

LiDAR metrics enhance our understanding of habitat selection beyond ecoforest map habitat categories

Brendan Blanchard^a, Robert Schneider^b, Frédéric Lesmerises^c,
Martin-Hugues St-Laurent^{d,*}

^a Centre for Forest Research, Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

^b Centre for Forest Research, Chaire de Recherche sur la Forêt Habitée, Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

^c Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

^d Centre for Forest Research, Centre for Northern Studies, Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

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ABSTRACT

Habitat selection studies in large mammals typically rely on photo-interpreted forest maps to link the telemetry locations of individuals to environmental data. Such forest maps mainly provide information on forest composition, age, and disturbance history but say little about the structure of stands. In contrast, airborne LiDAR (Light Detection and Ranging) can provide 3D metrics of vegetation structure, but its application to the study of wildlife–habitat relationships remains limited. We aim to determine if combining these products could improve our capacity to understand the habitat selection patterns of large mammal species representative of the eastern Canadian boreal forest: caribou (*Rangifer tarandus caribou*), moose (*Alces alces americana*) and eastern coyote (*Canis latrans*). We built resource selection functions with mixed logistic regressions to characterize habitat selection patterns, using telemetry data and the different sources of information on forest composition and structure. We evaluated model performance with a *k*-fold cross-validation. Our results suggest that integrating LiDAR data with forest maps substantially improves the ability to characterize habitat selection patterns across species, though benefits varied with periods and study areas. For example, vegetation structure, mostly detailed by LiDAR data, was the main determinant for caribou and eastern coyotes in the snow-covered period, whereas forest composition, described in the forest maps, was most important to characterize habitat selection patterns for moose in both periods. These differences may be partly attributed to contrasting compositions between northernmost and southernmost forests in our study area (i.e. province of Quebec), species ecology, as well as potential temporal discrepancies between data sources. When used appropriately, combining LiDAR with traditional forest maps provides richer ecological insight and a more comprehensive characterization of habitat selection patterns of large boreal mammals. Based on an average population-level description of habitat selection patterns, this integrated approach can guide practitioners to preserve sparse understory to support caribou, promote complex shrub structure for moose, and limit dense cover that may favor eastern coyotes.

1. Introduction

Habitat is defined by an area that is characterized by a set of environmental conditions, resources and risks for the species of interest (Northrup et al., 2022). Thus, habitat selection refers to the process where an animal's use of a resource (or a habitat component) is

disproportionate to its availability in the environment (Johnson, 1980). Quantifying habitat selection patterns therefore requires linking the locations of individuals to a description of their habitat in both space and time (Potvin et al., 1999; Rettie and McLoughlin, 1999). According to Johnson (1980), habitat selection is a hierarchical process that applies at several spatial scales.

* Corresponding author.

E-mail addresses: brendan.blanchard@uqar.ca (B. Blanchard), robert.schneider@uqar.ca (R. Schneider), frederic.lesmerises@uqar.ca (F. Lesmerises), martin-hugues.st-laurent@uqar.ca (M.-H. St-Laurent).

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The spatial scale is defined by its extent (i.e. the size of the study area) and by its grain (i.e. the size of the observation units) (Wiens, 1989; Boyce et al., 2003; Boyce, 2006). The ecological question or process under study determines the spatial scale at which the habitat is studied (Boyce, 2006). This choice must also consider the size of the organism studied (and its associated daily movements and home range size), its motion and navigation capacity, and its internal state (Nathan et al., 2008). In general, questions that require the characterization of fine-grained features call for higher-resolution data to capture the heterogeneity of resources and risks (Wiens, 1989; Dussault et al., 2001; Boyce, 2006). Finally, the accuracy of telemetry devices sets practical limits on the minimum grain that can be meaningfully analyzed. For instance, Schweiger et al. (2021) used variables at a 10 m spatial resolution to study the microhabitat selection of the Organ Mountains Colorado chipmunk (*N. quadrivittatus australis*), but used a coarser 90 m spatial resolution for second-order selection (*sensu* Johnson, 1980). Recent technological advances in telemetry monitoring, land cover mapping, and computing power have significantly reduced the dependency on data acquisition and availability (Kays et al., 2015; Wulder et al., 2018; Foley and Sillero-Zubiri, 2020; Oeser et al., 2020; Robinson et al., 2020). These innovations have spurred scientists to characterize environments using data that covers a greater extent at a finer resolution (Vierling et al., 2008).

Land cover maps, whether derived from satellite imagery or aerial photographs, represent a fundamental tool to describe habitat when studying species that can travel over several square kilometers, such as large mammals. Indeed, extracting environmental variables from remote sensing data, such as vegetation indices, land cover classifications, and indicators of urban development, has proven effective in describing habitat selection patterns across a range of wildlife species. For instance, satellite imagery has been successfully used in Europe for the Eurasian lynx (*Lynx lynx*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*; Oeser et al., 2020), and gray wolf (*Canis lupus*; Vorel et al., 2024), while forest maps have been used for the Iberian lynx (*Lynx pardinus*; Gastón et al., 2019) and brown bear (*Ursus arctos*; Thorsen et al., 2022). Similarly, in Canada, both satellite-derived and photo-interpreted land cover data have been applied to species such as caribou (*Rangifer tarandus caribou*; Wilson et al., 2023), moose (*Alces alces americana*; DeMars et al., 2019), brown bear (*Cristescu et al., 2016*), black bear (*Ursus americanus*; Latham et al., 2011), wood bison (*Bison bison athabasca*; DeMars et al., 2020), and gray wolf (Benson et al., 2015). These applications are made possible by forest mapping programs, which are implemented by several Canadian provinces (White et al., 2025).

In Quebec (eastern Canada), such maps—named “ecoforest maps”—were originally created in the early ‘80s to plan and support timber harvesting by the forestry industry (Ministère des Forêts, de la Faune et des Parcs, 2015), although they have been frequently used to evaluate wildlife habitats (e.g. Ouellet et al., 1996; Potvin et al., 1999; Dussault et al., 2001). Indeed, they are considered reliable and are still used to describe habitat selection patterns of large mammals such as caribou, black bear, gray wolf (Derguy et al., 2025), moose (Leblond et al., 2010), and white-tailed deer (*Odocoileus virginianus*, Courbin et al., 2017). Ecoforest maps provide information on both canopy characteristics and site conditions (Dussault et al., 2001; Ministère des Forêts, de la Faune et des Parcs, 2015). Their spatial resolution is relatively coarse, with a grain of 4 ha for productive forest polygons and less than 2 ha for non-productive polygons (e.g. agricultural fields and water bodies). Their temporal resolution is also relatively low because stand structure and composition inventories are conducted only once per decade, albeit the maps are manually updated each year to integrate natural (e.g. fire, insect outbreak) and anthropogenic (e.g. cutblock, gravel pit) disturbances (Potvin et al., 1999; Ministère des Forêts, de la Faune et des Parcs, 2022). According to Dussault et al. (2001), some variables of the ecoforest map (e.g. density, height, and age of stands) may be less accurate than expected and should be validated *in situ*, a logistically heavy

and costly task, especially for remote sites or large study areas (Ouellet et al., 1996; Potvin et al., 1999; Morgan et al., 2010). This problem stems from the difficulty to differentiate through photo interpretation the parts of a stand that have different structure or composition attributes but that are merged into one polygon (Wiens, 1989; Nolet et al., 1995).

Ecoforest maps and satellite imagery share an important technological limitation: being photography-based, they only capture information from the top of the canopy and therefore provide little to no information about understory structures and conditions beneath the canopy (Vierling et al., 2008). However, vegetation structure (i.e. “the organisation in space and time, including position, extent, quantity, type and connectivity, of the aboveground components of vegetation”; Pardini et al., 2019), both vertical and horizontal, is known to influence the quality, diversity, and availability of food resources for large mammals (Searle et al., 2007; Russo et al., 2023; Souza et al., 2023) and to provide shelter from predation (van Beest et al., 2013) and harsh weather conditions (Tveraa et al., 2003; van Beest et al., 2011). For example, vegetation cover protects moose from predation, heat stress, and thick snow, thus benefiting to their mobility, survival, and reproduction (Schwab and Pitt, 1991). Also, Russo et al. (2023) explored the bidirectional interactions between three-dimensional vegetation structure and animal ecological functions, showing how medium-sized to large mammals influence vegetation structure, which in turn affects their behaviour and ecological functions.

LiDAR (Light Detection and Ranging) is an active remote sensing technology that uses lasers to gather precise information about vegetation structure (Lefsky et al., 2002; Vierling et al., 2008; Davies and Asner, 2014). While airborne LiDAR (also known as Airborne Laser Scanning, ALS) is also acquired from above the canopy, the laser pulses are only partly reflected by the vegetation, allowing them to pass through all vegetation layers (from canopy to ground), sending part of the light back to the sensors at each interaction, resulting in a 3D “point cloud” dataset (Lefsky et al., 2002). The data acquisition can be carried out at very high spatial resolution and over regional to global extents (Coops et al., 2021) but has some drawbacks such as a very low acquisition frequency (i.e. a single snapshot for the current period) and heavy data processing (Ciuti et al., 2018). The use of LiDAR in ecology began in forestry and was then more recently incorporated into wildlife studies (Vierling et al., 2008; Acebes et al., 2021), particularly on birds (Bakx et al., 2019; Shokirov et al., 2023), taxa known to use complex vegetation structures throughout their annual life cycle (Acebes et al., 2021), and herpetofauna (Shokirov et al., 2024). LiDAR has also recently provided new insights about the use of vertical vegetation structure in small mammals, like the Pacific marten (*Martes caurina*; Tweedy et al., 2019) and the savanna glider (*Petaurus ariel*; Stobo-Wilson et al., 2021), medium-sized mammals, for instance primates (McLean et al., 2016; Singh et al., 2018; Seaman et al., 2019) and large mammals, such as lions (*Panthera leo*; Loarie et al., 2013; Davies et al., 2016a, 2016b) and several cervids (Coops et al., 2010; Ewald et al., 2014; Lone et al., 2014; Melin et al., 2014; Kroeger et al., 2020; Blouin et al., 2021). However, field-based research or other remote sensing techniques are required to supplement LiDAR structural data because LiDAR cannot readily identify variations in plant composition. Since LiDAR struggles to accurately detect variations in tree composition, it is essential to couple this tool with field studies or alternative remote sensing methods (Davies and Asner, 2014). This growing technology provides an important opportunity to develop new data-driven habitat models by combining LiDAR-derived habitat variables with GPS animal location data to guide habitat management (Vierling et al., 2008; Merrick et al., 2013; Davies and Asner, 2014; Simonson et al., 2014), which has not yet been done specifically with large mammals in eastern Canada. These two remote sensing tools may offer a complementary and synergistic view of habitat, providing the potential for a more complete understanding of habitat selection patterns.

Consequently, our study aimed at determining if the combination of ecoforest maps and airborne LiDAR data can improve our understanding

of the habitat selection patterns of different species of large mammals that have different habitat requirements and face distinct management challenges. Boreal caribou is threatened and of conservation concern in Canada (Environment Canada, 2011), moose holds significant socio-economic importance in Quebec (Desgagnés et al., 2022, but see Lefort and Massé, 2015), and eastern coyote (*Canis latrans*) is a predator involved in human-wildlife conflicts (Brooks et al., 2020). Assessing how LiDAR-derived vegetation structure complements ecoforest composition data may provide finer descriptions of habitat features relevant to these management contexts. We hypothesized that including LiDAR metrics of vertical and horizontal vegetation structure in addition to ecoforest map categories would improve habitat selection model parsimony and performance compared to models based on the ecoforest map alone. More precisely, we anticipated LiDAR-derived structural information to be particularly informative for caribou, a lichen specialist that seeks open habitats and depends on understory resources typically found in spruce-moss forests, and also useful for eastern coyotes, a medium-sized generalist predator whose habitat selection may be influenced by fine-scale structural features. In contrast, we anticipated a more limited added value of LiDAR for moose, a generalist herbivore mostly associated with mixed stands where vegetation composition may play a more prominent role than understory structure.

2. Methods

2.1. Study areas

We used three different GPS telemetry datasets collected on caribou, moose and eastern coyotes in three distinct study areas distributed across three bioclimatic domains (Fig. 1). This allowed us to account for contrasting habitat requirements, stand structure, and forest composition, and to assess whether the relevance of LiDAR data in explaining habitat selection varies with species-specific ecology and regional environmental conditions.

Caribou telemetry data were collected in the Assinica caribou population range, located close to the Mistassini Lake, in the Northern Quebec administrative region (western part of the province, Fig. 1). This range is in the black spruce (*Picea mariana*) – moss bioclimatic domain (Robitaille and Saucier, 1998), and the dominant tree species is black spruce, with a codominance of balsam fir (*Abies balsamea*) and jack pine (*Pinus banksiana*) (Lafontaine et al., 2019). This study region borders the northern limit of commercial forests (Fig. 1), above which wildfires are the main disturbance, while timber harvesting and the associated road network are the main disturbances south of the limit (Lafontaine et al., 2019). Mean annual temperatures vary with latitude from -2.5°C to 0°C in this area, while annual precipitations average 900 mm

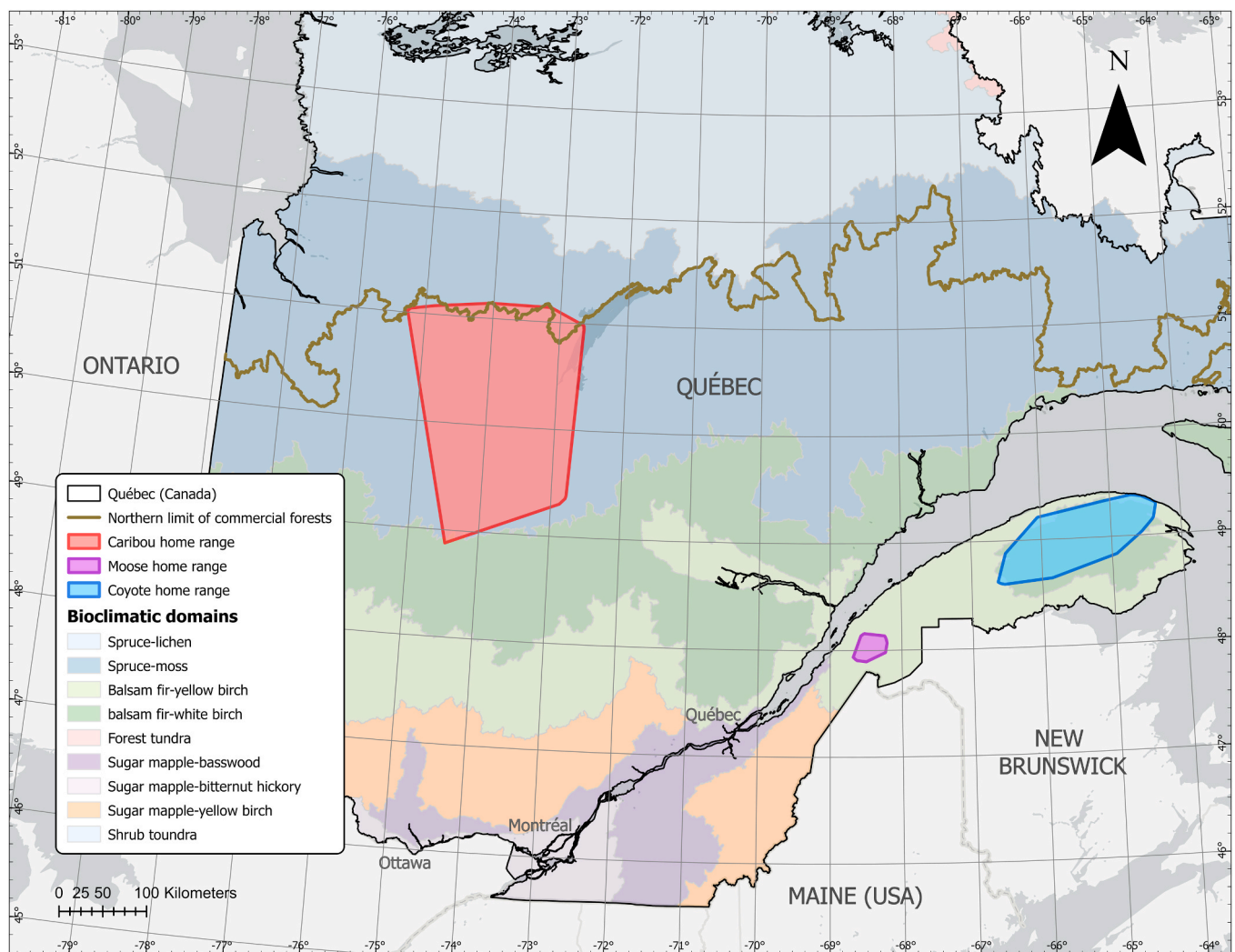


Fig. 1. Study areas as defined by a 100% minimum convex polygon encompassing GPS telemetry locations of all collared caribou (red) and moose (purple), and a 95% minimum convex polygon (to prevent the influence of extraterritorial excursions, Shivik and Gese, 2000) for coyote (blue) in different bioclimatic domains found in Quebec (eastern Canada).

(Robitaille and Saucier, 1998). Other large mammal species found in this area include the gray wolf, black bear, and moose.

We used moose telemetry data collected in the balsam fir – yellow birch (*Betula alleghaniensis*) bioclimatic domain, in the Bas-Saint-Laurent region (southeastern Québec) (Fig. 1). In this area, forests are mainly composed of balsam fir, white birch (*Betula papyrifera*), yellow birch, and white spruce (*Picea glauca*) (Robitaille and Saucier, 1998). Timber harvesting, small urban settlements and paved roads are the main disturbance types encountered (~85%), but agriculture covers ~15% of the landscape. The mean annual temperature is ~ 2.5 °C, and mean precipitation varies from 900 to 1100 mm annually (Robitaille and Saucier, 1998). Other large- and medium-sized mammal species present in the area include white-tailed deer, black bears, and eastern coyotes. The gray wolf was extirpated from the area 170 years ago (Villemure and Jolicoeur, 2004).

Eastern coyotes were monitored in the Gaspésie region (eastern Québec), between the Matane Wildlife Reserve and the north-eastern tip of the Gaspé Peninsula (Fig. 1). This area is divided in three ecological zones distributed along an elevation gradient (see Mosnier et al., 2008 for more details). From the valleys to the mountain tops, the vegetation varies from a closed forest composed of balsam fir, black spruce, white spruce and white birch, to a belt of krummholz and finally to alpine tundra (shrubs, mosses, and lichens) (Mosnier et al., 2008; Lesmerises et al., 2018). Timber harvesting is common in this area—except within the limits of the Gaspésie National Park, a protected area—and the most common natural disturbances are spruce budworm (*Choristoneura fumiferana*) outbreaks and windthrows. The annual mean temperature reaches ~ 2.5 °C, and mean annual precipitations vary from 1000 to 1300 mm (Robitaille and Saucier, 1998). Within this study area, we also find moose, caribou, white-tailed deer, and black bears. Gray wolves were extirpated from this region ~170 years ago as well (Villemure and Jolicoeur, 2004). Eastern coyotes, larger and behaviorally distinct from their western counterparts, may have partially filled the gray wolf ecological niche by preying on larger ungulates such as white-tailed deer (Messier et al., 1986).

Taken together, these three study areas span a gradient in forest composition, disturbance intensity, and climate across Quebec, which provides a broad context for evaluating the complementarity between LiDAR and ecoforest maps, but also entails some confounding between species and regional environmental conditions.

2.2. Capture and telemetry data

We used data from 58 boreal caribou, 18 moose and 15 eastern coyotes that were captured and collared in the three different study areas. Caribou were all females and were captured using a netgun fired from a helicopter by biologists and technicians of the Quebec government and fitted with GPS telemetry collars (Telonics Inc. models TGW 4680, Vectronic Aerospace model GPS-Plus) programmed to collect locations every 13 h. Caribou were monitored between January 2017 and May 2023. For moose, our dataset was also composed of females only, that were darted in February 2017 from a helicopter to receive a dose of chemical immobilizer (9 mg of etorphine per animal), fitted with a GPS/Iridium collar (Vectronic Vertex Lite 3D) programmed to record a location every two hours, and monitored for 2.5 years (see Laliberté and St-Laurent, 2020; Gagnon et al., 2024 for more details). Finally, 15 eastern coyotes (seven females, eight males) were captured using leg-hold traps with rubber jaws (Victor Soft Catch #3) and fitted with GPS/Iridium collars (Vectronics Vertex Lite); each eastern coyote was monitored for one year at a six-hour fix rate. All capture and handling procedures were approved by the Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs (wildlife management permit SEG # 2017-02-10-010-01-S-F for moose, CPA certificate #11-03, #12-03, #12-07, #13-09 and #14-05 for caribou) and by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate CPA #68-17-183 for moose,

CPA-MFFP-20-21 / CPA-MFFP-21-20 for eastern coyote).

For the three species, we removed from the datasets all the locations for which the position dilution value (PDOP) was ≥ 10 to have a tracking accuracy ≤ 20 m (Dussault et al., 2001). We chose two contrasted biological periods for each species, corresponding to the “snow-covered” and “snow-free” parts of the year, to have the possibility to contrast the LiDAR contribution (acquired in the leaf-on period only) between periods. We thus defined the following biological periods: for caribou, “early winter” (15 Nov.–17 Feb.) and “summer” (28 Jun.–6 Sep.) according to Rudolph and Drapeau (2012), and Lessard et al. (2025); for moose, “winter” (26 Nov.–26 Apr.) and “summer” (7 Jun.–2 Oct.) following Gagnon et al. (2024); and finally, for eastern coyotes, “mating” (1 Jan.–15 Mar.) and “hunting dispersion” (7 Sep.–31 Dec.) based on Boisjoly et al. (2010). Note that the coyote hunting-dispersion period represents a transitional season spanning early snow-covered and late snow-free conditions, rather than a truly snow-free period. This broader temporal window was retained because restricting to a true snow-free period yielded an insufficient sample size (10 individual-years) to support model complexity, whereas the extended period provided adequate data (25 individual-years). The terms “snow-covered period” and “snow-free period” will be used from here on to make comprehension and comparisons easier.

We aimed at retaining as many individual-year combinations (and GPS locations) as possible to maximize the power of our statistical analyses. However, airborne LiDAR data were taken in different years, dividing our study areas into “1 ha tiles” acquired between 2017 and 2022. We therefore kept the GPS locations temporally matching the LiDAR tiles within a range of ± 3 years to reduce the biases associated with the evolution of the vegetation structure over time (Campbell et al., 2018; Hull and Shipley, 2019). Individuals with $< 75\%$ of their locations matching LiDAR data (within ± 3 years) tiles were removed from our analyses to keep enough locations to be representative of the animals' habitat selection. In addition, and to make sure that the LiDAR representation of habitat structure was as accurate as possible, we checked that no disturbance occurred between the acquisition of the LiDAR and that of the telemetry locations.

2.3. Data processing

2.3.1. Habitat selection patterns

We characterized habitat selection patterns for our three species during each biological period at the 3rd order of selection (*sensu* Johnson, 1980) using resource selection functions (hereafter RSF; Manly et al., 2002) including landcover types, LiDAR metrics and other covariates (topography and linear features; all described below). To do so, we delineated seasonal home ranges for each individual-year using 100% minimum convex polygons (hereafter MCP; Mohr, 1947) for caribou and moose and 95% MCP for eastern coyotes (to prevent the influence of extraterritorial excursions, quite common for canids, see Shivik and Gese, 2000; and Gehrt et al., 2023). Thus, we compared characteristics under GPS locations (coded 1) with those of the same number of random points (coded 0) distributed in the seasonal home range of each individual.

2.3.2. Ecoforest map

In order to match telemetry data to habitat, we used the 1: 20,000 digitized ecoforest maps provided by the Ministère des Ressources Naturelles et des Forêts (hereafter MRNF; Ministère des Forêts, de la Faune et des Parcs, 2022). Ecoforest maps provide information about the canopy composition, density, and height, the mean age of the dominant and codominant tree layers (when applicable), as well as the type of soil, its slope, and drainage (Dussault et al., 2001; Ministère des Forêts, de la Faune et des Parcs, 2022). We grouped forest polygons into a given number of landcover types. This categorization process was guided by the ecology and needs of caribou (Hins et al., 2009; Leblond et al., 2011), moose (Laliberté and St-Laurent, 2020; Gagnon et al., 2024), and

eastern coyotes (Boisjoly et al., 2010; Latham et al., 2013), and reflected the composition of the different study areas and the precision of the ecoforest map. Landcover types with limited representation (e.g. flooded sites, islands) were merged into the “Other” category (see Appendix A). One habitat map per year was generated to consider the chronology of cutting operations and to include new natural disturbances (e.g. fires).

2.3.3. Airborne Lidar data

Nearly 500,000 km² of airborne LiDAR data has been collected since 2016 in Quebec, covering the province from the southern border to the northern extent of the commercial forestry area (Fig. 1) at a very high spatial resolution (1 × 1 m; Ministère des Forêts, de la Faune et des

Parcs, 2020). We used raw LiDAR point cloud data (.laz format) provided by the Quebec government authorities (MRNF and the Ministère des Transports et de la Mobilité durable). These raw LiDAR point cloud data covered our three study areas and were obtained between 2017 and 2022 at a density ranging from 2.5 to 4 points/m². We processed the raw LiDAR data to calculate several metrics relevant to describing vegetation (see Fig. 2 and Appendix B for more details). In order to facilitate the selection and ecological interpretation of LiDAR metrics and the comparison with other studies, we followed the recommendations of Bakx et al. (2019) and Moudry et al. (2023) and prioritized standard metrics. Knowing that the vegetation structure affects the distribution of resources (forage or prey availability), microclimate refugia (Schwab and

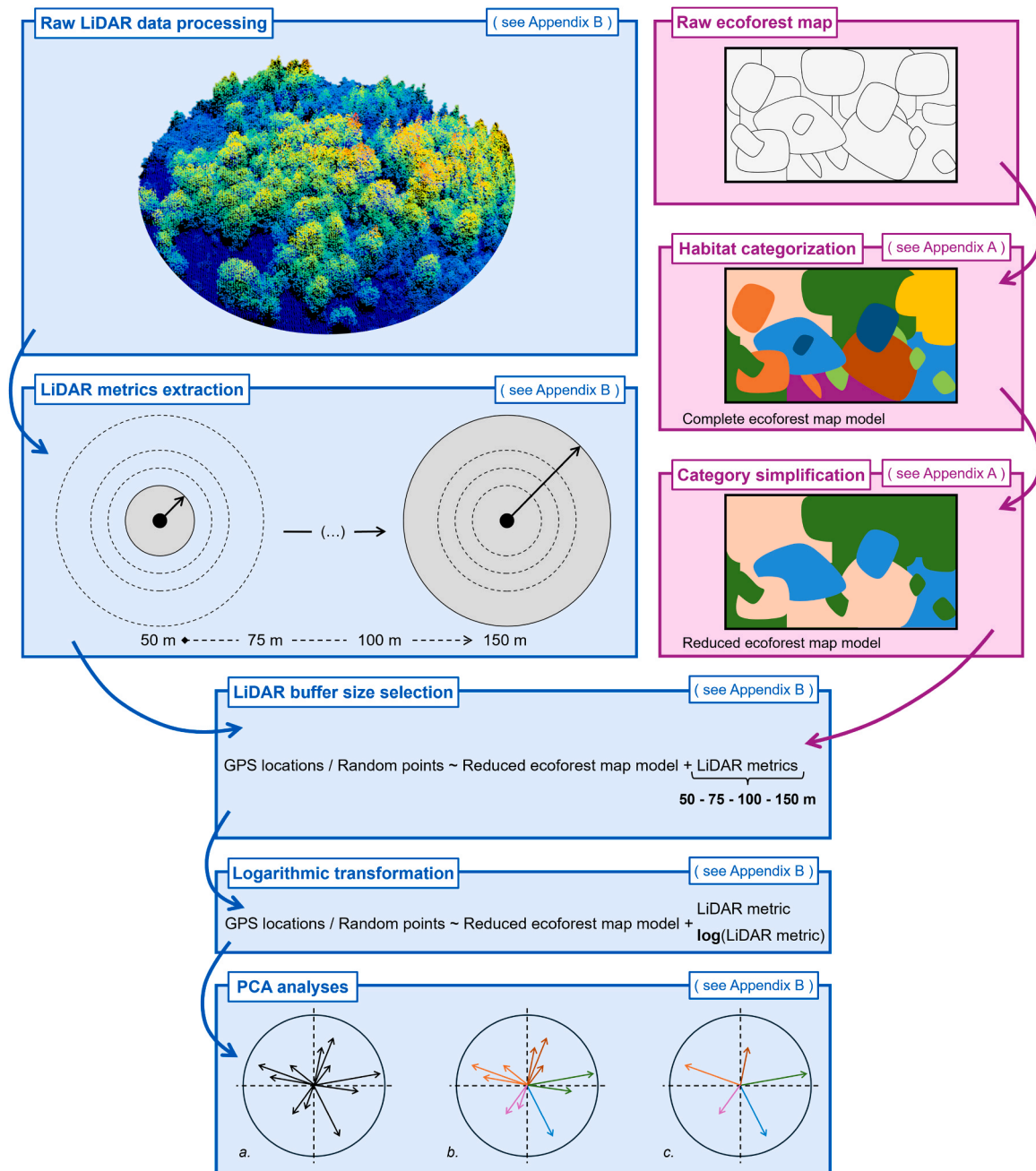


Fig. 2. Conceptual workflow illustrating the processing steps and integration of LiDAR metrics (blue boxes) and ecoforest map categories (purple boxes) used in habitat selection analyses. Structural metrics are extracted from processed raw airborne LiDAR data (see Appendix B) within multiple buffer sizes (50–150 m, see Appendix B) around GPS and random locations. These metrics are then log-transformed and used in a PCA (see Appendix B). Ecoforest maps are simplified through habitat categorization to generate a reduced ecoforest map model (see Appendix A). Both sources of information are then combined to represent complementary dimensions of forest composition and structure (see Statistical analyses).

Pitt, 1991), and predation risk (Briand et al., 2009), and plays a role in the energetic costs of movements (Shepard et al., 2013), we extracted the relevant LiDAR metrics (Table 1) to characterize these needs for caribou (Lantin et al., 2003; Briand et al., 2009; Dickie et al., 2017), moose (Dussault et al., 2005a; Lone et al., 2014; Melin et al., 2014), and eastern coyotes (Thibault and Ouellet, 2005; Kays et al., 2008; Boisjoly et al., 2010). To account for location accuracy (Dussault et al., 2001) and maximize model performance, vegetation metrics were calculated within species-specific buffer radii (from 50 m to 150 m). We followed the methodological approach used by Leblond et al., (2011) and recommended by McGarigal et al. (2016) for estimating road-effect distances (see Fig. 2 and Appendix B for more details). This process provided an empirical estimate of the range of influence of vegetation structure relevant to our analysis. Moreover, we added 0.5 m to the height of the shrub layer during the snow-covered period, corresponding approximately to the average snow depth over the winter since 2018 (Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs, 2024), to account for the important

Table 1
Vegetation structure metrics (Moudry et al., 2023) extracted from airborne LiDAR in a buffer around GPS locations and random points for each species.

Vegetation structure metrics	Description	Equation
Maximum vegetation height	Gives information about the tallest vegetation (m).	Mean height of the returns in the 95th percentile (Z_{95th}); used to avoid potential artefacts (Kane et al., 2010)
Mean vegetation height	The higher the value (m), the more the canopy is developed. The lower the value is, the more the canopy is scattered, and the more the shrub and herbaceous layer is represented.	Mean height of the returns below Z_{95th} vegetation height
Standard deviation of vegetation height	Represent the vertical variability of the vegetation. The higher the value (in meters), the more the vegetation is heterogeneous. The lower the value, the more the vegetation is homogenous.	$SD = \sqrt{\frac{\sum (z - \bar{z})^2}{N}}$ Z = vegetation height; N = number of returns below Z_{95th}
Rumple Index of vegetation	Represent the 3D variability of the vegetation (no unit). The higher the value, the more the vegetation is vertically and horizontally heterogeneous.	Ratio between area of triangle (Delaunay triangulation) on LiDAR returns and its projected area on the ground (Kane et al., 2010)
"Herbaceous" layer cover	Proportion of vegetation within the herbaceous layer. A value of 30 indicates that 30% of the vegetation is under 0.50 m.	$(N_H/N_{Total}) \times 100$ N_H = number of LiDAR returns below 0.50 m N_{Total} = total number of LiDAR returns below Z_{95th}
"Shrub" layer cover	Proportion of vegetation within the shrub layer. A value of 30 indicates that 30% of the vegetation is under x meters, with x being 3 m for moose, 2 m for caribou and 1 m for eastern coyotes, representing the maximum height of accessible food. The shrub layer is raised by 0.50 m in the snow-covered periods.	$(N_S/N_{Total}) \times 100$ N_S = number of LiDAR returns below x meters N_{Total} = total number of LiDAR returns below Z_{95th}
"Canopy" layer cover	Proportion of vegetation within the canopy layer. A value of 85 indicates that 85% of the vegetation is over $[0.66 \times Z_{95th}]$. If the value of maximum vegetation height was less than 6 m, we fixed the canopy layer cover to 0%.	$(N_C/N_{Total}) \times 100$ N_C = number of LiDAR returns between $[0.66 \times Z_{95th}]$ and Z_{95th} . N_{Total} = total number of LiDAR returns below Z_{95th}

influence that snow accumulation can have on animal behaviour (e.g. Johnson et al., 2004; Pozzanghera et al., 2016; Melin et al., 2023) and on vegetation structure near the ground (Musselman et al., 2008; Varhola et al., 2010). For example, the "shrub layer cover" metric for moose in the snow-covered period is the proportion of LiDAR returns between 0.5 m and 3.5 m instead of the 0–3.0 m range used for the snow-free period (Table 1). All these operations were carried out in R using the lidR package (Roussel et al., 2020) and ForestGapR (Silva et al., 2019). We also evaluated the effect of a logarithmic transformation on LiDAR metrics, which resulted in the transformation of most metrics (see Fig. 2 and Appendix B for more details).

Exploratory analyses revealed a strong collinearity between several LiDAR metrics. We thus grouped metrics based on their similarity with a principal component analysis (hereafter PCA) using the Factoextra package (Kassambara and Mundt, 2016) to ascertain whether LiDAR metrics were similar (King and Jackson, 1999; Keough and Quinn, 2023; but see Schneider et al., 2020) for the two biological periods of each species. From each group, a single metric was retained based on its ecological interpretability and relevance for habitat management (see Fig. 2 and Appendix B for methodological details).

2.3.4. Topography and linear features

We used the 1:20,000 topographic maps published by the MRNF to build a digital elevation model, knowing that the studied species respond to topography (caribou: Jones et al., 2007; moose: Leblond et al., 2010; coyote: Koehler and Hornocker, 1991), and extracted elevation (m) from the digital elevation model as a topographic variable. Road networks also influence the distribution of caribou (Leblond et al., 2011), moose (Laurian et al., 2008) and coyotes (Kolbe et al., 2007), so we used the 1:20,000 Routard numerical map, published by the MRNF as well. We acknowledge that the species studied, particularly eastern coyotes, may exhibit differential use of major (paved and large forestry roads) vs. minor roads (small forestry roads) (Kolbe et al., 2007; Dowd et al., 2014), but we combined these two types into a single class, as the fine-scale effects of roads were outside the scope of our study. We also calculated the Euclidian (i.e. minimum) distance between GPS locations (and random points) and roads, and applied a decay function to this variable (Carpenter et al., 2010, see Fig. 2 and Appendix C for more details).

2.4. Statistical analyses

2.4.1. Habitat selection patterns

We used mixed logistic regression models to describe habitat selection patterns for the three studied species using the lme4 package (Bates et al., 2015). We considered the individual-year as a random factor to account for statistical non-independence among locations sampled from the same individual (Gillies et al., 2006). This modelling approach estimates an average habitat-selection coefficient shared across individuals. By specifying random intercepts only, the model assumes homogeneous slopes across individuals and does not estimate among-individual variation in selection responses (Schielzeth and Forstmeier, 2009; Arnqvist, 2020). While random-slope models are generally recommended to quantify individual heterogeneity in habitat selection analyses (Muff et al., 2020; Northrup et al., 2022), they were not feasible due to limited sample sizes for certain species-period combinations in our dataset. Our comparison of methodologies therefore evaluates how habitat selection by the average individual (caribou, moose, and coyote) varies depending on the data source considered (airborne LiDAR, forest maps, and their combination). We built three types of candidate models for each biological period for each species: (1) "Ecoforest map only" models using landcover types derived from the ecoforest map, (2) "LiDAR only" models using vegetation structure metrics obtained from airborne LiDAR, and (3) "Fusion" models, combining both data sources (recently put forward by Shokirov et al., 2024, between terrestrial and airborne LiDAR). As proposed by Street

et al. (2021), we made sure that the number of parameters (k) for all candidate models was less than the number of individual-year (sample size, n) to prevent overparameterization.

2.4.2. Ecoforest map only models

For each species and biological period, we built different candidate models with varying numbers of landcover types, ranging from detailed models incorporating comprehensive stand composition information to simplified models where landcover types were systematically merged according to the use-availability ratios and their relative extent within the study areas (Table 2). Each candidate model was duplicated four times: with elevation and/or minimum distance to roads or neither (Table 3). The more complex models used landcover types that maximized forest stand differentiation (Table 2), leveraging the ecoforest map's key strength in identifying stand composition. Using Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson, 2001), we selected the most parsimonious model for each species and biological period, built only with the ecoforest map (Table 2). These "Ecoforest map only" models were based on a priori habitat categories defined according to ecological relevance and already used in previous habitat selection studies, without exhaustive testing of all possible category merging. This approach aimed to preserve ecological interpretability, facilitate comparison to other studies, and avoid the overfitting associated with overly detailed habitat categories. Subsequently, we selected a reduced model with fewer landcover types to facilitate the integration of LiDAR metrics in order to create the "Fusion" model (see Section 2.4.3) while continuing to prevent model overfitting (Table 2). This two-level approach allowed us to fully exploit both the detailed forest composition data and three-dimensional structural information derived from airborne LiDAR. Due to our limited sample size, we had to reduce the number of ecoforest map categories to avoid overparameterization; we first merged habitat categories and then quantified the information loss (i.e., the increase in AIC_c) caused solely by this simplification by comparing the AIC_c of complete and reduced ecoforest map models. This allowed us to approximate how much of the improvement in AIC_c observed in the "Fusion" models could be attributed to the addition of LiDAR metrics rather than to the merging of habitat categories.

2.4.3. LiDAR only and Fusion models

"LiDAR only" candidate models were built by generating all the possible combinations of LiDAR metrics retained after the PCA analyses (ranging from one to seven metrics; seven metrics were used for moose during the snow-free period), including elevation or minimum distance to roads or both (Table 3). We repeated the same process of generating combinations for "Fusion" models but added landcover types from the reduced models (see Section 2.4.2) to LiDAR metrics and/or elevation and/or minimum distance to roads or neither (Table 3). We selected the most parsimonious model with the best fit using AIC_c for the "Ecoforest map only" model, "LiDAR only" models, and "Fusion" models for the two biological periods of caribou, moose and eastern coyotes.

2.4.4. Model validation

Robustness of the top-ranking models for both periods for each species was obtained by using a k -fold cross validation (Boyce et al., 2002), in which all individual locations were pooled before partitioning the data into training (75%) and validation (25%) subsets, because individual-level partitioning led to model convergence issues in some folds. Following that, the RSF scores were sorted and divided into 10 equal bins that were scaled to percentile classes. We calculated the RSF value for each observation that was withheld by using the model built using the training dataset. To evaluate the model's performance, we computed a Spearman rank correlation (r_s) between the frequency of withheld data occurrences and the ranked RSF-availability bins (Boyce et al., 2002). We standardized all our numeric variables (i.e. LiDAR metrics, minimum distance to roads and elevation) to facilitate model

Table 2

Description of landcover types derived from the ecoforest map for caribou (●), moose (■) and eastern coyotes (▲). The symbols indicate the use of the category in the complete or reduced ecoforest map models for each species. Complete models are divided into snow-free and snow-covered periods. The same landcover types are used between periods for reduced models.

Habitat category	Description	Complete model		Reduced model
		Snow-free	Snow-covered	
Regenerating stands	21–40-year-old stands (all species confounded)	■	■	■
Immature/mature coniferous stands	≥ 41-year-old coniferous stands (all coniferous species confounded)	▲	▲	▲
Regenerating spruce stands	21–40-year-old spruce stands	●	●	■
Immature spruce stands	41–80-year-old spruce stands	●	●	▲
Mature spruce stands	> 80-year-old spruce stands	●	●	■
Immature/mature spruce stands	≥ 41-year-old spruce stands	▲		
21 + spruce stands	≥ 21-year-old spruce stands			●
Immature/mature fir stands	≥ 41-year-old fir stands	▲		
Regenerating pine stands	21–40-year-old pine stands	●	●	
Immature pine stands	41–80-year-old pine stands	●	●	
Mature pine stands	> 80-year-old spruce stands	●	●	
21 + pine stands	≥ 21-year-old pine stands			●
Other coniferous stands	≥ 21-year-old coniferous stands (except spruce and pine stands)	●	●	
Other coniferous stands	≥ 41-year-old coniferous stands (except fir and spruce stands)	▲		
Coniferous stands #1	> 80-year-old spruce, and ≥ 41-year-old other coniferous stands	■	■	
Coniferous stands #2	≥ 41-year-old fir, 41–80-year-old spruce, and ≥ 41-year-old coniferous-dominated mixed stands	■	■	
21 + mixed or deciduous stands	≥ 21-year-old deciduous and mixed stands	●	●	●
Immature/mature deciduous-mixed stands	≥ 41-year-old deciduous and mixed stands	▲	▲	▲
Deciduous stands #1	≥ 41-year-old maple (<i>Acer</i> spp.), 41–80-year-old deciduous, and > 80-year-old deciduous-dominated mixed stands	■	■	■

(continued on next page)

Table 2 (continued)

Habitat category	Description	Complete model		Reduced model
		Snow-free	Snow-covered	
Deciduous stands #2	> 80-year-old deciduous, and 41–80-year-old deciduous-dominated mixed stands	■	■	■
Open lichen woodlands	Non-productive dry forest	●	●	●
Alder (<i>Alnus</i> spp.) stands	Alder stands	▲		
Peatlands	Non-productive humid forest or flooded area	●	●	●
		■	■	■
Water	Lakes and rivers	▲		
		●	●	●
Wetlands	Non-productive humid forest or flooded area, alder stands, and lakes and rivers	▲	▲	
0–5-year-old cuts	All types of cut 5-years-old or less	●	●	
		▲	■	
6–20-year-old cuts	All types of cut between 6 and 20 years old	●	●	
		▲	■	
			▲	
0–20-year-old cuts	All types of cut between 0 and 20 years old	■		▲
0–20-year-old natural disturbances	0–20-year-old fires and insect outbreaks	●	●	▲
		■	■	
		▲	▲	
0–20-year-old disturbances	0–20-year-old cuts, fires, and insect outbreaks			●
				■
Human	Human disturbances, non-forest land (urban areas, power transmission line and agricultural, industrial, mining activities)	■	■	■
Other	Polygons that did not fit any of the previous criteria or are weakly represented	●	●	●
		■	■	■
		▲	▲	▲

convergence. All the statistical and geomatics analyses were conducted using R statistical software (R Core Team, 2023) and ArcGIS Pro 3.1.2 (ESRI Inc, 2023).

3. Results

Across all species and biological periods, “Fusion” models consistently showed the lowest AIC_c values (see Tables 4–6 for caribou, moose and eastern coyotes, respectively). All three types of models were robust to cross-validation with mean *r*_s values ranging from 0.805 to 0.993 for caribou (Table 4), 0.849–0.994 for moose (Table 5) and 0.919–0.982 for eastern coyotes (Table 6), but the cross-validation scores of “Fusion” models were the highest (except for eastern coyotes in the snow-covered period). The parsimony of models based on “LiDAR only” versus those based on ecoforest maps only varied between species and periods.

Table 3

Variables (landcover types, LiDAR metrics, topography and linear features) included in the three groups of candidate models, i.e. “Ecoforest map only”, “LiDAR only” and “Fusion” models. The building of candidate models was conducted for each species and biological period (see Table 2 for complete and reduced model information).

Model	Equation
“Ecoforest map only”	Complete model + (1 ID-year)
	Complete model + Elevation + (1 ID-year)
	Complete model + Minimum distance to roads + (1 ID-year)
	Complete model + Elevation + Minimum distance to roads + (1 ID-year)
“LiDAR only”	LiDAR metric combinations + (1 ID-year)
	LiDAR metric combinations + Elevation + (1 ID-year)
	LiDAR metric combinations + Minimum distance to roads + (1 ID-year)
	LiDAR metric combinations + Elevation + Minimum distance to roads + (1 ID-year)
“Fusion”	Reduced model + LiDAR metric combinations + (1 ID-year)
	Reduced model + LiDAR metric combinations + Elevation + (1 ID-year)
	Reduced model + LiDAR metric combinations + Minimum distance to roads + (1 ID-year)
	Reduced model + LiDAR metric combinations + Elevation + Minimum distance to roads + (1 ID-year)
	Reduced model + LiDAR metric combinations + Elevation + Minimum distance to roads + (1 ID-year)

During the snow-covered period, LiDAR-derived metrics emerged as the primary determinant of caribou and eastern coyote habitat selection, while categories from “Ecoforest map only” models proved to be the most influential factor for these two species during the snow-free period (Tables 4 and 6, respectively), as well as for moose (Table 5) throughout both phenological periods.

LiDAR metrics contributed to explain the average habitat selection patterns shared by individuals for each of the three focal species. More precisely, caribou selected habitats characterized by a taller mean height of the shrub layer and a lower shrub layer cover across both periods (Table 4). During the snow-free period, they selected areas with a lower mean height of herbaceous vegetation, while avoiding a denser canopy cover during the snow-covered period (Table 4). Moose exhibited a selection for habitats with a denser shrub layer cover and a taller mean height of the shrub layer while avoiding a denser canopy cover throughout both periods (Table 5). Their selection patterns showed selection for areas with a lower maximum vegetation height during the snow-free period, and denser shrub layer heterogeneity during the snow-covered period (Table 4). Eastern coyotes displayed a selection for a denser shrub cover across both periods. During the snow-free period, they selected areas with a taller mean height of the shrub layer and a taller maximum vegetation height (all layers combined; Table 6). The selection for a greater heterogeneity of the shrub layer was detected during the snow-covered period (Table 6).

For all species and both periods, the reduction of model complexity by merging habitat categories together led to an increase in AIC_c values, indicating a loss of the balance between model adjustment and complexity (Table 7). The magnitude of information loss due to the category merging process ranged from a minimum ΔAIC_c of 45.9 (caribou during the snow-covered period) to a maximum of 746.5 (moose during the snow-covered period; see Table 7). Globally, this loss was consistently lower during the snow-covered period for both caribou and eastern coyotes compared to the snow-free period. For moose, we observed the opposite pattern, with a greater parsimony loss during the snow-covered period than during the snow-free period.

4. Discussion

In line with our hypothesis, we showed that integrating LiDAR data to habitat selection analyses improved our understanding of the behavioural responses of large mammals living in heterogenous landscapes. Indeed, the “Fusion” models had lower AIC_c, indicating a better

Table 4

ΔAIC_c values, cross-validation scores ($r_s \pm S.D.$) and variables with associated coefficients and 95% confidence intervals (CI) [lower bound : upper bound] from the highest-ranking RSF for the three types of models for caribou studied over the snow-free (left of dividing line) and snow-covered periods (right of the dividing line). The reference habitat (*Ref.*) corresponds to the category with a use/availability ratio closest to 1. Bold coefficients are statistically significant (95% CI does not include 0).

	Snow-free period			Snow-covered period		
	Ecoforest map only	LiDAR only	Fusion	Ecoforest map only	LiDAR only	Fusion
ΔAIC_c value	73.7	136.2	0.0	404.4	252.7	0.0
$r_s \pm S.D.$	0.885 ± 0.057	0.805 ± 0.081	0.907 ± 0.054	0.968 ± 0.019	0.991 ± 0.008	0.993 ± 0.012
Regenerating spruce stands	1.39 [0.77 : 2.01]			0.01 [-0.35 : 0.36]		
Immature spruce stands	0.26 [-0.03 : 0.54]			0.04 [-0.15 : 0.22]		
Mature spruce stands	0.63 [0.43 : 0.82]			<i>Ref.</i>		
All spruce stands			0.60 [0.32 : 0.88]			0.28 [0.02 : 0.53]
Regenerating pine stands	-0.37 [-0.91 : 0.17]			0.41 [0.17 : 0.65]		
Immature pine stands	-0.14 [-0.62 : 0.34]			0.47 [0.26 : 0.67]		
Mature pine stands	0.43 [0.01 : 0.86]			0.92 [0.72 : 1.12]		
All pine stands			<i>Ref.</i>			0.69 [0.42 : 0.97]
Other coniferous stands	-1.40 [-2.11 : -0.69]			-0.07 [-0.35 : 0.21]		
All mixed or deciduous stands	-0.67 [-1.22 : -0.18]		-1.01 [-1.61 : -0.41]	-1.22 [-1.57 : -0.88]		-0.79 [-1.22 : -0.37]
Open lichen woodlands	-0.54 [-0.96 : -0.12]		-0.05 [-0.53 : 0.44]	0.48 [0.28 : 0.68]		0.65 [0.34 : 0.96]
Peatlands	<i>Ref.</i>		0.63 [0.29 : 0.96]	-0.57 [-0.69 : -0.44]		-0.31 [-0.58 : -0.03]
Water	-1.31 [-1.74 : -0.88]		-0.94 [-1.45 : -0.43]	0.31 [0.14 : 0.49]		0.55 [0.25 : 0.86]
0–5-year-old cuts	0.44 [-0.31 : 1.19]			-0.44 [-1.12 : 0.24]		
6–20-year-old cuts	-3.09 [-5.08 : -1.11]			-0.59 [-0.99 : -0.19]		
0–20-year-old natural disturbances	-1.67 [-2.35 : -0.99]			-2.02 [-2.42 : -1.61]		
0–20-year-old disturbances			-0.73 [-1.29 : -0.18]			-0.94 [-1.30 : -0.58]
Other	0.21 [-0.53 : 0.95]		-0.42 [-0.97 : 0.14]	-1.16 [-1.71 : -0.61]		<i>Ref.</i>
Canopy cover (<i>log</i>)					-0.10 [-0.14 : -0.05]	-0.04 [-0.11 : 0.02]
Shrub cover (<i>log</i>)		-0.05 [-0.41 : 0.30]	-0.57 [-0.69 : -0.46]		-0.37 [-0.42 : -0.31]	-0.25 [-0.31 : -0.19]
Mean height of the shrub layer (<i>log</i>)		0.11 [0.02 : 0.21]	0.03 [-0.07 : 0.12]		0.59 [0.53 : 0.65]	0.51 [0.45 : 0.57]
S.D. of the shrub layer (<i>log</i>)					0.05 [-0.01 : 0.11]	-0.04 [-0.11 : 0.03]
Mean height of the herbaceous layer (<i>log</i>)		-0.35 [-0.44 : -0.26]	-0.28 [-0.37 : -0.19]			
Elevation		-0.20 [-0.30 : -0.10]	-0.17 [-0.28 : -0.07]	-0.18 [-0.24 : -0.11]	-0.21 [-0.27 : -0.16]	-0.19 [-0.25 : -0.13]
Min. dist. roads	1.10 [0.97 : 1.22]	1.03 [0.92 : 1.15]	0.97 [0.85 : 1.10]	0.74 [0.67 : 0.81]	0.72 [0.65 : 0.78]	0.66 [0.59 : 0.72]

Table 5

ΔAIC_c values, cross-validation scores ($r_s \pm S.D.$) and variables with associated coefficients and 95% confidence intervals (CI) [lower bound : upper bound] from the highest-ranking RSF for the three types of models for moose studied over the snow-free (left of dividing line) and snow-covered periods (right of the dividing line). The reference habitat (*Ref.*) corresponds to the category with a use/availability ratio closest to 1. Bold coefficients are statistically significant (95% CI does not include 0).

	Snow-free period			Snow-covered period		
	Ecoforest map only	LiDAR only	Fusion	Ecoforest map only	LiDAR only	Fusion
ΔAIC_c value	268.9	736.3	0.0	438.1	3219.2	0.0
$r_s \pm S.D.$	0.954 $\pm$ 0.034	0.933 $\pm$ 0.032	0.968 $\pm$ 0.021	0.849 $\pm$ 0.053	0.954 $\pm$ 0.038	0.994 $\pm$ 0.007
Regenerating stands	0.15 [0.08 : 0.22]		0.24 [0.18 : 0.29]	-0.22 [-0.28 : -0.15]		-0.29 [-0.34 : -0.23]
Immature/mature coniferous stands			<i>Ref.</i>			<i>Ref.</i>
Coniferous stands #1	<i>Ref.</i>			-0.60 [-0.70 : -0.50]		
Coniferous stands #2	-0.05 [-0.14 : 0.04]			0.49 [0.41 : 0.58]		
Deciduous stands #1	-0.22 [-0.31 : -0.14]		-0.04 [-0.11 : 0.04]	-0.76 [-0.84 : -0.67]		-0.69 [-0.77 : -0.61]
Deciduous stands #2	0.42 [0.32 : 0.52]		0.57 [0.48 : 0.66]	0.55 [0.44 : 0.65]		0.48 [0.39 : 0.58]
Wetlands	-0.03 [-0.12 : 0.06]		-0.18 [-0.26 : -0.10]	-1.78 [-1.92 : -1.64]		-1.81 [-1.95 : -1.67]
0–5-year-old cuts				<i>Ref.</i>		
6–20-year-old cuts				0.50 [0.44 : 0.56]		
0–20-year-old cuts	0.29 [0.22 : 0.36]					
0–20-year-old natural disturbances	-0.27 [-0.35 : -0.19]			0.46 [0.38 : 0.54]		
0–20-year-old disturbances			0.20 [0.15 : 0.25]			0.36 [0.31 : 0.41]
Human	-1.18 [-1.35 : -1.02]		-1.40 [-1.57 : -1.25]	-1.12 [-1.27 : -0.96]		-1.16 [-1.32 : -1.01]
Other	0.92 [0.68 : 1.16]		0.90 [0.67 : 1.13]	0.77 [0.61 : 0.92]		0.63 [0.48 : 0.79]
Canopy cover		-0.05 [-0.08 : -0.03]	-0.11 [-0.13 : -0.09]		-0.13 [-0.15 : -0.11]	-0.18 [-0.20 : -0.16]
Shrub cover (log)		0.12 [0.09 : 0.15]	0.10 [0.07 : 0.13]		0.15 [0.13 : 0.18]	0.04 [0.02 : 0.06]
Mean height of the shrub layer (log)		0.09 [0.08 : 0.11]			0.20 [0.18 : 0.21]	0.16 [0.14 : 0.17]
S.D. of the shrub layer (log)					0.25 [0.23 : 0.27]	0.23 [0.21 : 0.24]
Max. height (zq95th)		-0.03 [-0.05 : -0.01]	-0.04 [-0.06 : -0.01]			
Elevation	0.36 [0.34 : 0.38]	0.40 [0.37 : 0.42]	0.38 [0.36 : 0.40]	-0.04 [-0.07 : -0.02]	0.01 [-0.01 : 0.04]	-0.05 [-0.07 : -0.02]
Min. dist. roads	0.29 [0.27 : 0.30]	0.27 [0.26 : 0.28]	0.28 [0.27 : 0.29]	0.22 [0.21 : 0.24]	0.21 [0.20 : 0.23]	0.25 [0.23 : 0.26]

Table 6

ΔAIC_c values, cross-validation scores ($r_s \pm S.D.$) and variables with associated coefficients and 95% confidence intervals (CI) [lower bound : upper bound] from the highest-ranking RSF for the three types of models for eastern coyotes studied over the snow-free (left of dividing line) and snow-covered periods (right of the dividing line). The reference habitat (*Ref.*) corresponds to the category with a use/availability ratio closest to 1. Bold coefficients are statistically significant (95% CI does not include 0).

	Snow-free period			Snow-covered period		
	Ecoforest map only	LiDAR only	Fusion	Ecoforest map only	LiDAR only	Fusion
ΔAIC_c value	145.0	162.5	0.0	151.7	63.0	0.0
$r_s \pm S.D.$	0.921 $\pm$ 0.030	0.942 $\pm$ 0.051	0.982 $\pm$ 0.014	0.919 $\pm$ 0.054	0.953 $\pm$ 0.027	0.928 $\pm$ 0.041
Regenerating stands	0.15 [-0.02: 0.32]		Ref.	Ref.		Ref.
Immature/mature coniferous stands			-0.44 [-0.54 : -0.34]	-0.22 [-0.37 : -0.06]		-0.05 [-0.21 : 0.11]
Immature/mature spruce stands	<i>Ref.</i>					
Immature/mature fir stands	-0.37 [-0.53 : -0.21]					
Other coniferous stands	-0.34 [-0.83 : 0.14]					
Immature/mature deciduous-mixed stands	-0.68 [-0.96 : -0.40]		-0.80 [-1.06 : -0.54]	-1.43 [-1.91 : -0.95]		-1.33 [-1.82 : -0.84]
Alder stands	0.56 [-0.05 : 1.16]					
Peatlands	0.64 [0.01 : 1.26]					
Water	-0.09 [-0.67 : 0.49]					
Wetlands				-0.09 [-0.71 : 0.52]		
0–5-year-old cuts	-0.37 [-0.59 : -0.15]			-1.11 [-1.45 : -0.76]		
6–20-year-old cuts	0.46 [0.29 : 0.62]			0.45 [0.28 : 0.61]		
0–20-year-old cuts			-0.13 [-0.24 : -0.02]			0.01 [-0.15 : 0.17]
0–20-year-old natural disturbances	-0.57 [-0.79 : -0.34]		-0.71 [-0.91 : -0.52]	-0.95 [-1.26 : -0.65]		-0.84 [-1.15 : -0.53]
Other	-2.16 [-2.87 : -1.46]		-0.87 [-1.17 : -0.57]	-2.49 [-3.95 : -1.03]		-1.00 [-1.54 : -0.47]
Shrub cover (log)		0.29 [0.25 : 0.33]	0.28 [0.23 : 0.33]		0.53 [0.46 : 0.59]	0.52 [0.45 : 0.58]
Mean height of the shrub layer (log)		0.27 [0.23 : 0.31]	0.26 [0.22 : 0.30]			
S.D. of the shrub layer					0.08 [0.01 : 0.14]	0.09 [0.02 : 0.16]
Max. height (zq95th, log)		0.07 [0.03 : 0.11]	0.10 [0.05 : 0.14]			
Elevation	0.26 [0.21 : 0.30]	0.15 [0.11 : 0.19]	0.18 [0.14 : 0.23]	0.10 [0.03 : 0.18]	0.07 [0.004 : 0.14]	0.10 [0.03 : 0.17]
Min. dist. roads	-0.22 [-0.27 : -0.18]	-0.32 [-0.36 : -0.28]	-0.22 [-0.27 : -0.18]	-0.50 [-0.58 : -0.43]	-0.66 [-0.74 : -0.59]	-0.57 [-0.65 : -0.49]

Table 7

Information loss between complete and reduced ecoforest map models and Fusion models (Reduced ecoforest map + LiDAR model) for caribou, moose and eastern coyotes for the snow-free and snow-covered periods.

Species	Period	Complete ecoforest map model (AIC _c)	Reduced ecoforest map model (AIC _c)	Reduced ecoforest map + LiDAR model (AIC _c)
Caribou	Snow-free	4527.0	4575.2	4453.3
	Snow-covered	12033.6	12079.5	11629.2
Moose	Snow-free	115133.6	115570.6	114864.7
	Snow-covered	106169.2	106915.7	105731.1
Eastern coyote	Snow-free	15811.5	15963.8	15666.5
	Snow-covered	6638.1	6737.3	6486.4

fit to the data and a greater explanatory power regarding behavioural variation for the three species studied, which have contrasting ecological requirements, limiting factors, and conservation or socio-economic statuses. LiDAR data and forest maps thus seem to be complementary, as LiDAR data captured fine-scale structural attributes not available in the ecoforest maps, the latter providing relevant information on stand composition that airborne LiDAR cannot capture.

Several studies have also pointed out the importance of stand structure information provided by LiDAR data when conducting habitat selection analyses for different species (caribou: Dickie et al., 2023; gray wolf: Gregovich et al., 2025; moose: Blouin et al., 2021; Johnson and Rea, 2023). In addition, some studies have shown that the combination of LiDAR with maps describing vegetation composition outperformed these maps when used alone (Hagani et al., 2024; but see Gregovich et al., 2025). Part of the improved performance of our Fusion models may stem not only from LiDAR's ability to capture three-dimensional structural detail, but also from the use of quantitative predictors, which better represent subtle ecological changes than qualitative, discrete land cover categories. Such an advantage was also highlighted by Coops and Wulder (2019), who recommended the use of continuous variables for habitat assessments, since they provided a more realistic representation of habitat than discrete classifications.

Differences in model parsimony between “Ecoforest map only” and “LiDAR only” models likely reflect how species-specific ecological strategies interact with forest composition and structure. The interspecific variation observed in our study aligns with Nieman et al. (2022) and Russo et al. (2023), who showed that large mammals responded differently to habitat composition and structure. For example, caribou showed stronger associations with LiDAR metrics than with habitat categories during the snow-covered period, suggesting a greater reliance on structural attributes in winter. This likely reflects the need to access terrestrial lichens under snow (Johnson et al., 2004) and avoid predators (James et al., 2004) in sparse understory (Hins et al., 2009), features best captured by LiDAR. However, this pattern may also reflect the limited variation in forest cover during winter, as caribou tend to remain in mature coniferous stands, which reduces the explanatory power of ecoforest maps despite the ongoing importance of cover type. Additionally, seasonal shifts in model performance within species (i.e. caribou and eastern coyote) further support the idea that habitat selection is dynamic and sensitive to environmental changes or the ecological needs of species (Dupke et al., 2016; Dagtekin et al., 2023; Dejeante et al., 2024).

4.1. Airborne LiDAR structural metrics refine our understanding of habitat selection patterns

Ecoforest map categories confirmed well-documented habitat selection behaviour for caribou, with consistent avoidance of disturbed stands, whether logged or naturally disturbed (Stevenson et al., 2025), and selection for mature coniferous stands, particularly black spruce forests, known to support terrestrial lichens availability (Lantin et al., 2003; Hins et al., 2009; Thompson et al., 2015; Webber et al., 2022). LiDAR data added a layer of detail by revealing selection for structurally simple understory across periods: lower shrub cover in both periods, shorter mean herbaceous height in the snow-free period, and taller mean

shrub height in the snow-covered period. Such findings align with those obtained by Briand et al. (2009), who documented the same fine-scale selection, associated with higher terrestrial lichen biomass, using *in situ* vegetation surveys. Such structurally simple habitats may enhance predator detection by reducing visual obstruction and minimize spatial overlap with moose, an alternative prey for wolves (Seip, 1992) and black bears (Brodeur et al., 2008), thereby potentially lowering the associated predation risk for caribou (James et al., 2004; Lambert et al., 2006). This supports the idea that predation is a key limiting factor for caribou (Rettie and Messier, 2000), and suggests that fine-scale understory structure, quantified here using LiDAR, can help identify the specific habitat features that mitigate this constraint. During the snow-covered period, selection for sparse understory may reflect adaptations to snow-related constraints. Such a structure can facilitate movement and improve access to terrestrial lichens beneath the snow (Johnson et al., 2004). This interpretation is supported by Lesmerises et al. (2011), who observed a negative relationship between stand density and lichen biomass.

For moose, ecoforest maps revealed established patterns of selection toward disturbed areas (Gagné et al., 2016; Sand et al., 2021), mature deciduous stands and immature mixed stands dominated by deciduous species (Potvin et al., 2005; Bjørneraas et al., 2011). However, LiDAR data sharpened our understanding of these patterns, documenting selection for complex understory across both periods, characterized by a higher shrub cover throughout, and by a taller mean shrub height with greater heterogeneity (i.e. vertical variability) during the snow-covered period. This complexity likely suggests higher forage availability: dense understories are known to offer abundant shrubs during the growing season and remnant twigs during dormancy (Renecker and Hudson, 1992). This selection mirrors that observed by Melin et al. (2013), (2016) using airborne LiDAR and point to the importance of fine-scale vegetation structure in moose habitat selection. The LiDAR-derived metrics of canopy we used showed that moose selected for sparser canopy cover in both periods, and vegetation of lower height during the snow-free period, which could be explained by the greater abundance of deciduous vegetation in such open habitats (Bjørneraas et al., 2011). Put together, these findings suggest that, in the absence of major predators such as wolves (Villemure and Jolicœur, 2004), moose habitat selection in this region may be primarily shaped by forage availability rather than by the need for structural features that facilitate predator detection. The selection for open canopies during the snow-covered period may also reflect the need to optimize thermal balance and movement efficiency in snowy conditions by favouring stands with greater solar exposure at ground level (Leblond et al., 2010). Altogether, LiDAR can help better illustrate the trade-offs between forage accessibility and thermal cover that moose may face (Schwab and Pitt, 1991; Dussault et al., 2004, 2005b) by revealing structural habitat attributes associated with these ecological constraints.

Ecoforest maps highlighted eastern coyote-selected habitats—which, in agreement with previous studies, included regenerating stands (21–50 years) providing forage, cover, and prey—and the avoidance of closed-canopy forests (Boisjoly et al., 2010; Youngmann et al., 2022). Airborne LiDAR metrics documented eastern coyote selection for dense, heterogeneous understories in both periods, with a higher shrub cover, and a greater vertical structure variability during the snow-free period.

They also selected for taller canopy height during the snow-free period and for taller shrubs during the snow-covered period. These structural attributes, difficult to quantify with ecoforest maps alone, likely reflect important ecological functions such as foraging opportunities and cover. In the snow-free period, dense vegetation may provide fruit-bearing shrubs (Richer et al., 2002; Schrecengost et al., 2008; Melville et al., 2015) and ambush concealment (Pietz and Tester, 1983; Hodges, 2020). Similarly, canopy height may further act as a proxy for overall vegetative cover (Moudry et al., 2023), previously linked to snowshoe hare (*Lepus americanus*) abundance (Ivan et al., 2014). Tall woody cover may also buffer temperature extremes through microclimatic effects (De Frenne et al., 2019; Greiser et al., 2020) and could be used by eastern coyotes for thermoregulation (Melville et al., 2020). During the snow-covered period, structurally complex habitats may help eastern coyotes access key prey such as snowshoe hares, which themselves favor dense understory for cover and foraging (Boisjoly et al., 2010; Ivan et al., 2014; Simard et al., 2018). A dense and heterogeneous shrub layer may also reduce locomotion costs by intercepting snow and facilitating movement for eastern coyotes (Thibault and Ouellet, 2005), suggesting that snow-related mobility constraints could act as a limiting factor during winter.

4.2. Limitations

Our integration of airborne LiDAR data with ecoforest maps provided clear advantages but also revealed some limitations that should inform future research. One central challenge stemmed from the temporal and seasonal mismatch between data sources and animal movements. Airborne LiDAR was acquired during a snow-free campaign, capturing vegetation structure with full foliage, which does not accurately reflect the physical environment encountered by animals during the snow-covered period, especially in mixed or deciduous forests, where foliage presence and canopy cover vary drastically between seasons. In contrast, coniferous-dominated stands, offer more structurally stable habitats year-round, which may partly explain the stronger performance of “LiDAR only” models for caribou and coyotes in winter. To mitigate this temporal bias, we adjusted the definition of understory strata upward in the snow-covered models to account for snow accumulation and better approximate the vegetation structure accessible to animals. This simple correction likely improved realism, though it remains a simplification. Similarly, a temporal gap of up to ± 3 years between LiDAR and telemetry data introduced uncertainty, as forest structure can change due to growth or disturbances. Nevertheless, only a small proportion of GPS telemetry relocations were affected by disturbances with a ± 3 -year temporal window: 0.5% for caribou, 2.5% for moose and 2.2% for eastern coyotes, making us confident that the LiDAR data accurately reflect the habitat conditions experienced by the animals. The ecoforest map also suffers from limitations in update frequency, with forest stand attributes refreshed only every 10 years despite annual disturbance updates.

A further limitation arises from the spatial design of our study. Each focal species was monitored in a distinct study area and bioclimatic domain, characterized by its own combination of forest composition, disturbance regime, and climatic conditions. As a result, differences observed between species partly reflect this contextual variation in addition to species-specific ecology. Furthermore, LiDAR penetration decreases in dense canopies (Shokirov et al., 2023), potentially leading to better habitat characterization in open versus closed forest stands. Given that our study species occupy habitats with varying canopy closure, this differential performance could affect the comparison between LiDAR and forest map data sources. Our strongest inferences therefore stem from within-species comparisons of model types (Ecoforest map-only, LiDAR-only, Fusion) and periods, which were implemented consistently in each region. Inter-species comparisons are better interpreted as qualitative, context-dependent contrasts illustrating how LiDAR-derived structure can inform habitat selection in different boreal

settings, rather than as strictly controlled interspecific tests.

A methodological caveat warrants mention regarding the coyote seasonal periods. In contrast with the caribou and moose periods, the coyote “hunting-dispersion” period (Sep-Dec) encompasses a transitional window from snow-free to snow-covered conditions, an issue driven by sample size constraints that may influence the selection patterns revealed during this period. Future studies with larger sample sizes could refine these periods to better isolate snow-free effects for coyotes.

Finally, methodological differences in model building must be considered. Our use of predefined habitat categories in “Ecoforest map only” models limited model flexibility and may have constrained performance compared to the more exploratory approach used for LiDAR data. While merging habitat categories inevitably led to some information loss, this was compensated by gains from LiDAR integration in “Fusion” models.

5. Conclusions and management implications

Our findings illustrate both the potential and the limitations of using remote sensing data to model wildlife habitat selection across boreal landscapes. By integrating data from different sources—vegetation structure from airborne LiDAR and stands composition from forest maps—we showed that no single dataset can fully capture the complexity of animal-habitat relationships. Rather, integrating complementary data sources offers the most ecologically meaningful and accurate representation of habitat selection. Improving the temporal alignment between datasets by acquiring LiDAR more frequently and during key seasons, especially winter, would increase ecological relevance. Likewise, expanding the size and temporal resolution of telemetry datasets would allow for less constrained modeling, including testing interactions between LiDAR metrics and habitat types. Altogether, this would increase the robustness and comparability of models and deepen the understanding of species- and period-specific habitat selection patterns. Finally, adopting mixed-effects models with random slopes in future work would broaden inferential capacity by explicitly quantifying how habitat-selection responses vary among individuals, rather than assuming a uniform response across the population.

Our results reinforce previous recommendations highlighting the importance of considering the preservation, restoration or creation of specific forest stand structures to support specific large mammal requirements when planning forest management practices (Boan et al., 2011; Tomita and Hiura, 2021; Chevaux et al., 2022). They also underline the importance of incorporating forest structure into habitat management and planning strategies across boreal landscapes, as reflected in the average habitat-selection patterns identified for each species. For caribou, a threatened and iconic ungulate, maintaining areas dominated by coniferous stands, with low shrub cover and limited vertical heterogeneity, is essential to provide foraging opportunities and reduce predation risk. In contrast, promoting a structurally rich understory, particularly in regenerating or mixed stands, can enhance habitat quality for moose by increasing forage availability. Maintaining areas with dense, tall and vertically heterogeneous understory appears beneficial for this species, which holds a significant economic value through sport hunting. Finally, for eastern coyotes, managing landscapes to limit the representation of dense, vertically complex understory and regenerating stands could help decrease habitat attractiveness for this generalist predators in sensitive areas where human-coyote conflicts occur, or near ranges of ungulate prey (e.g. Atlantic-Gaspésie caribou; see Frenette et al., 2020) in order to reduce indirect predation pressure.

When used alongside forest maps, LiDAR allows practitioners to move beyond broad habitat categories and toward more refined, structure-informed planning tailored to species-specific needs. Integrating structural data into landscape management provides a valuable opportunity to reconcile the habitat requirements of vulnerable species, support sustainable ungulate populations, and mitigate emerging predator-related risks in the boreal forests of Quebec.

CRediT authorship contribution statement

Robert Schneider: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Frédéric Lesmerises:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Martin-Hugues St-Laurent:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Brendan Blanchard:** Writing – original draft, Methodology, Investigation, Formal analysis.

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. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123665](https://doi.org/10.1016/j.foreco.2026.123665).

Data availability

Data will be made available on request.

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