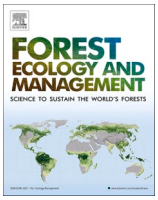
Forest Ecology and Management 580 (2025) 122538

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Linking overstory relative density to light availability and understory plant community composition in disturbance-dependent, *Pinus rigida* -dominated forests of the mid-Atlantic coastal plain, USA

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ARTICLE INFO

Keywords:
Relative Density
Leaf Area Index
Light availability
Pine barrens
Tradeoffs
Urban-rural divide

ABSTRACT

There is a vigorous debate around whether and how to manage forests for climate mitigation or for other goals such as biodiversity. To achieve any of these goals it is necessary to define the parameters within which they can exist; ideally, the metrics used to evaluate progress towards one goal should be able to speak to other goals, especially when there are competing objectives at play. In the pitch pine (*Pinus rigida*) dominated coastal plain of New Jersey, open-canopy habitats are the locus of biodiversity, so we sought to define 'open-canopy' using a common metric of forest occupancy, Relative Density (RD). Using forest inventory data and light intensity measurements we found non-linear relationships between overstory RD and metrics of canopy light use. We then used RD to define upper limits of forest occupancy for fairly common open-canopy understory taxa above which one is very unlikely to find these plants. Our methods found credible thresholds in overstory density for four of five taxa, placing boundaries on the envelope of survivable conditions for these open-canopy community members. Native warm-season grasses (subfamily *Panicoideae*), *Carex*, *Quercus ilicifolia,* and *Q. marilandica* were not present in pitch pine forests above RD of roughly 0.57, aligning well with the approximate stocking level for stem exclusion. Separate validation data supported our quantified limits for warm-season grasses and demonstrated the importance of considering ground-layer competition but did not support overstory density thresholds for *Hudsonia spp*. Managers of similar pine forests with social goals in tension may be better able to quantify or illustrate tradeoffs between objectives using these results.

1. Introduction

In fire- and disturbance-dependent pine forests, biodiversity hotspots are those patches of the landscape where open-canopy conditions predominate (Hanberry et al., 2020b). Restoration of open-canopy conditions for pine-oak systems entails silvicultural methods that require creative and diligent application of management actions (Bragg et al., 2020; Mitchell et al., 2006). Calls for restoring pitch pine (*Pinus rigida* Mill.) barrens (Bried et al., 2014) echo the ecological and social arguments made for restoring longleaf pine ecosystems (Mitchell et al., 2006; Van Lear et al., 2005), albeit across a smaller range and fewer jurisdictions.

National surveys show clear differences between how rural and suburban/urban residents prioritize addressing environmental problems, with the latter much more likely to cite the need to deal with climate change (Bonnie et al., 2020). In pitch-pine dominated northeastern coastal pine barrens, local residents are in support of treatments that support reduced density for fire mitigation and biodiversity (Ryan, 2012). In contrast, state-level policy goals involve increasing carbon storage in the forest (New Jersey Department of Environmental Protection, New Jersey Department of Agriculture, 2021), which is predicated on increased tree growth and higher densities of aboveground carbon. Within a site, management to reduce overstory density is inherently in tension with management to increase carbon, as

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https://doi.org/10.1016/j.foreco.2025.122538
Received 14 August 2024; Received in revised form 22 January 2025; Accepted 24 January 2025
Available online 5 February 2025
0378-1127/Published by Elsevier B.V.

aboveground net primary production and ground-level light availability are inversely related (Reich et al., 2001). Thus, management for open pine woodlands in the northeast illustrates an urban/suburban-rural divide: land ownership goals may not be in alignment between the people who live in the forest and those who do not but whose political representation presides over the forest. With calls to expand public ownership of forestland and restrict tree cutting to address climate change (DellaSala et al., 2022; Dinerstein et al., 2019) this dynamic will likely accelerate.

In order to build the foundational trust that is required to successfully address natural resource management affairs, public resource management agencies must meaningfully address the concerns of stakeholder groups, especially when tradeoffs and compromise are necessary (Toman et al., 2021). Individuals who have the least trust in government agencies and those who do not believe those agencies share their values are the most likely to have active involvement in management planning (Smith et al., 2013), a dynamic that can amplify tension when there is antinomy between social objectives for the resource. Moreover, the human dimensions of resource management can become more complicated in the absence of clear technical metrics; empirical guideposts to justify choices are a key component of trust between stakeholders and managers, and of critical importance for successful land management (Moffat et al., 2016).

We examined the pitch pine forests in the outer coastal plain of southern New Jersey to link ecological and carbon stocking goals in the context of conflicting public goals for the resource. Existing quantitative metrics for carbon stocks involve traditional forest measurements of attributes such as tree size and density (Hoover et al., 2021; Jenkins et al., 2004; Smith et al., 2006). In contrast, many of the ecological investigations of pitch pine forests instead characterize tree or canopy cover as being the relevant attribute of interest (Akresh et al., 2022; Bried et al., 2014; King et al., 2011; Šrůtek et al., 2008; Wieren and Simons, 2019).

Field-based ocular measurements of canopy cover can be biased and inconsistent with one another (Korhonen et al., 2006). Remote sensing observations are heavily dependent on sensor characteristics and can fundamentally vary depending on whether one is looking up at the overhead canopy or down through layers of vegetation to the ground (Smith et al., 2009). However, when considered within a forest type, metrics of stocking and average tree size can consistently predict canopy cover (McIntosh et al., 2012) and have the added benefit of being inherently related to the live carbon pools.

We sought to bridge ecological and biometric views of the pitch pine forest resource by empirically relating a metric of forest site occupancy to understory light availability and its effect on plant communities. To do this we asked two questions: (1) Is there a relationship between a common forest inventory metric of overstory occupancy (Relative Density, RD) and the light environment experienced by ground-layer plants in this system? (2) Can RD be used to find the limit of the distributions of indicator taxa for open woodland communities? If the answer to both is 'yes', then metrics that speak to carbon (such as the number of trees per area and their size) can be linked to local ecological stocking indicators (Isaacson et al., 2024). This should aid in conservation of the unique ecology of this landscape while at the same time informing the costs to other goals from management actions, which is indispensable in balancing disparate social objectives.

2. Materials and methods

2.1. Data sources

2.1.1. Forest inventory data

The New Jersey Forest Service (NJFS) collected forest inventory data in Wharton State Forest and Penn State Forest between 2017 and 2019 as part of the agency's process for developing forest management plans (Fig. 1). NJFS staff delineated forest types by aerial photo interpretation, with stratification intended to reduce type-level variance in basal area (BA) per hectare. Each of the 6000 inventory plot clusters had an overstory plot, an advanced regeneration (sapling) plot, and a ground-layer plot. Of these plots, 2960 met the criteria for inclusion in this study.

All overstory plots used in this study were completed using variable-radius sampling and a basal area factor (BAF) of 2.30 m^2 ha^{-1} (10 ft^2 ac^{-1}). Advanced regeneration was measured using an 81 m^2 (1/50th ac) fixed radius plot (5.1 m radius) and ground cover was measured using an 8.1 m^2 (1/500th ac) fixed radius plot (1.6 m radius). All three levels of

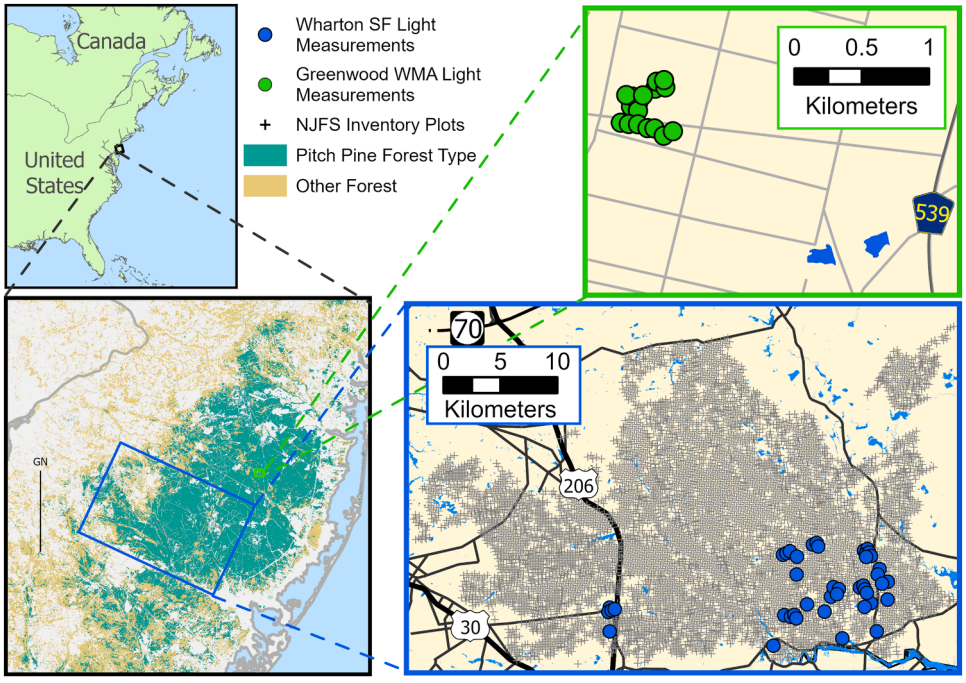

Fig. 1. Map of study locations, forest inventory points, and locations of leaf area index (LAI) measurements.

sampling used the same plot center point. State forest inventory plot summary statistics can be found in Table 1.

Overstory observations included species, diameter at breast height (DBH), total height, and other tree attributes. Only tree species were counted in the middle-sized advanced regeneration plots, and only those stems taller than 1.37 m in height and less than 10.2 cm DBH. Plants not counted in the overstory or advanced regeneration plot but inside the 1.6 m radius ground cover plot were assessed by taxon as to the percentage of the plot area over which their foliage was superimposed (% of 8.1 m^2 plot). Plots could have a sum of more than 100 % cover in the ground data, which was often the case in plots with mixed composition or multiple layers of vegetation. Most species were identified in ground plots, but for more diverse taxa whose management prescriptions would not change with species-level information, NJFS recorded coarser groupings at the scale of genus (for *Alnus*, *Amelanchier*, *Carex*, *Hudsonia*, *Ribes*, *Rubus*, *Viburnum* & *Vitis*), subfamily (*Panicoideae*), or growth form (crustose, foliose, or fruticose lichens).

We collected additional partial inventory points at Greenwood Wildlife Management Area (WMA), located roughly 13 km NNE of Penn State Forest. These points consisted solely of the variable-radius overstory plot collected at BAF 2.3 m^2 ha^{-1} and were necessary to capture LAI levels under the lowest-density overstory. Additional points were needed because we found exceedingly few places in Wharton and Penn State Forests where overstory density was low, while portions of Greenwood WMA are managed for this very attribute. Understory and ground layer data were not collected in these additional plots because brush mowing had occurred in the preceding weeks to maintain open habitat.

2.1.2. Leaf area index & diffuse non-interceptance measurements

We collected measurements of Leaf Area Index (LAI) and diffuse non-interceptance (DIFN) across a range of overstory occupancy values during August 2020 and June 2021 (Fig. 1, Table 1) using a LI-COR 2200c Plant Canopy Analyzer. All data were processed using FV2200 software (version 2.1). For each plot measurement, we visited pure or nearly pure plots of pitch pine, defined as those stands where *P. rigida* comprised > 90 % of the living relative BA of the plot. Other observed tree species included black oak (*Quercus velutina* Lam.), blackjack oak (*Q. marilandica* Müenchh.), post oak (*Q. stellata* Wangenh.), southern red oak (*Q. falcata* Michx.), and scarlet oak (*Q. coccinea* Müenchh.), though these cumulatively comprised less than 10 % of the total BA on any plot. We excluded plots with recent processes that interfered with light measurements above the shrub layer. This included areas that had major disturbance (wildfire, regeneration harvest) in the last fifteen years to ensure that measurements above the shrub layer were not additionally shaded by a new cohort of regeneration. Similarly, plots that had undergone prescribed burning in the previous five years were excluded as some prescribed fires in this landscape are hot enough to entirely denude trees of leaf area, which would interfere with a relationship between overstory occupancy from stem measurements and leaf area.

We made all light measurements on cloudless days, mainly when the sun was below the horizon during civil twilight in the morning and evening. For those measurements when the sun was above the horizon, we collected sky brightness scattering correction records ('K' records) every 60–90 mins to perform bright sky scattering corrections (Kobayashi et al., 2013), and where possible, used the closest two K readings to interpolate corrections. Both above- and below-canopy measurements used the 90° sensor field of view cap, oriented north, to keep the sun at the side and out of the sensor field of view. Above-canopy ('A' records) measurements were collected using a second wand logging every 30 s in a grassy field with at least 80 m to the nearest trees in the sensor field of view. Mean canopy height surrounding the fields was 15 m to 20 m.

We measured below-canopy ('B' records) observations at overstory inventory plot locations at two heights. First, we measured light above the shrub layer (at 1.7 m height) beginning over the plot center, then took readings at 1 m radii, starting at 1 m north and separated by 45° of azimuth from the plot center. We added four more measurements in the cardinal directions at 2 m radii, for a total of 13 measurements per plot. After these data were collected, we lowered the height of the sensor to 5–15 cm from the ground. For these we recorded light at the plot center, and at 1 m and 2 m radii in the cardinal directions, for a total of 9 measurements per plot.

To scale the observations, for all 'B' records we used the 'A' record that corresponded closest-in-time. Ring 5 was excluded from analysis for all records due to noise and to maintain consistency in sampled area; in our overstory inventory plots, the limiting distance of a tree of the quadratic mean diameter and mean canopy height for each plot usually corresponded to the projected amount of canopy observed by the outside of rings 3 and 4. For the few records where noise caused the reading from a ring of the B sensor to slightly exceed the ring from the A sensor, we clipped the offending ring's B reading at 1; since the A sensor is the above-canopy measurement, the reading level for each ring of the A sensor should theoretically be 1 and cannot be exceeded by the corresponding ring from B. We only collected measurements on plots where the shrub layer was lower than the height of the upper measurement as we sought to relate the light environment to metrics of overstory occupancy.

2.1.3. Validating observations for select taxa

We also collected below-canopy (B) light measurements where we found isolated and less vigorous individuals of three indicator species: broomsedge bluestem (*Andropogon virginicus* L.), switchgrass (*Panicum virgatum* L.), and golden-heather (*Hudsonia ericoides* L.). Vigor was visually estimated by the overall density and size of culms for the grasses; we considered plants with sparse, small culms to be of low vigor. Where these individuals were found, we took at least 6 and as many as 9 light intensity measurements corresponding to the inner ring of measurements taken on the overstory plot, both at 1.7 m and 5–15 cm height. By sampling isolated, low-vigor individuals of these indicator species, we speculated that these measurements would indicate the upper limit of competition, or the location of the shade constraint on

Table 1
Summary information for state forest inventory data and under canopy light measurements.

Dataset	Attribute	N	Mean	St. Dev.	Median	2.5 % Quantile	97.5 % Quantile
State Forest Inventory Data	TPHa	2960	745	515	627	79	2046
	BA (m^2/ha)		21.6	9.6	23.0	2.3	41.3
	QMD (cm)		21.3	5.8	20.8	12.0	34.2
	Relative Density		0.474	0.21	0.474	0.094	0.923
Understory Light Measurements	Property	N	Attribute	Overstory		Understory, additional	
				Mean	St. Dev.	Mean	St. Dev.
	Greenwood WMA	17	LAI	0.906	0.338	NA	NA
	Wharton SF	43	LAI	2.55	0.506	1.89	0.96
	Greenwood WMA	17	DIFN	0.586	0.11	NA	NA
	Wharton SF	43	DIFN	0.228	0.084	0.149	0.073

their realized niches.

2.2. Analysis

2.2.1. Plot summary statistics

For the light measurements and ground-based taxon validation we restricted all analysis to those plots where southern yellow pines (*Pinus rigida, P. echinata* Mill., *P. virginiana* Mill., *P. taeda* L.) together represented at least 90 % of total live BA. To summarize overstory characteristics we calculated forest occupancy metrics following the protocols from the US Forest Service (USFS) Forest Vegetation Simulator (FVS, Dixon, 2002). Stand Density Index (SDI) calculations used in this analysis followed the form of Zeide (Shaw, 2006; Zeide, 1983), and were converted to Relative Density (RD) by using the species-specific maximum SDI for pitch pine (FVS Staff, 2008):

$$\textit{Relative Density}_j = \frac{\sum_0^n \left(TPHa_i * \left(\frac{DBH_i}{25.41} \right)^{1.605} \right)}{SDI_{\max}} \quad \text{(A)}$$

where $RelativeDensity_j$ represents RD for forest stand j, $TPHa_i$ represents the number of trees per hectare represented by observation i, DBH_i represents diameter at 1.37 m of tree i in centimeters, SDI_{max} was set to 983 (converted from English formulation at 398), and n represents all of the overstory tree observations in stand j.

Although stem diameters less than 10.2 cm were not measured in the overstory data, taller advanced regeneration stems were present in many plots. Without diameter information for these stems, their contribution to shade (as measured at 1.7 m height) could not be assessed. However, advanced regeneration near the plot center would affect the light environment experienced by plants in the 1.6 m diameter ground plots. To account for the marginal increase in shade from advanced regeneration stems we assumed a diameter of 1.27 cm and combined the regeneration's cumulative contribution with overstory RD.

2.2.2. Modeling RD against LAI & diffuse non-interceptance

The size of our dataset presented an opportunity to test the robustness of different models by comparing their performance through simulated subsets. To describe the effects of overstory occupancy on attenuation of diffuse sky radiation as it passes through the canopy, we fit five candidate models to LAI (equations B-F) and four candidate models to DIFN (equations G-J). We broke the dataset into random training and testing halves, fit each candidate model to the training half, and recorded model parameters, the standard deviation of the model residuals, the model Bayesian Information Criterion (BIC), and the model Akaike Information Criterion (AIC). Applying the models to the withheld testing half of the data, we recorded the root mean squared error of the model's predictions. We repeated this process 10,000 times and compared model performance using the relative distributions of the model assessment statistics. This allowed us to get a better sense of the appropriateness of each model in predicting the underlying behavior of the data. The candidate models were as follows:

LAI	*Linear*	$LAI = \beta_1 * RD + \beta_2$	*(B)*
	Logarithmic	$LAI = \beta_1 * \log_{10}(RD) + \beta_2$	*(C)*
	Asymptotic	$LAI = \beta_1 - \beta_2 * \left(1 - 10^{(-\beta_3 * RD)}\right)$	*(D)*
	Log-Log	$LAI = 10^{(\beta_1 + \beta_2 * \log_{10}(RD))}$	*(E)*
	Michaelis-Menten	$LAI = (\beta_1 * RD)/(\beta_2 + RD)$	*(F)*
DIFN	*Linear*	$DIFN = \beta_1 * RD + \beta_2$	*(G)*
	Exponential Decay	$DIFN = \beta_1 * (-\beta_2 * RD) + \beta_3$	*(H)*
	Power Law	$DIFN = \beta_1 * RD^{-\beta_2}$	*(I)*
	Inverse	$DIFN = \beta_1/(\beta_2 + RD)$	*(J)*

2.2.3. Maximum RD for taxa of interest

We also used the inventory data to describe the environment of the realized niche for different taxa for the ground plot observations. We chose five taxa that were well-represented in the understory data and that are viewed as evidence of more open-canopy conditions: native warm-season grasses (subfamily *Panicoideae*), sedges (genus *Carex* L.), heather (genus *Hudsonia*), scrub oak (*Quercus ilicifolia* Wangenh.), and blackjack oak (*Q. marilandica* Müenchh.).

At any point in time (as when observed in an inventory) an individual plant may be growing/increasing, surviving/unchanged, or dying/declining. We assumed that plots with greater cover of a taxon were more reflective of suitable growing conditions for that taxon than plots where the indicator taxon were absent or sparse. For each taxon, to get the upper envelope of suitability we plotted two variables against RD: total percent cover of that taxon found in the ground plot (0–100 scale), and the proportion of the total ground cover for a plot occupied by that taxon (0–1 scale).

To get a robust sense of when each taxon would be in decline or disappear from a plot we used logistic regression on the upper envelope of 10,000 random 50 % samples of the ground level plot data. After sorting the data by RD value (x axis), we started at the highest observed RD and worked down to lower RD values, evaluating for each point whether the cover value (y axis) for a taxon was equal to or greater than the second highest cover observation already encountered at higher RD values. If a point met that criterion, we included it in the 'upper envelope'; if not, the point was excluded. We fit a logistic model to the points selected as the upper envelope of suitability for each sample dataset, in the form:

$$p(\textit{Taxon Cover}) = \frac{B_1}{(1 + \exp(B_2 * (RD - B_3)))} \quad \text{(K)}$$

where p*(Taxon Cover)* is the % ground cover or proportion of total plot cover for the selected taxon, *RD* is the relative density, $B_1 = 100$ or $B_1 = 1$ depending on whether we were examining the percent of ground cover for that species or the proportion of total plot cover coming from that species, and B_2 is the slope of the curve at inflection point B_3. We recorded the model parameter values (B_2 and B_3) for each run and used the distributions to describe a likely upper-envelope threshold for overstory suitability.

2.2.4. Estimated gamma distributions

To ensure that the modeled RD upper limits were not just a function of the sampling rate of RD values from the full dataset, we also tested whether the distributions of observed RD values for each species were different than a similarly sized random drawing of the full inventory data. For this analysis we took a random 50 % subsample of the plots where each taxon of interest occurred and estimated a gamma distribution from the corresponding RD values. We then took a similarly sized random sample of RD values from the full dataset and estimated a gamma distribution for this 'null' dataset, repeating the subsampling routine 10,000 times. We used the credible interval approach (middle 95 % between 2.5 % and 97.5 % quantiles) to evaluate whether the null and the taxon shape/scale parameters were comparable.

2.2.5. Ground-based validation for select taxa

We thought that a real-world method for testing the models would be to observe the light environment for individual plants of low vigor and compare it with our predicted limits. If our models for the relationships of LAI~RD, DIFN~RD, and maximum RD suitable for a taxon were

accurate, we could define a threshold light interception level that, if exceeded, would make a site unsuitable for that taxon. We expected that robust models would show all our light measurements of low-vigor individuals occurring within the product of the prediction intervals for the two functions (1: either LAI~RD or DIFN~RD, and 2: maximum RD for survival).

3. Results

3.1. RD vs. LAI & DIFN

We observed non-linear relationships between RD both LAI and DIFN, with increased RD producing increased LAI and decreased DIFN (Fig. 2 and Fig. 3). The dynamic interval was concentrated at lower levels of RD; adding RD when less growing space was occupied made a bigger difference in the light environment than adding the same amount of RD when there was already much more growing space occupied. Of the candidate models used, we found that a Michaelis-Menten equation was the most robust predictor of LAI based on RD alone (Table 2). For LAI, the Michaelis-Menten equation, the asymptotic model, and the logarithmic model had the lowest RMSE on the subsampled data (Fig. 2b). These three models also had the lowest standard deviation of residuals on the training data (Fig. 2d). However, the logarithmic and Michaelis-Menten formulations had the lowest Bayesian Information Criteria across all subsamples, with the asymptotic model paying a penalty for its third parameter (Fig. 2c).

For modeling DIFN as a function of RD, the inverse and exponential decay models had the lowest model RMSE and lowest standard deviation of residuals in the training data (Fig. 3, Table 3). However, the inverse decay model used one fewer parameter, producing consistently better BIC values across subsample runs (Fig. 3c). At an RD of 0 both the Michaelis-Menten model for LAI as a function of RD and the inverse decay model to predict DIFN matched the phenomenon of interest, e.g. that at an RD of 0 there should be no leaf area nor any light interceptance.

The models to predict LAI and DIFN from overstory occupancy displayed a small to moderate amount of heteroskedasticity in their residuals. We observed increased variance in residuals for the LAI models

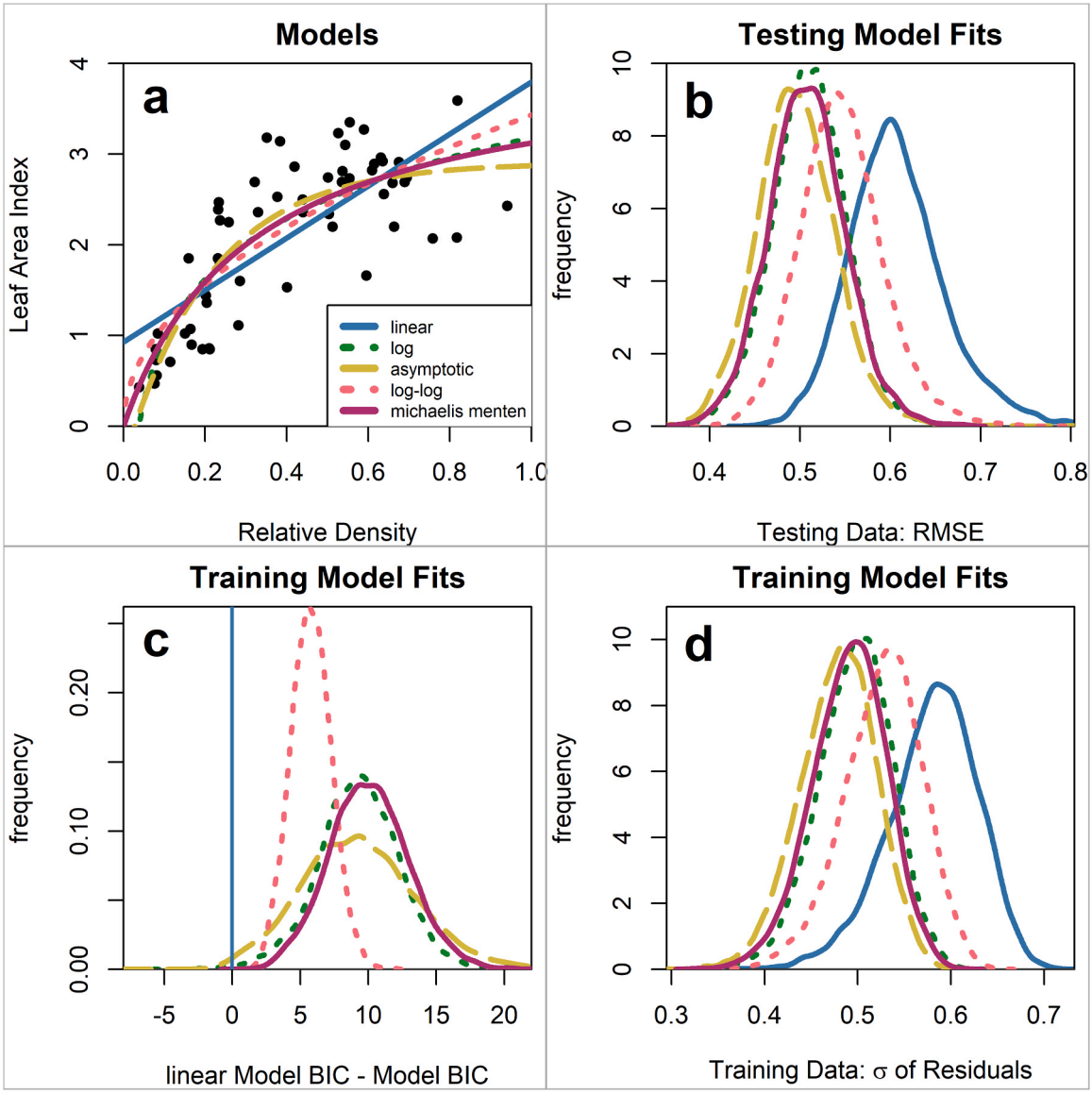

Fig. 2. Model evaluations to describe the effect of Relative Density on Leaf Area Index in pure Pitch Pine. (a) shows the model predicted value on the observed data, while (b-d) show the performance of each candidate model assessed using randomly subsampled replicates. Note that (c) shows the difference between the linear model and the indicated model, so that a higher value represents a lower BIC.

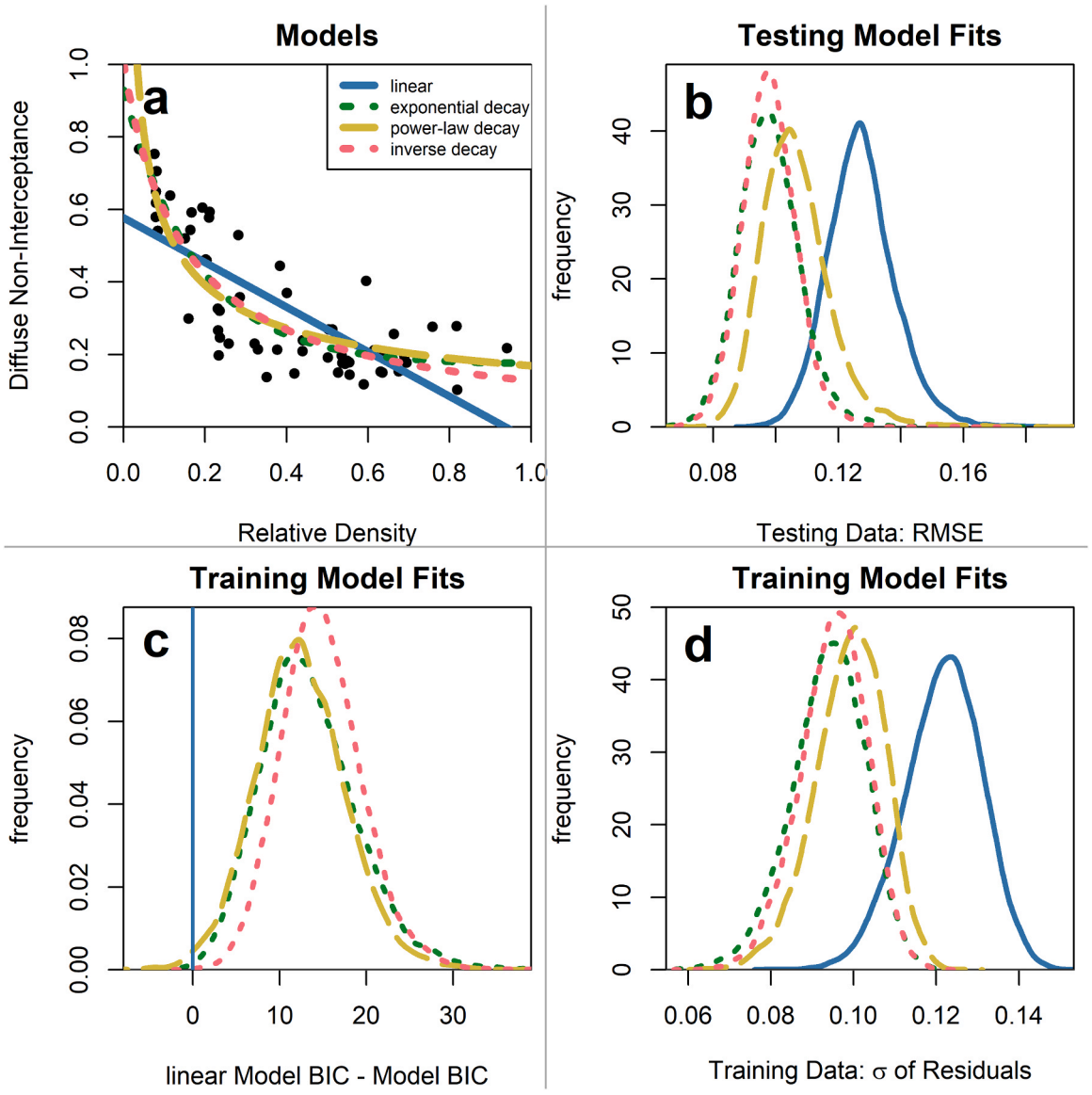

Fig. 3. Model evaluations to describe the effect of Relative Density on Diffuse Non-Interceptance in pure Pitch Pine. (a) shows the model predicted valueon the observed data, while (b-d) show the performance of each candidate model assessed using randomly subsampled replicates. Note that (c) shows the difference between the linear model and the indicated model, so that a higher value represents a lower BIC.

Table 2
Mean model parameters and 95 % quantiles for the 5 candidate models to predict leaf area index from Relative Density. Each model fit on 10,000 subsamples.

Model	Response Variable	Model Term	Mean	2.5 % Quantile	97.5 % Quantile	AIC	BIC	Sigma
B – Linear	LAI	β_1	0.932	0.63	1.28	110	116	0.584
		β_2	2.88	2.14	3.71			
C – Logarithmic		β_1	3.18	2.97	3.42	90.5	96.8	0.498
		β_2	2.24	1.92	2.61			
D – Asymptotic		β_1	−0.459	−1.17	−0.00447	86.6	94.9	0.478
		β_2	−3.39	−4.02	−2.99			
		β_3	2.07	1.24	2.98			
E – Log-Log		β_1	0.537	0.494	0.591	97.8	104	0.529
		β_2	0.491	0.385	0.61			
F – Michaelis-Menten		β_1	4.17	3.51	5.24	89.2	95.5	0.492
		β_2	0.327	0.206	0.518			

at higher levels of RD and an smaller increase in variance in residuals for the DIFN models at lower levels of RD. Observation time of day displayed no relationship with residual size for either dependent variable.

3.2. Maximum RD for taxa of interest

For most of the indicator taxa the proportional cover model (0−1) produced a narrower range of estimates of maximum RD (parameter B_3), but for the *Panicoideae* (grasses), the original % cover observations

Table 3
Mean model parameters and 95 % quantiles for the 4 candidate models to predict diffuse non-interceptance from relative density. Each model fit on 10,000 subsamples.

Model	Response Variable	Model Term	Mean	2.5 % Quantile	97.5 % Quantile	AIC	BIC	Sigma
G- Linear	DIFN	β_1	0.576	0.491	0.647	−77.7	−71.5	0.122
		β_2	−0.617	−0.783	−0.455			
H-Exponential Decay		β_1	3.18	3.18	3.18	−109	−100	0.094
		β_2	2.23	2.23	2.23			
		β_3	0.169	0.112	0.209			
I-Power Law		β_1	0.165	0.136	0.194	−102	−95.6	0.1
		β_2	0.541	0.461	0.652			
J-Inverse		β_1	0.146	0.12	0.175	−108	−102	0.0952
		β_2	0.146	0.0991	0.195			

(0−100) were more consistent (Fig. 4). Distributions of the modeled slope of the lines (B_2) followed the same pattern: values were more tightly grouped using the proportional cover model for all taxa except grasses (Fig. 5, Table 4).

Scaled as a proportion of the total plant coverage on the plot (0−1), the modeled inflection point for maximum RD for grasses occurred at 0.67 (95 % CI 0.57–0.89) (Fig. 4a). From the original % cover observations (0−100), however, the median inflection points for grasses occurred at 0.56 (95 % CI 0.48–0.60) (Fig. 4b). When applied to the relationship of LAI~RD (equation F) the predicted value and 95 % prediction interval for LAI at RD 0.56 were 2.64 and 1.63–3.63, respectively.

For *Carex spp.* (sedges) the proportional model (0–1, Fig. 4c) produced more consistent estimates of the upper RD limit than the total cover model (0–100, Fig. 4d). The scatter for *Carex* showed nearly no observations above RD 0.88, and wide variation within and between the distributions of the modeled inflection points. Scaled to the proportion of total ground cover (0−1), the median was 0.60, with a narrower range for the 95 % confidence interval (0.44–0.65). An upper limit of RD centered at 0.60 can be interpreted as sedge having intermediate shade tolerance – the model value and prediction interval for LAI at this RD level were 2.69 and 1.68–3.68, respectively.

Rarely was *Hudsonia spp.* (heather) a frequent component of the ground data, nor did it cover more than 75 % of any single plot. For this reason, the 95 % confidence interval of the modeled data for % ground cover extended into a negative range of RD, which is nonsensical (Table 4). The median simulated inflection point for the genus occurred at RD 0.05 when looking at the recorded % ground cover (0–100, Fig. 4f, Table 4), and at RD 0.12 when using the proportion of total plot cover (0–1, Fig. 4e). For % ground cover and the proportion of plot cover, the 95 % confidence intervals of the simulated inflection points were between −0.09 and 0.19, and 0.05–0.17, respectively.

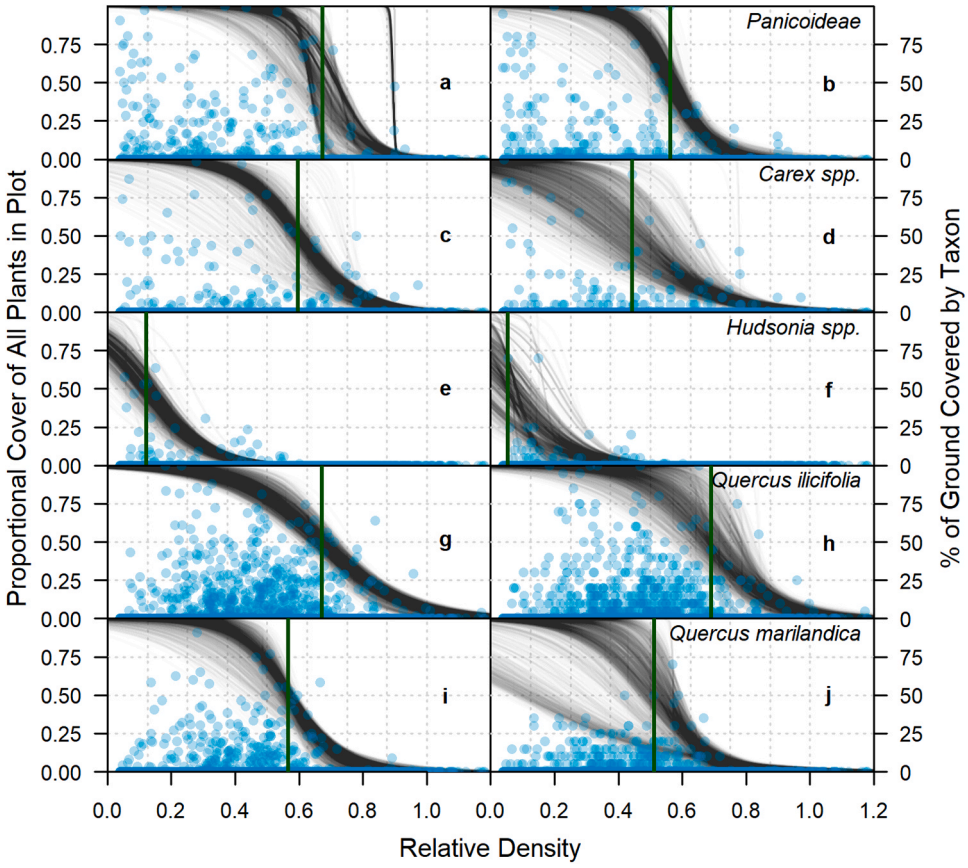

Fig. 4. Modeled upper limit of Relative Density for indicator taxa. Left column (a, c, e, g, i) shows proportion of all plot cover observations comprised of that taxon (0−1); right column (b, d, f, h, j) uses the original collection units (0–100 % coverage of the ground in the 8.1 m^2 subplot). Transparent gray lines each represent a subsampled replicate; vertical line is the median inflection point of the simulations.

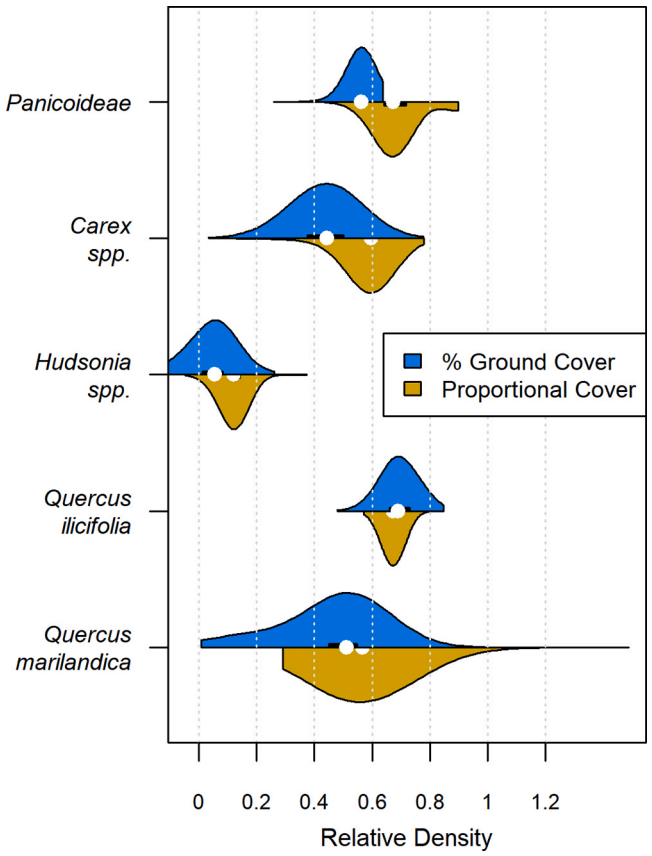

Fig. 5. Distributions of modeled Relative Density-limit inflection points. % Ground cover is in the original collection units (range 0–100 %). Proportional cover is the proportion of all vegetation in the subplot represented by the taxon, range 0–1. Data from 10,000 subsamples of the original dataset.

Quercus ilicifolia (scrub oak) seldom occurred at the lowest RD levels but did reach a threshold of RD where it was no longer present. Using % total ground cover (original units, 0–100 %, Fig. 4h), the median inflection point occurred at RD 0.69, with the middle 95 % of the simulations placing the inflection point between 0.59 and 0.80. Scaled as a proportion of the total plot cover (0–1, Fig. 4g), the median inflection point occurred at 0.67, with a 95 % CI of 0.62–0.72

Q. marilandica (blackjack oak) showed a wide range for the simulations based on total ground cover (0−100), as there was only one plot where its cover exceeded 55 % of the ground plot data (Fig. 4j); since the maximum value was set to 100, this made for inherently unstable fits. These simulations showed a median inflection point of 0.51, with a 95 % CI between 0.09 and 0.59. From the simulations based on the data scaled as a proportion of plot cover (0−1), the median inflection point was 0.57, with a 95 % CI between 0.46 and 0.59.

3.3. Estimated gamma distributions

For four of the taxa, there were differences in the parameters of the species-based estimated gamma and the estimated 'null' gamma distribution based on the rest of the pure pine plot data (Fig. 6, supplemental table). For significance of each gamma distribution parameter we used the 'credible interval' approach, where significance was determined by whether the middle 95 % quantiles of the parameter differences included zero (not significant) or excluded zero (significant). For grasses and sedges, the shape parameter was significantly smaller than the null shape parameter, while scrub oak showed a significantly larger shape parameter. For scrub oak and blackjack oak, the scale parameter was significantly smaller than the null. Only for heather was there no significant difference in the gamma distribution parameters compared to the null, most likely due to the small sample size of plots with heather. For all but *Hudsonia*, random samples from the overall dataset produced more high relative density values than random samples drawn from the points that contain each indicator taxon. This confirmed that for all indicator taxa except *Hudsonia*, the absence of observations of these taxa at high RD values is not an artefact of the overall distribution of RD values.

3.4. Ground-based validation for select taxa

All but one of the low-vigor individuals in the warm-season grasses occurred between the prediction intervals of maximum RD, but for heather the low-vigor plants did not correspond with the predicted regions of suitability (Fig. 7, Fig. 8). These figures show validation instances of low-vigor grasses and heather, superimposed on the best-fit models and prediction intervals for the product of models K*F (LAI as a function of RD, Fig. 7) and K*J (DIFN as a function of RD, Fig. 8). The prediction intervals shown were calculated by first finding the 2.5 % and 97.5 % quantiles for the RD value at the species-wise inflection point (model term β_3) from equation K, then determining the 2.5 % and 97.% prediction interval for models F and J at those values, respectively. The shaded areas correspond to the products of K*F and K*J along the median values for K's best fit parameters and at the deciles of the dependent variable for K; the darkest areas represent the leftmost RD values in Fig. 4 for a taxon, with decreased shading along the declining RD value, and no color beyond the RD limit for either species. If both models are accurate, low-vigor individuals should fall between the prediction interval lines, near the edge of the shaded region. The results for *Panicoideae* show robust formulation of both model F (LAI~RD) and model K (taxon presence~RD).

The validation plot using LAI (Fig. 7) showed more utility than that based on DIFN (Fig. 8). LAI was unconstrained above 0 but DIFN was

Table 4
Modeled parameter values for logistic curves of upper relative density limits for five taxa, % ground cover. Summary quantiles collected from 10,000 simulated subsamples of the data. Evaluations shown are for: −0–100 % of the ground plot area covered by the taxon and −0–1 the proportion of the ground plot observations occupied by the taxon. B_2 is the slope of the curve, B_3 is the inflection point.

Taxon	Evaluation	B_2			B_3		
		Median	Quantile 2.5 %	Quantile 97.5 %	Median	Quantile 2.5 %	Quantile 97.5 %
Panicoideae	0–100 %	0.564	0.482	0.602	16.1	7.94	28.1
	0–1	0.673	0.565	0.894	17.8	9.73	307
Carex	0–100 %	0.444	0.24	0.606	7.56	4.99	14.6
	0–1	0.597	0.439	0.65	11.4	7.6	17.6
Hudsonia	0–100 %	0.0544	−0.0928	0.187	10.6	8.11	75.4
	0–1	0.122	0.0486	0.167	10.8	9.14	16
Quercus ilicifolia	0–100 %	0.69	0.585	0.798	11	6.68	36.8
	0–1	0.672	0.619	0.724	8.12	6.4	13.4
Quercus marilandica	0–100 %	0.512	0.094	0.59	11	4.13	31.9
	0–1	0.567	0.459	0.589	12.9	7.04	24.6

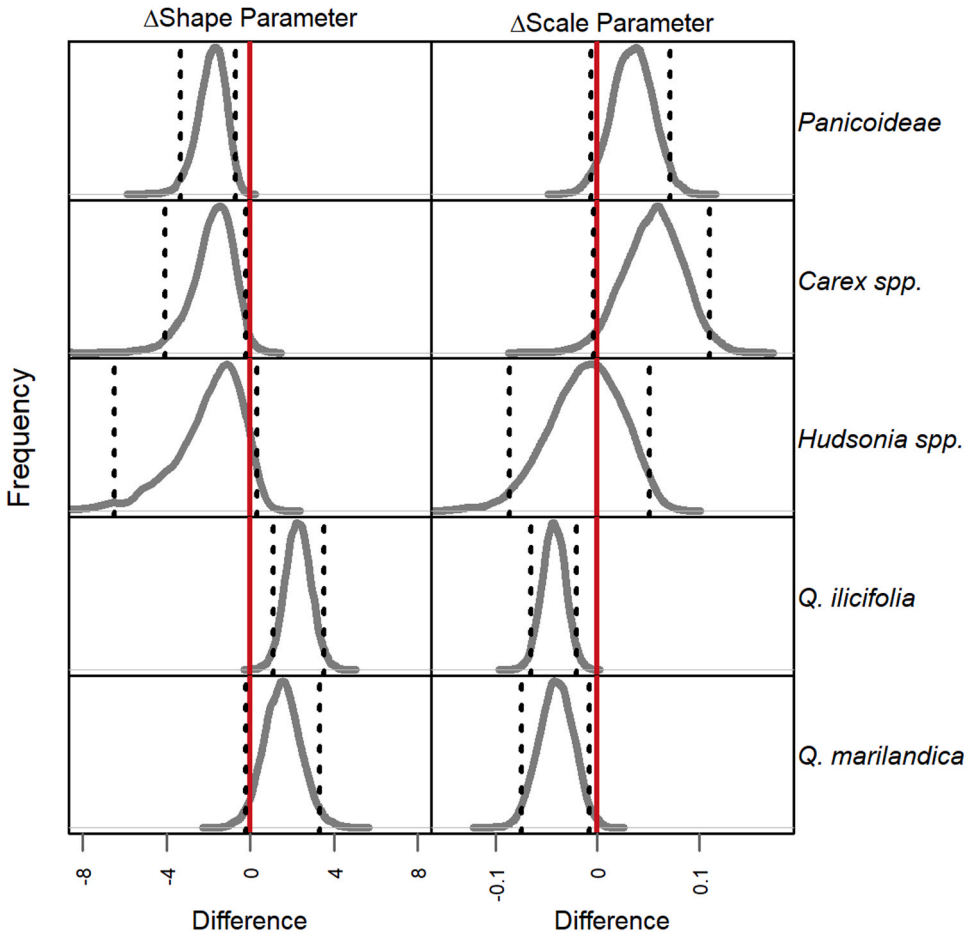

Fig. 6. Comparison of estimated gamma distribution parameters of taxon occurrences by Relative Density (RD). Taxon distributions reflect estimated gamma distribution parameters from 10,000 replicates of 50 % subsamples of RD values on plots where the species occurs. Null distributions are drawn from the RD observations across all plots, of sample size corresponding to the number observations for each taxon. Column 1 shows the difference between the shape parameter for the taxon's estimated gamma and that of the null. Column 2 shows the differences in the scale parameters. Vertical dotted lines show the 2.5 % and 97.5 % quantiles for the difference, with the solid line showing 0.

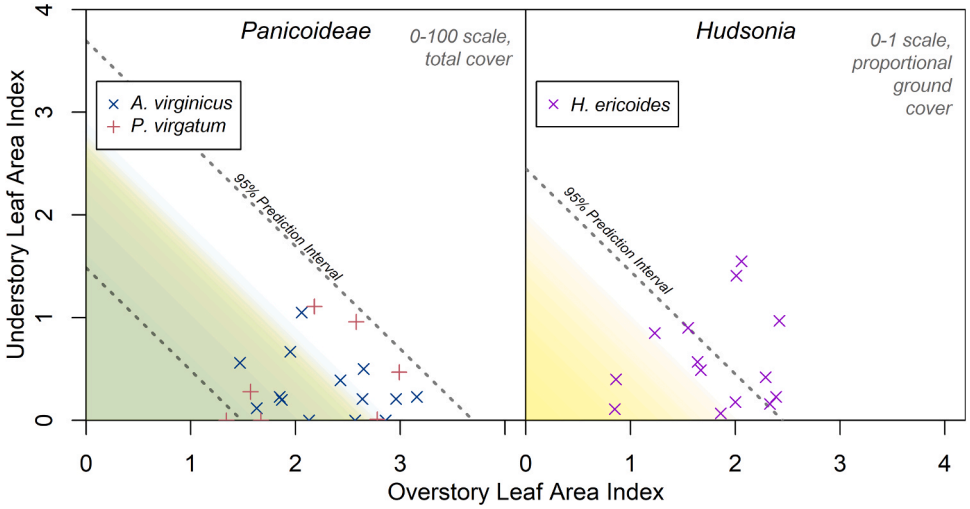

Fig. 7. Overstory LAI, understory LAI, and ground-based validation data for selected taxa. Instances of taxa of interest are low-vigor individuals. Colored region corresponds to Relative Density (RD) levels below the maximum RD threshold for specified taxon using the 2.5 % quantiles of the simulated model parameters, fading color corresponds to the downward slope of the same, with no color indicating RD values above the 97.5 % quantiles of the simulated model parameters. All RD values have been converted to LAI values using the Michaelis-Menten formulation of the LAI~RD function (equation F). The dotted lines correspond to the 2.5 % and 97.5 % prediction intervals for this function, using the same quantiles of the maximum RD function parameters.

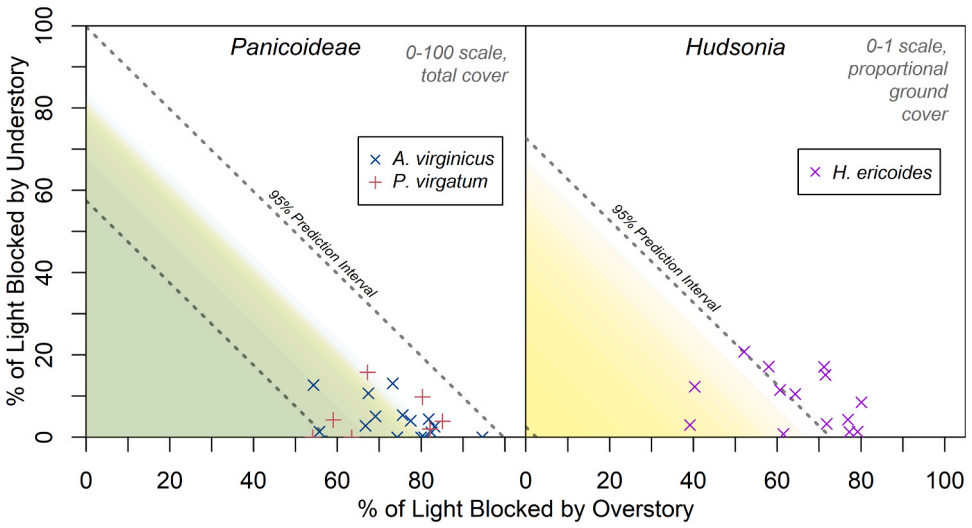

Fig. 8. Overstory Light Interception, understory Light Interception, and ground-based validation data for selected taxa. Instances of taxa of interest are low-vigor individuals. Colored region corresponds to Relative Density (RD) levels below the maximum RD threshold using the 2.5 % quantiles of the simulated model parameters, fading color corresponds to the downward slope of the same, with no color indicating RD values above the 97.5 % quantiles of the simulated model parameters. All RD values have been converted to DIFN values using the inverse decay formulation of the DIFN~RD function (equation J). The dotted lines correspond to the 2.5 % and 97.5 % prediction intervals for this function, using the same quantiles of the maximum RD function parameters.

constrained between 0 and 1. For this reason, the inverse decay model prediction interval for DIFN at and above the RD limits for the different taxa included 0. A modeled DIFN of 0 was the extinction value, meaning no light reached the sensor (or plant on the ground). This meant that there could still be low-vigor individuals present all the way to the point of no ground-level light, which removed any utility as validation for the modeled RD limits. Further, indicator taxa were largely absent above the RD limit, demonstrating that there was some upper limit to overstory density in which the indicator taxa could survive.

4. Discussion

4.1. Attenuation of diffuse sky radiation as a function of overstory occupancy

Our observations showed RD useful for estimating the understory light environment in pitch pine forests, answering our first research question. Methodologies to measure LAI are numerous but require significant instrumentation, expertise, and resources (Xu et al., 2020); there are similarly a diversity of methods for measuring canopy cover, the most reliable of which require significant time expenditure (Korhonen et al., 2006). For these reasons, light interception is not commonly measured in operational forest inventories. In contrast, RD is easily calculated from forest inventory data (Shaw, 2000). Linking RD and light connects a simple metric of tree-tree competition to the biophysical conditions experienced by understory plants.

RD could be used to reasonably predict LAI with the Michaelis-Menten formulation, and to predict DIFN with the inverse decay function. Both of these models made theoretical sense, as they started at 0 and 1, respectively; at an RD of 0, there should be no foliage to contribute leaf area or stems to block sunlight. McLaughlin et al. (2013) used the Michaelis-Menten form to predict LAI using stand BA in slash pine (*P. elliottii* Engelm.) plantations. However, LAI as a function of RD has also been previously formulated as a linear relationship in uneven-aged Ponderosa pine (*P. ponderosa* Lawson & C. Lawson) forests (Ex and Smith, 2013), albeit for a narrower and lower range of RD values. Others have observed non-linear relationships between under-canopy light availability and stand variables like BA (Hale et al., 2009; Palik et al., 1997) and the less-common Overstory Abundance Index (Battaglia et al., 2003).

Maximum LAI (our model term β_1 for the Michaelis-Menten formulation) is dependent on the physiology of the species of interest and is not uniform even amongst the closely related southern yellow pines (Gonzalez-Benecke et al., 2011; Sharma et al., 2012). Further, site-level LAI for pine can be increased through fertilization (Gholz et al., 1991; Gonzalez-Benecke et al., 2012; Jokela et al., 2004), indicating a strong influence of site quality on the parameters of the relationship. There is, however, a strong relationship between stem increment and total leaf area at lower levels of LAI that becomes noisier at higher LAI (Jokela et al., 2004), indicating that stand occupancy is the limiting factor for stand-scale light harvesting at lower LAI.

The reduced responsiveness of LAI to RD at higher levels of the latter indicates that above a threshold, increasing overstory occupancy does less to increase the amount of light attenuated by the overstory. This is consistent with the idea of full site occupancy by trees, which Long (1985) placed at a RD of 0.35, or 35 % of maximum possible SDI for a species ($SDI/SDI_{max} = 0.35$). Our mean value of 0.33 for the Michaelis-Menten constant (model term B_2) from equation F shows agreement with this placement of full-site occupancy. To put this point of site occupancy in the context of BA observations from the plot data, RD values of 0.32–0.34 were observed in our dataset to have a mean BA of 15.3 $m^2\ ha^{-1}$ with a standard deviation of 1.8 (English: 66.8 $ft^2\ ac^{-1}$, σ =7.9, n = 128). The formulation we used for the numerator in RD underpredicts site utilization in older trees and overpredicts for young trees (Woodall et al., 2003), making the physiological basis for using stocking metrics to quantify the use of growing space somewhat tenuous in uneven-aged stands (Long and Daniel, 1990). However, sapwood area is proportional to mean size-density in even-aged systems (Long and Dean, 1986), and slightly more than 92 % of our overstory points could be considered even-aged using the ratio method employed by Shaw and Long (2007). Also, our use of fixed value of 398 for the SDI_{max} (the denominator for Relative Density) for pitch pine did not reflect that maximum possible SDI for a species varies depending on many factors. However, SDI_{max} is mainly influenced by forest type and structure (Woodall and Weiskittel, 2021); all of our sample plots occurred in the same forest type (USFS FIA Forest Type Code 167, Pitch Pine) in the same landscape, with state public land management agency ownership. These shared attributes, along with the vast majority of points being even-aged, suggests that our use of RD accounts for the limitations of the concept.

We noted the presence of slightly-to-moderately heteroskedastic model residuals for both the LAI and DIFN models. Since RD is a stand metric we did not account for the spatial arrangement of trees within plots, but clumping is widely known to impact the Beer-Lambert law assumption of homogeneity in LAI measurements, particularly in open-canopy pine forests (Battaglia et al., 2002; Davi et al., 2008; Gholz et al., 1991; Sharma et al., 2012) like those of our study area. The noise generated by different clumping patterns around the plot center should have increased the variance in LAI and DIFN at low to medium RD values; while this agreed with our observations for DIFN we observed the opposite with LAI, which had greater variance at higher RD values. The pattern in the residuals for the LAI models might be better explained by spatial autocorrelation of sampling locations: the higher RD plots were collected across a wide range of sites spanning roughly 20 km and several soil series (Atsion, Downer, Evesboro, Lakewood, Lakehurst, Woodmansie), while the lower RD plots were collected in a narrow range across 0.5 km in a single soil series (Woodmansie). Leaf Area Index is responsive to soil nutrition and fertilization in other coastal plain pine forests (Fox et al., 2007) so increased variance at higher RD plots is likely a reflection of wider diversity of soil types. This was the unfortunate consequence of difficulty in locating low RD/low LAI plots anywhere on this landscape, which is suggestive of the relative paucity of habitat for shade-intolerant species on the public lands used for sampling.

4.2. Light needs of indicator taxa

Our second question aimed at linking a metric of overstory density (RD) with an ecological condition. Our results confirmed that in pitch pine forests the presence of open-canopy communities requires overstory density well below the maximum possible density for the overstory trees. Using relative density we would expect competition-induced mortality in overstory stems at around 0.60 (Long, 1985). Our modeled inflection points expressed as relative density were 0.56 for Panicoideae, 0.60 for *Carex*, 0.67 for *Q. ilicifolia*, and 0.57 for *Q. marilandica*. Together, these indicate, unsurprisingly, that stands reaching stem exclusion for the overstory are also reaching complete light exclusion for shade-intolerant shorter-stature plants. These relative density results may be slight overestimates however, as the point measurements we used are known to skew the numerator in Eq. A higher than if collected across a whole stand (Shaw and Long, 2010). Further, pitch pine is a relatively shade intolerant species (Niinemets and Fernando, 2006); even a site fully occupied by pitch pine (RD above 0.3 or 0.35) may allow enough light to allow shade-intolerant shrubs to survive.

Our results for grasses agree with previous investigations into grass yield for agroforestry and restoration purposes. Albaugh et al. (2014) used greenhouse studies to experimentally determine biomass yield for switchgrass in the context of intercropping with loblolly pine, noting that there would be significant reductions in biomass starting above LAI values between 1.95 and 2.25. Using our modeled relationship with RD, those values correspond to an RD range of 0.29–0.38, which brackets our finding for the onset of full site occupancy by the overstory (model F, parameter β_2). It is important to note, however, that the number from Albaugh et al. (2014) was for a modeled 50 % reduction in biomass, not the limit for survival used in this study. Mulligan et al. (2002) underplanted wiregrass (*Aristida beyrichiana*) in a longleaf pine plantation across a thinning gradient. In that case, some plants survived at all overstory densities (25, 16, and 8 $m^2\ ha^{-1}$; 109, 70 and 35 $ft^2\ ac^{-1}$), but survivorship increased with any level of thinning, and almost all reproduction occurred in the treatment with the lowest residual density. Wolters (1981) examined herbage production for silvopasture under longleaf pine with grass species seen in this study; that work recommended BA targets of 12–20 $m^2\ ha^{-1}$ (52–87 $ft^2\ ac^{-1}$) for productive balance of timber and grazing, with BA above 28 $m^2\ ha^{-1}$ (122 $ft^2\ ac^{-1}$) eliminating production of grass herbage entirely. Though BA does not map exactly to RD, plots from our study within the BA interval for productive grazing as determined by Wolters (1981) had a mean RD of 0.35 ($\sigma = 0.06$, n = 664), and plots close to Wolters' (1981) threshold BA for survival of grass (27–29 $m^2\ ha^{-1}$) had a mean RD of 0.60 ($\sigma = 0.06$, n = 263). This threshold for survival agrees well with our result for survival of local *Panicoideae* species.

The two grasses we used for validation (broomsedge bluestem, *Andropogon virginicus*; switchgrass, *Panicum virgatum*) are not only different species with potentially different light requirements but are also not an exhaustive representation of the full breadth of species of native warm-season grasses that can be found in this landscape; the most common others include little bluestem (*Schizachyrium scoparium*) and Indiangrass (*Sorghastrum nutans*). Different forage species have unique abilities to adjust to life in the partial shade (Pang et al., 2019), although the species we observed in the New Jersey Pinelands landscape do have some physiology in common, being taxonomically grouped and all using C4 photosynthesis. In tropical savannah-forest transitions, C4 grasses are mainly found in higher light environments, while C3 grasses and bare ground occur at higher LAI values (Charles-Dominique et al., 2018). While it is possible that some of the instances of grass in the state forest inventory data include C3 species outside of these native warm-season grasses, we did not encounter any other grass species than these four when conducting this study.

Our results for sedges are largely in agreement with those for grasses. Previous qualitative assessments for *Carex* show it surviving at middling levels of shade but being a better competitor in somewhat brighter sunlight (Abrams and Dickmann, 1982; Crins and Ball, 1983; Houseman and Anderson, 2002). As with grasses, sedges were dominant in lower RD plots but disappeared at around the same RD level.

For the understory oaks we examined, the estimated gamma distributions for both species indicated that they occurred on points with RD values significantly different from the overall dataset, with fewer instances at the highest and lowest RD values. Scarcity at the lowest RD values was likely the result of disturbances like wildfires, which may require site re-colonization by scrub oak if rootstocks are killed. However, our observations of these species under higher shade are somewhat different from most published descriptions. Smith (1992) described both *Q. ilicifolia* and *Q. marilandica* as 'very intolerant' of shade, Halls (1977) described the former as 'light demanding,' while Niinemets and Fernando (2006) treated the latter as of low to moderate shade tolerance, closer to our findings. However, most descriptions of these species are biased towards characterizing their current distributions, not their physiological abilities.

Several authors have documented disappearance of *Q. marilandica* in forested lands of the inland southeastern US, with complementary explanations of shade exclusion (Clark et al., 2005), lack of appropriate fire (Brewer, 2001), and both acting together (DeSantis et al., 2010; Surrette et al., 2008). Contemporaneous to this disappearance from forestlands has been blackjack oak recruitment into grasslands and savannahs, attributable to climatic effects (Rogers and Russell, 2014). It may be that there are interacting controls on the occurrence of blackjack oak: appropriate climatic and fire effects for recruitment, followed by light availability requirements for persistence. Surrette et al. (2008) noted in reference to an observation from Hilgard (1860) that blackjack oak may be more flexible in response to shade than is typically thought: on fertile loams blackjack oak was seen to produce straight, tall stems, very unlike its typical growth form today. While anecdotal, this account from two centuries ago highlights the difference between today's realized niche and the fundamental niche that a species might be capable of occupying. Changes in land use (e.g. reduced disturbance) on the more fertile sites where blackjack oak once grew may have removed from its range the sites where it was best able to tolerate moderate shade through expression of other growth forms. In the Cross Timbers region of Central Oklahoma and Texas, both *Q. stellata* and *Q. marilandica* co-occur, but *Q. stellata* has seen less decline in importance on sites undergoing mesophication (DeSantis et al., 2010; Hoff et al., 2018). Though there is a

clear relationship between *Q. marilandica* and fire, the different responses to mesophication may at least be partially attributable to differences in shade tolerance – the undisturbed environment experiences both less fire and more shade (Hanberry et al., 2020a).

As silvopasture research has shown with grasses, survival of understory oaks under shade does not necessarily translate to productivity. Little et al. (1958) observed that shaded *Q. ilicifolia* produced fewer acorns than open-grown plants, suggesting that light was important to fecundity and the population dynamics of the species. In contrast, Wolgast (1978) demonstrated that genetic differences are also responsible for the size of an individual's acorn crop. There is likely an interaction between the two, where there is selective pressure for individuals that persist under sub-optimal conditions at the expense of other adaptations, like higher reproductive output. Our observations of slightly more shade tolerance for understory oaks may be best explained by our having described the edge of shade tolerance for the species, rather than the most suitable conditions described by others.

Our results demonstrate the fundamental niche boundary for light, not the specific realized niche boundaries on a given site. At our modeled inflection points of overstory occupancy, the variance in light availability as function of RD leaves enough small openings for at least sparse survival of indicator taxa we considered. For grasses, we observed individuals to be present but of low vigor when occurring in the LAI interval describing the product of uncertainty associated with the relationship of RD to LAI and the RD limit for the taxon. These individuals may survive but are not thriving due to the marginal site conditions.

In contrast to the results for the above indicator taxa, our results for *Hudsonia* spp. (heather) were primarily an artefact of its non-dominance on any plots. As a result of the smaller sample size plots where heather occurred, the estimated gamma distribution of RD values of plots with heather was largely similar to the distribution of RD plots for the full dataset (Fig. 6). This undermines the upper RD limit we determined from the logistic models for this taxon. Validation data (Figs. 7 and 8) showed that heather occurred at higher LAI and lower DIFN than calculated from the prediction intervals for these variables based on the maximum RD inflection point. While strongly light-dependent, the observed distribution of heather in this environment (Fig. 4) probably has more to do with other factors such as soils. Heather is a component of the plant community on the driest sites and sites with abundant bare soil. These observations point to edaphic and disturbance effects as alternative explanations for the distribution of heather. Though we expect there is a limit for the amount of shade that heather can tolerate, this study was unable to determine that limit.

4.3. Disturbance, open-canopy, and goals of public ownership

Keeping a pitch pine forest below RD 0.60 requires at least intermediate disturbance. Though there may be specific disturbance types, methods, intensities, or frequencies that promote the recruitment of our indicator taxa, we did not observe a relationship between proportional cover of any taxa of interest and time since disturbance for any of the disturbance types (Supplementary material). While this may be a shortcoming of our method of using available inventory data, an alternative explanation is that the type of disturbance matters less than intensity to the overstory – for disturbance to make understory light available a stand must get below the RD threshold. Along this vein, we did not seek to answer whether RD is more important than a specific type of or time since disturbance in predicting the presence of a taxon. We instead attempted to determine an overstory stocking-related boundary to the niche space.

Overstory stocking is not the only forest attribute that increased the LAI experienced by open-canopy taxa. The most common understory taxon in the data were members of the *Vaccinieae*, whose distribution was insensitive to overstory stocking owing to their shade tolerance. In the majority of the overstory plots for which we collected light measurements cumulative LAI as measured on the ground was well beyond the limits for our open-canopy dependent taxa, mainly from the contributions of shade-adapted shrubs. The maximum LAI that we observed at ground level (maximum 6.1; upper 97.5 % quantile 5.9) corresponded with the values of 5.5–6.0 reported by Clark et al. (2012), who used destructive sampling in the same ecosystem and forest type. Competition from non-tree species plays a role in determining community composition at the ground layer, and open-canopy taxa were not dominant on all low-RD plots throughout the inventory dataset. In a similar environment with a notable absence of trees, clonal expansion of black huckleberry alone was enough to replace the more diverse sandplain grassland community (Harper, 1995). Thus, management intended to improve the light environment for open-canopy species likely requires actions to diminish shrubs in addition to overstory.

Even so, similar to fire-dependent oak systems (Dey et al., 2017), biodiversity in pitch pine dominated forests is dependent on low overstory density. Many of the endangered plants of this landscape are dependent on open, sunny conditions, such as Pickering's morning glory (*Stylisma pickeringii* var. *pickeringii* Torr.), broom crowberry (*Corema conradii* Torr.), American chaffseed (*Schwalbea americana* L.), and eastern silvery aster (*Symphyotrichum concolor* L.) (CU Maurice River, 2010; NatureServe, 2021; Peters, 1995). Open, sunny ground conditions also provide much-needed habitat for rare wildlife, such as Northern Pine Snake (*Pituophis melanoleucus melanoleucus*) (Golden et al., 2009), northern bobwhite quail (*Colinus virginianus*) (Castelli et al., 2011; Coppola et al., 2021), and frosted elfin (*Callophrys irus*) (Albanese et al., 2007).

High overstory stocking has negative implications for other management goals in this landscape. Climate trends combined with overstocked conditions are creating a high risk of disturbance from southern pine beetle in New Jersey coastal plain pine stands (Lesk et al., 2017), as well as an elevated risk of wildfire (Clark et al., 2022). On the other hand, high stocking is associated with increased forest carbon, which is a major state-level objective for these forests (New Jersey Department of Environmental Protection, New Jersey Department of Agriculture, 2021). A society interested in using forests for emissions mitigation may strike a different balance than one maximizing biodiversity, especially since removing enough trees to increase suitable habitat for open-canopy taxa involves reducing the aboveground live carbon pool.

Further complicating this dynamic is that forest carbon in this landscape is not limited to the stands where such management might occur. Adjacent to the drier-site pine stands considered in this study are abundant wetlands with a seasonally fluctuating water table, and several wetland soil series in this landscape feature a shallow peaty layer (Atsion, Berryland, and Mullica series) or are organic-rich histosols (Manahawkin series) (Soil Survey Staff, 2015). On account of soil carbon, forested peatlands on a per-area basis contain in general (USGCRP, 2018) and can sequester in temperate regions (Bernal and Mitsch, 2012) orders of magnitude more carbon than uplands. Climate change in our study region is expected to exacerbate late summer drought, further drawing down water table levels when they are already at their annual low (Butler-Leopold et al., 2018). Surface peat deposits are particularly vulnerable to combustion from wildfire when water table levels are low (Wilkinson et al., 2020). Looking only at combustion losses of peat (and not aboveground biomass) in a very similar wetland forest type to a major wetland forest type in our study region, Reddy et al. (2015) demonstrated carbon losses of ~44 kg m^{-2} following peat-consuming fire. This is one to two orders of magnitude greater than the carbon emissions from prescribed fire in our landscape: Clark et al. (2015) measured 0.3–0.6 kg m^{-2} carbon emitted from fire, Mueller et al. (2017) measured 1.1–1.4 kg m^{-2} biomass consumed by fire, and Clark et al. (2024) estimated 1.55 kg m^{-2} cumulative carbon lost from 3 fires over 18 years. Carbon losses per area from wildfire in western conifer-dominated uplands are close in magnitude to these prescribed fire emissions (Restaino and Peterson, 2013). For pitch pine stands in this landscape with current levels of tree density (stems per area), higher levels of aboveground live carbon are associated with very high risk of

active crown fire (Isaacson et al., 2024). Combustion losses of carbon have the potential to be greatly magnified when fire crosses into lowlands on this landscape; this nonlinearity in overall carbon risk adds a complicating spatial/scale component to the balance of different objectives.

Even within upland pine stands, the stability of residual carbon impacts management choices. In dry, fire-prone pine forests in the western US, Stenzel et al. (2021) found that stands thinned to a much lower density incur a persistent carbon deficit relative to unmanaged stands, but that including the possibility of losses due to disturbance such as insect outbreak or wildfire negated the difference. Similarly, thinned stands of southern yellow pines give up carbon for a lower risk from southern pine beetle outbreaks (Nowak et al., 2015), and active management to reduce density can improve resilience in growth for red pine stands following drought (D'Amato et al., 2013), all of which increase the stability of the residual forest carbon.

A lower level of overstory occupancy, in line with our findings for inclusion of open-canopy indicator taxa, may be closer to a sustainable condition in these forests (Hanberry et al., 2020b, 2018). Lower density woodland conditions are closer to the historic range of variability on the coastal plain landscape of New Jersey (Day, 1953; Hanberry et al., 2020a; Muntz, 1959). Management to maximize carbon in coastal pine ecosystems is likely to result in worse ecological function (Puhlick et al., 2022), and strategies to mitigate climate change through increased standing biomass come at the expense of adaptability to the coming climate (D'Amato et al., 2011).

When it comes to building trust between stakeholders who may have opposing goals, making the effort to use interpretable language, a common vocabulary, and tools that can translate between disciplines enables the demonstration of shared values between all parties. This expression is key to trust and advancing solutions to natural resource challenges (Smith et al., 2013). With this work one could illustrate the region of suitability for open-canopy habitat on a density management diagram that has isolines for carbon mass, crown fire risk, or southern pine beetle outbreak, similar to previous work visually demonstrating the interplay between these and other meaningful goals here (Isaacson et al., 2024) and in other landscapes (Shaw and Long, 2007; Smith and Long, 1987; Vacchiano et al., 2013, 2008).

5. Conclusions

Forest management must successfully balance competing goals to reflect the desires of the society in which it occurs. In our study landscape, where land management activities are interface with the regulatory environment at the stand scale rather than a broader scale, the goals of increased biodiversity and increased forest carbon are often perceived as being in conflict. Our method confirms a robust connection between common plants in the open-canopy community and a level of overstory occupancy that can be determined by forest inventory. When paired with density management tools from other work in this ecosystem, one can illustrate the limits of survival for open-canopy plant communities in the context of multiple management goals. In this way, a manager could quantitatively describe the aboveground live carbon costs of different actions to support our indicator taxa and the biodiversity with which they are associated, clearly illustrating the tradeoff between maximizing carbon and conserving biodiversity. Management actions that aim to at least maintain the survival of open-canopy taxa in a pitch pine forest need to keep overstory occupancy below taxon-specific RD levels, with open-canopy understory taxa disappearing around RD of 0.57.

CRediT authorship contribution statement

Grabosky Jason C: Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Serbin Shawn P:** Writing – review & editing, Supervision, Software, Methodology, Conceptualization. **Isaacson Bernard N.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Support for this study was provided by the USDA National Institute of Food and Agriculture grant #NJ17318. The authors wish to acknowledge the Rutgers Center for Remote Sensing and Spatial Analysis for their computating support. Many thanks also to William Zipse, Rosa Yoo, and Courtney Willitts for supporting the state data streams. Thanks also to Richard Lathrop and Peter Smouse for reviewing and editing, and to Frank Gallagher for sharing equipment. The authors thank the anonymous reviewers whose suggestions greatly improved the quality and clarity of this article.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122538.

Data availability

The data used for this study are being made available through the New Jersey Forest Service GitHub site at https://github.com/New-Jersey-Forest-Service

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