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Leveraging United States Forest Inventory Analysis data to project mature and old-growth forest conditions, with three wildlife case studies showing utility

Daniel J. Herrera [a,*], Christopher M. Schalk [b], Andrew N. Gray [c], Margaret Woodbridge [d], Deanna H. Olson [c], Michael V. Cove [a]

[a] North Carolina Museum of Natural Sciences, Raleigh, NC, USA
[b] USDA Forest Service, Southern Research Station, Nacogdoches, TX, USA
[c] USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA
[d] USDA Forest Service, Southern Research Station, Asheville, NC, USA

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ABSTRACT

Although many species display relationships – both positive and negative – with various forest successional stages, researchers often rely on datasets that describe forest presence rather than forest age (i.e., National Landcover Database). In 2023, the USDA Forest Service introduced standardized region-specific mature and old-growth (MOG) forest definitions for the United States, but these definitions have not been readily integrated to address questions in ecology and conservation. Here, we introduce 'mapMOG'—an open access R function that applies the recently adopted federal MOG definitions to Forest Inventory and Analysis (FIA) plots across the contiguous United States (US). Additionally, our novel function interpolates MOG status across US forested lands between FIA plots. To demonstrate the utility of these data for forest landscape ecological modeling, we compare the predictive power of the MOG covariate against binary forest/non-forest and percent canopy cover covariates to examine forest habitat associations across three taxa, geographies, and modelling frameworks: avian richness in Mid-Atlantic national parks; Seminole bat (*Lasiurus seminolus*) occupancy in the Southeastern Coastal Plain; and Cascade torrent salamander (*Rhyacotriton cascadae*) distribution associated with US National Forests in the Pacific Northwest. In all three cases, our MOG covariate produced by our function explained variation in the wildlife occurrence data better than the alternative forest metrics. Finally, we compared imputed results across multiple spatial scales and found notable but statistically insignificant differences in interpolated MOG scores.

1. Introduction

Many wildlife species are adapted to habitat conditions within specific successional stages of vegetation, with numerous species depending on the complex habitat structures and microhabitats provided by late-stage successional habitats such as mature and old-growth forests (*hereafter, 'MOG';* Fox, 1990; Nyberg et al., 1987; Pinotti et al., 2012; Thompson and Donnelly, 2018). In the United States (US), iconic old-growth associated species in the Pacific Northwest region — such as the northern spotted owl (*Strix occidentalis*) and Roosevelt elk (*Cervus canadensis roosevelti*) — clearly have demonstrated this dependence on late-successional forests (Bart and Forsman, 1992; Jenkins and Starkey, 1984; Lamphear et al., 2025; Mills et al., 1993; Silvergieter and Lank, 2011). Beyond the Pacific Northwest, many species have similar, albeit lesser-known associations with MOG forests. For example, numerous bird and mammal species nest in tree cavities, which are most prevalent in MOG (Clement and Castleberry, 2013; Czeszczewik et al., 2008; Edworthy et al., 2018; Van Der Hoek et al., 2017). Species of amphibians and reptiles which require woody debris and buttressed trees have been disproportionately found in MOG forests with abundant large trees and logs (Thompson and Donnelly, 2018). Likewise, MOG forests host unique assemblages of salamanders and invertebrates associated with the stable temperatures and humidities within the relatively deep layers of accumulated litter under multi-layered canopies, and through symbiotic relationships between wildlife and old-growth-obligate plant and fungal communities (Komonen, 2001; Schowalter, 2017; Welsh, 1990).

* Corresponding author.
E-mail address: herrerawildlife@gmail.com (D.J. Herrera).

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Conversely, many species have negative relationships with the conditions prevalent in MOG forests. In general, pre-forest and mid-successional forest stages have been shown to be less structurally complex than MOG but can maintain high vegetative diversity (Burton et al., 2013; Franklin et al., 2017; Franklin and Van Pelt, 2004; King and Schlossberg, 2014; Swanson et al., 2011; Zenner, 2004). The habitat conditions of non-MOG (i.e., pre-forest, early, and mid-successional) forests can create a similarly unique array of niches to which many species have ties (Franklin et al., 2017), such as New England cottontails (*Sylvilagus transitionalis*) and chestnut-sided warblers (*Dendroica pensylvanica*; DeGraaf and Yamasaki, 2003). Additionally, abundant flowers and berries from heliophilic plants have been shown to attract nectar-dependent arthropods such as bees and butterflies (Favorito et al., 2023; Hanula et al., 2015; Ulyshen et al., 2024). Likewise, frugivorous and insectivorous bird species can be attracted to early-successional habitats, especially in the post-breeding period (Major and Desrochers, 2012). Thus, while some forest-dwelling species hold strong positive associations with MOG, others are negatively associated with MOG (DeGraaf and Yamasaki, 2003; Olson et al., 2017). Given the nuanced taxa-specific associations between wildlife, complex forest conditions and successional stage, an improved understanding of the distribution of MOG forests may contribute to a deeper understanding of the distribution and conservation of biodiversity across North America.

Although the consideration of MOG may enhance insights in forest ecological modelling, many studies have used simplified forest metrics like forest presence or percent canopy cover instead (Martinuzzi, 2009; Tavernia et al., 2016). One reason for this decision may be because variables such as canopy cover and land use are relatively easy to access, define, and interpret, and can easily bridge the science-management interface for everyday use in forest management or policy decisions. Conversely, defining a forest as mature or old-growth can be difficult. Past studies have often used *in-situ* data collection rather than remotely sensed data, especially as MOG definitions may vary based on the ecological community, and because land managers in different regions have adhered to different MOG definitions (Nyberg et al., 1987; Spies, 2004). In 2023, a set of standardized definitions were introduced by the USDA Forest Service which clarified the MOG criteria across regions, ecosystems, and forest types (USDA Forest Service, 2023a; Pelz et al., 2023; Woodall et al., 2023). However, MOG has remained an elusive forest stage designation and these definitions have not yet been widely adopted by ecologists or systematically mapped across non-federal lands in the US.

To illustrate and increase the applicability of MOG definitions to ecological research, we wrote an analytical function that uses the most recent and publicly-available Forest Inventory Analysis (FIA) data across the contiguous US to identify MOG in the programming language R (Available in Supplemental Material 1; R Core Team, 2025). This MOG function uses a shapefile of the user's study area to accesses data from FIA to determine the regionally-appropriate MOG definitions, and processes the FIA data to determine where each FIA plot sits along the MOG continuum (Spies, 2004). Additionally, the function interpolates the MOG status of forested land between measured FIA plots. The function classifies forests on a continuous gradient between zero (non-MOG) and one (old-growth forest). Within this continuum, values greater 0.5 are considered mature, while values greater than 0.9 are considered old-growth. Using this function, we produced rasters of MOG for each state of the contiguous US at a $1590 \times 1{,}590$-m resolution (Supplemental Material 2). Future use of the function will automatically use the most recent FIA data, however, which may yield more timely insight.

Herein, we demonstrate the utility of FIA data analyzed with our MOG function for wildlife research and management through several case studies. In each case study we compare the explanatory power of MOG vegetation conditions against two frequently used forest metrics in characterizing wildlife habitat: binary forest/non-forest data, and continuous percent canopy cover data. We use a variety of modelling frameworks, taxa, and geographies to explore the utility of this novel metric and approach, including avian species richness in National Park sites across the Mid-Atlantic region, Seminole bat (*Lasiurus seminolus*) occupancy across the Southeast Coastal Plains ecoregion, and occurrences of the Cascade torrent salamander (*Rhyacotriton cascadae*) in the western Cascade Range of the Pacific Northwest region. In all three cases, we predicted that models incorporating MOG data would outperform models containing other more commonly used metrics of forested habitat. Although we use a resolution of $1590 \times 1{,}590$-m in this study, we also explore how changes in the spatial resolution of interpolation influences the results. The function presented herein, along with its derived outputs, was developed to increase the accessibility of MOG data, with the goal that these data might inform management of MOG-associated species and expedite forest management decisions that aim to balance species conservation with forest management.

2. Methods

2.1. MOG assessment

We applied the mature (Woodall et al., 2023) and old-growth (Pelz et al., 2023) definitions put forth by the USDA Forest Service (USDA Forest Service, 2023a) to publicly accessible forest plot data from FIA. FIA is a standardized survey of both public and private forested lands in the US. The survey is administered by the USDA Forest Service, and consists of counting, measuring, and identifying all living and dead trees within an extensive network of fixed-radius plots. Additional data pertaining to saplings, herbaceous vegetation, lichen, and coarse woody debris are also collected in select regions. Forests are re-surveyed every 5–10 years following the same protocol (Gray et al., 2012). Although these data are public, the geographic coordinates of each FIA plot are obscured by ~800-m to protect the privacy of landowners who permit their forests to be sampled (Coulston and Reams, 2004). While FIA data are collected in Alaska, wilderness areas are not currently sampled. MOG definitions were not developed for Hawaii, the District of Columbia or US territories. Thus, we exclude Alaska, Hawaii, the District of Columbia and US territories from our analysis.

To streamline the MOG assessment process, we wrote a function in the programming language R (R Core Team, 2025) called 'mapMOG.' The function is available in Supplemental Material 1 and is published on Dryad (https://doi.org/10.5061/dryad.gmsbcc31s). Tutorials explaining how to use the function are available on both Dryad and Github (https://github.com/Dan-Herrera/Mature-and-Old-Growth-Forest-Assessment). The user begins by specifying a study area as a shapefile. The function determines the state in which the study area resides using the 'sf' package (Pebesma et al., 2024), and calls upon the R package 'rFIA' to download all FIA data for that state (Stanke et al., 2020). Once the data are downloaded, the function determines which USDA Forest Service administrative region the FIA plot resides within, as well as the forest type that the FIA plot represents. Based on these criteria, the function calculates the forest metrics required for the plot's region, such as density of trees surpassing a particular diameter, the basal area of live trees, or the age of the forest stand. Plot-specific forest metrics are then assessed to see if they meet the thresholds for old-growth, which vary by region and forest type. Plots that meet these thresholds are assigned a MOG value of one. Regional old-growth definitions can be found in Pelz et al. (2023).

If an FIA plot is determined to not be old-growth forest, the plot is tested to see if it is mature. Similar to the old-growth forest definitions, mature forest definitions vary by region and forest type. While some regions use unique metrics to assess old-growth, all regions use a combination of the same set of metrics to assess maturity, including: density of dominant trees greater than 2.54 cm (1-inch) diameter at breast height (DBH), total basal area of dominant trees greater than 2.54 cm DBH, quadratic mean diameter of dominant trees, diameter diversity

index, mean height of the tallest 25 % of trees, standard deviation of height of all trees, and total basal area of standing dead trees (Woodall et al., 2023). The function compares each plot's calculated metrics against the maturity thresholds specific to the plot's region and forest type. If a metric meets the threshold for maturity, a threshold-specific score is attributed to the plot. The sum of the threshold scores is then considered the maturity score. If this composite score is great than 0.5, the plot is considered mature (Woodall et al., 2023). Although thresholds are used to indicate if a plot is mature (0.5) or old-growth (1), the function provides MOG scores on a continuous scale between 0 and 1, which are interpreted as a continuum of "old-growthness" (*C. Woodall, personal communication*; Spies, 2004).

2.2. MOG interpolation

The function uses the National Canopy Cover Dataset (USDA Forest Service, 2023b) to identify forested lands that were not sampled in the FIA program, and are thus in need of interpolation. To account for nuances in forest cover across ecosystems, ecoregion-specific canopy cover thresholds are used to determine whether an unsampled area is considered forested. The FIA data specifies if a plot is considered forested or not. Within each ecoregion, all forested FIA plots are joined to the canopy cover dataset to determine the mean canopy cover of sites which the USDA Forest Service recognizes as forest. If a local canopy cover threshold surpasses 50 %, the local threshold is lowered to 50 % to avoid excluding lands that are predominantly forested but do not reach the regional canopy cover threshold. Although the National Canopy Cover Dataset has a resolution of 30 × 30-m, the function aggregates cells to a coarser resolution to account for geographic imprecision of FIA data. The function's default resolution is approximately double the maximum geographic fuzzing distance to create an interpolation grid that accurately captures most FIA plots rather than assigning plots to cells in which they are not actually located. By default, the canopy cover dataset is aggregated to the same resolution and the new cell is assigned the mean canopy cover value of the original cells within it. However, the function allows users to override the default resolution with an alternate resolution. All enlarged cells whose mean canopy cover value meet the local canopy threshold are retained as forest and are available for interpolation.

Our function uses an inverse distance weighting function to interpolate the MOG status of forested areas which are not sampled in the FIA program (Coulston and Reams, 2004). The MOG value of each forested cell is estimated using the MOG value of the three nearest FIA plots, with values from closer plots receiving greater weight than values from further plots. The function uses a default power parameter of two for interpolation, which emphasizes the importance of distance in interpolation and produces clearer delineation amongst interpolated surfaces. However, the function allows users to override the default power parameter. Finally, the function returns the interpolated MOG data for the study area as a SpatRaster (Hijmans et al., 2024). Although the threshold to be considered old-growth forest is one, the interpolation process makes it extremely unlikely for any cell that does not contain an FIA plot to achieve this value. For this reason, we continue to use a threshold of 0.5 for mature forests but lowered our old-growth threshold to 0.90. Thus, we consider any forest with a score between 0.50 and 0.89 to be mature, and any forest with a score between 0.90 and 1.00 to be old-growth. Because MOG includes both mature and old-growth forests, we consider any forest with a score greater than 0.5 to be MOG. For this analysis, we ran this function individually for each state. The resulting data are visualized in Fig. 1 and are available in Supplementary Material 2 and Github (https://github.com/Dan-Herrera/Mature-and-Old-Growth-Forest-Assessment).

Although we conducted interpolation at the 1590 × 1,590-m scale, we subdivided each cell into 2890 30 × 30-m cells and clipped them to a 30 × 30-m national landcover database raster cells identified as deciduous, evergreen, or mixed forest, as well as woody wetlands (Dewitz, 2023). Henceforth, we refer to this clipped dataset as the "fine scale" MOG dataset, and the original MOG dataset as the "coarse scale" MOG dataset. This approach reduces the number of canopy gaps or otherwise non-forested areas that are falsely labeled as MOG during the interpolation process while still accounting for the obscured FIA coordinate data. We conducted all case studies using both the fine (30 ×30-m) and coarse (1590 ×1,590-m) MOG layers to explore if the two processes produced different inferences. Competing alternative forest metrics in these analyses always matched the spatial resolution of the MOG layer for consistency. We opted to use the fine-scale MOG dataset to quantify MOG across the US to avoid counting non-forested land as MOG. For facilitate direct comparison to previous studies estimating MOG across the US, we also summed the area of fine-scale MOG cells within lands owned by the USDA Forest Service or Bureau of Land Management in addition to quantification of MOG across public and private lands.

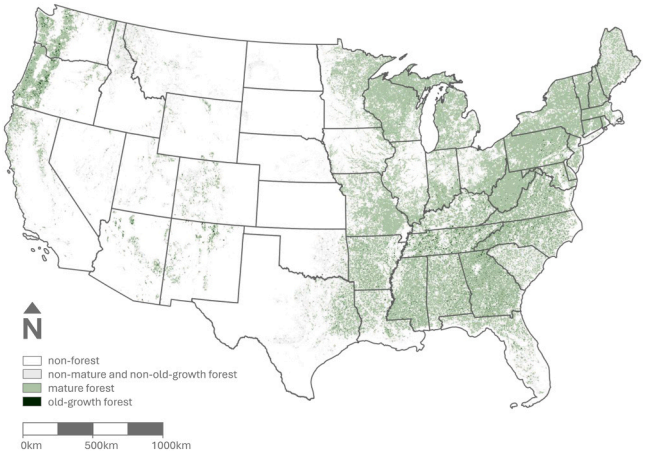

Fig. 1. Estimated mature and old-growth (MOG) forests across the contiguous United States. Colored areas depict forested lands, with light gray indicating non-MOG forests (MOG score < 0.5), light green indicating mature forests (MOG score between 0.5 and 0.89), and dark green indicating old-growth forests (MOG score ≥ 0.9).

2.3. Forest metrics for comparison

To demonstrate the utility of MOG as a covariate in wildlife studies, we compared it against two other commonly used forest metrics: presence of forest (binary) and percent canopy cover (Martinuzzi, 2009; Tavernia et al., 2016). For consistency between metrics, we altered the resolution of the National Landcover Dataset (Dewitz, 2023) to match the resolution of the MOG dataset. The new 1590 × 1590-m raster cells were classified as "forest" if most 30 × 30-m cells within each new 1590 × 1590-m cell were identified as deciduous forest, evergreen forest, mixed forest, or woody wetlands. We similarly altered the resolution of the National Canopy Cover Dataset to match the other forest rasters and assigned each 1590 × 1590-m raster cell the mean value of the 30 × 30-m cells within it. In both cases, the original 30 × 30-m resolution datasets were employed when the fine-scale MOG dataset was used, since that dataset was adjusted to achieve a 30 × 30-m resolution despite being interpolated at a resolution of 1590 × 1590-m.

2.4. Avian species richness

Birds exhibit strong responses to changes in forest structure and age, which can be readily seen in the eastern US where otherwise comparable forests are prevalent (King and Schlossberg, 2014; Major and Desrochers, 2012). We used the 'NPSpecies' database to obtain the number of bird species documented in each property managed by the National Park Service throughout the Mid-Atlantic region as of March 14, 2025. We

defined the Mid-Atlantic region as Virginia, West Virginia, Maryland, Delaware, New Jersey, Pennsylvania, and New York (See Supplementary Material 3 for a list of parks used in this analysis). NPS sites in Washington, DC, were excluded from this analysis because FIA data in the District of Columbia follow different sampling protocols and render MOG estimation impossible. Additionally, we excluded the Appalachian Trail from this analysis since it extends beyond the Mid-Atlantic region and its species list reflects additional birds from the Southeast and Northeast regions. Parks without species lists were also omitted from analyses. We then used the 'sf' (Pebesma et al., 2024) and 'terra' (Hijmans et al., 2024) packages in R to measure the area of each park polygon, and to calculate the proportion of forested land in the park, the mean percent canopy cover in the park, and the mean MOG value in the park.

To assess the relationship between our forest variables and avian species richness, we performed a Poisson regression in which the number of documented bird species was the dependent variable. We constructed three competing models that each contained the area of the park, and one of the three forest metrics as independent variables. Each independent variable was scaled to have a mean of zero and standard deviation of one prior to our analyses. Models were ranked by their Akaike Information Criterion (AIC) scores.

2.5. Seminole bat occupancy

Seminole bats (*Lasiurus seminolus*) roost in southeastern upland pine forests or wetland habitat (Wilkins, 1987). When roosting in deciduous trees, Seminole bats select for trees with ample Spanish moss (*Tillandsia usneoides*), which predominantly grows on large mature trees associated with MOG (Garth, 1964; Wilkins, 1987). We obtained bat presence-absence data from the NABat database (Loeb et al., 2015). For this analysis, we subset the national dataset to only include surveys within the Southeast Coastal Plains ecoregion (Level II ecoregion, category 8.5; United States Environmental Protection Agency, 2024) in the year 2022. NABat surveys provide nightly detection data from passive acoustic recorders. Thus, we were able to construct nightly detection histories for Seminole bats at each survey location (1 = detected, 0 = not detected). The NABat program aggregates surveys using a national grid and presents survey data at the grid cell level. Within each bat survey cell, we calculated the proportion of forested area, the mean percent canopy cover, and the mean MOG value using the same methods described in the previous case study. A variable number of acoustic detectors were deployed within each survey cell, producing inconsistent survey effort. We controlled for this difference by recording the number of acoustic detectors deployed in each sampling cell each night.

We constructed our occupancy models using the 'unmarked' package in R (Fiske and Chandler, 2011). We compared three models that each considered the nightly number of acoustic detectors on detection probability (ρ). Each of the competing models contained one of the three forest metrics as a variable explaining occupancy (ψ). Each forest metric was scaled to have a mean of zero and standard deviation of one prior to analysis. Models were ranked by their AIC score.

2.6. Cascade torrent salamander distribution

Cascade torrent salamanders (*Rhyacotriton cascadae*) live in low-order cool streams in the Pacific Northwest region (Nijhuis and Kaplan, 1998; Thurman et al., 2022). Although such streams exist in younger forests, these salamanders are reported to be found exclusively in streams buffered by MOG (Steele et al., 2003). Historical records and contemporary observations of Cascade torrent salamanders were compiled in 2011 to enable a conservation assessment (Howell and Maggiulli, 2011). Georeferenced observations were recorded between the years of 1932 and 2009 and were originally stored across museum collections and a variety of federal, state, academic, and nonprofit databases. See Howell and Maggiulli (2011) for a detailed list of data sources. Additional surveys occurred in 2019 across Oregon and Washington, and newly documented observations from that project were also included in our dataset (Thurman et al., In Press). Although there is a temporal mismatch between some of our salamander data and our forest cover data, forests in this region must be approximately 200 years old to qualify as old-growth. Because all salamander data were collected within the last 200 years, historical observations are assumed to have been collected in a forest which resembles those that exists today. We used the 'sf' and 'terra' packages in R (Hijmans et al., 2024; Pebesma et al., 2024) to associate these data points with the three forest metrics. Each salamander observation point was assigned a value for forest/non-forest, percent canopy cover, and MOG based on the value of the raster cell that contained the observation point. Due to the computational demands of this model, we limited our analysis to salamander observations and landcover variables within four proximate national forests and scenic areas in Washington and Oregon: Columbia River Gorge National Scenic Area, Gifford Pinchot National Forest, Mt. Hood National Forest, and Willamette National Forest.

We used a MaxLike species distribution model to assess habitat associations for Cascade torrent salamanders. Similar to MaxEnt models, MaxLike models use presence-only data to assess relationships between species and landscape variables (Royle et al., 2012). MaxLike models have been found to be less biased than MaxEnt models, and offer the additional benefit of producing results on the probability scale rather than relative probability (Fitzpatrick et al., 2013). We used the 'maxlike' package in R to fit each competing distribution model (Royle et al., 2012). Similar to the previous analyses, each competing model contained a single forest metric, and models were ranked using AIC scores. Each forest metric was scaled to have a mean of zero and standard deviation of one prior to analysis.

2.7. Comparison of interpolation across spatial scales

Although our function defaults to interpolating MOG status at a resolution of 1590 × 1,590-m, the resolution can be modified by the user. To test the similarity of the interpolated datasets at different spatial scales, we ran the 'mapMOG' function for the state of Maryland at four spatial scales: 1590 × 1590; 1200 × 1200; 780 × 780; and 390 × 390-m. We then removed raster cells that overlapped the Chesapeake Bay, and calculated the mean and standard deviation of MOG values for the remaining cells at each resolution. Although each imputed raster was created at a different resolution, we reprojected each raster to the smallest resolution to facilitate direct comparison. Thus, we reprojected each raster to have a resolution of 390 × 390-m, using the 'terra' package in R, where each new cell retained the maximum MOG value of the overlapping original cell(s). To compare the imputed outcome of each survey, we subtracted each reprojected raster value from the reprojected reference raster value. Finally, we conducted a Bayesian *t*-test by calculating the 95 % highest density interval of differences between rasters (Kruschke, 2013). If the range between those quantiles overlapped zero, we determined that the difference between interpolated values was not significant.

3. Results

3.1. MOG interpolation

Using ecoregion-specific canopy cover thresholds, our MOG function estimated that there are approximately 3892,882 km^2 of forested land within the contiguous US. After reducing the resolution from 1590 × 1,590-m to 30 × 30-m and clipping forested land to lands defined as forest by the National Landcover Database, we estimated that approximately 1952,589 km^2 of forested land exists within the contiguous US. This area comprises roughly 48 % of the contiguous US. Within that forested landscape, approximately 59.18 % (1155,452.06 km^2) of forests were estimated to meet the federal definition of mature forest,

and only 1.53 % (29,955.68 km^2) of forests were estimated to meet the federal definition of old-growth forest (Pelz et al., 2023; Woodall et al., 2023). MOG was disproportionately concentrated in the eastern US, with much of the forested land east of the Great Plains estimated to be mature forest. Eastern old-growth forests were concentrated in the southeastern region but tend to be small and dispersed relative to old-growth forests elsewhere in the country. The central and western US were characterized by a paucity of MOG, with the notable exception of isolated clusters of old-growth forests roughly aligned with the boundaries of the Colorado Plateau in the Southwestern, Rocky Mountain, and Intermountain regions. The Pacific Northwest region contained notably high concentrations of contiguous mature forest as well as the highest concentration of contiguous old-growth forests in the country (Table 1; Fig. 1). Across federal lands (i.e., Bureau of Land Management and USDA Forest Service), we estimated 169,015.50 km^2 of mature and 7549.62 km^2 of old-growth forest.

3.2. Avian species richness

Avian species richness data were available for 46 NPS sites across ten states, with a mean of 156.33 (SD = 69.13) species per site. The MOG model was the top ranked model across both the fine-scale (30 ×30-m resolution) and coarse-scale (1590 ×1,590-m) resolution, indicating that it fit the data better than the forest or canopy cover models (Table 2). This model indicated a significant negative association between species richness and MOG at both the fine scale ($\beta = -0.20$, 95 % CI = −0.23 - −0.18, $p < 0.001$; Fig. 2) and coarse scale ($\beta = -0.19$, 95 % CI = −0.21 - −0.17, $p < 0.001$; Fig. 2). We also observed a significant positive relationship with site area at both the fine ($\beta = 0.13$, 95 % CI = 0.11–0.15, $p < 0.001$) and coarse spatial scales ($\beta = 0.12$, 95 % CI = 0.10–0.14, $p < 0.001$). Estimated parameters for the forest and canopy cover models are in Supplemental Material 3.

3.3. Seminole bat occupancy

Bat surveys from 74 sites within the Mississippi Alluvial and Southeast Coastal Plains ecoregion in 2022 were conducted over a mean survey length of 38.86 (SD = 49.55) nights/site using an average of 1.84 (SD = 1.14) acoustic monitors/site. Seminole bats were detected at 41 (55 %) sites. The MOG model had the lowest AIC score for both spatial resolutions (Table 2) and was the only occupancy model for which the habitat variable had a statistically significant relationship with bat occupancy. The effect size of MOG was larger at the fine spatial scale ($\beta = -1.00$, 95 % CI = −1.58 – −0.41, $p < 0.05$; Fig. 2) than it was at the coarse spatial scale ($\beta = -0.63$, 95 % CI = −1.14 – −0.12, $p < 0.05$). The number of acoustic recorders operating each night also had a significant positive relationship with bat detection probability at both the fine ($\beta = 1.36$, 95 % CI = 1.21 – 1.51, $p < 0.001$) and coarse scales ($\beta = 1.36$, 95 % CI = 1.20 – 1.52, $p < 0.001$). Estimated parameters for the forest and canopy cover models are in Supplemental Material 3.

3.4. Cascade torrent salamander distribution

Cascade torrent salamanders from 291 sites across public and private lands were within US National Forests in the western Cascade Range of Washington and Oregon. The MOG model was the highest-ranking model (Table 2) and reported a significant positive relationship between salamander occurrence and MOG at both the fine ($\beta = 0.32$, 95 % CI = 0.19 – 0.46, $p < 0.001$; Fig. 2) and coarse spatial scales ($\beta = 0.53$, 95 % CI = 0.36 – 0.69, $p < 0.001$). Estimated parameters for the forest and canopy cover models are in Supplemental Material 3.

3.5. Comparison of interpolation across spatial scales

Our analyses found the 95 % highest density interval of differences between MOG values across spatial scales contained zero, suggesting the

Table 1
Estimates of forested land, mature and old-growth forests, and old-growth forests across the continental United States. Estimates were produced using the 'mapMOG' function presented in this paper, and interpolated at a scale of 1590 × 1,590-m with a power parameter of 2. These data represent the results when each 1590 × 1,590-m cell was subdivided into 2890 30 × 30-m cells and clipped to raster cells identified as forested land in the US National Land Cover Database. Land was considered forested if it had a MOG value ≥ 0.10, was considered mature if its value was ≥ 0.50–0.89, and was considered old-growth if its value was ≥ 0.90. An identical table using data from the unmodified 1590 × 1,590-m resolution is available in Supplemental Material 3.

State	Area (km^2) of forested land (percentage of state that is forested)	Area (km^2) of mature and old-growth forest (percentage of forested land that is mature/old-growth [MOG])	Area (km^2) of mature forest (percentage of forested land that is mature)	Area (km^2) of old-growth forest (percentage of forested land that is old-growth)
Alabama	79591.95 (58.62 %)	53777.47 (67.57 %)	51830.77 (65.12 %)	1946.70 (2.45 %)
Arizona	27603.93 (9.35 %)	10907.46 (39.51 %)	10253 (37.14 %)	654.46 (2.37 %)
Arkansas	70597.49 (51.24 %)	47074.49 (66.68 %)	45514.94 (64.47 %)	1559.55 (2.21 %)
California	49798.64 (11.75 %)	17180.94 (34.50 %)	16884.29 (33.91 %)	296.65 (0.60 %)
Colorado	48274.62 (17.91 %)	9370.29 (19.41 %)	9234.44 (19.13 %)	135.85 (0.28 %)
Connecticut	7730.50 (53.84 %)	6959.94 (90.03 %)	6943.82 (89.82 %)	16.12 (0.21 %)
Delaware	1515.68 (23.51 %)	1139.24 (75.16 %)	1124.36 (74.18 %)	14.88 (0.98 %)
Florida	59048.37 (31.93 %)	26201.71 (44.37 %)	25794.93 (43.68 %)	406.78 (0.69 %)
Georgia	84663.62 (55.01 %)	68186.67 (80.54 %)	64254.22 (75.89 %)	3932.45 (4.64 %)
Idaho	35636.69 (16.46 %)	4275.03 (12.00 %)	4264.54 (11.97 %)	10.49 (0.03 %)
Illinois	21495.37 (14.73 %)	16580.59 (77.14 %)	16465.05 (76.6 %)	115.54 (0.54 %)
Indiana	21655.12 (23.11 %)	18306.22 (84.54 %)	18000.6 (83.12 %)	305.62 (1.41 %)
Iowa	11483.54 (7.88 %)	7163.23 (62.38 %)	7119.63 (62 %)	43.60 (0.38 %)
Kansas	82.84 (0.04 %)	7.76 (9.37 %)	7.76 (9.37 %)	0.00 (0.00 %)
Kentucky	53389.57 (51.02 %)	30610.48 (57.33 %)	29605.83 (55.45 %)	1004.65 (1.88 %)
Louisiana	52983.77 (39.06 %)	25152.28 (47.47 %)	24710.91 (46.64 %)	441.37 (0.83 %)
Maine	67783.74 (73.97 %)	35156.66 (51.87 %)	35098.84 (51.78 %)	57.82 (0.09 %)
Maryland	10790.80 (33.58 %)	8669.40 (80.34 %)	8454.75 (78.35 %)	214.65 (1.99 %)
Massachusetts	12320.03 (45.07 %)	10241.68 (83.13 %)	10226.75 (83.01 %)	14.93 (0.12 %)
Michigan	82194.74 (54.62 %)	63943.02 (77.79 %)	63783.19 (77.6 %)	159.83 (0.19 %)
Minnesota	72854.73 (33.30 %)	42983.33 (59.00 %)	42754.5 (58.68 %)	228.83 (0.31 %)
Mississippi	67733.40 (53.99 %)	51981.72 (76.74 %)	49937.61 (73.73 %)	2044.11 (3.02 %)
Missouri	65358.99 (36.20 %)	49513.78 (75.76 %)	49457.53 (75.67 %)	56.25 (0.09 %)
Montana	49783.82 (13.07 %)	4673.22 (9.39 %)	4670.78 (9.38 %)	2.44 (0.00 %)
Nebraska	1961.35 (0.98 %)	113.95 (5.81 %)	113.65 (5.79 %)	0.30 (0.02 %)
Nevada	14820.22 (5.18 %)	1007.19 (6.80 %)	989.49 (6.68 %)	17.70 (0.12 %)
New Hampshire	19257.73 (79.52 %)	14728.11 (76.48 %)	14698.51 (76.33 %)	29.60 (0.15 %)

(continued on next page)

Table 1 (*continued*)

State	Area (km^2) of forested land (percentage of state that is forested)	Area (km^2) of mature and old-growth forest (percentage of forested land that is mature/old-growth [MOG])	Area (km^2) of mature forest (percentage of forested land that is mature)	Area (km^2) of old-growth forest (percentage of forested land that is old-growth)
New Jersey	8540.01 (37.82 %)	6465.61 (75.71 %)	6411.48 (75.08 %)	54.13 (0.63 %)
New Mexico	33399.10 (10.61 %)	10965.61 (32.83 %)	10158.97 (30.42 %)	806.64 (2.42 %)
New York	76193.72 (58.30 %)	61566.51 (80.80 %)	61433.97 (80.63 %)	132.54 (0.17 %)
North Carolina	70664.58 (50.70 %)	48374.69 (68.46 %)	45448.92 (64.32 %)	2925.77 (4.14 %)
North Dakota	1864.99 (1.02 %)	43.78 (2.35 %)	43.78 (2.35 %)	0.00 (0.00 %)
Ohio	33084.71 (30.95 %)	26101.75 (78.89 %)	25963.58 (78.48 %)	138.17 (0.42 %)
Oklahoma	26319.49 (14.54 %)	4229.02 (16.07 %)	4113.95 (15.63 %)	115.07 (0.44 %)
Oregon	64997.00 (25.51 %)	44872.00 (69.04 %)	41958.41 (64.55 %)	2913.59 (4.48 %)
Pennsylvania	70905.57 (60.46 %)	62855.88 (88.65 %)	62182.19 (87.7 %)	673.69 (0.95 %)
Rhode Island	1513.57 (37.83 %)	1300.96 (85.95 %)	1296.92 (85.69 %)	4.04 (0.27 %)
South Carolina	44730.05 (53.93 %)	19033.15 (42.55 %)	18810.86 (42.05 %)	222.29 (0.50 %)
South Dakota	3264.70 (1.63 %)	41.87 (1.28 %)	41.87 (1.28 %)	0.00 (0.00 %)
Tennessee	56491.06 (51.77 %)	37254.04 (65.95 %)	33702.65 (59.66 %)	3551.39 (6.29 %)
Texas	65172.56 (9.37 %)	24636.11 (37.80 %)	24035.18 (36.88 %)	600.93 (0.92 %)
Utah	23620.85 (10.74 %)	3678.12 (15.57 %)	3638.29 (15.4 %)	39.83 (0.17 %)
Vermont	18504.47 (74.31 %)	14952.48 (80.80 %)	14943.05 (80.75 %)	9.43 (0.05 %)
Virginia	62131.18 (56.08 %)	46095.78 (74.19 %)	44653.1 (71.87 %)	1442.68 (2.32 %)
Washington	62763.22 (33.99 %)	37722.49 (60.10 %)	35879.87 (57.17 %)	1842.62 (2.94 %)
West Virginia	50444.34 (80.38 %)	46689.55 (92.56 %)	46274.03 (91.73 %)	415.52 (0.82 %)
Wisconsin	69779.04 (47.95 %)	59147.83 (84.76 %)	58912.07 (84.43 %)	235.76 (0.34 %)
Wyoming	17793.22 (7.02 %)	3474.65 (19.53 %)	3354.23 (18.85 %)	120.42 (0.68 %)
Contiguous USA	1952588.68 (24.59 %)	1185407.74 (60.71 %)	1155452.06 (59.18 %)	29955.68 (1.53 %)

difference between resolutions is statistically non-significant (Kruschke, 2013). However, projected MOG across the state of Maryland varied by 2178.53 km^2, amounting to approximately 8 % of the state's land area. The mean MOG value across the state of Maryland was 0.37 (SD = 0.38) at the 1590 × 1,590-m scale, 0.40 (SD = 0.40) at the 1200 × 1,200-m scale, 0.45 (SD = 0.41) at the 780 × 780-m scale, and 0.39 (SD = 0.40) at the 390 × 390-m scale (Table 3; Fig. 3).

4. Discussion

We introduced a novel function that uses recently adopted federal definitions and publicly available FIA data to map MOG across the continental US. Our analysis estimated that the US contains approximately 1155,452 km^2 of mature forest and 29,956 km^2 of old-growth forest, with MOG disproportionately concentrated in the eastern US and the Pacific Northwest regions (Fig. 1). In addition to mapping and quantifying MOG, we used these data as a covariate in three wildlife habitat-association case studies and found that MOG better explained variation in wildlife detection data than simpler, more widely applied forest variables. Finally, we explored how interpolated values differed under alternative spatial resolutions and found that differences can be notable but not statistically significant. Altogether, the 'mapMOG' function presented herein increases the accessibility of large-scale MOG data and provides a path to assess ecological relationships pertaining to MOG broadly.

In total, our assessment estimated approximately 1185,408 km^2 of MOG across the continental US, indicating that that approximately 59 % of the country's forested land is mature and only 2 % is old-growth (Table 1). These estimates are substantially greater than those previously reported, as DellaSala et al. estimated that the contiguous US contains roughly 672,000 km^2 of MOG, whereas Barnett et al. (2023) proposed a value of 1021,286 km^2. However, these estimates used MOG definitions that were not aligned with the now-adopted definitions put forth by the USDA Forest Service (USDA Forest Service, 2023a). Pelz et al. (2023) and Woodall et al. (2023) jointly estimated 403,578 km^2 of MOG using the federal MOG definition but only assessed forests on lands managed by the National Forest Service and Bureau of Land Management. Our methods reach beyond those federal lands, and it is therefore not surprising that our estimate was substantially greater than those provided in Pelz et al. (2023) and Woodall et al. (2023). Interestingly, when we limit our estimates to federal lands only, our estimate (176, 565.10 km^2) was less than half of what Pelz et al. (2023) and Woodall et al. (2023) reported. Our estimates of forested land irrespective of MOG were also less than those previously reported from FIA data (Oswalt et al., 2019). One reason for this discrepancy might be because our interpolation process is conservative compared to the standard method of extrapolating FIA data (i.e., expansion factors; Van Deusen,

Table 2
Model comparisons for each wildlife case study from three US regions. Models were ranked by AIC score, with the lowest AIC score indicating the best model fit. Parameter estimates for each model are available in Supplemental Material 3.

Taxa	Locale	Model framework	Model (by rank)	Coarse scale (1590 ×1,590-m)				Fine scale (clipped to 30 ×30-m)			
				AIC	Model rank (ΔAIC)	K	Negative log likelihood	AIC	Model rank (ΔAIC)	K	Negative log likelihood
Avian species richness	US National Parks in the Mid-Atlantic region	Poisson regression	MOG	1180.21	1(0.00)	3	586.82	1142.54	1 (0.00)	3	567.98
			Canopy	1229.80	2 (49.59)	3	611.62	1259.91	2 (117.38)	3	626.67
			Forest	1348.20	3 (167.99)	3	670.82	1279.17	3(136.63)	3	636.30
Seminole bat (*Lasiurus seminolus*)	Southeastern coastal plains	Occupancy analysis	MOG	3112.49	1 (0.00)	4	1552.25	3108.01	1 (0.00)	4	1550.00
			Canopy	3116.56	3 (4.07)	4	1554.28	3119.38	2 (11.37)	4	1555.67
			Forest	3116.37	2 (3.88)	4	1554.19	3121.33	3 (13.32)	4	1556.16
Cascade torrent salamander (*Rhyacotriton cascadae*)	Pacific Northwest region	MaxLike	MOG	5204.45	1 (0.00)	2	2600.20	9791.21	1 (0.00)	2	4893.58
			Canopy	5216.91	2 (12.46)	2	2606.43	9797.00	2 (5.79)	2	4896.48
			Forest	5247.57	3 (43.12)	2	2621.76	9805.77	3 (14.57)	2	4900.87

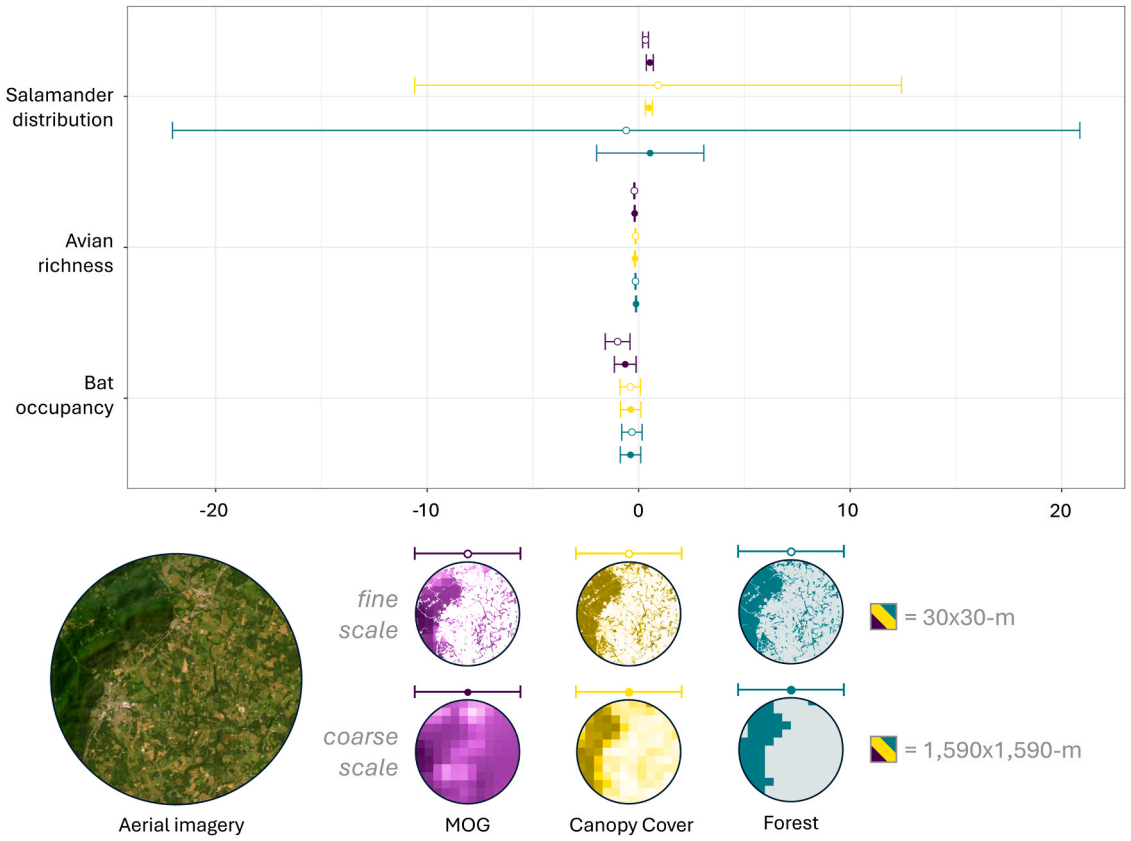

Fig. 2. Estimated effect of each forest metric (points) and associated 95% confidence intervals (horizontal bars). Closed, solid-filled points indicate the effect of forest metrics at the coarse (1,590 × 1,590-m) spatial scale, whereas open points indicate the effect of forest metrics at the fine (30 × 30-m) spatial scale. Maps beneath the effect plot illustrate how each forest metric describes the same landscape (large map insert on left) differently. In each forest metric map, darker colors indicate higher values (e.g., greater canopy cover). Aerial imagery is shown for reference.

Table 3
Comparison of interpolated MOG values across the state of Maryland at four spatial scales. The 1590 × 1,590-m scale is regarded as the reference scale here and in Fig. 3. All interpolation used a power parameter of 2.

Resolution	Area (km^2) of MOG [MOG ≥ 0.50] (% of terrestrial area in state)	Area (km^2) of old-growth forest [MOG ≥ 0.90] (% of terrestrial area in state)	Mean MOG score (SD)	Mean difference in MOG score from largest resolution (SD)	95 % Highest density interval of differences in MOG scores
1590 × 1,590-m	9964.98 (37.00 %)	4500.49 (16.61 %)	0.37 (0.38)	NA	NA
1200 × 1,200-m	10,670.88 (39.62 %)	5521.53 (20.50 %)	0.40 (0.40)	−0.03 (0.23)	−0.59 – 0.47
780 × 780-m	12,190.82 (45.27 %)	6679.02 (24.80 %)	0.45 (0.41)	−0.08 (0.27)	−0.73 – 0.46
390 × 390-m	10,558.78 (39.21 %)	5702.08 (21.17 %)	0.39 (0.40)	−0.02 (0.31)	−0.75 – 0.68

2007). We used an ecoregion-specific approach to identify non-sampled forested land available for interpolation. However, alternative definitions of forested land will identify variable amounts of forest (Oswalt et al., 2019), which will impact the final estimate of MOG. Although our estimates differed from previous attempts to estimate MOG across the continental US, our analyses offer valuable insights into the distribution of MOG nationally and produce the first national map of MOG across the continental US using the federal definitions.

Our national map produced by the 'mapMOG' function suggests that most MOG is concentrated in the eastern US, with additional concentrations of old-growth forest in the Pacific Northwest (Fig. 1). Indeed, our analyses indicate that 70 % of MOG is located east of the Mississippi River despite these states only comprising 23 % of the contiguous US land area (Table 1). This disparity is likely attributed to multiple factors. First, 59 % of forested land occurs in the eastern US (Table 1), so the region is predisposed to contain disproportionately more MOG than the less-forested US West. Furthermore, western forests have been subject to different frequencies and intensities of disturbance. For instance, western forests are increasingly exposed to intense stand-replacing fires that shift mature forests back to an early-successional state, while fires in the east tend to be lower in intensity (Abella et al., 2007; Mitchell et al., 2014; Singleton et al., 2019). Likewise, anthropogenic actions such as logging and fire suppression vary spatially, and may further explain the disparities between western and eastern forests (Davis et al., 2017; Naficy et al., 2010). Additionally, our workflow only considers an area to be forested if it meets a canopy cover threshold based on local data. Many forests in the central and western US tend to have lower canopy cover compared to eastern forests, which may result in forest stands failing to meet the minimum canopy cover threshold to be included in interpolation. We attempted to overcome this shortcoming by using ecoregion-specific canopy cover thresholds within each state, but this method likely still omitted some forested lands from our analyses and

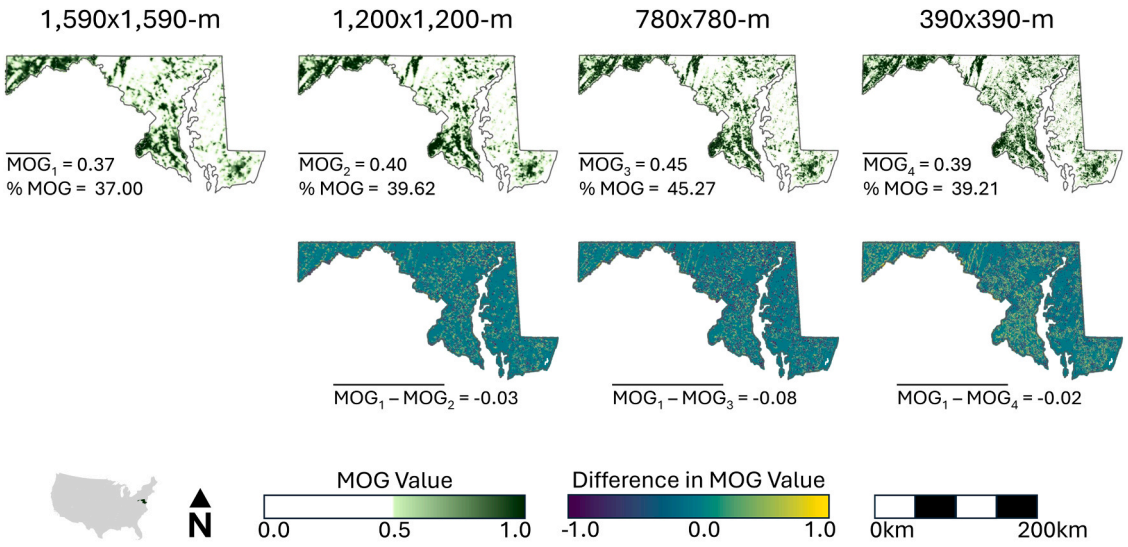

Fig. 3. Comparison of interpolated Maryland MOG results across four spatial scales. The top row of maps depicts the interpolated MOG at each spatial scales, while the bottom row of maps shows the difference in interpolated MOG values between the 1,590 × 1,590-m reference resolution and the alternative resolution.

warrants further investigation. Finally, it is possible that the sensitivity of the current MOG definitions varies across regions, leading to artificial concentrations and disparities of MOG between regions.

Although our interpolation method produces a dataset that differs from existing landcover datasets, our MOG dataset proved to be a better predictor of wildlife occurrences across our three case studies. In each case study, the effect size of forest presence, canopy cover, and MOG were estimated to be similar values, yet the model ranking consistently revealed that MOG best explained variation in the wildlife data. As predicted, Cascade torrent salamander distribution was positively correlated with MOG. Prior research has found this species to be associated with MOG, but the structural aspects of MOG that drive this relationship remain unclear (Steele et al., 2003; Thurman et al., In Press). Thus, this case study eloquently demonstrates the utility of our FIA-derived MOG dataset, since individual components of MOG forests failed to predict species distributions while the composite MOG index readily identified this relationship. Contrary to our prediction, avian species richness displayed a negative association with MOG, possibly because many bird species are adapted to regular disturbances and living in forest edges (Brawn et al., 2001; Valente and Betts, 2019). In the Mid-Atlantic region, MOG may provide conditions which are too uniform for many species and thus supports less speciose communities than non-MOG areas featuring regular fragmentation (Batáry et al., 2014; Brawn et al., 2001; Fahrig, 2017; Fahrig et al., 2019). Indeed, the heterogenous landscapes associated with forest edges, canopy gaps, early successional habitats, and forest-matrix edges support higher diversity of birds and other taxa at this scale (Fahrig et al., 2019; Greenberg et al., 2016). Seminole bats also displayed a negative relationship with MOG, perhaps because their ideal roost sites – mature deciduous trees with Spanish moss – are not widespread (Garth, 1964). Seminole bats also roost in conifers, but few coniferous forests in the southeastern US meet the federal MOG definition (Woodall et al., 2023). Thus, disproportionate sampling of bats roosting in non-MOG coniferous forests in lieu of suboptimal deciduous MOG may have driven the negative relationship identified by our analysis. Although our MOG dataset facilitates the mapping of large-scale patterns, consideration of additional data, such as specific forest types or characterizing forest structure at smaller spatial scales, may better explain such phenomena and should be integrated into future analyses.

We produced our MOG dataset at a 1590 × 1,590-m scale to account for the spatial uncertainty of listed FIA plot coordinates and clipped this resolution to a 30 × 30-m forest layer to achieve more fine-scale estimations. The true coordinates of an FIA plot can be obscured as far as 800-m from the location shown in the dataset to protect landowner privacy (Coulston and Reams, 2004). By selecting a resolution roughly double the positional error of the FIA data, we aimed to capture most FIA plots within the raster cell that they reside. This approach allowed us to account for many of the inaccurate plot locations while still maintaining a relatively fine spatial resolution. MOG can also be interpolated using alternative resolutions to avoid post-hoc processing (i.e., clipping data to forest layers), but interpolating at finer resolutions may not account for uncertainty in spatial coordinates. We compared several MOG maps for the state of Maryland at different resolutions and found the differences between interpolated datasets to be statistically insignificant. Despite this finding, the differences between datasets were substantial. Estimates of MOG area differed by as much as 2225.8 km^2 (8.3 % of Maryland's land area), which is larger than the state's ten largest cities combined (Table 3). In general, finer resolutions tended to report higher MOG values than the 1590 × 1,590-m resolution, especially at forest edges (Fig. 3). We acknowledge that no single resolution is inherently optimal (Dark and Bram, 2007; Gallo et al., 2018). Instead, we encourage users to critically consider their data needs when selecting a resolution and workflow, and to compare interpolated MOG data against ground-truthed data when possible.

5. Conclusions

We introduced publicly-available R code that maps MOG across the continental US using FIA data and the federal MOG definitions (Gray et al., 2012; Pelz et al., 2023; Woodall et al., 2023). While state-specific MOG rasters (1590 ×1,590-m resolution) from our analyses in 2025 can be found in Supplemental Material 2, the 'mapMOG' function automatically uses the most recent FIA data available. Thus, using the function to map MOG across individual study areas may produce more timely insights. In addition to introducing this function and dataset, we demonstrated its utility using three wildlife habitat-association case studies. In each case study, models using MOG data outperformed models with alternative forest data. We thus contend that MOG is an important consideration for many taxa, and that the inclusion of MOG in ecological models can introduce greater nuance and advance conservation and management efforts. In creating and sharing the mapMOG function, we hope to better position practitioners and researchers to

apply the federal definitions of mature and old-growth forests to their own systems and thereby systematically consider forest successional stage in a wide variety of management applications.

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CRediT authorship contribution statement

Andrew N. Gray: Writing – review & editing, Methodology. **Margaret Woodbridge:** Writing – review & editing, Validation, Methodology. **Deanna H. Olson:** Writing – review & editing, Data curation. **Michael V. Cove:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Daniel J. Herrera:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Christopher M. Schalk:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Daniel Herrera reports financial support was provided by USDA Forest Service Southern Research Station. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123085.

Data availability

The authors do not have permission to share data.

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