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Forest management affects the functional traits of birds and mammals differently

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Abstract

Forest management is an important component of global change as more than half of the world's forests are managed for human use. Although the effect of forest management on taxonomic diversity is well-studied, we do not fully understand its impact on functional diversity. Understanding this is important to better predict how ecosystem processes will respond to global change scenarios and to implement efficient conservation actions. We conducted two large-scale (~81 800 km^2) research projects over 4 years in temperate forests of the northeastern USA to investigate how the functional structure of bird and mammal communities are affected by forest disturbance. We surveyed 85 bird species distributed in 115 sites using point counts, and 14 mammal species across 197 sites using camera traps. For each species, we selected functional traits that summarize key features of their biology, and for each site, we collected data on the level of forest disturbance based on forest loss events. We found that functional richness increased with forest disturbance for mammals but not for birds. Our results also showed that niche breadth (diet), morphological (body mass and wing length), and physiological (litter size) factors were the main determinants of the functional structure of both groups. These findings emphasize the complexity of making predictions about responses to forest management given the heavy dependence on the context and taxa studied. Overall we observed a limited response of functional diversity to forest management, which might indicate that the environmental changes generated by forest management in this region are less extreme than deforestation or conversion of natural forest to plantations of exotic species. Nonetheless, our results underscore the importance of investigating the effects of forestry on individual traits to develop strategies for managing for ecosystem functions.

Introduction

54% (2.05 billion ha) of the world's forests are managed, primarily for timber production (Food and Agriculture Organization of the United Nations, 2020) and this has been a common practice, especially in temperate regions, for thousands of years (Canham, Rogers, & Buchholz, 2013). In many cases, timber harvesting only removes tree cover temporarily without leading to land use change *per se*, as forest regeneration commonly follows harvesting (Keenan *et al*., 2015). Even in tropical regions where timber demand is often met by commercial tree plantation of exotic species managed forests can still retain high numbers of species (Barlow *et al*., 2007). Nevertheless, the global scale of forests and forestry makes them important drivers of change, and thus we must improve our understanding of how forestry practices affect ecosystem functioning and services.

Timber harvest can have short- and long-term consequences on forest structure, composition, function, and microclimate (Hunter, 1999; Lindenmayer *et al*., 2009), ultimately affecting individuals and populations of animals. At the individual level, management practices can mediate survival rates and the distribution of behavioral types (Srinivasan, Hines, & Quader, 2015; Gasperini *et al*., 2016; Mortelliti & Brehm, 2021). At the population level, it can affect population size and occupancy probability (Kalies *et al*., 2012; c2016; Schulze, Malek, & Verburg, 2019). Species richness of communities can increase or decrease in response to forest management (Paillet *et al*., 2010; Chaudhary *et al*., 2016), and even if richness is unaffected, species composition can change, creating a new community with different species and dynamics (Werner & Raffa, 2000; Politi, Hunter, & Rivera, 2012; Solar *et al*., 2016). However, population and taxonomic community metrics may not fully demonstrate whether ecological dynamics and ecosystem services are resilient to forest management (Yguel *et al.*, 2019).

Functional diversity (the ability of species and their traits to influence ecosystem functioning; Tilman (2001)) is a strong indicator of ecosystem resilience to both natural and anthropogenic forest disturbance as it measures the functional role of species (Tilman, 2001; Aquilué *et al.*, 2020). Functional diversity in forests is driven mostly by vegetation structure rather than climate or topography (Thom *et al.*, 2021), but recent studies have found that it is not consistently affected by forest management practices. For example, some studies have shown that forest disturbance leads to an increase in functional diversity due to vegetation heterogeneity (Sitters *et al.*, 2016; Murray *et al.*, 2017; Szymañski *et al.*, 2021), but other studies have found the opposite pattern: a decrease in functional diversity as a response to forest disturbance (Cosset & Edwards, 2017; Murray *et al.*, 2017; Rodriguez, Pohjoismäki, & Kouki, 2019). In addition to overall functional diversity, forest disturbance can also modify the *average* distribution of individual traits (e.g. body mass, habitat breadth), for example, by shifting from large, specialized species to small generalists (Carreño-Rocabado *et al.*, 2012).

These contrasting patterns highlight the complexity of the relationship between functional diversity and forest management and call for more research. We still do not fully understand: (1) how species with different functional traits respond to management practices; and (2) what functional traits are the main drivers of responses. This is not surprising because forest management can be very complex, and its influence varies among taxa (Barlow *et al.*, 2007; Paillet *et al.*, 2010; Chaudhary *et al.*, 2016). In addition, terms like “forest management” and “forest disturbance” cover a wide array of impactful events, although they can be simplified to a disturbance index tied to the extent of tree mortality (Franklin, Johnson, & Johnson, 2018).

To help fill this critical knowledge gap on animal responses to commercial forestry, we conducted two large-scale (~81 800 km^2) field studies over 4 years in temperate forests of the northeastern USA (Rolek *et al.*, 2018a, 2018b, 2021; Evans, Mosby, & Mortelliti, 2019; Evans & Mortelliti, 2022; Evans *et al.*, 2024) to investigate how forest management practices and other forest covariates influence the functional structure of bird and mammal communities. More specifically, we asked: (1) how does forest disturbance caused by timber harvest and the resulting vegetation structure (e.g. tree species composition and size) affect the functional diversity of bird and mammal communities? (2) what are the functional traits driving these associations? We expect forest disturbance to affect the functional diversity of birds and mammals, but the direction of this effect should depend on whether forestry practices increase or decrease communities’ trait variation (Fig. 1). Because forest disturbance can lead to functionally simplified communities (Carreño-Rocabado *et al.*, 2012; Costantini, Edwards, & Simons, 2016), we expect functional traits associated with niche breadth and specialization to be especially influential in determining functional diversity patterns.

Materials and methods

Study area

Our study was carried out primarily in Maine with a few sites in New Hampshire, and Vermont, in the northeastern USA. Forests cover over 85% of this region and are mostly (>70%) intensively managed for commercial forestry (Morin *et al.*, 2012). Commercial forestry in this area has resulted in a mosaic of mixed-age stands. These are hemi-boreal forests described as a transition from temperate deciduous to boreal forest (Brandt, 2009) with dominant trees such as balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), and paper birch (*Betula papyrifera*). The climate is humid continental, with summer (July) temperatures ranging from 12 to 25°C with 55 cm of rainfall, and winters (January) ranging from −16 to −5°C with 51 cm of snowfall (National Oceanic and Atmospheric Agency [NOAA], 2020).

We established two large-scale field studies to collect data on the composition of bird (Rolek *et al.*, 2018a, 2018b, 2021) and mammal (Evans, Mosby, & Mortelliti, 2019; Evans & Mortelliti, 2022; Evans *et al.*, 2024) communities across a range of forest disturbance regimes characteristic of northeastern USA forests (Fig. 2).

Bird survey

Birds were surveyed in 115 sites (i.e. forest stands with relatively uniform years since harvest and forest management; sampling unit) between 2013 and 2015 using point counts across six areas in Maine, New Hampshire, and Vermont, USA (Fig. 2) (Rolek *et al.*, 2018a, 2018b, 2021). Sites were selected based on (1) years since harvest (including five to >113 years since harvest disturbance), (2) intensity of forest management (from most intense to least intense), (3) composition of coniferous trees (>50%), and (4) site size (>12 ha) to minimize edge effects (King, Griffin, & DeGraaf, 1997; Ortega & Capen, 2002). The surveys focused on conifer-associated birds because practices of partial and selection harvests coincide with a decrease in coniferous forests in our study area (Legaard, Sader, & Simons-Legaard, 2015) and birds dependent on such forests are showing declines in their populations and thus are of conservation interest (Ralston *et al.*, 2015).

Sites were sampled during the breeding and post-breeding season (June–August), with the number of points per site varying from two to 18 (mean = 5; SD = 2.6). At each point, a 10 min multi-species point count survey was conducted with a radius of 50 m from the observer (Bibby *et al.*, 2000). Most points (71%) were visited once a month during the 3 years of our fieldwork totaling nine visits per point (remaining points were visited from four to eight times) (Rolek *et al.*, 2018a, 2018b, 2021). Therefore, sites had both spatial (points) and temporal (visits per point) replicates to increase the detection of rare species. Twenty-eight trained observers conducted the surveys, and they were rotated among repeated visits to minimize observer bias.

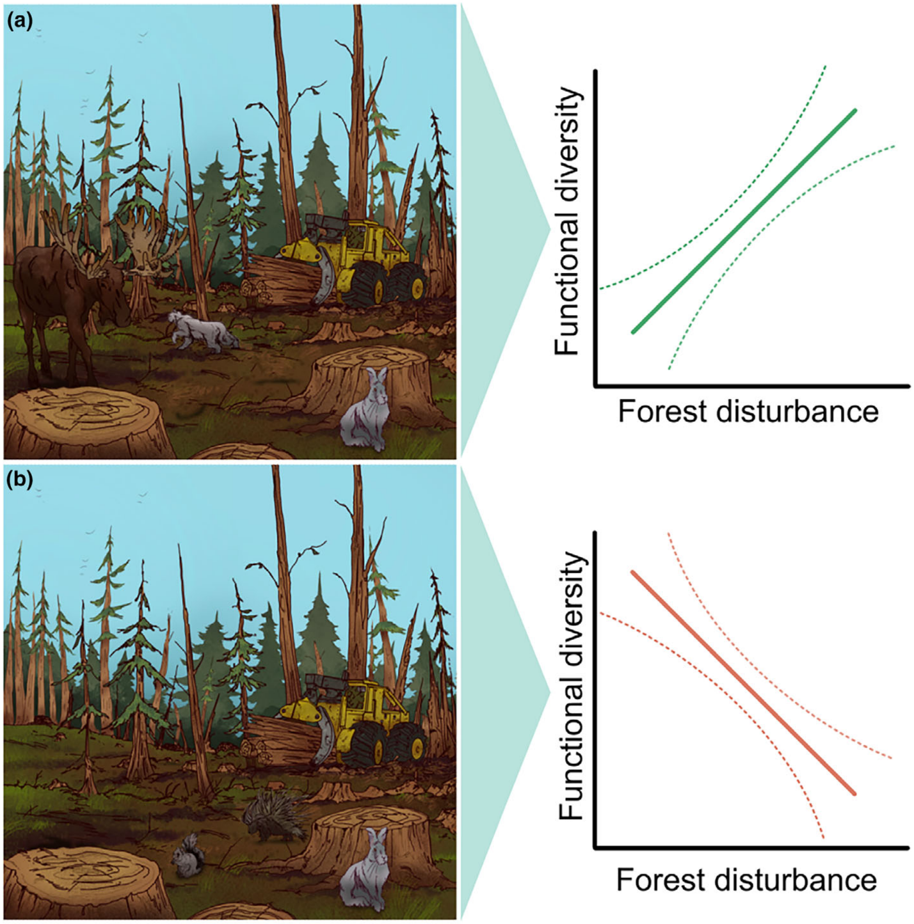

Figure 1 Conceptual framework of the study. Forest management activities such as logging can determine the abundance of species with different traits in the community. Panel (a) shows a scenario in which forest management promotes trait variation within the community represented by a large herbivore (moose), a carnivore (lynx), and a small herbivore (snowshoe-hare) and this is reflected in an increase of functional diversity. Panel (b) shows a scenario in which forest management reduces community trait variation represented by three small herbivores (red squirrel, porcupine, and snowshoe hare), ultimately decreasing functional diversity.

Surveys were conducted during good weather conditions, avoiding excessively windy (Beaufort scale <7, strong breeze or less) or rainy days (moderate rain and thunderstorms). Points were at least 100-m apart and at least 130-m from the forest edge, and sites were about 1-km apart within an area, on average. We created a species presence/absence matrix for each site based on the species detected at each point. We removed species detected in less than five points and flyovers, and we combined data for two vireo species (*Vireo philadelphicus* and *Vireo olivaceus*) because they are very difficult to distinguish by song in the field. Thus, we included in the analyses 85 species from 24 families.

Mammal survey

Mammals were surveyed in 197 sites between 2017 and 2020 using camera traps in Maine, USA (Fig. 2). Sites were selected based on (1) forest disturbance (from low to high levels of forest disturbance), (2) latitude (from low to high latitude), and (3) forest composition (deciduous vs. coniferous trees; Evans, Mosby, & Mortelliti, 2019; Evans & Mortelliti, 2022; Evans *et al.*, 2024). We focused our survey on the northern two-thirds of Maine excluding the coastal and less forested southern portion of the state.

Sites were sampled at least once in the summer (JuneSeptember) and once in the winter (January-April), totaling a minimum of two seasons per site, but some sites had up to seven seasons. Sites were at least 6 km apart to ensure independence among detections between sites. Each site had three passive infrared cameras (Bushnell Trophy Cam E2/E3) about 100 m apart in a linear transect (Evans, Mosby, & Mortelliti, 2019) which were active for 15 to 21 days. Cameras were set about 40 cm from the ground facing a tree with bait (beaver meat) and scent lure scent (skunk essence and Vaseline based) to attract carnivores (Evans & Mortelliti, 2022). Importantly, in our study area, the combined use of bait and lure increases the detection of carnivores while not influencing the detection of non-carnivore mammals

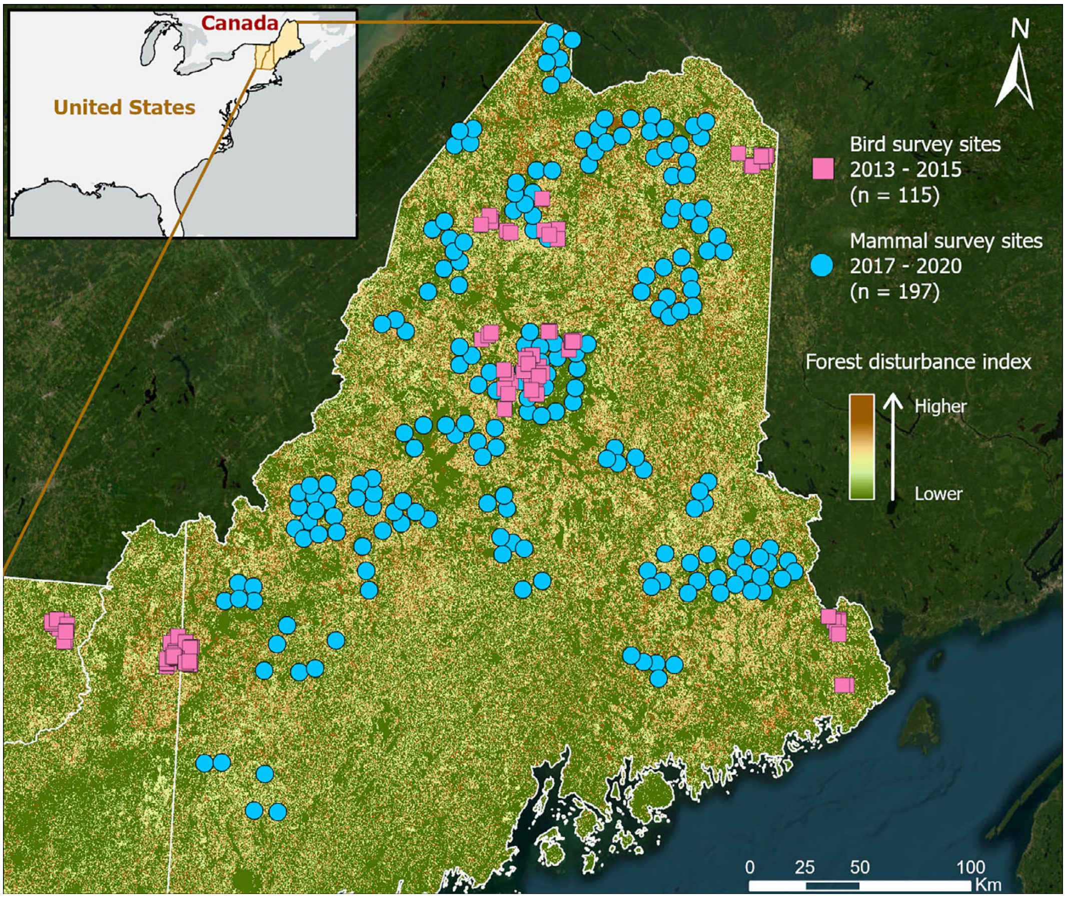

Figure 2 Study area in northeastern USA including the states of Maine, New Hampshire, and Vermont. Survey sites were distributed among different levels of forest disturbance from low (in green) to high (in brown). Pink squares indicate point count sites to survey birds between 2013 and 2015 and blue circles indicate camera trap sites to survey mammals between 2017 and 2020.

(Buyaskas, Evans, & Mortelliti, 2020). For the species presence/absence data for each site, we pooled images from all three cameras for each site. In total, we included 14 mammal species from nine families in the analyses. Our field methods were approved by the University of Maine Institutional Animal Care and Use Committee, protocol #A2018-05-06.

Forest covariates

We collected two GIS forest-related covariates at each survey site: forest disturbance and proportion of conifer forest. Forest disturbance was measured from Landsat imagery from 1984 to 2017 and processed by Kilbride (2018) using a novel method to combine multiple individual change detection algorithms calibrated for New England forests. These algorithms capture forest loss events, primarily due to timber harvest activity. Using spectral properties, Kilbride (2018) derived metrics describing the year of the most recent forest disturbance event and the intensity of this event at a 30-m resolution. We categorized the intensity into four classes where one indicated no disturbance event and four indicated a high-intensity event. We also categorized the year of the most recent disturbance event into four classes, one indicating no disturbance event (or prior to 1989) and four indicating a very recent event (after 2010 for birds and after 2013 for mammals). We then multiplied these two variables (intensity and year) to create a single variable that incorporates both intensity and time since the forest loss hereafter called the forest disturbance index (Evans & Mortelliti, 2022; Mortelliti, Brehm, & Evans, 2022; Dri *et al.*, 2022; Figure S1). The disturbance index covered from 1984 to 2015 for birds and from 1984 to 2017 for mammals to fit the respective survey periods. The proportion of conifer forest was extracted from the National Land Cover Database (NLCD) from 2013 for birds and 2019 for mammals. Because these variables may affect the functional diversity at different scales, we created buffers (300 m, 1 km, 3 km, and 6 km) around the centroid of each site and extracted the average values of forest disturbance and proportion of conifer forest for each buffer. These distances are appropriate because they are comparable to home-range sizes of target species and they also capture changes in the landscape from local (300 m) to broader (6 km) scales. This data processing was performed in ArcGIS Pro 2.8.

We also calculated the diversity of forest structure variables in the field that characterize the fine-scale vegetation structure related to forest management. For birds, the covariates include trees' DBH, canopy cover, and midstory cover (Rolek *et al.*, 2018b). For mammals, they include tree's DBH and the number of logs and stumps on the ground (Evans & Mortelliti, 2022). We calculated the coefficient of variation of these variables that represents the diversity of each forest element by calculating the variable standard deviation and dividing it by the variable mean, using program R version 4.2.3 (R Core Team, 2023). See Supplementary Material for a full description of these variables.

Functional traits collection and processing

We selected functional traits for birds and mammals that summarize key features of their biology, ultimately influencing their interaction with the environment (Sitters *et al.*, 2016). For birds, traits included body mass, diet, habitat breadth, foraging strata, wing length, and migration status, whereas for mammals they included body mass, diet, habitat breadth, litter size, and activity period. Body mass, diet, and foraging strata were obtained from the ELTON Traits 1.0 database (Wilman *et al.*, 2014), migration and wing length were obtained from the AVONET trait database (Tobias *et al.*, 2022), litter size was obtained from the panTHERIA database (Jones *et al.*, 2009), activity was obtained from Cox, Gardner, & Gaston (2021), and habitat breadth was obtained from the IUCN Habitats Classification Scheme (IUCN, 2023). All functional traits were continuous except for migration for birds (long distance, partial-migrant, or sedentary) and activity period for mammals (diurnal, crepuscular, nocturnal, or cathemeral).

Body mass (g) was the average weight of a reproductive adult (Wilman *et al.*, 2014). Diet was calculated as a synthetic value representing the invertivore gradient for birds (i.e. species that consume mainly invertebrates have a higher value than granivore or frugivore species), and the herbivore gradient for mammals (i.e. species that consume mainly plant items have a higher value than carnivore species). To process the diet data, we followed Cox, Gardner, & Gaston (2021) in which we transformed the percent use of each diet item (invertebrates, vertebrates, fruit, plants, etc) from Elton Traits into a distance matrix and then performed a Principal Coordinate Analysis (PCoA) on this matrix. The first axis explained sufficient diet variation across species (43% for birds and 65% for mammals) and thus we used the loading values of the first PCoA axis as synthetic trait values hereafter referenced as diet (Figure S2; Cox, Gardner, & Gaston, 2021). Foraging strata was the number of different forest strata listed for each species in the Elton Traits database (e.g. ground, understory, mid-high, and canopy). Wing length (mm) was the length from the carpal joint to the tip of the longest primary on the unflattened wing. Litter size was the average number of offspring born in a single litter. Habitat breadth was the number of "suitable" habitats listed for each species by the IUCN (2023). More details on the functional traits used with a direct demonstration of the linkage between each trait and its ecological importance are available in the Table S1.

Data analysis

To quantify the effect of forest covariates on the functional structure of animal communities, we calculated the functional richness (FRic) and functional originality (FOri) of these communities. Functional richness describes the volume of the functional space occupied by species in a community (i.e. it is a measure of the amount of different traits; Villéger, Mason, & Mouillot, 2008). Functional originality measures how isolated a species is in the functional space in relation to other species in the community and it can be interpreted as the opposite of functional redundancy (i.e. it is a measure of trait uniqueness) (*sensu* Mouillot *et al.*, 2013). We calculated functional richness for all traits combined and also for each trait separately. By assessing the variation of each trait within communities we can identify which traits are more important for the functional structure and drivers of potential associations with the environment. We also calculated functional specialization (FSpe) which represents how far a species is from the center of the functional space and it can be interpreted as a generalist vs. specialist gradient (Mouillot *et al.*, 2013). However, this index was highly correlated ($cor > 0.6$) with functional originality for both birds and mammals so we elected to remove this variable from the analyses (Figure S3). We used species presence/absence data rather than abundance because converting camera trapping data into abundance can be problematic (Johansson *et al.*, 2020).

We standardized the functional traits to create a multi-trait distance matrix using Gower distance allowing the treatment of mixed-type traits (Pavoine *et al.*, 2009) using the funct.dist from the mFD package version 1.0.4 (Magneville *et al.*, 2022). We used this distance matrix to calculate functional richness using the dbFD function from the FD package version 1.0.12.1 (Villéger, Mason, & Mouillot, 2008). To calculate functional originality, we performed a PCoA from the distance matrix to ordinate species into a functional space (Villéger, Mason, & Mouillot, 2008). From the PCoA, we assessed the quality of the functional space of birds and mammals through the mean squared deviation (mSD; Maire *et al.*, 2015) and selected the first four PCoA axes to calculate FOri following Mouillot *et al.* (2013, Figures S4 and S5). To calculate these indices, we combined all data from a site (both spatial and temporal replicates per site), so each site had one value per variable. We verified that there was no spatial autocorrelation in all response variables by performing a spcorrelogram analysis using the package ncf version 1.3–2 (Bjornstad, 2022, Figures S6 and S7).

Because functional richness is strongly influenced by species richness (Villéger, Mason, & Mouillot, 2008; Mouillot *et al.*, 2013), and species richness is influenced by sampling artifacts, we created null models to tease apart the correlation between species and functional richness and used the null deviation from the expectations as an unbiased measure of FRic. To do so, we maintained the observed species richness and composition for each community while randomizing species traits 999 times and recalculating FRic in each randomization. Null models allowed us to create a distribution of expected FRic values and compare them to the observed values. The new FRic ($\mathrm{FRic_{SES}}$) resulting from the comparison between the observed ($\mathrm{FRic_{obs}}$) and null ($\mathrm{FRic_{null}}$) with their standard deviation ($\mathrm{SD_{null}}$) calculated as the Standardized Effect Size for each community (equation 1) (Gotelli & McCabe, 2002):

$$\mathrm{FRic_{SES}} = \frac{(\mathrm{FRic_{OBS}} - \mathrm{FRic_{NULL}})}{\mathrm{SD_{NULL}}} \quad (1)$$

We calculated the corrected functional richness ($\mathrm{FRic_{SES}}$) for all traits combined and for each functional trait separately. To examine the effect of forest covariates on functional diversity, we fitted linear mixed-effect models using site as a random variable for birds with the R package lme4 version 1.1.32 (Bates *et al.*, 2015), and linear models for mammals as there was no hierarchical structure in the mammal dataset (Evans & Mortelliti, 2022). We ran a separate set of models for each response variable ($\mathrm{FRic_{SES}}$ and FOri) and associated them with forest covariates. For both animal groups, predictor variables were the proportion of conifer forest (all buffer sizes), forest disturbance index (all buffer sizes), and diversity of DBH. For birds, we also included the diversity of midstory cover, and canopy cover, while for mammals we included the diversity of logs and stumps on the ground. To identify which traits were driving the observed association of $\mathrm{FRic_{SES}}$ and FOri with forest covariates or how they respond to forest covariates individually, we generated another set of models with $\mathrm{FRic_{SES}}$ of individual traits as the response variable and forest disturbance index (all buffer sizes) and proportion of conifer forest (all buffer sizes) as predictor variables.

We used the Akaike Information Criterion (AIC) to rank competing models (Burnham & Anderson, 2002) with the R package AICcmodavg version 2.3.2 (Mazerolle, 2023) and performed multi-model inference using models within 2 ΔAIC of the top model. We first tested single variable models and then tested additive and interaction term models if more than one model ranked within 2 ΔAIC. We did not include highly correlated variables (>0.6) or the same variable at different buffer scales in the same model. If the null model was within 2 ΔAIC, we interpreted it as no predictor having an important association with the response variable, and if the top model set contained nested models, we reported on the simpler model. We quantified mixed-effect models fit using Nagelkerke's *R*-squared through the R package MuMIn version 1.47.5 (Barton, 2023). All variables were z-standardized prior to the analysis. We checked linear model assumptions for all models, and the residual plots of the top-ranked models are available in the Figures S8 and S9.

Results

Bird communities varied from 22 to 54 species (37 ± 6) per site and mammal communities varied from 3 to 13 species (8 ± 1) per site. Birds were mostly insectivorous with body mass ranging from 3.09 g to 5.7 kg. For mammals, we detected a similar number of carnivores, herbivores, and omnivores with body masses ranging from 119 g to 357 kg. See archived data for the full list of species with their traits (Rolek *et al.*, 2018a, 2018b, 2021; Dri, 2024).

Functional richness and originality

The top-ranked model for mammal functional richness included a positive effect on the proportion of conifer forest at a 3-km scale ($\beta = 0.18$; SD = 0.05) and forest disturbance at a 1-km scale ($\beta = 0.14$; SD = 0.05; Fig. 3; Table 1). Mammal functional originality also included a slight positive effect of both the proportion of conifer forest at a 3-km scale ($\beta = 0.01$; SD = 0.004) and forest disturbance at a 300-m scale ($\beta = 0.009$; SD = 0.004). We did not find an association between bird functional richness and originality and any forest covariates at any spatial scale (Fig. 3; Table 1).

Functional richness for individual traits

The top-ranked models for individual traits included the effect of forest disturbance and the proportion of conifer forest for birds. Specifically, we found that bird communities in areas with higher forest disturbance had a higher variation in diet ($\beta = 0.329$; SD = 0.09; 500-m scale) but a lower variation in body mass ($\beta = -0.11$; SD = 0.03; 300-m scale) and wing length ($\beta = -0.35$; SD = 0.11; 300-m scale; Fig. 4; Table 2). We also found that the variation in foraging strata slightly decreased with the proportion of conifer forest at 1-km scale ($\beta = -0.18$; SD = 0.07; Table 2). We did not find evidence for an association between the variation in habitat breadth and migration status with forest covariates.

For mammals, we found that both the variation in body mass and litter size increased with forest covariates. The top-ranked model for body mass variation showed a positive effect with the proportion of conifer forest at a 3-km scale ($\beta = 0.182$; SD = 0.05; Table 2). The proportion of conifer forest at a 6-km scale was a competitive model and had a similar positive association with the variation in body mass. The top-ranked model for litter size variation included a positive effect of forest disturbance ($\beta = 0.241$; SD = 0.06) and proportion of conifer forest ($\beta = 0.174$; SD = 0.06) both at a 3-km scale (Fig. 4; Table 2). We did not find evidence for an association between the variation in habitat breadth, diet, and activity pattern with forest covariates.

Discussion

Our results using two large-scale field studies on birds and mammals revealed that mammal' functional richness increased with forest disturbance while birds showed no significant trend. We also found interesting results at the trait

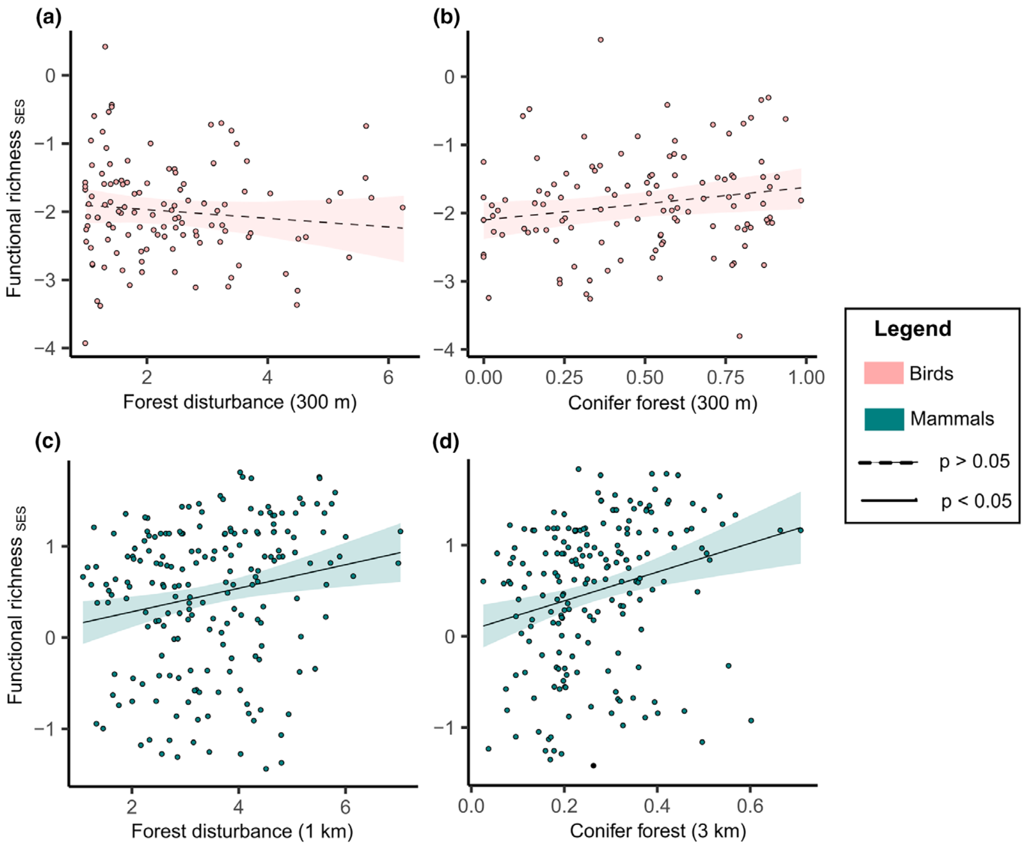

Figure 3 Predictions from the top-ranked linear (mixed) model for bird and mammal functional diversity with all traits analyzed together. While bird functional diversity is slightly negatively affected by forest disturbance and the proportion of conifer forest, both at the 300-m scale (panels a and b), mammal functional richness increases with forest disturbance at a 1-km scale and conifer forest at the 3-km scale (panels c and d). Functional richness$_{\text{SES}}$ is the functional richness corrected by species richness (standard effect size). Color ribbons indicate the 95% confidence interval. Bird data were collected from point count surveys conducted from 2013 to 2015 in 115 sites across Vermont, New Hampshire, and Maine, USA. Mammal data were collected from camera trap surveys conducted from 2017 to 2019 in 197 sites across Maine, USA.

level for both animal groups. Partially in line with our predictions that niche breadth traits (e.g. diet and habitat breadth) would be particularly influential in determining functional diversity patterns, we found that niche breadth (diet) along with morphological (body mass and wing length) and physiological (litter size) factors were the main determinants of the functional structure of both groups. Importantly, each trait category responded differently to forest disturbance, and birds and mammals were sensitive to disturbance at different spatial scales (Fig. 4). Our results indicate that the effects of forest management on functional diversity are less extreme than other types of land use change (e.g. forest plantation; Keenan *et al.*, 2015) but the moderate effects that we observed may have unknown long-term consequences, including filtering out species with certain traits.

Bird functional richness was not associated with forest disturbance at any spatial scale, indicating the complexity of this process: previous research has found that bird functional diversity can increase (Sitters *et al.*, 2016; Murray *et al.*, 2017) or decrease (Cosset & Edwards, 2017) with forest management, depending on the system. This inconsistent association could be because individual traits are masking each other's effect. Our trait analyses showed that bird communities in areas with high forest disturbance tend to have species with similar body mass and wing length but they also tend to have species with different diet preferences (Fig. 4; Table 2). Interestingly, all these patterns were at small spatial scales (300-m), potentially because their territories are often fixed during the breeding season (Krebs, Ashcroft, & Webber, 1978). The morphological filtering promoted by forest management could be a consequence of the loss of uncommon species that are more functionally distinct than common species (Seymour *et al.*, 2015). For example, the homogenization in body mass size and wing length could mean the loss of small and large species (e.g. hummingbirds and vultures) that contribute to different functions in the ecosystem, potentially degrading long-term ecosystem integrity (Seymour *et al.*, 2015). On the other hand, the increase in diet variation may suggest that forest management promotes

Table 1 Results of the functional diversity analyses. This table shows the top-ranked models of the models with all traits together using functional richness ($FRic_{SES}$) and functional originality (FOri) as response variables. Linear mixed-effect models were used for birds and linear models for mammals. Functional traits used for birds are body mass, diet, habitat breadth, wing length, foraging strata, and migration. For mammals, traits included body mass, diet, habitat breadth, litter size, and activity. Only models within 2 ΔAICc from the top model are shown. For the bird models, we used "site" as a random effect. Note that linear models used in the mammal dataset do not have a hierarchical structure and thus only R^2_m is reported. Bird data were collected from point count surveys conducted from 2013 to 2015 in 115 sites across Vermont, New Hampshire, and Maine, USA. Mammal data were collected from camera trap surveys conducted from 2017 to 2019 in 197 sites across Maine, USA

Group	Response variable	Model	*K*	ΔAICc	AICc weight	R^2_m	R^2_c
Birds	$FRic_{SES}$	Prop. conifer forest (300 m)	4	0.00	0.25	0.03	0.09
		Prop. conifer forest (1 km)	4	0.23	0.22	0.04	0.13
		Forest disturbance index (6 km)	4	1.48	0.12	0.02	0.05
		Null	3	1.57	0.11		
	FOri	Forest disturbance index (300 m)	4	0.00	0.22	0.03	0.14
		Forest disturbance index (1 km)	4	0.14	0.21	0.03	0.13
		Forest disturbance index (500 m)	4	0.95	0.14	0.02	0.12
		Prop. conifer forest (6 km)	4	1.05	0.13	0.07	0.07
		Null	3	1.55	0.10		
Mammals	$FRic_{SES}$	Forest disturbance index (1 km) + Prop. conifer forest (3 km)	4	0.00	0.49	0.09	
		Forest disturbance index (1 km) * Prop. conifer forest (3 km)	5	0.03	0.48	0.10	
	FOri	Forest disturbance index (300 m) + Prop. conifer forest (3 km)	4	0.00	0.61	0.05	

K = number of parameters, ΔAICc = Delta Akaike Information Criterion, AICc weight = Akaike's cumulative weight, R^2_m = coefficient of variation attributed to fixed effects, R^2_c = coefficient of variation attributed to both fixed and random effects.

vegetation heterogeneity allowing species with different diets to coexist (MacArthur, 1958). The mismatch between overall and individual trait patterns has been observed in assemblages of plant species in the Neotropics and can be an indication of the low impact of forest management on the functional structure of such communities (Carreño-Rocabado *et al.*, 2012). In our case, different traits may respond differently to forest management, further corroborating the complex effects of forestry practices on wildlife.

Unlike birds, mammal functional richness increased with forest disturbance at a larger spatial scale (Fig. 3) likely due to their larger home ranges, and the most influential trait in this association was litter size (Fig. 4). In other words, in areas with high forest disturbance, mammal communities tend to have high interspecific variation in litter size, suggesting a mixture of species with *r* vs. *K* life strategies, for example snowshoe hare (*Lepus americanus*) representing *r* and moose (*Alces alces*) representing *K* strategy. In our study system, many mammalian species are associated with early successional forests including coyote (*Canis latrans*), Canada lynx (*Lynx canadensis*), snowshoe hare, and moose (Mortelliti, Brehm, & Evans, 2022). Notably these species are very different from each other in terms of functional traits and ecosystem functions, and this could increase functional richness in more disturbed habitats. Forest management often increases vegetation heterogeneity and previous studies have shown that species richness positively responds to vegetation heterogeneity (Sukma *et al.*, 2019; Szymański *et al.*, 2021). Nonetheless, the increase in diversity due to anthropogenic vegetation heterogeneity may not always be beneficial for the ecosystem as it can also mean habitat degradation for more sensitive species (Hunter & Schmiegelow, 2011) especially those associated with old forests that disappear when forests are logged before reaching full maturity. For example, the extirpation of caribou (*Rangifer tarandus*) in this region may be linked to the loss of old forests (Vors *et al.*, 2007), but overhunting also played a role. Therefore, these results should be interpreted carefully.

Other important forest covariates related to disturbance include forest composition and structure (Lindenmayer *et al.*, 2009; Hunter & Schmiegelow, 2011), which can modify habitat quality for many species (Flaspohler, Temple, & Rosenfield, 2001). We tested the effect of variables such as the proportion of conifer forest and the diversity of DBH on the functional structure of bird and mammal communities, and we found that the functional richness of mammals increased with the proportion of conifer forest. For birds, the proportion of conifer forest was in the top-model set with a slightly positive effect, but the null model was among the top models so the evidence for this relationship is weak. Nonetheless, forestry practices that retain high proportions spruce-fir trees may be an effective strategy to maintain species with different traits, and thus the ecosystem functions, while also promoting economic growth.

We acknowledge that our bird surveys did not cover some mixed and deciduous forests that are common in the northeastern USA, limiting wide generalizations. However, we elected to focus on conifer-specialist birds because there is much concern about links between timber harvests and their population declines in our study area (Ralston *et al.*, 2015, but see Rolek *et al.*, 2021). Regarding data analysis, our model residuals did not always fit a perfect normal

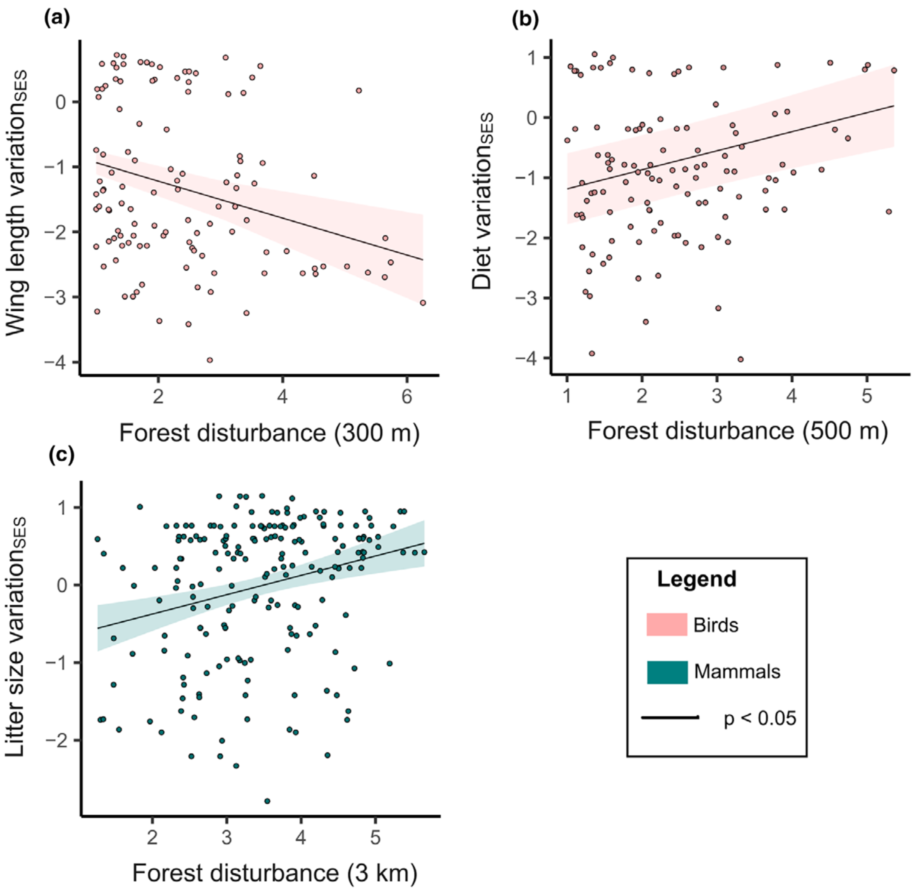

Figure 4 Predictions from the top-ranked linear (mixed) model for bird and mammal functional diversity of traits analyzed separately. Bird communities have (a) lower variation in wing length but (b) higher variation in diet in areas with higher forest disturbance at the 300-m and 500-m scale, respectively. Mammal communities (c) have a higher variation of litter size in areas with higher forest disturbance at the 3-km scale. Specific trait variation$_{\text{SES}}$ is the functional richness of the specific trait corrected by species richness (standard effect size). Color ribbons indicate the 95% confidence interval. Bird data were collected from point count surveys conducted from 2013 to 2015 in 115 sites across Vermont, New Hampshire, and Maine, USA. Mammal data were collected from camera trap surveys conducted from 2017 to 2019 in 197 sites across Maine, USA.

distribution, nevertheless, the models we used are relatively robust to deviations from distribution assumptions since we have independent points (Schielzeth *et al*., 2020; Knief & Forstmeier, 2021). We also acknowledge that the effect size of our models was not particularly strong, potentially because we did not model the variation in detectability among species which often relates to traits, and used presence/absence data rather than abundance. However, this moderate response of species traits corroborates past literature indicating that forest management is complex and context-dependent (Barlow *et al*., 2007; Chaudhary *et al*., 2016; Oettel & Lapin, 2021). Notably, forestry practices are deployed in a mosaic of patches that rarely cover the entire landscape. Additionally, forest disturbance in this region is significant, but they are not as extreme as those resulting from forest plantations (e.g. oil palm or eucalyptus; Keenan *et al*., 2015).

We showed that the functional traits of birds and mammals are differently affected by forest disturbance, highlighting the complexity of this process. Indeed, although forest management for timber production has been a common practice in the majority of temperate and boreal forests (Canham, Rogers, & Buchholz, 2013), our results indicate that making global generalizations and predictions may be challenging as this process is heavily dependent on the context and taxa studied (Paillet *et al*., 2010; Chaudhary *et al*., 2016). For example, different patterns may arise in tropical forests, where timber production often consists of the plantation of exotic species (Food and Agriculture Organization of the United Nations, 2020). Our results advance the field by showing that different traits have contrasting responses to forest management, underscoring the importance of investigating the effects of forestry on individual traits to develop strategies for managing for ecosystem functions.

Table 2 Results of the functional diversity analyses for individual traits. Functional traits used for birds are body mass, diet, habitat breadth, wing length, foraging strata, and migration. For mammals, traits included body mass, diet, habitat breadth, litter size, and activity. Linear mixed-effect models were used for birds and linear models for mammals. Only models within 2 ΔAICc from the top model are shown. For the bird models, we used "site" as a random effect. Note that linear models used in the mammal dataset do not have a hierarchical structure and thus only R^2_m is reported. Bird data were collected from point count surveys conducted from 2013 to 2015 in 115 sites across Vermont, New Hampshire, and Maine, USA. Mammal data were collected from camera trap surveys conducted from 2017 to 2019 in 197 sites across Maine, USA

Group	Response variable	Model	K	ΔAICc	AICc weight	R^2_m	R^2_c
Birds	Body mass$_{\text{SES}}$	Forest disturbance index (300 m)	4	0.00	0.85	0.08	0.20
	Wing$_{\text{SES}}$	Forest disturbance index (300 m)	4	0.00	0.77	0.07	0.16
	Diet$_{\text{SES}}$	Forest disturbance index (500 m)	4	0.00	0.72	0.10	0.49
	Foraging strata$_{\text{SES}}$	Prop. conifer forest (1 km)	4	0.00	0.50	0.05	0.05
	Habitat breadth$_{\text{SES}}$	Null	3	0.00	0.20		
	Migration$_{\text{SES}}$	Forest disturbance index (1 km)	4	0.00	0.14	0.01	0.03
		Null	3	0.03	0.14		
Mammals	Body mass$_{\text{SES}}$	Prop. conifer forest (3 km)	3	0.00	0.50	0.04	
		Prop. conifer forest (6 km)	3	1.21	0.27	0.03	
	Litter size$_{\text{SES}}$	Forest disturbance index (3 km) + Prop. conifer forest (3 km)	4	0.00	0.66	0.09	
		Forest disturbance index (3 km) × Prop. conifer forest (3 km)	5	1.81	0.27	0.09	
	Diet$_{\text{SES}}$	Prop. conifer forest (6 km)	3	0.00	0.15	0.005	
		Null	2	0.12	0.15		
	Habitat breadth$_{\text{SES}}$	Forest disturbance index (300 m)	3	0.00	0.26	0.01	
		Forest disturbance index (500 m)	3	1.16	0.15	0.008	
		Prop. conifer forest (500 m)	3	1.49	0.12	0.007	
		Null	2	1.87	0.10		
	Activity$_{\text{SES}}$	Forest disturbance index (300 m)	3	0.00	0.27	0.01	
		Forest disturbance index (500 m)	3	1.38	0.13	0.006	
		Null	2	1.64	0.12		

K = number of parameters, ΔAICc = Delta Akaike Information Criterion, AICc weight = Akaike's cumulative weight, R^2_m = coefficient of variation attributed to fixed effects, R^2_c = coefficient of variation attributed to both fixed and random effects.

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Author contributions

GFD, MLH, and AM conceived the ideas. BR and BE collected the data. BR provided edits and suggestions. GFD analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

Data and R codes to replicate our results are available in Figshare repository (https://doi.org/10.6084/m9.figshare.25193018) and in https://doi.org/10.5066/F76Q1W53.

References

Aquilué, N., Filotas, É., Craven, D., Fortin, M.J., Brotons, L. & Messier, C. (2020). Evaluating forest resilience to global threats using functional response traits and network properties. *Ecol. Appl.* **30**, e02095.

Barlow, J., Gardner, T.A., Araújo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N., da Silva Motta, C. & Peres, C.A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. USA* **104**, 18555–18560.

Barton, K. (2023). MuMIn: multi-model inference. – R package ver. 1.47.5. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (2000). *Bird census techniques*. 2nd edn. London: Academic Press.

Bjornstad, O.N. (2022). ncf: spatial Covariance Functions. R package version 1.3–2. https://CRAN.R-project.org/package=ncf

Brandt, J.P. (2009). The extent of the north American boreal zone. *Environ. Rev.* **17**, 101–161.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information–theoretic approach*. 2nd edn. New York: Springer.

Buyaskas, M., Evans, B.E. & Mortelliti, A. (2020). Assessing the effectiveness of attractants to increase camera trap detections of North American mammals. *Mamm. Biol.* **100**, 91–100.

Canham, C.D., Rogers, N. & Buchholz, T. (2013). Regional variation in forest harvest regimes in the northeastern United States. *Ecol. Appl.* **23**, 515–522.

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J.C. & Poorter, L. (2012). Effects of disturbance intensity on species and functional diversity in a tropical forest. *J. Ecol.* **100**, 1453–1463.

Chaudhary, A., Burivalova, Z., Koh, L.P. & Hellweg, S. (2016). Impact of forest management on species richness: global meta-analysis and economic trade-offs. *Sci. Rep.* **6**, 23954.

Cosset, C.C. & Edwards, D.P. (2017). The effects of restoring logged tropical forests on avian phylogenetic and functional diversity. *Ecol. Appl.* **27**, 1932–1945.

Costantini, D., Edwards, D.P. & Simons, M.J. (2016). Life after logging in tropical forests of Borneo: a meta-analysis. *Biol. Conserv.* **196**, 182–188.

Cox, D.T.C., Gardner, A.S. & Gaston, K.J. (2021). Diel niche variation in mammals associated with expanded trait space. *Nat. Commun.* **12**, 1753.

Dri, G.F. (2024). Data from: Forest management affects the functional traits of birds and mammals differently. https://doi.org/10.6084/m9.figshare.25193018

Dri, G.F., Blomberg, E.J., Hunter, M.L., Vashon, J.H. & Mortelliti, A. (2022). Developing cost-effective monitoring protocols for track-surveys: an empirical assessment using a Canada lynx *Lynx canadensis* dataset spanning 16 years. *Biol. Conserv.* **276**, 109793.

Evans, B.E., Brehm, A.M., Franzoi Dri, G., Bolinjkar, A., Archambault, G. & Mortelliti, A. (2024). Differential habitat use between demographic states of black bears in managed timber forests. *J. Wildl. Manag.* **88**, e22501.

Evans, B.E. & Mortelliti, A. (2022). Effects of forest disturbance, snow depth, and intraguild dynamics on American marten and fisher occupancy in Maine, USA. *Ecosphere* **13**, e4027.

Evans, B.E., Mosby, C.E. & Mortelliti, A. (2019). Assessing arrays of multiple trail cameras to detect North American mammals. *PLoS One* **14**, e0217543.

Flaspohler, D.J., Temple, S.A. & Rosenfield, R.N. (2001). Effects of forest edges on ovenbird demography in a managed forest landscape. *Conserv. Biol.* **15**, 173–183.

Food and Agriculture Organization of the United Nations. (2020). *Global forest resources assessment 2020* (FRA 2020): main report. Rome. https://doi.org/10.4060/ca9825en

Franklin, J.F., Johnson, K.N. & Johnson, D.L. (2018). *Ecological forest management*. Long Grove Illinois, USA: Waveland Press.

Gasperini, S., Mortelliti, A., Bartolommei, P., Bonacchi, A., Manzo, E. & Cozzolino, R. (2016). Effects of forest management on density and survival in three forest rodent species. *For. Ecol. Manag.* **382**, 151–160.

Gotelli, N.J. & McCabe, D.J. (2002). Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology* **83**, 2091–2096.

Hunter, M.L. (1999). *Maintaining biodiversity in forest ecosystems*. Cambridge: University Press.

Hunter, M.L. & Schmiegelow, F.K.A. (2011). *Wildlife, forests and forestry: Principles of managing forests for biological diversity*. 2nd edn. New Jersey: Prentice Hall.

IUCN. (2023). The IUCN red list of threatened species. Version 2023-1. Accessed 04 May 2023. https://www.iucnredlist.org

Johansson, Ö., Samelius, G., Wikberg, E., Chapron, G., Mishra, C. & Low, M. (2020). Identification errors in camera-trap studies result in systematic population overestimation. *Sci. Rep.* **10**, 6393.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C., Price, S., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O., Gittleman, J.L., Mace, G. & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: ecological archives E090-184. *Ecology* **90**, 2648.

Kalies, E.L., Dickson, B.G., Chambers, C.L. & Covington, W.W. (2012). Community occupancy responses of small mammals to restoration treatments in ponderosa pine forests, northern Arizona, USA. *Ecol. Appl.* **22**, 204–217.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A. & Lindquist, E. (2015). Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manag.* **352**, 9–20.

Kilbride, J.B. (2018). *Forest disturbance detection and aboveground biomass modeling using moderate-resolution, time-series satellite imagery*. Master's thesis. Maine, USA: University of Maine https://digitalcommons.library.umaine.edu/etd/291

King, D., Griffin, C. & DeGraaf, R. (1997). Effect of clearcut borders on distribution and abundance of forest birds in Northern New Hampshire. *Wilson Bull.* **109**, 239–245.

Knief, U. & Forstmeier, W. (2021). Violating the normality assumption may be the lesser of two evils. *Behav. Res. Methods* **53**, 2576–2590.

Krebs, J., Ashcroft, R. & Webber, M. (1978). Song repertoires and territory defence in the great tit. *Nature* **271**, 539–542.

Legaard, K., Sader, S. & Simons-Legaard, E. (2015). Evaluating the impact of abrupt changes in forest policy and management practices on landscape dynamics: analysis of a Landsat image time series in the Atlantic Northern Forest. *PLoS One* **10**, 1–24.

Lindenmayer, D.B., Hunter, M.L., Burton, P.J. & Gibbons, P. (2009). Effects of logging on fire regimes in moist forests. *Conserv. Lett.* **2**, 271–277.

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**, 599–619.

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D. & Villeger, S. (2022). mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* **2022**, e05904. https://doi.org/10.1111/ecog.05904

Maire, E., Grenouillet, G., Brosse, S. & Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob. Ecol. Biogeogr.* **24**, 728–740.

Mazerolle, M.J. (2023). AICcmodavg: model selection and multimodel inference based on (Q)AIC. – R package ver. 2.3-2. https://cran.r-project.org/package=AICcmodavg

Morin, R.S., Barnett, C.J., Butler, B.J., Crocker, S.J., Domke, G.M., Hansen, M.H., Hatfield, M.A., Horton, J., Kurtz, C.M., Lister, T.W., Miles, P.D., Nelson, M.D., Piva, R.J., Wilmot, S., Widmann, R.H., Woodall, C.W. & Zaino, R. (2012). *Forests of Vermont and New Hampshire 2012*. Newtown Square, PA: U.S. Forest Service, United States Department of Agriculture, and Northern Research Station.

Mortelliti, A. & Brehm, A.M. (2021). Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. *Proc. R. Soc. Lond. B* **287**, 20201713.

Mortelliti, A., Brehm, A.M. & Evans, B.E. (2022). Umbrella effect of monitoring protocols for mammals in the Northeast US. *Sci. Rep.* **12**, 1893.

Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177.

Murray, B.D., Holland, J.D., Summerville, K.S., Dunning, J.B., Jr., Saunders, M.R. & Jenkins, M.A. (2017). Functional diversity response to hardwood forest management varies across taxa and spatial scales. *Ecol. Appl.* **27**, 1064–1081.

National Oceanic and Atmospheric Agency [NOAA]. (2020). Climate normals. Accessed 30 July 2024. www.ncei.noaa.gov/access/us-climate-normals

Oettel, J. & Lapin, K. (2021). Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. *Ecol. Indic.* **122**, 107275.

Ortega, Y. & Capen, D. (2002). Roads as edges: effects on birds in forested landscapes. *For. Sci.* **48**, 381–390.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* **24**, 101–112.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. & Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* **118**, 391–402.

Politi, N., Hunter, M. & Rivera, L. (2012). Assessing the effects of selective logging on birds in Neotropical piedmont and cloud montane forests. *Biodivers. Conserv.* **21**, 3131–3155.

R Core Team. (2023). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-pro ject.org/

Ralston, J., King, D.I., DeLuca, W.V., Niemi, G.J., Glennon, M.J., Scarl, J.C. & Lambert, J.D. (2015). Analysis of combined data sets yields trend estimates for vulnerable spruce-fir birds in northern United States. *Biol. Conserv.* **187**, 270–278.

Rodriguez, A., Pohjoismäki, J.L. & Kouki, J. (2019). Diversity of forest management promotes parasitoid functional diversity in boreal forests. *Biol. Conserv.* **238**, 108205.

Rolek, B., Loftin, C., Harrison, D. & Wood, P. (2018*b*). Avian point count survey-specific data in Northern New England 2013 to 2015: U.S. Geological Survey data release https://doi.org/10.5066/F76Q1W53

Rolek, B.W., Harrison, D.J., Linden, D.W., Loftin, C.S. & Wood, P.B. (2021). Habitat associations of breeding conifer-associated birds in managed and regenerating forested stands. *For. Ecol. Manag.* **502**, 119708.

Rolek, B.W., Harrison, D.J., Loftin, C.S. & Wood, P.B. (2018*a*). Regenerating clearcuts combined with postharvest forestry treatments promote habitat for breeding and post-breeding spruce-fir avian assemblages in the Atlantic Northern Forest. *For. Ecol. Manag.* **427**, 392–413.

Schielzeth, H., Dingemanse, N.J., Nakagawa, S., Westneat, D.F., Allegue, H., Teplitsky, C., Réale, D., Dochtermann, N.A., Garamszegi, L.Z. & Araya-Ajoy, Y.G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods Ecol. Evol.* **11**, 1141–1152.

Schulze, K., Malek, Ž. & Verburg, P.H. (2019). Towards better mapping of forest management patterns: a global allocation approach. *For. Ecol. Manag.* **432**, 776–785.

Seymour, C.L., Simmons, R.E., Joseph, G.S. & Slingsby, J.A. (2015). On bird functional diversity: species richness and functional differentiation show contrasting responses to rainfall and vegetation structure in an arid landscape. *Ecosystems* **18**, 971–984.

Sitters, H., Di Stefano, J., Christie, F., Swan, M. & York, A. (2016). Bird functional diversity decreases with time since disturbance: does patchy prescribed fire enhance ecosystem function? *Ecol. Appl.* **26**, 115–127.

Solar, R.C.R., Barlow, J., Andersen, A.N., Schoereder, J.H., Berenguer, E., Ferreira, J.N. & Gardner, T.A. (2016). Biodiversity consequences of land-use change and forest disturbance in the Amazon: a multi-scale assessment using ant communities. *Biol. Conserv.* **197**, 98–107.

Srinivasan, U., Hines, J.E. & Quader, S. (2015). Demographic superiority with increased logging in tropical understorey insectivorous birds. *J. Appl. Ecol.* **52**, 1374–1380.

Sukma, H.T., Di Stefano, J., Swan, M. & Sitters, H. (2019). Mammal functional diversity increases with vegetation structural complexity in two forest types. *For. Ecol. Manag.* **433**, 85–92.

Szymañski, C.R., Tabeni, S., Alvarez, J.A. & Campos, C.M. (2021). Diversity of plants and mammals as indicators of the effects of land management types in woodlands. *For. Ecosyst.* **8**, 1–15.

Thom, D., Taylor, A.R., Seidl, R., Thuiller, W., Wang, J., Robideau, M. & Keeton, W.S. (2021). Forest structure, not climate, is the primary driver of functional diversity in northeastern North America. *Sci. Total Environ.* **762**, 143070.

Tilman, D. (2001). Functional diversity. *Encyclopedia Biodivers* **3**, 109–120.

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J., Yang, J., Sayol, F., Neate-Clegg, M.H.C. et al. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581–597.

Villéger, S., Mason, N.W. & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R. & Patterson, B.R. (2007). Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *J. Wildl. Manag.* **71**, 1249–1256.

Werner, S.M. & Raffa, K.F. (2000). Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *For. Ecol. Manag.* **139**, 135–155.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027.

Yguel, B., Piponiot, C., Mirabel, A., Dourdain, A., Hérault, B., Gourlet-Fleury, S., Forget, P.-M. & Fontaine, C. (2019). Beyond species richness and biomass: Impact of selective logging and silvicultural treatments on the functional composition of a neotropical forest. *For. Ecol. Manag.* **433**, 528–534.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Distribution of survey sites in relation to forest disturbance index in the northeast USA.

Figure S2. Principal Coordinate Analysis (PCoA) of diet categories for (A) birds ($n = 85$) and (B) mammals ($n = 14$).

Figure S3. Association between functional specialization and functional originality of (A) bird ($n = 115$) and (B) mammal ($n = 197$) communities.

Figure S4. Functional space quality of bird species ($n = 85$) in the Northeastern USA describing six functional traits (five continuous and one categorical).

Figure S5. Functional space quality of mammal species ($n = 14$) in the Northeastern USA describing five functional traits (four continuous and one categorical).

Figure S6. Spatial autocorrelation calculated using spline correlograms for all bird functional diversity indices used in the analysis.

Figure S7. Spatial autocorrelation calculated using spline correlograms for all mammal functional diversity indices used in the analysis.

Figure S8. Residual plots for the bird top-ranked models reported in Table 2 of the main text.

Figure S9. Residual plots for the mammal top-ranked models reported in Tables 1 and 2 of the main text.

Table S1. Functional traits used in the derivation of functional diversity indices and their ecological importance for birds ($n = 85$) and mammals ($n = 14$).