



Spaceborne LiDAR and animal-environment relationships: An assessment for forest carnivores and their prey in the Greater Yellowstone Ecosystem

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ABSTRACT

Animal conservation requires understanding animal-habitat relationships. The integration of novel remote sensing platforms such as Light Detection and Ranging (LiDAR) technology has dramatically improved the resolution of insight when evaluating animal-habitat relationships by characterizing forest structure. However, conventional LiDAR collection (e.g., airborne or terrestrial laser scanning) may be limited by small spatial extents and logistical constraints (e.g., budget) associated with sampling. NASA's Global Ecosystem Dynamics Investigation (GEDI) mission provides an alternative and complement to conventional LiDAR sampling with globally available waveform LiDAR, which is being collected to characterize vertical and horizontal structure of Earth's forests. Forest carnivores are wide-ranging species occupying forested ecosystems, and are generally associated with vertical and horizontal forest structure for their survival and reproduction. We evaluated patterns in occurrence and habitat use of forest carnivores, which included Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), and coyotes (*Canis latrans*) and patterns in occurrence of their prey; American red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hares (*Lepus americanus*). Camera trap data were collected during the 2014–2017 winters in the Greater Yellowstone Ecosystem in Wyoming, USA. Our objectives were to (1) combine GEDI samples with multispectral satellite imagery from Landsat 8 to upscale vertical forest structure metrics; (2) assess the relative importance of environmental characteristics influencing occurrence and habitat use of forest-associated predators and prey; and (3) determine if GEDI-derived variables aided our efforts in characterizing animal-environment relationships. We used Random Forest regression models to upscale GEDI samples across our study area and implemented a multi-tiered approach using generalized linear mixed effect models to simultaneously evaluate animal-environment relationships and how GEDI-derived metrics improved the animal-habitat models. GEDI-derived metrics of relative height and foliage height diversity improved our animal-environment models and were among the strongest covariates (effect sizes were 1.3–1.8 times larger than the next closest) in the coyote, red squirrel, and snowshoe hare models. All five species were influenced to some degree by the frequency of rebaiting a camera trap and varying conditions of snow depth. Collectively, our work indicates forest canopy height and complexity variables significantly improved our ability to assess the importance of forest characteristics on forest carnivores and their prey. Indeed, there is an untapped opportunity to enhance animal ecology and conservation planning with continued integration of GEDI information with freely available satellite data to characterize attributes of forest structure across expansive areas.

1. Introduction

Animal conservation and management requires information about

habitat use and quality by evaluating animal-environment relationships. Wildlife occurrence and habitat use are affected by a combination of resources (e.g., forage quality) and environmental constraints (e.g.,

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snow depth; Morrison et al., 1999; Creel et al., 2005) that vary in space and time. The coexistence of multiple sympatric species can also influence how resources are used, and ultimately lead to spatial or temporal shifts in habitat use by a particular species (Garneau et al., 2007; Atwood et al., 2009; Hearn et al., 2018). Remote camera traps are a common tool used to assess spatio-temporal patterns of animal occurrence and habitat use. In recent studies, analytical approaches have been applied to examine occurrence and habitat use, highlighting spatio-temporal interactions among species and how they vary with respect to resource availability and seasonality (Vanak et al., 2013; Karanth et al., 2017; Keim et al., 2019; Ruprecht et al., 2021). Keim et al. (2019) applied a count-based, recurrent event model that uncovered the intensity of use (i.e., photos/day) by wolves (*Canis lupus*) was strongly influenced by temporal effects of season and the activity of humans and white-tailed deer (*Odocoileus virginianus*). Keim et al. (2019) further identified that forest habitat treatments dramatically influenced habitat use by wolves, presumably through restricting movement. In another study, Ruprecht et al. (2021) used camera traps to record daily visits of coyotes (*C. latrans*) at mountain lion (*Puma concolor*) kill sites, and uncovered a temporal trend in coyote use that peaked one day after a lion kill and declined thereafter. Analytical approaches such as these allow for a unique look into the nuances of camera trap data with the intent of characterizing spatio-temporal patterns in animal-environment relationships.

The discoveries generated from animal-habitat evaluations are directly related to the resolution of environmental data (Olsoy et al., 2015; Forbey et al., 2017). For example, within the last decade, numerous studies have integrated Light Detection and Ranging (LiDAR) — a remote sensing technique that uses laser pulses to measure the distance of objects (e.g., vegetation or buildings) from the laser instrument (Dubayah and Drake, 2000; García-Feced et al., 2011) to characterize wildlife habitat (García-Feced et al., 2011; Palminteri et al., 2012; Vogeler et al., 2013; Holbrook et al., 2015; Tweedy et al., 2019). The integration of novel remote sensing platforms such as LiDAR can dramatically increase the resolution of the environment and provide information on vertical and horizontal vegetation structure, leading to finer resolution questions aimed at animal-habitat evaluations. One such platform that captures spatially extensive LiDAR was the 2018 launch of NASA's Global Ecosystem Dynamics Investigation (GEDI)—a spaceborne LiDAR instrument installed on the International Space Station. Within the originally planned two-year mission, GEDI is expected to collect over 10 billion cloud-free shots covering the Earth's tropical and temperate forests (Dubayah et al., 2020). These data can be used to spatially characterize canopy height, canopy cover, and vertical cover as well as other structural metrics (Dubayah et al., 2020). The application of airborne LiDAR has proven successful for small-footprint studies (e.g., Vogeler et al., 2016; Davies et al., 2019; Hagar et al., 2020); however, for wide-ranging species such as carnivores, a spatially extensive sample of LiDAR data with the potential of upscaling (e.g., Asner et al., 2018) is needed for landscape to region scale habitat assessments.

Forest carnivores are a guild of species that can benefit from characterizations of vertical and horizontal forest structure when assessing habitat relationships. These species not only occupy forested environments, but for some, their survival and reproductive success depend on vertical and horizontal forest structure (e.g., downed woody debris, large trees, foliage height diversity, or snags for nesting/rooting; Ruggiero et al., 1994; Kosterman et al., 2018). Examples of forest carnivores include wolverines (*Gulo gulo*), Canada lynx (*Lynx canadensis*), Pacific martens (*Martes caurina*), and Rocky Mountain red foxes (*Vulpes vulpes macroura*). The dependence on forest characteristics varies for these species. For example, lynx and martens are closely associated with forests, whereas wolverines and red foxes are more habitat generalists (Buskirk and Ruggiero, 1994; Powell et al., 2003; Holbrook et al., 2019). Pacific martens require late-successional conifer and mature lodgepole pine (*Pinus contorta*) forests characterized by abundant large dead and down trees and live trees with snags (Buskirk and Ruggiero, 1994; Ellis,

1998; Powell et al., 2003). Martens utilize the upper canopy for resting and rearing young (Buskirk and Ruggiero, 1994) and exploiting downed woody debris as foraging grounds (Andruskiw et al., 2008). In contrast, Rocky Mountain red foxes may occupy and use the lower sections of trees and occur in areas with sparse understory and mesic meadows near forest edges for foraging and escape cover (Fuhrmann, 1998; Perrine, 2005). Some prey species of forest carnivores, however, can be closely associated with vertical variation in forest structure. For instance, mature and late-successional forests with dense horizontal cover provide a temporally stable habitat for snowshoe hares (*Lepus americanus*; Buskirk et al., 1999; Ellsworth and Reynolds, 2006), generally leading to higher survival, abundance, and population density (Berg et al., 2012; Ivan et al., 2014; Holbrook et al., 2017). American red squirrels (*Tamiasciurus hudsonicus*) are closely associated with forest characteristics, including tall trees with closed canopies and downed woody debris (Steele, 1998). Red squirrels occupy the entire forest canopy among various tree species compositions (Klugh, 1927; Rothwell, 1979; Steele, 1998) and create middens (cone-scale piles) to cache food (Posthumus et al., 2015). Collectively, forest carnivores and their associated prey represent a suite of species in which extensive LiDAR data could be instrumental in characterizing and advancing our understanding of animal-environment relationships.

The goal of our study was to evaluate patterns in occurrence and habitat use (i.e., photos/day as our index) among forest-associated predators and their prey while integrating cutting-edge remote sensing information. To address this goal, we used camera trap data of Pacific martens, Rocky Mountain red foxes, coyotes, red squirrels, and snowshoe hares collected during the 2014–2017 winters in the Greater Yellowstone Ecosystem (GYE) in Wyoming, USA. This study addresses three objectives: (1) combine GEDI LiDAR samples with multispectral satellite imagery from Landsat 8 to upscale vertical forest structure metrics; (2) assess the relative importance of Landsat 8 products/indices, predicted GEDI-derived variables, and other environmental variables in influencing occurrence and habitat use of forest-associated predators and prey; and (3) determine if and how GEDI-derived forest structure variables demonstrate appreciable gains in characterizing animal-environment relationships. We hypothesized spaceborne LiDAR would significantly enhance efforts to characterize habitat relationships for martens and squirrels by capturing variation in forest canopy height and relative density within high canopy cover stands. Conversely, we hypothesized weak improvements for our fox and coyote models when including spaceborne LiDAR metrics because they are mostly habitat generalists, potentially not requiring specific conditions of vertical forest structure to meet life requirements. Overall, this work provides a timely evaluation of how spaceborne LiDAR might improve characterizations of animal-environment relationships, with a particular focus on an understudied guild of forest-dwelling species.

2. Materials and methods

2.1. Study area

Our study occurred in the mountains of the GYE of Wyoming (Fig. 1). The GYE is situated in the central Rocky Mountains and covers approximately 38,900 ha, of which 90% was federal lands consisting of two national parks (Yellowstone and Grand Teton), portions of three national forests (Shoshone, Bridger-Teton, and Caribou-Targhee), one national wildlife refuge (National Elk), and Bureau of Land Management holdings (BLM, 2016). Elevation ranged from 1,340 to 4,205 m, with an average of 2,616 m across the study area. Sagebrush (*Artemisia* spp.) and grassland steppe inhabit the lower elevation of the GYE, and dominant forests included lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Riparian vegetation (e.g., *Salix* spp.) occupied the drainage bottoms throughout the elevation gradient, and subalpine vegetation (e.g., whitebark pine [*P. albicaulis*]), sparse vegetation, and barren terrain

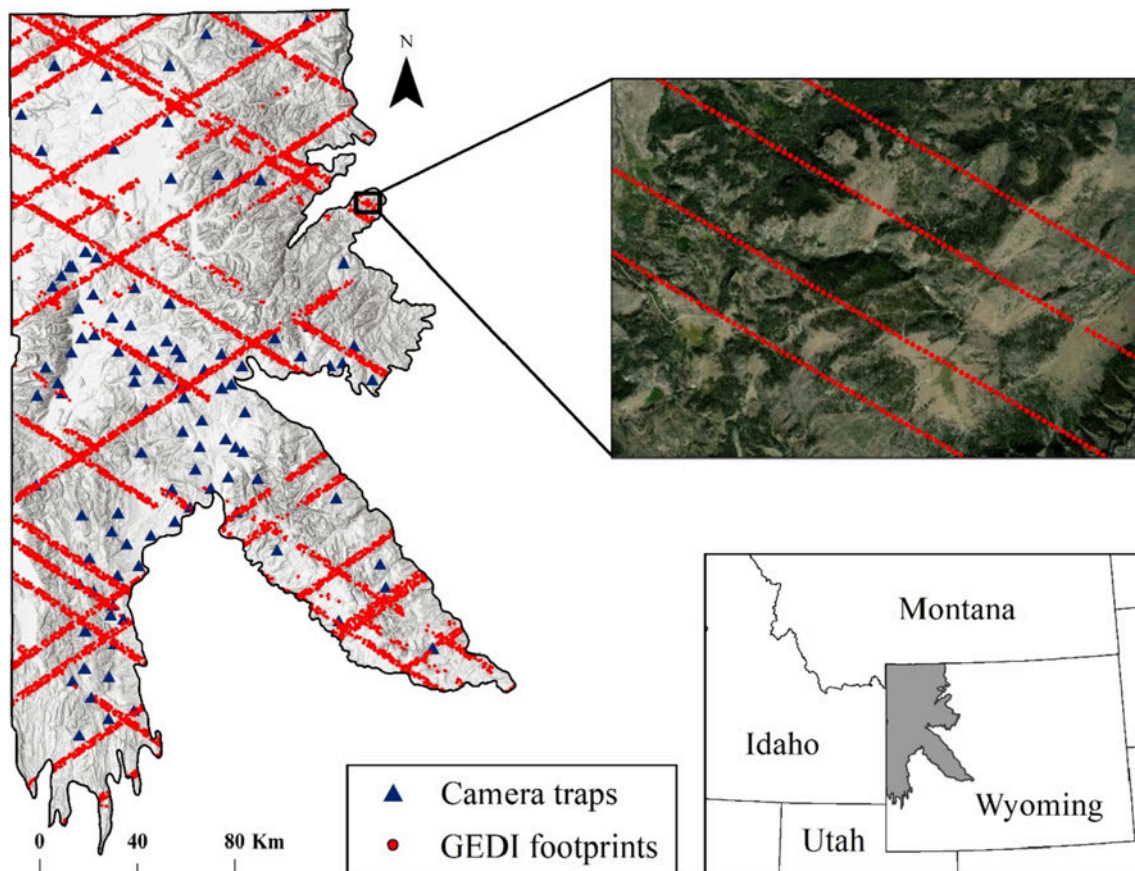


Fig. 1. The Greater Yellowstone Ecosystem study area in Wyoming, USA with camera trap locations ($n = 107$) and the 15,000 GEDI footprints. The inset map illustrates an example of full GEDI tracks across the landscape.

inhabited the upper-elevation of the GYE (Despain, 1990; LANDFIRE, 2021). Snow accumulation generally started in early November and ended in early May. The average snow depth in the GYE during our study (i.e., November 1 to April 30) was 0.99 m (NOHRSC, 2004).

2.2. Camera trap data

We conducted forest carnivore camera trap surveys during the 2014–2015, 2015–2016, and 2016–2017 winter seasons in the GYE (Fig. 1). We deployed 107 camera traps (Reconyx Hyperfire, models PC 800, PC 850, or PC 900; Reconyx, Holmen, WI) based on expected habitat suitability of wolverine and Canada lynx and expert opinion to increase the likelihood of photographing the forest carnivore assemblage. Camera trap elevation ranged from 1,935 to 3,231 m, with an average elevation of 2,591 m. Camera settings were as followed: sensitivity = high; pictures per trigger = three or five; and picture interval = one second between one-shot or three-shot pulses. Each camera trap was set 1.5 m above the mean annual snowfall on the northern aspect of a tree with attractants on an adjacent tree. Attractants varied from a leg of roadkill mule deer (*O. hemionus*) or half a beaver (*Castor canadensis*) carcass, Caven's Gusto (Minnesota Trapline Products, Pennock, MN) scent lure (e.g., Lukacs et al., 2020), and visual objects (e.g., pie plates, compact discs, and feathers). Camera placement occurred within natural movement corridors in mature, multi-storied spruce/fir forest types from November to April. Camera traps placed at inaccessible locations (e.g., winter access restrictions, Yellowstone National Park restrictions, unsafe—avalanche risk, or too remote) were deployed with an automatic long-call scent lure dispenser and a cow (*Bos taurus*) femur and left until the end of the survey season. We archived and identified camera photos using Colorado Parks and Wildlife Photo Warehouse (Ivan and

Newkirk, 2016).

We defined animal occurrence as whether a particular species was detected (i.e., 1) or not detected (i.e., 0) at a camera trap within 24-hours. If a camera trap detected an animal within 24-hours, then we defined habitat use as the total number of detections, or total counts, of the species at a camera trap during the 24-hour period. Habitat use represents how frequently a spatial unit is used each day (Keim et al., 2019). To generate distinct detection events, we applied a 15-minute quiet period from the first detection (Keim et al., 2019) and counted sequences of photos within this period as a single event. We calculated habitat use for Pacific martens, Rocky Mountain red foxes, coyotes, red squirrels, and snowshoe hares across every camera trap from November 1 to April 30 for 2014–2017.

2.3. Environmental data

We considered a suite of abiotic and biotic factors, including camera trap baiting, topographic, vegetative, and climate variables. In terms of biotic factors, we assessed whether baiting camera traps (e.g., using deer legs, cow bones, etc.) strongly influenced the habitat use of a given species. Average rebaiting occurred approximately every 39 days. To test whether occurrence or high habitat use was a function of rebaiting, we generated a variable of time since rebaiting. Every date a camera trap was rebaited, the rebait count started at zero and sequentially increased until the next rebaiting.

To characterize topography, we calculated derivatives of a digital elevation model (DEM; sourced from Shuttle Radar Topography Mission; Farr et al., 2007) downloaded from Google Earth Engine (GEE; Gorelick et al., 2017). We computed aspect, slope, roughness (Jenness, 2004), vector ruggedness measure (VRM; Sappington et al., 2007),

topographic position index (TPI; Guisan et al., 1999; De Reu et al., 2013), and heat load index (HLI; McCune and Keon, 2002). VRM, TPI, and HLI represent the terrain ruggedness relative to concavity or convexity, and hot-dry to cool-wet areas across the landscape, respectively. All topographic metrics were calculated using the *raster* (v.3.4–13, Hijmans, 2021) or *spatialEco* (v.1.3–6, Evans, 2021) packages in the R programming environment (v.4.1.0, R Core Team, 2021), and were summarized to a 500×500 m window (Table 1).

We used LANDFIRE Existing Vegetation Type (EVT; LANDFIRE, 2014) data to represent the dominant vegetation types of forests (Despain, 1990). We reclassified the aggregated existing vegetation types within the LANDFIRE EVT dataset to derive (1) lodgepole pine and (2) spruce-fir (*P. Abies*). Then, we calculated the percentage of occurrence of each classification within a 500×500 m window around a given cell using the Geomorphometric and Gradient Metric Toolbox, version 2 (Evans et al., 2014) within ArcGIS (v.10.8.1, ESRI, 2020).

We generated Landsat 8 Surface Reflectance (SR) and Landsat 8 Top of Atmosphere (TOA) medoid composites to calculate vegetation indices within GEE. The medoid takes the median in multi-dimensional band space so that the values for a given pixel for all of the bands are coming from the same image date (Flood, 2013). This method is vital for maintaining the relationship of values between the different bands for

Table 1

Biotic and abiotic covariates used in our multi-tiered occurrence and habitat use modeling for Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), coyotes (*Canis latrans*), American red squirrels (*Tamiasciurus hudsonicus*), and snowshoe hares (*Lepus americanus*) across the Greater Yellowstone Ecosystem, Wyoming, USA.

Theme	Variables	Units	Resolution (m ²)	Reference
Base metrics	Topographic position index (TPI)	Index	30	Guisan et al. (1999)
	Heat load index (HLI)	Index	30	McCune and Keon (2002)
	Vector ruggedness measurement (VRM)	Index	30	Sappington et al. (2007)
	Snow depth	m	1000	NOHRSC (2004)
	Rebait	Day since rebait	NA	This study
Landsat metrics	Spruce-fir forest	Proportion	30	LANDFIRE (2014)
	Lodgepole pine forest	Proportion	30	LANDFIRE (2014)
	Normalized difference vegetation index (NDVI)	Index	30	Huang et al. 2021
	Normalized burn ratio (NBR)	Index	30	Key and Benson (2006)
GEDI-derived metrics	Relative height-100% (RH100)	m	30	Potapov et al. 2021
	Relative height-100%-standard deviation (RH100-SD)	m	30	This study
	Foliage height diversity (FHD)	–	30	This study
	Pacific marten	Detections per day	NA	This study
Predator/Prey metrics	Rocky Mountain red fox	Detections per day	NA	This study
	Coyote	Detections per day	NA	This study
	American red squirrel	Detections per day	NA	This study
	Snowshoe hare	Detections per day	NA	This study

realistic combinations of values from a single date image to calculate spectral indices that are ratios of those bands for the values. We filtered Landsat 8 imagery from June 1 to September 30 for each year (2014–2016) to capture the entire growing season across the elevation gradient of our study area and removed scenes with $\geq 50\%$ cloud cover. During our image processing, we discovered minimal cloud-free coverage within our 2014 Landsat composite across the western portion of our study area. We corrected the NoData created by the masked clouds and smoke by filling the data gaps with 2015 Landsat 8 imagery. We generated Landsat 8 SR composites to calculate Normalized Difference Vegetation Index (NDVI; Huang et al., 2021), Normalized Burn Ratio (NBR; Key and Benson, 2006), Normalized Difference Water Index (Gao, 1996), Modified Normalized Difference Water Index (Xu, 2006), Soil Adjusted Vegetation Index (Huete, 1988), and each band (i.e., ultra-blue, blue, green, red, near-infrared, shortwave infrared 1, shortwave infrared 2, brightness temperature 1, and brightness temperature 2). We also used Landsat 8 TOA to calculate tasseled cap vegetation indices (e.g., brightness, greenness, and wetness), which indicate soil reflectivity, amount of green vegetation, and soil and vegetation moisture, respectively (Huang et al., 2002). We extracted NDVI and NBR median values from the 2014–2016 composites from each camera trap location with a 500 m buffer and appended the values to the occurrence and habitat use data set. Collectively, the derived NDVI, NBR, lodgepole pine, and spruce-fir covariates will here-on be referred to as Landsat metrics (Table 1).

Lastly, because our camera traps occupied rugged, forested environments during the winter months, we incorporated spatially explicit snow depth data from the Snow Data Assimilation System within the National Operational Hydrologic Remote Sensing Center (NOHRSC, 2004; Table 1). We downloaded snow depth data from November 1 to April 30 for 2014–2017. We appended the $1 \text{ km} \times 1 \text{ km}$ snow depth value intersecting each active day of a camera trap to the occurrence and habitat use data set, providing daily estimates of snow depth. We expected a negative relationship between snow depth and occurrence and habitat use for coyotes because of larger foot-loading (Murray and Boutin, 1991), a positive relationship for hares given their morphological adaptations to be successful in deeper snow (Gigliotti et al., 2017), and no relationship between martens and squirrels as these species are more adaptable to coexist with varying snow depths (Pruitt and Lucier, 1958; Raine, 1983; Brigham and Geiser, 2012; Jung et al., 2021).

2.4. GEDI data and pre-processing

We integrated GEDI footprint-level structure information into remote sensing data fusion models to evaluate how spaceborne LiDAR might improve our ability to characterize habitat relationships for our focal species. GEDI is a full waveform LiDAR instrument providing analysis ready products related to canopy cover, cover height, vertical cover profiles, and surface topography within ~ 25 m footprint samples at near-global extents (Dubayah et al., 2020). Our study utilized Version 2, Level 2A (footprint-level elevation and height; Dubayah et al., 2021a) and Level 2B (footprint-level canopy cover and vertical profile; Dubayah et al., 2021b) metrics, specifically relative height-100% (RH100) from Level 2A and foliage height diversity (FHD) from Level 2B to characterize three-dimensional forest structure. Relative height is defined as the height at which a specified percentage of the laser's returned energy is reached relative to the ground (Healey et al., 2020). For instance, when the waveform reaches 100% of the total energy, the canopy height along the elevational gradient equals RH100 (Fig. 2). Based on exploratory analyses, GEDI RH100 was an adequate indicator of maximum forest height (e.g., when compared to other potential metrics, such as RH98). FHD describes the vertical variability of the foliage profile and measures the complexity of forest structure, independent of plant area index (MacArthur and Horn, 1969; Simonson et al., 2014) and has been suggested as an important indicator of habitat quality for wildlife (MacArthur and Horn, 1969; August 1983). GEDI's FHD measurement is

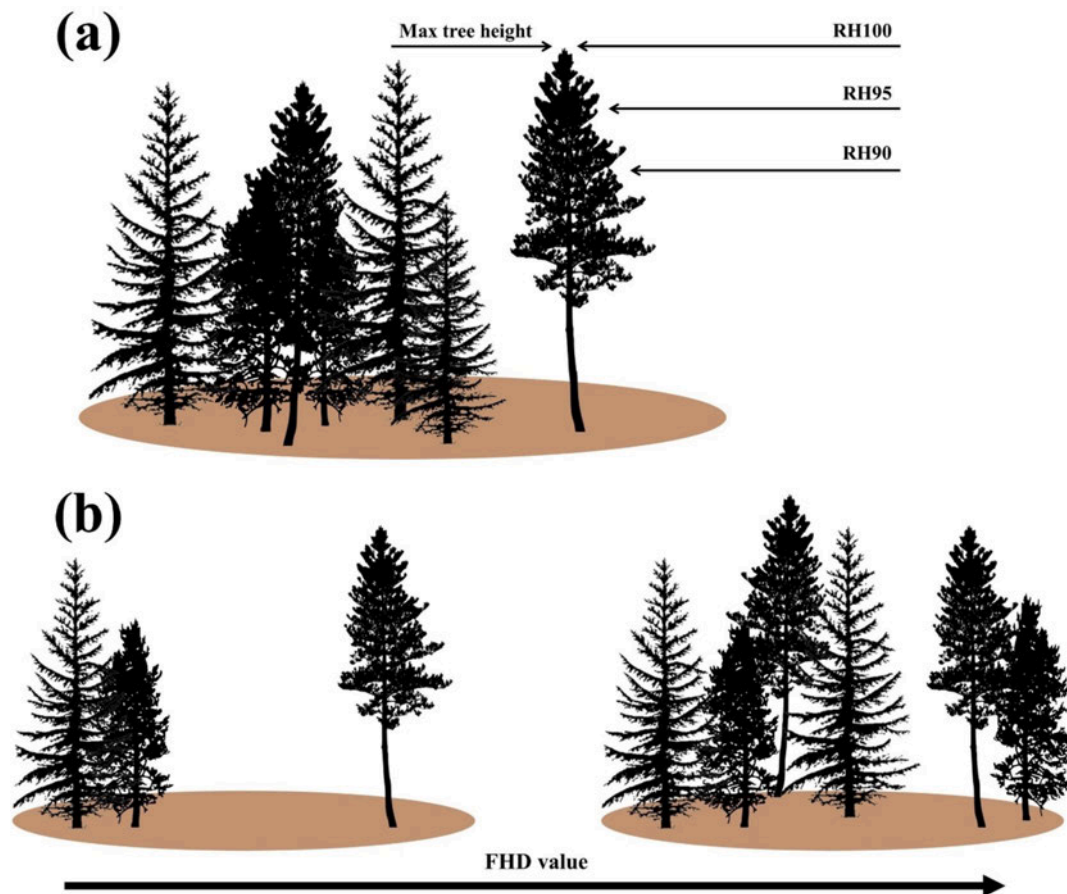


Fig. 2. Representation of a GEDI footprint illustrating metrics (a) relative height- 100% (RH100) and (b) foliage height diversity (FHD). RH100 is the 100th percentile of waveform energy relative to ground elevation. FHD describes the vertical variability of the foliage profile and measure the forest complexity. Note the value of FHD increase with forest complexity. This figure is an artistic representation and not a true GEDI output illustration.

largely based on estimates of the vertical leaf area index profile (Tang and Armston, 2019). High FHD values indicate complex forest structure associated with multiple canopy layers, whereas lower FHD values indicate less complex forest structure and fewer layers in the canopy (MacArthur and Horn, 1969; Fig. 2).

GEDI Level 2A and Level 2B metrics were filtered between June 1 through September 30, 2019, and downloaded from NASA Earthdata (Earthdata Search, 2019) using the GEDI finder tool from the *rGEDI* package (v.0.2.1 Silva et al., 2021). Selected GEDI footprint observations included (1) shots from full power only beams, (2) shots captured during the night, (3) shots with high beam sensitivity (e.g., > 0.9), and (4) with a Level 2A and Level 2B quality flag = 1. The filtering process ensures that the highest quality GEDI footprints were retained to use as training and test sample data for developing models to map forest structure variables across the study area. After filtering, the remaining GEDI footprints were cropped to our study area ($n = 336,041$). We sampled the available 336,041 GEDI footprints down for computational efficiency, resulting in approximately 15,000 randomly selected footprints (split into 70% training and 30% testing sets) to be used for the RH100 and FHD models (Fig. 1).

2.5. GEDI random forest modeling

We used Random Forest (RF) regression (Breiman, 2001; Holbrook et al., 2017) to develop models of GEDI RH100 and FHD. RF is a supervised machine learning approach using either regression or classification data that produces multiple decision trees using random bootstrapped samples with replacement for model training and setting aside approximately one-third of the data for error assessment at each

iteration (Breiman, 2001). To fine-tune the RF algorithm, the number of random variables selected and tried in each tree for prediction (i.e., *mtry*) can be selected. We modeled RH100 and FHD using topographic covariates and a suite of 2019 Landsat spectral indices described above in the *Environmental data* section (see Table 2). The RF models were generated using the *caret* package (v. 6.0–88, Kuhn, 2021) in program R. We divided the training data into five folds cross-validation with no repeats. Both models identified *mtry* = 12 as the optimal number of variables sampled at each split. RF regression model performance was assessed by the root mean square error (RMSE). We predicted RH100 and FHD onto the 30% withheld data, and then calculated the R^2 and RMSE for this testing set. We then applied the RH100 and FHD models across the topographic and Landsat index rasters to predict the GEDI structure metrics across the GYE at a 30 m resolution (Asner et al., 2018). We did this for the year of the GEDI model creation (2019), as well as hind-casted to topographic and annual Landsat rasters back through 2016 to better temporally match our wildlife camera data.

We performed moving window analyses on our modeled GEDI metrics using the median value of a 500×500 m pixel window around a given cell. We then extracted and appended predicted RH100 and FHD to the occurrence and habitat use data sets at each camera trap location (Table 1). To characterize horizontal heterogeneity in canopy heights, we also generated an RH100 standard deviation (RH100-SD) layer by calculating the standard deviation of RH100 at the 500×500 m neighborhood. If RH100-SD has a value of 0, the canopy height is homogeneous, whereas higher values are indicative of heterogeneous canopy height (e.g., variations in forest structure height across the area). Collectively, the modeled GEDI metrics (i.e., RH100, RH100-SD, and FHD) will here-on be referred to as GEDI-derived metrics.

Table 2

Topographic and vegetative covariates used in GEDI Random Forest regression models to characterize relative height-100% (RH100) and foliage height diversity (FHD) metrics across the Greater Yellowstone Ecosystem, Wyoming, USA. Variable importance is measured by residual sum of squares and represents how much removing each variable reduces the accuracy of the model. The top five variables for each model are bolded.

Data type	Variables	RH-100% variable importance	FHD variable importance
Topographic	Elevation	7	7
	Aspect	8	8
	Slope	3	3
	Roughness	5	5
	Ultra-blue band	15	18
Vegetative	Blue band	9	11
	Green band	2	4
	Red band	6	6
	Near-infrared band	18	15
	Shortwave infrared 1	4	2
	Shortwave infrared 2	16	12
	Brightness temperature 1	14	16
	Brightness temperature 2	13	17
	Heat load index	10	10
	Normalized difference vegetation index	21	22
	Existing vegetation index	11	14
	Soil Adjusted vegetation index	23	23
	Normalized difference water index	19	20
	Modified normalized difference water index	12	13
	Normalized burn ratio	20	19
	Tasseled cap brightness	1	1
	Tasseled cap greenness	22	21
	Tasseled cap wetness	17	9

2.6. Animal occurrence and habitat use modeling

Prior to model development, we assessed multicollinearity and standardized covariates. We evaluated collinearity by calculating variation inflation factors (VIF; [Zuur et al., 2009](#)) and ensured each model never contained a variable with a $VIF \geq 3$ ([Zuur et al., 2007](#)). We standardized and centered the covariates using the equation, $\bar{x} - \text{mean}(x) / \text{sd}(x)$ to compare relative effect sizes among covariates.

We modeled the probability of occurrence of Pacific marten, Rocky Mountain red fox, coyote, red squirrel, and snowshoe hare and the habitat use of marten, fox, and coyote using generalized linear mixed-effects models with binomial and negative binomial error distributions, respectively. We incorporated random effects for camera location and for year to account for repeated measures within a camera station and block for among-year variation (similar to [Ruprecht et al., 2021](#)). Our mixed-effects models had the general structure:

$$y = \beta_0 + \beta_1(TPI) + \beta_2(HLI) + \beta_3(VRM) + \beta_4(Snow\ Depth) + \beta_5(Time\ Since\ Rebait) + \dots + \beta_i(x_i) + \gamma_{\text{Camera ID}} + \gamma_{\text{Year}} + \varepsilon$$

Where y is the observed species occurrence or habitat use of a particular species; β_1 – β_5 are the base model fixed effects applied to every model; $\beta_i(x_i)$ indicates additional effects we tested as part of our modeling process; γ s are random effects associated with camera station and year; and ε is residual error. The binary models allowed us to evaluate what factors influence occurrence patterns across the full extent of our camera trap network. We developed count models to assess how environmental resources influenced habitat use for a particular species in areas where the species was detected at least once. Count models were not created for red squirrels and snowshoe hares because of low variation in total detections per day, with most detections being one

to two per day. We expected marten, squirrel, and hare occurrence and habitat use to be a function of taller, denser forest stands, particularly in lodgepole pine and spruce-fir forest and the presence of prey species to be positively significant for marten. We expected Rocky Mountain red fox occurrence and habitat use to be positively associated with ruggedness to provide escape cover from intraguild competition with coyotes and to be positively associated with the presence of hares. Because of fitness constraints, we expected a negative relationship between foxes and deep snow and no relationship with the forest characteristics because of their plasticity among forested environments. We expected that coyote occurrence and habitat use would be associated with convex terrain and lower snow depth. Coyotes' diet is predominantly carrion during the winter; therefore, we expected no association with the presence of squirrels and hares. Because coyotes are not forest specialists, we expected a positive association with more patchy forest structures. Lastly, we anticipated that occurrence and habitat use would increase as a function of earlier rebaiting for all three forest carnivores.

We implemented a multi-tiered approach to develop candidate models for characterizing species occurrence and habitat use. We first developed a “base” model to account for expected variation in species occurrence and habitat use. Our base model included TPI, HLI, VRM, snow depth, and time since rebaiting. We then evaluated how Landsat metrics (i.e., spruce-fir, lodgepole pine, NDVI, and NBR) influenced our ability to characterize species occurrence and habitat use. At our third tier, we assessed if the addition of GEDI-derived structure metrics (i.e., RH100, RH100-SD, and FHD) improved models (based on Akaike's information criterion; AIC_c) by showing better performance than our base covariates coupled with our Landsat metrics. Lastly, we utilized the top model, either the base or Landsat metrics or GEDI-derived metrics model, and added predator/prey species counts (i.e., total detections per day for a given species) to the model to evaluate if the presence of a predator or prey species improved and contributed to the final model.

We assessed model performance using AIC_c ([Burnham and Anderson, 2002](#)) and selected the model with the smallest AIC_c as the top model when there was clear separation from the candidate set (i.e., ΔAIC_c for the second model was > 2 ; [Burnham and Anderson, 2002](#)). If multiple models were within a ΔAIC_c of 2, we selected the most parsimonious (i.e., the model with the fewest coefficients). For each of the top models selected, we assessed model fit or predictive performance. For binary outcomes (i.e., species occurrence at a camera station), we calculated the area under the curve (AUC) of a receiver operating characteristic (ROC; [Robin et al., 2011](#)) for the generalized linear mixed-effects models. A ROC plot illustrates the sensitivity (i.e., the proportion of true positive values) and specificity (i.e., the proportion of true negative values) as the threshold for classification changes of all possible values ([Robin et al., 2011](#)). The AUC ranges from 0 to 1 and measures the performance of a model's ability to distinguish between plots with occurrences and no occurrences ([Robin et al., 2011](#)). When AUC is near one, the model classified positive and negative values well, whereas $AUC = 0.5$ indicates random discrimination. When $AUC \geq 0.6$, the model has indicated better discrimination ability ([Hosmer and Lemeshow, 2000](#)). For counts, we calculated Spearman's rank correlation coefficients (r_s) between observed and predicted values for our top habitat models to measure the goodness-of-fit. We used program R for all analyses, which included packages *car* (v.3.0–11, [Fox and Weisberg, 2019](#)), *lme4* (v.1.1–27.1, [Bates et al., 2015](#)), *AICcmodavg* (v.2.3–1, [Mazerolle, 2020](#)), *pROC* (v.1.17.0.1, [Robin et al., 2011](#)), and *MuMIn* (v.1.43.17, [Barton, 2020](#)).

3. Results

In total, we collected data over 24,622 active camera days across 107 camera traps and three winter seasons from November 1 to April 30, with the opportunity to detect Pacific martens, Rocky Mountain red foxes, coyotes, red squirrels, and snowshoe hares. The highest detections per day for each species at a single camera trap were for marten (51),

followed by red fox (45), coyote (15), red squirrel (11), and snowshoe hare (7). Of the three forest carnivores, marten had the highest number of days with at least one detection per day (2,280), followed by red fox (953) and coyote (329). The naïve occupancy rate (i.e., the total number of cameras with at least one species detection divided by the total number of cameras) across camera traps was greatest for martens (0.96) and the lowest for hares (0.52). The average detections per species per day across the study period ranged from 0.02 – 0.33 detections/day.

3.1. GEDI forest structure models

Our RF regression models predicting the GEDI footprint metrics, RH100 and FHD, using Landsat 8 spectral indices and topographic information performed well (see Table 2, which includes variable importance). Model performance was high within the training data (RH100: RMSE = 4.77; MAE = 2.89; R^2 = 0.65 and FHD: RMSE = 0.42; MAE = 0.30; R^2 = 0.65). When predicting RH100 and FHD values onto the validation data, model performance remained high (RMSE = 4.74; MAE = 2.88; R^2 = 0.66 for the RH100 model, and RMSE = 0.42; MAE = 0.30; R^2 = 0.66 for the FHD model; Fig. 3).

3.2. Occurrence models

3.2.1. Forest carnivores

Our top model for Pacific marten contained only base covariates coupled with daily detections of red squirrels. This model was 972.9 ΔAIC_c values better than the null model (i.e., random effects only; Appendix A) and exhibited an AUC = 0.82, indicating relatively strong predictive performance. Of the base covariates, marten occurrence increased with flat, valley-like terrain and the presence of squirrels. Marten occurrence had a strongly negative effect with the time since

rebaitying, indicating that as days increased since the last rebait, marten occurrence declined (Table 3). Our top model for Rocky Mountain red fox contained base covariates coupled with Landsat metrics (spruce-fir and lodgepole pine), as well as daily detections of coyotes. The top model was 266.4 ΔAIC_c values better than the null model (Appendix A) and presented an AUC = 0.82, indicating relatively strong predictive performance. Occurrence of red fox was positively related to deep snow and negatively related to the timing since last rebait. Further, red fox had a slight positive, yet statistically significant, association with daily coyote detections. Landsat metrics improved the base model, with red fox occurrence being significantly lower in lodgepole pine forests and demonstrating no significance in the proportion of spruce-fir cover (Table 3). Lastly, our top coyote model contained base covariates, daily detections of red squirrels, and a GEDI-derived metric (i.e., RH100-SD) that outperformed all Landsat metrics (Appendix A). Our top model was 35.8 ΔAIC_c values better than the null model (Appendix A) and exhibited an AUC = 0.80, indicating fairly strong predictive performance (Table 3). Models coupling the base covariates with Landsat metrics did not improve our ability to characterize coyote occurrence; however, when incorporating the GEDI-derived metric, RH100-SD, models improved by 6 ΔAIC_c . RH100-SD exhibited the strongest effect and was positively related to coyote occurrence (Fig. 4). Like marten, coyote occurrence increased in flat, valley-like terrain and decreased with time since rebait. Coyote occurrence strongly increased with deep snow and was positively related with detections of red squirrels (Table 3). Because all the carnivore models indicated relatively strong predictive performance, we mapped predictions for Pacific marten, Rocky Mountain red fox, and coyote occurrence across our study area (Fig. 5).

3.2.2. Prey

Occurrence patterns for both prey species were strongly influenced

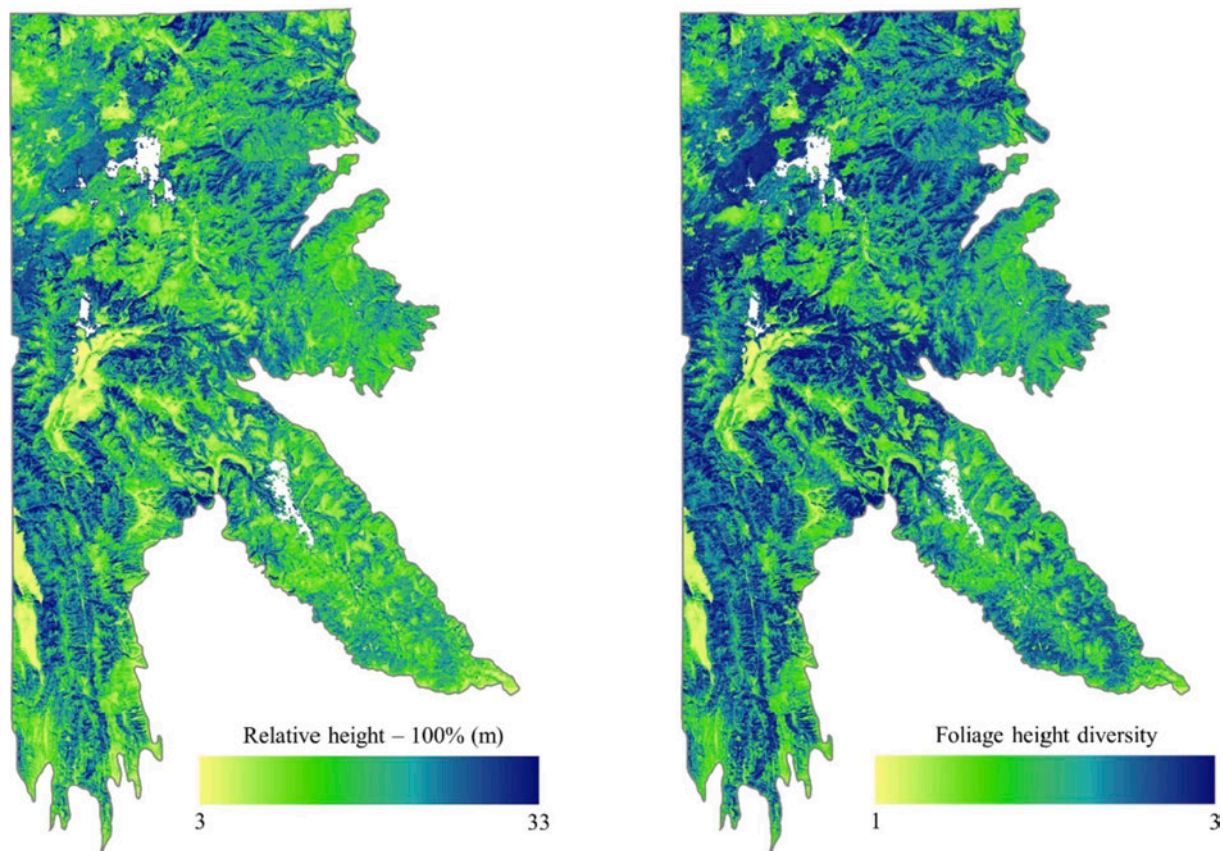


Fig. 3. Predicted GEDI relative height-100% and foliage height diversity coverage across our study area in the Greater Yellowstone Ecosystem, Wyoming, USA.

Table 3

Standardized coefficients and variance of random effects from our top occurrence models for Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), coyotes (*Canis latrans*), American red squirrels (*Tamiasciurus hudsonicus*), and snowshoe hares (*Lepus americanus*) across the Greater Yellowstone Ecosystem, Wyoming, USA. P-values ≤ 0.05 were determined as significant and bolded. The symbol σ (camera ID and year) represents variance of the random effect. See Appendix A for full model selection with number of parameters, model weights, and AIC_c (Akaike's information criterion) values.

Species	Covariates	Beta coefficients	Standard Error	P-value
Pacific marten	Intercept	-0.28	0.19	<0.01
	TPI	-0.23	0.08	0.01
	HLI	-0.08	0.10	0.40
	VRM	-0.13	0.09	0.12
	Snow depth	-0.03	0.04	0.42
	Rebait	-1.42	0.06	<0.01
	Red squirrel	0.05	0.02	0.02
	$\sigma_{\text{Camera ID}} = 0.88$		$\sigma_{\text{Year}} = 0.08$	
Rocky Mountain red fox	Covariates	Beta coefficients	Standard Error	P-value
	Intercept	-4.20	0.40	< 0.01
	TPI	0.11	0.13	0.28
	HLI	0.19	0.11	0.09
	VRM	0.17	0.10	0.09
	Snow depth	0.35	0.06	<0.01
	Rebait	-0.78	0.07	<0.01
	Spruce-fir	0.07	0.13	0.55
	Lodgepole pine	-0.26	0.11	0.02
	Coyote	0.07	0.02	<0.01
	$\sigma_{\text{Camera ID}} = 1.05$		$\sigma_{\text{Year}} = 0.44$	
	Covariates	Beta coefficients	Standard Error	P-value
Coyote	Intercept	-5.20	0.22	< 0.01
	TPI	-0.33	0.15	0.03
	HLI	0.19	0.16	0.22
	VRM	0.07	0.15	0.65
	Snow depth	0.32	0.09	<0.01
	Rebait	-0.21	0.08	<0.01
	RH100-SD	0.44	0.16	0.01
	Red squirrel	0.10	0.03	<0.01
	$\sigma_{\text{Camera ID}} = 1.69$		$\sigma_{\text{Year}} = 0.04$	
	Covariates	Beta coefficients	Standard Error	P-value
American red squirrel	Intercept	-4.94	0.51	< 0.01
	TPI	-0.05	0.23	0.82
	HLI	0.02	0.22	0.94
	VRM	-0.47	0.22	0.04
	Snow depth	0.48	0.06	<0.01
	Rebait	0.33	0.04	<0.01
	FHD	0.61	0.17	<0.01
	$\sigma_{\text{Camera ID}} = 3.48$		$\sigma_{\text{Year}} = 0.61$	
Snowshoe hare	Covariates	Beta coefficients	Standard Error	P-value
	Intercept	-5.29	0.34	< 0.01
	TPI	0.52	0.21	0.02
	HLI	0.23	0.22	0.30
	VRM	-0.22	0.21	0.30
	Snow depth	0.36	0.01	<0.01
	Rebait	0.14	0.05	0.01
	FHD	0.96	0.20	<0.01
	$\sigma_{\text{Camera ID}} = 3.56$		$\sigma_{\text{Year}} = 0.39$	

by GEDI metrics. Our top model for red squirrels contained base covariates, along with GEDI-derived FHD (Fig. 4); predator occurrence did not influence squirrel occurrence. This model was 104.3 ΔAIC_c values better than the null model (Appendix A) and had a strong fit with an AUC = 0.89. Foliage height diversity was the most important covariate with a significantly positive relationship, indicating squirrel occurrence increased with more variability in the vertical distribution of vegetation. Squirrel occurrence decreased with earlier time since rebaiting and increased with deeper snow, while occurrence decreased with rugged terrain (Table 3). Our top model for snowshoe hares matched red

squirrels, containing the base model coupled with GEDI-derived metrics and no predator covariates. This model was 44.4 ΔAIC_c values better than the null model (Appendix A) and exhibited an AUC = 0.87 indicating strong predictive performance. Snowshoe hare occurrence increased with dense and tall forest conditions indexed by FHD (Fig. 4); FHD was the most influential covariate (Table 3). Hare occurrence increased on ridgelines compared to flatter valleys, decreased with earlier time since rebaiting, and increased with deeper snow (Table 3). Like the carnivores, we used our top models to map red squirrel and snowshoe hare occurrence across our study area (Fig. 5).

3.3. Habitat use models

Habitat use models for our forest carnivores illustrated patterns similar to our occurrence models. For instance, the coyote model was improved by the GEDI-derived metric RH100-SD, while no forest metrics (Landsat nor GEDI-derived) improved the Pacific marten model. Our top model for marten habitat use contained only the base covariates coupled with daily detections of red squirrels. This model was 94.0 ΔAIC_c values better than the null model (Appendix B) and had relatively poor predictive performance ($r_s = 0.41$; p-value < 0.01). Like the marten occurrence model, habitat use was related to flatter, valley-like terrain and significantly reduced as time since rebait increased. Conversely, the daily detections of red squirrels were significantly less important for marten habitat use than occurrence (Table 4). Our top model for red fox contained only base covariates coupled with daily detections of red squirrels. This model was 7.3 ΔAIC_c better than the null model (Appendix B) and had relatively poor predictive performance ($r_s = 0.41$; p-value < 0.01). Habitat use for red fox decreased with time since rebait, was negatively related to snow depth, and decreased with daily detections of red squirrels (Table 4). Our top model for coyote contained the base covariates coupled with a GEDI-derived metric (i.e., RH100-SD). This model was 8.2 ΔAIC_c better than the null model (Appendix B) and had the weakest predictive performance ($r_s = 0.35$; p-value < 0.01). Rebaiting and patchy forest structure remained highly influential for coyote habitat use, while basin terrain was no longer significant compared to coyote occurrence patterns (Table 4).

4. Discussion

Conservation and management of highly mobile species requires an understanding of animal-environmental relationships, which may be aided by new and expansive remote sensing platforms. Spaceborne LiDAR from the GEDI mission is an example of such a platform, yet it is still novel with little integration into applications within animal ecology. Forest-dwelling species can be particularly dependent on vertical and horizontal forest structure for successful breeding, survival, and movement. Here, we coupled active and passive remote sensing platforms to extend habitat information from GEDI-sampled locations to unsampled areas to evaluate how information on vertical and horizontal forest structure may improve habitat modeling for a suite of forest carnivores (Pacific martens, Rocky Mountain red foxes, and coyotes) and their prey (red squirrels and snowshoe hares). Through our analytical process, we successfully upscaled GEDI LiDAR metrics (relative height-100% (RH100) and foliage height diversity (FHD)) across the GYE, leveraging continuous topographic and Landsat spectral information. Our animal-environment modeling indicated FHD significantly improved red squirrel and snowshoe hare occurrence models, whereas neither Landsat metrics nor GEDI-derived metrics improved marten occurrence or habitat use models. Our work indicated that GEDI-derived metrics did not enhance the red fox models, whereas, contrary to our expectations, RH100-SD (i.e., horizontal heterogeneity in canopy heights) significantly improved both the occurrence and habitat use models for coyotes. We also evaluated if other biotic and abiotic factors affected species occurrence and habitat use, in addition to whether GEDI-derived metrics improve characterizing animal-environmental relationships. We found

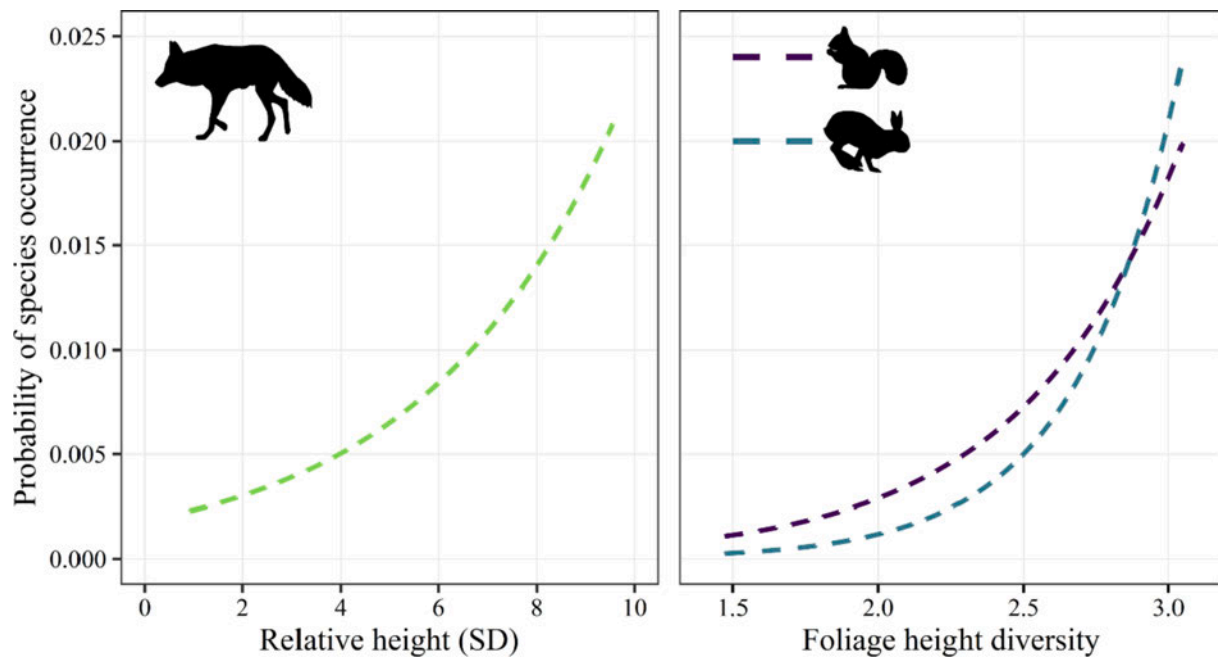


Fig. 4. Predicted species occurrence of coyotes (*Canis latrans*) as a function of relative height-100%-standard deviation (i.e., heterogeneity of tree height) and snowshoe hares (*Lepus americanus*), and American red squirrels (*Tamiasciurus hudsonicus*) as a function of foliage height diversity.

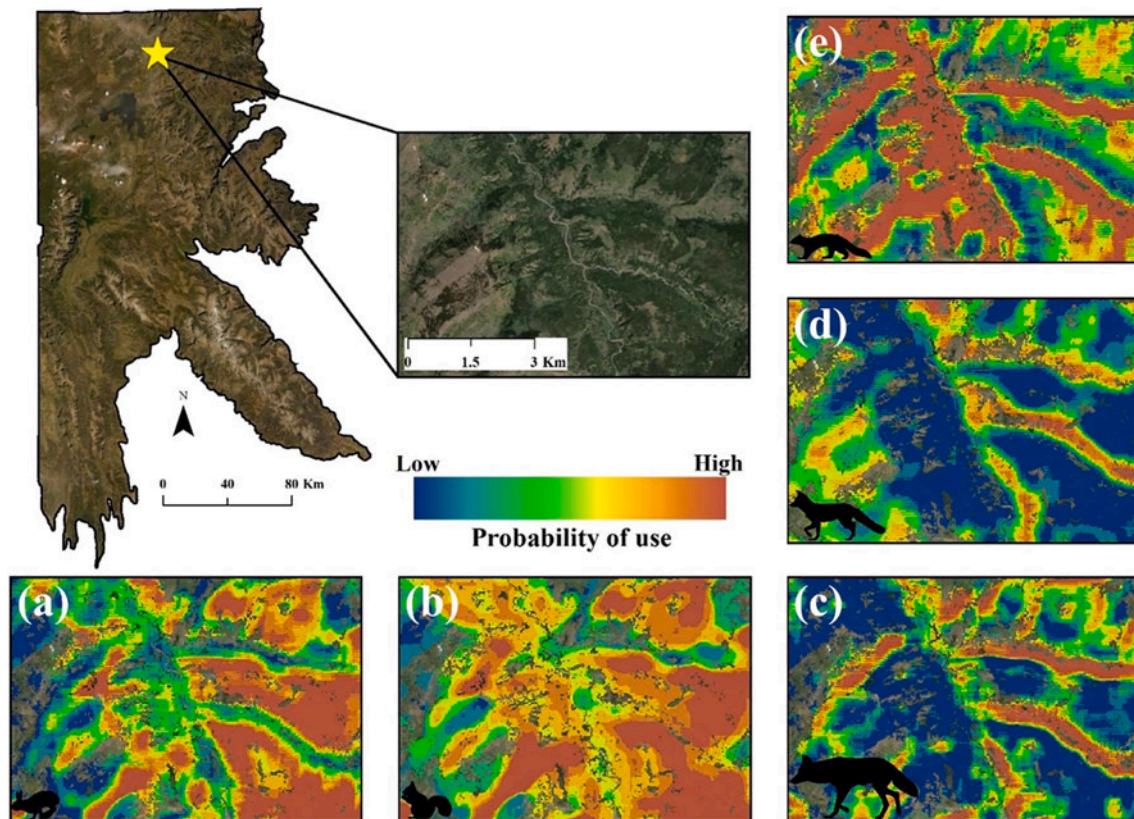


Fig. 5. Predicted probability of occurrence for Pacific martens (*Martes caurina*; (e)), Rocky Mountain red foxes (*Vulpes vulpes macroura*; (d)), coyotes (*Canis latrans*; (c)), American red squirrels (*Tamiasciurus hudsonicus*; (b)), and snowshoe hares (*Lepus americanus*; (a)) across the Greater Yellowstone Ecosystem, Wyoming, USA. The species-specific maps are small samples from the overall study area. The blank (i.e., no data) areas within the species-specific inset maps represent non-forested areas.

the frequency of rebaiting a camera trap and varying snow depth was influential across all species. The effect of rebaiting was relatively consistent with predator species generally attracted to baiting, whereas prey species were not; the effect of snow was more variable. Collectively,

our work advanced the understanding of animal-environment relationships among our forest-associated species by effectively combining GEDI samples with other data sources (i.e., Landsat) to generate spatially contiguous rasters. More broadly, we highlighted the utility of

Table 4

Standardized coefficients and variance of random effects from our top habitat use models for Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), and coyotes (*Canis latrans*) across the Greater Yellowstone Ecosystem, Wyoming, USA. P-values ≤ 0.05 were determined as significant and bolded. The symbol σ (camera ID and year) represents variance of the random effect. See Appendix B for full model selection with number of parameters, model weights, and AIC_c (Akaike's information criterion) values.

Species	Covariates	Beta coefficients	Standard Error	P-value
Pacific marten	Intercept	0.09	0.07	<0.01
	TPI	-0.10	0.04	0.02
	HLI	-0.09	0.05	0.06
	VRM	-0.03	0.04	0.52
	Snow depth	-0.05	0.04	0.18
	Rebait	-0.33	0.04	<0.01
	Red squirrel	-0.05	0.02	<0.01
	$\sigma_{\text{Camera ID}} = 0.15$		$\sigma_{\text{Year}} = 0.00$	
	Covariates	Beta coefficients	Standard Error	P-value
	Intercept	-0.40	0.27	0.14
Rocky Mountain red fox	TPI	0.07	0.06	0.24
	HLI	-0.02	0.06	0.78
	VRM	0.00	0.06	0.98
	Snow depth	-0.19	0.06	<0.01
	Rebait	-5.99	1.27	<0.01
	Spruce-fir	-0.05	0.07	0.51
	Lodgepole pine	-0.19	0.09	0.03
	Red squirrel	-0.06	0.03	0.01
	$\sigma_{\text{Camera ID}} = 0.22$		$\sigma_{\text{Year}} = 0.05$	
	Covariates	Beta coefficients	Standard Error	P-value
Coyote	Intercept	0.22	0.14	0.11
	TPI	-0.04	0.06	0.51
	HLI	0.08	0.06	0.18
	VRM	-0.03	0.07	0.64
	Snow depth	-0.09	0.08	0.23
	Rebait	-0.29	0.08	<0.01
	RH100-SD	0.15	0.06	0.02
	$\sigma_{\text{Camera ID}} = 0.04$		$\sigma_{\text{Year}} = 0.04$	
	Covariates	Beta coefficients	Standard Error	P-value
	Intercept	0.22	0.14	0.11

integrating novel remote sensing tools in animal ecology and conservation.

4.1. Predator-prey habitat insights

Counter to our expectations for Pacific marten, our modeled GEDI metrics had no detectable influence on marten occurrence and habitat use. Rather, marten occurrence and use were consistently influenced by lower-laying basins and the frequency of rebaiting. The frequency of rebaiting was by far the most influential covariate, which is not surprising as baiting camera traps is an effective method to detect *Martes* (Long and MacKay, 2012). The daily detections of red squirrels positively influenced marten occurrence, yet was negatively associated with habitat use. Many western North American studies have found red squirrel middens are used by martens for resting and denning, and that martens may predate on red squirrels during the winter (Murie, 1961; Raine, 1983; Buskirk, 1984; Sherburne and Bissonette, 1993; Coffin, 1994; Ruggiero et al., 1998). Based on our results, martens do not appear to be impacted by variation in snow depth, at least within the sampling frame of our camera traps. Snow does not seem to limit marten habitat use (Raine, 1983; Martin et al., 2021), and indeed marten may take advantage of deeper snow to avoid predators (e.g., bobcats [*L. rufus*] and coyotes; Krohn et al., 2005; Moriarty et al., 2015). We expected GEDI-derived metrics and/or Landsat metrics to influence marten occurrence and habitat use; however, neither were supported in our top model. Martens are strongly associated with structurally complex, mature forests (Buskirk and Powell, 1994; Moriarty et al., 2015) and avoid areas with more than 25% forest cover removed (Hargis et al., 1999; Thompson et al., 2012). Our camera traps were placed in mostly

mature, multi-storied forest stands; therefore, it was surprising that no GEDI-derived or Landsat metrics improved the models. Using airborne LiDAR, Tweedy et al. (2019) found the probability of selection for martens increased with higher canopy cover surrounding rest structures and increased structural complexity at finer spatial scales. Perhaps different characterizations of forests using LiDAR, GPS monitoring of marten, or both would shed additional light on the relationship between marten and forest structural attributes. Alternatively, because most of our camera traps were deployed in mature, multi-storied forests (i.e., a likely habitat to detect martens), we may have constrained sampling such that detecting variation in occurrence and habitat use associated with forest conditions was limited (see Appendix C for comparisons of GEDI-derived metrics and elevation at camera traps and random locations across the GYE). The naïve occupancy rate for marten across camera stations was 96%; thus, there was little spatial variation among forest types and structures to evaluate.

Rocky Mountain red fox occurrence and habitat use were influenced by some forest characteristics (Landsat metrics—spruce-fir and lodgepole pine) but not GEDI-derived metrics. We expected ruggedness to influence red fox occurrence as a strategy to avoid intraguild competition with coyotes (Fuhrmann, 1998; Crabtree and Sheldon, 1999). However, red fox occurrence and habitat use were not influenced by any topographic variables (i.e., TPI, HLI, and VRM). Predator-prey questions associated with red fox yielded different results between the occurrence model, which indicated a negative effect from daily detections of red squirrels, and the habitat use model, which indicated a positive effect from daily detections of coyotes. Red foxes are noted to rarely eat red squirrels (Aubry, 1983; Cross and Crabtree, 2021) and have opposing diel activity patterns (Smith, 2021; thus, no relationship may be expected. The positive association between use by red foxes and daily detections of coyotes may indicate a degree of tolerance by coyotes. Studies have demonstrated that coyotes tolerate foxes in the absence of ungulate carcasses (Gese et al., 1996). Further, Rocky Mountain red foxes are well adapted to deep snow with larger, furrier feet than European red foxes and have less foot-loading than coyotes, which may explain their tendency to occur in deeper snow (Fuhrmann, 1998). GEDI-derived metrics did not aid our efforts to explain red fox occurrence or habitat use, yet some Landsat metrics were selected in our top models. Our findings indicated that lodgepole pine was negatively associated with red fox occurrence and habitat use, perhaps illustrating increased fox use in more mesic areas. Van Etten et al. (2007) observed Rocky Mountain red fox home ranges were primarily within Douglas-fir habitats, while lodgepole pine only accounted for approximately 6% across home ranges. Further, red foxes preferred subalpine/montane forests to open areas (Fuhrmann, 1998), but also were associated with sagebrush, which was presumed to be important for escape cover (Fuhrmann, 1998; Van Etten et al., 2007). Our results, coupled with others (e.g., Fuhrmann, 1998; Van Etten et al., 2007), may indicate that Rocky Mountain red foxes are habitat generalists within forested environments, or that additional work is needed at a finer resolution (i.e., GPS monitoring of foxes) to assess fine-scale conditions that may affect habitat selection.

Our study was one of a few (e.g., Gantz and Knowlton, 2005; Kolbe et al., 2007; Gese et al., 2013) to investigate coyote habitat relationships in rugged, mountainous terrain. Coyotes are often associated with lower elevation, relatively flat areas (Crabtree and Sheldon, 1999; Arjo et al., 2002) during the winter, where they scavenge for ungulate carrion (Crabtree and Sheldon, 1999; Sivy et al., 2017). In our study's rugged/mountainous terrain, coyote occurrence was associated with flat, basin-like terrain. Coyotes are not morphologically adapted to deep snow landscapes (Murray and Boutin, 1991; Penczykowski et al., 2017), yet studies have found coyotes occur in deep snow conditions (e.g., Crête and Larivière, 2003; Kolbe et al., 2007; Dowd et al., 2014). Our findings indicated coyotes occurred in structurally heterogeneous habitats (i.e., GEDI RH100-SD), with deep snow and a greater occurrence of red squirrels, whereas their habitat use increased in patchy habitats and was

not impacted by varying snow depths. We presume that the positive relationship between coyotes and RH100-SD was related to food diversity and availability (e.g., small mammals, grouse [*Bonasa umbellus*; *Dendragapus obscurus*]). Although, additional work is needed to determine the function of uneven canopy structure or intermittent gaps in canopy cover to help distinguish the functional role to coyotes. In northwestern Wyoming, Dowd et al. (2014) found that coyotes used dense canopy cover with increased snow penetration and an abundance of rodents (*Microtines*) and red squirrel snow tracks. Additionally, when snow depth increased, coyotes used less canopy cover, and were often found in open woodlands for travel (Dowd et al., 2014; Pozzanghera et al., 2016). Gese et al. (2013) found that coyotes increased their use of snowmobile trails with increased snow depth and penetrability off-trail; however, other studies found that when the snow column was supportive, coyotes traveled off-trail (Kolbe et al., 2007; Whiteman and Buskirk, 2013) extensively. In many forested ecosystems, ungulate carion is one of the most common winter food items for coyotes (Crabtree and Sheldon, 1999; Dowd and Gese, 2012; Sivy et al., 2017), although other studies have pointed to the role of rodents for forested-living coyotes (O'Donoghue et al., 1997; Dumond et al., 2001). In our study, camera trap rebaiting was one of the most influential factors in coyote occurrence and habitat use, which illustrates the importance of scavenging for coyotes. Additional work is needed to clarify coyote ecology and resource requirements in high-elevation environments during winter.

In western North America, red squirrels are dependent on mature, coniferous forests with an abundance of large diameter spruce-fir and lodgepole pine stands for greater food production (e.g., cones, seeds, and fungi; Steele, 1998; Frey, 2003), nest sites, thermoregulation, and escape cover from predators (Steele, 1998). As we expected, red squirrel occurrence was strongly related to the GEDI-derived FHD and snow depth. The strong positive association between red squirrels and FHD likely supports the notion that squirrels require dense, mature forests for high-quality and quantity food resources (Frey, 2003; Haughland and Larsen, 2004; Posthumus et al., 2015; Elkins et al., 2018). In Scotland, Flaherty et al. (2014) tested whether airborne LiDAR could aid in characterizing habitat suitability for the endangered Eurasian red squirrel (*Sciurus vulgaris* L.), and found that incorporating habitat heterogeneity was very advantageous for characterizing suitability. This study went further to illustrate that only 27% of the forest had highly suitable habitat for Eurasian red squirrels, while the remaining forest had low-canopy cover (e.g., lack of protection from predators) or low tree density and young trees (e.g., not able to produce seeds; Flaherty et al., 2014). Lastly, Robold and Huettmann (2021) found that LiDAR-derived covariates helped generate accurate predictions of red squirrel middens within interior Alaska. Our work, along with others, suggests that LiDAR can be powerful for assessing squirrel-habitat relationships.

As we expected, snow depth and GEDI-derived FHD were two of the strongest effects on snowshoe hare occurrence. Snowshoe hares depend on contiguous habitats with high horizontal cover (Hodges et al., 2009; Lewis et al., 2011) and are often found in mature and late-successional multi-storied forests (Buskirk et al., 1999; Ellsworth and Reynolds, 2006; Berg et al., 2012; Ivan et al., 2014). Our results reinforced that dense forests are strong drivers of hare occurrence. Because hares are an ecologically important herbivore, and a primary prey species of the federally threatened Canada lynx (Squires and Ruggiero, 2007), extensive research has been conducted to advance our understanding of hare-habitat relationships. In recent years, airborne LiDAR has been used to characterize forest structure at landscape scales (e.g., Jensen et al., 2021). Holbrook et al. (2017) found that increased hare occupancy and use was associated with multi-storied forest with dense canopy cover and medium-sized trees (e.g., 12.7–24.4 cm in diameter at breast height). Further, studies have demonstrated a close association with relative density of snowshoe hares and density of horizontal cover (Lewis et al., 2011; Holbrook et al., 2017). Likewise, Jensen et al. (2021) found that hare density increased as canopy and horizontal cover

increased, and medium-height trees (~5–10 m) were present. Although our study did not truly capture understory structure, an overall increase in FHD may indicate an increase in horizontal cover associated with multi-storied stands, thus increasing the probability of hare occurrence. In addition to forest structure, our results indicated increased snow depth influenced hare occurrence. Our findings add to the growing literature indicating snow cover may be just as important as forest cover and heterogeneity for predicting the occurrence of snowshoe hares (Lewis et al., 2011; Sultaire et al., 2016a; Sultaire et al., 2016b; Holbrook et al., 2017; Peers et al., 2020).

4.2. Spaceborne LiDAR applications

Characterizing forest structure has been limited to photo interpretation or on-the-ground field measurements and, more recently, airborne LiDAR systems, which provide estimates of forest biomass and volume to monitor forest degradation, habitat, and biodiversity. Current methods, however, are often expensive and impractical for large spatial extents (Potapov et al., 2021) or expansive time-series. A significant benefit of spaceborne LiDAR with GEDI, in particular, is providing consistent samples of forest structure across the planet that are spatially dense and freely available (Randin et al., 2020; Jensen et al., 2021). GEDI products can likely improve animal-environment assessments in other parts of the world, where discrete return LiDAR is lacking or unlikely to arrive anytime soon. For forest carnivores such as Pacific martens, Rocky Mountain red foxes, and coyotes, which rely on large spatial extents, advancing our understanding of how forest structure characteristics influence occurrence and habitat use is critical for adequate management and conservation. In our study, data fusion leveraging the forest structure information of GEDI and the continuous extent of Landsat aided our efforts to characterize animal-environment relationships, particularly for coyotes, red squirrels, and snowshoe hares. On the other hand, marten and red fox models did not improve when GEDI-derived metrics were coupled with topographic and climate variables. Predicting forest structure metrics to unsampled areas using Landsat 8 did not sufficiently represent conditions important to marten and red fox. There are several reasons why our forest structure metrics might not have aided our modeling efforts with these species, given our wildlife sampling (Appendix C). However, additional work incorporating animals with GPS monitors would provide more opportunities to assess the power of mapped forest structure information in characterizing animal-environment relationships at varying temporal and spatial scales. From our observations, GEDI data helped improve knowledge about wildlife-habitat relationships in ways not previously attainable and will have a rich future in animal habitat ecology.

4.3. Conclusions

The ability to scale-up vertical vegetation structure sampled from space fills an important research gap with implications for animal ecology and management (Ehrlén and Morris, 2015). GEDI is a consistent and dense sample of forest structure information obtained at near-global extents. When paired with other sensors, such as Landsat 8, GEDI can greatly improve habitat information at spatial and temporal scales commensurate with field data collected on animals. Our top models characterizing coyote, red squirrel, and snowshoe hare occurrence all had either GEDI RH100-SD or FHD as the most important covariate, indicating that GEDI-derived products significantly improved our ability to assess the importance of forest characteristics for these species. Although our work successfully applied spaceborne LiDAR to map and assess the importance of forest characteristics for forest-associated species, future work would benefit from expanding on these spatio-temporal questions. For instance, incorporating GEDI metrics and upscaling processes to pair with GPS collaring of forest carnivores would allow resolute questions aimed at animal movement, habitat selection, and variation in home range size. Alternatively, asking longer-term

questions and integrating a time-series of GEDI metrics could shed light on forest disturbance consequences on focal species or biodiversity. Our work indicated that spaceborne LiDAR collected from the GEDI mission provided a ready sampling of forest structure that could be combined with other remotely sensed data to improve our understanding of animal-habitat relationships. Our successes are likely transferable to other landscapes and animal species.

Credit authorship contribution statement

Austin B. Smith: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Jody C. Vogeler:** Methodology, Software, Writing – review & editing, Supervision. **Nichole L. Bjornlie:** Resources, Data curation, Writing – review & editing. **John R. Squires:** Resources, Data curation, Writing – review & editing. **Neal C. Swayze:** Methodology, Software, Validation, Data curation, Writing – review & editing. **Joseph D. Holbrook:** Conceptualization, Data curation, Formal analysis, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Model selection for occurrence models for Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), coyotes (*Canis latrans*), snowshoe hares (*Lepus americanus*), and American red squirrels (*Tamiasciurus hudsonicus*) in the Greater Yellowstone Ecosystem, Wyoming, USA. The table includes full models with covariates; *k* represents the number of parameters, AIC_c indicates Akaike's information criterion, and *w* represents the model's weight.

Pacific marten					
Model tier	Models	<i>k</i>	AIC _c	ΔAIC _c	<i>w</i>
Null	(1 CameraID) + (1 Year)	3	13799.39	972.92	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	8	12829.60	3.13	0.06
Base + Landsat	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	9	12827.78	1.31	0.14
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	10	12827.86	1.40	0.13
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	10	12829.73	3.27	0.05
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	10	12829.78	3.31	0.05
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	9	12830.71	4.25	0.03
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	9	12831.22	4.75	0.02
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	9	12830.00	3.54	0.05
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	9	12830.12	3.65	0.04
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	9	12831.27	4.81	0.02
	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + (1 CameraID) + (1 Year)	9	12826.46	0.00	0.27
Base + Top Landsat/GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	10	12828.18	1.72	0.11
	TPI + HLI + VRM + Snow depth + Rebait + Snowshoe hare + (1 CameraID) + (1 Year)	9	12831.12	4.66	0.03
Rocky Mountain red fox					
Null	(1 CameraID) + (1 Year)	3	7274.37	266.35	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	8	7023.79	15.77	0.00
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	10	7021.40	13.39	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	9	7024.68	16.66	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	9	7025.67	17.65	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	9	7025.79	17.77	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	10	7025.86	17.84	0.00
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	10	7026.38	18.36	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	9	7025.35	17.33	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	9	7025.72	17.71	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	9	7025.74	17.72	0.00
	TPI + HLI + VRM + Snow depth + Rebait + Coyote + (1 CameraID) + (1 Year)	11	7008.02	0.00	0.97
Base + Top Landsat or GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + (1 CameraID) + (1 Year)	11	7016.37	8.35	0.01
	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	12	7016.90	8.89	0.01
	TPI + HLI + VRM + Snow depth + Rebait + Snowshoe hare + (1 CameraID) + (1 Year)	11	7021.38	13.36	0.00
Coyote					
Null	(1 CameraID) + (1 Year)	3	3272.31	35.80	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	8	3249.09	12.57	0.00
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	9	3249.41	12.90	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	9	3250.28	13.77	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	9	3250.64	14.12	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	10	3250.87	14.35	0.00

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Pacific marten					
Model tier	Models	k	AIC _c	ΔAIC _c	w
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	10	3251.33	14.82	0.00
	(1 CameraID) + (1 Year) + TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine	10	3251.97	15.46	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	9	3243.05	6.54	0.03
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	9	3249.65	13.14	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	9	3250.76	14.25	0.00
Base + Top GEDI or Landsat + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Red squirrel + (1 CameraID) + (1 Year)	10	3236.51	0.00	0.68
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	11	3238.30	1.79	0.28
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Snowshoe hare + (1 CameraID) + (1 Year)	10	3244.45	7.94	0.01
American red squirrel					
Null	(1 CameraID) + (1 Year)	3	6517.24	104.28	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	8	6425.16	12.20	0.00
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	10	6421.41	8.45	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	9	6425.01	12.05	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	9	6425.50	12.54	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	10	6426.37	13.41	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	9	6427.16	14.2	0.00
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	10	6427.21	14.25	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	9	6412.97	0.01	0.26
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	9	6423.14	10.18	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	9	6425.10	12.14	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Coyote + (1 CameraID) + (1 Year)	10	6412.96	0.00	0.26
Base + Top Landsat/GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + Coyote + (1 CameraID) + (1 Year)	11	6414.77	1.81	0.10
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + (1 CameraID) + (1 Year)	10	6414.87	1.91	0.10
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + Coyote + (1 CameraID) + (1 Year)	11	6414.90	1.94	0.10
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + (1 CameraID) + (1 Year)	10	6414.92	1.96	0.10
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + Rocky Mountain red fox + Coyote + (1 CameraID) + (1 Year)	12	6416.72	3.76	0.04
Snowshoe hare	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + Pacific marten + (1 CameraID) + (1 Year)	11	6416.84	3.88	0.04
	(1 CameraID) + (1 Year)	3	4841.51	44.43	0.00
	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	8	4820.79	23.72	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	9	4812.38	15.30	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	10	4813.50	16.42	0.00
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	10	4814.12	17.05	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	9	4818.25	21.18	0.00
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	10	4819.45	22.37	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	9	4819.67	22.59	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	9	4797.07	0.00	0.33
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	9	4808.85	11.77	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	9	4822.28	25.21	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Coyote + (1 CameraID) + (1 Year)	10	4798.34	1.27	0.18
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + (1 CameraID) + (1 Year)	10	4798.80	1.72	0.14
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + (1 CameraID) + (1 Year)	10	4799.02	1.95	0.13
Base + Top Landsat or GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + Coyote + (1 CameraID) + (1 Year)	11	4800.02	2.94	0.08
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + Coyote + (1 CameraID) + (1 Year)	11	4800.31	3.23	0.07
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Rocky Mountain red fox + Pacific marten + (1 CameraID) + (1 Year)	11	4800.73	3.66	0.05
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + Rocky Mountain red fox + Coyote + (1 CameraID) + (1 Year)	12	4801.97	4.90	0.03
	TPI + HLI + VRM + Snow depth + Rebait + FHD + Pacific marten + Rocky Mountain red fox + Coyote + (1 CameraID) + (1 Year)	12	4801.97	4.90	0.03

Appendix B. Model selection results for habitat use models for Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), and coyotes (*Canis latrans*) in the Greater Yellowstone Ecosystem, Wyoming, USA. The table includes full models with covariates; *k* represents the number of parameters, AIC_c indicates Akaike's information criterion, and *w* represents the model's weight.

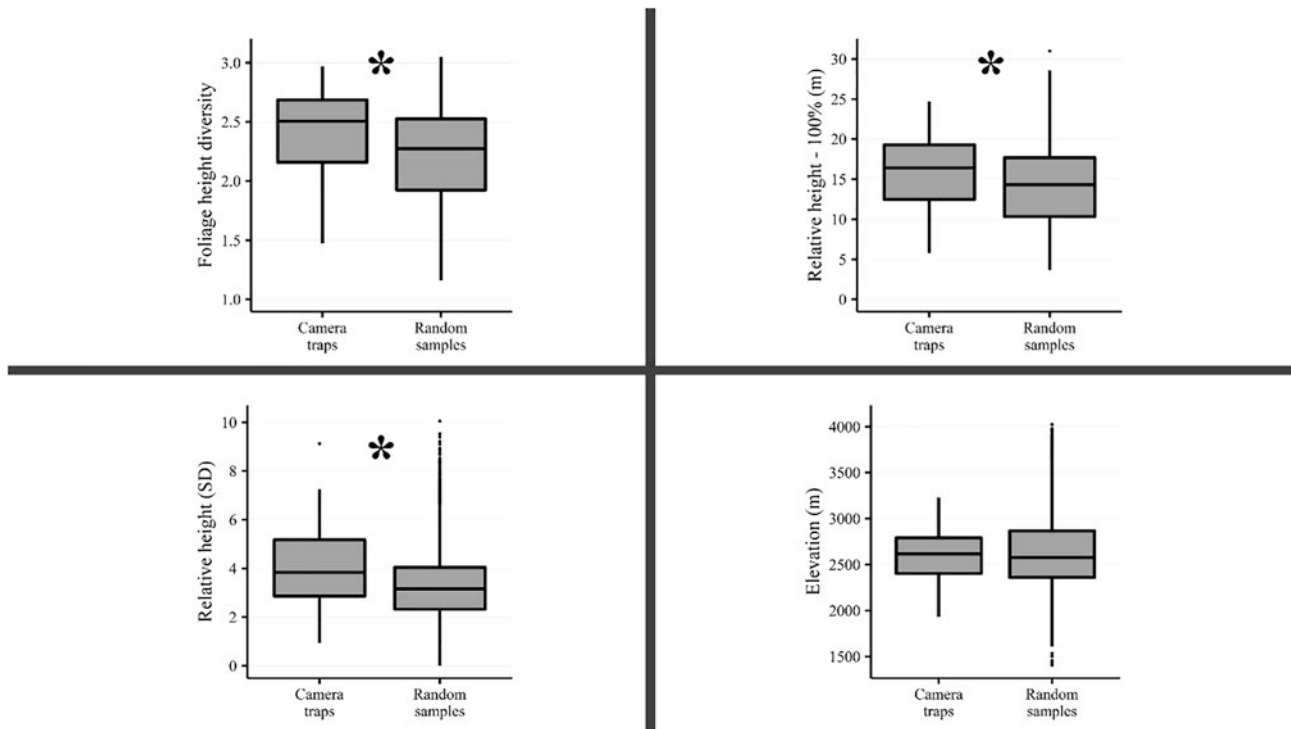
Pacific marten					
Model tier	Models	k	AIC _c	ΔAIC _c	w
Null	(1 CameraID) + (1 Year)	4	10436.04	93.98	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	9	10350.41	8.35	0.01
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	10	10352.04	9.98	0.00
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	10	10352.37	10.31	0.00
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	10	10352.42	10.36	0.00
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	11	10352.55	10.49	0.00

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Pacific marten					
Model tier	Models	k	AIC _c	ΔAIC _c	w
Base + GEDI	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	11	10353.99	11.93	0.00
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	11	10354.35	12.29	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	10	10352.32	10.26	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	10	10352.37	10.31	0.00
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	10	10352.43	10.37	0.00
Base + Top Landsat or GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	11	10342.06	0.00	0.58
	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + (1 CameraID) + (1 Year)	10	10342.98	0.92	0.37
	TPI + HLI + VRM + Snow depth + Rebait + Snowshoe hare + (1 CameraID) + (1 Year)	10	10348.85	6.79	0.02
Rocky Mountain red fox					
Null	(1 CameraID) + (1 Year)	4	3764.22	29.30	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	9	3740.35	5.43	0.03
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	11	3739.78	4.86	0.04
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	10	3741.67	6.75	0.02
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	10	3742.18	7.26	0.01
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	10	3742.38	7.46	0.01
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	11	3742.68	7.76	0.01
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	11	3744.19	9.28	0.00
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	10	3741.78	6.86	0.01
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	10	3742.07	7.15	0.01
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	10	3742.16	7.24	0.01
	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	11	3734.92	0.00	0.46
Base + GEDI	TPI + HLI + VRM + Snow depth + Rebait + Red squirrel + (1 CameraID) + (1 Year)	10	3736.47	1.56	0.21
	TPI + HLI + VRM + Snow depth + Rebait + Snowshoe hare + (1 CameraID) + (1 Year)	10	3737.26	2.34	0.14
	TPI + HLI + VRM + Snow depth + Rebait + Coyote + (1 CameraID) + (1 Year)	10	3741.01	6.09	0.02
Coyote					
Null	(1 CameraID) + (1 Year)	4	992.05	8.16	0.00
Base	TPI + HLI + VRM + Snow depth + Rebait + (1 CameraID) + (1 Year)	9	987.27	3.38	0.05
Base + Landsat	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + NBR + (1 CameraID) + (1 Year)	11	986.64	2.75	0.07
	TPI + HLI + VRM + Snow depth + Rebait + NBR + (1 CameraID) + (1 Year)	10	987.41	3.52	0.05
	TPI + HLI + VRM + Snow depth + Rebait + NDVI + (1 CameraID) + (1 Year)	10	988.32	4.43	0.03
	TPI + HLI + VRM + Snow depth + Spruce-fir + (1 CameraID) + (1 Year)	10	988.51	4.62	0.03
	TPI + HLI + VRM + Snow depth + Spruce-fir + NDVI + (1 CameraID) + (1 Year)	11	988.64	4.75	0.02
	TPI + HLI + VRM + Snow depth + Rebait + Spruce-fir + Lodgepole pine + (1 CameraID) + (1 Year)	11	990.64	6.75	0.01
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + (1 CameraID) + (1 Year)	10	983.89	0.00	0.26
	TPI + HLI + VRM + Snow depth + Rebait + RH100 + (1 CameraID) + (1 Year)	10	989.02	5.13	0.02
	TPI + HLI + VRM + Snow depth + Rebait + FHD + (1 CameraID) + (1 Year)	10	989.33	5.44	0.02
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Red squirrel + (1 CameraID) + (1 Year)	11	984.05	0.16	0.24
Base + Top Landsat or GEDI + Predator/prey	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Red squirrel + Snowshoe hare + (1 CameraID) + (1 Year)	12	985.77	1.88	0.10
	TPI + HLI + VRM + Snow depth + Rebait + RH100-SD + Snowshoe hare + (1 CameraID) + (1 Year)	11	985.82	1.93	0.10

Appendix C. Boxplots comparing GEDI metrics (i.e., relative height- 100% (m), relative height- 100%- standard deviation, and foliage height diversity) and elevation between camera trap locations ($n = 107$) and randomized sampling points ($n \approx 19,400$) from across the Greater Yellowstone Ecosystem (GYE), Wyoming, USA. To generate the random sample, we created a 1 km² grid across the GYE, and randomly sampled 50% of the 1 km² grids (i.e., $n \approx 19,400$). The centroid of the 1 km² grids were used to append 2015 GEDI metrics and elevation values. The asterisks below indicate if there was statistical difference ($\alpha = 0.05$) between camera traps and random samples.



References

- Andruskiw, M., Fryxell, J.M., Thompson, I.D., Baker, J.A., 2008. Habitat-mediated variation in predation risk by the American marten. *Ecology* 89 (8), 2273–2280.
- Arjo, W.M., Pletscher, D.H., Ream, R.R., 2002. Dietary overlap between wolves and coyotes in northwestern Montana. *J. Mammal.* 83 (3), 754–766.
- Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., Heckler, J., Evans, L.J., Jucker, T., Goossens, B., Stark, D.J., Reynolds, G., Ong, R., Renneboog, N., Kugan, F., Coomes, D.A., 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biol. Conserv.* 217, 289–310.
- Atwood, T.C., Gese, E.M., Kunkel, K.E., 2009. Spatial partitioning of predation risk in a multiple predator–multiple prey system. *J. Wildl. Manage.* 73 (6), 876–884.
- Aubry, K.N., 1983. The Cascade red fox: distribution, morphology, zoogeography and ecology. Dissertation. University of Washington, Seattle.
- August, P.V., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64 (6), 1495–1507.
- Barton, K., 2020. MuMIn: Multi-model inference. R package version 1.43-17. <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.
- Berg, N.D., Gese, E.M., Squires, J.R., Aubry, L.M., 2012. Influence of forest structure on the abundance of snowshoe hares in western Wyoming. *J. Wildl. Manage.* 76 (7), 1480–1488.
- BLM, 2016. Federal mineral ownership. University of Wyoming GeoHub. <https://service.s.wygis.org/hostgis/rest/services/GeoHub/BLMFederalMineralOwnership/MapServer> (accessed April 2021).
- Breiman, L., 2001. Random Forests. *Mach. Learn.* 45, 5–32.
- Brigham, R.M., Geiser, F., 2012. Do red squirrels (*Tamiasciurus hudsonicus*) use daily torpor during winter? *Ecoscience* 19 (2), 127–132.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference, second ed. Springer, New York.
- Buskirk, S.W., 1984. Seasonal use of resting sites by marten in south-central Alaska. *J. Wildl. Manage.* 48 (3), 950. <https://doi.org/10.2307/3801445>.
- Buskirk, S.W., Powell, R.A., 1994. Habitat ecology of fishers and American martens. In: Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), *Martens, sables, and fishers: Biology and conservation*. Cornell University Press, Ithaca, pp. 283–296.
- Buskirk, S.W., Ruggiero, L.F., 1994. American marten. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J. (Eds.), *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States*. Gen. Tech. Rep. RM-254. U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, pp. 7–37.
- Buskirk, S.W., Ruggiero, L.F., Krebs, C.J., 1999. Habitat fragmentation and interspecific competition: Implications for lynx conservation. In: Ruggiero, L.F., Aubry, K.A., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and conservation of lynx in the United States*. Gen. Tech. Rep. RMRS-GTE-30WWW. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, pp. 83–100.
- Coffin, K.W., 1994. Population characteristics and winter habitat selection by pine martens in southwest Montana. Thesis. Montana State University, Bozeman.
- Crabtree, R.L., Sheldon, J.W., 1999. Coyotes and canid coexistence. In: Clark, S.T.W., Curlee, A.P., Kareiva, P. (Eds.), *Carnivores in ecosystems: the Yellowstone experience*. Yale University Press, New Haven, pp. 127–163.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86 (12), 3387–3397.
- Crête, M., Larivière, S., 2003. Estimating the costs of locomotion in snow for coyotes. *Can. J. Zool.* 81 (11), 1808–1814.
- Cross, P.R., Crabtree, R.L., 2021. Recent findings suggest adding red fox (*Vulpes vulpes*) to climate-threatened whitebark pine (*Pinus albicaulis*) trophic system. *Can. J. Zool.* 99 (7), 618–623.
- Davies, A.B., Oram, F., Ancrenaz, M., Asner, G.P., 2019. Combining behavioural and LiDAR data to reveal relationships between canopy structure and orangutan nest site selection in disturbed forests. *Biol. Conserv.* 232, 97–107.
- De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., Finke, P., Van Meirvenne, M., Verniers, J., Crombé, P., 2013. Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186, 39–49.
- Despain, D.G., 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder.
- Dowd, J.L.B., Gese, E.M., 2012. Seasonal variation of coyote diet in northwestern Wyoming: implications for dietary overlap with Canada lynx? *Northwest Sci.* 86, 289–299.

- Dowd, J.L.B., Gese, E.M., Aubry, L.M., 2014. Winter space use of coyotes in high-elevation environments: behavioral adaptations to deep-snow landscapes. *J. Ethol.* 32 (1), 29–41.
- Dubayah, R.O., Drake, J.B., 2000. Lidar remote sensing for forestry. *J. For.* 98, 44–46.
- Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P., Marselis, S., Patterson, P.L., Qi, W., Silva, C., 2020. The Global Ecosystem Dynamics Investigation: high-resolution laser ranging of the Earth's forests and topography. *Sci. Remote Sens.* 1, 100002. <https://doi.org/10.1016/j.srs.2020.100002>.
- Dubayah, R., Hofton, M., Blair, J., Armston, J., Tang, H., Luthcke, S., 2021a. GEDI L2A elevation and height metrics data global footprint Level V002 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/GEDI/GEDI02_A.002 (accessed August 2021).
- Dubayah, R., Tang, H., Armston, J., Luthcke, S., Hofton, M., Blair, J., 2021b. GEDI L2B canopy cover and vertical profile metrics data global footprint level V002 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/GEDI/GEDI02_B.002 (accessed August 2021).
- Dumond, M., Villard, M.-A., Tremblay, É., 2001. Does coyote diet vary seasonally between a protected and an unprotected forest landscape? *Ecoscience* 8 (3), 301–310.
- Earthdata Search, 2019. Greenbelt, MD: Earth Science Data and Information System (ESDIS) Project, Earth Science Projects Division (ESPD), Flight Projects Directorate, Goddard Space Flight Center (GSFC) National Aeronautics and Space Administration (NASA). <https://urs.earthdata.nasa.gov/> (accessed August 2021).
- Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* 18 (3), 303–314.
- Elkins, E.K., Tyers, D.B., Frisina, M.R., Rossi, J.L., Sowell, B., 2018. Red squirrel (*Tamiasciurus hudsonicus*) midden site selection and conifer species composition. *Environ. Manag. Sustain. Dev.* 7 (2), 15. [https://doi.org/10.5296/emsd.v7i2.12674](https://doi.org/10.5296/emsd.v7i210.5296/emsd.v7i2.12674).
- Ellis, L.M., 1998. Habitat-use patterns of the American marten in the southern Cascade Mountains of California, 1992–1994. Thesis. Humboldt State University, Arcata.
- Ellsworth, E., Reynolds, T.D., 2006. Snowshoe hare (*Lepus americanus*): a technical conservation assessment. United States Forest Service, Rocky Mountain Region.
- ESRI (Environmental Systems Research Institute), 2020. ArcGIS desktop. Release 10.8.1. Environmental Systems Research Institute, Redlands.
- Evans, J.S., Oakleaf, J., Cushman, S.A., Theobald, D., 2014. An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0-0. <https://evansmurphy.wixsite.com/evansspatial/arcgis-gradient-metrics-toolbox> (accessed December 2020).
- Evans, J.S., 2021. spatialEco. R package version 1.3-6. <https://github.com/jeffrejevans/spatialEco>.
- Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D., 2007. The shuttle radar topography mission. *Rev. Geophys.* 45, RG2004.
- Flaherty, S., Lurz, P.W.W., Patenaude, G., 2014. Use of LiDAR in the conservation management of the endangered red squirrel (*Sciurus vulgaris* L.). *J. Appl. Remote Sens.* 8 (1), 083592. <https://doi.org/10.1117/1.JRS.8.083592>.
- Flood, N., 2013. Seasonal composite Landsat TM/ETM+ images using the medoid (a multi-dimensional median). *Remote Sens.* 5 (12), 6481–6500.
- Forbey, J.S., Patricelli, G.L., Delparte, D.M., Krakauer, A.H., Olsoy, P.J., Fremgen, M.R., Nobler, J.D., Spaete, L.P., Shipley, L.A., Rachlow, J.L., Dirksen, A.K., Perry, A., Richardson, B.A., Glenn, N.F., 2017. Emerging technology to measure habitat quality and behavior of grouse: examples from studies of greater sage-grouse. *Wildlife Biol.* 2017.
- Fox, J., Weisberg, S., 2019. An R companion to applied regression, third ed. Sage, Thousand Oaks.
- Frey, J.K., 2003. Initiation of red squirrel (*Tamiasciurus hudsonicus*) monitoring on Carson National Forest, New Mexico, A Final Contract R3-02-03-12 Completion Report. U.S. Department of Agriculture, Forest Service, Taos.
- Fuhrmann, R.T., 1998. Distribution, morphology, and habitat use of the red fox in the northern Yellowstone ecosystem. Thesis. Montana State University, Bozeman.
- Gantz, G.F., Knowlton, F.F., Morgart, 2005. Seasonal activity areas of coyotes in the Bear River Mountains of Utah and Idaho. *J. Wildl. Manage.* 69 (4), 1652–1659.
- Gao, B.-C., 1996. NDWI-A Normalized Difference Water Index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58 (3), 257–266.
- García-Pecec, C., Tempel, D.J., Kelly, M., 2011. LiDAR as a tool to characterize wildlife habitat: California spotted owl nesting habitat as an example. *J. For.* 109, 436–443.
- Garneau, D.E., Post, E., Boudreau, T., Keech, M., Valkenburg, P., 2007. Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. *Wildlife Biol.* 13 (2), 186–194.
- Gese, E.M., Stotts, T.E., Grothe, S., 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. *J. Mammal.* 77 (2), 377–382.
- Gese, E.M., Dowd, J.L.B., Aubry, L.M., Hayward, M., 2013. The influence of snowmobile trails on coyote movements during winter in high-elevation landscapes. *PLoS ONE* 8 (12), e82862.
- Gigliotti, L.C., Diefenbach, D.R., Sheriff, M.J., 2017. Geographic variation in winter adaptations of snowshoe hares (*Lepus americanus*). *Can. J. Zool.* 95 (8), 539–545.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27.
- Guisan, A., Weiss, S.B., Weiss, A.D., 1999. GLM Versus CCA spatial modeling of plant species distribution. *Plant Ecol.* 143, 107–122.
- Hagar, J.C., Yost, A., Haggerty, P.K., 2020. Incorporating LiDAR metrics into a structure-based habitat model for a canopy-dwelling species. *Remote Sens. Environ.* 236, 111499. <https://doi.org/10.1016/j.rse.2019.111499>.
- Hargis, C.D., Bissonette, J.A., Turner, D.L., 1999. The influence of forest fragmentation and landscape pattern on American martens. *J. Appl. Ecol.* 36 (1), 157–172.
- Haughland, D.L., Larsen, K.W., 2004. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. *J. Mammal.* 85 (2), 225–236.
- Healey, S.P., Yang, Z., Gorelick, N., Ilyushchenko, S., 2020. Highly local model calibration with a new GEDI LiDAR asset on google earth engine reduces Landsat forest height signal saturation. *Remote Sens.* 12, 1–10.
- Hearn, A.J., Cushman, S.A., Ross, J., Goossens, B., Hunter, L.T.B., Macdonald, D.W., Bosso, L., 2018. Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? *PLoS ONE* 13 (7), e0200828.
- Hijmans, R.J., 2021. Raster: Geographic data analysis and modeling. R package version 3.4-13. <https://CRAN.R-project.org/package=raster>.
- Hodges, K.E., Mills, L.S., Murphy, K.M., 2009. Distribution and abundance of snowshoe hares in Yellowstone National Park. *J. Mammal.* 90 (4), 870–878.
- Holbrook, J.D., Vierling, K.T., Vierling, L.A., Hudak, A.T., Adam, P., 2015. Occupancy of red-naped sapsuckers in a coniferous forest: using LiDAR to understand effects of vegetation structure and disturbance. *Ecol. Evol.* 5, 5383–5393.
- Holbrook, J.D., Squires, J.R., Olson, L.E., Lawrence, R.L., Savage, S.L., 2017. Multiscale habitat relationships of snowshoe hares (*Lepus americanus*) in the mixed conifer landscape of the Northern Rockies, USA: cross-scale effects of horizontal cover with implications for forest management. *Ecol. Evol.* 7, 125–144.
- Holbrook, J.D., Squires, J.R., Bollenbacher, B., Graham, R., Olson, L.E., Hanvey, G., Jackson, S., Lawrence, R.L., Savage, S.L., 2019. Management of forests and forest carnivores: relating landscape mosaics to habitat quality of Canada lynx at their range periphery. *For. Ecol. Manage.* 437, 411–425.
- Hosmer, D.W., Lemeshow, S., 2000. Applied logistic regression, second ed. John Wiley and Sons, New York.
- Huang, C., Wylie, B., Yang, L., Homer, C., Zylstra, G., 2002. Derivation of a tasseled cap transformation based on Landsat 7 at-satellite reflectance. *Int. J. Remote Sens.* 23 (8), 1741–1748.
- Huang, S., Tang, L., Hupy, J.P., Wang, Y., Shao, G., 2021. A commentary review on the use of normalized difference vegetation index (NDVI) in the era of popular remote sensing. *J. For. Res.* 32 (1), 1–6.
- Huete, A.R., 1988. A Soil-Adjusted Vegetation Index (SAVI). *Remote Sens. Environ.* 25 (3), 295–309.
- Ivan, J.S., White, G.C., Shenk, T.M., 2014. Density and demography of snowshoe hares in central Colorado. *J. Wildl. Manage.* 78 (4), 580–594.
- Ivan, J.S., Newkirk, E.S., 2016. CPW Photo Warehouse: a custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. *Meth. Ecol. Evol.* 7, 499–504.
- Jenness, J.S., 2004. Calculating landscape surface area from digital elevation models. *Wildl. Soc. Bull.* 32 (3), 829–839.
- Jensen, P.O., Meddens, A.J.H., Fisher, S., Wirsing, A.J., Murray, D.L., Thornton, D.H., 2021. Broaden your horizon: the use of remotely sensed data for modeling populations of forest species at landscape scales. *For. Ecol. Manage.* 500, 119640. <https://doi.org/10.1016/j.foreco.2021.119640>.
- Jung, T.S., Slough, B.G., McEwan, C.A., Johnston, W.G., 2021. Snow tracking provides insights on the hunting behaviour of marten (*Martes americana*). *Mammal Res.* 66 (4), 663–668.
- Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., Kumar, N.S., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proc. R. Soc. B.* 284 (1848), 20161860. <https://doi.org/10.1098/rspb.2016.1860>.
- Keim, J.L., Lele, S.R., DeWitt, P.D., Fitzpatrick, J.J., Jenni, N.S., Auger-Méthé, M., 2019. Estimating the intensity of use by interacting predators and prey using camera traps. *J. Anim. Ecol.* 88 (5), 690–701.
- Key, C.H., Benson, N.C., 2006. Landscape Assessment (LA) sampling and analysis methods. In: Lutes, D.C., Keane, R.E., Caratti, J.F., Key, C.H., Benson, N.C., Sutherland, S., Gangi, L.J. (Eds.), FIREMON: fire effects monitoring and inventory system. Gen. Tech. Rep. RMRS-GTR-164-CD. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, pp. LA-1–55.
- Klugh, A.B., 1927. Ecology of the red squirrel. *J. Mammal.* 8 (1), 1. <https://doi.org/10.2307/1373393>.
- Kolbe, J.A., Squires, J.R., Pletscher, D.H., Ruggiero, L.F., 2007. The Effect of snowmobile trails on coyote movements within lynx home ranges. *J. Wildl. Manage.* 71 (5), 1409–1418.
- Kosterman, M.K., Squires, J.R., Holbrook, J.D., Pletscher, D.H., Hebblewhite, M., 2018. Forest structure provides the income for reproductive success in a southern population of Canada lynx. *Ecol. Appl.* 28 (4), 1032–1043.
- Krohn, W., Hoving, C., Harrison, D., Phillips, D., Frost, H., 2005. *Martes* foot-loading and snowfall patterns in eastern North America: Implications to broad-scale distributions and interactions of mesocarnivores. In: Harrison, D.J., Fuller, A.K., Proulx, G. (Eds.), *Martens and fishers (Martes) in human-altered environments*. Springer, Boston, pp. 115–131.
- Kuhn, M., 2021. caret: Classification and regression training. R package version 6.0-88. <https://CRAN.R-project.org/package=caret>.
- LANDFIRE, 2014. Existing vegetation type layer. U.S. Department of Agriculture and U.S. Department of the Interior. <https://landfire.cr.usgs.gov/viewer/> (accessed January 2020).
- LANDFIRE, 2021. U.S. Department of Agriculture and U.S. Department of the Interior. <https://landfire.cr.usgs.gov/viewer/> (accessed September 2021).

- Lewis, C.W., Hodges, K.E., Koehler, G.M., Mills, L.S., 2011. Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. *J. Mammal.* 92 (3), 561–567.
- Long, R.A., MacKay, P., 2012. Noninvasive methods for surveying martens, sables, and fishers. In: Aubry, K.B., Zielinski, W.J., Raphael, M.G., Proulx, G., Buskirk, S.W. (Eds.), *Biology and conservation of martens, sables, and fishers*. Cornell University Press, Ithaca, pp. 320–342.
- Lukacs, P.M., Evans Mack, D., Inman, R., Gude, J.A., Ivan, J.S., Lanka, R.P., Lewis, J.C., Long, R.A., Sallabanks, R., Walker, Z., Courville, S., Jackson, S., Kahn, R., Schwartz, M.K., Torbit, S.C., Waller, J.S., Carroll, K., 2020. Wolverine occupancy, spatial distribution, and monitoring design. *J. Wildl. Manage.* 84 (5), 841–851.
- MacArthur, R.H., Horn, H.S., 1969. Foliage profile by vertical measurements. *Ecology* 50, 802–804.
- Martin, M.E., Moriarty, K.M., Pauli, J.N., 2021. Landscape seasonality influences the resource selection of a snow-adapted forest carnivore, the Pacific marten. *Landsc. Ecol.* 36 (4), 1055–1069.
- Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. <https://CRAN.r-project.org/package=AICcmodavg>.
- McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. *J. Veg. Sci.* 13 (4), 603–606.
- Moriarty, K.M., Epps, C.W., Betts, M.G., Hance, D.J., Bailey, J.D., Zielinski, W.J., 2015. Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. *Landsc. Ecol.* 30 (10), 1865–1877.
- Morrison, M.L., Marcot, B.G., Mannan, R.W., 1999. *Wildlife-habitat relationships: concepts and applications*. NCASI Tech. Bull. 2, 371.
- Murie, A., 1961. *Am. Soc. Mammal.* 42, 516–521.
- Murray, D.L., Boutin, S., 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia* 88 (4), 463–469.
- NOHRS (National Operational Hydrologic Remote Sensing Center), 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, Version 1. [snow depth]. NSIDC Natl. Snow Ice Data Cent., Boulder. <https://doi.org/10.7265/N5TB14TC> (accessed March 2020).
- O'Donoghue, M., Boutin, S., Krebs, C.J., Hofer, E.J., 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80 (1), 150. <https://doi.org/10.2307/3546526>.
- Olsoy, P.J., Forbey, J.S., Rachlow, J.L., Nobler, J.D., Glenn, N.F., Shipley, L.A., 2015. Fearscape: mapping functional properties of cover for prey with terrestrial LiDAR. *Bioscience* 65, 74–80.
- Palmer, S., Powell, G.V.N., Asner, G.P., Peres, C.A., 2012. LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate. *Remote Sens. Environ.* 127, 98–105.
- Peers, M.J.L., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T.S., Kenney, A.J., Krebs, C.J., Murray, D.L., Boutin, S., 2020. Climate change increases predation risk for a keystone species of the boreal forest. *Nat. Clim. Chang.* 10 (12), 1149–1153.
- Penczykowski, R.M., Connolly, B.M., Barton, B.T., 2017. Winter is changing: trophic interactions under altered snow regimes. *Food Webs* 13, 80–91.
- Perrine, J.D., 2005. *Ecology of red fox (Vulpes vulpes) in the Lassen Peak region of California*. USA. Dissertation, University of California, Berkeley.
- Posthumus, E.E., Koprowski, J.L., Steidl, R.J., Mousseau, T.A., 2015. Red squirrel middens influence abundance but not diversity of other vertebrates. *PLoS ONE* 10 (4), e0123633.
- Potapov, P., Li, X., Hernandez-Serna, A., Tyukavina, A., Hansen, M.C., Kommareddy, A., Pickens, A., Turubanova, S., Tang, H., Silva, C.E., Armston, J., Dubayah, R., Blair, J. B., Hofton, M., 2021. Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote Sens. Environ.* 253, 112165. <https://doi.org/10.1016/j.rse.2020.112165>.
- Powell, R.A., Buskirk, S.W., Zielinski, W.J., 2003. Fisher and marten: *Martes pennant* and *Martes americana*. In: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), *Wild mammals of North America: Biology, management and conservation*. John Hopkins University Press, Baltimore, pp. 635–649.
- Pozzanghera, C.B., Sivy, K.J., Lindberg, M.S., Prugh, L.R., 2016. Variable effects of snow conditions across boreal mesocarnivore species. *Can. J. Zool.* 94 (10), 697–705.
- Pruitt, W.O., Lucier, C.V., 1958. Winter activity of red squirrels in interior Alaska. *J. Mammal.* 39 (3), 443. <https://doi.org/10.2307/1376165>.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://R-project.org/>.
- Raine, R.M., 1983. Winter habitat use and responses to snow cover of fisher (*Martes pennant*) and marten (*Martes americana*) in southeastern Manitoba. *Can. J. Zool.* 61 (1), 25–34.
- Randin, C.F., Ashcroft, M.B., Bolliger, J., Cavender-Bares, J., Coops, N.C., Dullinger, S., Dirnböck, T., Eckert, S., Ellis, E., Fernández, N., Giuliani, G., Guisan, A., Jetz, W., Joost, S., Karger, D., Lembrechts, J., Lenoir, J., Luoto, M., Morin, X., Price, B., Rocchini, D., Schaepman, M., Schmid, B., Verburg, P., Wilson, A., Woodcock, P., Yoccoz, N., Payne, D., 2020. Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sens. Environ.* 239, 111626. <https://doi.org/10.1016/j.rse.2019.111626>.
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Vutsits, L., Sanchez, J.-C., Mueller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinf.* 12, 1–8.
- Robold, R.B., Huettmann, F., 2021. High-resolution prediction of American red squirrel in Interior Alaska: a role model for conservation using open access data, machine learning, GIS and LiDAR. *PeerJ* 9, e11830.
- Rothwell, R., 1979. Nest sites of red squirrels (*Tamiasciurus hudsonicus*) in the Laramie Range of southeastern Wyoming. *J. Mammal.* 60 (2), 404–405.
- Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J., 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. Gen. Tech. Rep. RM-254. U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins.
- Ruggiero, L.F., Pearson, E., Henry, S.E., 1998. Characteristics of American marten den sites in Wyoming. *J. Wildl. Manage.* 62 (2), 663. <https://doi.org/10.2307/3802342>.
- Ruprecht, J., Eriksson, C.E., Forrester, T.D., Spitz, D.B., Clark, D.A., Wisdom, M.J., Bianco, M., Rowland, M.M., Smith, J.B., Johnson, B.K., Levi, T., 2021. Variable strategies to solve risk-reward tradeoffs in carnivore communities. *Proc. Natl. Acad. Sci.* 118 (35) <https://doi.org/10.1073/pnas.2101614118>.
- Sappington, J.M., Longshore, K.M., Thompson, D.B., 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* 71 (5), 1419–1426.
- Sherburne, S.S., Bissonette, J.A., 1993. Squirrel middens influence marten use of subnivean access points. *Am. Mid. Nat.* 129, 204–207.
- Silva, C.A., Hamamura, C., Valbuena, R., Hancock, S., Cardil, A., Broadbent, E.N., de Almeida, D.R.A., Silva Junior, C.H.L., Klauber, C., 2021. rGEDI: NASA's Global Ecosystem Dynamics Investigation (GEDI) data visualization and processing. R package version 0.2.1. <https://github.com/carlos-alberto-silva/rGEDI> (accessed August 2021).
- Simonson, W.D., Allen, H.D., Coomes, D.A., Tatem, A., 2014. Applications of airborne lidar for the assessment of animal species diversity. *Methods Ecol. Evol.* 5 (8), 719–729.
- Sivy, K.J., Pozzanghera, C.B., Grace, J.B., Prugh, L.R., 2017. Fatal attraction? Intraguild facilitation and suppression among predators. *Am. Nat.* 190 (5), 663–679.
- Smith, A.B., 2021. Spatio-temporal variation in habitat use and interspecific interactions among forest carnivores and their associated prey in the Greater Yellowstone Ecosystem. Thesis. University of Wyoming, Laramie, Wyoming.
- Squires, J.R., Ruggiero, L.F., 2007. Winter Prey Selection of Canada Lynx in Northwestern Montana. *J. Wildl. Manage.* 71 (2), 310–315.
- Steele, M.A., 1998. *Tamiasciurus hudsonicus*. *Mamm. Species* (586), 1. <https://doi.org/10.2307/3504443>.
- Sultaite, S.M., Pauli, J.N., Martin, K.J., Meyer, M.W., Notaro, M., Zuckerberg, B., 2016a. Climate change surpasses land-use change in the contracting range boundary of a winter-adapted mammal. *Proc. R. Soc. B Biol. Sci.* 283 (1827), 20153104. <https://doi.org/10.1098/rspb.2015.3104>.
- Sultaite, S.M., Pauli, J.N., Martin, K.J., Meyer, M.W., Zuckerberg, B., 2016b. Extensive forests and persistent snow cover promote snowshoe hare occupancy in Wisconsin. *J. Wildl. Manage.* 80 (5), 894–905.
- Tang, H., Armston, J., 2019. Algorithm theoretical basis document (ATBD) for GEDI L2B footprint canopy cover and vertical profile metrics, version 1.0. The Land Processes Distributed Active Archive Center, Goddard Space Flight Center, Greenbelt, MD. http://lpdaac.usgs.gov/documents/588/GEDI_FCCVPM_ATBD_v1.0.pdf (accessed April 2022).
- Thompson, I., Fryxell, J., Harrison, D., Aubry, K., Zielinski, W., Raphael, M., Proulx, G., Buskirk, S., 2012. Improved insights into use of habitat by American martens. In: Aubry, K.B., Zielinski, W.J., Raphael, M.G., Proulx, G., Buskirk, S.W. (Eds.), *Biology and conservation of martens, sables, and fishers*. Cornell University Press, Ithaca, pp. 209–230.
- Tweedy, P.J., Moriarty, K.M., Bailey, J.D., Epps, C.W., 2019. Using fine scale resolution vegetation data from LiDAR and ground-based sampling to predict Pacific marten resting habitat at multiple spatial scales. *For. Ecol. Manage.* 452, 117556. <https://doi.org/10.1016/j.foreco.2019.117556>.
- Van Etten, K.W., Wilson, K.R., Crabtree, R.L., 2007. Habitat use of red foxes in Yellowstone National Park based on snow tracking and telemetry. *J. Mammal.* 88 (6), 1498–1507.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., Slotow, R., 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* 94 (11), 2619–2631.
- Vogeler, J.C., Hudak, A.T., Vierling, L.A., Vierling, K.T., 2013. Lidar-derived canopy architecture predicts brown creeper occupancy of two western coniferous forests. *Condor* 115 (3), 614–622.
- Vogeler, J.C., Yang, Z., Cohen, W.B., 2016. Mapping suitable Lewis's woodpecker nesting habitat in a post-fire landscape. *Northwest Sci.* 90 (4), 421–432.
- Whiteman, J.P., Buskirk, S.W., 2013. Footload influences wildlife use of compacted trails in the snow. *Wildlife Biol.* 19 (2), 156–164.
- Xu, H., 2006. Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. *Int. J. Remote Sens.* 27 (14), 3025–3033.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing ecological data*. Springer, New York.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York.