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Habitat alteration or climate: What drives the densities of an invading ungulate?

Melanie Dickie[1,2,3] | Robert Serrouya[1] | Marcus Becker[3] | Craig DeMars[1] | Michael J. Noonan[2,4,5] | Robin Steenweg[6] | Stan Boutin[7] | Adam T. Ford[2]

[1]Wildlife Science Centre, Biodiversity Pathways, University of British Columbia, Kelowna, British Columbia, Canada

[2]Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada

[3]Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada

[4]Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada

[5]Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada

[6]Canadian Wildlife Service – Pacific Region, Environment and Climate Change Canada, Kelowna, British Columbia, Canada

[7]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Correspondence
Melanie Dickie, Wildlife Science Centre, Biodiversity Pathways, University of British Columbia, Kelowna, British Columbia, Canada.
Email: mvezina@ualberta.ca

Abstract

Anthropogenic habitat alteration and climate change are two well-known contributors to biodiversity loss through changes to species distribution and abundance; yet, disentangling the effects of these two factors is often hindered by their inherent confound across both space and time. We leveraged a contrast in habitat alteration associated with the jurisdictional boundary between two Canadian provinces to evaluate the relative effects of spatial variation in habitat alteration and climate on white-tailed deer (*Odocoileus virginianus*) densities. White-tailed deer are an invading ungulate across much of North America, whose expansion into Canada's boreal forest is implicated in the decline of boreal caribou (*Rangifer tarandus caribou*), a species listed as Threatened in Canada. We estimated white-tailed deer densities using 300 remote cameras across 12 replicated 50 km^2 landscapes over 5 years. White-tailed deer densities were significantly lower in areas where winter severity was higher. For example, predicted deer densities declined from 1.83 to 0.35 deer/km^2 when winter severity increased from the lowest value to the median value. There was a tendency for densities to increase with increasing habitat alteration; however, the magnitude of this effect was approximately half that of climate. Our findings suggest that climate is the primary driver of white-tailed deer populations; however, understanding the mechanisms underpinning this relationship requires further study of over-winter survival and fecundity. Long-term monitoring at the invasion front is needed to evaluate the drivers of abundance over time, particularly given the unpredictability of climate change and increasing prevalence of extreme weather events.

KEYWORDS
camera traps, climate change, invasive species, land-use, *Odocoileus virginianus*, weather

1 | INTRODUCTION

Disentangling the effects of anthropogenic habitat alteration and climate change on global biodiversity loss is a pressing ecological challenge (Caro et al., 2022; Williams et al., 2022), complicated by the fact that habitat alteration and climate change are often correlated in space and time. Both factors can alter species distribution and abundance, which can disrupt food webs (Bartley et al., 2019; Wang et al., 2020) and facilitate the spread of novel diseases and parasites (Patz et al., 2000), potentially leading to extirpations of native biota. For most species, anthropogenic habitat alteration (hereafter termed habitat alteration) is considered to have a stronger effect (Caro et al., 2022), though the relative influence of habitat alteration and climate is species- and context-specific (Tourani et al., 2023; Weiskopf et al., 2020). As climate change accelerates and its effects strengthen (Smith et al., 2015), it is incumbent to understand the relative contributions of habitat alteration and climate change to observed biodiversity changes, their interactive effects, and, importantly, the mechanisms through which these factors act. Such knowledge is essential for developing evidence-based conservation actions that take into account predicted effects of climate change going forward (Dirzo et al., 2014; Gilbert et al., 2019; Mantyka-Pringle et al., 2013).

Across North America, white-tailed deer (*Odocoileus virginianus*) have greatly expanded their distribution and abundance in the last century, with the potential to disrupt ecological processes (Côté et al., 2004; Patterson & Power, 2002; VerCauteren, 2003). The historic expansion of this species into mixedwood forests and grasslands of the United States and southern Canada was facilitated by food subsidies through the conversion of land for agriculture and forest harvest, reduced predation through intensive carnivore reductions, and deer harvest management (Côté et al., 2004 and references therein). In many places, white-tailed deer have since become highly abundant, and are considered ecosystem disruptors via overgrazing, disease transmission, and altered predator–prey interactions (Côté et al., 2004; Greenspoon et al., 2023; Rooney, 2001). White-tailed deer have also expanded into boreal forests throughout Canada, where they have been implicated in the decline of boreal caribou—an ecotype of woodland caribou facing extirpation across much is its range (*Rangifer tarandus caribou*; Environment and Climate Change Canada, 2020; Latham et al., 2011). Increased prevalence and densities of white-tailed deer supports higher wolf densities (Latham et al., 2011; Mech & Boitani, 2003), leading to increased incidental predation on caribou (Holt, 1977; Serrouya et al., 2021). Additionally, white-tailed deer expansion may increase the transmission of disease and parasites, including ticks, brainworm, chronic wasting disease, and COVID-19 (Christina, 2008; Hannaoui et al., 2017), potentially impacting human health and sustenance.

At the northern edge of white-tailed deer range in Canada's western boreal forests, changes in forage availability and physiological constraints imposed by harsh climates are implicated in the expansion of white-tailed deer (Dawe et al., 2014; Kennedy-Slaney et al., 2018; Laurent et al., 2020). In these northwestern boreal forests, there is an underlying habitat productivity gradient as the highly productive Parkland ecosystem in the south transitions into less productive Boreal Plains and then Boreal Shield farther north (Dickie et al., 2022). Generally, this productivity gradient occurs along a northwest–southeast axis. Though agriculture is rare in the Boreal Plains and Boreal Shield, land clearing for oil and gas exploration and forest harvest are hypothesized to increase forage availability beyond the baseline variation in productivity (Serrouya et al., 2021), potentially supporting higher densities of deer (Fuller et al., 2022). However, concomitant with changes in habitat alteration, climate change has resulted in less severe winters that increase white-tailed deer survival, and longer growing seasons that increases food availability (Beier & McCullough, 1990; Dawe & Boutin, 2016; Kennedy-Slaney et al., 2018). The covariation of habitat alteration and climate change in time can also play out over space. In western Canada, human activity tends to decrease with increasing latitude, while climate severity increases with latitude. Thus, we expect white-tailed deer densities to decrease with latitude, but it is currently unclear to what extent habitat alteration, climate, or their combined effects might be underpinning this pattern.

Here, we assessed the relative influence of habitat alteration and climate change on deer densities by taking advantage of a decoupling of the typical habitat alteration–climate change pattern (i.e., decreasing alteration and increasing winter severity with increasing latitude) that occurs at the Alberta-Saskatchewan provincial border (Figure 1). Habitat alteration is on average 3.6-fold higher in Alberta's eastern boreal plains than in the neighboring Saskatchewan western boreal plains (i.e., an east–west habitat alteration gradient; Environment and Climate Change Canada, 2017). Unlike habitat alteration, climate does not vary significantly across the provincial border for a given latitude. We leveraged this unique contrast in habitat alteration, along with a latitudinal gradient in climate, to evaluate factors affecting white-tailed deer density estimated from remote camera clusters situated in 12 replicated 50 km^2 landscapes. If white-tailed deer densities are primarily driven by habitat alteration, we expected densities to be higher in study sites with higher habitat alteration (i.e., in Alberta). In contrast, if white-tailed deer densities are primarily driven by climate, we expected densities to be lower in study sites that are characterized by more severe winters (i.e., more northerly). If these factors interact beyond their additive effects, we expected deer densities to be highest in areas with high habitat alteration and less severe winters, and that the deer density would be lowest in areas with low habitat alteration and more severe winters.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located at the interface of the Boreal Plains and Boreal Shield ecozones (Ecological Stratification Working Group, 1996). Both ecozones are characterized by a mosaic of upland and wetland forests, though the plains contain relatively more broadleaf forest than the shield, whereas the shield has relatively more cover of barren areas,
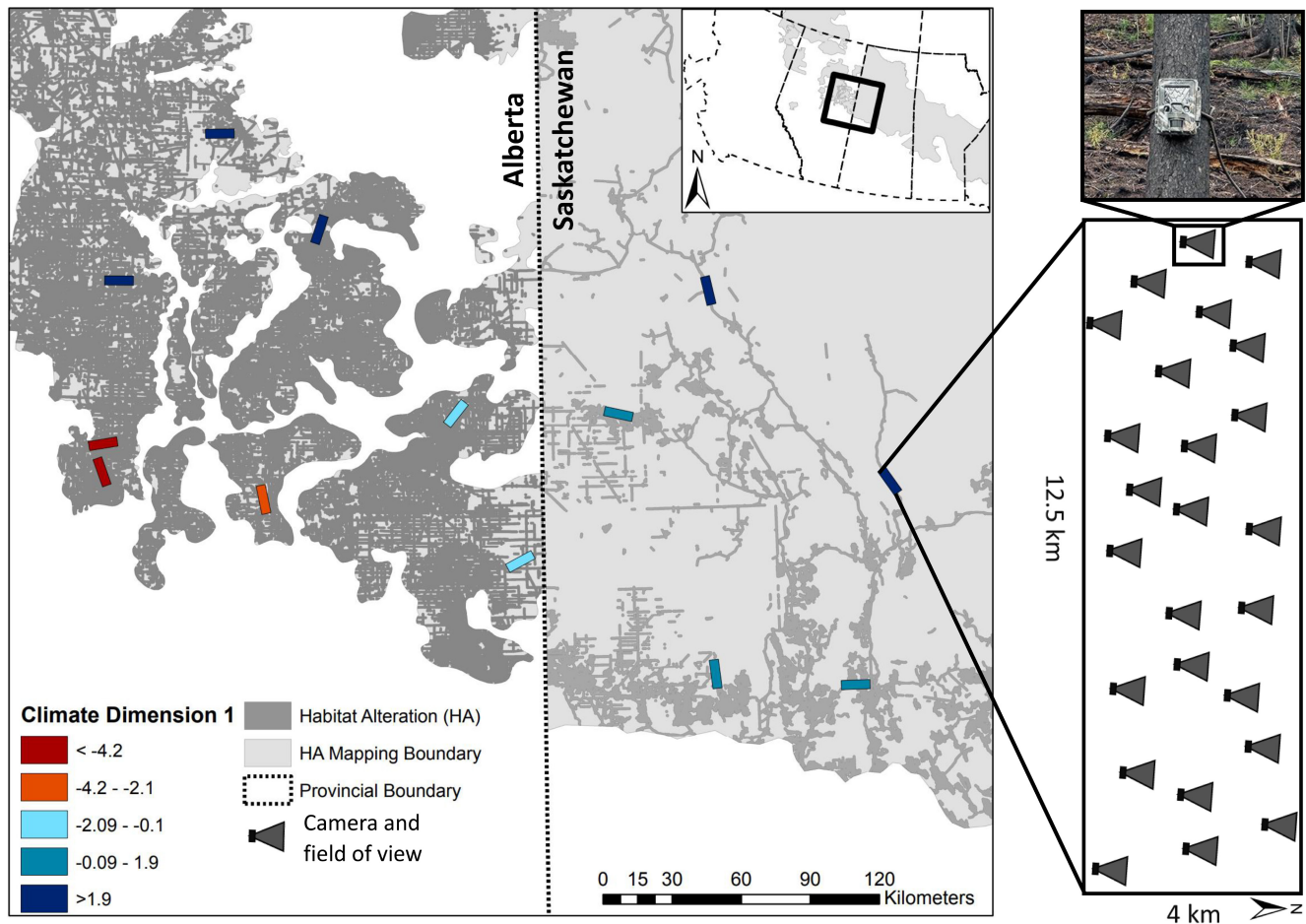
FIGURE 1 Location of camera clusters used to evaluate the relative effects of anthropogenic habitat alteration (HA) and climate on white-tailed deer. Dark gray shading depicts HA as mapped by Environment and Climate Change Canada, buffered by 500m (Environment and Climate Change Canada, 2017), and light gray shading depicts the mapping boundary in which HA was mapped. Camera clusters are colored by the Climate Dimension 1 identified using a 5-year multiple factor analysis, such that higher values (i.e., cooler colors) represent more severe winters. Cameras were placed randomly within a 12.5km by 4km area on trees with a minimum distance of 1km apart using a random location generator, and all cameras faced north to avoid solar interference with images. The inset map depicts the study area in relation to Canada, whereas the outset images depict an example of random camera trap placement within each camera cluster. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

shrubland, and grassland peatlands. The study area has a relatively low human influence index (Wildlife Conservation Society & Center for International Earth Science Information Network, 2005), with human population densities typically less than 1 person/km². The majority of anthropogenic habitat alteration within the study area is related to the forestry and energy sectors, with some occurrence of agriculture in localized areas. Geophysical exploration within the boreal shield is less prominent than on the boreal plains, in part due to the depth of the oil and gas deposits. The divergence between Saskatchewan and Alberta's human land-use is a result of complex sociopolitical drivers (Herbert Emery & Kneebone, 2008).

2.2 | Camera deployment

Beginning in 2017, we deployed twelve 50 km² (12.5 km × 4 km) clusters of camera traps, with 25 cameras per cluster, across

approximately 55,375 km² in northeastern Alberta and northwestern Saskatchewan (Figure 1). Camera clusters were placed on both sides of the Alberta-Saskatchewan border to maximize the variation in habitat alteration (east–west gradient), and across a range of latitude to capture climatic variation (northwest–southeast axis). For example, minimum temperatures in the snow season varied from −35 to −45°C and maximum temperatures in the snow-free season varied from 28 to 39°C. Initially, six camera clusters were placed in Alberta (i.e., high habitat alteration) in January of 2017. In fall and winter of 2017/2018, four additional clusters were added to sample areas with low habitat alteration in both eastern Alberta and western Saskatchewan. An additional cluster was added in Saskatchewan in 2019, and another in 2021. Finally, the southwestern most cluster in Alberta was moved in 2020 due to imminent forest harvest. Cameras collected data year-round to increase the cumulative detection probability, and were typically serviced once per year.

We used Reconyx Hyperfire2 and Recoynx PC900 camera models (Holmen, WI, USA). Cameras were programmed to take motion-triggered photos during day and night, and to take a time-lapse photo every 2 h. Detailed camera trigger settings are documented in Alberta Biodiversity Monitoring Institute (2019). Camera clusters were placed within reasonable access to roads to facilitate camera servicing, such that roads typically bisect the shorter edge of the cluster and run parallel to the longest edge. Within clusters, cameras were placed randomly, with a minimum distance of 1 km apart using a random location generator. While this design results in clusters biased toward areas with roads, this bias was consistent across the strata of interest.

2.3 | Estimating deer density

We estimated white-tailed deer density for each camera using the Time in Front of Camera method (TIFC; Becker et al., 2022). The TIFC model uses basic sampling logic in which the number of animals observed within a defined area, sampled using camera traps, is multiplied by the time those animals were observed, and divided by the area and time monitored, using the formula:

$$D = \frac{\sum (N \cdot T_F)}{A_F \cdot T_O}$$

where density D is calculated as the total number of individuals observed N multiplied by the time in front of the camera field-of-view T_F, divided by the area of the camera field-of-view A_F multiplied by the total camera operating time T_O. The units are animal-seconds per area-seconds, which simplifies to the number of animals per unit area. The probability of detecting an animal decreases as the distance from the camera increases, and this is species- and habitat-specific. To account for this, we modified the area monitored by the effective detection distance in which white-tailed deer, in each season, can be detected following the methods of Becker et al. (2022). Furthermore, we accounted for the probability of the animal leaving the field of view as a function of time between images when quantifying T_O (Becker et al., 2022). Lastly, we added the average time between images in all series to the duration of each series to account for how long animals are typically in the field of view before and after the first and last images, respectively, are taken (Becker et al., 2022). TIFC is an appropriate density estimator for our system given white-tailed deer are unmarked populations, and our cameras were placed randomly (Becker et al., 2022), though like the example provided by Becker and colleagues, our sampling likely violates the assumption of true random placement across microhabitats.

We calculated the density of deer at each camera separately for each year, defined as April 16–April 15 in the following year, roughly corresponding to camera servicing dates and time periods used to calculate effective detection distances (Becker et al., 2022). To obtain cluster-level density estimates, we then averaged the density across all cameras and calculated 90% confidence intervals treating density estimates as a compound distribution of presence (1) and absence

(0), and abundance given presence (Becker et al., 2022), similar to a zero-inflated log-normal distribution. While annual densities smooth over potential seasonal variation, for example, resulting from seasonal migrations, snow-free and snow season density estimates were correlated, and correlated to annual estimates (Appendix S1).

2.4 | Environmental variables

We quantified habitat alteration, here defined as the area modified by human land-use, using two approaches. First, we used a dataset extending across Alberta and Saskatchewan's boreal forest where anthropogenic habitat alteration identified at a 1:50,000 scale using Landsat imagery is buffered by 500 m (hereafter termed "buffered disturbance"; Environment and Climate Change Canada, 2017). This definition of anthropogenic habitat alteration is used by the Federal Recovery Strategy for boreal caribou (Environment Canada, 2011; Environment and Climate Change Canada, 2020). A known drawback to this dataset is that it underestimates the footprint of linear disturbances, such as roads, pipelines, and seismic lines (Dickie, Bampfylde, et al., 2023). Therefore, we also quantified "direct alteration" by calculating the mean percent area altered by human land-use in each cluster using the best available data from Saskatchewan and Alberta's Footprint Inventories (Alberta Biodiversity Monitoring Institute, 2018; Government of Saskatchewan, 2021). We used the Alberta Human Footprint Inventory with the same vintage data available in Saskatchewan (i.e., 2018), and converted into a 1 km by 1 km raster of the percent area disturbed by habitat alteration to match the Saskatchewan Footprint Inventory.

To quantify spatial variation in climate, we conducted a multiple factor analysis (MFA) to reduce climate variables expected to impact deer demographic rates (survival and recruitment), and thus density, during the period when deer were monitored. The MFA accounted for sampling variables across years at the same location, grouping each of the variables over the 5-year monitoring period, and hence represents medium-term "climate" dimensions for each cluster. For each year, we extracted the maximum and mean precipitation, maximum and minimum temperature, and the mean vapor pressure (i.e., a measure of humidity) for two seasons, defined as snow-free (May 1–August 31) and snow (September 1–March 31) from DAYMET Version 4 (Thornton et al., 2022). We extracted the mean value of each variable for each pixel, then averaged the pixel-level average values for each camera cluster, season, and year combination. Metrics of temperature, precipitation, and humidity have been linked to over-winter survival, energy reserves available for reproduction, and nutrition of ungulates through energy balances associated with how these variables interact to influence winter severity and resource availability throughout the growing season (Delguidice et al., 2002; Michel et al., 2018; Patterson & Power, 2002). Additionally, we quantified snow season length by conducting a breakpoint analysis on snow water equivalent data to identify the period when the ground was continuously covered by snow (Appendix S2). We also used snow water equivalent data to estimate cumulative snowfall over the

snow season. We used package FactoMineR (Lê et al., 2008) in R (R Core Team, 2019) to conduct the MFA. Recognizing that annual variation in weather may contribute to annual variation in deer density, we additionally quantified spatiotemporal variability in weather (i.e., annual variation in "climate" dimensions) in addition to evaluating the effect of medium-term climate (i.e., the 5-year medium-term "climate" dimensions). We used a principal component analysis (PCA) to identify annual weather dimensions for each cluster using package factoextra (Kassambara & Mundt, 2020) in R (R Core Team, 2019), using the same variables described above.

In addition to anthropogenic habitat alteration and climate, deer density is expected to vary depending on landscape context, such as primary productivity (Dawe et al., 2014; Kennedy-Slaney et al., 2018). To account for landscape context, we used the change in the Enhanced Vegetation Index (ΔEVI) as a measure of deciduous vegetation availability (Gagné et al., 2016), which has been found to impact the density of terrestrial herbivores in boreal forests, including moose (*Alces alces*) and deer species (Dickie et al., 2022; Serrouya et al., 2021). We used MODIS Terra Vegetation Indices 16-Day Global data (500m resolution) to extract the median EVI values during the leaf-on period when deciduous vegetation is at or near peak production (July 1–August1), and the leaf-off period when vegetation has senesced but snow has not yet accumulated (September 1–October 1). We calculated ΔEVI by subtracting the leaf-off median EVI from the leaf-on median EVI (Appendix S3). To eliminate pixels covered by clouds or shadows, we retained only those classified as "VI produced, good quality" and removed pixels covered by water, following Hansen et al. (2013).

2.5 | Analytical framework

We used a two-stage modelling framework to first identify the metrics that best represented the two main variables of interest (habitat alteration and climate), and second, to evaluate their relative effects on deer density while controlling for habitat productivity. For habitat alteration, we evaluated the relative support for direct habitat alteration versus buffered habitat alteration. For climate, we evaluated the relative support for the inclusion of the 5-year climate and annual climate dimensions, specifically contrasting the support for Dimension 1 only, Dimension 2 only, or the additive effect of Dimensions 1 and 2. We included the metrics for habitat alteration and climate with the lowest Akaike Information Criterion, corrected for small sample size (AICc; Akaike, 1974), in the final global model. If metrics fell within 2 AICc units, the simplest model formulation was included (Sutherland et al., 2023). We also explored the inclusion of heterogeneity in habitat alteration and productivity within camera clusters, measured using the coefficient of variation of each variable, but found no support for including the variation in habitat alteration or productivity rather than their means (Appendix S4). Because weather or climate may have a lag effect on deer densities (Patterson & Power, 2002 and references therein), we additionally conducted the MFA and the PCA analyses to include a 1-year lag in the climate metrics. We found little

evidence to support the inclusion of a 1-year lag, and so present these analyses in Appendix S5.

Finally, we modelled average deer density in each camera cluster as a function of the top variables identified to quantify habitat alteration and climate, each interacting with ΔEVI, as well as the interaction between the top metrics of habitat alteration and climate. We calculated the marginal R^2 to evaluate model performance using Nakagawa's R^2 (Nakagawa & Schielzeth, 2013). For all models, we used a tweedie distribution and included temporal autocorrelation using an ar1 covariance structure in *glmmTMB* (Brooks et al., 2017). Because some cameras failed or were displaced from their field of view, we weighted each density estimate by the number of cameras operating in that cluster-year, thereby giving higher weight to clusters-year combinations where more cameras were operating. We checked that all covariates did not covary (i.e., all correlation coefficients were less than .6; the Pearson's correlation between direct habitat alteration and habitat productivity was .37, between direct habitat alteration and climate dimension 1 was .38, and habitat productivity and climate dimension 1 was −.41). We found no support for spatial autocorrelation based on model residuals using Moran's *I*, which was estimated using package *DHARMa* (Hartig & Lohse, 2022; Moran's $I = -0.230$, $p = .120$). Individual cameras within a cluster were considered replicated samples of mean deer density; however, the mean may not represent the variation in deer densities within cluster. We therefore tested if using each individual camera density estimate as the sample unit influenced our results, and found that model interpretations and coefficients were similar between the analytical approaches (Appendix S6).

3 | RESULTS

Camera traps operated between 53,506 and 96,096 trap days from 2017 to 2021. During this time, we recorded 7738, 9775, 17,785, 19,071, and 24,547 images of white-tailed deer in each of the study years, respectively.

For the MFA, Dimensions 1 and 2 explained 40.37% and 21.90% of the variance, respectively, for a total of 62.27% of the climate variance explained across cameras clusters by these two axes (Appendix S7). Dimension 1 was primarily related to cumulative snow water equivalent, maximum snow water equivalent, and snow season length (each with square cosine >0.8), such that increasing values of Dimension 1 represents longer, snowier winters. Dimension 2 was primarily related to the maximum snow season precipitation (each with square cosine >0.60), and to a lesser extent, snow-free season mean precipitation, snow season minimum and maximum temperatures (square cosine >0.2), having a less clear ecological interpretation than Dimension 1. For the PCA, Dimensions 1 and 2 explained 38.25% and 15.84% of the weather variance, respectively, for a total of 54.09% (Appendix S7). Dimension 1 was primarily related to cumulative snow water equivalent and maximum snow water equivalent (square cosine >0.8), representing snowier winters, and axis 2 was primarily related to minimum snow season

temperatures (square cosine >0.4), with increasing values representing warmer winters. Both Dimensions 1 and 2 varied across years, though clusters tended to follow the same annual patterns (Appendix S7).

Of the competing habitat alteration models, percent direct habitat alteration was the best model, being 6 AIC units lower than the second-ranked model (Table 1). Of the competing climate models, the MFA Climate Dimension 1 and MFA Climate Dimensions 1 and 2 models were within 2 AICc units (Table 1). We therefore chose the simplest model structure of the two competing models, MFA Dimension 1, to include within the final modelling stage (Arnold, 2010).

Results from the global model (marginal $R^2 = .90$), which assessed for the effects of habitat alteration and climate after accounting for habitat productivity, showed that deer densities were primarily influenced by winter severity (i.e., climate). Specifically, deer densities were significantly lower in areas with increasing values of climate Dimension 1 ($\beta = -6.794$, SE = 2.523; Table 2). When habitat alteration and productivity were held at their mean value, predicted deer densities declined from 1.83 to 0.35 deer/km^2 when winter severity increased from the lowest value to the median value (Figure 2). There was a tendency for increasing habitat alteration and habitat productivity to partially mediate the effect of climate Dimension 1 (% Habitat alteration: Climate Dimension 1 $\beta = 3.871$, SE = 2.357; Habitat productivity: Climate Dimension 1: $\beta = 4.586$, SE = 3.818), though the effect was not statistically significant (Table 2).

TABLE 1 Akaike Information Criterion corrected for small sample size (AICc) and degrees of freedom for models used to select metrics to quantify habitat alteration and climate when evaluating the effects on white-tailed deer density.

Variables	Metrics	df	AICc
Habitat alteration	% Direct habitat alteration	**8**	**−10.159**
	% Buffered habitat alteration	8	−4.537
Climate	MFA Dimension 1	**8**	**−11.119**
	MFA Dimension 2	8	−4.266
	MFA Dimension 1 + MFA Dimension 2	**9**	**−12.337**
	PCA Dimension 1	8	−5.291
	PCA Dimension 2	8	−2.518
	PCA Dimension 1 + PCA Dimension 2	9	−2.653

Note: Bold indicates the top performing model(s) for each variable (habitat alteration and climate).

Abbreviations: MFA, multiple factor analysis; PCA, principal component analysis.

TABLE 2 Model coefficient estimates, standard errors (SE), and *p*-values of the global model used to test the relative effects of habitat alteration and climate, given habitat productivity, on average deer density (animals/km^2).

| Variables	Estimates	SE	*p*-Value
Intercept	1.562	2.107	.458
Habitat productivity	−2.241	3.008	.456
% Habitat alteration	−0.328	2.060	.873
Climate Dimension 1	**−6.794**	**2.523**	**.007**
Habitat productivity:% Habitat alteration	0.553	2.290	.809
Habitat productivity:Climate Dimension 1	4.586	3.818	.230
% Habitat alteration:Climate Dimension 1	3.871	2.357	.100

Note: All independent metrics were scaled between 0 and 1 as $(x - \text{minimum}(x))/(\text{maximum}(x) - \text{minimum}(x))$. Bold indicates significant values defined as *p*-Value < 0.05.

4 | DISCUSSION

In a rapidly changing world, one of the most pressing issues facing ecologists is disentangling the relative effects of habitat alteration and climate change on shifting animal communities. We contrasted the relative effects of habitat alteration and climate, measured here using an index of winter severity across a 5-year monitoring period, on white-tailed deer densities in a region where spatial variation in habitat alteration and climate were decoupled. Our data supports the climate hypothesis: White-tailed deer densities were significantly lower in areas where winter severity was higher. While there was a tendency for deer densities to increase with increasing habitat alteration the magnitude of this effect was approximately half that of climate, and was statistically insignificant.

For many wildlife species, more severe winters can lead to longer or more intense phases of energy deficits. These energy deficits manifest as poor body condition and put individuals at risk of abortions, reduced offspring condition, starvation, and increased risk of disease, parasites, and predation (Delguidice et al., 2002; Mysterud & Østbye, 2006; Tverra et al., 2007). While the physiological effects of severe winters could potentially be mediated by higher forage availability (Dumont et al., 2000, 2005; Tverra et al., 2007)—for example, in areas with high productivity or through forage subsidies associated with human land-use—this mechanism was not statistically supported by our results. Though we established a link between climate and deer densities, the ecological mechanisms behind this linkage remain unclear without detailed information about cause-specific mortality and recruitment. Future analyses could explore temporal variation in distribution and abundance as well as finer resolution information on attributes of altered habitat (e.g., vegetation regeneration and forage availability), or the relative influence of the various components of climate expected to influence survival and reproduction.

Winter severity is expected to decline as climate change progresses (Notaro et al., 2014), and therefore white-tailed deer are expected to keep expanding northward and increase in abundance (Dawe & Boutin, 2016; Fisher et al., 2020; Kennedy-Slaney et al., 2018). The deer densities we observed were similar to those estimated by Latham et al. (2011) for a nearby region in the mid to late
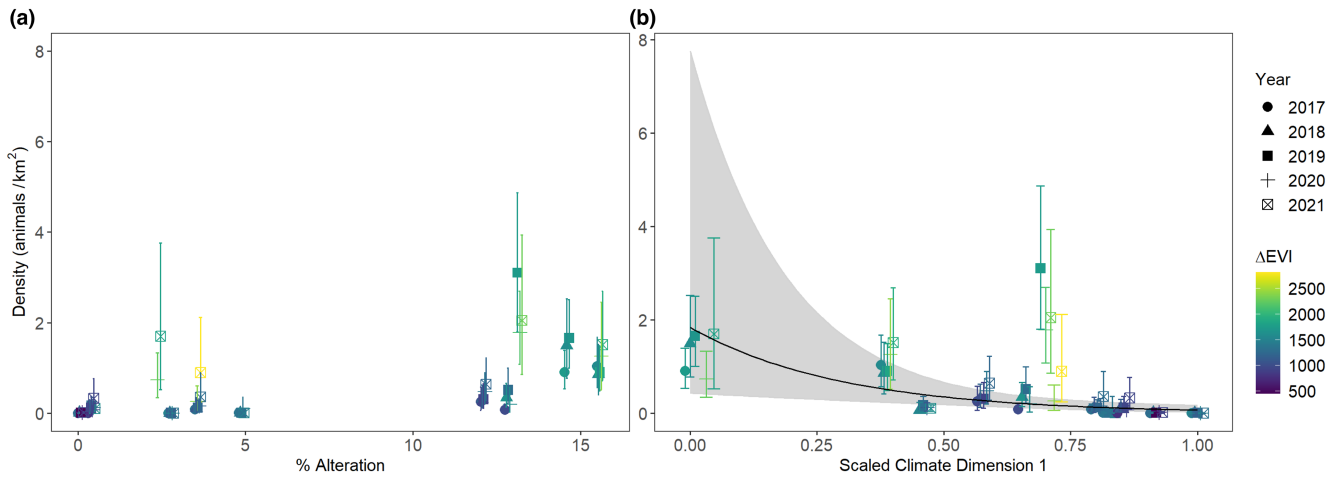
FIGURE 2 Average density of white-tailed deer (animals/km²) as a function of (a) habitat alteration (%) and (b) winter severity (Scaled Climate Dimension 1; such that winter severity increases as Dimension 1 increases). Density estimates are colored by habitat productivity (ΔEVI) and symbols represent different years. The significant predicted relationship and 95% confidence intervals between Climate Dimension 1 and average deer densities from the global model presented in Table 2 is shown. Percent alteration is displayed in its original units to aid in interpretation, whereas Climate Dimension 1 is displayed as scaled between 0 and 1 as $(x - \text{minimum}(x))/(\text{maximum}(x) - \text{minimum}(x))$. EVI, Enhanced Vegetation Index.

2000s, suggesting that deer have continued to have a strong presence in this region, though we note that higher densities appear to be more common now, at least in the more southerly portions of the study area. Even over a small geographic area relative to the overall distribution of white-tailed deer, we found a large increase in deer densities (from 0 to 2 animals/km²), which suggests that even a small change in winter severity over time could trigger a substantial increase in deer densities in northern areas. However, forecasting future deer distribution and abundance using retrospective relationships (see examples Dawe & Boutin, 2016; Kennedy-Slaney et al., 2018) is complicated by the mounting frequency and intensity of wildfires that can drastically influence habitat composition and population demographics (Neilson et al., 2020), as well as the spatial variation in the velocity of climate change (Li et al., 2019). The annual unpredictability of overall climate change and extreme weather events underscores the need to evaluate the mechanisms in which weather and climate influences population demographics (i.e., disentangling how various components of climate link to reproduction, adult female survival, etc.), though long-term monitoring at the invasion front is needed to evaluate the drivers of abundance over time.

When seeking to understand the drivers of a species' abundance and distribution, it is important to consider that ecological processes are often hierarchical (Tourani et al., 2023). Our finding that climate drives the population density of white-tailed deer, aligns with studies on factors affecting deer distribution (Dawe & Boutin, 2016; Kennedy-Slaney et al., 2018). In contrast, some studies, even within these same regions, have consistently demonstrated that habitat alteration influences relative habitat use (Fisher et al., 2020; Fuller et al., 2022), and thus emphasizes the significance of habitat composition and structure in shaping deer behavior (i.e., habitat use). While drivers of habitat use are often inferred to influence demographics, this is not always the

case and is rarely tested (Avgar et al., 2020; Courbin et al., 2017). Localized habitat-driven processes are nested within a larger scale framework that dictates overall population dynamics (Tourani et al., 2023). Climate may set the envelope within which white-tailed deer can persist in the boreal forests of western Canada, while habitat alteration may influence their abundance or finer scale spatial distribution within this climatic envelope (Elmhagen et al., 2017; Kennedy-Slaney et al., 2018).

Creating robust designs to study large-scale drivers of population abundance for wide-ranging species is notoriously difficult. The strength of our study design is underscored by two fundamental components. First, we were able to leverage a jurisdictional boundary to decouple spatial variation in climate and habitat alteration. Second, we leveraged the strengths of camera traps to estimate densities in an area where abundance is otherwise difficult to quantify. The use of cameras to estimate population abundance for unmarked populations is undergoing rapid methodological development. Many such approaches are afflicted by low precision resulting from the small area monitored by each individual camera, coupled with low sample sizes, both of which contribute to high measurement error (Becker et al., 2022; Palencia et al., 2021). By treating each cluster of camera traps as a sample estimate of deer densities, we were able to contrast densities across landscape units of interest that varied in the environmental strata of interest. Despite poor precision inherent with many camera studies, particularly with unmarked populations (Palencia et al., 2021), the magnitude of effect sizes we documented overcame the lack of precision in estimates, supported by the similar results between analyses using the mean density at each cluster versus the individual camera.

White-tailed deer—one of the largest contributors to terrestrial mammal biomass (Greenspoon et al., 2023)—are considered ecosystem disruptors that alter predator–prey dynamics and spread diseases

(Hannaoui et al., 2017; Patz et al., 2000). Specifically, in the boreal forests of western Canada, white-tailed deer are implicated in the decline of woodland caribou (Latham et al., 2011). Increasing deer densities affect predator–prey dynamics by shifting the diets of predators and triggering a predator numerical response (Latham et al., 2011; Serrouya et al., 2015). Wolves in particular have been shown to have densities an order of magnitude higher when deer are available as prey (Fuller et al., 2002). Habitat alteration is widely believed to be the ultimate cause of caribou declines, acting through increased predator hunting efficiency and disturbance-mediated apparent competition (Johnson et al., 2020; Serrouya et al., 2021). Habitat restoration and protection are therefore proposed management actions to recover caribou populations, with the goal of reducing predation by restoring predator–prey dynamics. However, if climate is indeed favoring the northward expansion of white-tailed deer to a greater degree than habitat alteration, restoring habitat is less likely to be effective on its own as white-tailed deer will continue to support high abundances of wolves (Ford et al., 2021; Fuller et al., 2002; Latham et al., 2011). In such cases, complementary management strategies such as predator or prey reduction programs (McShea, 2012; Serrouya et al., 2019), perhaps even through intervention-forward adaptive management (Dickie, Ford, et al., 2023), may warrant consideration. Additionally, understanding the mechanism leading to deer expansion will have implications for the management of pathogens common in deer that are transmittable to caribou or moose, such as chronic wasting disease (Hannaoui et al., 2017).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

DATA AVAILABILITY STATEMENT

ORCID

Melanie Dickie https://orcid.org/0000-0003-2177-2352
Robert Serrouya https://orcid.org/0000-0001-5233-6081
Marcus Becker https://orcid.org/0000-0002-4182-4044
Craig DeMars https://orcid.org/0000-0001-7984-633X
Michael J. Noonan https://orcid.org/0000-0003-4512-0535
Robin Steenweg https://orcid.org/0000-0002-6399-372X
Stan Boutin https://orcid.org/0000-0001-6317-038X
Adam T. Ford https://orcid.org/0000-0003-2509-7980

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SUPPORTING INFORMATION

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