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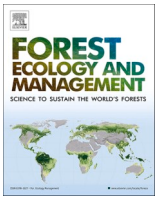

Influence of landscape composition and structure on habitat selection of a large herbivore in managed forests along a latitudinal gradient

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ABSTRACT

Large herbivores are keystone species in forest ecosystems, influencing forest structure and biodiversity through their selective browsing. Therefore, understanding herbivore habitat selection across spatiotemporal scales in managed forest landscapes is crucial for wildlife and forest management. This study examines how landscape structure (patch size and contiguity, distance to the nearest road) and composition (habitat type and heterogeneity) influence the seasonal habitat selection of moose (*Alces alces*) across five ecological zones. Using GPS data from 392 adult moose across 21 study sites (56–67°N) in Sweden, we combined Hidden Markov Models and Integrated Step-Selection Analysis to apply a patch-landscape approach that considers animals' behavior-specific responses at the scale of individual habitat patches and the broader landscape matrix. This approach allowed us to assess the role of small-scale habitat features and their spatial arrangement within the larger landscape context for moose movement and patch selection, thereby considering both landscape structure and composition. We found a dominance of landscape composition (i.e. habitat type) shaping moose selection at the patch scale, but also context-specific relevance of landscape structure (e.g. distance to the nearest road, patch size and contiguity). Moose preferred deciduous-mixed and young forests and generally avoided proximity to roads. Individuals occasionally selected for large and well-connected forest patches. Our findings highlight that forest management should prioritize preserving and connecting young and mixed-deciduous forest patches to facilitate moose access to their preferred habitats, thereby helping to distribute moose (and potentially browsing pressure) across forest patches within the managed landscape.

1. Introduction

Understanding how external environmental factors linked to internal cognitive processes drive animal movement and resource selection in changing environments is essential for studying animal ecology in the Anthropocene (Turner et al., 2001; Nathan et al., 2008; Wittemyer et al., 2019). Following the conceptual framework on animal movement (Nathan et al., 2008), movement decisions can be understood as the outcome of an interplay between internal states (e.g., needs related to feeding, resting, or parturition), motion and navigation capacities, and external factors such as the surrounding environment (biotic and abiotic). Together, these factors operate across multiple scales in space and time, resulting in a hierarchical habitat selection process, through which animals adaptively fulfill their needs (Johnson, 1980). Animal movements and habitat selection encompass both, daily 'within-area' decisions and broader seasonal patterns, offering key insights into ecological interactions and ecosystem functioning. For instance, animals adjust their selection spatially and temporally to cope with new threats or opportunities, such as the presence of predators and other risks, or changing foraging opportunities (Candolin, 2023; Zhang et al., 2023). Extensive research has examined how animals respondto dynamic environments, including seasonal variability (Fryxell et al., 2008; Bjørneraas et al., 2011; Owen-Smith, 2014). Assessing the internal state is challenging in wild animals, but methodological advances allow today differentiating behavioral patterns that can be used as indices for some internal states (e.g. resting, foraging, Wilmers et al., 2015; Whoriskey

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et al., 2017). Exploring scale-dependent patterns of movement and selection, recognizing internal and external factors, may be further advanced through a 'behavior-patch-landscape matrix'. Such an approach provides a more detailed prspective on how different landscape features influence animals' decisions, influenced not only by resource availability, but are also shaped by internal states (Klappstein et al., 2022).

Earlier work has quantified how landscape-scale features influence seasonal movement patterns across landscapes (e.g. migration and species distribution, Singh et al., 2012; Holloway and Miller, 2017; Van Moorter et al., 2021) and how herbivores, such as moose (*Alces alces*) (Herfindal et al., 2009; Leblond et al., 2010; Stewart et al., 2010; Neumann et al., 2013; Allen et al., 2016; Borowik et al., 2021), elk (*Cervus elaphus*) (Fryxell et al., 2008), fallow deer (*Dama dama*) and red deer *(Cervus elaphus)* (Giralt-Rueda and Santamaría, 2023), and roe deer (*Capreolus capreolus*) (Dupke et al., 2017; Giralt-Rueda and Santamaría, 2023) adjust habitat selection based on resource availability, landscape structure and composition, and environmental conditions. Landscape configuration, such as patchiness, plays a critical role in habitat selection and movement of large herbivores (e.g. *Cervus elaphus*, (Schippers et al., 2014; Seidel and Boyce et al., 2015)). Larger, contiguous patches often provide more resources and shelter, attracting herbivores, while smaller or fragmented patches can limit resources and increase movement costs. Patch size further influences movement dynamics, affecting foraging strategies and forage quality (WallisDeVries et al., 1999; Schippers et al., 2014; Seidel and Boyce, 2015; Borowik et al., 2020; Qi et al., 2021). Connectivity between patches is essential for facilitating movement and reducing energy expenditure, enabling species to access resources more efficiently, which is particularly important for large herbivores species roaming in managed landscapes. For example, bison (*Bison bison*; Seidel and Boyce et al., 2015), elk (Ling et al., 2023), and African elephants (*Loxodonta africana*) rely on connected habitats to reach widely distributed foraging areas (Crego et al., 2021). Yet, we still lack a good understanding of the interplay between landscape structure and composition across different landscapes, and how the surrounding landscape matrix influences the individuals' decision to utilize a patch during a given time in a given landscape.

Buildning on the conceptual framework that external factors and internal cognitive processes shape animal movement decisions (Nathan et al., 2008), recent research has highlighted the importance of integrating behavioral states into habitat selection models to improve model inference and enhance our understanding of how animals respond to environmental variation (Pohle et al., 2024). Considering behavior-specific habitat selection allows researchers to incorporate internal factors more explicity, providing deeper insights into animals' habitat use as individuals track resources for different purposes in changing landscapes (e.g. resting, forage, cover; Fryxell et al., 2008; Dupke et al., 2017; Giralt-Rueda and Santamaría, 2023). For example, studies on birds, such as gouse (Picardi et al., 2022) and golden eagles *(Aquila chrysaetos)* (Sur et al., 2021), and ungulates (e.g. mule deer *(Odocoileus hemionus)* (Paterson et al., 2023) and African zebra *(Equus quagga)* (Klappstein et al., 2022)) have demonstrated how movement behaviors, such as foraging versus resting, influence individuals' habitat preferences. The consequences of decisions in behavior-specific habitat selection create cascading ecological effects. For instance, in herbivores, behavior-specific decisions can influence their browsing pressure in a given place, and thus herbivores' impacts on vegetation dynamics, habitat structure, and composition. Large herbivores, often referred to as "ecosystem engineers" (Pastor et al., 1988; Côté et al., 2004) or "biological switches" (Hobbs, 1996), can generate strong ecological impacts, particularly in regenerating forests in managed landscapes like temperate and boreal forests (Bowyer and Kie, 1997; Fuller and Gill, 2001; Côté et al., 2004; Stewart et al., 2006; Spitzer et al., 2021). Understanding the features characterizing patches preferred within managed forest landscapes may help to manage the distribution of herbivores in a way that allows mitigating browsing hotspots.

Globally, intensive rotation forestry has transformed forest ecosystems, often replacing structurally diverse landscapes with extensive monocultures, changing ecosystems' preconditions (Hobbs, 2009; Radeloff et al., 2015; Girona et al., 2023). In Europe, large-scale forestry operations (Schippers et al., 2014; Haddad et al., 2015; Kuemmerle et al., 2016) create simplified landscapes that, while providing plenty of forage for herbivores, lack the diversity needed to support a range of wildlife species and bear the risk for conflicts where large herbivores roam in regenerating forests (Côté et al., 2004; Girona et al., 2023). In managed landscapes, herbivores closely interact with different types of land use (Neumann et al., 2022). Land use (Allen et al., 2016; Singh et al., 2016; Olofsson, 2017; Muthiuru et al., 2024) and roads (Yost and Wright, 2001; Laurian et al., 2012; Neumann et al., 2013; Prokopenko et al., 2017; Wattles et al., 2018) can lower habitat connectivity by breaking continuous forests into a mosaic of smaller, isolated patches and thereby altering animal distributions as they adapt to these modified landscapes (Fahrig, 2013). For instance, Giraffes (*Giraffa tippelskirchi*) exhibit altered space use in response to human presence (Muthiuru et al., 2024). However, relatively little attention has been given to the influence of structural landscape features such as patchiness, and how fine-scale habitat features interact with behavior-specific selection in different managed forest landscapes.

For a large herbivore like moose previous studies show that habitat selection is shaped by a combination of factors such as food availability, predation risk, hunting pressure, snow depth, and ambient temperature (Dussault et al., 2006; Bjørneraas et al., 2012; Van Beest et al., 2012). For example, within an agricultural-forest landscape moose show distinct daily and seasonal patterns where animals alternated their use of cultivated land and different forests (Bjørneraas et al., 2011). In managed forest-dominated landscapes, moose require spatially adjacent patches of young forest stands and older forests (Johnson and Rea, 2024). Moose have a varied diet to ensure nutritional balancing, which demands access to different food items within hetergeneous forage landscapes (Spitzer 2019; Felton et al., 2020). Food availability and habitat quality increase habitat preferences and lower space use (Dussault et al., 2006; Allen et al., 2016). Importantly, moose show scale- and state-dependent selection, often choosing areas with abundant low-quality forage at the landscape level while selecting high-quality forage or shelter from predators within their home range (Van Beest et al., 2010). Moreover, factors related to the landscape features generate variation within populations, whereas climatic factors affect variation among populations (Allen et al., 2016).

Using moose in managed forest landscapes in Sweden as a model species and building on previous work, we apply a novel "behavior-patch-landscape matrix" approach, which incorporates behavioral states as a departure point, to analyse animal habitat selection as a spatio-temporal process of different habitat features such as patchiness (i.e. patch size and contiguity), habitat types and heterogeneity, and distance to roads among seasons and along a latitudinal gradient. Sweden provides an ideal case study for examining animal-habitat relationships in managed forest landscapes due to its significant land-use transformation over the past century and high-intensity rotation forestry on large scale that has shaped the forest landscape (68 % of country's terrestrial surface, Antonson and Jansson et al., 2011; FOA, 2020; Girona et al., 2023). Sweden spans over a gradient from temperate to subalpine biome. Whereas Southern Sweden is characterized by more fragmented forest-agricultural landscapes. Northern Sweden features are larger and more connected forest patches that offer greater habitat continuity, allowing us to study the effect of different landscape matrices on moose habitat selection.

Our integrative perspective will not only enhances our understanding of herbivore ecology in anthropogenic landscapes where human land use largely defines the distribution of forage quantity and quality. Furthermore, we offers a scalable method for assessing the broader ecological consequences of forest management on large herbivores behavior and vice versa (Fraser et al., 2018; Katzner and Arlettaz, 2020).

Using a high-resolution dataset of 392 GPS-collared adult moose, spanning 11 degrees of latitude, we apply a combined approach of Hidden Markov Models and Integrated Step Selection Functions (HMM-iSSF, Klappstein et al., 2022; Picardi et al., 2022; Pohle et al., 2024) to explore different angles that together provide a multidimensional understanding of seasonal habitat selection. We apply a general model for a more broad perspective as well as zone-specific models to discriminate possible patterns across ecological zones:

1) How does **latitudinal variation** influence moose responses to landscape structure and composition? We expect that moose generally favor large habitat patches if available in each season to fulfil their daily needs (e.g. forage and lower disturbance risk). Given zone-specific differences in landscape structure, we expect moose in the two northern inland zones to select more for large contiguous patches, while moose in the Hemiboreal and Boreal Coastal zone select for smaller habitat patches. This pattern may not solely reflect active habitat selection but could also be largely driven by differences in landscape configuration itself, namely, the greater availability of large patches and lower fragmentation in the northern inland zones compared to the more fragmented landscapes in the southern and coastal zones, while still indicating behavioral flexibility in adaptation to environmental modifications (Sih, 2013).
2) How does **landscape structure**, including patch size, contiguity, and distance to the nearest road, shape moose habitat selection across different behavioral states and seasons? We expect moose to prefer larger patches in general, but in the Boreal Coastal and Hemiboreal zones, where human activity and habitat fragmentation are higher, we expect that moose might be restricted to using smaller patches, based on availability.
3) Which **forest types** (e.g. young coniferous stands, mixed-deciduous stands) are selected by moose in a given behavioral state and season in relation to coniferous forests? We predict young and mixed-deciduous forests to be attractive forage habitats across seasons in most ecological zones (Cassing et al., 2006; Bjørneraas et al., 2011; Spitzer et al., 2019).
4) How does habitat selection relate to **behavioral states**? We predict that during exploratory movements (i.e. longer and more directed steps), moose will select areas with larger, patchy habitats in all ecological zones and seasons, as these areas support larger movement distances to access diverse resources. In contrast, during restrictive movements (i.e. shorter and more torturous steps), we expect moose to prefer patches with high contiguity and heterogeneity, during the growing seasons, likely reflecting a need for concentrated foraging or resting sites.

2. Materials and methods

2.1. Study area

The study covered data from 21 sites in Sweden, stretching from South in Växjö (Kronoberg county) to North in Gällivare (Norrbotten county), thereby encompassing 11 degrees of latitude (56–67 °N), representing different environmental settings (Fig. 1). Sweden consists of four distinct biomes that encompass substantial differences in climate, habitat composition and configuration, and human influence, which are ecologically meaningful to consider when investigating moose habitat selection. Previous studies have shown that external factors influence moose habitat distribution and movement behaviour (Allen et., 2016; van Moorter etal., 2021) such as weather conditions (Singh et al., 2012), likely also light conditions (different timing of sunrise and sunset along the 11 degrees of latitude during most times of the year) and seasonality in life history events (Neumann and Ericsson, 2018; Neumann et al., 2020), but also in relation to human land use (Neumann et al., 2022). To reduce possible noise caused by variation among individuals and areas that would be needed to handle within an approach considering data of all study sites in the same model (e.g., Allen et al., 2016), we decided for two modelling approaches. One considering all data in the same model to test for general patterns, and one where we split our analyses according to the ecological zones that have been identified in previous studies to explore zone-specific patterns. We viewed regional differences, using zone-specific models, not as redundant replications, but as an opportunity to investigate how moose adjust habitat use and behavioral state expression under different ecological conditions.

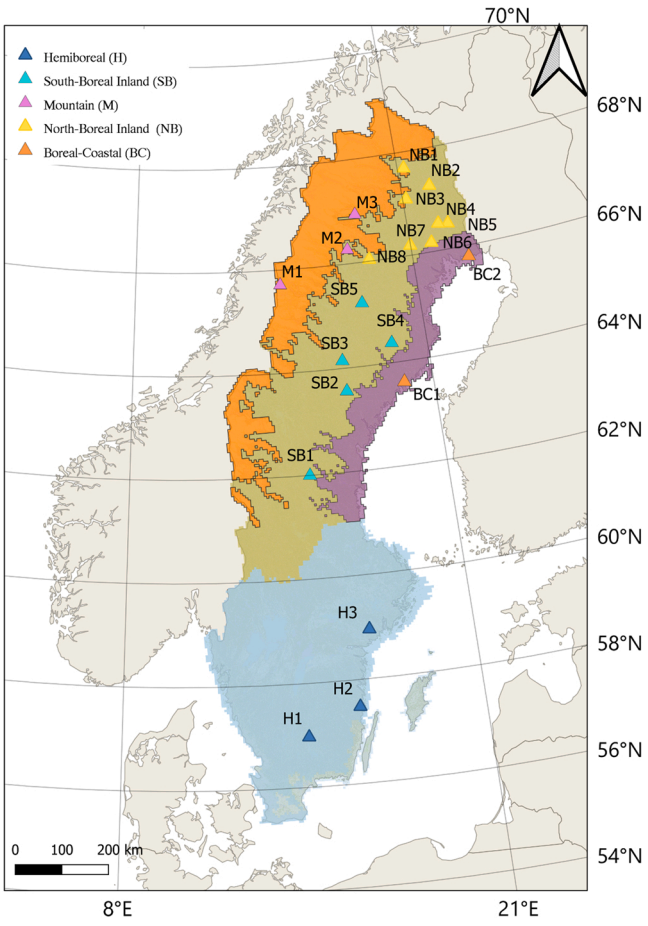

Fig. 1. Distribution of the 21 study sites across different ecological zones derived from the adjusted strata applied within the National Inventory Landscape Sweden (Swedish University of Agricultural Sciences, 2024). We subdivided the inland region into two zones to account for environmental differences, resulting in five ecological zones: (1) Hemiboreal (blue triangles – H1-H3); (2) South-Boreal Inland (SB) (light blue triangles -SB1-SB5); (3) Mountain (violet triangles – M1-M3); (4) North-Boreal Inland (yellow triangles – NB-NB8) and (5) Boreal Coastal (orange triangles - BC1-BC2).

Accordingly, we divided our study area into five major ecological zones following different biomes and a longitudinal distribution from the mountains to the coast, to group the data based on similarity of environmental preconditions: (1) the *Hemiboreal* zone (H, three study sites in the counties Kronoberg, Kalmar, and Södermanland, 2009–2017), (2) the *South-Boreal Inland* zone (SB, five study sites in the counties Gävleborg, Västernorrland, and Västerbotten, 2003–2007 and 2019–2023), (3) the *Mountain* zone (M, three study sites in the counties Västerbotten and Norrbotten, 2003 to 2016) (4) the *North-Boreal Inland* zone (NB, eight study sites in the county Norrbotten, 2008–2010 and 2013–2022), and (5) the *Boreal Coastal* zone (BC, two study sites in the counties Västerbotten and Norrbotten, 2004–2005 and 2016 – 2023), (Fig. 1). Ecological zones varied in climate with longer growing seasons, higher mean temperatures, and less snow in the South in contrast to the longer winters and greater snow depth in the North (www.smhi.se).

Temperatures in winter and summer average around 0°C to 2°C and 16°C and 18°C, respectively, in the Hemiboreal zone; −2°C to −7°C and 15°C and 17°C in the South-Boreal Inland zone; −11∘C and 8∘C in the Mountain zone; −10°C to −15°C and 10°C to 15°C in the North-Boreal Inland zone, and 2°C and 18°C in the Boreal Coastal zone. The human footprint on the landscape, such as road density, urban areas, and agricultural activities, was more prominent in the Southern regions (i.e. about 90 % of the inhabitants live below latitude 61°N) (www.scb.se, accessed 18 August 2022; Swedish National Atlas 1991). The heterogeneity of the landscape was characterized by different forest types following a south-north gradient. The Hemiboreal zone was characterized by patches of mixed-deciduous forest (e.g., birch, elm (*Ulmus glabra)*, oak (*Quercus robur*), maple (*Acer platanoides)*, and beech (*Fagus sylvatica*)) and coniferous forest, and agricultural fields in a flat to gently rolling terrain (Swedish Land Cover, 2012). Coniferous forests dominated in the northern inland zones with monocultures of Scots pine *(Pinus silvestris)*, Norway spruce *(Picea abies)* and birch *(Betula spp.)*, including also partly *Salix ssp,* interspersed with mires or bogs, and patches of agricultural activity. We decided to consider a Southern and Northern Boreal inland zone to acknowledge different climatic conditions (winter severity, light conditions), forest productivity, as well as human footprint. Mountainous birch forests and open areas with heaths, meadows, grass, bare rock, and sparsely vegetated areas above the tree line define the Mountain zone. A larger imprint of agriculture within the boreal forest landscape and higher human density compared to both inland zones characterize the Boreal Coastal zone.

Moose hunting in Sweden is a deep tradition and varies by region to reflect differences in climate and moose distribution (Apollonio et al., 2010; Neumann et al., 2022). In northern Sweden, the season typically begins in September and extends into January. In southern Sweden, hunting usually starts in early October and continues through December or January. Harvest is most intensive during the first three weeks following the start of the hunt (www.viltdata.se). During the rut, hunting is typically prohibited for about two weeks to allow for undisturbed breeding.

2.2. Moose capture and data handling

A total of 392 free-ranging adult moose have been followed across Sweden. Out of these, 320 were females (F) and 72 males (M). The distribution of individuals across zones varied slightly with 97 moose in the Hemiboreal zone (79 F, 18 M), 96 in the South-Boreal Inland (85 F, 11 M), 58 in the Mountain zone (46 F, 12 M), 77 in the North-Boreal Inland (52 F, 25 M), and 64 in the Boreal Coastal zone (57 F, 7 M), covering a study period of two decades (2003–2023). This extensive dataset is unique in its latitudinal and longitudinal distribution and includes continuous annual data in all zones. Moose were immobilized from a helicopter with a pre-pressurized dart using a CO2-powered rifle (Kreeger and Arnemo 2018). Capturing occurred during February and March, when moose were in their winter range, except at site M1, where it was conducted in November and December, while animals were still in their summer range. The intramuscular injection area preferred was the large muscle mass of the rump. The combination of the injection was made of 50 mg xylazine (Xylased® 500 mg, Bioveta, Ivanovice na Hané, Czech Republic) and 4.5 mg etorphine, an opioid (Captivon® 98 Etorphine HCl, 9.8 mg/ml, Wildlife Pharmaceuticals (Pty) Ltd, White River, South Africa). Immobilization was reversed using naltrexone and atipamezole. The procedure to handle free-ranging wildlife is described in more detail by (Græsli et al., 2020). All personnel handling the moose were certified according to the Swedish Animal Welfare Agency and the Swedish Board of Agriculture standards. All animal marking and handling had been approved by the Animal Care Committees in Umeå (DNR A116–09, A12–12, DNR 77–06, A205–12, A124–06, A124–05, A50–12, A14–15, A7–03, A3–16, A28–17, DNR A 11–2020). The GPS devices of Vectronic Aerospace calculated positions were stored and managed in the Wireless Remote Animal Monitoring (WRAM) database system for data validation and management at the Swedish University of Agricultural Sciences (Dettki et al., 2014).

To ensure consistency across the annual cycle, data were resampled at a regular rate of one GPS location every 3 h for all individuals using the R packages "momentuHmm" (Mcclintock, 2018) and “amt” (Signer and Fieberg, 2019). Quality control measures were implemented to ensure high data accuracy. The dataset was cleaned by removing duplicates, and GPS positions collected after death or collar removal. Furthermore, individuals located only in Norway were excluded. We filtered out outliers, such as high movement rates (>10 km per hour, which seems biologically unrealistic), and excluded individuals with fewer than 50 locations, ensuring data reliability, improving statistical power, and enhancing the interpretability of movement patterns and habitat selection. Finally, the data were divided into four seasons, summer, fall, winter, and spring, adjusted according to the latitude gradient of the study area, using information on the start and end of the seasons provided by the Swedish Meteorological and Hydrological Institute (SMHI 2023).

2.3. Landscape metrics – configuration and composition

We applied a behavior-patch-landscape matrix approach to analyse the influence of landscape structure on moose habitat selection, (Prieto-Remírez, 2023). We analysed landscape metrics at the individual home range level, focusing on three key aspects (Fig. 2):

i) *Patchiness* encompasses patch size, patch core area, and patch contiguity.
ii) *Habitat diversity*, considers five land cover types, the Shannon’s diversity index (SHDI) as an indicator of heterogeneity.
iii) *Fragmentation*, represented by patch contiguity and distance to the nearest road. Reflecting, respectively, the degree to which patches of a given habitat are physically connected, but also capturing the anthropogenic fragmentation and potential barriers to movement.

To efficiently calculate these landscape metrics for large spatial datasets, we used the R package “landscapemetrics” (Hesselbarth et al., 2019), leveraging parallel processing via the R packages “parallel” and “doSNOW”.

Specifically, we calculated the following metrics:

1. **Patch size** (AREA): Defined as the area of a given habitat type that is distinct from its surroundings. In movement ecology, patch size represents the annual available area to an individual or population.
2. **Patch core area** (CORE): Defined as the interior of the patch within a 100 m wide band inside the patch boundary. This metric complements patch size by capturing the undisturbed interior portion of habitat, which may offer higher refuge quality or reduced edge effects, factors potentially influencing moose foraging behavior.
3. **Patch contiguity** (CONTIG): Measures the spatial connectedness among patches of the same habitat type, indicating corridors, fragmentation, and connectivity of these patches within a landscape. Values range from 0 to 1, where values close to 0 represent low internal connectivity, (i.e. highly fragmented or irregularly shaped patches of the same habitat type are more isolated). Values near 1 indicate high contiguity, meaning that a given patch is more connected to patches of the same habitat type.
4. **Distance to the nearest road:** Euclidean distance (meter) of a given GPS position to the nearest paved and major road. Paved and major roads were defined as roads with a hard surface (e.g., asphalt, concrete, or bitumen) and classified as high-capacity, high-traffic routes, such as major regional roads, national highways, primary highways, and motorways.
5. **Shannon’s diversity index** (SHDI): A metric of landscape heterogeneity that incorporates both the richness (number of land cover

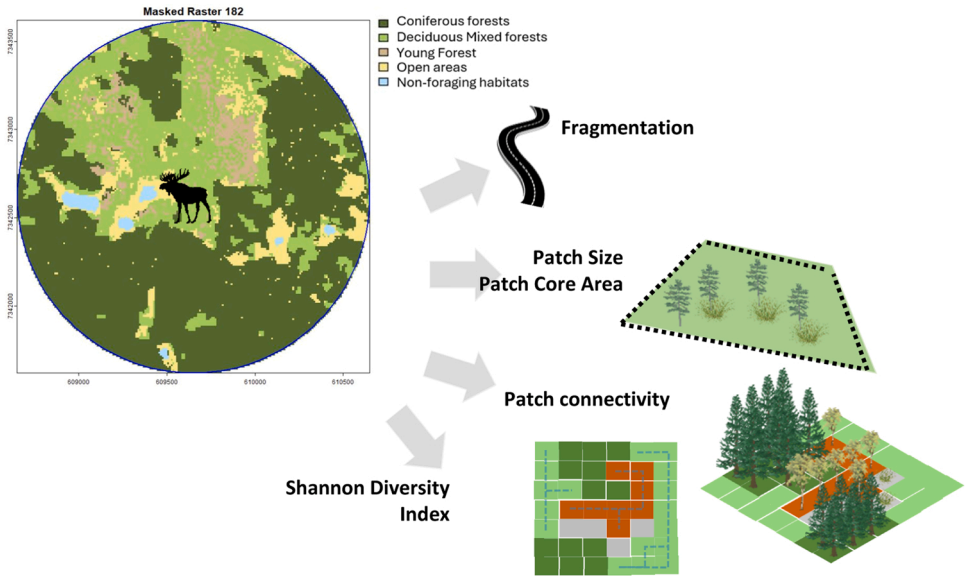

Fig. 2. Key landscape metrics influencing animals' habitat selection, including fragmentation (index of landscape subdivision), patch size and patch core area (index of overall dimensions and interior space among habitat patches), and patch contiguity (index of linkage between habitat areas). Shannon Diversity Index as an index for heterogeneity among land cover types within the landscape.

types) and evenness (relative adundance) of those types within a given area. Values close to 2 suggest a relatively high diversity and an even distribution of land cover types, while values between 0 and 1 indicate a low diversity and a dominance of one (or few) land cover types.

We calculated each index within a 1 km buffer around each animal's step (i.e. movement between two consecutive GPS locations), reflecting the average distance traveled by individuals within a 3-hour interval and allowing us to assess habitat influence for two behavioral states: "exploratory", which we considered as a state reflecting movement or transition, and "restricted", which we considered as a state reflecting foraging or resting. For AREA, calculations considered the extent of a given study site. For example, if a location fell within a large patch, the full patch size was measured rather than just a fragment within the 1 km buffer to ensure the ecological context was kept. Our data set covered two decades, therefore, we used land cover from two national land cover maps that had diffent timestamps: for data collected from 2003 to 2017 we updated the Swedish Land Cover Data from 2002 with official information on year-specific clearcuts dates up to 2018 (Swedish Forest Agency, www.skogsstyrelsen.se), at a spatial resolution of 50 m. This allowed us to accurately match clearcut events to the corresponding year of GPS data; for data collected after 2017, we used the Swedish EPA from year 2019 at a spatial resolution of 10 m (The Swedish Environmental Protection Agency). We grouped the 26 land cover classes into 5 main habitat classes considered biologically relevant for moose (Bjørneraas et al., 2011; Spitzer et al., 2020): 1) coniferous forests (hereafter *Coniferous*), 2) mixed and deciduous forests (hereafter *Mixed-Deciduous*), 3) temporarily non-forest (i.e. tress < 5 m, representing, for example, clear-cuts, burnt areas, young forests, hereafter *Young*), 4) open areas and arable land (hereafter *Open*), and 5) non-foraging habitat (including anthropogenic infrastructures, water sources and areas non-classified, hereafter *Non-Foraging*). We generated a raster of the Euclidean distance to the nearest paved and major roads (hereafter ROAD, 25-m resolution) based on the Swedish road map (Swedish Transport Administration (Trafikverket, 2014)).

2.4. Data analysis

To investigate moose habitat selection in relation to behavioral states and landscape structure, thereby considering internal and external factors, we applied a combined approach using Hidden Markov Models (HMM, R package "momentuHMM" (Mcclintock, 2018)) and integrated Step Selection Analysis (iSSA, R package *amt* (Signer and Fieberg, 2019), Fig. 3). While HMM alone does not address resource selection (Chandler, 2022), its combination with iSSA provides a robust framework for state-dependent habitat selection (Klappstein et al., 2022) by considering behavioral states, reducing bias, and better accounting for temporal autocorrelation, thereby enhancing overall accuracy (Pohle et al., 2024). We used two data streams derived from GPS location time series: step length (distance between successive GPS points) and turning angle (change in direction between three consecutive locations). Both were calculated from temporally regularized GPS fixes at 3-hour intervals. We defined two behavioral states using HMM based on a gamma distribution for step lengths and a Von Mises distribution for turning angles (Picardi et al., 2022). The HMM can infer the most likely hidden state at that time step based on adjacent data (before and after), which is helpful in dealing with GPS data gaps or period of signal loss. We fitted the Viterbi algorithm (Zucchini et al., 2016) to derive the most likely behavioral state for each step: "exploratory"(characterised by longer movement steps (mean $=$ 800 m $\pm$ 1000 m standard deviation (SD)) and more directed movement (mean $=$ 0.001 concentration $=$ 0.99)) and "restricted" (characterised by shorter steps (mean $=$ 100 m $\pm$ 100 m SD) and more tortuous movement (mean $=$ 3, concentration $=$ 0.1)). We interpret these two stages as indices for directed travel or movement (exploratory) and foraging or resting (restricted) as suggested by previous research (Graf et al., 2024, Paterson et al., 2023; Picardi et al., 2022). Steps were assigned a state only if both step length and turning angle could be calculated (i.e. requiring at least one GPS fix before and one after the current point).

Next, to quantify individuals' habitat selection in a given behavioral state, we applied iSSA (Avgar et al., 2016). For each empirically observed step, we generated five random steps based on gamma distribution for step lengths and Von Mises distribution for turning angles (Signer and Fieberg, 2019). Our decision to use five random steps is a practical balance between computational limitations and efficiency, ensuring sufficient coverage of available habitat options. The choice of the number of random steps is thus a trade-off between very many steps (commonly $>$20) and the lowest number (1) possible. Thurfjell et al. (2014) suggest that even a single random step per day is sufficient when

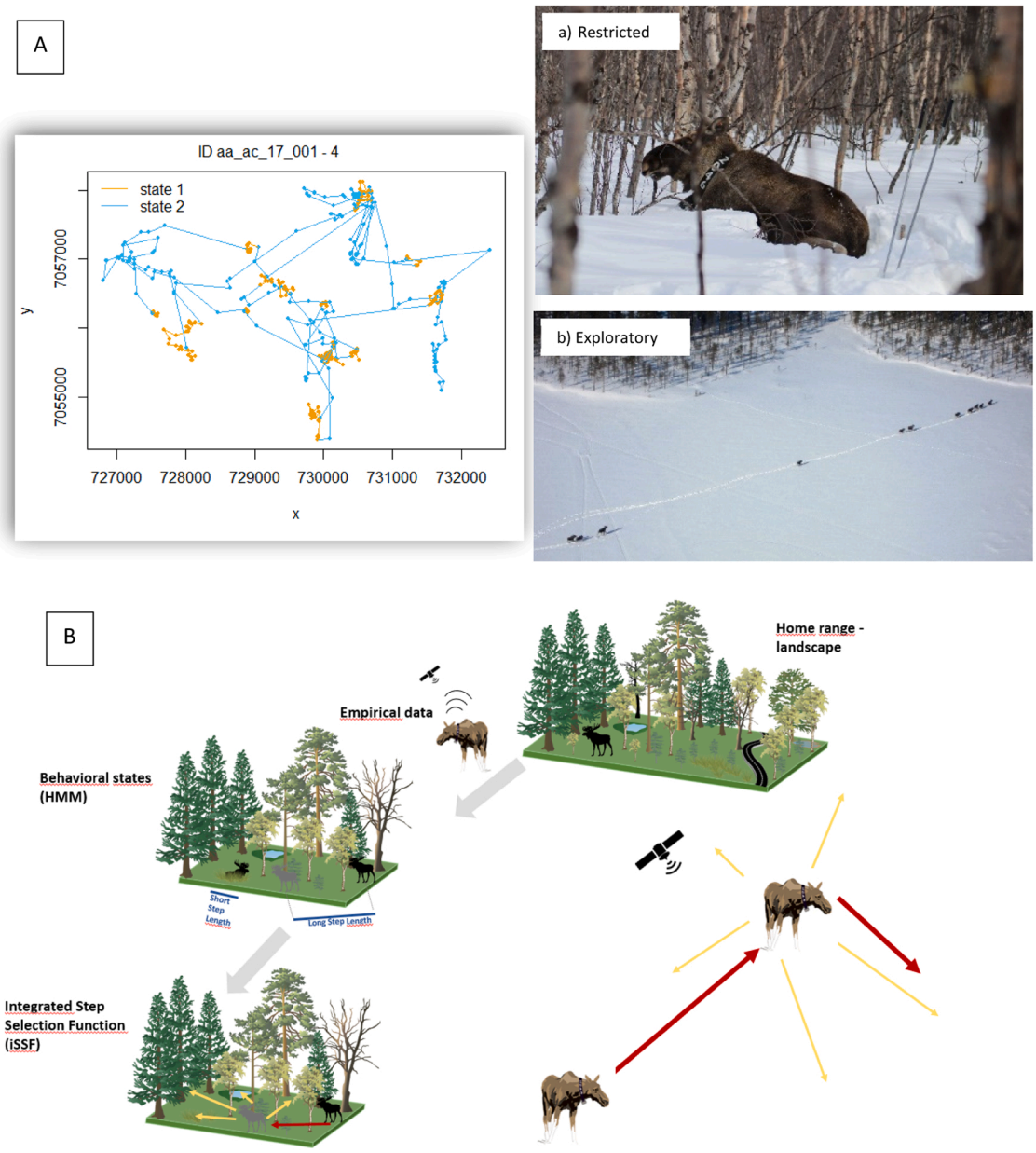

Fig. 3. A: Application of Hidden Markov Models (HHM) on empirical data from GPS-tracked moose to estimate state-specific movement; exploratory movement steps involve longer step lengths and more directed movements, while restricted movement steps correspond to shorter step lengths and more turning movements. B: Combination of HHM and Integrated Step Selection Function (iSSF)to comparing state-specific observed movement steps (empirical data) with random steps (n = 5) generated at the same starting point to calculate the probability that an animal selects a given habitat feature in relation to the reference feature and feature's availability.

rare habitats are not the focus. Additionally, Van Beest et al., (2012) used five random steps to study moose habitat selection with a similar approach used in our study. In our dataset, the proportion of discarded invalid positions relative to the total was 5.6 %. At each step endpoint (observed and random), we extracted the environmental covariates.

2.4.1. *Modelling*

We considered all environmental variables as continuous (Thurfjell et al., 2014), except habitat type, which was categorical (with Coniferous forest as reference habitat type). To allow for comparability and a better interpretation of the modelling results, we log-transformed and normalized continuous variables to have a zero mean and unit standard deviation. We screened all continuous variables for collinearity using Spearman's correlation (i.e. patch size (AREA), patch core area (CORE), patch contiguity (CONTIG), Shannon's Diversity Index (SHDI), distance from the nearest road, and terrain ruggedness). Patch core area exhibited strong collinearity with patch size ($r = 1.0$), and thus was excluded from the following analyses. Patch size was retained as it offers a more comprehensive measure of habitat selection. For each season and ecological zone, we built separate generalized linear mixed models (GLMMs, R package "glmmTMB", (Brooks et al., 2017; Muff et al., 2020) with Poisson family and stratum-specific fixed intercepts (Muff et al., 2020). Each model included fixed effects for habitat characteristics and their interactions with parameters on landscape structure (Table 1). In each model, we also considered two random effects to account for stratum-specific intercept *(1 | step_id)* and individual variation *(1 | animal_id)*. We summarized the estimated selection coefficients in a single dataset and visualized them in the same figure to provide a comprehensive picture of habitat selection among seasons for a given zone.

Table 1
Design of the conditional generalized linear mixed models (glmmTMB) to test individual-based selection of different landscape features by adult moose separately during two behavioral states, four seasons, in five ecological zones across Sweden, 2009–2022.

Generalized linear mixed model (GLMM)	Data sets
y_[a] ~	2 Behavioral states (restricted and exploratory)
log step length[b] +	
cosine turning angle[c] +	
State[d] * AREA[e] +	4 Seasons
State[d] * SHDI[f] +	(winter, spring, summer, fall)
Habitat types[g] * AREA[e] +	
State[d] * CONTIG[h] +	
AREA[e] * Roads[i] +	5 Ecological Zones
AREA[e] * SHD[f] +	(Hemiboreal, South-Boreal Inland, Mountain, North-Boreal Inland and Boreal Coastal)
(1 | step_id)[l] +	
(1 | animal_id)[m]	

[a] Observed and random steps; binary
[b] Logarithm of Step length
[c] Cosine of Turning Angle
[d] Two behavioral states, restricted and exploratory
[e] Patch size of a given habitat class within one km buffer
[f] Shannon-Diversity Index
[g] Five habitat types taken at the end of the step length. Coniferous forest is the reference level
[h] Patch contiguity of a given habitat class within one km buffer
[i] Euclidean distance to the nearest road[ill] Stratum-specific intercept
[m] Individual variation

We tested the interaction between patch size and habitat types in our models. However, in certain winter ecological zones, this resulted in excessively high coefficients and confidence intervals. These implausibly large values indicated potential issues with model stability, overfitting, or data sparsity, despite the absence of explicit convergence warnings. To address these concerns, we simplified the models by removing the interaction between patch size and habitat type, thereby improving model stability and ensuring more robust and interpretable results.

2.4.2. Daily behavioral rhythms

To investigate how the expression of moose behavioral states varied over the diel cycle, we used the decoded Viterbi sequence from the Hidden Markov Models, assigning each GPS location to either the exploratory or restricted state. We extracted the time of day from each GPS timestamp (converted to local solar time) and binned data into hourly intervals. For each hour, we calculated the proportion of GPS fixes classified as either state, summarized by season and ecological zone. These proportions were then averaged across individuals to visualize patterns of behavioral state expression throughout the day. This allowed us to quantify activity rhythms and investigate potential seasonal and regional differences in diel behavior.

3. Results

The general model emphasized overarching seasonal patterns in forest type selection, road avoidance, and state-dependent effects of patch structure, whereas the zone-specific models highlighted how the strength and even direction of these effects varied locally across ecological regions. Both approaches converged on a stable core: moose selected young and mixed-deciduous forests year-round, avoided non-foraging habitats (and often open areas in spring and fall) and roads in most seasons. During restricted movement in summer–fall, moose favored larger, more contiguous patches. Compared to the general model, the region-varying models indicated three things: (1) weak or neutral relevance of structural metrics (patch size, contiguity, heterogeneity) in several regions despite the pooled trend; (2) road avoidance was not universal, with some regions and seasons showing neutral or reversed effects; and (3) patch-size preferences can flip (smaller vs. larger patches) in specific contexts, particularly in summer.

3.1. General patterns in moose habitat selection

Across all seasons, several predictors on both landscape composition and structure significantly influenced moose habitat selection, but with varying seasonal effects. Moose consistently showed strong selection for both young and deciduous-mixed forest throughout the year and distinct selection against non-foraging areas. Open areas were selected against in spring and fall (Fig. 4a, Appendices Table A.1). In summer, moose tended to select larger and more connected patches and young forest and mixed-deciduous forests, when in a restricted movement state. Patches with higher levels of contiguity were preferred during summer (Fig. 5a). In spring, summer, and fall, moose strongly selected areas further away from roads (Appendices Table A.1). Interaction effects revealed important context-dependent relationships. The positive effect of patch area and contiguity on habitat selection was stronger during restricted movement in summer and fall. In winter and summer, large patches located closer to roads were more likely to be used than expected from the main effects alone (Appendices Table A.1). Animals selected for habitat heterogeneity (SHDI) only in spring, but especially during restricted movement. Across all seasons, moose showed stronger selection for large patches when these patches were embedded within landscapes of high habitat heterogeneity (Appendices Table A.1).

3.2. Zone–specific patterns in moose habitat selection

We found also dinstinct zone specific patterns of moose selecting for different features of landscape composition and structure features over the annual cycle (Appendices Table B.1–5).

In contrast to our expectations, we found that patch size and contiguity, alongside compositional metrics, such as habitat heterogeneity (SHDI) had limited influence on moose habitat selection in most ecological zones and seasons. Moose selected localities farther from roads, except in the North-Boreal Inland during spring and in the Boreal Coastal zone during winter, Appendices Table B.2–4).

Consistent with our predictions and as supported by the general model, individuals selected more for young and mixed-deciduous forests compared to coniferous forests in all zones (Fig. 4b), Appendices Table B.1–5), whereas they selected always against non-foraging and often against open habitats (except in the Hemiboreal zone, Fig. 4b, Appendix Table B.1). Patch size influenced habitat selection by moose only in the Boreal Coastal zone, where individuals consistently selected smaller patches across all seasons. While in the South-Boreal Inland and in the Mountain zone selection for larger patch size is particular relevant during summer, as also shown by the general model, Appendix Table B.2–3). Still, the size of patches became relevant in specific contexts such as in relation to distance to the nearest road or behavioral state. For instance, moose selected larger patches closer to roads in the Mountain, North- and South-Boreal Inland and Boreal Coastal zones. They were more likely to show restricted movement behavior during fall in the Hemiboreal, South- and North-Boreal Inland zones, but also during summer in the Mountain and North-Boreal Inland zones (Fig. 5b). Restricted movement was common in larger patches (especially in summer and fall, in the Mountain and North-Boreal Inland zones). Patch contiguity was also relevant for restricted movement in these same zones and seasons, with moose responding strongly to the spatial connectedness of habitat during summer and fall (Figs. 5b, 6). The distribution of movement steps classified as restricted and exploratory behavioral states followed diurnal patterns, exhibiting a bimodal activity pattern (e.g., higher share of restricted steps during daytime and more exploratory steps in the morning and evening) in most ecological zones and seasons, specifically in summer (Fig. 7). With few exceptions, the overall share of restricted movement steps dominated, particularly during winter in all zones.

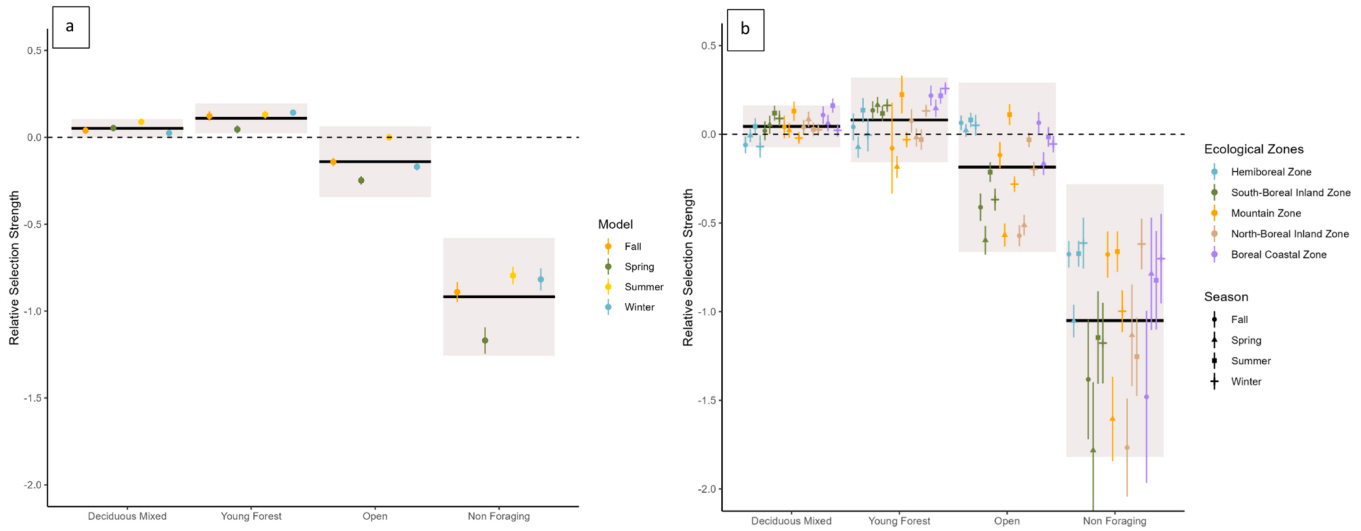

Fig. 4. Estimated relative selection strength (mean estimates ± 95 % confidence intervals) for key habitat types by season*:* (a) General model results across all ecological zones showing seasonal selection for mixed-deciduous forest, young forest, open habitats, and non-foraging areas*;* (b) Zone-specific model results illustrating seasonal habitat selection patterns within each ecological zone in Sweden. Coniferous forest is taken as reference. Values above the line represent positive selection for patch contiguity, while values below indicate negative selection.

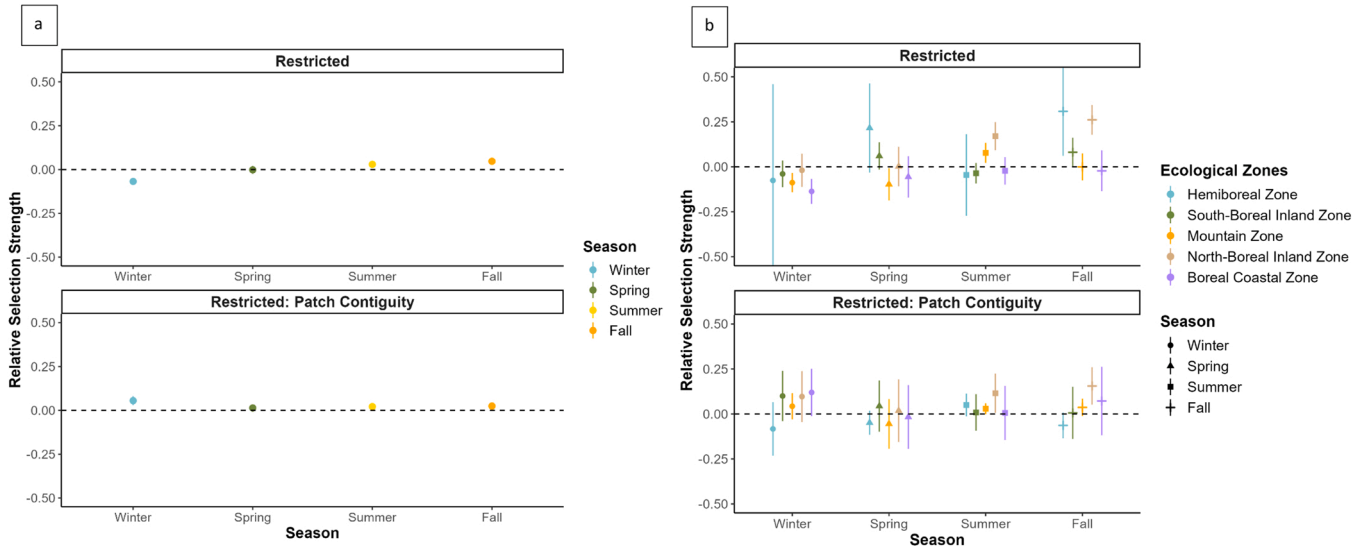

Fig. 5. Estimated relative selection strength (RSS, and 95 % CI) for the behavioral state Restricted (upper panels) and its interaction with patch contiguity (lower panels) across seasons: (a) General model results showing seasonal variation in selection strength across all ecological zones combined; (b) Zone-specific model results illustrating seasonal patterns within each ecological zone in Sweden. The overall selection strength during restricted movement, with the exploratory state serving as the reference category (intercept at RSS=0, indicated by the dashed line). The bottom panel shows the effect of patch contiguity during restricted state, with the exploratory state as reference. Values above the line represent positive selection for patch contiguity, while values below indicate negative selection.

4. Discussion

Using an extensive data set, we found general patterns but also zone-specific responses in the annual habitat selection of a large herbivore, as moose in relation to both landscape composition (habitat type, habitat heterogeneity) and landscape structure (including patch size and contiguity, and distance to the nearest road). From our work, four key findings emerged, each shedding light on the complex landscape-specific interplay between landscape composition, structure, and behavioral states in shaping the habitat selection in adult moose.

First, we found landscape composition (i.e. habitat type) to be an important feature shaping the habitat selection in adult moose. In support of our hypothesis and previous research, both the general model and the zone-specific models consistently showed selection for habitats composed of a mosaic of mixed-deciduous stands (Courtois et al., 2002; Dussault et al., 2006; Street et al., 2015; Borowik et al., 2024) and regenerating young forest stands (Blouin et al., 2021). This aligns with the ecological interplay between moose and the surrounding forest landscape as synthesized by Johnson and Rea, (2024) who emphasize that moose in managed forests largely depend on a matrix of mixed-deciduous, early successional, and mature coniferous forests to meet their daily needs. In line with previous research, our observed selection pattern on vegetation-rich habitats (i.e. mixed-deciduous and regenerating young forest stands) likely reflects the importance of these habitat types in fulfilling the dietary and shelter needs for a browser during different seasons (Borowik et al., 2024). Young forests provide abundant, high-quality forage for a large-bodied herbivore like moose (Spitzer et al., 2019; Felton et al., 2020), while mature coniferous stands

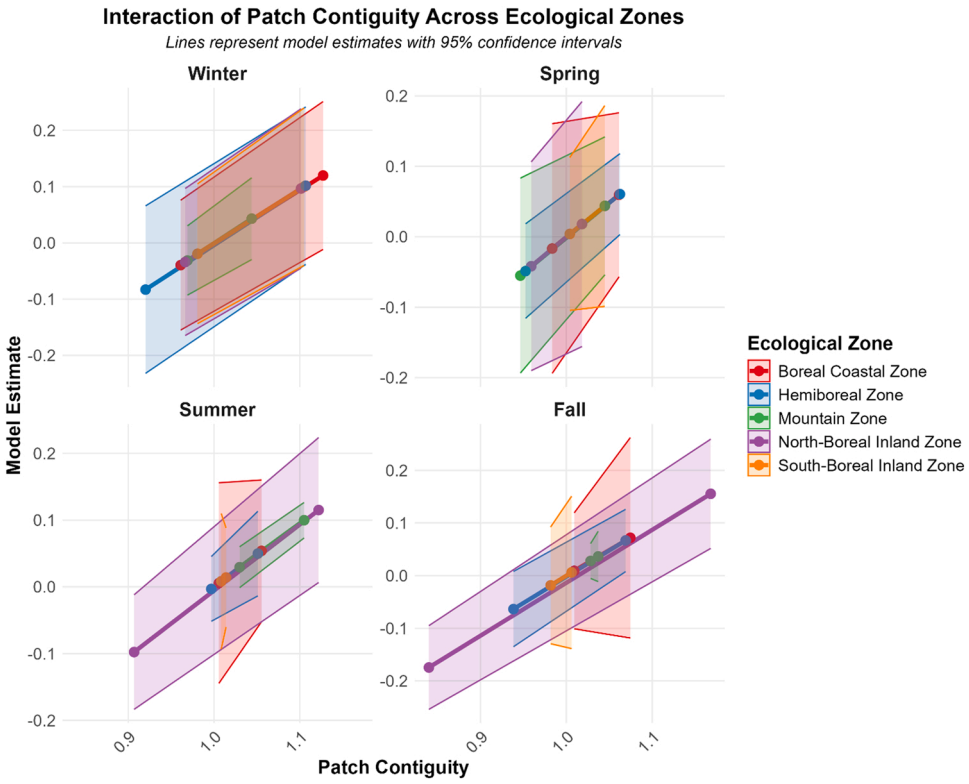

Fig. 6. Estimated relative selection strength (y-axis) of log-transformed patch contiguity (x-axis, and corresponding 95 % confidence intervals) selected by moose in a given season and ecological zone as given by the conditional logistic regression (glmmTMB), Sweden 2003–2022.

offer field-layer forage alongside thermal and security cover (Cederlund and Okarma, 1988; Crête and Courtois, 1997). Widespread natural and industrial disturbances in many parts of North America have cast doubt on the presumed tolerance of moose for vast, uniform expanses of young forest (Thompson and Stewart, 1998). However, in Sweden and other places in Fennoscandia, young forests differ in scale and structure compared to their North American counterparts (i.e. usually smaller size), offering significantly more forage (woody browse) compared to the surrounding older forests (Ball et al., 2001; Bergqvist et al., 2018; Loosen et al., 2021). This feature makes them attractive foraging habitats patches within the forest landscape in winter, but also during other seasons, as supported by our results. Thinning practices, however, can influence the extent of mixed-deciduous forage availability within young forests. Aspen (*Populus tremula*), willow (*Salix* spp.), and rowan (*Sorbus aucuparia*) are highly preferred by moose, making stands of deciduous and mixed forests attractive to satisfy animals' diet demands (Shipley et al., 1998; Bergqvist et al., 2018; Felton et al., 2020; Spitzer et al., 2020). Importantly, we found that individuals consistently selected against open and non-foraging areas across all seasons and ecological zones, suggesting that these habitats are of very little interest for moose, supporting findings in other systems (e.g. Canada (Gagnon et al., 2024)). We found one notable exception in this selection pattern: open areas in the Hemiboreal zone, which individuals selected in summer and fall, while in the Mountain zone during summer and in the Boreal Coastal zone during fall. Our findings suggest that within the agricultural-forest landscapes of this zone, selection of open areas likely reflects the utilization of forage-rich agricultural fields, such as cereal crops, that provide attractive forage sources (e.g., cereals, Felton et al., 2024; Widén et al., 2024). This indicates individual plasticity and flexibility in habitat selection in this forest-dwelling cervid species, as also found in other Cervidae and systems (e.g., roe deer in France, (Morellet et al., 2011) and moose in Norway (Bjorneraas et al., 2011))

Second, contrary to expectation, the selection of patch-level structural features, such as patch size and contiguity, alongside compositional metrics like habitat heterogeneity, was context-specific (i.e. depending on the ecological zone, season and behavioral state). For example, larger and more connected patches were preferred in certain seasons and zones (e.g. in winter and summer in the South-Boreal Inland zones; fall in the Mountain zone and North Boreal Inland zone), supporting our hypothesis that moose select larger patches, in these zones, compared to the more human-imprinted and fragmented Hemiboreal and Boreal Coastal zone. Interestingly, moose in the Boreal Coastal zone consistently selected smaller patches year-round. This different selection pattern might reflect individuals' responses to the unique landscape composition and spatial habitat configuration along the coast, supporting our expectation of higher flexibility in selection patterns in this zone. This is characterised by a fragmented forest landscape under the strong influence of rotation forestry (Svensson et al., 2020). It also includes islands and peninsulas, which naturally limit the size of forest habitat patches, but are relatively easily accessible for moose (by swimming or moving on ice). Transition among these patches allows animals to access a mosaic of resources distributed across the fragmented landscape, possibly compensating for the smaller patch sizes and highlighting moose's environmental adaptability. During restricted movement, we found that larger patches were preferred (e.g., summer and fall in the Mountain and only in fall in the North-Boreal Inland zones), whereas smaller patches were preferred during spring in the North-Boreal Inland zone, and during winter in the South-Boreal Inland and Boreal Coastal zones. Previous research pinpoints that patch size affects herbivore selectivity, with larger patches allowing for better discrimination between feeding sites within a given patch, enhancing the overall foraging efficiency of herbivores (WallisDeVries et al., 1999). Larger patches are more attractive than smaller ones (e.g. elk, (Seidel and Boyce et al., 2015)), while smaller patches may lead to more random or localised movement patterns due to even resource distribution (Borowik et al., 2020). Studies including red deer, bison, and moose demonstrate that larger, resource-rich patches can provide the necessary forage and protection required during

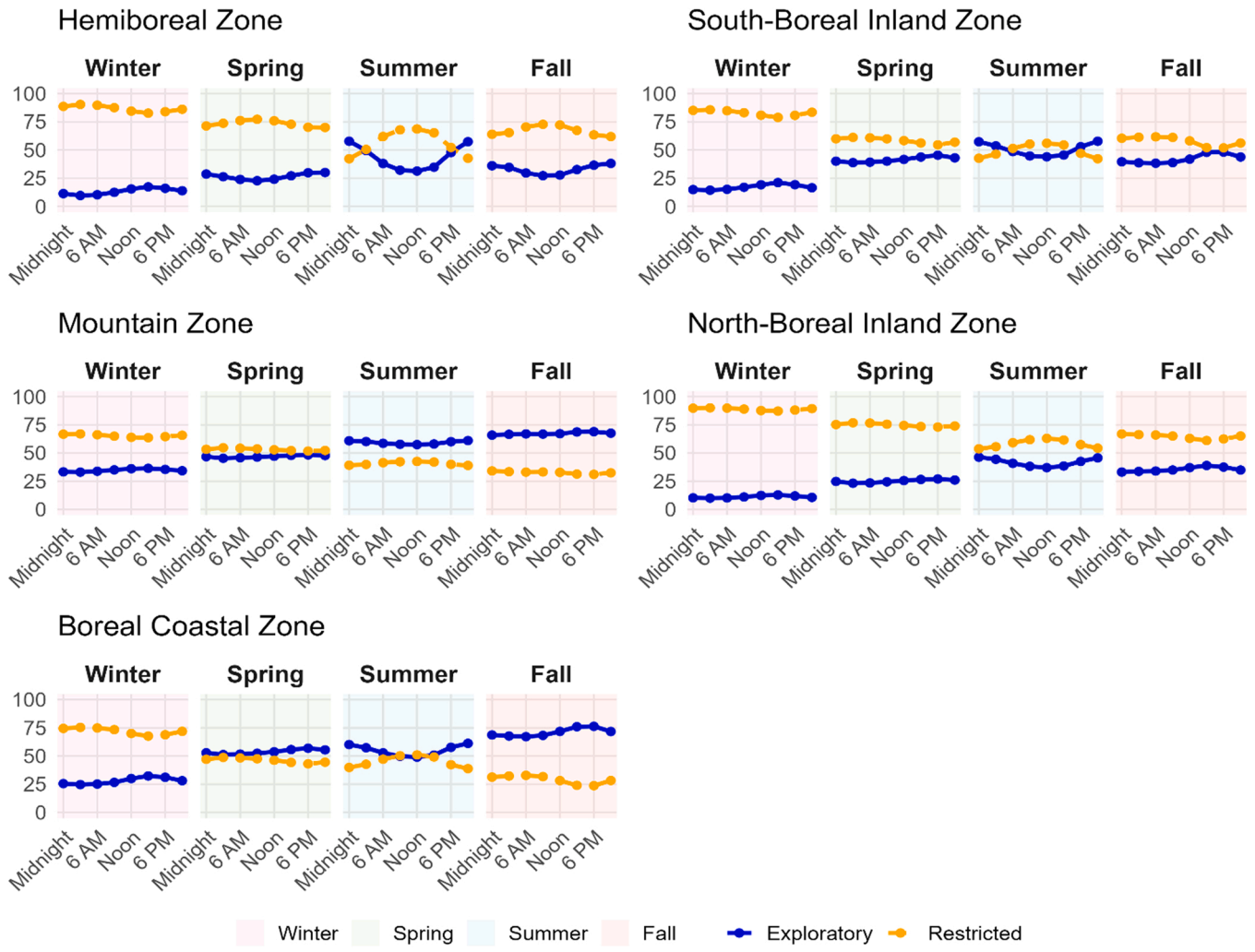

Fig. 7. Percentage of moose movement positions during a given time of the day (hour) being exploratory (blue lines) or restricted (orange dashed lines), stratified by ecological zones and seasons. Each subplot represents a specific ecological zone, with seasons (Winter, Spring, Summer, and Fall).

restrictive behavioral states (Van Beest et al., 2010; Avgar et al., 2016). Even though we see a context-specific component, this finding supports the overarching idea that a large-bodied herbivore like moose may favor larger patches for energy efficiency when their movement is restricted, as these patches likely provide sufficient resources within a more confined area, reducing the need for extensive movement.

Similar to patch size, patch contiguity emerged as a context-dependent factor. In the North-Boreal Inland zone in particular, moose selected more contiguous patches during restricted movements (i.e., likely foraging and resting) in summer and fall. Contiguous patches likely provide easy movement and access to foraging resources, particularly in fragmented or harsh environments, as seen in large herbivores, such as African elephants (*Loxodonta africana*) (Codron et al., 2011), reticulated giraffes (*Giraffa reticulata*) (Kearney et al., 2003) and plains zebras (*Equus quagga*) (Owen-Smith et al., 2010) that have been found to prioritize patch contiguity to maintain movement and resource access in fragmented landscapes (Crego et al., 2021). Likewise, in the European context, roe deer or the European bison (*Bison bonasus*) demonstrate strong preferences for connected habitat patches in fragmented landscapes (Bluhm et al., 2023).

Selection for habitat patch contiguity appears to vary along latitudinal gradients and seasons, as supported by our hypothesis (e.g. general model also showing a significant positive effect in summer). More specifically, we found selection for patch contiguity in zones with lower human activity and during the vegetation period (e.g. during summer for the North- Boreal Inland and Mountain zones, during spring and fall in the Hemiboreal zones). From the forest management perspective, higher levels of contiguity might facilitate the distribution of herbivores across attractive forage patches, which in turn may help to dilute the browsing pressure in a given patch. Here, we encourage future research to investigate quantitatively whether more diverse and connected forest landscapes help to distribute herbivores to a larger degree across attractive forest patches, which in turn may mitigate the gathering and over-utilization of isolated patches.

Interestingly, habitat heterogeneity (SHDI) played a nuanced role in moose habitat selection. In the general model, animals selected for higher levels of SHDI in spring, particularly during restricted movements when moose likely engaged in foraging—suggesting that diverse habitat mosaics offer critical resources during this nutritionally demanding period. Moreover, across all seasons, the positive interaction between patch size and SHDI indicates that large patches embedded within heterogeneous landscapes—likely combining abundant forage with proximal shelter or cover—were preferentially selected. This finding is consistent with previous work showing that interspersion of forage and cover (akin to landscape heterogeneity) enhances habitat suitability at broader scales (e.g., Dussault et al., 2006). The weaker signal of this interaction in the zone-specific models, suggests that the influence of heterogeneity may be most apparent at landscape-wide scales, underscoring the importance of multiscale approaches to fully capture habitat selection dynamics.

Thirdly, our study pinpointed the relevance of paved and major roads for habitat selection in this large-bodied herbivore where individuals consistently selected against road proximity, suggesting that roads were generally avoided year-round (i.e. in South-Boreal and North-Boreal Inland, and Mountain zones but also in the general model). Similarly, roe deer and red deer (Coulon et al., 2008; Bastianelli et al., 2024), elk (Prokopenko et al., 2017), and reindeer *(Rangifer tarandus)* (Beyer et al., 2016; Dyer et al., 2002) show distinct adjustments towards roads (e.g. roads are avoided during day) or general avoidance (Borowik et al., 2024). In moose, linear features like roads can funnel animal movement (Bartzke et al., 2015), and roads might be perceived as intrusive features, particularly in remote areas with low human presence (e.g. Canada, Dussault, 2007; Laurian et al., 2008; Beyer et al., 2013; Sweden, Neumann et al., 2013; USA, Wattles et al., 2018). In areas where road density and human activity are relatively higher (e.g. the Hemiboreal and Coastal zone), we found little effect of roads on individuals' habitat selection, suggesting a reduced sensitivity to roads, potentially due to habituation or the availability of forage along roadsides, particularly along smaller roads (Dyer et al., 2002; Beyer et al., 2013, Johnson and Rea, 2024). Notably, our finding on the interactions between road proximity and patch size highlighted a context-specific dynamic in our system with individuals selecting larger habitat patches closer to roads differently across seasons and zones. This finding underscores the importance of considering regional context when assessing habitat accessibility and availability.

Lastly, our study emphasizes the importance of considering behavioural-state-specific habitat selection as the selection of landscape features like structural components, dependent on individuals' movement state (Klappstein et al., 2022; Pohle et al., 2024). Behavioral states may reflect different prioritization and trade-offs in selection. For example, our findings pinpoint the relevance of larger habitat patches within the landscape matrix for moose during their restricted movement, which may indicate refuges within the dynamic managed forest landscapes. Moose generally showed a higher share of restrictive movements than explorative during a diurnal cycle, making large patches places where animals spent most time (which in turn may affect the browsing pressure in those patches). The diel rhythm of behavioral states, particularly the pronounced crepuscular exploratory state peaked during summer, which provides further insights into how moose adjust their activity in response to seasonal photoperiod, potentially thermoregulation but also seasonal energetic demands (Graesli et al., 2020). Compared to the more stable behavioral profiles observed in winter and spring, the summer activity pattern suggests a shift in foraging strategy or movement to avoid midday heat, but might also be influenced by the lack/reduction of clear day-night patterns in summer at higher latitudes (i.e. midsummer nights). In summary, the observed daily rhythms highlight behavioral plasticity in response to the surrounding environment within this herbivore. Additionally, preference for forage (availability and quality) and safety might be prioritized, as during this time of the day, individuals focus on intake and rumination. In contrast, selection for easier pathways and access to attractive habitats might be more relevant during transit among habitats under exploratory movement.

4.1. Limitations

We used a comprehensive dataset on individual movement data across a latitudinal gradient and several years to quantify the seasonal habitat selection of adult moose in relation to landscape structure and composition. Yet, some limitations need to be mentioned. First, the data resolution might not have been ideal. Three-hour intervals might bear the risk of missing fine-scale movements and brief interactions with landscape features between GPS locations (e.g. short foraging bouts, rapid responses to environmental stimuli or the use of small and fragmented habitat patches). This could affect the detection of moose preferences for or avoidance of specific landscape features (e.g. forest edges or water bodies). Second, we acknowledge that the interpretations of the behavioral states are not confirmed by direct observations or independent data, and thus should be viewed as indicative rather than definitive. We use these states as behavioral indices, as done in previous research. For example, similar movement patterns have previously been used as proxies for such behaviors in large herbivores (e.g. Paterson et al., 2023), Future studies with complementary data (such as accelerometers or field observations) could further validate this classification. Third, we also want to acknowledge that the number of individuals varied across ecological zones with the Boreal Coastal zone including fewer moose and a higher proportion of females compared to the other zones. While we consider our sample size per zone to be sufficient to capture individual-level variation, we cannot exclude that sex-specific differences in habitat selection, movement behavior, or dispersal (e.g. male-biased dispersal) may have influenced observed selection patterns. This is particularly relevant in the Boreal Coastal zone, where restricted patch selection may reflect not only landscape configuration but also underlying demographic structure and sex-specific selection patterns. Last but not least, our dataset spans two decades (2003–2023), a period over which notable changes in climate, forest structure, and management practices have occurred in Sweden (Bergkvist et al., 2025). These temporal changes may include increased clearcutting, changes in thinning practices (Lundmark et al., 2017) as well as milder winters or altered snow conditions (Berteaux et al., 2016). While our analysis does not explicitly account for temporal trends, the broad temporal coverage may integrate long-term variability in landscape use. We suggest that future studies could benefit from explicitly testing temporal effects or stratifying analyses by time periods to disentangle the influence of climate change or policy shifts on moose habitat selection.

4.2. Implications for conservation and management

The present study highlights the intricate interplay between landscape composition, structure, and behavioral states in shaping the habitat selection of a large-bodied herbivore. Our findings emphasize the critical role of composition but also structural features such as distance to the nearest road, patch size, and contiguity in combination with behavioral state for animal habitat selection in forest landscapes shaped by humans. Our findings suggest that managing populations of large herbivores such as moose in forest-rich countries where intensive rotation forestry is common, requires maintaining a mosaic of mature, mixed-deciduous and young forests in suitable patch size and contiguity to facilitate distribution of individuals across different habitat types (Felton et al., 2024; Johnson and Rea, 2024). While our results focus on patterns of habitat selection, they may have broader implications for the ongoing herbivore–forestry conflict (Beguin et al., 2016; Widemo et al., 2019; Neumann et al., 2024). Our findings suggest that landscape matrices composed of a variety of attractive habitats could encourage a more spatially dispersed use of the landscape by moose. Such dispersion could, in theory, lead to a more even distribution of foraging pressure, potentially alleviating concentrated browsing damage on economically valuable tree species. However, we caution that habitat selection alone does not necessarily equate to actual browsing impact, and further research linking selection patterns to browsing intensity at fine spatial scales would be necessary to support this hypothesis. Nevertheless, integrating landscape-level planning with ecological knowledge on herbivore habitat selection behavior could offer promising pathways toward more sustainable coexistence in managed forest systems.

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CRediT authorship contribution statement

Wiebke Neumann: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Göran Ericsson:** Writing – review & editing, Writing – original draft, Validation, Resources, Funding acquisition. **Marco Heurich:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology. **Navinder J Singh:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Funding acquisition. **Matteo L. Bastianelli:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Formal analysis. **Desirée Guidobaldi Stenbacka:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, 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

Appendix Table A.1
Coefficients, confidence intervals (CI), and statistics from the full conditional generalized linear mixed model (glmmTMB) for seasonal general patterns in habitat selection of adult moose across all ecological zones. Ecological zone was included as a random effect. Coniferous forest, exploratory state, medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength, and values above 1 indicate higher relative selection strength, for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				**Spring**				**Summer**				**Fall**			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	0.27	0.26 – 0.28	−77.01	< 0.001	0.20	0.19 – 0.20	−89.94	< 0.001	0.13	0.12 – 0.15	−50.21	< 0.001	0.15	0.14 – 0.15	−79.08	< 0.001
log Step Length	0.92	0.92 – 0.93	−34.00	< 0.001	1.00	0.99 – 1.00	−0.90	0.370	1.07	1.06 – 1.08	24.41	< 0.001	1.06	1.05 – 1.06	17.81	< 0.001
Cosine Turning Angles	1.10	1.09 – 1.11	20.09	< 0.001	1.00	0.99 – 1.01	0.60	0.551	0.77	0.77 – 0.78	−50.75	< 0.001	0.91	0.90 – 0.92	−16.60	< 0.001
state [Restricted]	0.94	0.92 – 0.95	−6.81	< 0.001	1.00	0.98 – 1.02	−0.17	0.865	1.03	1.01 – 1.05	3.34	0.001	1.05	1.03 – 1.07	4.58	< 0.001
Area	1.03	1.00 – 1.06	2.26	0.024	0.98	0.94 – 1.03	−0.64	0.524	1.02	1.00 – 1.04	1.57	0.116	1.00	0.97 – 1.02	−0.38	0.705
SHDI	1.01	0.99 – 1.02	0.93	0.351	1.05	1.03 – 1.07	4.58	< 0.001	0.99	0.98 – 1.00	−1.68	0.094	0.99	0.98 – 1.01	−1.01	0.313
Contig	0.97	0.95 – 1.00	−2.12	0.034	1.00	0.98 – 1.02	−0.04	0.966	1.07	1.05 – 1.09	8.21	< 0.001	1.01	0.99 – 1.02	0.61	0.543
Road	1.04	1.02 – 1.05	6.09	< 0.001	1.06	1.04 – 1.08	5.07	< 0.001	1.03	1.01 – 1.04	4.55	< 0.001	1.02	1.01 – 1.03	4.69	< 0.001
Mixed-Deciduous	1.02	1.01 – 1.04	2.53	0.011	1.06	1.04 – 1.08	5.58	< 0.001	1.10	1.08 – 1.12	9.89	< 0.001	1.04	1.02 – 1.06	3.69	< 0.001
Young	1.16	1.14 – 1.18	16.16	< 0.001	1.05	1.02 – 1.07	3.94	< 0.001	1.15	1.12 – 1.18	11.01	< 0.001	1.13	1.10 – 1.16	8.39	< 0.001
Open	0.84	0.82 – 0.86	−15.89	< 0.001	0.78	0.76 – 0.80	−20.26	< 0.001	1.00	0.98 – 1.03	0.38	0.702	0.87	0.85 – 0.89	−11.37	< 0.001
Non-foraging	0.44	0.41 – 0.47	−25.26	< 0.001	0.31	0.29 – 0.34	−30.13	< 0.001	0.45	0.42 – 0.47	−30.72	< 0.001	0.41	0.39 – 0.43	−30.28	< 0.001
state [Restricted] x Area	1.02	1.00 – 1.04	1.84	0.065	1.03	0.97 – 1.10	0.96	0.336	1.04	1.02 – 1.05	4.97	< 0.001	1.05	1.03 – 1.07	5.66	< 0.001
state [Restricted] x Contig	1.06	1.03 – 1.08	4.08	< 0.001	1.01	1.00 – 1.03	1.64	0.100	1.02	1.01 – 1.04	2.92	0.004	1.03	1.01 – 1.04	3.18	0.001
state [Restricted] × SHDI	0.99	0.97 – 1.01	−1.06	0.290	0.97	0.95 – 0.99	−2.81	0.005	1.01	0.99 – 1.03	1.27	0.203	1.00	0.99 – 1.02	0.47	0.639
Area × Road	0.99	0.99 – 1.00	−2.96	0.003	1.02	1.00 – 1.04	1.89	0.059	0.99	0.99 – 0.99	−4.24	< 0.001	1.00	0.99 – 1.00	−1.41	0.157
Area × SHDI	1.01	1.00 – 1.02	2.48	0.013	1.06	1.02 – 1.10	3.12	0.002	1.01	1.00 – 1.02	3.17	0.002	1.01	1.00 – 1.01	2.12	0.034

Appendix Table B.1

Coefficients, confidence intervals (CI), and statistics given by the conditional generalized linear mixed model (glmmTMB) for the seasonal habitat selection of adult moose in the **Hemiboreal zone**. Coniferous forest, exploratory state and medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength and values above 1 indicate higher relative selection strength for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				**Spring**				**Summer**				**Fall**			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	1.40	0.22 – 8.96	0.36	0.722	0.27	0.13 – 0.57	−3.45	0.001	0.33	0.17 – 0.66	−3.17	0.002	0.22	0.09 – 0.51	−3.50	< 0.001
log Step Length	0.89	0.87 – 0.90	−13.77	< 0.001	0.96	0.95 – 0.97	−7.23	< 0.001	1.04	1.03 – 1.06	6.38	< 0.001	1.01	1.00 – 1.03	2.24	0.025
Cosine Turning Angles	1.01	0.98 – 1.04	0.43	0.670	1.02	1.00 – 1.04	1.70	0.089	0.88	0.86 – 0.90	−10.79	< 0.001	0.98	0.95 – 1.00	−2.20	0.028
state [Restricted]	0.93	0.54 – 1.58	−0.28	0.781	1.24	0.97 – 1.59	1.71	0.088	0.96	0.76 – 1.20	−0.39	0.694	1.36	1.06 – 1.74	2.44	0.015
Area	702.53	0.10 – 4742427.78	1.46	0.145	0.47	0.01 – 16.36	−0.42	0.675	2.07	0.08 – 56.92	0.43	0.667	0.82	0.01 – 51.07	−0.10	0.923
SHDI	1.06	0.83 – 1.34	0.45	0.653	1.10	0.96 – 1.28	1.34	0.181	1.15	1.01 – 1.29	2.19	0.028	1.13	0.99 – 1.29	1.80	0.072
Contig	1.11	0.96 – 1.27	1.42	0.155	1.06	1.00 – 1.13	2.07	0.039	1.00	0.95 – 1.05	−0.13	0.900	1.07	1.01 – 1.13	2.21	0.027
Road	114.58	0.70 – 18633.35	1.83	0.068	4.64	0.64 – 33.82	1.51	0.130	11.29	1.73 – 73.64	2.53	0.011	4.08	0.40 – 42.05	1.18	0.237
Mixed-Deciduous	0.93	0.88 – 0.99	−2.14	0.032	0.99	0.96 – 1.03	−0.38	0.706	1.05	1.00 – 1.09	1.96	0.050	0.94	0.90 – 0.99	−2.52	0.012
Young	1.00	0.91 – 1.09	−0.09	0.926	0.93	0.88 – 0.99	−2.38	0.017	1.15	1.07 – 1.23	3.88	< 0.001	1.04	0.97 – 1.12	1.09	0.277
Open	1.05	0.99 – 1.11	1.71	0.088	1.02	0.99 – 1.06	1.19	0.233	1.08	1.04 – 1.13	3.97	< 0.001	1.07	1.02 – 1.11	3.05	0.002
Non-foraging	0.54	0.47 – 0.63	−8.35	< 0.001	0.35	0.32 – 0.38	−22.37	< 0.001	0.51	0.47 – 0.55	−18.13	< 0.001	0.51	0.47 – 0.55	−17.66	< 0.001
state [Restricted] x Area	0.37	0.04 – 3.13	−0.91	0.362	2.02	0.73 – 5.59	1.35	0.176	1.04	0.43 – 2.54	0.10	0.923	1.98	0.78 – 5.02	1.44	0.149
state [Restricted] x Contig	0.92	0.79 – 1.07	−1.09	0.274	0.95	0.89 – 1.02	−1.42	0.155	1.05	0.99 – 1.12	1.54	0.123	0.94	0.87 – 1.01	−1.74	0.081
state [Restricted] × SHDI	1.01	0.93 – 1.10	0.28	0.783	0.97	0.93 – 1.01	−1.36	0.175	1.00	0.95 – 1.05	−0.08	0.933	1.00	0.96 – 1.05	0.12	0.903
Area × Road	71372867.57	0.00 – 3513084130248517120.00	1.44	0.150	3.46	0.00 – 53646.32	0.25	0.801	9.19	0.00 – 96211.36	0.47	0.639	2.65	0.00 – 254482.55	0.17	0.868
Area × SHDI	1.27	0.41 – 3.92	0.42	0.675	1.22	0.61 – 2.42	0.56	0.575	1.51	0.83 – 2.75	1.35	0.177	1.69	0.88 – 3.25	1.59	0.113

Appendix Table B.2
Coefficients, confidence intervals (CI), and statistics given by the conditional generalized linear mixed model (glmmTMB) for the seasonal habitat selection of adult moose in the **South-Boreal Inland zone**. Coniferous forest, exploratory state and medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength and values above 1 indicate higher relative selection strength for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				**Spring**				**Summer**				**Fall**			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	0.27	0.25 – 0.30	−28.17	< 0.001	0.17	0.15 – 0.19	−29.24	< 0.001	0.17	0.15 – 0.18	−43.93	< 0.001	0.13	0.11 – 0.14	−36.91	< 0.001
log Step Length	0.92	0.91 – 0.93	−14.17	< 0.001	1.05	1.03 – 1.06	6.24	< 0.001	1.04	1.03 – 1.05	6.34	< 0.001	1.09	1.07 – 1.11	10.80	< 0.001
Cosine Turning Angles	1.16	1.14 – 1.19	13.44	< 0.001	1.06	1.03 – 1.09	3.87	< 0.001	0.75	0.74 – 0.77	−24.17	< 0.001	0.91	0.88 – 0.93	−6.58	< 0.001
state [Restricted]	0.96	0.89 – 1.04	−1.04	0.296	1.06	0.98 – 1.15	1.55	0.120	0.96	0.91 – 1.02	−1.24	0.215	1.08	1.00 – 1.18	1.98	0.047
Area	1.39	1.26 – 1.54	6.28	< 0.001	1.13	0.91 – 1.39	1.13	0.260	1.13	1.03 – 1.25	2.46	0.014	1.09	0.94 – 1.26	1.14	0.254
SHDI	1.01	0.95 – 1.08	0.41	0.684	1.08	1.01 – 1.14	2.41	0.016	1.02	0.98 – 1.06	1.00	0.320	1.01	0.96 – 1.07	0.44	0.658
Contig	0.98	0.87 – 1.11	−0.31	0.760	1.00	0.90 – 1.12	0.07	0.942	1.01	0.94 – 1.09	0.37	0.711	0.98	0.88 – 1.10	−0.33	0.743
Road	1.02	0.93 – 1.11	0.40	0.688	1.35	1.09 – 1.69	2.69	0.007	1.06	1.00 – 1.11	2.03	0.042	1.07	1.00 – 1.13	1.97	0.049
Mixed-Deciduous	1.09	1.05 – 1.14	3.97	< 0.001	1.05	1.00 – 1.11	2.06	0.040	1.13	1.08 – 1.18	5.53	< 0.001	1.02	0.97 – 1.08	0.72	0.472
Young	1.18	1.13 – 1.22	8.71	< 0.001	1.18	1.13 – 1.24	7.01	< 0.001	1.12	1.08 – 1.17	5.28	< 0.001	1.14	1.09 – 1.21	5.03	< 0.001
Open	0.69	0.65 – 0.74	−11.60	< 0.001	0.55	0.51 – 0.60	−14.52	< 0.001	0.81	0.76 – 0.85	−7.57	< 0.001	0.66	0.61 – 0.72	−10.34	< 0.001
Non-foraging	0.31	0.25 – 0.39	−10.16	< 0.001	0.17	0.11 – 0.25	−9.10	< 0.001	0.32	0.25 – 0.41	−8.63	< 0.001	0.25	0.18 – 0.35	−8.03	< 0.001
state [Restricted] x Area	0.90	0.82 – 0.99	−2.09	0.037	0.91	0.79 – 1.05	−1.30	0.193	1.10	0.99 – 1.22	1.82	0.068	1.12	0.97 – 1.28	1.59	0.112
state [Restricted] x Contig	1.10	0.96 – 1.27	1.40	0.162	1.04	0.91 – 1.20	0.60	0.547	1.01	0.91 – 1.12	0.16	0.870	1.01	0.87 – 1.16	0.08	0.934
state [Restricted] × SHDI	1.01	0.94 – 1.09	0.27	0.785	0.96	0.89 – 1.04	−0.95	0.345	1.02	0.97 – 1.07	0.75	0.454	0.99	0.93 – 1.05	−0.39	0.694
Area × Road	0.90	0.78 – 1.04	−1.42	0.157	0.41	0.25 – 0.69	−3.39	0.001	0.98	0.89 – 1.08	−0.41	0.679	0.97	0.85 – 1.11	−0.47	0.640
Area × SHDI	0.91	0.84 – 1.00	−2.01	0.045	0.94	0.85 – 1.05	−1.04	0.300	1.11	1.03 – 1.19	2.85	0.004	0.98	0.89 – 1.08	−0.41	0.680

Appendix Table B.3
Coefficients, confidence intervals (CI), and statistics given by the conditional generalized linear mixed model (glmmTMB) for the seasonal habitat selection of adult moose in the **Mountain zone**. Coniferous forest, exploratory state and medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength and values above 1 indicate higher relative selection strength for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				**Spring**				**Summer**				**Fall**			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	0.26	0.24 – 0.28	−41.25	< 0.001	0.23	0.21 – 0.25	−32.79	< 0.001	0.15	0.14 – 0.16	−49.79	< 0.001	0.19	0.18 – 0.21	−35.60	< 0.001
log Step Length	0.95	0.94 – 0.96	−10.68	< 0.001	1.00	0.99 – 1.01	0.23	0.820	1.07	1.05 – 1.08	11.58	< 0.001	1.02	1.01 – 1.03	2.97	0.003
Cosine Turning Angles	1.04	1.02 – 1.06	4.30	< 0.001	0.94	0.91 – 0.96	−5.14	< 0.001	0.73	0.72 – 0.75	−28.83	< 0.001	0.78	0.76 – 0.80	−18.89	< 0.001
state [Restricted]	0.92	0.87 – 0.97	−3.22	0.001	0.91	0.83 – 0.99	−2.12	0.034	1.08	1.02 – 1.14	2.72	0.007	1.00	0.93 – 1.08	−0.01	0.994
Area	1.01	0.98 – 1.04	0.54	0.591	1.00	0.92 – 1.10	0.05	0.956	1.05	1.02 – 1.08	3.07	0.002	1.04	1.01 – 1.07	2.46	0.014
SHDI	1.02	1.00 – 1.04	1.79	0.073	1.05	1.02 – 1.09	3.01	0.003	0.99	0.97 – 1.01	−1.39	0.164	0.98	0.95 – 1.01	−1.58	0.115
Contig	0.97	0.91 – 1.03	−1.00	0.317	1.04	0.95 – 1.15	0.88	0.378	1.11	1.08 – 1.13	7.36	< 0.001	1.03	0.99 – 1.06	1.65	0.099
Road	1.03	1.02 – 1.05	4.50	< 0.001	1.04	1.01 – 1.07	2.71	0.007	1.01	1.00 – 1.02	2.30	0.022	1.01	1.00 – 1.03	2.30	0.022
Mixed-Deciduous	0.98	0.95 – 1.01	−1.20	0.230	1.02	0.98 – 1.07	1.06	0.291	1.14	1.08 – 1.20	4.71	< 0.001	1.04	0.98 – 1.11	1.29	0.198
Young	0.97	0.93 – 1.01	−1.39	0.165	0.83	0.78 – 0.89	−5.82	< 0.001	1.25	1.12 – 1.39	4.10	< 0.001	0.92	0.72 – 1.20	−0.60	0.549

(*continued on next page*)

Appendix Table B.3 (*continued*)

	Winter				Spring				Summer				Fall			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
Open	0.76	0.72 – 0.79	−12.71	< 0.001	0.57	0.53 – 0.60	−17.17	< 0.001	1.12	1.05 – 1.19	3.70	< 0.001	0.89	0.83 – 0.96	−3.10	0.002
Non-foraging	0.37	0.33 – 0.41	−16.59	< 0.001	0.20	0.16 – 0.25	−13.21	< 0.001	0.52	0.46 – 0.58	−11.35	< 0.001	0.51	0.45 – 0.58	−10.20	< 0.001
state [Restricted] x Area	1.02	1.00 – 1.05	2.42	0.016	1.11	1.02 – 1.21	2.52	0.012	1.05	1.03 – 1.07	5.71	< 0.001	1.06	1.04 – 1.08	5.67	< 0.001
state [Restricted] x Contig	1.04	0.97 – 1.12	1.16	0.246	0.95	0.82 – 1.09	−0.78	0.435	1.03	1.00 – 1.06	1.88	0.059	1.04	0.99 – 1.09	1.50	0.135
state [Restricted] × SHDI	0.98	0.96 – 1.01	−1.40	0.160	1.01	0.96 – 1.05	0.30	0.760	1.06	1.03 – 1.09	3.85	< 0.001	1.06	1.02 – 1.10	3.18	0.001
Area × Road	1.00	0.99 – 1.00	−1.62	0.105	1.02	1.00 – 1.05	1.69	0.091	0.99	0.99 – 1.00	−3.78	< 0.001	0.99	0.99 – 1.00	−2.15	0.032
Area × SHDI	1.00	0.99 – 1.01	0.68	0.494	1.04	1.00 – 1.09	1.97	0.049	1.02	1.01 – 1.03	4.93	< 0.001	1.02	1.01 – 1.03	4.01	< 0.001

Appendix Table B.4

Coefficients, confidence intervals (CI), and statistics given by the conditional generalized linear mixed model (glmmTMB) for the seasonal habitat selection of adult moose in the **North-Boreal Inland zone**. Coniferous forest, exploratory state and medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength and values above 1 indicate higher relative selection strength for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				Spring				Summer				Fall			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	0.31	0.28 – 0.34	−22.93	< 0.001	0.17	0.14 – 0.19	−25.19	< 0.001	0.10	0.09 – 0.11	−48.50	< 0.001	0.09	0.08 – 0.10	−45.54	< 0.001
log Step Length	0.90	0.89 – 0.90	−24.45	< 0.001	1.01	1.00 – 1.02	1.39	0.166	1.12	1.11 – 1.13	19.05	< 0.001	1.14	1.13 – 1.16	19.15	< 0.001
Cosine Turning Angles	1.18	1.16 – 1.20	17.55	< 0.001	1.05	1.02 – 1.08	3.48	0.001	0.76	0.74 – 0.78	−24.77	< 0.001	0.92	0.90 – 0.95	−6.28	< 0.001
state [Restricted]	0.98	0.89 – 1.08	−0.41	0.680	1.00	0.90 – 1.12	0.03	0.977	1.19	1.10 – 1.28	4.29	< 0.001	1.30	1.20 – 1.41	6.21	< 0.001
Area	1.07	0.98 – 1.16	1.55	0.121	0.50	0.34 – 0.72	−3.70	< 0.001	1.00	0.95 – 1.07	0.16	0.873	1.09	1.02 – 1.17	2.47	0.014
SHDI	1.00	0.95 – 1.06	0.14	0.886	0.97	0.92 – 1.03	−0.89	0.374	1.01	0.98 – 1.05	0.78	0.434	0.98	0.94 – 1.02	−1.13	0.258
Contig	0.97	0.85 – 1.10	−0.51	0.609	0.96	0.83 – 1.11	−0.55	0.581	0.91	0.83 – 0.99	−2.23	0.026	0.84	0.78 – 0.91	−4.30	< 0.001
Road	1.10	1.03 – 1.18	2.85	0.004	0.70	0.56 – 0.87	−3.23	0.001	1.05	1.01 – 1.09	2.37	0.018	1.04	1.01 – 1.07	2.66	0.008
Mixed-Deciduous	1.03	0.99 – 1.06	1.41	0.158	1.09	1.04 – 1.14	3.75	< 0.001	1.03	0.99 – 1.07	1.39	0.163	1.04	1.00 – 1.08	1.94	0.053
Young	1.14	1.10 – 1.18	7.77	< 0.001	0.98	0.93 – 1.03	−0.69	0.488	0.97	0.92 – 1.03	−1.00	0.316	1.08	1.01 – 1.15	2.29	0.022
Open	0.82	0.79 – 0.86	−9.59	< 0.001	0.60	0.57 – 0.63	−17.36	< 0.001	0.97	0.93 – 1.01	−1.50	0.135	0.56	0.53 – 0.60	−19.06	< 0.001
Non-foraging	0.54	0.47 – 0.62	−8.48	< 0.001	0.32	0.24 – 0.43	−7.76	< 0.001	0.29	0.23 – 0.36	−11.12	< 0.001	0.17	0.13 – 0.23	−12.53	< 0.001
state [Restricted] x Area	0.95	0.87 – 1.02	−1.41	0.158	0.85	0.73 – 0.99	−2.13	0.033	1.01	0.94 – 1.09	0.37	0.709	1.11	1.03 – 1.18	2.94	0.003
state [Restricted] x Contig	1.10	0.96 – 1.27	1.34	0.181	1.02	0.86 – 1.21	0.20	0.838	1.12	1.01 – 1.25	2.08	0.038	1.17	1.05 – 1.30	2.94	0.003
state [Restricted] × SHDI	0.95	0.89 – 1.01	−1.61	0.107	1.02	0.95 – 1.09	0.45	0.654	0.99	0.95 – 1.04	−0.24	0.807	1.00	0.95 – 1.05	−0.03	0.979
Area × Road	0.91	0.84 – 0.98	−2.51	0.012	0.08	0.03 – 0.21	−5.11	< 0.001	1.00	0.96 – 1.04	−0.02	0.985	0.98	0.95 – 1.01	−1.21	0.225
Area × SHDI	0.98	0.94 – 1.03	−0.74	0.462	0.93	0.81 – 1.07	−0.99	0.320	1.03	1.00 – 1.05	1.93	0.053	1.03	1.00 – 1.05	1.82	0.069

Appendix Table B.5
Coefficients, confidence intervals (CI), and statistics given by the conditional generalized linear mixed model (glmmTMB) for the seasonal habitat selection of adult moose in the **Boreal Coastal zone**. Coniferous forest, exploratory state and medium-sized patches, contiguity, and road distances are in the intercept. Significant differences are indicated in bold. Values below 1 indicate lower relative selection strength and values above 1 indicate higher relative selection strength for a given predictor in relation to coniferous forest (for habitats) and its availability

	Winter				**Spring**				**Summer**				**Fall**			
Predictors	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*	*Odds Ratios*	*CI*	*z-value*	*p-value*
(Intercept)	0.18	0.15 – 0.21	−20.33	< 0.001	0.16	0.14 – 0.18	−33.24	< 0.001	0.11	0.10 – 0.12	−45.27	< 0.001	0.13	0.11 – 0.14	−33.60	< 0.001
log Step Length	0.94	0.93 – 0.95	−11.55	< 0.001	1.02	1.00 – 1.03	2.12	0.034	1.08	1.07 – 1.10	12.07	< 0.001	1.07	1.05 – 1.09	8.74	< 0.001
Cosine Turning Angles	1.07	1.05 – 1.09	6.53	< 0.001	0.95	0.93 – 0.98	−3.52	< 0.001	0.75	0.74 – 0.77	−24.71	< 0.001	0.94	0.92 – 0.97	−4.19	< 0.001
state [Restricted]	0.87	0.81 – 0.93	−3.85	< 0.001	0.95	0.84 – 1.06	−0.96	0.339	0.98	0.91 – 1.06	−0.57	0.569	0.98	0.87 – 1.10	−0.39	0.698
Area	0.27	0.14 – 0.54	−3.72	< 0.001	0.47	0.35 – 0.63	−5.02	< 0.001	0.54	0.42 – 0.69	−4.98	< 0.001	0.66	0.46 – 0.96	−2.19	0.029
SHDI	0.98	0.92 – 1.05	−0.48	0.633	0.98	0.91 – 1.04	−0.72	0.474	0.92	0.87 – 0.98	−2.68	0.007	0.95	0.89 – 1.00	−1.83	0.067
Contig	0.96	0.86 – 1.08	−0.67	0.501	1.06	0.94 – 1.19	1.00	0.315	1.06	0.95 – 1.17	1.00	0.320	1.01	0.90 – 1.13	0.16	0.871
Road	0.49	0.32 – 0.74	−3.42	0.001	0.99	0.91 – 1.09	−0.11	0.915	0.94	0.85 – 1.04	−1.20	0.231	0.87	0.75 – 1.01	−1.84	0.066
Mixed-Deciduous	1.02	0.99 – 1.06	1.23	0.219	1.06	1.02 – 1.12	2.64	0.008	1.18	1.13 – 1.22	7.86	< 0.001	1.11	1.06 – 1.17	4.29	< 0.001
Young	1.29	1.25 – 1.34	14.71	< 0.001	1.16	1.10 – 1.22	5.85	< 0.001	1.24	1.19 – 1.30	9.44	< 0.001	1.24	1.18 – 1.32	7.58	< 0.001
Open	0.95	0.90 – 0.99	−2.30	0.021	0.85	0.79 – 0.90	−5.03	< 0.001	0.99	0.93 – 1.04	−0.53	0.595	1.07	1.00 – 1.13	2.11	0.034
Non-foraging	0.50	0.39 – 0.64	−5.45	< 0.001	0.46	0.33 – 0.62	−4.87	< 0.001	0.44	0.33 – 0.58	−5.81	< 0.001	0.23	0.14 – 0.37	−5.98	< 0.001
state [Restricted] x Area	0.78	0.63 – 0.95	−2.48	0.013	1.02	0.66 – 1.56	0.07	0.942	0.96	0.73 – 1.26	−0.32	0.748	0.92	0.62 – 1.38	−0.39	0.698
state [Restricted] x Contig	1.13	0.99 – 1.29	1.79	0.074	0.98	0.82 – 1.17	−0.18	0.854	1.01	0.87 – 1.17	0.07	0.941	1.07	0.89 – 1.30	0.74	0.459
state [Restricted] × SHDI	1.04	0.97 – 1.11	1.06	0.287	1.04	0.95 – 1.14	0.83	0.404	1.07	1.01 – 1.13	2.23	0.025	1.03	0.95 – 1.13	0.74	0.458
Area × Road	0.03	0.00 – 0.19	−3.69	< 0.001	0.69	0.46 – 1.02	−1.86	0.063	0.47	0.31 – 0.72	−3.44	0.001	0.41	0.21 – 0.80	−2.64	0.008
Area × SHDI	1.14	0.95 – 1.38	1.40	0.162	1.18	0.97 – 1.45	1.65	0.099	0.97	0.79 – 1.19	−0.28	0.782	1.11	0.92 – 1.33	1.11	0.268

Data availability

Data will be made available on request.

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