019 wherein all trees ≥ 10 cm in diameter at breast height (dbh) were inventoried, measured, mapped using a Nomad GPS with a Crescent A100

backpack antenna with a horizontal accuracy of <0.6 m (Hemisphere GPS, Calgary, Canada). Stem maps were generated using data for tree dbh and spatial location of trees. Stem maps for years 2010, 2017, and 2018 were inferred based on post-disturbance information on tree mortality collected following initial forest treatment harvest in 2010, tornado damage in 2017, and Hurricane Michael damage in 2018, respectively (Cannon et al. 2022), and we assumed no change between these dates to infer remaining years.

Leaf litter data collection began in summer 2010 (into 2011) and ended in 2021, and annual litterfall measurements were calculated from April to March of the following year, resulting in 10 years of annual litterfall data. To capture a gradient of canopy structure, litter traps were stratified under three classes of overstory abundance indices (OAI) that ranged from low (0–471), medium (472–1414), to high (1415–3359). OAI was calculated at the center of each 4 m grid cell using the formula:

$$\text{OAI} \left(\frac{\text{cm}^2}{\text{m}} \right) = \sum_{i=1}^n \frac{BA}{d}$$

where BA is the cross-sectional area (cm^2) at breast height of each tree i (≥ 10 cm dbh) within 15 m of the center of each grid cell, and d is the distance to each tree (Whelan et al. 2018). OAI is higher in locations with larger trees and when trees are nearer to the point of interest. Litterfall biomass was collected from litter traps approximately every 3 months and oven-dried at 70°C for at least 48 h to a constant mass. Pine needles were sorted from other non-pine species and were assumed to originate from longleaf pine because of its dominance in the study plots ($\sim 95\%$ density).

To assess how well the best spatial model performed in a new setting, we collected an independent validation dataset from 68 additional traps across 12 different 0.25-hectare plots from years 2019–2021 (i.e., two years of litterfall data) using the previously described litter trap design and processing method. We established these plots in stands that were also dominated by longleaf pine but varied by site edaphic condition hereafter referred to as xeric, intermediate, and mesic sites ($n=3$ per edaphic condition). The mesic site was characterized by poorly-drained sandy loam over sandy clay loam with a water holding capacity of 40 cm per m of soil, the intermediate site was characterized by well-drained loamy sand over sandy loam with 28 cm per m of soil, and the xeric site was characterized by deep, sandy soils with a water holding capacity of 18 cm per m of soil (Goebel et al. 1997; Mitchell et al. 1999). Mean basal area ranged from 11.1 to $18.4 \text{ m}^2 \text{ ha}^{-1}$

(Wiesner et al. 2020). We inventoried all longleaf pine trees ≥ 10 cm dbh within the validation plots in the summer of 2021 and mapped tree locations relative to previously mapped litter collection traps using a Tru-Pulse 360° laser rangefinder.

Model descriptions

To predict field-measured annual litterfall, we developed four spatially explicit models of litterfall with increasing complexity, a spatially null model that accounted for interannual variability in litter production, and an intercept-only version of this model to assess the relative contribution of year-to-year variability. Starting with the simplest model, the intercept-only null model estimated a parameter (ϵ) for the mean litterfall at any point of interest (litter trap) across all years, assuming no spatial relationship to the surrounding trees. We also constructed a model which included a different parameter (α_y) estimate for each year (y) of the 10-year data collection to account for annual differences in litter production (interannual null model). However, we did not measure variables that may have accounted for these differences because this study primarily concerned spatial variability in litter dispersal rather than temporal variability.

We defined two area-based models based on stand density: a basal area model (Eq. 1) which predicted leaf litterfall (LLF_i) at a point of interest representing a litter trap (i) based on the basal area of n trees within a specified radius r :

$$LLF_i = \alpha_y \left[\sum_{r=1}^n BA_{ir} \right] + \epsilon \quad (1)$$

where α_y is a litter production scaling parameter with separate estimates for each of the 10 years of calibration data to account for interannual variation, BA_{ir} is the basal area ($\text{m}^2 \text{ ha}^{-1}$) within radius r (m), and ϵ is an intercept parameter. We also defined a model based on OAI (Eq. 2) which predicts litter fall based on individual tree size and distance from a point of interest i .

$$LLF_i = \alpha_y \left[\sum_{j=1}^n \frac{BA_j^\beta}{dist_{ij}^\gamma} \right] + \epsilon \quad (2)$$

where α_y is an annual litter production scaling parameter, β and γ are scaling parameters, $dist_{ij}$ represents the distance from the i th point to the j th tree for all n trees, and ϵ is an intercept parameter.

We included two individual-tree-based models based on previous studies in mixed hardwood stands (Ferrari and Sugita 1996; Staelens et al. 2003). These models incorporated the influence of individual tree size and location to determine how their combined litter production and dispersal kernels contributed to predicted

litterfall at a point of interest. The first individual-tree model (hereafter referred to as isotropic model) assumed isotropic leaf dispersal and consisted of an allometric function to represent foliage biomass production in the model. The allometric function (Eq. 3) predicts foliar production based on tree diameter (dbh in cm):

$$\frac{\text{Foliage biomass}}{\text{tree}}(g) = \alpha dbh^{\beta} \exp(-\delta dbh) \quad (3)$$

where α and β are scaling parameters that affect foliar litter production with increasing tree size and δ attenuates the rate of foliage biomass increase as dbh increases. The litter dispersal kernel component incorporates an exponential decay function (4)

$$LLF\left(\frac{g}{m^2}\right) = \frac{1}{N} \exp(-\gamma dist_{ij}) \quad (4)$$

where N is a normalizing parameter that ensures the spatial kernel integrates to one, γ is a parameter that determines the dispersal kernel shape, and $dist_{ij}$ represents distance from the i th trap to the j th tree. Data from a study on litter dispersal in isolated trees validated that a negative exponential function is appropriate for characterizing leaf litterfall patterns from trees (Ferrari and Sugita 1996). Combining these model components results in the following isotropic model (Eq. 5):

$$LLF_i = \frac{\gamma^2}{2\pi} \alpha_y \left[\sum_{j=1}^n dbh_j^{\beta} \exp(-\gamma dist_{ij} - \delta dbh_j) \right] + \varepsilon \quad (5)$$

We combined α and $1/N$ into a single parameter (α_y) to simplify parameter estimation, ε is an intercept parameter, and the $\gamma^2/2\pi$ term integrates the distance-based function to calculate total biomass (following Ferrari and Sugita 1996). The second individual-tree model (hereafter referred to as the anisotropic model (Eq. 6) is a modification of Eq. 5 that incorporates the influence of prevailing wind direction (Staelens et al. 2003).

$$LLF_i = \frac{\gamma^2}{2\pi} \alpha_y \left[\sum_{j=1}^n dbh_j^{\beta} \exp \left\{ \left[-\gamma + \gamma' \cos(\theta_{ij} - \theta_d) \right] dist_{ij} - \delta dbh_j \right\} \right] + \varepsilon \quad (6)$$

where the additional parameter γ' modifies dispersal distance due to the effects of wind. The variable θ (in radians) represents the angle clockwise from north, from location i to source tree j , and the term $\theta_{ij} - \theta_d$ accounts for the difference between the angle of tree j and point i and the relative wind direction (θ_d in radians). The term $\cos(\theta_{ij} - \theta_d)$ is positive when downwind of a tree of interest and negative in upwind locations, which slightly increases and decreases litter, respectively. Parameter γ determines the shape of the litterfall curve. We also

combined α and $1/N$ into a single parameter (α_y) for the anisotropic model.

Parameter estimation and model comparison

We estimated parameters for litter dispersal models using the simulated annealing function in the likelihood package (Murphy 2015) in R 4.0.3 (R Core Team 2013). Simulated annealing is a global optimization search algorithm that attempts to find the global maximum of the likelihood surface produced by all possible values of the given model parameters being estimated. We used a maximum number of iterations of 10,000 and reported upper and lower parameter support intervals. We compared model fit using the corrected Akaike information criterion (AIC_c) as well as the coefficient of determination (R^2) from the linear regression of predicted litterfall versus observed litterfall (Anderson and Burnham 2002).

Model validation

We used an independently collected validation dataset to evaluate the predictive power of the models in novel longleaf pine stands that varied across a gradient of edaphic conditions. To evaluate model performance, we used a linear regression analysis, using the observed litterfall values as the predictor variable and the predicted litterfall values from the validation dataset as the response variable. We used the coefficient of determination (R^2) to compare the performance of the different models with the validation data. We also obtained daily wind direction data over the study period from an onsite environmental monitoring station to validate the anisotropic model parameter estimate for prevailing wind direction (Newton GA, JWJERC, Hoogenboom et al. 1991).

Because previous studies on litter dispersal used only internal validation, we also used a subset of the original calibration dataset (108 traps) for comparison with previous studies which did not use an independent validation dataset. We re-trained the models with a random selec-

tion of two-thirds of the data from the litter traps (72 traps; $n=720$) across the 10-year period and used the remaining one-third (36 traps; $n=360$) of litter trap data to validate the models. This internal validation allowed comparison of model performance to similar studies.

Results

Model fit comparison

Overall model fit increased with model complexity. The two individual-tree models characterized by isotropic

Table 1 Model fit of intercept-only and interannual null models and four spatially explicit leaf litter dispersal models in longleaf pine forests in southwestern Georgia, USA from 2011–2020. The optimal parameter estimates are shown with 95% support intervals (in parentheses) except for the annual intercept model where the range across the 10-year period is shown. Parameters are defined in the methods section. R^2 : adjusted R^2 for the model, k : number of model parameters, ΔAIC_c : corrected Akaike information criterion. A “-” indicates that the model does not include the parameter denoted in the column

Parameter	Litter models					
	Intercept only	Annual intercept	Basal area	OAI	Isotropic	Anisotropic
α_y	-	0.1908 (0.1392–0.2405)	0.0062 (0.0028–0.0096)	0.5739 (0.1892–0.8561)	0.3817 (0.2506–0.5146)	0.1428 (0.0979–0.1897)
β	-	-	-	0.3114 (0.2989–0.3389)	0.9709 (0.9612–0.9709)	1.1617 (1.1617–1.1617)
r	-	-	8.349 (8.349–8.600)	-	-	-
γ	-	-	-	1.8926 (1.8926–1.9116)	0.1969 (0.1832–0.2088)	0.2566 (0.2437–0.2642)
γ'	-	-	-	-	-	0.0966 (0.0927–0.1038)
δ	-	-	-	-	0.0000 (0.0000–0.0012)	0.0000 (0.0000–0.0006)
θ_d	-	-	-	-	-	5.659 (5.376–5.772)
ε	0.1915 (0.1838–0.1991)	-	0.1153 (0.1130–0.1242)	0.0861 (0.0783–0.0897)	0.0670 (0.0596–0.0695)	0.0694 (0.0659–0.0749)
R^2	0.016	0.099	0.488	0.416	0.612	0.656
k	2	11	13	14	15	17
ΔAIC_c	736.53	681.14	276.86	373.66	82.11	0

and anisotropic litter dispersal had the highest R^2 and lowest AIC_c values (Table 1). The anisotropic model had the best fit compared to measured litter trap data ($R^2=0.656$), while the isotropic model was comparable in performance ($R^2=0.612$). The basal area model performed moderately well ($R^2=0.488$), followed by the OAI model ($R^2=0.416$). As expected, all spatially explicit models explained more variation in litterfall than the spatially independent null models. Annual variability in litterfall production accounted for about ~10% of variation in litterfall predictions for the interannual null model ($R^2=0.099$) relative to the intercept-only null model ($R^2=0.016$).

To demonstrate how models can be used to predict the spatial patterns of litter, we generated heat maps depicting the model predictions of litterfall based on stem map data (Fig. 1). Spatial configuration of canopy trees drives the availability of litter in the understory at fine scales, and within the 4-hectare area shown. Litterfall varies from 95 to 360 g m⁻² for all models except the OAI model which ranged from 135 g m⁻² to an unrealistic 42.6 kg m⁻².

Leaf litter production and dispersal pattern

Over the 10-year study period, mean annual litter production (g m⁻²) varied by a factor of greater than 1.5.

Individual year estimates of the parameter for scaling litter production (α) varied by a factor of 1.3 to 1.7 among the models. The trends in annual litter production are similar for mean annual litter production and α parameter estimates, indicating an effect of temporal variability on model parameter estimates (Fig. 2).

The two individual-tree models included an allometric litter production function as well as a negative exponential decay dispersal function. The isotropic and anisotropic models predicted similar litterfall at diameter sizes < 30 cm, whereas predictions differed by about 5% at stem diameters ≥ 60 cm (Fig. 3a). For trees up to 60 cm in diameter, the isotropic model predicted that >80% of litterfall occurs within 15 m of the source tree (Fig. 3b).

Wind direction influenced predicted litterfall dispersal patterns upwind and downwind of source trees. The anisotropic model predicted litterfall was concentrated within 10 m on the upwind side and within 20 m of the downwind side of a 30 cm diameter tree (Fig. 4a), demonstrating the directional influence of wind on litter dispersal. The estimated prevailing wind direction θ_d was between 5.376 and 5.772 radians corresponding to 308° to 331° which is between the prevailing wind direction which oscillates from ~225° to 20° between July and January (peak needle cast) (Fig. 4b), resulting in litterfall concentration slightly to the southeast of individual trees (Fig. 5).

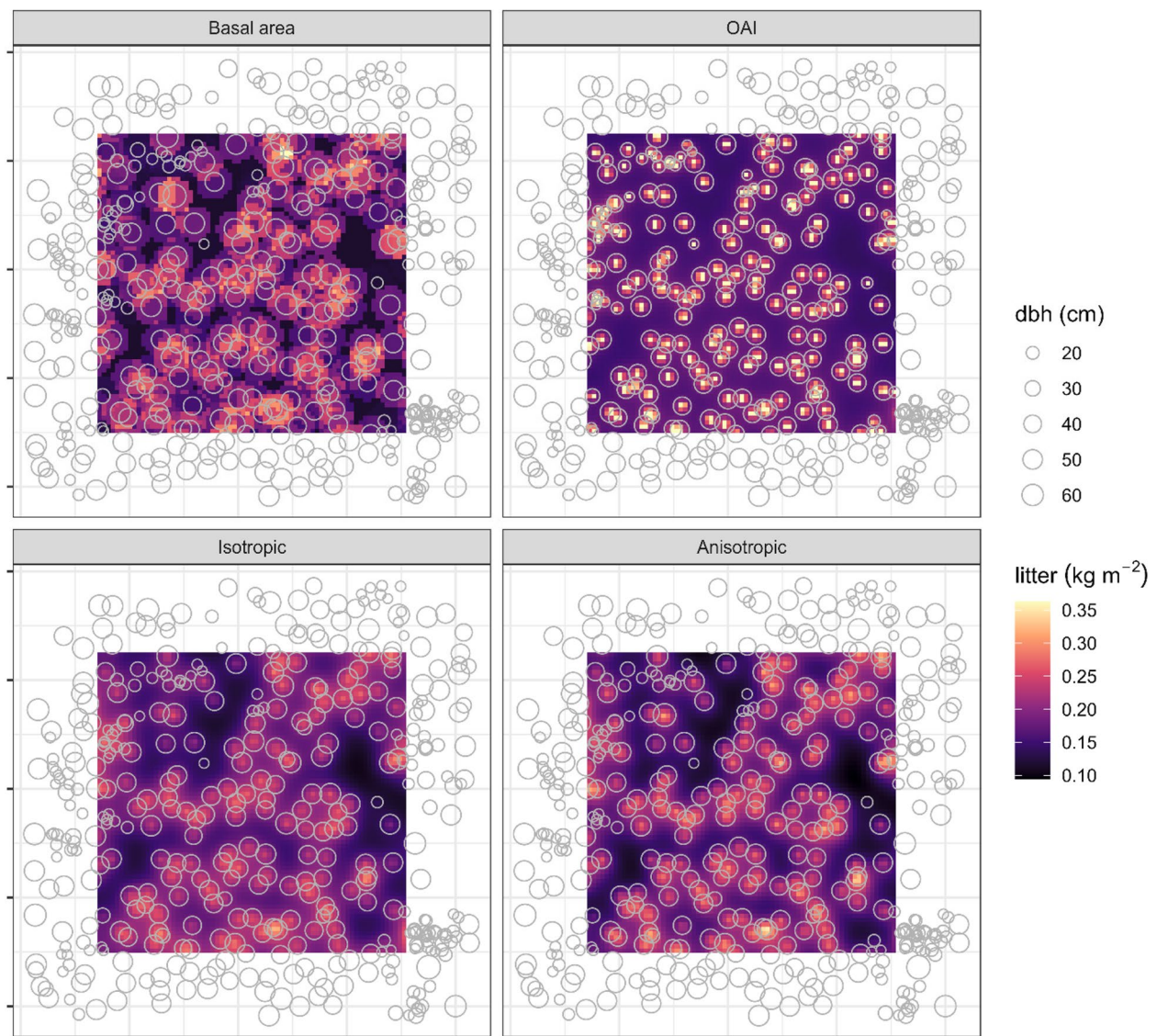


Fig. 1 Example litterfall predictions for four spatially explicit litter models within a 200×200 m study plot. Predictions are shown with a 2 m resolution for basal area, OAI, isotropic, and anisotropic models. The locations of longleaf pine trees ≥ 10 cm are indicated with grey circles. Values > 0.363 kg m⁻² are truncated in the OAI model for clarity and a 30-m buffer was clipped from each side to reduce edge effects. We used the mean α from each model to represent an average year

Although the basal area model was only the third best model based on AIC, we present further results from this model to allow for litter prediction when only stand level data rather than individual tree data is available. For the basal area model, Fig. 6 describes the litterfall amount shed with increasing basal area around a point of interest at a set neighborhood radius of 8.3 m. Litterfall increased by approximately 0.00621 kg m⁻² as basal area increased by one unit (m² ha⁻¹), based on the median α value, but this coefficient varied from 0.0028 to 0.0096 over the 10-year study period.

Model validation

Predictive capability varied greatly among the models when tested against the independently collected, external validation dataset (Table 2; $R^2=0.122\text{--}0.319$). For all models, the regression line deviated significantly from the 1:1 line, often overpredicting litterfall, especially at litterfall amounts < 0.1 kg m⁻² (Fig. 7). The isotropic model performed best on independently derived data ($R^2=0.319$). The second best-performing model was the anisotropic model ($R^2=0.242$). Both the isotropic and anisotropic models overpredicted litterfall

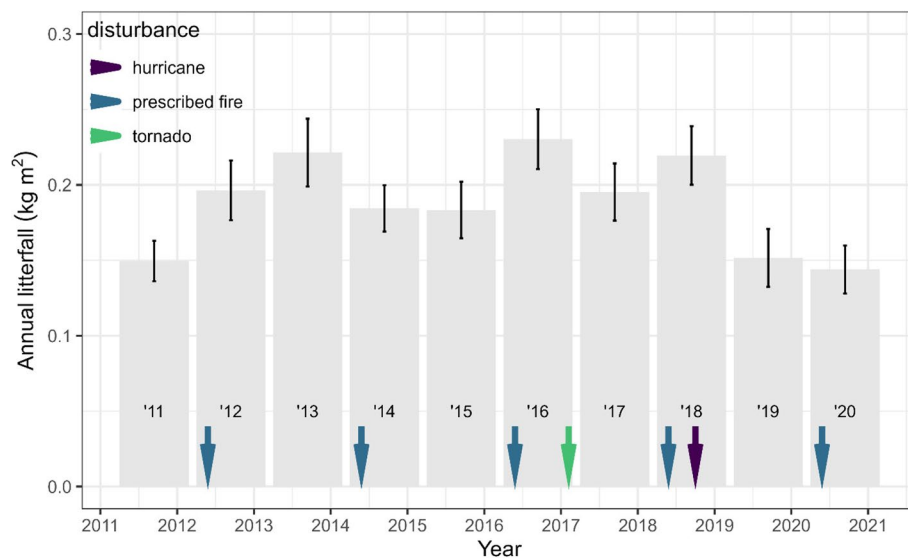


Fig. 2 Study-wide annual litterfall from 2011 to 2020 calculated from 108 total 0.25 m² litter traps among eighteen 4-ha research plots. Disturbances from prescribed fire, tornado, and hurricane are shown. Error bars represent two standard errors of the mean. Note that sampling for a nominal year spans into April of the following year

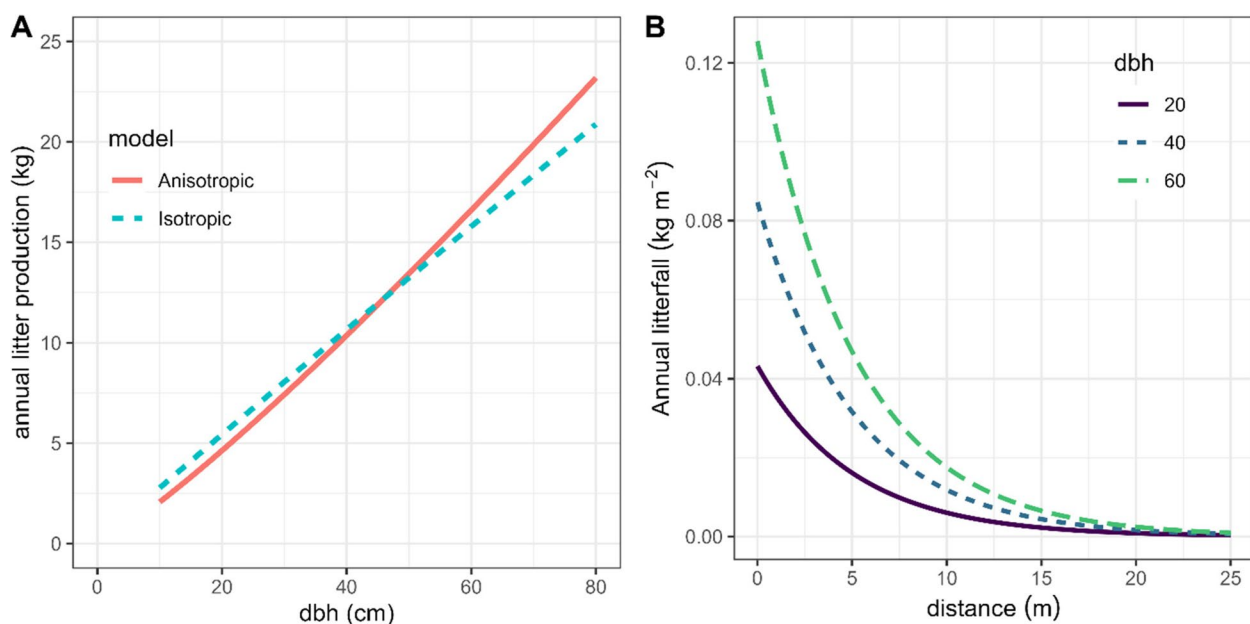


Fig. 3 Comparison of (A) isotropic and anisotropic litter kernel models as a function of tree diameter of individual tree (cm); B individual-tree leaf litter dispersal predicted by an isotropic model as a function of distance (m) from the source tree at three tree size classes. Models use the mean α parameter to represent an average year

values at values $< 0.3 \text{ kg m}^{-2} \text{ yr}^{-1}$. The basal area and OAI models performed poorly in comparison to the individual-tree models ($R^2 = 0.122$ and $R^2 = 0.129$, respectively) when applied to an independently collected dataset. The basal area model overpredicted litterfall at values $< 0.2 \text{ kg m}^{-2} \text{ yr}^{-1}$ and the OAI model had the highest root mean square error and underpredicted litterfall

at all levels of litter production. Site edaphic condition showed a marked difference in litterfall amounts and accuracy of model predictions among sites (Table 2). In particular, all models performed poorly in the xeric site, and model performance was best in the mesic site.

Because many existing studies do not validate models with an independent dataset, we used internal validation

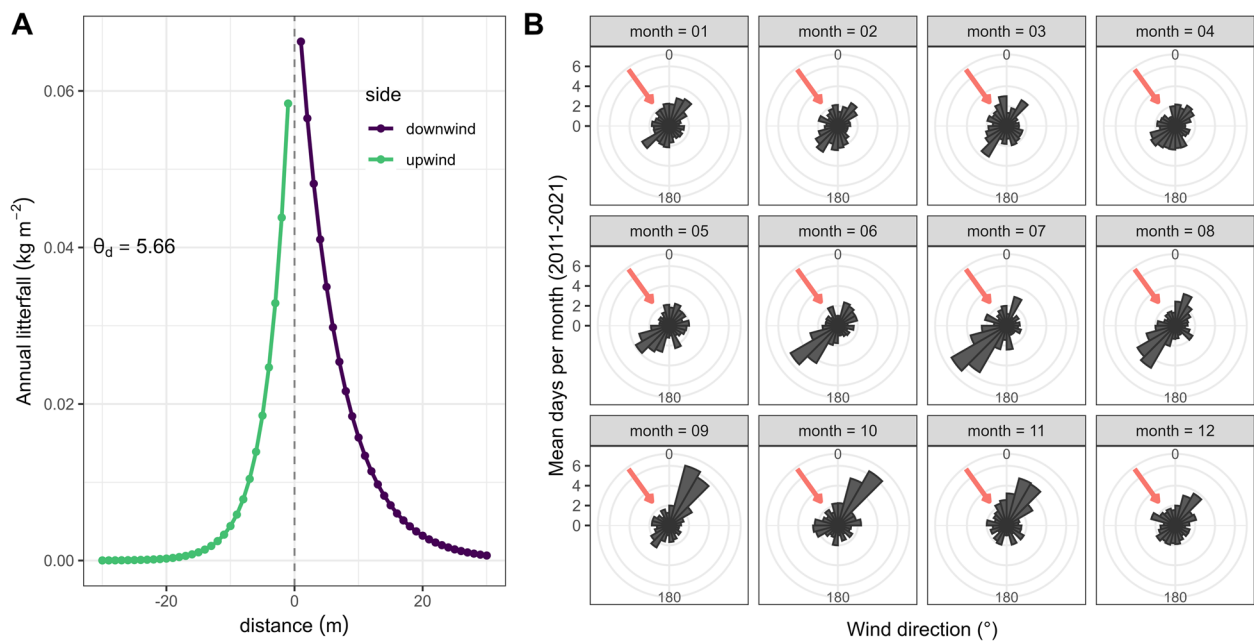


Fig. 4 Predictions of leaf litter dispersal from anisotropic model as a function of distance from a source tree (dbh = 30 cm) in the upwind and downwind directions using a mean value of a parameter to represent an average year; **b** frequency distribution of daily wind direction for all months from 2011–2021. The red arrow indicates the parameter estimate for $\theta_d = 5.66$ radians (324.3°)

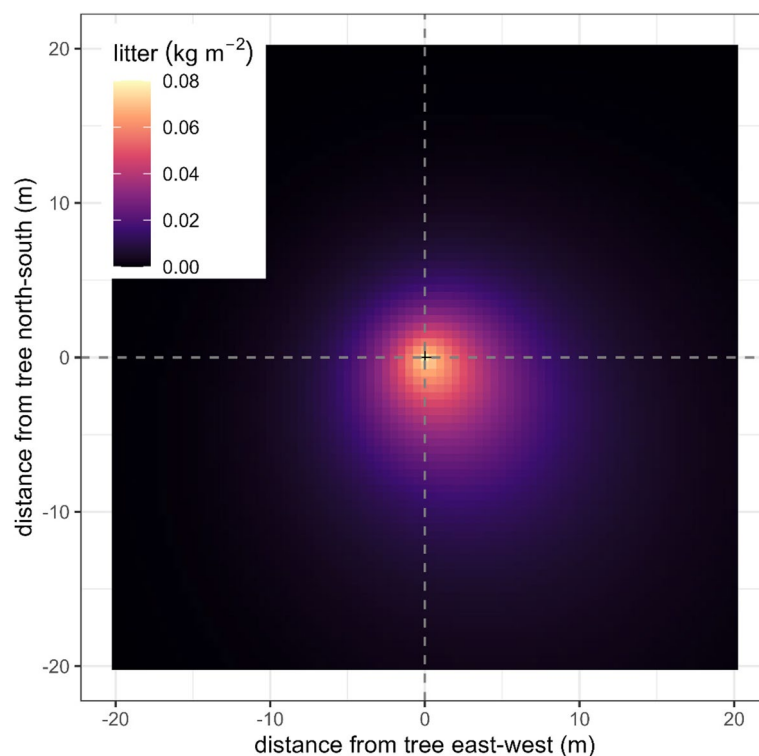


Fig. 5 Simulated litterfall predicted for an isolated 30 cm dbh longleaf tree (located at origin), in all directions using the anisotropic model for estimated wind direction $\theta_d = 5.66$ (324.3°) and the mean α parameter to represent an average year. Output resolution is 0.5 m

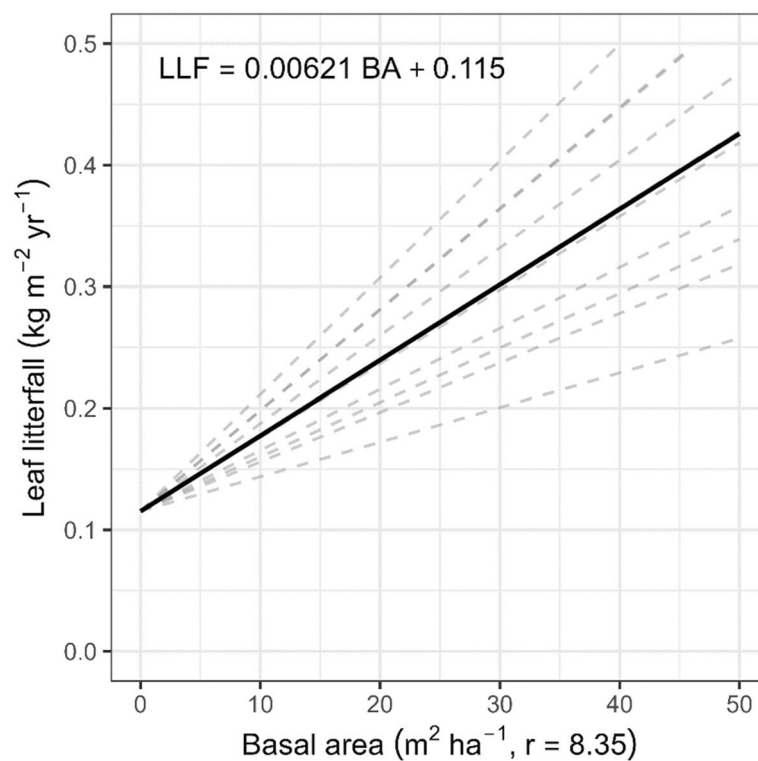


Fig. 6 Annual leaf litterfall as predicted by basal area within radius of 8.35 m. Dashed lines show basal area model for a range of values of α representing annual variability in litter production (see Table 1). Dark line and equation correspond to mean value of the α parameter to represent an average year

to allow for comparison with other studies. Results of internal validation appeared to have much better fit than suggested by external validation using the novel dataset (Table 3; $R^2 = 0.196\text{--}0.549$). All models were significant when challenged with the internal validation dataset. Additionally, the anisotropic model performed the best in this internal validation and the OAI model performed the worst (Table 3; Fig. S1).

Discussion

This study supports three major findings on leaf litter dispersal in longleaf pine forests: (1) leaf litter was best predicted by individual-tree-based models using

an exponential decay function, (2) mean annual litterfall production by plot varied by a factor of ~ 1.5 over a 10-year span, and (3) incorporating dispersal distances as an exponential decay function was more important for model performance than prevailing wind direction. This is the first known study to utilize a 10-year dataset to parameterize models of pine needle dispersal. In addition, we evaluated models using an external, independently collected dataset as well as a subset of the original calibration dataset. Models performed more poorly when challenged with a novel dataset than when challenged with a subset of the original data. Although most litter dispersal studies use only internal validation, our study highlights that validation of litter models may require external datasets to verify the predictive capability of litter dispersal models in novel forest stands.

Table 2 Comparison of coefficient of determination (R^2) for regressions of observed litterfall from the validation dataset versus model predictions of litterfall in longleaf forests in southwestern Georgia, USA. P values ≥ 0.05 indicated by “-”

	Basal Area	OAI	Isotropic	Anisotropic
Overall	0.122	0.129	0.319	0.242
Xeric	-	-	-	-
Intermediate	0.153	-	0.196	-
Mesic	-	0.179	0.148	0.117

Model fit and validation

Incorporating the influence of individual trees greatly improved model fit. This modeling approach accounted for the complexity due to leaf litter contribution of individual trees based on tree location and size. However, the basal area model was surprisingly well-fit to

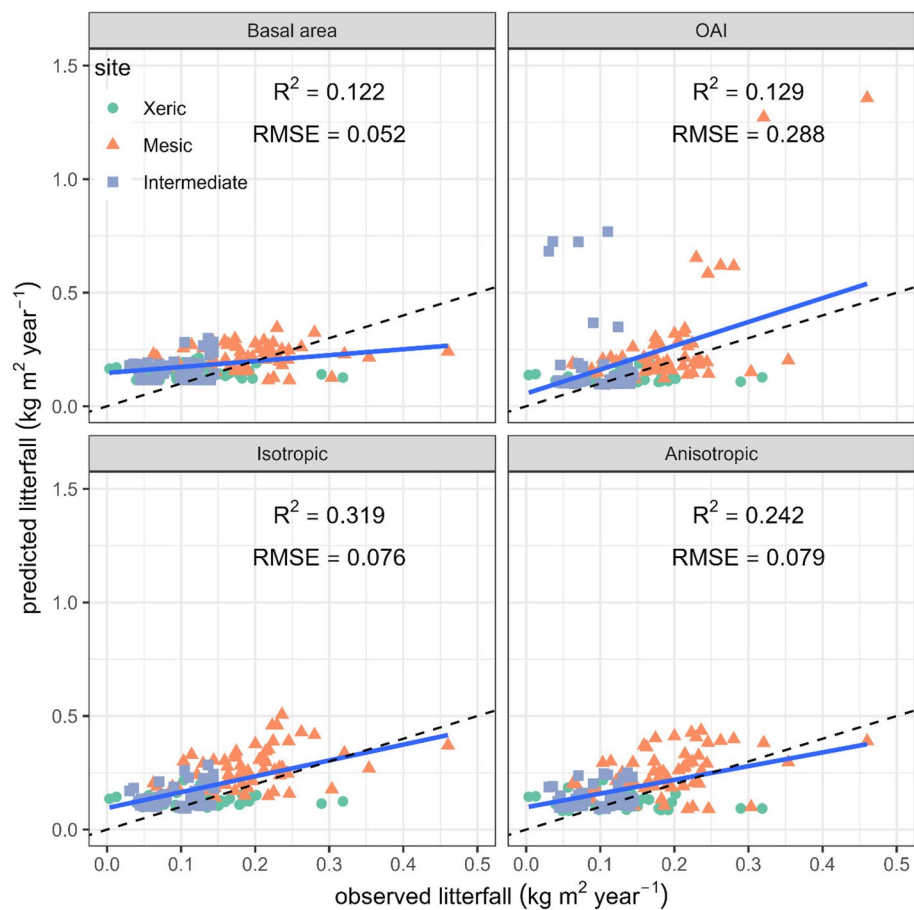


Fig. 7 Comparison of regressions for predicted needle litterfall vs. observed litterfall of the external validation data. Observed data are of three different longleaf pine forest sites varying along an edaphic gradient (xeric, intermediate, and mesic) in southwestern Georgia, USA from years 2019–2021. The dashed line represents a 1:1 relationship

Table 3 Comparison of coefficient of determination (R^2) for the model performance in initial calibration, internal, and external validation tests from litterfall data collected from longleaf pine forests in southwestern Georgia, USA. The best model in each category is indicated in bold

	Basal area	OAI	Isotropic	Anisotropic
Calibration	0.488	0.416	0.612	0.656
Internal Validation	0.484	0.196	0.510	0.549
External Validation	0.122	0.129	0.319	0.242

the calibration data. Compared to the best-fit model (anisotropic) that explained 66% of the variation in litterfall, the basal area model explained only 17% less of the variation in litterfall. Since stem maps are often not available for forest stands, this model can be more broadly useful for predicting longleaf pine litter dispersal as it requires basal area within a specified radius, rather than individual tree data from a stem map. This

would be more relevant to spatially uniform forests such as even-aged pine plantations. Conversely, the individual-tree models may be more useful for predicting litterfall in uneven-aged stands with more complex canopy structure. However, given the growing availability of lidar datasets and algorithms for tree segmentation (Silva et al. 2016; Blackburn et al. 2021; Whelan et al. 2023), individual tree-based litter prediction models will likely increase in utility. The OAI model had relatively low explanatory power and large over-predictions in litter. As seen in Fig. 1, the OAI model predicts unrealistically high litterfall at short distances from trees, and low litterfall elsewhere. This is likely because the model structure imposes an inverse relationship between litterfall and distance. Although it is useful as a competition index (Bigelow and Canham 2015), OAI may have less utility for modeling litterfall.

Regardless of whether internal or external validation was used, the isotropic and anisotropic models always provided the best predictions of litterfall. We expected

that the internal and external validation data sets would rank models consistently, but this was not the case (Table 3). Although the anisotropic model predicted litterfall comparably well to the isotropic model, it did not perform as well with the external validation data as it did with the calibration data. The anisotropic model may not have predicted as well with the external dataset because the unmeasured factors that contribute to the influence of wind influence during peak litterfall months could have deviated from our calibration dataset study sites. For instance, canopy structure has an effect on the influence of wind flows (Finnigan 2000; Pimont et al. 2011), and the model may not have been able to account for considering the wide range of canopy spatial configurations across the three edaphic categories of our external validation dataset. Future modeling studies in longleaf pine forests could take a ballistic approach like Jonard et al. (2006) that considers wind speed and release height to refine the model for wider applicability in model forest types.

We externally validated our model with multiple datasets because we expected differences in forest structure and primary productivity across an edaphic gradient to influence litterfall. Mitchell et al. (1999) found that overstory annual net primary productivity was significantly higher in mesic than xeric sites, largely due to greater density of overstory trees in mesic sites. Sheffield et al. (2003) found that at the individual tree level, needles were longer in mesic than in more xeric sites. Stand level characteristics that differ between soil moisture regimes are more likely to contribute to differences in litterfall predictions.

This study found that incorporating wind direction modestly improved litterfall predictions by explaining an additional 4% of variation in litterfall, but the importance of wind influence varies among other studies. No other pine-based studies that evaluated the influence of prevailing wind direction could be compared to our results. However, previous studies tested the influence of wind direction in hardwood forests and found an effect of wind on prevailing dispersal direction (Staelens et al. 2003; Jonard et al. 2006; Bigelow and Canham 2015; Nickmans et al. 2019). One study modeling leaf dispersal of basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton.), eastern hemlock (*Tsuga canadensis* L.), and sugar maple (*Acer saccharum* Marsh.) trees did not detect a strong influence of wind direction on litterfall (Ferrari and Sugita 1996). However, this may have been due to the closed canopy nature of the stands studied, whereas the influence of wind may have been more important in the open structure of the longleaf pine woodlands in this study. In more closed canopy longleaf

pine stands, the effect of wind may be less important. Leaf characteristics such as morphology and litterfall timing can also determine the influence of wind on dispersal (Staelens et al. 2003; Jonard et al. 2006). For instance, needle size in longleaf pine may be of significance compared to other species with smaller needles. The influence of wind on leaf dispersal in pine-based studies may differ from deciduous hardwood studies because their canopies retain foliage year-round, which may diminish the influence of wind in peak litterfall months. The incorporation of wind in the anisotropic model explained only 4% more variation in litterfall than the isotropic model, and the fitted parameter of wind direction θ_d was intermediate between the prevailing wind direction of summer (June–August) and autumn (September–December). Determining prevailing wind from nearby weather stations is fairly easy and may improve models more substantially in sites with consistent wind direction during peak periods of litterfall.

The results of this study shed light on the relevant radius of litterfall shedding around a tree of interest. We estimated that the relevant radius of leaf shedding (r) of the basal area model was 8.35 m. In the isotropic and anisotropic dispersal models, relevant distances of litterfall deposition ranged from 10–20 m depending on wind direction. These estimates span a range of litterfall influence slightly higher than the basal area model, but the majority of litter is concentrated within the first 10 m when modeled at the individual tree level. Staelens et al. (2004) found that cumulative basal area and leaf litterfall (*Q. rubra*, *Q. robur*, and *B. pendula*) were highly correlated at a radius of about 12–18 m around litter traps. Another study, Ferrari and Sugita (1996), found that the average radius within which 90% of leaf litter falls to a trap is 17.1 m. The smaller relevant radius we observed is comparable to findings from other studies that have documented the extent of longleaf pine needle cast in relation to individual trees and gap edges. For example, O'Brien et al. (2008) found that needle loading into a canopy gap greatly diminishes by about 8–12 m. A study by Bigelow and Whelan (2019) attributed lower fire temperature and less hardwood topkill to diminishing needle availability, as predicted by a neighborhood model that estimated there was a marked decrease in time over 60° C about 10 m from 30 cm adult longleaf pine trees. Another study by Rebertus et al. (1989) demonstrated that the influence of longleaf pine crowns on turkey oak (*Quercus laevis* Walt.) survival extended about 4 m beyond the crown edges. The range of variability among studies for the relevant litterfall radius of longleaf pine is broad, and this study supports a mechanistic basis to estimate this value.

Sources of litterfall variability

We found high interannual variability in leaf litter production across the 10 years of litterfall data, as indicated by a wide range of α_y parameter estimates (Table 1). Other comparable studies found low interannual variability in litter production, but these were also conducted in forests dominated by deciduous trees (Ferrari and Sugita 1996; Staelens et al. 2003; Jonard et al. 2006). Though we did not measure variables that may account for temporal variability in litterfall, there are multiple explanations for the variability across the study period. Factors such as weather patterns and site conditions affect needle biomass production and timing of shedding (Hennessey et al. 1992). For instance, Hennessey et al. (1992), found that differences in annual litterfall patterns in a loblolly pine stand over a 5-year period varied with growing season precipitation, site water balance, and the occurrence of drought. Gresham (1982) found an effect of a hurricane causing an irregularly high increase in annual longleaf pine litterfall. Sheffield et al. (2003) found that needle life span varied by 8–24 months (15 months on average) in a mature longleaf forest, suggesting that needle fall timing can be highly variable. Incorporating climate parameters such as growing season precipitation or annual precipitation to estimate litter production could further enhance the predictive power of these models and improve performance with novel datasets.

There are additional tree characteristics that could be incorporated to improve the individual-tree models. For instance, tree height was not considered in this study, which can limit the ability to predict litterfall dispersal on sites with heterogeneous tree sizes (Jonard et al. 2006), but can be modeled (Loudermilk et al. 2011). Other studies used a ballistic model to predict litterfall, (Jonard et al. 2006; Nickmans et al. 2019), and this approach that incorporates tree height, leaf velocity, and wind speed may be of interest for future studies in longleaf needle dispersal. Furthermore, crown architecture can affect foliage biomass production and dispersal distance. Therefore, including a variable such as crown volume or live crown ratio may improve future models. Sánchez-López et al. (2023) used litter data from clip plots and crown attribute data via airborne laser scanning to predict litter biomass accumulation. They successfully modeled local fuel heterogeneity with this approach, which incorporated litter decomposition as well as litter consumption during prescribed fire. Though our study also predicts litter biomass production, we did not include parameters for litter removal from the fuelbed. Nevertheless, the predictions of explicit litter inputs are useful for understanding contributions of leaf litter to nutrient cycles and

fuel beds. Litter dispersal should be closely related to leaf area, so direct or indirect measures of leaf area of individual trees could improve models further.

The relationship between tree size, age, and needle production could be further explored in old-growth longleaf pine forests, as this study took place in second-growth forests that are about 80–100 years old. Adding parameter δ , which determines the decline in litter production as tree dbh increases, approached zero in both the isotropic and anisotropic models, and thus did not contribute to the allometric relationship between dbh and annual litterfall (Eq. 3). This finding was similar to Staelens et al. (2003), likely because there were not many large trees (Ruark 1987). This study could be expanded in old growth longleaf to see if there is a significant reduction in foliage production in much larger, older trees (i.e., $\delta > 0$). Repeated studies in forests across a wider range of stand structures can improve the robustness of individual-tree litter dispersal modeling.

Conclusion and management implications

Spatially explicit models of leaf litterfall can improve our understanding and practice of fire-dependent ecosystem management. In frequently burned ecosystems, fuel distribution varies at fine scales resulting in variable fire effects at fine scales (Loudermilk et al. 2018). Therefore, it is important to understand how leaf litter fuels affect fire at fine scales, and particularly biophysical fire effects such as fire-induced plant mortality (O'Brien et al. 2018). The ability to predict the spatial pattern and quantity of leaf litter fuels could contribute to existing models of fire behavior such as QUIC-fire (Linn et al. 2020) as well as next generation fire behavior models that are currently under development. In addition, terrestrial LIDAR (Light Detection and Ranging) technology can decrease the time spent on acquiring accurate tree data to model litter dispersal (Dassot et al. 2011). Information on litter abundance can also be useful for modeling ecosystem processes such as mortality from fire. For example, spatially explicit models of growth, competition, and mortality have been developed for longleaf pine ecosystems that require information of fuel accumulation of pine litter to estimate fire intensity and resulting tree mortality but currently are based on coarser empirical models (Loudermilk et al. 2011). In addition, litter dispersal models could be useful for understanding spatial patterns of other species found to have fire intensity, duration, and flammability comparable to longleaf pine needles such as turkey oak (*Quercus laevis* Walt.) and post oak (*Quercus stellata* Wangenh.) (Kane et al. 2008). Leaf

litter models can also be used to better understand the effects of forest tree species shifts on litter composition. The positive feedback cycle known as mesophication whereby fire-tolerant species with highly flammable litter are replaced by fire-sensitive, shade-tolerant species (Nowacki and Abrams 2008; Alexander et al. 2021) results in a dampening effect on fire behavior in formerly fire-prone ecosystems (Kreye et al. 2018). Understanding the impacts of these compositional shifts on leaf litter patterns can be assisted by these dispersal models. Besides fire, other ecosystem processes such as carbon and nitrogen and other nutrients are linked to leaf litter production and deposition (Bigelow and Canham 2015; Liu et al. 2009). The models of litter deposition explored here can be incorporated into spatially explicit models of ecosystem succession which consider litter input and decomposition (e.g., Landis-II NECN extension; Scheller et al. 2011) to improve predictions and understanding of nutrient cycling.

An overall advantage of these models is that they can provide predictions of litterfall patterns at various scales from a patch in the forest to the landscape level. In the context of prescribed fire, these models may help predict continuity of fuels in conjunction with other models (Pimont et al. 2011; Bigelow and Whelan 2019). Effective fuels management is critical for fire-dependent plant and wildlife species and the ecosystems they inhabit, as well as for human recreation and aesthetic purposes. Predicting needle litter deposition based on canopy structure is not only applicable to the effective management of prescribed fire, but also for sustainable harvesting of timber and pine straw. For instance, these models may be useful to land managers interested in pine straw production from longleaf pine and other pine species, particularly in stands where composition and structure are not uniform, but a straw harvest is desired. These models also inform management decisions regarding the density of adult trees to maintain while harvesting timber to sustain sufficient pine litter in the fuelbed. Indeed, all these models could potentially converge under a homogenous overstory canopy with homogenous litter dispersal. We expect this may occur in pine or other planted stands, where simpler models may suffice. However, many ecological forestry approaches in longleaf pine aim for more complex structure (Cannon et al. 2022). In these cases, models that incorporate spatial information on trees can improve predictions substantially as our results support. The use of these and future litter dispersal models holds potential for understanding and predicting prescribed fire and other management outcomes in longleaf pine forests as well as other frequently burned forest ecosystems.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-023-00209-z>.

Additional file 1.

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Authors' contributions

SHB and JBC participated in data curation, formal analysis, and visualization. JBC and DPA participated in funding acquisition, project administration, and supervision. JBC contributed resources and software. All authors participated in conceptualization, investigation, methodology, validation, writing and revising original draft.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors report no conflict of interest.

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References

- Alexander, H.D., C. Siegert, J. Stephen Brewer, J. Kreye, M.A. Lashley, J.K. McDaniel, A.K. Paulson, H.J. Renninger, and J. Morgan Varner. 2021. Mesophication of Oak landscapes: evidence, knowledge gaps, and future research. *BioScience* 71 (5): 531–542. <https://doi.org/10.1093/biosci/biaa169>.
- Anderson, David R., and Kenneth P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management* 66 (3): 912–918.
- Bigelow, S.W., and C.D. Canham. 2015. Litterfall as a niche construction process in a northern hardwood forest. *Ecosphere* 6 (7): art117.
- Bigelow, S.W., & Whelan, A.W. 2019. Longleaf pine proximity effects on air temperatures and hardwood top-kill from prescribed fire. *Fire Ecology*, 15(27). <https://doi.org/10.1186/s42408-019-0039-7>.

- Blackburn, R.C., R. Buscaglia, and A.J. Sánchez Meador. 2021. Mixtures of airborne lidar-based approaches improve predictions of forest structure. *Canadian Journal of Forest Research* 51 (8): 1106–1116. <https://doi.org/10.1139/cjfr-2020-0506>.
- Canham, C.D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications* 16 (1): 62–73. <https://doi.org/10.1890/04-0657>.
- Cannon, J.B., S.W. Bigelow, J.K. Hiers, and S.B. Jack. 2022. Effects of silvicultural selection treatments on spatial pattern and dynamics in a *Pinus palustris* Mill. woodland. *Forest Ecology and Management* 505: 119888.
- Dassot, M., T. Constant, and M. Fournier. 2011. The use of terrestrial LiDAR technology in forest science: Application fields, benefits and challenges. *Annals of Forest Science* 68 (5): 959–974. <https://doi.org/10.1007/s13595-011-0102-2>.
- Drew, M.B., L.K. Kirkman, and A.K. Gholson. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. *Castanea* 63 (1): 1–24.
- Facelli, J.M., and S.T.A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review* 57 (1): 1–32. <https://doi.org/10.1007/BF02858763>.
- Ferrari, J.B., and S. Sugita. 1996. A spatially explicit model of leaf litter fall in hemlock-hardwood forests. *Canadian Journal of Forest Research* 26: 1905–1913.
- Finnigan, John. 2000. Turbulence in plant canopies. *Annual Reviews of Fluid Mechanics* 32: 519–571. <https://doi.org/10.1146/annurev.fluid.32.1.519>.
- Goebel, P.C., Palik, B.J., Kirkman, L.K., and West, L. 1997. *Field guide: landscape ecosystem types of Ichauway*.
- Grace, S.L., and W.J. Platt. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *The Journal of Ecology* 83 (1): 75. <https://doi.org/10.2307/2261152>.
- Gresham, C.A. 1982. Litterfall patterns in mature loblolly and longleaf pine stands in coastal South Carolina. *Forest Science* 28 (2): 223–231.
- Hennessey, T.C., P.M. Dougherty, B.M. Cregg, and R.F. Wittwer. 1992. Annual variation in needle fall of a loblolly pine stand in relation to climate and stand density. *Forest Ecology and Management* 51 (4): 329–338. [https://doi.org/10.1016/0378-1127\(92\)90332-4](https://doi.org/10.1016/0378-1127(92)90332-4).
- Hiers, J.K., J.J. O'Brien, R.J. Mitchell, J.M. GREGO, and E.L. Loudermilk. 2009. The wildland fuel cell concept: An approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. *International Journal of Wildland Fire* 18 (3): 315–325. <https://doi.org/10.1071/WF08084>.
- Hiers, J.K., Joseph J. O'Brien, J. Morgan Varner, Bret W. Butler, Matthew Dickinson, James Furman, Michael Gallagher, David Godwin, Scott L. Goodrick, Sharon M. Hood, Andrew Hudak, Leda N. Kobziar, Rodman Linn, E. Louise Loudermilk, Sarah McCaffrey, Kevin Robertson, Eric M. Rowell, Nicholas Skowronski, Adam C. Watts, and Kara M. Yedinak. 2020. Prescribed fire science: the case for a refined research agenda Abstract Resumen *Fire Ecology* 16(1). <https://doi.org/10.1186/s42408-020-0070-8>
- Hoogenboom, G., Verma, B. P., & Threadgill, E. D. 1991. The Development of the Georgia Automated Environmental Monitoring Network. *Proceedings of the 1991 Georgia Water Resources Conference, Held March 19 and 20, 1991, at the University of Georgia.*, 285–287.
- Jonard, M., F. Andre, and Q. Ponette. 2006. Modeling leaf dispersal in mixed hardwood forests using a ballistic approach. *Ecological Society of America* 87 (9): 2306–2318.
- Kane, J.M., J.M. Varner, and J.K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impiders. *Forest Ecology and Management* 256 (12): 2039–2045. <https://doi.org/10.1016/j.foreco.2008.07.039>.
- Kirkman, L.K., R.J. Mitchell, R.C. Helton, and M.B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88 (11): 2119–2128. <https://doi.org/10.2307/3558437>.
- Kreye, J.K., J.M. Varner, G.W. Hamby, and J.M. Kane. 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. *Ecosphere* 9 (1): e02078.
- Linn, R. R., Goodrick, S. L., Brambilla, S., Brown, M. J., Middleton, R. S., O'Brien, J. J., & Hiers, J. K. 2020. QUIC-fire: A fast-running simulation tool for prescribed fire planning. *Environmental Modelling and Software*, 125(August 2019). <https://doi.org/10.1016/j.envsoft.2019.104616>.
- Liu, L., J.S. King, F.L. Booker, C.P. Giardina, H.L. Allen, and S. Hu. 2009. Enhanced litter input rather than changes in litter chemistry drive soil carbon and nitrogen cycles under elevated CO₂: A microcosm study. *Global Change Biology* 14: 441–453.
- Loudermilk, E.L., J.P. Cropper, R.J. Mitchell, and H. Lee. 2011. Longleaf pine (*Pinus palustris*) and hardwood dynamics in a fire-maintained ecosystem: a simulation approach. *Ecological Modelling* 222 (15): 2733–2750. <https://doi.org/10.1016/j.ecolmodel.2011.05.004>.
- Loudermilk, E. Louise, Hiers, J. K., & O'Brien, J. J. 2018. The Role of Fuels for Understanding Fire Behavior and Fire Effects. In *Ecological Restoration and Management of Longleaf Pine Forests* (pp. 107–122). CRC Press, Taylor & Francis Group. <https://doi.org/10.1201/9781315152141-6>.
- McIntyre, R. K., Jack, S. B., Mitchell, R. J., Kevin Hiers, J., & Neel, W. L. 2008. *Multiple value management: the Stoddard-Neel approach to ecological forestry in longleaf pine grasslands*. 32. http://www.americaslongleaf.org/media/3536/multiple_value_management_the_stoddard-neel_approach_to_ecological_forestry.pdf.
- Mitchell, R.J., J.K. Hiers, J.J. O'Brien, S.B. Jack, and R.T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. *Canadian Journal of Forest Research* 36 (11): 2724–2736. <https://doi.org/10.1139/X06-100>.
- Mitchell, Robert J., Kirkman, L. K., Pecot, S. D., Wilson, C. A., Palik, B. J., & Boring, L. R. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research*, 29(6), 743–751. <https://doi.org/10.1139/x99-051>.
- Mitchell, R.J., J.K. Hiers, J.J. O'Brien, G. Starr. 2009. Ecological forestry in the southeast: understanding the ecology of fuels. *Journal of Forestry* 107: 391–397.
- Murphy, L. 2015. *Methods for Maximum Likelihood Estimation* (Version 1.7). R Package. <https://cran.r-project.org/package=likelihood>.
- Nickmans, H., M. Jonard, K. Verheyen, and Q. Ponette. 2019. Modelling leaf dispersal and nutrient return in tree species mixtures. *Forest Ecology and Management* 436: 68–78.
- Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58 (2): 123–138. <https://doi.org/10.1641/B580207>.
- O'Brien, J.J., J.K. Hiers, A. MacCallahan, R.J. Mitchell, and S.B. Jack. 2008. Interactions among overstory structure, seedling life-history traits, and fire in frequently burned neotropical pine forests. *Ambio* 37: 542–547.
- O'Brien, J.J., E.L. Loudermilk, B. Hornsby, A.T. Hudak, B.C. Bright, M.B. Dickinson, J.K. Hiers, C. Teske, and R.D. Ottmar. 2016. High-resolution infrared thermography for capturing wildland fire behaviour: RxCADRE 2012. *International Journal of Wildland Fire* 25: 62–75. <https://doi.org/10.1071/WF14165>.
- O'Brien, J.J., J.K. Hiers, J.M. Varner, C.M. Hoffman, M.B. Dickinson, S.T. Michaelitz, E.L. Loudermilk, and B.W. Butler. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports* 4 (4): 161–177. <https://doi.org/10.1007/s40725-018-0082-7>.
- Pimont, F., J.-L. Dupuy, R.R. Linn, and S. Dupont. 2011. Impacts of tree canopy structure on wind flows and fire propagation simulated with FIRETEC. *Annals of Forest Science* 68: 523–530. <https://doi.org/10.1007/s13595-011-0061-7>.
- Platt, W.J., D.P. Ellair, J.M. Huffman, S.E. Potts, and B. Beckage. 2016. Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecological Monographs*. 86 (3): 352–372. <https://doi.org/10.1002/ecm.1224>.
- R Core Team. 2013. *A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.r-project.org/>.
- Rebertus, A.J., G.B. Williamson, and E.B. Moser. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. *Ecology* 70 (1): 60–70.
- Ruark, G. A. 1987. Comparison of constant and variable allometric ratios for estimating *Populus tremuloides* biomass. In *Forest science*. (Vol. 33, Issue 2, p. 294). Society of American Foresters.
- Rutledge, B.T., J.B. Cannon, R.K. McIntyre, A.M. Holland, and S.B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. *Forest Ecology and Management* 481: 118724. <https://doi.org/10.1016/j.foreco.2020.118724>.
- Sánchez-López, N., A.T. Hudak, L. Boschetti, C.A. Silva, B.C. Bright, and E.L. Loudermilk. 2023. A spatially explicit model of litter accumulation in fire

- maintained longleaf pine forest ecosystems of the Southeastern USA. *Advances in Forest Fire Research* 2022 481: 1383–1389.
- Scheller, R.M., Dong Hua, P.V. Bolstad, R.A. Birdsey, and D.J. Mladenoff. 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling* 22: 144–153.
- 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 (1–3): 157–167. [https://doi.org/10.1016/S0378-1127\(02\)00523-6](https://doi.org/10.1016/S0378-1127(02)00523-6).
- Silva, C.A., A.T. Hudak, L.A. Vierling, E.L. Loudermilk, J.J. O'Brien, J.K. Hiers, S.B. Jack, C. Gonzalez-Benecke, H. Lee, M.J. Falkowski, and A. Khosravipour. 2016. Imputation of Individual Longleaf Pine (*Pinus palustris* Mill.) Tree Attributes from Field and LiDAR Data. *Canadian Journal of Remote Sensing* 42 (5): 554–573. <https://doi.org/10.1080/07038992.2016.1196582>.
- Staelens, J., L. Nachtergale, S. Luyssaert, and N. Lust. 2003. A model of wind-influenced leaf litterfall in a mixed hardwood forest. *Canadian Journal of Forest Research* 33 (2): 201–209. <https://doi.org/10.1139/x02-174>.
- Staelens, J., L. Nachtergale, and S. Luyssaert. 2004. Predicting the spatial distribution of leaf litterfall in a mixed deciduous forest. *Forest Science* 50 (6): 836–847. <https://doi.org/10.1093/forests/50.6.836>.
- Walker, J., and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp. *North Carolina. Vegetatio* 55 (3): 163–179. <https://doi.org/10.1007/BF00045019>.
- Whelan, A. W., Bigelow, S. W., Nieminen, M. F., & Jack, S. B. 2018. Fire season, overstory density and groundcover composition affect understory hardwood sprout demography in longleaf pine Woodlands. *Forests*, 9(7). <https://doi.org/10.3390/f9070423>.
- Whelan, A. W., Cannon, J. B., Bigelow, S. W., & Sanchez Meador, A. J. 2023. Improving generalized lidar estimates of forest structure in complex forest types using area- and voxel-based approaches. *Submitted to Remote Sensing of the Environment*, 284(November 2022). <https://doi.org/10.1016/j.rse.2022.113362>.
- Wiesner, S., P.C. Stoy, C.L. Staudhammer, and G. Starr. 2020. Using metabolic energy density metrics to understand differences in ecosystem function during drought. *Journal of Geophysical Research: Biogeosciences* 125 (3): 1–20. <https://doi.org/10.1029/2019JG005335>.
- Wiggers, M.S., L.K. Kirkman, R.S. Boyd, and J.K. Hiers. 2013. Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. *Forest Ecology and Management* 310: 54–63. <https://doi.org/10.1016/j.foreco.2013.07.030>.
- Williamson, G.B., and E.M. Black. 1981. High temperature of forest fires under pines as a selective advantage over oaks. *Nature* 293: 643–644. <https://doi.org/10.1038/293643a0>.

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