

**LINKING ENVIRONMENTAL STOCHASTICITY WITH ANIMAL MOVEMENT USING
CONTINUOUS-TIME STOCHASTIC PROCESSES**

by

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B.Sc. Hons. Biology, University of Regina, 2021

B.Sc. Statistics, University of Regina, 2021

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE COLLEGE OF GRADUATE STUDIES

(Biology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Okanagan)

July 2023

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The following individuals certify that they have read, and recommend to the College of Graduate Studies for acceptance, a thesis entitled:

Linking environmental stochasticity with animal movement using continuous-time stochastic processes,

submitted by Stefano Mezzini in partial fulfillment of the requirements of the degree of Doctor of Philosophy.

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Abstract

Animals adapt their movement in response to many factors, including resource abundance, competitive pressure, predation, weather, and climate. While the effects of many of these factors have been studied extensively, little is known about how animals respond to environmental stochasticity. This thesis will quantify how environmental stochasticity, specifically stochasticity in resources and climate, affect where, how, when, and how much animals move. It will begin by proposing new, foundational hypotheses of how resource abundance and stochasticity affect animals' spatial needs, and it will support such hypotheses using quantitative simulations. Next, it will quantify resource abundance and stochasticity worldwide during the last five decades using the Normalized Difference Vegetation Index (NDVI) and a location-scale hierarchical generalized additive model. It will then test the again hypotheses using tracking data from over 3000 mammals across more than 85 globally-distributed species. Finally, it will assess how temperature, precipitation, and snow depth alter when, how fast, and where mammals moved in what is often referred to as British Columbia, Canada. Each of the chapters will create products that will be of direct use to Land Protectors, conservationists, and fellow scientists. The introductory chapter's conceptual framework will be useful for assessing how animals' spatial needs change in response to changes in resource abundance, including following unpredictable events such as firest and floods. The second chapter's model of mean and variance in NDVI will be available for managers to evaluate the quality and stability of lands and for scientists to use in their own research. The third chapter will contain appendices for reproducing the analyses with other datasets. Finally, the fourth chapter will present maps of current BC habitat quality and predictions in 2100 based on climate change projections. With the exception of sensitive data, all code and raw data will be made openly and freely available on GitHub, such that all who are interested can reproduce, evaluate, and learn from the work. Additionally, each project will be carried out in close contact with conservation experts and organizations to ensure the work is relevant and directly applicable in conservation.

Lay Summary

Animals adapt their movement in response to many factors, including resource abundance, competitive pressure, predation, weather, and climate. While the effects of many of these factors have been studied extensively, little is known about how animals respond to environmental unpredictability. This thesis aims to quantify how unpredictability in resources and climate affect animal movement. It will begin by proposing new hypotheses of how resource abundance and unpredictability affect animals' spatial needs, and it will support the hypotheses using simulations. Next, it will quantify resource abundance and unpredictability worldwide during the last five decades using satellite-derived measures of habitat greenness. It will then test the hypotheses again using tracking data from over 3000 mammals across more than 85 globally-distributed species. Finally, it will assess how temperature, precipitation, and snow depth alter when, how fast, and where mammals moved in what is often referred to as British Columbia, Canada.

Foreword: Recognizing Traditional Indigenous Knowledge

The lands managed and protected by Indigenous Peoples are often markedly different from those inhabited by urban societies or conserved by Western organizations. While acknowledging that there is great diversity between Indigenous Peoples (as well as other colonized Peoples), it is important to recognize that many different Peoples hold great knowledge on how to safeguard habitats, protect biodiversity, and live sustainably as an integral part of Nature (Schuster *et al.*, 2019), and that many have been doing so for millennia (Bennett *et al.*, 2021). While Indigenous leaders, representatives, and Knowledge keepers have recently taken a more active role in conservation-related decision-making, their perspective is often still not valued (Lamb *et al.*, 2023). Instead, many Western institutions continue to dismiss, ignore, and contradict the ancestral and traditional Knowledge of Indigenous and and other colonized Peoples (Kimmerer, 2020; Smith, 2021). Consequently, the development of Western science is frequently assumed to clash with the (often sacred) Knowledge many colonized Peoples hold. Western science is often viewed as more objective, more methodical, and more unbiased than Traditional Knowledge, and as such Western institutions and people often consider it to be superior to Indigenous Knowledge (Smith, 2021). However, the refusal to recognize traditional Knowledge and cooperate with non-Western institutions often results in a loss of time, resources, and funds for the Western institutions as well as severe (and potentially irreparable) damage to the Land and to those who inhabit the It (Smith, 2021). The development of Western science at the exclusion of Indigenous Peoples perpetuates colonialism and brings harm all parties involved, and reinforces “research” as the ‘dirtiest word’ for many Indigenous Peoples (see page 1 of Smith, 2021).

The concept of *two-eyed seeing* refers to an approach to knowledge and growth that braids Indigenous Knowledge and science together with Western science (Kutz & Tomaselli, 2019; Kimmerer, 2020). Since Traditional Indigenous Knowledge tends to be qualitative, while biological sciences tend to be quantitative, connecting the two is not always simple (Bowles *et al.*, 2021). Although this project does not focus on Indigenous Knowledge or Data, I intend to carryout the work with an anti-imperial and anti-colonial sentiment. I recognize my ignorance in the field in the hopes of receiving valuable critiques, direction, and suggestions. During the project, I intend connecting with local Indigenous groups and Nations to offer help, develop relationships, and exchange knowledge (while recognizing that I do not have the right to all knowledge and that many forms and sources of Knowledge are sacred and private).

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Acknowledgements

I would like to thank Dr. Noonan for offering me the opportunity to pursue a PhD with such an interesting project and cutting-edge statistical methods for movement ecology. I have already learned much and I expect to learn much more.

I would like to thank Dr. Bourbonnais, Dr. Ford, and Dr. Pither for agreeing to be on my committee. Your feedback and mentorship will help me ensure this project is relevant and directly applicable to current issues regarding quantitative biology, conservation, and biogeography.

I would like to thank Sandra Fox for providing me with resources to ensure my perspective and work are inclusive and supportive of different ways of knowing, including Indigenous Knowledge, and that my attitude remains anti-colonial and anti-imperial.

Dedication

A is Terras chi m'ant imbuconau e m'ant donau su logu aundi bivi, imparai e giogai.

Alle Terre che mi hanno nutrito e dato un luogo dove vivere, imparare e giocare.

To the Lands that have nourished me and given me a place to live, learn, and play.

1 Chapter 1: Literature review and quantitative simulations

The amount of resources an organism is able to access is a strong determinant of its odds of survival and reproduction. Resource limitations can cause individuals to experience a negative energetic balance, which can then result in lower fitness (Le Bot *et al.*, 2019; Hou *et al.*, 2020), changes to community structure (Burson *et al.*, 2018; Haney & Siepielski, 2018; Ghislandi *et al.*, 2018; Riotte-Lambert & Matthiopoulos, 2020), altered physiology (Wessling *et al.*, 2018; Le Bot *et al.*, 2019; Rocha *et al.*, 2021; Dai Pra *et al.*, 2022), lower chance of reproduction (Douglas & Pearce-Higgins, 2014; Le Bot *et al.*, 2019; Schmidt *et al.*, 2020; Stefanescu, Ubach & Wiklund, 2021), and even death (Foley, Pettorelli & Foley, 2008; Berger *et al.*, 2018). Thus, many organisms will adapt their behaviors in response to changes in local resource abundance to ensure their needs are met. Some species may respond to fluctuations in resource abundance by, if possible, switching to other food sources (Le Bot *et al.*, 2019; Steinmetz *et al.*, 2021), reducing energetic costs by reducing body heat (Schmidt *et al.*, 2020), or entering hibernation or torpor (Boyles *et al.*, 2020; Mohr, Bagriantsev & Gracheva, 2020; Fjelldal, Wright & Stawski, 2021), but movement represents one of the most readily available traits that species can adjust, whether this be by modifying their home range (Lucherini & Lovari, 1996; Relyea, Lawrence & Demarais, 2000; Arechavala-Lopez *et al.*, 2019; Bista *et al.*, 2022; Bradsworth *et al.*, 2022; Yu *et al.*, 2022), migrating (Middleton *et al.*, 2018; Geremia *et al.*, 2019), dispersing (framework: Southwood, 1977; amphibians: Cayuela *et al.*, 2020; Wheat *et al.*, 2017; birds: Pretorius *et al.*, 2020; mammals: Singh *et al.*, 2012), or moving nomadically (Teitelbaum & Mueller, 2019; Nandintsetseg *et al.*, 2019).

The relationship between animal movement and resource abundance has been of interest to biologists for over half a century. Burt (1943) considered the search for food as the primary driver for animal movement within an animal's home range. Three decades after, Southwood (1977) suggested that change in resource abundance is a strong determinant of how animals decide where to live and when to reproduce. Two years later, Harestad & Bunnel (1979) proposed that the simplest relationship between resource abundance and an animal's home-range size is

$$H = C/R, \quad (1)$$

where H is the animal's **home-range size**, C is the animal's resource consumption, and R is the **resources** an animal can access. Harestad and Bunnel's model is simple to conceptualize and allows for testable predictions, but a species' spatial requirements likely depend on numerous other factors, such as competition, metabolic rate, diet, and body weight (Harvey & Clutton-Brock, 1981; Gittleman & Harvey, 1982; Lindstedt,

Miller & Buskirk, 1986; Reiss, 1988; Jetz *et al.*, 2004; Boratyński, 2020; Noonan *et al.*, 2020). While many researchers have since demonstrated that animals adapt their home ranges in response to resources abundance, few studies build upon others' previous work. Instead, results are reported as independent, *de-novo* findings. Consequently, we currently lack a unifying framework for quantifying the effects of resource abundance on animals' spatial needs. In addition, while much work has been done on estimating animals' responses to average resource abundance, there is little to no information on how they respond to unpredictable changes in resources.

In this paper, we refer to a location's average amount of resources as **resource abundance**, while use the phrase **resource stochasticity** to indicate the variability in resource abundance due to unpredictable causes. We argue that, on its own, a habitat's long-term resource abundance is not sufficient to assess the habitat's quality, nor make predictions about how much space an animal might use. For instance, a grassland with relatively low but constant forage availability will clearly require drastically different behaviors and adaptations from a desert location with equally scarce forage but rare, sudden, and strong pulses of resources. In the first scenario, an animal may require a large but constant home range as it moves between locations in search of food (*sensu* Teitelbaum & Mueller, 2019), while an animal in the second scenario may switch between dispersal as it searches for high-resource patches and short-term range residency until the local resources are depleted. Although it may be possible for both habitats to have the same long-term average resource abundance, the differences in resource unpredictability result in substantially different movement strategies and life histories being selected for. Although it is generally expected that resource unpredictability will decrease animals' fitness and a landscape's energetic balance (Chevin, Lande & Mace, 2010), there is little empirical evidence to support this hypothesis (but see: Herfindal *et al.*, 2005; Nilsen, Herfindal & Linnell, 2005; Rizzuto *et al.*, 2021).

1.1 Thesis structure and aims

This thesis aims to quantify how animal's movement and use of space are affected by environmental stochasticity, with a focus on resource stochasticity. This work has four key objectives: (i) estimating individuals' spatial requirements in a way which is insensitive to variation in sampling protocols and data quality; (ii) quantifying resource stochasticity; (iii) estimating the effects of resource stochasticity on mammals worldwide using models that are robust to commonly-found issues (e.g., correlations within species); and (iv) understanding changes in weather and climate affect mammal movement within BC. The present section provides the structure for this thesis, where each chapter is structured as a stand-alone body of work to be submitted for publication. While each chapter is designed to address each objective independently, together the chapters provide convergent evidence towards the role of stochasticity and change in shaping animal

space use.

In this chapter, I will illustrate how animals' spatial needs depend on both the abundance and unpredictability of resources. First, I will set the theoretical background necessary for the successive sections by introducing key concepts and notation. Next, I will provide a review of the effects of resource *abundance* on animals' spatial needs while suggesting a unifying hypothesis. Afterwards, I will provide a review of the effects of resource *stochasticity* on animals spatial needs while suggesting a second unifying hypothesis. Subsequently, I will demonstrate the power of these two hypotheses using quantitative, simulated responses to changes in resource abundance and unpredictability. Finally, I will demonstrate how this framework can be used in practice to describe the movement ecology of a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado (Medici *et al.*, 2022). Results from the simulations and empirical example will be presented using a fully transparent approach that will allow researchers to replicate the work and apply the methods to their own tracking data.

In **Chapter 2**, I will produce a global raster of a new resource stochasticity index. This metric will then serve as the basis for my subsequent investigation into the relationship between resource stochasticity and animal movement.

Chapter 3 will use an unprecedented and conservation-relevant animal tracking dataset (>3000 animals from 87 globally-distributed species) to investigate how mammals' spatial needs change with environmental variance.

Chapter 4 will estimate how changes in BC's climate over the next century will affect where, how, when, and how much mammals in BC will move.

Finally, **Chapter 5** will summarize the work presented in this thesis and demonstrates its significance within the larger picture of movement ecology, conservation, and quantitative zoology.

Chapters 6-9 contain various supporting information, namely links to the code and data used in this thesis (**Chapter 6**), a table of all abbreviations used in the thesis (**Chapter 7**), a table of all mathematical notations and symbols used in the thesis (**Chapter 8**), and the tentative timeline (**Chapter 9**, which will not be present in the final version of the thesis). **Appendix 1** contains details on published works I made substantial contributions to.

2 Chapter 2: A new measure of environmental variance

2.1 Disentangling changes in mean and stochasticity

Whether an animal can perceive stochasticity depends strongly on the spatiotemporal scale of the process(es) involved. Organisms are most affected by stochastic events and processes that occur on time scales which are on the order of the organisms' life spans or generation times (Southwood, 1977). Weekly heavy rains that alter a lake's salinity may be perceived as stochastic events, while a slow, multi-centennial drought and the high salinity that follows it should be viewed as a (undetectable) change in average conditions. However, since the distinction between changes in mean and spikes in variance depends on the organism of reference, producing a reasonable estimate of resource stochasticity is not simple (Steixner-Kumar & Gläscher, 2020).

I will estimate resource stochasticity using rasters of Normalized Difference Vegetation Index (NDVI, see Pettorelli *et al.*, 2011) from the Advanced Very High Resolution Radiometer (AVHRR) satellites at a daily temporal frequency and a 0.5-degree resolution. While a finer spatial resolution would contain more information about landscapes' stochasticity, it would also increase the size of the dataset and computational costs unnecessarily, as the models will be designed for large-scale spatial changes (i.e., on the order of kilometers). In contrast, while coarsening the data temporally would greatly increase the risk of missing important stochastic events which occur over short time spans (e.g., short-term green-ups, floods, and small fires).

2.2 Quantifying environmental variance

Productivity varies strongly over both space and time. Equatorial and tropical regions tend to have higher productivity than polar regions, and productivity also tends to be higher in warmer seasons than in colder ones. However, the intensity of inter-annual variation strongly depends on location, too: Equatorial ecosystems experience very little seasonality, while arctic regions have marked growth and dormancy periods. Similarly, the stochasticity in productivity also varies spatiotemporally, since both highly productive habitats (e.g., the Amazon) and barren habitats (e.g., deserts) tend to be more predictable than environments with intermediate productivity, and stochasticity is highest during seasons of change (e.g., growth seasons and the timing of colder weather, including higher stochasticity in temperature in cold regions). Consequently, the model of mean and variance in NDVI should account for each of these complex spatiotemporal trends.

Generalized Additive Models (GAMs, see Wood, 2011; Wood, 2017) are flexible statistical models which allow analysts to estimate complex, smooth trends in a data-informed manner (Simpson, 2018). Importantly,

GAMs do not require the response to be (conditionally) normally distributed. Instead, they support a variety of families of distributions from the exponential set of distributions. This is important when modeling modeling biological data, such as NDVI, since the response's variance (i.e., $\mathbb{V}(R)$) often depends on its mean (i.e., $\mathbb{E}(R)$). This is because as the mean NDVI approaches a boundary (-1 or 1), the range of possible values decreases (due to the boundary) and it becomes increasingly more unlikely for NDVI to take a value near the opposite boundary. Biologically, this means that a location with a mean NDVI of +1 (e.g., the Amazon) is highly unlikely to have a value near -1 (or even 0).

Since NDVI is bounded in the $[-1, 1]$ range, I could model NDVI using a GAM with a beta family of distributions (after scaling NDVI to the interval $[0, 1]$ using the transformation $(\nu + 1)/2$, where ν is NDVI). The model could include a (cyclic) smooth of day of year to account for seasonal trends, a smooth of year to account for long-term trends, and a two-dimensional smooth of space to account for differences between habitats. Additionally, including a tensor interaction term of day of year and space would allow the seasonal trends to vary over space (including inverting the seasonal trend between hemispheres), while a tensor interaction term of year and space would allow locations to deviate from the average long-term. Since the beta distribution only supports values in the interval $[0, 1]$, the variance of a beta random distribution is bounded in the interval $(0, 0.25]$. Under the assumption of a constant scale parameter (as is the case with GAMs), the variance tends to 0 as the mean tends to 0 or 1. Consequently, the variance in NDVI depends on the mean and thus vary over time and space, but the mean-variance relationship is spatiotemporally.

Generalized Additive Models for Location and Scale [GAMLSs; Stasinopoulos & Rigby (2007)] are a class of GAMs which allow one to estimate smooth trends in both the mean and the variance around the mean while relaxing the assumption of a constant mean-variance relationship. While beta location-scale models are currently not supported by the `mgcv` package, we have been collaborating with the packages' main author, Dr. Simon Wood, to develop code for the `betals` family. The GAMLS would include all terms detailed above for both the mean and scale parameters' linear predictors.

To my knowledge, there currently is no large-scale measurement of environmental variance. High-resolution, worldwide, spatiotemporally dynamic estimates mean and variance in NDVI would allow researchers to begin studying the effects of spatiotemporal environmental variance on various aspects of animal behavior, including the timing and drivers of animals' spatial needs, movement (including migration and nomadism), and territoriality, and reproduction. The data could also be used to study large-scale phenology events and effects of climate change.

3 Chapter 3: Movement analyses

This chapter will test the hypotheses presented in chapter 1 using the estimated resource abundance and stochasticity from chapter 2 and a worldwide mammal tracking dataset with over 3,000 individuals across more than 85 species. The tracking data will be modeled using continuous-time movement models (CTMMs) via the `ctmm` package (Fleming & Calabrese, 2021) for R (R Core Team, 2022). Each of the movement models will then be used to estimate the animals' spatial needs via their Utilization Distributions (UDs) estimated via Autocorrelated Kernel Density Estimation (Noonan *et al.*, 2019b; AKDE, see Silva *et al.*, 2022). The effects of resource abundance and stochasticity will then be quantified using the estimates of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ from the previous chapter and a Hierarchical Generalized Additive Model (HGAM, see Pedersen *et al.*, 2019) fit via the `mgcv` package (Wood, 2017) for R. The HGAM will estimate effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on the mammals' spatial needs while accounting for differences in the animals' body size (Noonan *et al.*, 2020), diet type, and taxonomy. Additional analyses will also be performed to test whether the animals' range crossing time, long-term average speed, daily speed, and directional persistence also depend on $\mathbb{E}(R)$ and $\mathbb{V}(R)$.

Results from the HGAMs will allow researchers and conservation managers to predict mammals' spatial needs and movement via quantitative environmental variables ($\mathbb{E}(R)$ and $\mathbb{V}(R)$) and known traits (i.e., body size, taxonomy, and diet type). Consequently, the models will have the potential of predicting animals' spatial needs without any tracking data, which is of particular importance for animals which are hard to track and study, whether this be due to their small mass (e.g., rodents), their scarce numbers, their elusiveness, or ethical concerns.

4 Chapter 4: Effects of climate change on BC mammals

This chapter will provide a BC-focused analysis on the effects of weather and climate on mammal movement. Using more than a decade of pre-collected telemetry data on 5 species of terrestrial BC mammals (caribou, cougars, elk, grizzly bears, and mountain goats), I will estimate how mammalian movement ecology responded to historical weather conditions and predict how and mammalian movement will respond under different climate change scenarios in the current century. More specifically, I will determine how changes in temperature and precipitation will affect when, how, how much, and where BC mammals move over the next 80 years (see sections below). Additionally, in collaboration with Dayna Weststrate and Aimee Chhen (current students from the Quantitative Ecology Lab), I will produce quantitative and data-informed estimates of how climate change will shape Human Wildlife Conflict in BC's protected areas. A preprint on the work is available at <https://doi.org/10.1101/2023.07.11.548618>.

4.1 Weather and climate data

Short-term historical weather data will be estimated using hourly projections from the ERA5-Land dataset (Copernicus Climate Change Service, 2019) downloaded via the `ecmwfr` package (Hufkens, Stauffer & Campitelli, 2019) for R. While real-time measurements would provide more accurate estimates, the tracked animals were not sufficiently close to a weather station throughout the tracking period. Some of the elk datasets included collar measurements of air temperature, but such measurements are likely biased by solar radiation and the animals' body heat. Therefore, including such temperature data would result in species-level biases in the HGAM.

The climate data during the current century will be estimated using the latest Shared Socioeconomic Pathway (SSP) predictions by the IPCC (Riahi *et al.*, 2017), which will be downloaded via the `climatenetR` package (Burnett, 2023) for R. Since the SSPs only provide predictions for average monthly precipitation and average, maximum, and minimum montly temperatures, the predictions will likely fail to account for the heterogeneity within months and the effect of sub-monthly extreme weather, such as heat waves which last a week or less. If the movement models suggest highly heterogeneous and nonlinear responses to temperature or precipitation, it may be necessary to simulate daily fluctuations in weather.s

4.2 Determining when, how, and how much mammals move

The movement of each of the mammals in the dataset will be modeled using CTMMs via the `ctmm` package (Fleming & Calabrese, 2021) for R. Rather than imposing a model on the tracking data, the model will be determined based on a model selection process that accounts for the data's sampling frequency (Noonan *et*

al., 2019a). Next, I will use the subset of models with speed estimates and their associated data to estimate animals' instantaneous movement rates between known locations. Since CTMMs always predict a non-zero speed, movement rates will be standardized by subtracting the minimum speed, which will be assumed to be approximately equal to zero.

Finally, the chance that an animal will move and the animal's speed (given that it is moving) will be modeled using an HGAM with a hurdle Gamma distribution via the `brms` package (Bürkner, 2017, 2018) for R. The model will account for each species' changes in behavior throughout the day and throughout the year while also accounting for the effects of temperature and precipitation, as well as how the species' daily and seasonal trends are affected by changes in temperature and precipitation. While snow depth is also an important determinant of mammal movement (e.g., Pedersen *et al.*, 2021; Melin *et al.*, 2023), I will not include it in the analysis because I am unaware of any predictions of snow depth in future decades.

4.3 Determining where mammals will move

I will estimate the mammals' spatial selection using Hierarchical Resource Selection Functions (HRSFs). To avoid the common limitations of linear or polynomial feature selection which many RSFs suffer from, I will fit the HRSFs as Heterogeneous Poisson Processes (HPPPs) using HGAMs via the `mgcv` package (Aarts *et al.*, 2008). This will allow me to estimate common, nonlinear preferences between animals from the same species. However, since HPPPs require a large number of quadrature points (i.e., locations where the animal was *not*) relative to the number of GPS locations (i.e., $\gtrsim 200$), the computational requirements will likely be too high to fit a single hierarchical model for all mammal species in the dataset. However, this is not a serious issue, since the models can still be used independently at the species level, and a mammal-level estimate from an opportunistic sample of 5 species would likely be biased and lead to questionable predictions.

The HRSFs will account for animals' preference for three resources: forest cover, water, and elevation, which will be estimated using temporally static rasters of forest cover, distance to nearest freshwater body, and elevation. While temporally dynamic rasters would provide more accurate estimates (e.g., by accounting for deforestation and droughts), I am unaware of any such estimates. In addition, the models will also estimate how temperature and precipitation affect the species' preference for each of the resources. Each of the model terms will be estimated using sufficiently flexible yet reasonably constrained smooths. To decrease computation time (with no cost to accuracy), the models will be fit using the `bam()` function from the `mgcv` package with fast residual maximum likelihood and a discretization of covariates (Wood *et al.*, 2017; Li & Wood, 2020). The models and predictions produced by this chapter will be tailored specifically to the needs of conservation organizations within BC, including BC Parks, which whom I have been collaborating through a Living Labs project.

5 Chapter 5: Synthesis

The effect of environmental stochasticity on animals' spatial needs and movement at large has received little to no attention. However, recent increases in weather and climate stochasticity (@ Intergovernmental Panel On Climate Change, 2023), including an increase in the frequency and intensity of extreme events (Yao *et al.*, 2022) demonstrates that the topic is of high importance. Failure to account for the effects of environmental stochasticity will hinder our ability to make informed conservation decisions and take effective actions. This thesis will provide foundational framework with easily employable estimates of how mammal movement is affected by resource abundance, resource stochasticity, and changes in climate, with a focus on large-scale mammalian energetics.

The findings produced by this thesis will offer important considerations regarding the amount and quality of habitat mammals require to survive in heterogeneous, changing, and stochastic environments. Although the focus of this thesis will be on (large) mammals, the ideas and methods presented here can easily be applied to non-mammalian data. In addition, the global measure of environmental variance produced in **Chapter 2** will be designed so it is applicable to other fields of biology other than animal movement ecology, such as animal behavior, phenology, and forestry.

6 Open and transparent science: Code and data availability

All code and figures used in this project are available at the GitHub repository located at <https://github.com/StefanoMezzini/hr-environ-stoch-phd> and related repositories (linked in the former's main README file). The repositories will not include any publicly available data, unless the data was substantially wrangled or cleaned.

All scripts will include comments to help people replicate the analysis, but they will assume some basic knowledge of R (including referring to help files and vignettes). Comments and requests regarding the project can be placed in the repositories as issues, or sent directly to my email address.

7 List of abbreviations used

Table 1: A list of all abbreviations and acronyms used in the thesis.

Abbreviation	Phrase
CTMM	Continuous-time movement model
GAM	Generalized additive model
GAMLS	Generalized additive model for location and scale
HGAM	Hierarchical generalized additive model
HPPP	Heterogeneous poisson point process
NDVI	Normalized difference vegetation index
PCA	Principal components analysis

8 List of notations and symbols used

Table 2: A list of all mathematical notations and symbols used in the thesis.

Symbol	Meaning
$\mathbb{E}(\cdot)$	Expectation, mean
H	Home range, spatial needs, required area
$P(A)$	Probability of event A , e.g., A = successful foraging
R	Resources
$R \sim \text{Gamma}(k, \theta)$	R follows a Gamma distribution with parameters k and θ
$\mathbb{V}(\cdot)$	Variance
$a < b$	a less than b
$a > b$	a greater than b
$a \approx b$	a approximately equal to b
$a \geq b$	a greater than or equal to b
$a \leq b$	a less or equal to b
$a \lesssim b$	a approximately less than b
$c \in (a, b]$	c is in the interval from a (not included) to b (included)
$c \propto k$	c is proportional to k
$\mu(t)$	Time-varying mean in resource abundance
n	sample size
n_{eff}	effective sample size
$\sigma^2(t)$	Time-varying variance in resource abundance
τ_p	Positional autocorrelation, mean reversion to HR center, range crossing time
τ_v	Velocity autocorrelation, directional persistance

9 Project timeline

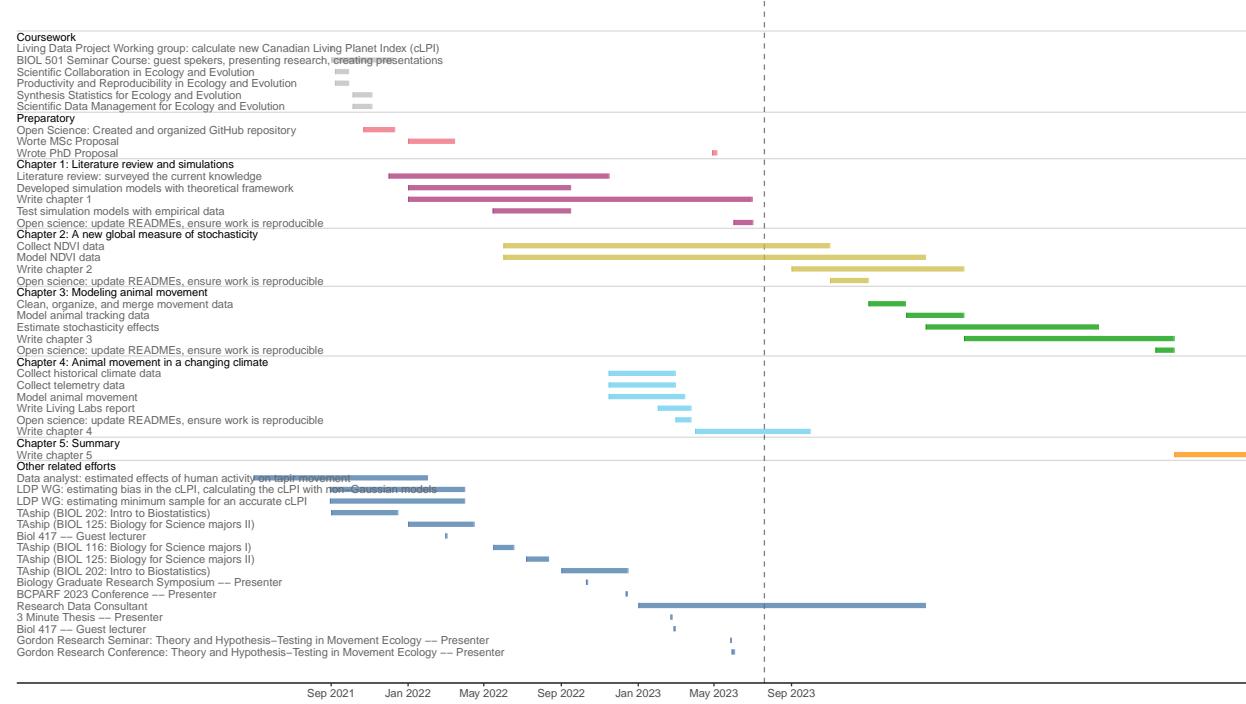


Figure 1: Visual representation of the estimated timeline for my Master’s project.

9.1 Progress to date

- Created and organized the GitHub repository (<https://github.com/StefanoMezzini/hr-environ-stoch-masters>);
- Completed all coursework necessary for a Master’s degree;
- Reviewed literature and have begun making theoretical predictions;
- Living Data Project Working group: calculated new Canadian Living Planet Index (cLPI);
- Data analyst: estimated effects of human activity on tapir movement using `ctmm` and `mgcv`. The manuscript has been accepted and is in press (preprint is available at <https://www.biorxiv.org/content/10.1101/2021.11.12.468362v1>, and the code and data are available at <https://github.com/StefanoMezzini/tapirs>);
- Data analyst: estimated changes paleolimnological time series from endorheic lakes due to 8-m lake-level variation using Hierarchical Generalized Additive Models (HGAMs) and location-scale HGAMs fit with `mgcv`. The manuscript is available at <https://doi.org/10.1002/lno.12054>, while code and data are available at <https://github.com/simpson-lab/kenosee-white-bear>;
- Presented the background theory behind the thesis and some simulations as a guest lecturer in Dr. Noonan’s BIOL 417 course (Evolutionary Ecology).

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Appendix 1: Manuscripts contributed to during the degree

Abrupt changes in the physical and biological structure of endorheic upland lakes due to 8-m lake-level variation during the 20th century

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Abstract

Climate-induced variation in lake level can affect physicochemical properties of endorheic lakes, but its consequences for phototrophic production and regime shifts are not well understood. Here, we quantified changes in the abundance and community composition of phototrophs in Kenosee and White Bear lakes, two endorheic basins in the parkland Moose Mountain uplands of southeastern Saskatchewan, Canada, which have experienced > 8 m declines in water level since ~ 1900. We hypothesized that lower water levels and warmer temperatures should manifest as increased abundance of phytoplankton, particularly cyanobacteria, and possibly trigger a regime shift to turbid conditions due to evaporative concentration of nutrients and solutes. High-resolution analysis of sedimentary pigments revealed an increase in total phototrophic abundance (as β-carotene) concurrent with lake-level decline beginning ~ 1930, but demonstrated little directional change in cyanobacteria. Instead, significant increases in obligately anaerobic purple sulfur bacteria (as okenone) occurred in both lakes during ~ 1930–1950, coeval with alterations to light environments and declines in lake level. The presence of okenone suggests that climate-induced increases in solute concentrations may have favored the formation of novel bacterial habitats where photic and anoxic zones overlapped. Generalized additive models showed that establishment of this unique habitat was likely preceded by increased temporal variance of sulfur bacteria, but not phytoplankton or cyanobacteria, suggesting that this abrupt change to physical lake structure was unique to deep-water environments. Such climate-induced shifts may become more frequent in the region due to hydrological stress on lake levels due to warming temperatures across the Northern Great Plains.

Local and regional declines in lake levels are of great concern as human water use is expected to increase over the next century (Vörösmarty et al. 2000; Gaeta et al. 2014). In

addition to anthropogenic uses, lake levels may vary in response to perturbations in regional hydroclimate, particularly where evaporation rates exceed precipitation levels (Pham et al. 2009; Xiao et al. 2018). Such hydroclimate changes and subsequent lake-level declines are widespread in the Northern Great Plains, particularly in hydrologically managed endorheic basins which depend on spring snowmelt for water replenishment (van der Kamp et al. 2008; Pham et al. 2009; Sereda et al. 2011). In these regions, general circulation models (GCMs) forecast warmer temperatures and only modest changes in precipitation (Tanzeeba and Gan 2012; Asong et al. 2016; Zhou et al. 2018), potentially resulting in increased volatility of regional lake levels due to evaporative forcing. Resultant changes in regional water quality may include variation in nutrient, carbon, and major ion concentrations, proportion of littoral and pelagic habitats, phytoplankton community composition and production, and food-web dynamics including zooplankton and fish communities (Vinebrooke et al. 1998; Fischer and Öhl 2005; Hambright et al. 2008; Pham et al. 2009; Gal et al. 2013; Wigdahl

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Additional Supporting Information may be found in the online version of this article.

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Author Contribution Statement: J.A.B. and C.A.C.G. are equal lead authors.

et al. 2014; Vogt et al. 2018). Despite on-going variation in lake levels in the Canadian Prairie region (Fritz 1990; van der Kamp et al. 2008), little is known of the long-term effects of enhanced evaporative stresses on production, community composition, and stability of phototrophic assemblages.

Variation in lake levels also affects water-column heating and circulation, as well as the degree to which irradiance penetrates to stable environments such as lake bottoms or chemoclines (Zohary and Ostrovsky 2011). Changes in thermal stratification may be particularly noteworthy in shallow prairie and parkland systems where polymixis is common due to frequent high winds (Plancq et al. 2018), while variation in ionic content can affect chemical stratification (Hodgson et al. 1998). In addition, evaporative concentration of nutrients associated with lake-level decline may favor increased primary production, particularly under warm conditions (Vinebrooke et al. 1998; Zinabu 2002). As shallower ecosystems warm more quickly than deeper ones (Dröscher et al. 2009; Dibike et al. 2016), such conditions can promote blooms of planktonic algae and potentially-toxic cyanobacteria (Davis et al. 2009; Paerl and Paul 2012; Huisman et al. 2018; Hayes et al. 2019).

Large and disproportionate increases in cyanobacterial abundance can arise as an abrupt change, or “regime shift” (*sensu lato*) in some lake systems (Taranu et al. 2015; Bunting et al. 2016; Vogt et al. 2018). In some cases, there is increased temporal variance in the abundance or concentration of phytoplankton or cyanobacteria prior to the shift, marking a “critical slowing down” arising from changes in the strength of internal feedbacks due to environmental driver(s) (Scheffer et al. 2001; Scheffer and Carpenter 2003; Carpenter and Brock 2006; Dakos et al. 2015; Ratajczak et al. 2018). In lake systems, variation in primary production can rise because of prolonged gradual increases in nutrient influx (e.g., paradox of enrichment; Cottingham et al. 2000), after which the regime shift to prolific cyanobacteria is initiated by relative minor forcing that push lakes beyond critical thresholds (Dakos et al. 2015; Bunting et al. 2016). These transitions may become self-enforcing through positive feedback mechanisms and result in a transition to an alternate stable state that exhibits self-maintenance and hysteresis (Scheffer et al. 2001; Scheffer and Carpenter 2003; Dakos et al. 2015; Ratajczak et al. 2018). Additional environmental drivers which may result in a regime shift in lakes include changes in ice-cover duration, vertical-mixing regime, and water-column warming (Paerl and Paul 2012; Taranu et al. 2015); although, in theory, variation in lake level, chemical stratification, or ionic concentration could also induce a regime shift (Garcés et al. 1995; Hodgson et al. 1998). On the Northern Great Plains, changes in the interactions between the predominant air masses (Gulf, Pacific, Arctic) can cause increased evaporative concentration and salinity (Liu et al. 2008; Pham et al. 2009), variation in water-column mixing (polymixis to meromixis; Michels et al. 2007), and large changes (5–10 m) in lake level (van der

Kamp et al. 2008) that could all initiate a regime shift with large biological responses (Scheffer et al. 2001; Carpenter et al. 2011).

To date, little is known of whether changes in the physical status of lakes (deep/shallow, mixed/stratified, etc.) are recorded by temporal variation in primary production or whether such changes in physical conditions can initiate true regime shifts (Bunting et al. 2016; Taranu et al. 2018). Furthermore, it has been established that some regime shifts are not preceded by rising variance (Burthe et al. 2016; Ratajczak et al. 2018) and that rising variance in environmentally sensitive proxies does not invariably lead to a regime shift (Burthe et al. 2016), which makes the establishment of regime shifts very difficult without abundant a priori knowledge of the impacted system (Scheffer and Carpenter 2003; Dakos et al. 2015; Burthe et al. 2016). In this context, it may be useful to retroactively examine systems which have experienced substantial environmental changes to discover if any regime shifts occurred, either with or without an associated rise in variance of key proxies, such as biological production (Randsalu-Wendrup et al. 2016; Taranu et al. 2018). The establishment of past regime shifts, or transitions between alternate stable states, may provide critical insights on how nonlinear and abrupt changes in ecosystem response to environmental change may improve lake management and mitigation strategies (Bunting et al. 2016; Randsalu-Wendrup et al. 2016).

To better understand how lake-level variation may influence the temporal variability of lakes, we quantified historical changes in the production, composition, and variance of phototrophic assemblages in two proximal endorheic parkland lakes located in the Moose Mountain uplands of southeast Saskatchewan, Canada. Kenosee and White Bear lakes are presently unstratified (Plancq et al. 2018) and have experienced > 8 m declines in water level over the past century (Vance et al. 1997; Vinebrooke et al. 1998; van der Kamp et al. 2008). Analyses of historical changes in biomarker pigments from algae and phototrophic bacteria (cyanobacteria, purple sulfur bacteria) were used to: (1) quantify how phytoplankton abundance and community composition have varied in response to lake-level changes since ~ 1900; (2) determine if climate and lake-level change resulted in disproportionate increases in toxic cyanobacteria as is expected in warming, shallowing waters (Taranu et al. 2015; Bunting et al. 2016; Vogt et al. 2018) and (3) determine if any changes in lake physical structure (i.e., mixing regime, oxygenation, light penetration) due to historical lake-level variation are related to increased temporal variance of phytoplankton, such as seen in other prairie lakes which have undergone regime shifts (Carpenter et al. 2011; Bunting et al. 2016). Analysis of temporal patterns of primary producers may provide insights into the ecological effects of regional changes in lake levels (Dakos et al. 2015; Taranu et al. 2018) and will help forecast lake response to future

environmental change under a warmer and potentially more arid climate (Asong et al. 2016).

Materials and methods

Study sites

Kenosee Lake and White Bear Lake are located in the Moose Mountain Uplands of southeastern Saskatchewan, Canada (Fig. 1). These lakes are separated by ~ 2 km and share a humid, cold, continental climate (Köppen Dfb) with a mean annual temperature of 3.7°C and 427 mm yr⁻¹ of precipitation during the 1981–2010 period (Estevan, Saskatchewan, station data; Environment and Climate Change Canada [ECCC]; https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnProv&lstProvince=SK&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2896&dispBack=0, accessed April 2021). Historical data suggest that while mean annual temperatures have increased by ~ 2°C over the past 80 yr, rainfall has increased only modestly and there has been little trend in snowfall (Supplemental Information Fig. S1; Homogenized Canadian Climate Station Data; ECCC; <https://www.canada.ca/en/environment-climate-change/service-s/climate-change/science-research-data/climate-trends-variability/adjusted-homogenized-canadian-data.html>, accessed August 2021).

<https://www.canada.ca/en/environment-climate-change/service-s/climate-change/science-research-data/climate-trends-variability/adjusted-homogenized-canadian-data.html>, accessed August 2021).

The two lakes are of similar size (~ 8–9 km²), although White Bear Lake is deeper ($Z_{\max} = 15$ vs. 8 m) and drains a larger area (172 vs. 60 km²) than Kenosee Lake (Table 1; Vance et al. 1997; van der Kamp et al. 2008). The catchments of Kenosee and White Bear lakes exhibit poor hydrological integration and neither lake has channelized inflows or outflows. Instead, wetlands, sloughs, and lakes in the Moose Mountain Uplands rely on complex subsurface connections of saline, carbonate-rich groundwater that is eventually discharged on the adjacent prairie surface ~ 150 m below (Vance et al. 1997). Historically, Kenosee Lake spilled into White Bear Lake when water levels reached over 742 m above sea level (asl), but water conveyance between lakes has not been recorded since 1954 due to water-level low stands (see below) and the construction of a highway between the basins (Godwin et al. 2013).

Land use is similar within catchments of Kenosee and White Bear lakes, with ~ 55–57% cover by broadleaf deciduous forest primarily comprised of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), green ash



Fig. 1. (A) Map of Kenosee and White Bear Lakes with marked coring locations. Coring depths are 7.6 and 9.2 m for Kenosee Lake and White Bear Lake, respectively. Map interpreted from photograph courtesy of the U.S. Geological Survey (Landsat 8 OLI/TIRS database). (B) The location of Kenosee and White Bear lakes in the Moose Mountain Uplands of southeast Saskatchewan in relation to the Province of Saskatchewan (SK) in Canada.

Table 1. Summary of physical and chemical characteristics of Kenosee and White Bear lakes. Surface area (km^2) and max depth (m) were obtained from van der Kamp et al. (2008), while physical (Secchi depth), chemical (total phosphorus [TP], total nitrogen [TN], total organic carbon [TOC]), salinity, pH, and Chl a were measured once per month from Jun to Sep in 2016 (mean \pm standard deviation).

Site	Kenosee Lake	White bear Lake
Surface area (km^2)	8	9
Drainage area (km^2)	60	172
Maximum depth (m)	8	15
Lake-level elevation (m asl)	741	729
TN ($\mu\text{g}\cdot\text{L}^{-1}$)	2048 \pm 38	2533 \pm 116
TP ($\mu\text{g}\cdot\text{L}^{-1}$)	27.50 \pm 9.57	14.46 \pm 10.41
TOC ($\text{mg}\cdot\text{L}^{-1}$)	26.75 \pm 0.44	35.03 \pm 1.97
Chl a ($\mu\text{g}\cdot\text{L}^{-1}$)	9.44 \pm 4.41	8.40 \pm 7.79
Salinity ($\text{g}\cdot\text{L}^{-1}$)	1.07 \pm 0.03	1.84 \pm 0.06
pH	8.58 \pm 0.14	8.72 \pm 0.07
Secchi depth (m)	1.84 \pm 1.36	2.58 \pm 1.07

(*Fraxinus pennsylvanica*), white birch (*Betula papyrifera*), and Manitoba maple (*Acer negundo*; Henderson et al. 2002), \sim 21–27% cover by other water bodies, \sim 9–10% by grasses and shrubs, and < 1% agricultural cover (Agriculture and Agri-Food Canada 2013). The catchments of Kenosee and White Bear lakes have never been cleared. A portion of the catchment of White Bear Lake is encompassed by White Bear First Nations reserve created in 1875, while the remaining catchment area of both lakes became part of a Canadian federal forest reserve in 1894 and a Saskatchewan provincial park in 1931 (Henderson et al. 2002). Despite these designations and protections, significant recreational development has occurred on the shorelines of both lakes since the 1960s including the construction of cottages and golf courses. Monthly sampling during June–September 2016 showed that both lakes are currently hyposaline, alkaline, and mesotrophic (Table 1). Currently, both basins do not stratify, although nothing is known of the interannual variation in mixing intensity.

Lake-level history

Annual lake-level data for Kenosee and White Bear lakes were recorded by the Government of Canada (Historical Hydrometric Data; https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html, accessed April 2021) between 1964 and 2016. Values for White Bear Lake between 1910 and 1964 were obtained from Cullimore and Griffin (1979). While no data are available regarding Kenosee Lake's water-levels prior to 1964, a strong linear relationship between lakes levels since 1964 ($R^2 = 0.72$, $p < 0.0001$) suggest that both basins would have experienced similar degrees of lake-level variation during the early 20th century.

Paleolimnological analyses

Sediment cores were collected from deep-water sites from Kenosee and White Bear lakes using a Glew gravity corer (Glew 1989) in August 2016 (Fig. 1). The Kenosee Lake core was collected at \sim 7.6 m depth ($49^\circ 49.455'\text{N}$, $102^\circ 18.882'\text{W}$) and was \sim 57 cm in length, while the White Bear Lake core was taken at \sim 9.2 m depth ($49^\circ 49.455'\text{N}$, $102^\circ 18.882'\text{W}$) and was \sim 56-cm long. Both cores were sectioned on site at 0.5-cm intervals, stored in the dark on ice during transport, and refrigerated until analysis within 4 months of collection. Sediments from the top 40 cm of each core were freeze-dried (72 h, 0.1 Pa) for subsequent analyses of ^{210}Pb and ^{137}Cs activities, stable isotope content (carbon [C], nitrogen [N]), and pigment biomarker concentrations in the Institute of Environmental Change and Society at the University of Regina.

Sediment chronology was based on ^{210}Pb and ^{137}Cs activities quantified using gamma spectrometric analysis of 12 evenly spaced sections of each core (Appelby et al. 1986). Sediment age and mass accumulation rates ($\text{g}\text{ cm}^{-2}\text{ yr}^{-1}$) were calculated using the constant rate of supply (CRS) model (Binford 1990). Sediment age-depth relationships were refined using shape-constrained additive models (SCAMs) with monotone decreasing P-splines via the *scam* package (Pya 2021) with generalized cross-validation smoothness parameter selection in R (R Core Team 2021).

Whole dried sediments were analyzed for stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) and elemental content (N%, C%) by combustion using a Thermoquest Delta Plus isotope ratio mass spectrometer equipped with a Thermoquest NC2500 elemental analyzer (Savage et al. 2004). Carbon and nitrogen isotope values were standardized against international standards (Pee Dee Belemnite and atmospheric N₂, respectively) and expressed using standard ‰ notation. Elemental composition of whole sediments were estimated as % dry mass for N (N%) and C (C%) content, and were used to estimate C : N mass ratios.

High-performance liquid chromatography (HPLC) was used to quantify fossil pigment concentrations from alternate sediment sections in the Kenosee and White Bear cores following Leavitt and Hodgson (2001). Pigments were extracted from 15 to 100 mg of freeze-dried sediments by an 80 : 15 : 5 (by volume) solution of HPLC-grade acetone, methanol, and water. Extracts were filtered (0.22-μm pore) and evaporated under inert N₂ gas, before being redissolved into injection solution. Concentrations of fossil pigments were measured using an Agilent model 1260 HPLC calibrated with authentic pigment standards and using Sudan II as an internal reference. Pigment interpretation followed Leavitt and Hodgson (2001) with concentrations of chlorophyll a (Chl a) derivative pheophytin a , and β-carotene used as indicators of total phototroph abundance (Leavitt and Hodgson 2001). Other taxon-specific pigments included fucoxanthin (siliceous algae), diatoxanthin (primarily diatoms), alloxanthin

(cryptophytes), pheophytin *b* (chlorophytes), echinenone (total cyanobacteria), and canthaxanthin (Nostocales cyanobacteria). Lutein and zeaxanthin could not be separated and were combined as indicators of bloom-forming taxa (Leavitt and Hodgson 2001). In addition, okenone was used as an indicator of purple sulfur bacteria (Leavitt et al. 1989; Leavitt and Hodgson 2001). All pigment concentrations were expressed as nmoles pigment g⁻¹ carbon (Leavitt et al. 1994). The ratio of Chl *a* to pheophytin *a* (Chl : pheo) was used as a metric of changes in preservation environment (Leavitt and Hodgson 2001), while the ratio of UVR-absorbing scytonemin derivatives to the sum of other carotenoids (alloxanthin, lutein-zeaxanthin, diatoxanthin) was used as an index of past exposure to UV irradiance (Leavitt et al. 1997).

Numerical analyses

Temporal trends in pigment and other geochemical proxies were estimated using generalized additive models (GAMs) using the *mgcv* package (Wood 2011, 2017; Simpson 2018). Specifically, pigment concentrations were estimated using a location-scale hierarchical GAM (HGAM) where both the mean and scale predictors used a global smooth of year and a factor smooth for each combination of the 2 lakes and

10 pigments for a total of 20 factors (model GS in Pedersen et al. 2019). The global smooth accounted for the common trend between both lakes and all pigments, while the factor smooth accounted for the deviations at the pigment and lake level from the global smooth. The model deviations were fit assuming a common smoothness parameter between lakes and pigments, but do not account for common trends between lakes or pigments separately. Both the global smooth and the factor smooth were fit using cubic regression splines. Finally, the scale predictor also accounted for the period of time represented by each core slice to account for changes in temporal averaging between adjacent samples. This was facilitated with the addition of a smooth of each sample's log-transformed temporal interval and by fitting the smooth with adaptive splines.

Pigment variances were extracted from pigment concentrations by calculating the product of the mean and shape estimates from the concentration HGAM. Credible intervals (95%) for the variance values were obtained by running 10,000 simulations and taking the 2.5% and 97.5% quantiles of the posterior distributions. Resultant pigment variances were also modeled using an HGAM under the same parameters as described above. In addition, Chl : pheo ratios and UV indexes were modeled individually using HGAMs with Gamma and Tweedie distributions, respectively. Both models used a smooth for year and lake, such that each lake had a different smoothness parameter (model *I* in Pedersen et al. 2019). In all models, observations were weighted by temporal resolution and the smoothness parameter was estimated using a restricted maximum likelihood approach (Simpson 2018). To identify periods of significant change, the first derivative of the estimated smooth trend was evaluated from the relevant model of each proxy (Bunting et al. 2016; Simpson 2018). Here, the first derivative of each proxy smooth was estimated using the *gratia* package in R (Simpson 2021). Periods of significant change were identified where the 95% credible interval on the estimated derivative excluded 0.

All statistical analyses were performed in the R statistical environment (R Core Team 2021). The *tidy* and *dplyr* packages (Wickham 2021; Wickham et al. 2021) were used for data wrangling, while plots were created using the *ggplot2* and *cowplot* packages (Wickham et al. 2016; Wilke 2020). Code for analyses is available on GitHub at <https://github.com/simpson-lab/kenosee-white-bear>.

Results

Lake-level

Historical records suggested that both Kenosee and White Bear lakes experienced water-level variation of > 8 m since the early 20th century (Fig. 2). Taking the first common year of record (1964) as a benchmark, water levels in White Bear Lake were ~ 4 m higher between ~ 1910 and ~ 1930 before

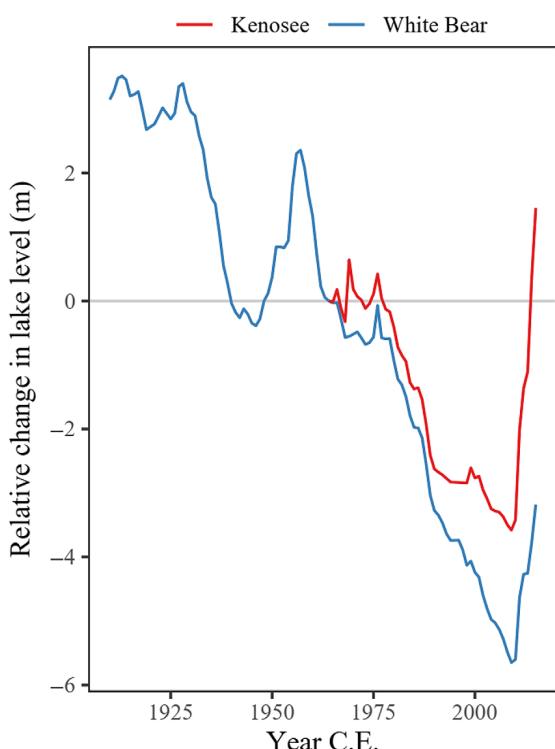


Fig. 2. Water levels of Kenosee Lake (red) and White Bear Lake (blue) relative to their levels in 1964. Data from 1964 to 2015 were obtained from the Government of Canada Water Office; data prior to 1964 for White Bear Lake were obtained from estimates from Cullimore and Griffin (1979).

declining toward a plateau by 1950. While lake levels rose ~ 2 m during the 1950s, values declined again to the late 1960s. The water levels of both lakes were stable until ~ 1975 when marked declines of up to 6 m and 3 m occurred in White Bear and Kenosee lakes, respectively. Water levels reached a minimum at ~ 2010 (-4 to -5.5 m) before rapidly rising by 2 m in White Bear Lake and 4 m in Kenosee Lake in recent years (Fig. 2). Given the strong

correlation between Kenosee and White Bear lake levels since 1964 ($R^2 = 0.72$, $p \leq 0.0001$), it is likely that Kenosee Lake experienced similar water-level fluxes prior to 1964. Together, these findings suggest that Kenosee and White Bear lakes have experienced water-level variations equivalent to $\sim 75\%$ and $\sim 55\%$ of their present depth, respectively, with only very recent increases toward historical benchmarks (Fig. 2).

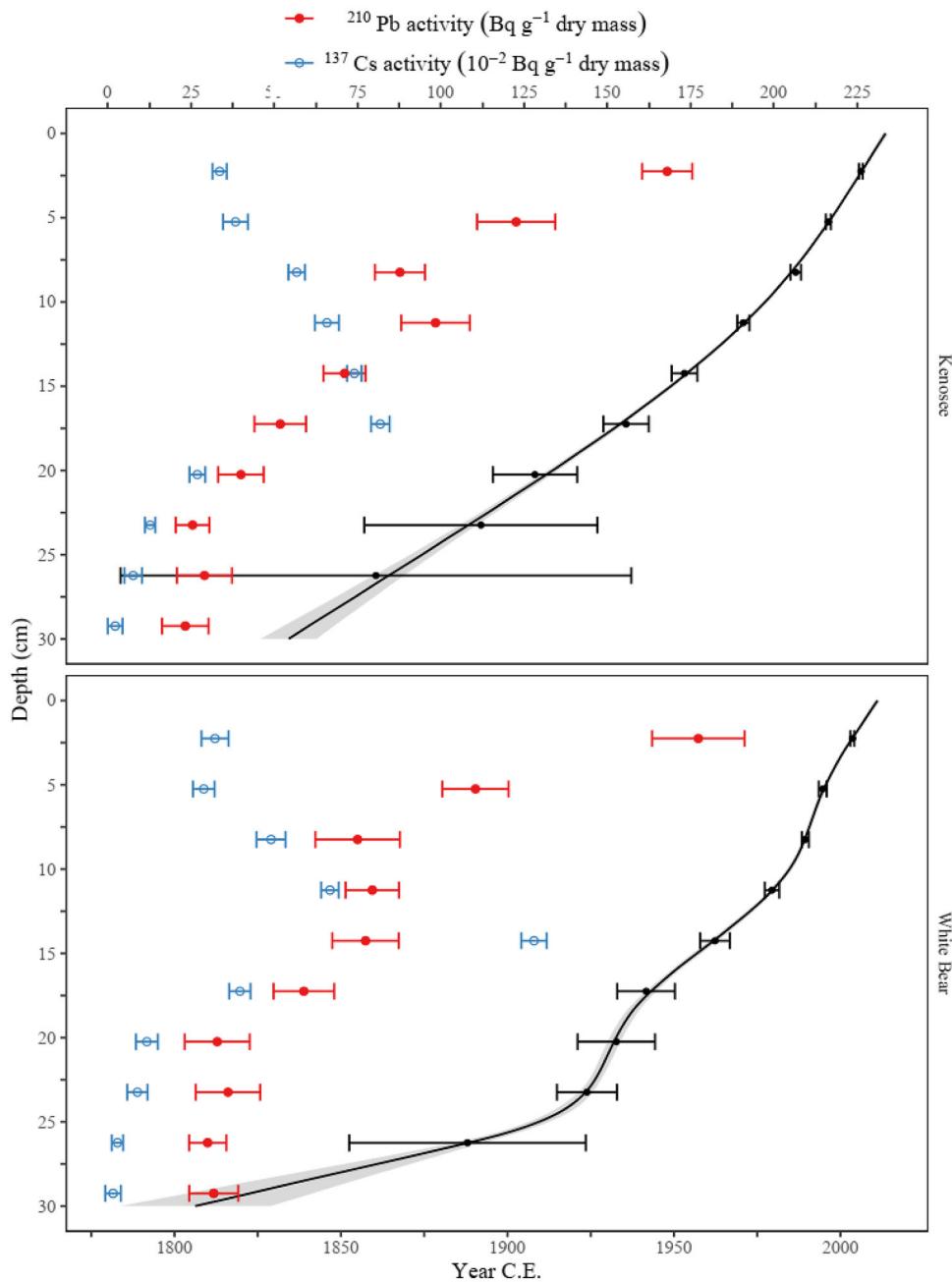


Fig. 3. Activities of ^{210}Pb and ^{137}Cs with associated error estimates (1σ) by core depth for Kenosee Lake and White Bear Lake. Age-depth relationships were estimated using SCAMs (shape-constrained additive models)-based CRS (constant rate of supply) models of ^{210}Pb activity in each core. Inferred dates are also presented with error ranges (1σ) by core depth for Kenosee Lake and White Bear Lake.

Sediment chronology

Activity of ^{210}Pb declined with sediment depth in the Kenosee and White Bear cores with little evidence of sediment mixing (Fig. 3). Activity profiles of ^{137}Cs were well defined in White Bear Lake sediments, with a clear maximum in ^{210}Pb -dated intervals corresponding to peak atmospheric nuclear testing in 1963 at 14 cm (Fig. 3). The ^{137}Cs peak was less well defined in Kenosee Lake, with a maximum at ~ 17 cm. Age-depth models suggested that bulk dry sediment accumulation rates were comparable between sites, whereas SCAMs based on the CRS models suggest that ages at ~ 30 cm were essentially the same; ~ 1830 and ~ 1810 for Kenosee and White Bear lakes, respectively (Fig. 3).

Geochemistry and stable isotopes

Geochemical trends in stable isotope values were generally similar in the cores from Kenosee and White Bear lakes (Fig. 4). In both cores, C and N content (% by mass) was low prior to ~ 1930 , but rose rapidly afterward to a transient

plateau ca. 1950–1975, before continuing to historical maxima in the most recently deposited sediments. The C : N ratios of both lakes exhibited an inverse relationship to C and N content, with stable values of ~ 18 prior to 1900, declining to a plateau before accelerating to a minimum after ca. 2000 (Fig. 4). Sedimentary $\delta^{13}\text{C}$ values were relatively stable and elevated at both sites before ~ 2000 ($\sim 15\text{\textperthousand}$), after which isotope values declined to $\sim -22.5\text{\textperthousand}$ in both lakes (Fig. 4). In contrast, trends in $\delta^{15}\text{N}$ were markedly different between lakes. In Kenosee Lake, $\delta^{15}\text{N}$ ratios decreased from $\sim 6\text{\textperthousand}$ to $\sim 4\text{\textperthousand}$ after approximately 1925 before returning to more enriched values after ~ 1960 (Fig. 4), whereas in White Bear Lake, $\delta^{15}\text{N}$ ratios continue to decline after ~ 1960 with depletions to $\sim 2\text{\textperthousand}$ in sediments deposited since ca. 2000 (Fig. 4).

Phototrophic pigments

Analysis of sedimentary carotenoid and chlorophyll pigments revealed significant changes in the composition, concentration, and variance of primary producers over the

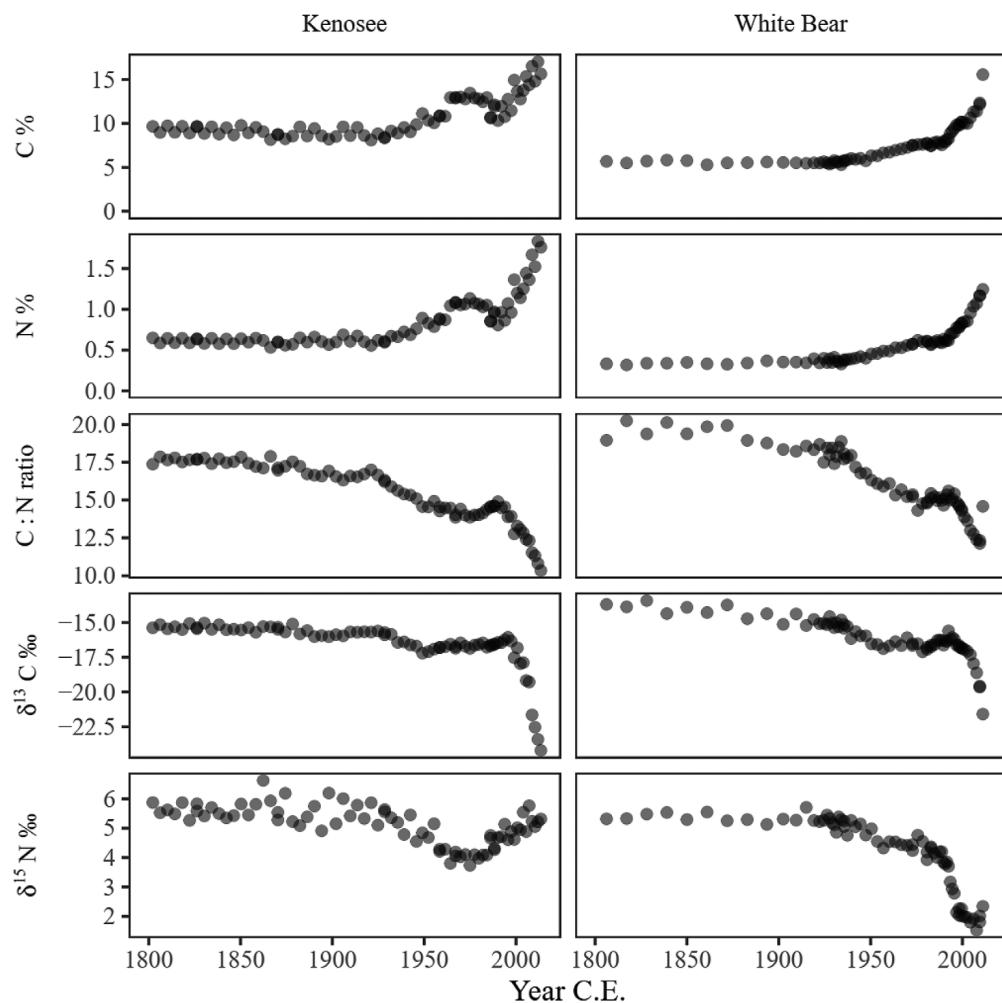


Fig. 4. Carbon (C%) and nitrogen (N%) content, C : N ratios, and stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\textperthousand) plotted by year for Kenosee Lake and White Bear Lake.

past ~200 yr of Kenosee and White Bear lakes (Fig. 5). In these analyses, significant changes refer to periods of time when the slope (i.e., the first derivative) of pigment concentrations and variances are statistically significant from 0 (see the Methods section). In Kenosee Lake, concentrations of pigments indicative of siliceous algae (fucoxanthin), diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*), and other bloom-forming taxa (lutein-zeaxanthin) were generally low, but did show periods of significant increase prior to ~1900. Abundances of chlorophytes (pheophytin *b*) increased significantly after ~1900, with the largest changes occurring after ~1930, concomitant with lake-level fall, whereas densities of diatoms (diatoxanthin),

cryptophytes (alloxanthin), and bloom-forming taxa (lutein-zeaxanthin) increased significantly across the 20th century with periods of minor declines centered at ~1975 and additional decreases in lake level (Figs. 2, 5). Trends in these phytoplankton were similar in White Bear Lake sediments, with the exception of a slightly delayed onset of significant increases at ~1930 (Fig. 5). In that lake, diatoxanthin exhibited distinctly high concentrations prior to 1900, but declined throughout the 20th century with statistically significant intervals of decline at ~1930 and ~1970 (Fig. 5).

In Kenosee Lake, concentrations of pigments from cyanobacteria (echinenone and canthaxanthin) were relatively elevated at ~1800 and rose significantly to ~1850 before

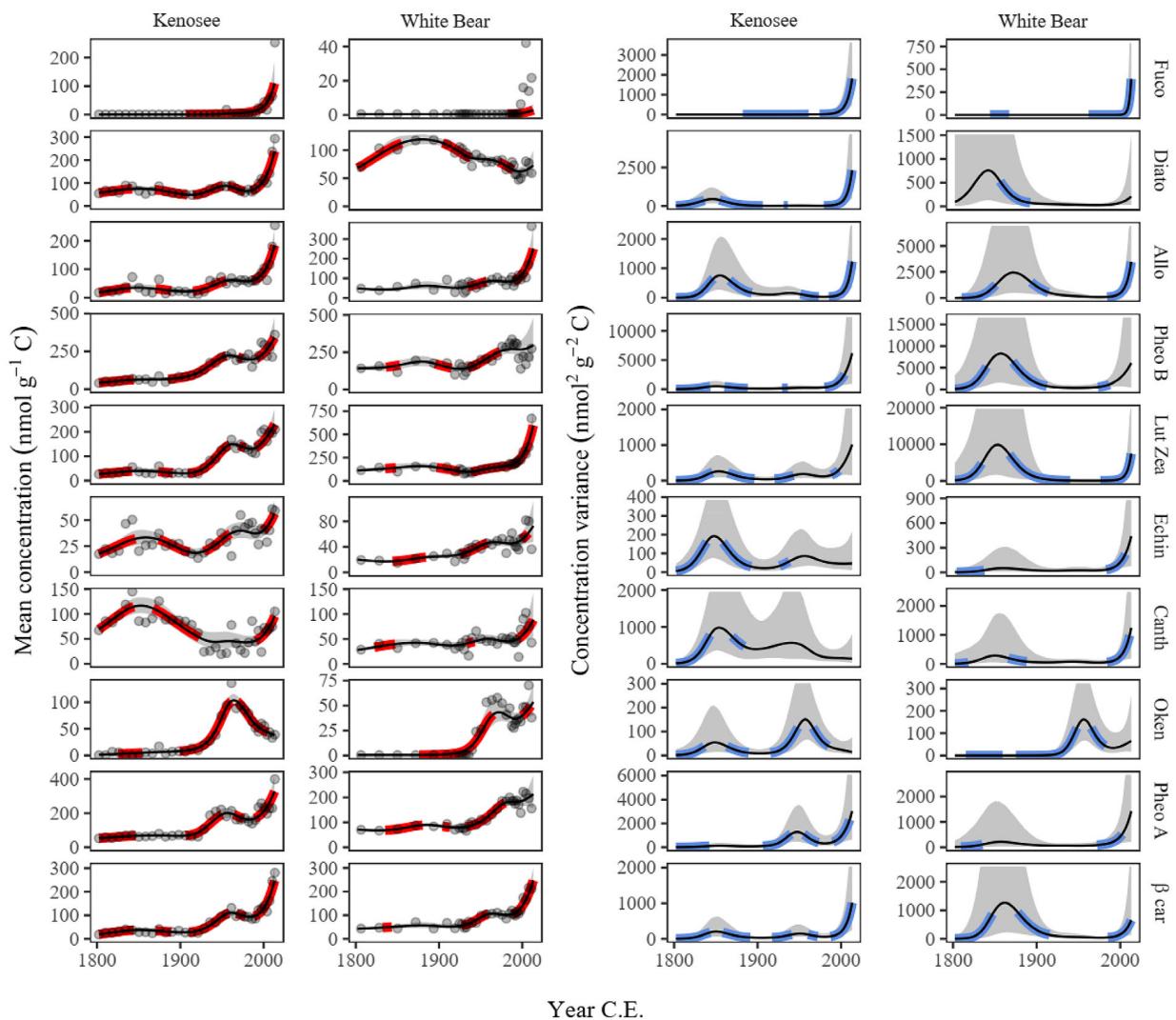


Fig. 5. Mean concentrations (left) and concentration variances (right) of fossil pigments by year in sediments from Kenosee Lake and White Bear Lake. Pigment mean concentrations and concentration variances are fitted with hierarchical generalized additive models (HGAMs). In all plots, solid lines are the fitted model trends, gray shading represents 95% confidence intervals of the trends, and emboldened sections of the trends represent significant changes in pigment mean concentration or concentration variance. Fuco = fucoxanthin (siliceous algae), Diato = diatoxanthin (primarily diatoms), Allo = alloxanthin (cryptophytes), Pheo B = pheophytin *b* (chlorophytes), Lut Zea = lutein-zeaxanthin (chlorophytes and cyanobacteria pigments, i.e., “bloom-forming” taxa), Echin = echinenone (total cyanobacteria), Canth = canthaxanthin (*Nostocales* cyanobacteria), Oken = okenone (purple sulfur bacteria), Pheo A = pheophytin *a* (total production), β car = β -carotene (total production).

declining significantly to 1900 (Fig. 5). Abundance of total cyanobacteria (echinenone) then rose significantly from ~ 1930 to 1950 alongside falls in lake level (Figs. 2, 5). In contrast, potentially N₂-fixing colonial cyanobacteria (canthaxanthin) declined throughout the early 20th century, reaching stable and relatively low concentrations between ~ 1930 and 2000 before rising significantly after ~ 2000 (Fig. 5). Concentrations of both pigments were low in White Bear Lake prior to 1900, despite periods of significant increases during this time, and slowly rose over the 20th century, with significant increases in echinenone at ~ 1930–1950 alongside declines in lake level (Figs. 2, 5). In both lakes, concentrations of okenone from obligately anaerobic purple sulfur bacteria were negligible prior to ~ 1900, but increased substantially during the early 20th century and reached maxima at ~ 1950, a period of stable water levels at both sites (Figs. 2, 5). Thereafter, concentrations of okenone declined significantly in Kenosee lake during periods of lake-level increase (~ 1950–1970) and subsequent decline (~ 1970–2010) (Figs. 2, 5). These declines in okenone concentration did not reach pre-1900 minimum values. In White Bear Lake, concentrations of okenone

plateaued during ~ 1950–2000 despite substantial lake-level changes, before rising significantly thereafter (Figs. 2, 5). In addition, overall biomarkers of total phototroph production (pheophytin *a*, β-carotene) were relatively stable before ~ 1900, but increased significantly between ~ 1900 and 1950 in Kenosee Lake and between ~ 1930 and 1970 in White Bear Lake (Fig. 5). Maximum values of these pigments occurred in both lakes after ~ 2000, coeval with recent increases in lake levels (Figs. 2, 5).

Temporal trends in variance of primary producers were similar in Kenosee and White Bear lakes sediments (Fig. 5). At both sites, variance of diatoms (diatoxanthin), cryptophytes (alloxanthin), and green algae (pheophytin *b*, lutein) was elevated during the mid-19th century, centered at ~ 1840–1860, before declining significantly to low values by 1900 (Fig. 5). Variance measures of these phytoplankton remained low through the period of lake-level variation during the 20th century before increasing significantly after ~ 2000 (Figs. 2, 5). In Kenosee Lake, variance in cyanobacterial abundance (echinenone, canthaxanthin) increased significantly prior to ~ 1850 then significantly declined to low values by 1900

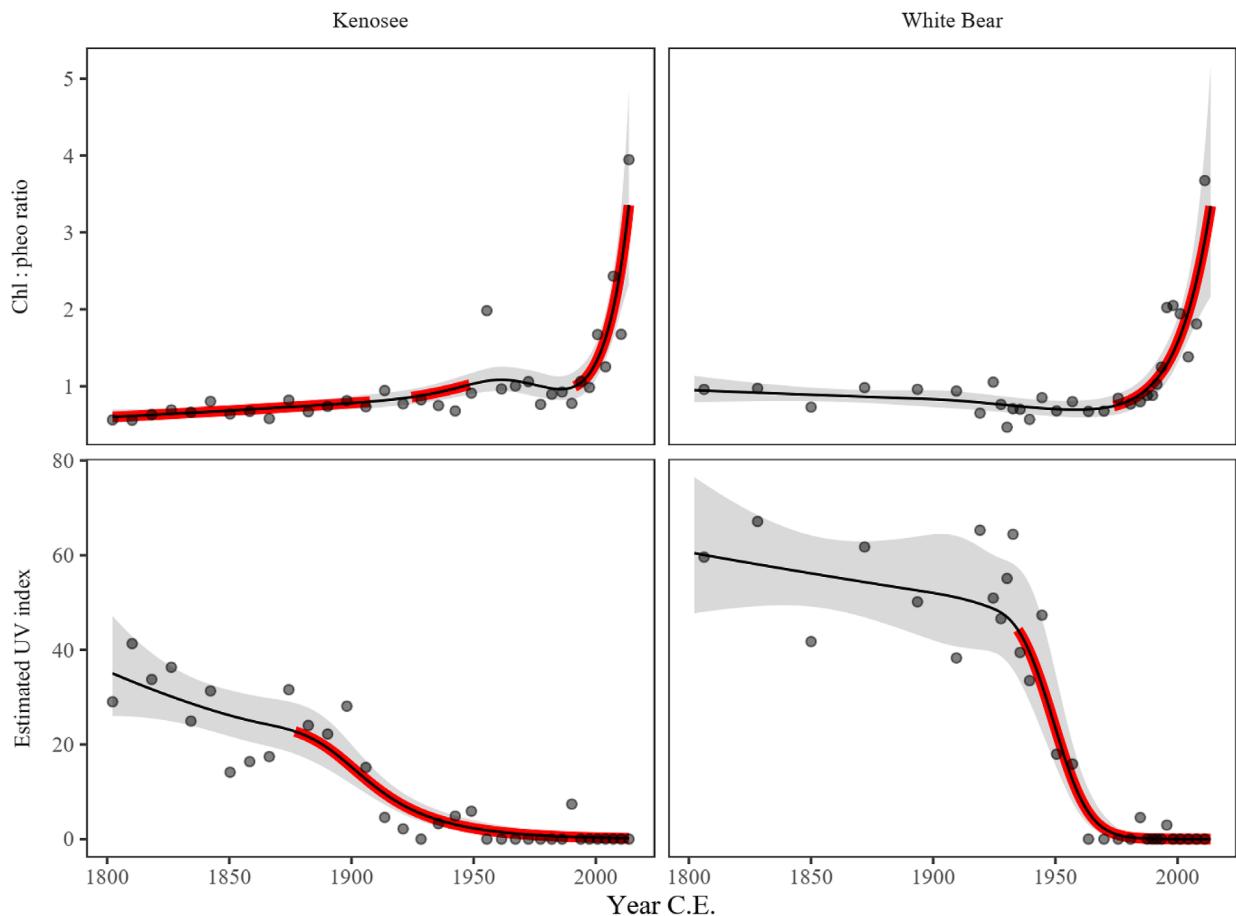


Fig. 6. Precursory Chl *a* to derivative pheophytin *a* (Chl : pheo) ratios and estimated UV index values plotted by year for Kenosee Lake and White Bear Lake. In all plots, solid lines are the fitted model trends, gray shading represents 95% trend confidence intervals, and emboldened sections represent periods of significant change.

(Fig. 5). In White Bear Lake, 19th century changes in variance of these pigments were much less marked, although still significant increases in cyanobacterial variance were recorded up to ~1850 (Fig. 5). Similarly, variance in purple sulfur bacteria (okenone) differed between lakes before ~1900, with slightly elevated values in Kenosee in the mid-19th century, but consistently low variance in White Bear Lake during the same interval (Fig. 5). Changes in okenone variance were more coherent between lakes after ~1900, rising significantly between ~1930 and ~1950 during the period of lake-level decline (Figs. 2, 5). These peaks in okenone variance were short-lived and declined significantly to ~1975, a period of substantial lake-level variation. In contrast to other pigments, variation in okenone time series did not rise again during late 20th century periods of lake-level decline, nor did it increase significantly when lakes refilled after ~2010 (Figs. 2, 5). Finally, there were few common patterns of historical change in variation of total primary producers (pheophytin *a*, β-carotene), with a higher amount of significant variance changes across the 20th century in Kenosee Lake and more significant changes during the 19th century at White Bear Lake (Fig. 5). In both basins, variance of these pigments rose significantly after ~2000 (Figs. 2, 5).

Analysis of changes in preservation environment (as Chl : pheo ratios) suggested that there was little variation in sedimentary pigment preservation in either lake until the most recently deposited sediments (Fig. 6). Although changes in Chl : pheo ratios were significant in Kenosee Lake for the first 150 yr of the record, these changes were minor relative to those seen after ~2000. Reconstruction of the UVR index suggested that phytoplankton were exposed to relatively high levels of UV radiation during the 19th century, but that exposure declined significantly through the 20th century, culminating in minimum values in the recent sediments of both lakes (Fig. 6).

Discussion

Kenosee and White Bear lakes have experienced lake-level variability of >8 m during the last century (Fig. 2), likely reflecting rising regional temperatures, increased evaporation, and complex interactions between Arctic, Gulf, and Pacific air masses which affect regional snowpack, spring runoff, and groundwater availability (Bonsal et al. 2006; Pomeroy et al. 2007; Liu et al. 2008; van der Kamp et al. 2008; McCullough et al. 2012). Lake-level decline was marked by coeval increases in primary production beginning ca. 1930, including elevated abundance of total phytoplankton, diatoms, cryptophytes, and chlorophytes (Fig. 5), concomitant increases in sedimentary C and N content (Fig. 4) and bulk sedimentation rates (Fig. 3). However, despite increasing temperatures and loss of over 50% of lake depth, neither total nor colonial diazotrophic cyanobacteria increased substantially during the 20th century relative to prior levels (Fig. 5). Instead,

fossil concentrations of okenone from anaerobic purple sulfur bacteria increased in both lakes during ~1930–1950 (Fig. 5), showing that light penetrated to anoxic habitats during this interval (Pfennig 1978; Leavitt et al. 1989). While variance in total primary production did not increase substantially prior to the development of illuminated anoxic habitats during intervals of stable and low lake level, temporally coherent and significant increases in okenone variance occurred during lake-level declines between ~1930 and 1950 suggesting that the development of illuminated and anoxic habitats in both Kenosee and White Bear lakes may represent a regime shift with respect to bacteria and physical lake structure (Scheffer et al. 2001; Dakos et al. 2015). These patterns are consistent with the establishment of bacterial plates within transient chemoclines following lake-level decline and evaporative concentrations of solutes in deep waters (Leavitt et al. 1989; Vinebrooke et al. 1998; Pham et al. 2009). This novel physical lake structure does not appear to represent an alternate stable state, as subsequent and substantial changes in lake-level restricted the anoxic and illuminated environments and suggests that any possible regime shift was transient and lacked hysteresis (Dakos et al. 2015; Ratajczak et al. 2018). Regardless, these abrupt changes in lake level, mixing, oxygenation, light penetration, and biotic structure may become more common in the Northern Great Plains, where future climate change is expected to increase evaporative forcing by 2050 due to a ~5°C warming and only a modest (<5%) increase in precipitation (Asong et al. 2016; Sauchyn et al. 2020).

Climate forcing of upland lakes

Lake levels at Kenosee Lake and White Bear Lake declined >8 m since 1910 (Fig. 2). While extraordinary relative to many boreal lakes, such large excursions are common in the Northern Great Plains (Fritz 1990; van der Kamp et al. 2008) due to water deficits (precipitation-evaporation) ranging -20 to -60 cm yr⁻¹ (Pham et al. 2009; Haig et al. 2020, 2021), and pronounced shifts in the relative importance of winter air masses that control the hydrodynamics of snow accumulation and melting (Bonsal et al. 2006; Pomeroy et al. 2007; Liu et al. 2008). In the Canadian Prairie region, >70% of annual precipitation falls as summer rain, but up to 80% of regional runoff is derived from spring snow melt (Akinremi et al. 1999). This snowmelt recharges surface and intermediary-depth aquifers (van der Kamp and Maathuis 1991) that can also contribute water to some prairie and parkland lakes (Shaw and Prepas 1990). In general, regional precipitation is regulated by a complex interplay between air masses from the Arctic, Pacific Ocean, and Gulf of Mexico (Bryson and Hare 1974) that is additionally influenced by the El Niño-Southern Oscillation, North Atlantic Oscillation, and Pacific Decadal Oscillation climate systems (Trenberth and Hurrell 1994; Hurrell 1995; Mantua et al. 1997). Paleoclimate and modeling analyses reveal that centennial- and continental-scale variation in these air masses

affect the position of the winter jetstream and, in turn, the precipitation supply which creates decadal-scale changes in runoff, lake level, and salinity (Fritz 1990; Michels et al. 2007; Liu et al. 2008; McCullough et al. 2012). Relationships between runoff and lake level are further complicated by the presence of numerous shallow water bodies within lake catchments (Fig. 1) that variously “fill and spill” depending on antecedent meteorological conditions (Coles and McDonnell 2018; Haig et al. 2021). Finally, land-use practices can alter lake levels by channelizing surface flow, removing wetlands, extracting for human use, modifying forests, or through agricultural irrigation (Fang et al. 2007; Mao and Cherkauer 2008).

Patterns of hydrology in White Bear and Kenosee lakes (Fig. 2) are consistent with known variability in regional climate and land-management practices (Vance et al. 1997; Vinebrooke et al. 1998). For example, stable elevated lake levels were recorded in White Bear Lake until onset of the prolonged prairie droughts of the 1920s and 1930s when blocking high pressure cells reduced the influx of moisture from the Gulf of Mexico (Bonsal et al. 2006). Lake levels recovered briefly during the 1950s before declining again to a plateau until the early 1970s. These events correspond to rapid changes between arid and pluvial conditions during the 1950s and 1960s (Henderson et al. 2002). After ~1970, lake levels declined continuously until the early 21st century, reflecting a both 0.95 cm yr⁻¹ decline in prairie winter precipitation during this interval (Akinremi et al. 1999; Henderson et al. 2002) and local water management practices which included water extraction for nearby golf courses and the construction of a highway that restricted flow between adjacent waterways, including Kenosee and White Bear lakes (Godwin et al. 2013). Finally, sudden recent increases in lake level of 2–4 m may reflect changes in the supply of moisture into the region, similar to the step-change increase in precipitation and runoff in nearby Manitoba during the 1990s (McCullough et al. 2012; Dumanski et al. 2015). In this case, delays in lake-level response (Fig. 2) may arise because antecedent arid conditions created substantial hydrological sinks in both lakes’ catchments by lowering water levels in many small water bodies (Fig. 1). The presence of empty hydrological sinks decoupled precipitation and runoff until the sinks were filled and regained a steady state (“fill and spill”) exchange of influx and outflow of water (Coles and McDonnell 2018; Haig et al. 2021), although further local research is needed to validate this mechanism.

Phototroph response to lake-level declines

Analysis of chemically stable algal and cyanobacterial pigments revealed similar increases in primary production in Kenosee and White Bear lakes during the 20th century (Fig. 5). Specifically, when analyzed using GAMs, mean concentrations of biomarkers for diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*, lutein), total

cyanobacteria (echinenone), and all primary producers (pheophytin *a*, β-carotene) increased significantly from ~1930 until the 21st century, although onset of eutrophication was delayed in White Bear Lake, compared to signals from Kenosee Lake (Fig. 5). Elevated lake production is consistent with trends seen in lowland lakes throughout the Canadian Prairies and normally reflect substantial changes in land use and nutrient influx (Leavitt et al. 2006; Pham et al. 2008; Maheaux et al. 2016). In contrast, catchments of upland Kenosee and White Bear lakes have not been subject to extensive modification, beyond shoreline development, suggesting that more extensive algal growth arose because of marked lake-level declines after ~1930 and ~1975 (Fig. 2). Although speculative, we note that shallow lakes are usually more productive than deeper basins of given size (Jeppesen et al. 2014) due to a higher fraction of profundal sediments in contact with warm surface waters and consequently elevated rates of internal nutrient loading (Søndergaard et al. 2013). Furthermore, phytoplankton production in prairie lakes can increase when evaporation concentrates epilimnetic nutrients and other solutes (Oduor and Schagerl 2007; Wissel et al. 2011; Vogt et al. 2018).

Historical variation in geochemical and isotopic sediment features were generally comparable in Kenosee and White Bear lakes and were consistent with pigment inferences of increased lake production after ~1930 (Figs. 3, 4). Specifically, variation in C and N content were inversely correlated with White Bear Lake water levels ($R^2_{adj} = 0.76, 0.89$), whereas C : N mass ratios varied with lake level until the ~2010 minimum. Similarly, bulk sedimentation in White Bear Lake, and to a lesser extent Kenosee Lake, exhibited marked acceleration during intervals of declining lake level in the 20th century, with more modest rates of accumulation between ~1940 and 1970 when lake levels were generally stable beyond a transitory 2 m change during the 1950s (Fig. 3). Together, these patterns are consistent with increased deposition of organic matter resulting from elevated autochthonous primary production (Meyers and Teranes 2001), as recorded by coeval declines in C : N ratios from values characteristic of terrestrial plants (C : N ~ 20–25) to those associated with autochthonous organic matter (C : N ~ 8–12; Gu et al. 2006; Woodward et al. 2012). Depleted $\delta^{13}\text{C}$ values in both lakes are also consistent with elevated in situ primary production during the 20th century, reflecting increased photosynthetic uptake of isotopically depleted CO₂ from respiration in situ sources (Meyers and Teranes 2001; Woodward et al. 2012) as seen in other eutrophied prairie lakes (Bunting et al. 2016).

Unlike most biogeochemical proxies, late 20th century measures of nitrogen cycling (as $\delta^{15}\text{N}$) differed between Kenosee and White Bear lakes, with sedimentary enrichment at the former site and depletion at the latter (Fig. 4). In general, historical patterns of $\delta^{15}\text{N}$ were correlated strongly with concentrations of okenone from purple sulfur bacteria ($R^2_{adj} = 0.79, p < 0.0001$), taxa known to fix nitrogen in

illuminated anaerobic habitats (Madigan 1995). We infer that cyanobacteria did not contribute substantially to fixed N pools (c.f., Hayes et al. 2019), as concentrations of canthaxanthin from potentially diazotrophic cyanobacteria (Leavitt and Hodgson 2001; Hayes et al. 2019) were uncorrelated to historical variation in $\delta^{15}\text{N}$ values (Figs. 3, 5). Thus, while it is possible that enhanced shoreline development since the 1960s (e.g., cottages and golf courses) may have added isotopically enriched N from fertilizers or wastes (Botrel et al. 2014), the absence of common patterns in $\delta^{15}\text{N}$ of the lakes since the 1960s is more consistent with differential supply of fixed N from diazotrophic purple sulfur bacteria.

Historical variation in *Nostocales* cyanobacteria (canthaxanthin) did not show a close correspondence to either observed changes in lake levels (Fig. 2) or other sediment proxies of lake production (Figs. 3–5), despite cyanobacterial preference for warm, nutrient-rich, shallow conditions (Paerl and Paul 2012; Vogt et al. 2018), their presence in the current phytoplankton (Bos et al. 2019), and fossil concentrations which were similar those in other regional eutrophic lakes (Leavitt et al. 2006; Bunting et al. 2016; Maheaux et al. 2016). For example, *Nostocales* were most abundant in Kenosee Lake during the 19th century and declined to stable low values until the 2000s, whereas this group varied little over the past 200 yr in White Bear Lake until recent years (Fig. 5). While we currently lack a definitive mechanistic explanation for either the 19th century maximum in Kenosee Lake, or the marked difference with nearby White Bear Lake, anecdotally low water levels during the late 19th century (Henderson et al. 2002) may have favored anthropogenic eutrophication either from initial settler recreational activities, or cultural use of the lakes by regional First Nations. Although further research is required to resolve the reasons for elevated cyanobacteria during the 19th century, the absence of marked increases in *Nostocales* during the 20th century contrasts sharply with other lakes that similarly underwent pronounced eutrophication and/or regime shifts (Scheffer et al. 2001; Carpenter and Brock 2006; Bunting et al. 2016).

Preferential increases in eukaryotic phytoplankton (diatoms, cryptophytes, and chlorophytes) over cyanobacteria during the past 200 yr appears to have reduced the mean exposure of phototrophs to UV radiation (Fig. 6). In general, changes in UVR exposure were unrelated to observed lake levels. Significant declines in UVR indices occurred earlier (late 1800s) in Kenosee Lake than in White Bear Lake (~ 1930), similar to timing of significant increases in biomarkers from eukaryotic phytoplankton and declines in lake level (Figs. 2, 5, 6). We infer that reduced UVR exposure arose from progressive, but slightly asynchronous, eutrophication of both lakes, as declines in lake level should have increased mean UVR exposure. Similar declines in UVR exposure are recorded elsewhere in lakes undergoing cultural eutrophication (Stevenson et al. 2016).

Concentrations of most fossil pigments increased significantly after ~ 2000 in both Kenosee and White Bear lakes

(Fig. 5), concomitant with 2–4 m increases in lake level (Fig. 2). In part, these changes reflect post-depositional pigment transformation, as indicated by rapid changes in Chl : pheo ratios in sediments deposited since ~ 2000 (Fig. 6). Such first-order decay is observed in sediments of other prairie lakes (Patoine and Leavitt 2006), but is usually restricted to labile pigments with oxygen- or N-rich functional groups (e.g., Chl *a*, fucoxanthin, and peridinin) rather than less-substituted hydrocarbons (e.g., β -carotene, alloxanthin, diatoxanthin, lutein-zeaxanthin, etc.; Cuddington and Leavitt 1999; Leavitt and Hodgson 2001). Given that chemically stable pigments also increased markedly toward the surface of the core, we infer that both Kenosee and White Bear lakes may be undergoing modern eutrophication, possibly reflecting increased nutrient transfer from the landscape due to increased runoff and subsequent lake-level rise (McCullough et al. 2012; Tanzeeba and Gan 2012; Asong et al. 2016). Furthermore, elevated concentrations of stable phototrophic biomarkers (e.g., ubiquitous β -carotene) in recent sediments from both study lakes are also consistent with documented water quality problems in both Kenosee and White Bear Lakes since 2000, including the formation of algal blooms (Godwin et al. 2013; Bos et al. 2019).

Evidence of possible regime shifts in upland lakes

Declines in regional lake level between ~ 1930 and ~ 1950 resulted in the formation of illuminated, anoxic, deep-water habitats that were ideal for the proliferation of obligately anaerobic purple sulfur bacteria (Pfennig 1978) in both Kenosee and White Bear lakes (Fig. 5). The development of such bacterial populations between ~ 1930 and 1950 prerequisites either the illumination of anoxic lake sediments (Jørgensen and Postgate 1982; Maheaux et al. 2016) or the formation of strong seasonal or semi-permanent chemoclines resulting from concentrating solutes associated with climate-mediated lake-level decline (Züllig and Rheineck 1985; Leavitt et al. 1989). We infer that permanent meromictic conditions were not established in either Kenosee Lake or White Bear Lake as there were few concomitant changes in the preservation of labile pigments as okenone concentrations increased (Fig. 6), total okenone concentrations were much lower than those seen in fully meromictic systems (Züllig and Rheineck 1985; Leavitt et al. 1989; Vinebrooke et al. 1998), and peak concentrations of okenone in Kenosee Lake were twofold greater than those in White Bear Lake (Fig. 5), as would be expected given the greater illumination of sediments in the shallower lake following lake-level declines (Table 1; Fig. 6). Alternatively, the observation that both lakes are currently hypersaline (Table 1), despite recent increases in lake level (Fig. 2), suggests that salt concentrations were substantially higher during the lake-level low-stands of the 20th century. As shown in other regional lakes, declines in lake level due to evaporative forcing and reduced runoff are associated with higher deep-water salt concentrations that favor establishment

of meromictic conditions in even shallow prairie lakes (Garcés et al. 1995; van der Kamp et al. 2008; Pham et al. 2009).

Alongside increases in pigment concentrations, variance of okenone time series also rose significantly, beginning at ~1930 and reaching maximum values at ~1950 (Fig. 5). Rising variance has been considered as a predictor of a regime shift in some lake systems undergoing eutrophication (Carpenter and Brock 2006; Bunting et al. 2016), although some work suggests that regime shifts can occur without preceding increases in variance, or that rising variance does not always result in a regime shift (Burthe et al. 2016; Ratajczak et al. 2018). As well, it has been noted that rising variance can also be indicative of changes in the variability of environmental forcing agents (e.g., climate, nutrient flux, etc.), independent of the occurrence of regime shifts (Dakos et al. 2015; Burthe et al. 2016). In our case, as pigment variances were calculated from pigment mean concentrations, an increase or decrease in the latter will result in the change in the former, making it difficult to assess the validity of any possible regime changes. Furthermore, differences in temporal averaging of core sediments (yr cm^{-1}) due to physical compression of deposits also makes it difficult to evaluate whether rising variance is truly antecedent to the peak okenone concentrations, despite our attempts to weight samples by temporal resolution in HGAM analyses (see the Methods section). Taken together, these observations suggest that further research is needed to determine how sedimentary records may be used to record changes in variance as a means of distinguishing between abrupt ecosystem changes, regime shifts, or true alternative stable states (Taranu et al. 2018). Regardless, we note that the marked rise in okenone is an unambiguous marker for the establishment of a novel, illuminated, anoxic environment, and that the coeval rise in variance of okenone ca. 1930–1950, but not algal or cyanobacterial pigments, is consistent with potential establishment of an abrupt change in the deep-water environment (Fig. 5). Further research is needed to evaluate these possibilities, including analysis of variance in potential forcing functions, addition of limnological proxies to complement paleolimnological knowledge, and other factors influencing variance (c.f., Bunting et al. 2016).

Periods of illuminated deep-water anoxic habitats appear to have been ephemeral or unstable in both Kenosee and White Bear lakes (Fig. 5). Therefore, in these cases, rising variance does not appear to signal lake transition to an alternate stable state nor represent the establishment of internal feedback mechanisms that favor hysteresis between states (Scheffer et al. 2001; Dakos et al. 2015; Ratajczak et al. 2018). Instead, the >8-m rise and fall of lake levels appears to have resulted in a series of novel phototroph communities whose composition reflected extant hydroclimate and lake-level conditions (McCullough et al. 2012; Asong et al. 2016), physical processes such as mixing and light penetration (Garcés et al. 1995; Hodgson et al. 1998), and landscape influences on nutrient supply (Taranu et al. 2015; Bunting et al. 2016). As well,

despite evidence of warming temperatures and increased nutrient concentrations during the 20th century, there was little evidence of increased cyanobacterial populations until after the large concentrations of okenone had abated in the latter half of the century (Fig. 5). These findings are in stark contrast to many studies that highlight increased cyanobacterial production under warm and nutrient-rich conditions such as those present at Kenosee and White Bear lakes (Paerl and Paul 2012; Vogt et al. 2018). We speculate that intervals of reduced mixing, anoxia, or even weak meromixis may have favored internal nutrient supply from sediments that sustained cyanobacteria through the last half of the 20th century (Fig. 5). However, we also note that continued lake-level declines may have eventually restricted anoxic, illuminated habitats and sulfur bacterial growth after 1950, possibly due to the influence of high regional winds (Plancq et al. 2018). This hypothesis is consistent with the more pronounced declines in okenone in shallower Kenosee Lake compared to deeper White Bear Lake (Fig. 5).

Conclusions

Kenosee and White Bear lakes have experienced >8 m declines in lake level over the last century due to increased temperature and evaporation rates, combined with variations in climate systems that regulate introduction of moist oceanic air and precipitation (Akinremi et al. 1999; Bonsal et al. 2006; Michels et al. 2007; Pham et al. 2009). Quantification of historical changes in sedimentary stable isotopes, geochemistry, and biomarker pigments suggests that both lakes began to eutrophy during the early 20th century, coeval with documented declines in lake levels (Fig. 2). By the mid-20th century, declines in lake levels and increased solute concentrations allowed the development of illuminated anoxic habitats that allowed expansion of obligately anaerobic purple sulfur bacteria (Züllig and Rheineck 1985; Leavitt et al. 1989). However, despite evidence of eutrophication in biomarkers from eukaryotic phytoplankton, Kenosee and White Bear lakes did not exhibit substantial increases in colonial cyanobacteria, nor the significant increases in temporal variation of primary producers typical of lakes undergoing nutrient-driven regime shifts (Taranu et al. 2015, 2018; Bunting et al. 2016). Instead, the establishment of anoxic habitats for photosynthetic sulfur bacteria was recorded by rising variance only in their biomarker okenone, and suggests that only deep-water habitat and taxa, rather than the entire ecosystem, underwent a transition to a novel structure. Overall, it appears that rising variance of okenone did not constitute either an alternate state change or true regime shift (sensu Burthe et al. 2016; Ratajczak et al. 2018), but instead illustrates that climate-induced changes in lake-level can result in abrupt variation in lake structure that reconfigures deep-water habitats and biological communities (Fig. 5). Given that GCMs predict that the northern Great Plains region will rapidly become more arid in

coming century (Tanzeeba and Gan 2012; Asong et al. 2016; Sauchyn et al. 2020), we anticipate the development of similar deep-water and biotic assemblages in other regional lakes.

Data Availability Statement

Data from this study is open and available on github at <https://github.com/simpson-lab/kenosee-white-bear>.

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Acknowledgments

The authors thank Kyle Hodder for GIS analysis using Arc 10.4.1 and ArcGISPro-2.0.1, Bjoern Wissel for stable isotope and geochemical analyses, and Zoraida Quinones-Rivera for assistance with HPLC analysis. We also thank Tiffany Blampied, Jessica Bos, and Corey McCowan for assistance with field sampling. Funding for this project was provided through NSERC Discovery grants to G.L.S., P.R.L., and K.F., the Saskatchewan Ministry of Parks, Culture, and Sport to K.F., the Canada Foundation for Innovation, the Canada Research Chair program, the Province of Saskatchewan, and University of Regina. We also thank two anonymous reviewers for their helpful comments that greatly improved the quality of this manuscript. Data in this study were obtained from samples collected

from part of Canada's Treaty 4, the traditional territories of Nêhiyawak, Anihšināpēk, Dakota, Lakota, and Nakoda First Nations, and the home-land of the Métis Nation.

Conflict of Interest

None declared.

Submitted 17 August 2021

Revised 02 February 2022

Accepted 20 February 2022

Associate editor: Grace M Wilkinson

RESEARCH

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Movement ecology of vulnerable lowland tapirs between areas of varying human disturbance

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Abstract

Background: Animal movement is a key ecological process that is tightly coupled to local environmental conditions. While agriculture, urbanisation, and transportation infrastructure are critical to human socio-economic improvement, these have spurred substantial changes in animal movement across the globe with potential impacts on fitness and survival. Notably, however, human disturbance can have differential effects across species, and responses to human activities are thus largely taxa and context specific. As human disturbance is only expected to worsen over the next decade it is critical to better understand how species respond to human disturbance in order to develop effective, case-specific conservation strategies.

Methods: Here, we use an extensive telemetry dataset collected over 22 years to fill a critical knowledge gap in the movement ecology of lowland tapirs (*Tapirus terrestris*) across areas of varying human disturbance within three biomes in southern Brazil: the Pantanal, Cerrado, and Atlantic Forest.

Results: From these data we found that the mean home range size across all monitored tapirs was 8.31 km² (95% CI 6.53–10.42), with no evidence that home range sizes differed between sexes nor age groups. Interestingly, although the Atlantic Forest, Cerrado, and Pantanal vary substantially in habitat composition, levels of human disturbance, and tapir population densities, we found that lowland tapir movement behaviour and space use were consistent across all three biomes. Human disturbance also had no detectable effect on lowland tapir movement. Lowland tapirs living in the most altered habitats we monitored exhibited movement behaviour that was comparable to that of tapirs living in a near pristine environment.

Conclusions: Contrary to our expectations, although we observed individual variability in lowland tapir space use and movement, human impacts on the landscape also had no measurable effect on their movement. Lowland tapir movement behaviour thus appears to exhibit very little phenotypic plasticity in response to human disturbance. Crucially, the lack of any detectable response to anthropogenic disturbance suggests that human modified habitats risk being ecological traps for tapirs and this information should be factored into conservation actions and species management aimed towards protecting lowland tapir populations.

Keywords: Anthropocene, Continuous-time movement modelling, Home range, Human Footprint Index, Space use

Background

While agriculture, urbanisation, and transportation infrastructure are critical to human socio-economic improvement [17], the associated habitat transformations represent a major threat to species survival [18, 54, 76]. Of particular concern is the impact of human activities

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on animal movement and space use [3, 16, 71]. Animal movement governs how individuals, populations, and species interact with each other and the environment [29, 39, 63] and mediates key ecological processes [6]. The capacity for individuals to move unhindered across complex landscapes is therefore critical for species survival and ecosystem function. Problematically, human development has reduced the amount of habitat available to wildlife [8, 13, 32]. This has spurred substantial changes in animal movement behaviour across the globe [16, 19, 71], with potential consequences including reduced fitness and survival, altered predator–prey dynamics, reduced seed dispersal, genetic isolation and local extinction [14, 15, 19, 72].

Notably, human disturbance has been shown to have differential effects across species [16, 70], even for closely related taxa occupying the same habitat [68]. Responses to human activities are thus largely context specific [16] and cannot be expected to be consistent across taxa. For instance, while Wall et al. [78] found a tendency for African elephants (*Loxodonta spp.*) to exhibit reduced movement in human modified landscapes, Morato et al. [47] noted that jaguars (*Panthera onca*) living in regions with high human population densities in South America occupied home ranges that were orders of magnitude larger than those of jaguars living in more pristine habitats. As human disturbance is only expected to worsen over the next decade it is critical to better understand how species respond to human disturbance to develop effective, case-specific conservation strategies.

Here we focus on understanding how the movement behaviour of lowland tapirs (*Tapirus terrestris*) varies across areas of varying human disturbance within the Pantanal, Cerrado, and Atlantic Forest biomes in southern Brazil. Lowland tapirs are herbivores of the order Perissodactyla that can reach over 2.5 m in length and weigh up to 250 kg [40]. While lowland tapirs are distributed throughout South America [27], their populations have suffered severe reductions, with local and regional extirpations, and are currently classified as vulnerable to extinction [74]. Although the incorporation of information on animal movement is a key component in designing effective conservation and recovery strategies [3], currently, very little is known about the movement ecology of tapirs (but see [22, 52, 69]). This knowledge gap is especially pertinent given that large terrestrial mammals, such as tapirs, tend to have larger home ranges and greater absolute mobility than do small mammals [11, 51], making them more susceptible to anthropogenic impacts than smaller bodied species [31, 71]. Here, we use an extensive telemetry dataset collected over 22 years to describe the movement ecology of tapirs and study how changes in habitat composition and human

disturbance influence their movement and space use. First, animals living in highly productive environments do not need to range over wide areas to meet their energetic needs [35, 48, 57]. As such, we expected that tapirs should exhibit plasticity in their movement and space use in relation to local environmental conditions as well as biome type. Furthermore, because human activity tends to result in increased movement for large herbivores [16] our underlying hypothesis was that tapirs should exhibit greater movement distances and larger home-range areas when living in human-modified landscapes.

Methods

Study area and data collection

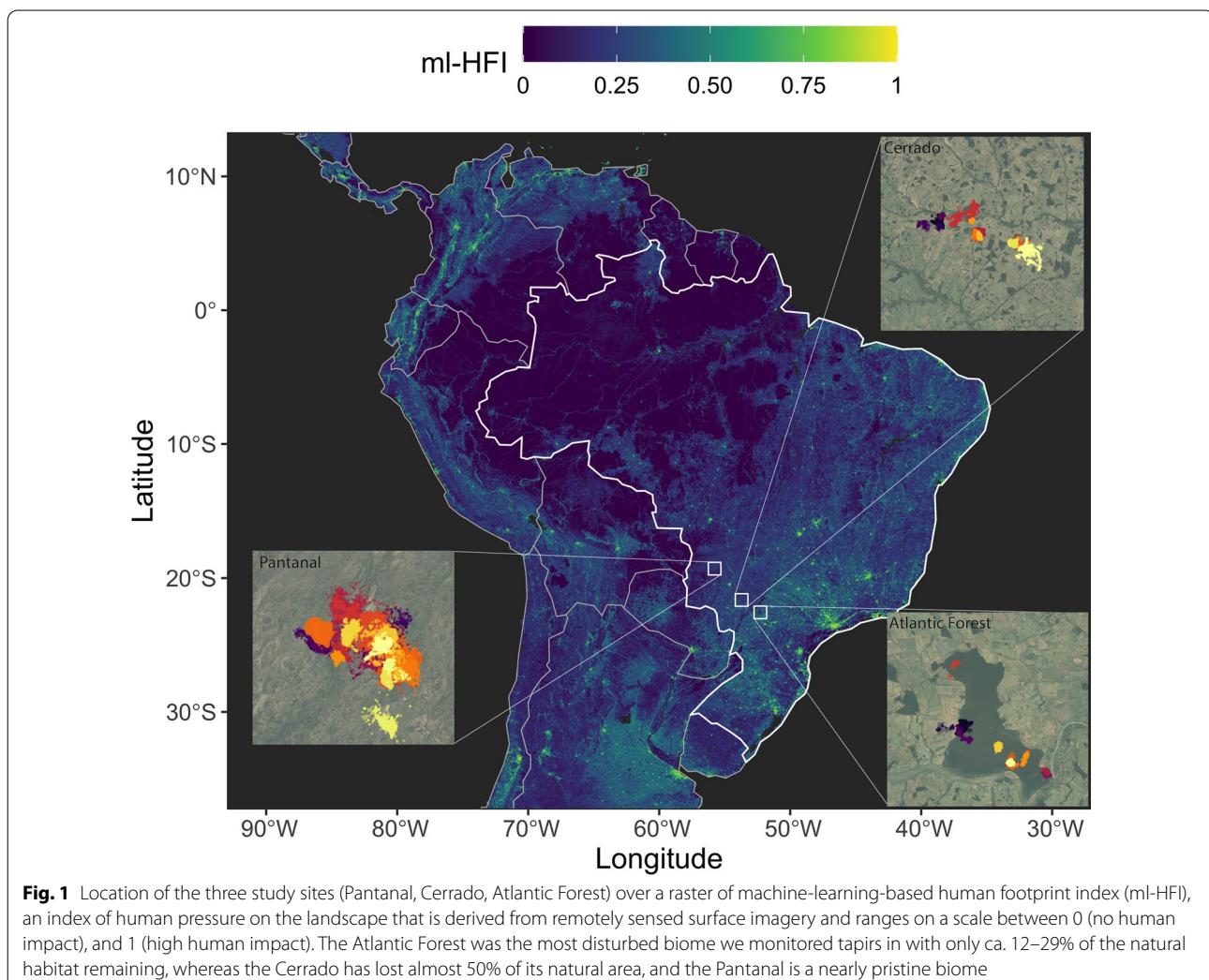
The data were collected in three different biomes in southern Brazil (Fig. 1): Atlantic Forest (1997–2007), Pantanal (2008–2019), and south-western Cerrado (2016–2018).

Atlantic forest

Morro do Diabo State Park is a protected area located in the Municipality of Teodoro Sampaio (22°32'S, 52°18'W), state of São Paulo, in the southeastern region of Brazil. The park has an area of 370 km² composed of a mosaic of mature and secondary deciduous forest, surrounded by the Paranapanema River in the south, and of a matrix of cattle ranches and agriculture, mostly sugar cane, in the remaining borders [73]. Its average annual temperature is 22 °C and annual rainfall is 1347 mm [28]. The park is part of the “Planalto Forest,” which is distinguished from the coastal forest of the Atlantic Forest biome by having lower annual rainfall and a marked dry season from May to September and is thus more similar to the Cerrado biome [61]. In fact, the semi-deciduous forests of the “Planalto Forest” are similar to those occurring within or on the edges of the Cerrado [61]. The Atlantic Forest was the most disturbed biome we monitored tapirs in, with only ca. 12–29% of the natural habitat remaining [37, 58, 59, 66].

Cerrado

The study site in the Cerrado biome is a 2200 km² mosaic of private properties (cattle ranches and farms) and landless people settlements within the Municipalities of Nova Alvorada do Sul and Nova Andradina, Mato Grosso do Sul State (21°37'S, 53°40'W). The area includes small fragments of natural Cerrado habitat (Cerradão fragments, gallery forests, and marshland—25% of the study area), surrounded by areas highly impacted by human activities such as agriculture (particularly sugarcane, soybean and corn), cattle-ranching (cultivated pastureland), eucalyptus plantations, rural communities, and highways. The average annual temperature is 25 °C and annual rainfall is



1185 mm. The Cerrado has lost almost 50% of its natural area due primarily to human driven land-use change to agriculture and cattle ranching [36, 45].

Pantanal

Baía das Pedras Ranch, a private property of 145 km², is located in the Nhecolândia Sub-Region of the Southern Pantanal, Municipality of Aquidauana (19°20'S, 55°43'W), Mato Grosso do Sul State, in the central-western region of Brazil. The ranch includes a mosaic of seasonally inundated grasslands, lakes, gallery forests, scrub, and deciduous forests that supports an abundance of wildlife and is situated far away from the edges of the biome where deforestation and other anthropogenic threats are occurring. Cattle are raised extensively on the native grasses. The average annual temperature is 25 °C and annual rainfall is 1185 mm [12]. The Pantanal is a nearly pristine biome with substantially less human disturbance than the Atlantic Forest and Cerrado.

In each study site, tapirs were captured by darting after physical restraint in either box traps or pitfall traps, or by darting from a distance [55]. Animals were anesthetized mostly using a combination of butorphanol, medetomidine and ketamine, as described by Medici et al. [41] and Fernandes-Santos et al. [20]. Reversal agents were administrated at the end of procedures. The procedures carried out during immobilization included the subcutaneous insertion of a microchip, morphometric measurements, sex and age class determination, physical examination, collection of biological samples for health and genetic studies, and placement of a telemetry collar on adults. Animals were tracked using VHF tracking (all three regions, Telonics® MOD500) and GPS tracking (Pantanal and Cerrado; Telonics® TGW SOB and GPS IRIDIUM models). A total of 74 tapirs were tracked starting in July of 1997 until October of 2019, with the majority of the individuals being

in the Pantanal (46), while 17 and 11 were from the Cerrado and Atlantic Forest regions, respectively.

Tapirs equipped with VHF collars were monitored for 5 days per month with data collection concentrated during crepuscular times, 3 h at dawn (04:00–07:00 h) and 3 h at dusk (17:00–20:00 h). These periods are the two main peaks of tapir activity [40]. Each tapir was located every 30 min during the sampling periods. GPS collars were programmed to obtain a fix every hour and operated for a median of 15.4 months across all tagged tapirs. GPS fix success rates were 75% in the Pantanal and 90% in the Cerrado. The full dataset comprised 232,622 location estimates collected over a period of 22 years (for full details see Additional file 1: File S1). In addition to the tapir location data, we collected 883 and 174 measurements from tags in fixed locations in the Pantanal and Cerrado, respectively in order to calibrate the measurement error of the GPS tracking collars.

Data analysis

Initial exploratory analyses were carried out in ctmmweb (version 0.2.11, [10]). All formal statistical analysis and plotting were performed using R (version 4.0.5, R Core Team 2021 [56]), with the packages ctmm (version 0.6.1, [9]), mgcv (version 1.8-36, [80]), ggplot2 (version 3.3.4, [79]), ggmap (version 3.0.0, [33]). The furrr package (version 0.2.2, [75]) was used for parallel computation on Windows machines. All R code can be found in the GitHub repository at <https://github.com/StefanoMezini/tapirs>. Details on the analyses are presented in Additional file 2: Appendix S2.

Data calibration and cleaning

Before analysis, we performed an error calibration and data cleaning process to minimise the impacts of GPS measurement error and outliers on our subsequent analyses [21]. Data cleaning and calibration were carried out using the methods implemented in the ctmm R package. For this process, measurement error for location estimates collected via VHF telemetry was assumed to be insubstantial relative to the coarsely sampled movement data (median step length: 260.7 m) and raw locations were carried forward in the analyses. Measurement error on the GPS data was calibrated using a unitless Horizontal Dilution of Precision (HDOP), which quantifies the accuracy of each positional fix. We then estimated an equivalent range error with the HDOP values from the tags in fixed locations. This allowed for the unitless HDOP values to be converted into estimates of measurement error in meters. Notably, we found no effect of sampling technique, and thus error handling protocols, on home range area estimates (see Additional file 1: Appendix S1). After calibration, data points were

considered as outliers (and removed) if they had a large (error-informed) distance from the median location and the minimum speed required to explain the displacement was unusually high ($\geq 1\text{m/s}$). The Atlantic Forest dataset contained a total of 4,082 observations, 8 (ca. 0.2%) of which were removed as outliers; the Pantanal dataset contained 139,138 observations, 914 (ca. 0.7%) of which were removed; while the Cerrado dataset contained 90,402 observations, 193 (ca. 0.2%) of which were removed.

Movement modelling and home range estimation

For each of the monitored tapirs we quantified a number of key movement metrics and home range-related characteristics that allowed us to test for an effect of habitat composition and human disturbance on tapir movement behaviour. For this we first identified the best Continuous-Time Movement Model (CTMM) for each animal using the ctmm.select function from the ctmm package. This fits a series of CTMMs to location data using perturbative Hybrid Residual Maximum Likelihood (pHREML, [22]) and chooses the best model using small-sample-sized corrected Akaike's Information Criterion (AICc). The models used here are insensitive to sampling frequency (Johnson et al. 2008; [7, 24]) and they account for spatio-temporal autocorrelation in the data (when necessary), so they are robust to irregular or frequent sampling frequency [23]. The parameter estimates from each individual's movement model provided information on the tapir's home range crossing time (τ_p , in days), and directional persistence timescale (τ_v , in hours).

We then conditioned on the selected CTMMs to estimate each animal's 95% home range (HR) area (in km^2) using small-sample-size bias corrected Autocorrelated Kernel Density Estimation (AKDE, [25, 49]), and average daily movement speed (in km/day) using continuous-time speed and distance (CTSD) estimation [50].

Movement pattern analyses

We were first interested in understanding whether home-range areas and movement metrics differed across the three biomes, as well as between animals of different age and sex. For these comparisons, home-range estimates were compared using the meta-analysis methods implemented in the ctmm package, which treats the individual home-range area estimates as having a chi-squared sampling distribution, and the population of home-range areas as having an inverse-Gaussian distribution [26]. This approach also allowed for uncertainty in the individual home-range estimates to be propagated to the population-level estimates. Home-range crossing time, directional persistence, and mean movement speed were analysed using generalized linear models (GLMs) with

a Gamma distribution and a log link function for the response. The GLMs were fit using the mgcv package [80] and Residual Maximum Likelihood (REML). Notably, because different tracking technologies were used to collect the tapir location data, we assessed whether tracking technique in-and-of-itself could have impacted the individual home range estimates. From these analyses found no effect of sampling technique on home range area (see Additional file 1: Appendix S1 for full details).

To test whether tapirs responded to different environment types, the HR sizes and average daily speeds were regressed against the proportions of the habitat types in each HR. For the Atlantic Forest, we used the habitat map provided in the park's management plan [28]. For the Pantanal and Cerrado, we obtained satellite imagery from the periods of data collection. Habitat classification was then carried out using GIS software, and a team of researchers confirmed the classifications in the field. The primary habitat types included: (1) forest, (2) savannah, (3) exposed soil, (4) floodplain, and (5) water. For full details on the habitat composition of the different study areas see Additional file 1: Figure S2 in Appendix S1. Similarly, the HR sizes and average daily speeds were regressed against their HR's average machine-learning-based human footprint index (ml-HFI) [34] to test whether human activity significantly altered the animals' behavior. Briefly, convolutional neural networks, are used to identify patterns of human activity from the Hansen Global Forest Change imagery version 1.7 (GFCv1.7, for full details see [34]). The resulting ml-HFI is an index of human pressure on the landscape that is derived from remotely sensed surface imagery and ranges on a scale between 0 (no human impact), and 1 (high human impact). For these models we applied Generalized Additive Models (GAMs) with a Gamma distribution and a log link function for the response. The Gamma distribution allows for more accurate significance testing and is an appropriate distribution for variables that range between 0 and ∞ , while the log link scale allows HFI to have a multiplicative effect on the response. The GAMs were fit using the mgcv package [80] and REML, and the best model was selected using AICc based model selection. All analyses were carried out at both the 95% and 50% quantiles. The findings were consistent between quantiles and only results at the 95% quantile are presented in the main text. Full results for the 50% core home ranges are presented in Additional file 2: Appendix S2.

Results

Individual variation in movement and space use

The mean home-range size across all monitored tapirs was 8.31 km^2 (95% CI: 6.53–10.42; Fig. 2), ranging between 1.0 km^2 and 29.7 km^2 (Fig. 3a). Tapirs had HR

crossing times of 0.72 days on average (95% CI 0.42–1.25), ranging from 0.05 to 12.8 days (Fig. 3b), and a mean velocity autocorrelation timescale of 0.44 h (95% CI 0.38–0.51), ranging from 0.17 to 1.88 h (Fig. 3c). We estimated that tapirs had mean movement speeds of 11.2 km/day (95% CI 10.1–12.3), ranging from 1.51 to 25.96 km/day (Fig. 3d). There was no evidence that average daily speed differed between sexes (females: 10.5 km/day, 95% CI 9.19–12.0; males: 11.9 km/day; 95% CI 10.3–13.7, $p = 0.22$, 4a), nor between age groups (adults: 11.8 km/day, 95% CI 10.6–13.2; sub-adults: 9.5 km/day, 95% CI 7.9–11.4; $p = 0.053$, Fig. 4b).

There was no evidence that home range sizes differed between sexes (males: 5.46 km^2 , 95% CI 4.03–7.23; females: 6.11 km^2 , 95% CI: 4.53–8.07 Fig. 4c), nor between age groups (adults: 5.37 km^2 , 95% CI: 4.39–11.64; sub-adults: 6.98 km^2 , 95% CI: 3.87–11.65; Fig. 4d). We estimated the male/female ratio of mean home-range areas to be 0.87 (0.56–1.30), and the adult/subadult ratio to be 0.70 (0.37–1.32), both of which include 1 and are thus non-significant.

Variation in movement across biomes and variation in human disturbance

The Atlantic Forest, Cerrado, and Pantanal vary substantially in habitat composition, levels of human disturbance, and tapir population densities. Despite these differences, we found that lowland tapir movement behaviour and space use were consistent across all three biomes (Fig. 3).

We also found that habitat type had little effect on HR area or average individual movement speeds. The best HR area regression model only accounted for the effect of areas of exposed soil (approximate p-value: 0.023, $R^2_{adj} = 0.48$; Fig. 5a), while no land use types had a significant effect on an animal's average speed. There was very little difference between the AIC of the full model (315.69, $df=10.18$, 7 predictors and an intercept) and that of the intercept-only model (310.89, $df=2$). However, the directional persistence term (τ_v) was marginally, though non-significantly lower for animals who had a higher amount of forested area ($p=0.093$; Fig. 5b) or water ($p=0.025$) in their home ranges. Importantly, we note here that the significant differences in directional persistence persisted even after adjusted for the increased location error in the forested areas.

HFI had no significant effect on lowland tapir home range size ($p=0.90$; Fig. 6a), nor average daily movement speed ($p=0.53$; Fig. 6b), nor directional persistence ($p=0.596$, $R^2_{adj} = -0.0184$). A tapir living in a near pristine environment (HFI=0.004) had a home range estimate of 7.77 km^2 (95% CI 2.12–28.6) and an average speed of 13.2 km/day (95% CI 7.8–22.1) with a

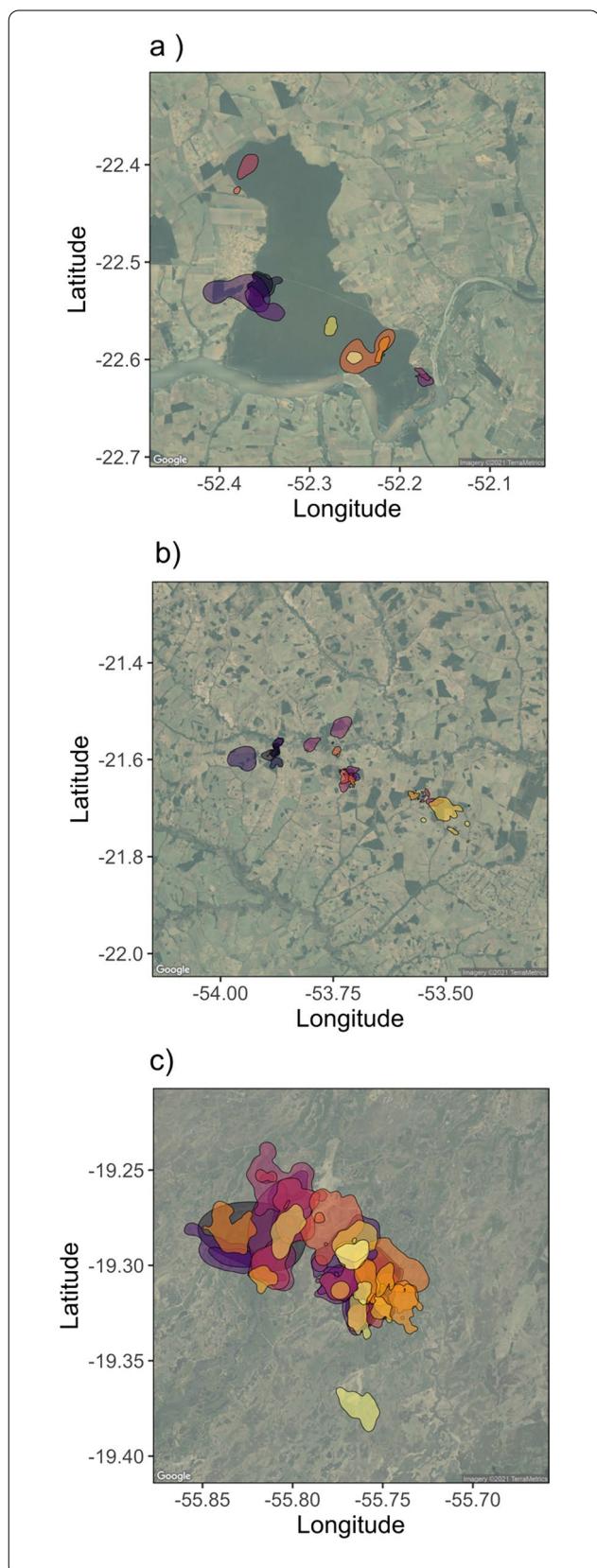


Fig. 2 Autocorrelated kernel density estimates of each tapir's 95% home range in each of the three regions: **a** Atlantic forest, **b** Cerrado, and **c** pantanal

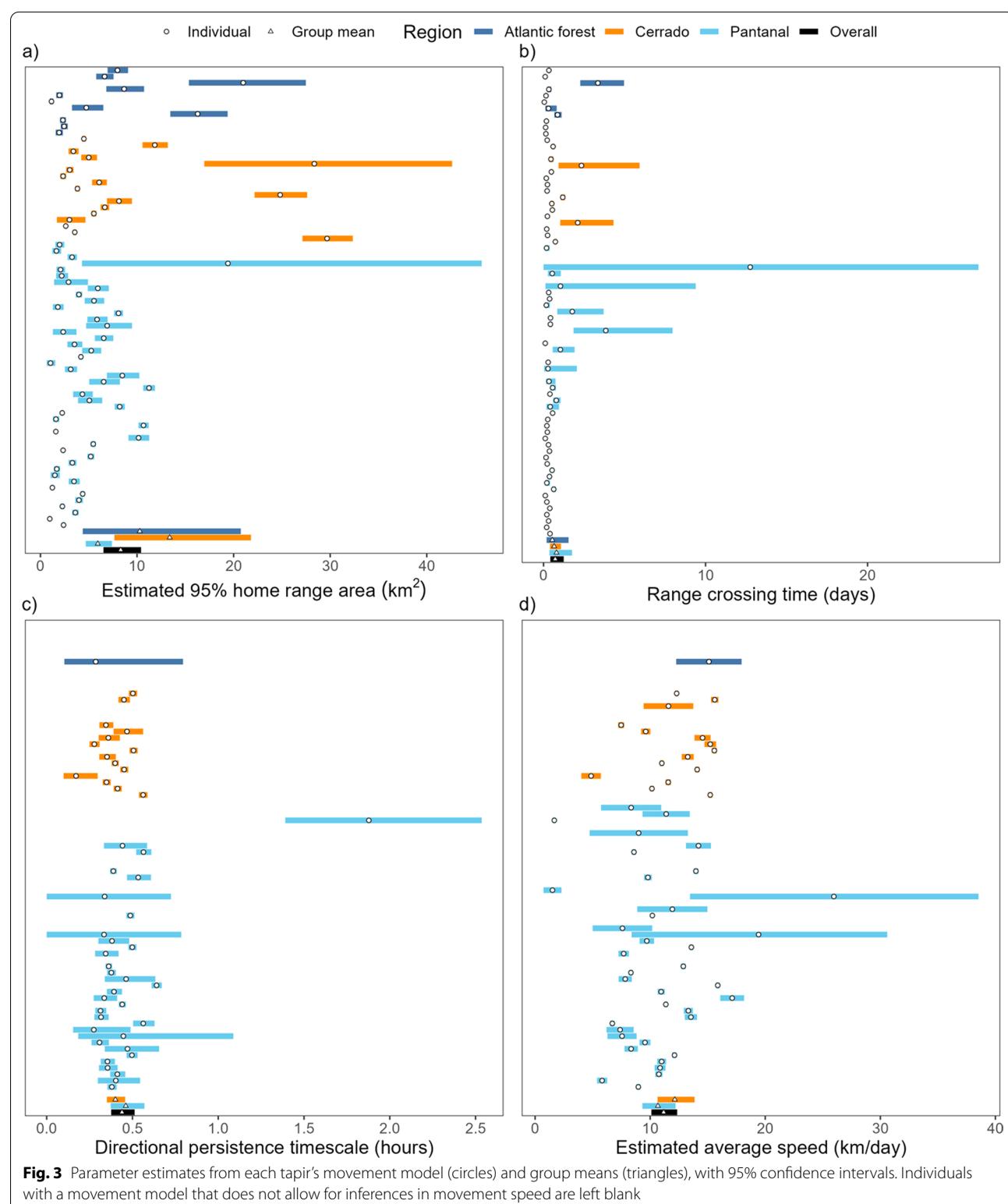
directional persistence of 0.36 h (95% CI 0.16–0.78), while a tapir from the most altered habitat we monitored ($HFI=0.31$) had an estimated home range area of 6.93 km^2 (95% CI 3.36–14.30) and an average speed of 10.4 km/day (95% CI 8.3–13.2) with a directional persistence of 0.48 h (95% CI 0.34–0.68).

Discussion

Understanding individual movement and space use requirements is a key step in conservation planning [3]. Prior to the present study, very little was known about the movement ecology of tapirs despite their vulnerable status and declining population sizes [74]. From detailed tracking of 74 tapirs collected over 22 years, we found that although individuals varied in their movement, these inter-individual differences were not explained by differences in age, sex, habitat composition, biome, nor human disturbance. Overall, human activity and land use change did not appear to significantly affect their behaviour one way or another. This contradicts patterns in large herbivores generally [16, 71], and further emphasizes the need to understand the movement ecology of target populations when designing conservation and recovery strategies.

The ecology of lowland tapir space use

Interestingly, we found that the home range sizes and mean daily movement speeds of lowland tapirs were consistent across the three study sites. This consistency in movement was surprising as these different biomes have substantially different habitat compositions, patterns of seasonality, and productivity [47], see also Additional file 1: Appendix S1). Tapirs living in the Pantanal, for instance, occupy a near pristine ecosystem but must cope with significant seasonal flooding, whereas individuals in the Cerrado occupied an agricultural and cattle ranching mosaic with more stability across seasons. The unique requirements of these three different biomes, however, did not impact the space use and movement speed of tapirs in any statistically detectable way. Furthermore, the only pre-existing study on tapir movement found that individuals had complex home range structures, with multiple core areas of use that were established according to the distribution of patches of preferred habitat types [69]. While individuals may exhibit differential use of patchily distributed resources, we found that habitat composition had no effect on home range sizes. In addition to exhibiting little inter-individual variation in



movement, variogram analysis [24] showed that tapir movement was extremely consistent over time (see also [22]. Here again, this seasonal stability in movement

was interesting, especially for animals living in the Pantanal where, every year, large parts of the biome change from terrestrial into aquatic habitats and vice-versa [1].

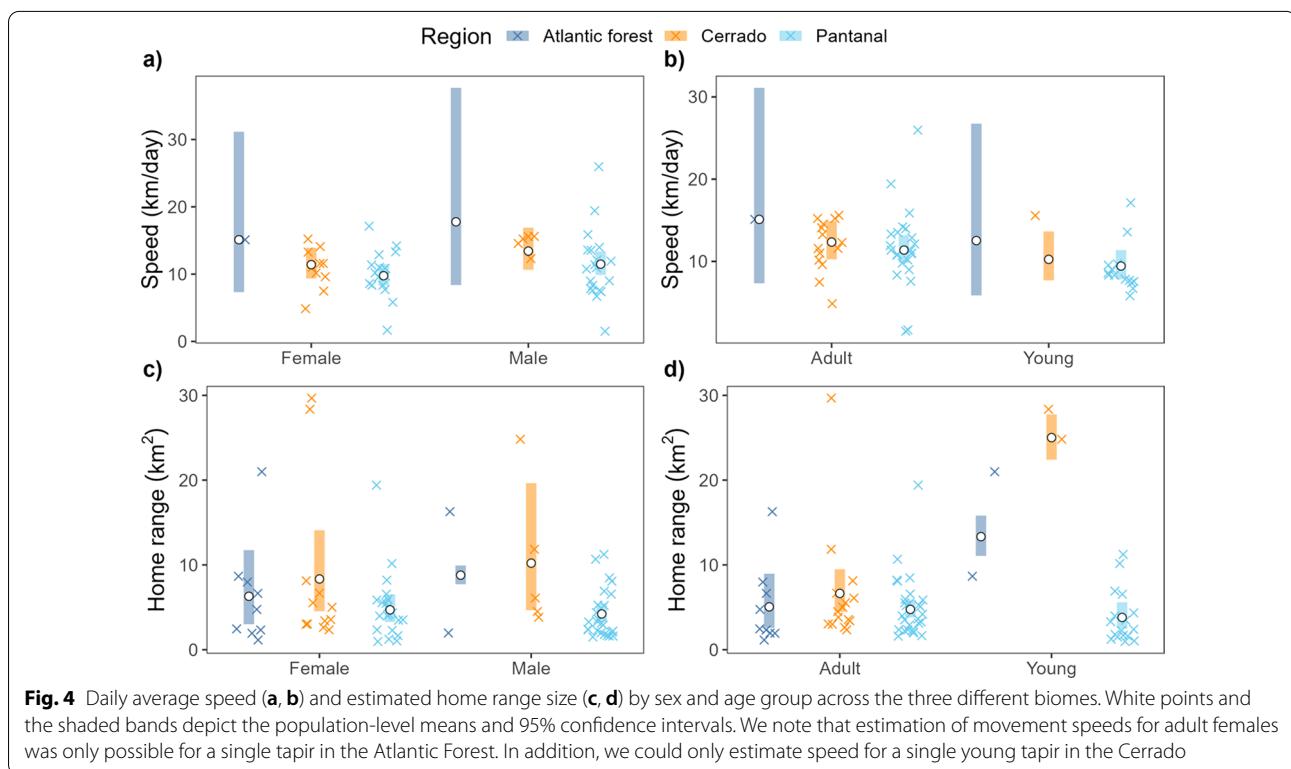


Fig. 4 Daily average speed (**a, b**) and estimated home range size (**c, d**) by sex and age group across the three different biomes. White points and the shaded bands depict the population-level means and 95% confidence intervals. We note that estimation of movement speeds for adult females was only possible for a single tapir in the Atlantic Forest. In addition, we could only estimate speed for a single young tapir in the Cerrado

We note though that the flooding regime in the Pantanal has been changing over the last decade and the biome is expected to become drier under the IPCC's climate change scenarios [38].

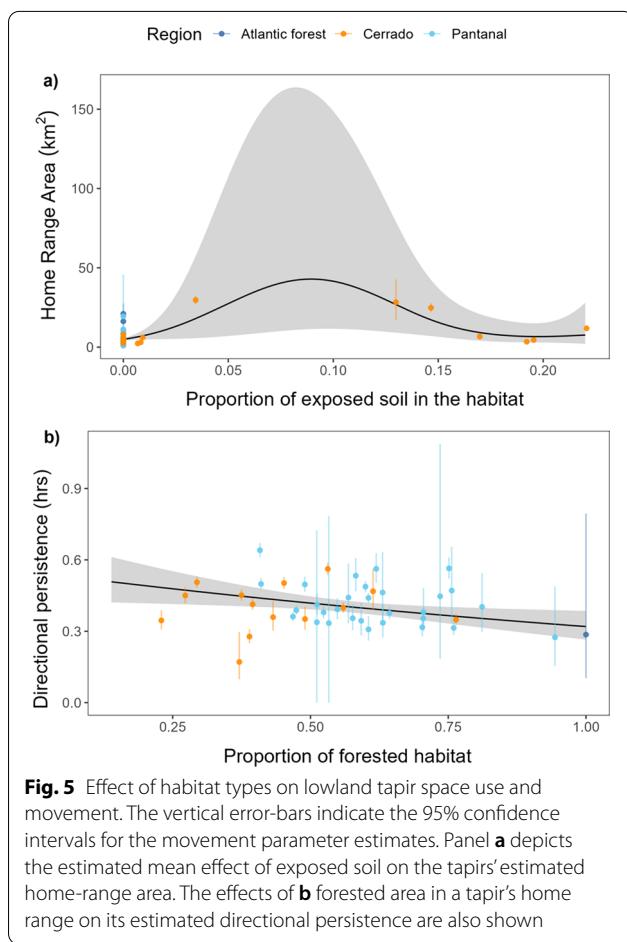
We did find that animals with a higher proportion of forest and/or more water bodies in their home ranges had reduced directional persistence. This shows how habitat complexity can impact movement [15], with potential implications for foraging efficiency and encounter rates [5, 39, 77]. Nonetheless, these differences did not translate into patterns in tapir home range sizes and mean daily movement speeds.

Lowland tapir movement and human disturbance

This is the first study aimed at understanding how lowland tapir space use and movement vary across differing biomes and degrees of human disturbance. Contrary to our initial expectations, and to patterns in large herbivores generally [16], human impacts on the landscape had no measurable effect on tapir movement. To put this landscape scale effect into perspective, tapirs inhabiting the Atlantic Forest, the most disturbed biome with only ca. 12–29% of habitat remaining [37, 58, 59, 66], had home ranges that were comparable in size to tapirs inhabiting the Cerrado, a biome that has lost almost 50% of its natural area (36, 45), and the Pantanal, a near pristine biome. Notably, the Lowland Tapir Conservation Action Plan

published by the IUCN SSC Tapir Specialist Group (TSG) in 2007 [43], and the Lowland Tapir National Action Plan (PAN—Plano de Ação Nacional, ICMBIO—Instituto Chico Mendes de Conservação da Biodiversidade, Brazil) published in 2019 prioritize the mitigation of the impacts of small, isolated tapir populations. Population isolation thus emerges as one of the most important threats to the species' long-term persistence. However, addressing this issue will require additional efforts as the average and maximum distances we recorded for tapir movements were substantially less than the distances between most tapir populations.

Humans are directly responsible for more than one-quarter of global terrestrial vertebrate mortality [30]. Mortality at this scale is expected to impose strong selection pressure on animal populations [53, 67]. As genotypic adaptation takes generations to occur [4], behavioral plasticity provides the most immediate response to the pressures of Human Induced Rapid Environmental Change (HIREC, [65]). The capacity for behavioural plasticity in movement and space use in response to human disturbance is especially important for long-lived, K-selected species such as tapirs [46, 60, 65] that take years to reach sexual maturity and have long inter-generational intervals [40]. Despite the key importance of behavioural adaptations in response to HIREC, tapir movement appeared to exhibit very little plasticity in



response to human disturbance. The lack of any measurable response to human activity suggests that tapirs living near humans may experience increased exposure to vehicle collisions [2, 42], pesticide and environmental pollutants [20, 41, 44] and poaching [62]. Human modified habitats thus risk being ecological traps [64] for tapirs as individuals showed no detectable responses to degradations in habitat quality. Although tapir home range area and mean daily movement speed exhibited no statistically detectable response to the human footprint index, it is possible that individuals are responding to human disturbance at a finer temporal and/or spatial scale than the long-term averages that were examined here. It may also be possible that tapirs exhibit non-linear, or even binary, responses to human disturbance that were not possible to detect. Future investigation into lowland tapir behaviour in more heavily modified habitats is clearly warranted.

Conclusions

We compared home range areas and movement behavior of lowland tapirs using telemetry data collected over 22 years across 3 biomes in southern Brazil: the

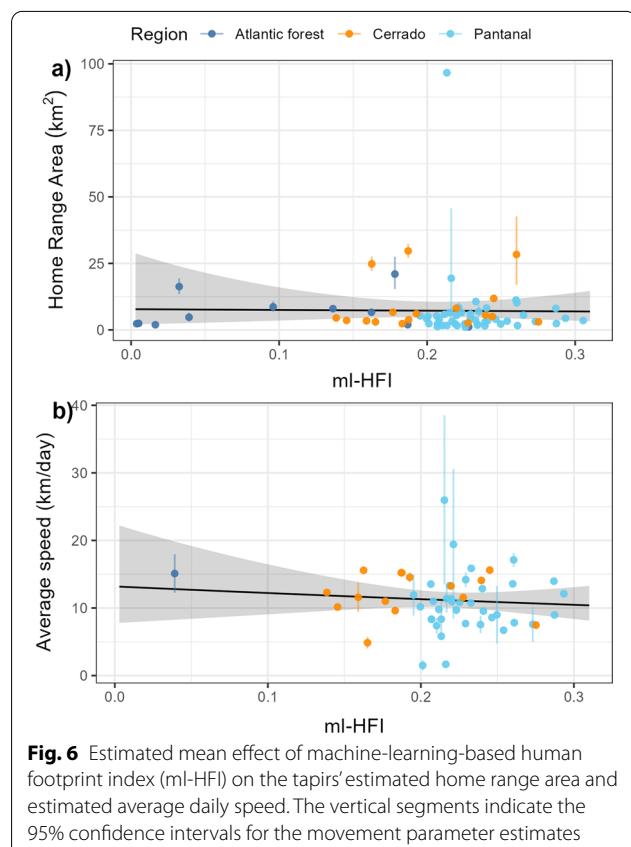


Fig. 6 Estimated mean effect of machine-learning-based human footprint index (ml-HFI) on the tapirs' estimated home range area and estimated average daily speed. The vertical segments indicate the 95% confidence intervals for the movement parameter estimates

Pantanal, Cerrado, and Atlantic Forest. These data represent the largest lowland tapir tracking dataset yet to be collected, with over 232,000 locations from 74 tracked individuals and fill a critical knowledge gap in lowland tapir ecology, which can contribute to long-term species management and conservation planning. Contrary to our expectations, we observed very little individual variability in lowland tapir space use and movement, and human impacts on the landscape also had no measurable effect on their movement. Lowland tapir movement behaviour thus appears to exhibit very little phenotypic plasticity. The lack of any adaptive response to anthropogenic disturbance suggests that human modified habitats risk being ecological traps for tapirs and this information should be factored into conservation actions aimed towards protecting lowland tapir populations.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-022-00313-w>.

Additional file 1: Details on the habitat composition of the different biomes.

Additional file 2: Details on the R scripts used to generate the results presented in the main text.

Acknowledgements

The study of tapir movement ecology has been an important component of the long-term activities of the Lowland Tapir Conservation Initiative (LTCI) – Instituto de Pesquisas Ecológicas (IPÊ) in Brazil. The LTCI has the institutional support from the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Tapir Specialist Group (TSG), Association of Zoos and Aquariums (AZA) Tapir Taxon Advisory Group (TAG), and European Association of Zoos and Aquariums (EAZA) Tapir Taxon Advisory Group (TAG). LTCI's financial support comes from national and international agencies, including zoological institutions, foundations, private businesses, and private individuals. EPM would like to thank the Smithsonian Conservation Biology Institute (SCBI) for hosting her for a 2-month research visit for initial data processing and analysis.

Authors' contributions

EPM devised the field study, collected the data, and performed preliminary analyses. EPM, JMC, and MJN conceived the scope of the project and analytical pipeline. SM, CHF, and MJN contributed to data analysis. All authors contributed to the writing. All authors read and approved the final manuscript.

Funding

MJN was supported by an NSERC Discovery Grant RGPIN-2021-02758. This work was partially funded by the Center of Advanced Systems Understanding (CASUS) which is financed by Germany's Federal Ministry of Education and Research (BMBF) and by the Saxon Ministry for Science, Culture and Tourism (SMWK) with tax funds on the basis of the budget approved by the Saxon State Parliament. CHF and JMC were supported by NSF IIBR 1915347.

Availability of data and materials

All R code and data necessary to reproduce the analyses in the main text can be found in the GitHub repository at <https://github.com/StefanoMezzini/tapirs>.

Declarations

Ethics approval and consent to participate

The Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) provided the required annual permits for the capture and immobilization of tapirs and collection of biological samples (SISBIO# 14,603). The Comissão Técnico-Científica (COTEC) do Instituto Florestal do Estado de São Paulo (IF-SP) provided the required permit to carry out research in Morro do Diabo State Park (SMA# 40624/1996). All protocols for the capture, anesthesia, handling and sampling of tapirs have been reviewed and approved by the Veterinary Advisors of the Association of Zoos and Aquariums (AZA) – Tapir Taxon Advisory Group (TAG), and the Veterinary Committee of the IUCN SSC Tapir Specialist Group (TSG).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 17 November 2021 Accepted: 2 March 2022

Published online: 14 March 2022

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Publisher's Note

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Assessing the representation of species included within the Canadian Living Planet Index

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OPEN ACCESS

Citation: Currie J, Burant JB, Marconi V, Blain SA, Emry S, Hébert K, Xie G, Moore NA, Wang X, Brown A, Grevstad L, McRae L, Mezzini S, Pata P, and Freeman R. 2022. Assessing the representation of species included within the Canadian Living Planet Index. *FACETS* 7: 1121–1141. doi:[10.1139/facets-2022-0063](https://doi.org/10.1139/facets-2022-0063)

Handling Editor: David Lesbarrères

Received: March 17, 2022

Accepted: June 9, 2022

Published: August 11, 2022

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Published by: Canadian Science Publishing

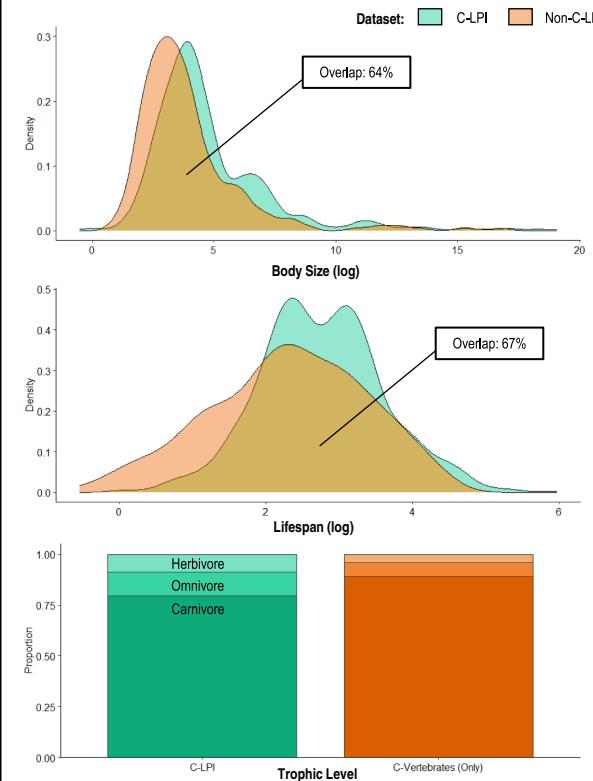
Abstract

To effectively combat the biodiversity crisis, we need ambitious targets and reliable indicators to accurately track trends and measure conservation impact. In Canada, the Living Planet Index (LPI) has been adapted to produce a national indicator by both World Wildlife Fund-Canada (Canadian Living Planet Index; C-LPI) and Environment and Climate Change Canada (Canadian Species Index) to provide insight into the status of Canadian wildlife, by evaluating temporal trends in vertebrate population abundance. The indicator includes data for just over 50% of Canadian vertebrate species. To assess whether the current dataset is representative of the distribution of life history characteristics of Canadian wildlife, we analyzed the representation of species-specific biotic variables (i.e., body size, trophic level, lifespan) for vertebrates within the C-LPI compared to native vertebrates lacking LPI data. Generally, there was considerable overlap in the distribution of biotic variables for species in the C-LPI compared to native Canadian vertebrate species lacking LPI data. Nevertheless, some differences among distributions were found, driven in large part by discrepancy in the representation of fishes—where the C-LPI included larger-bodied and longer-lived species. We provide recommendations for targeted data collection and additional analyses to further strengthen the applicability, accuracy, and representativity of biodiversity indicators.

INVESTIGATING DATA GAPS

Assessing the representation of species included within the Canadian Living Planet Index

To effectively combat the biodiversity crisis, we need ambitious targets and reliable indicators to accurately track trends and measure conservation impact. In Canada, the Living Planet Index (LPI) has been adapted to produce a national indicator by both WWF-Canada (Canadian Living Planet Index; C-LPI) and Environment and Climate Change Canada (Canadian Species Index) — to provide insight into the status of Canadian wildlife, by evaluating temporal trends in vertebrate population abundance. The indicator includes data for just over 50% of Canadian vertebrate species. To assess whether the current dataset is representative of the distribution of life history characteristics of Canadian wildlife, we analyzed the representation of species-specific biotic variables (i.e., body size, trophic level, lifespan) for vertebrates within the Canadian-LPI compared to native vertebrates lacking LPI data.



Generally, there was considerable overlap in the distribution of biotic variables for species in the C-LPI compared to native Canadian vertebrate species lacking LPI data. Nevertheless, some differences among distributions were found — driven in large part by discrepancy in the representation of fishes — where the C-LPI included larger-bodied and longer-lived species. We provide recommendations for targeted data collection and additional analyses to further strengthen the applicability, accuracy and representativity of biodiversity indicators.

Currie et al. 2022

Key words: Living Planet Index, representation, biodiversity indicator, Canada, conservation

Introduction

Combatting the biodiversity crisis requires ambitious targets, widespread action, and reliable indicators to accurately track the impact of conservation intervention and progress towards national (e.g., Canada's Federal Sustainable Development plan) and international (e.g., Convention on Biological Diversity) goals. The Living Planet Index (LPI)—conceived nearly 25 years ago—is a biodiversity indicator used to evaluate the state of wildlife by assessing temporal trends in vertebrate population abundance. The indicator has been applied at global ([WWF 2020](#)), regional (see for example [McRae et al. 2012](#)), and national ([Bayraktarov et al. 2020](#), [Marconi et al. 2021](#)) geographic scales and used as a public engagement and advocacy tool to motivate wildlife conservation ([Ledger et al. 2021; in preparation](#)).

Recently the discourse in the literature in relation to the LPI has been heightened, with papers exploring biases pertaining to the underlying data and calculation of aggregate measures ([Leung et al. 2020](#); [Buschke et al. 2021](#); [Leung et al. 2022a](#); [Leung et al. 2022b](#); [Leung et al. 2022c](#); [Loreau et al. 2022](#); [Murali et al. 2022](#); [Puurtinen et al. 2022](#)). For instance, random population fluctuations ([Buschke et al. 2021](#)) and extreme population trends, particularly declines, (i.e., outliers; [Leung et al. 2020](#)) introduce biases that can exaggerate declines in the global LPI. Despite these biases, the effect of random population fluctuations does not detract from global LPI messaging of substantial declines in average vertebrate population abundance ([Buschke et al. 2021](#)). Similarly, recent research has also noted that the removal of extreme population declines and increases (i.e., removing outliers from both tails of the distribution) has little effect on the overall LPI ([Murali et al. 2022](#)). Consequently, while biases can exist, the utility of the LPI and the messaging remains clear—nature is deteriorating ([IPBES 2019](#); [WWF 2020](#)). Nevertheless, these nuances around interpreting the LPI are also accompanied by calls for greater monitoring to address data gaps and ensure adequate representation of global biodiversity ([Leung et al. 2022b](#); [Murali et al. 2022](#)).

In Canada, the LPI methodology has been adapted to produce a biodiversity indicator within a national context by both World Wildlife Fund-Canada (Canadian Living Planet Index; C-LPI) ([WWF-Canada 2020](#)) and Environment and Climate Change Canada (Canadian Species Index; CSI) ([ECCC 2019](#)). These indicators reveal near-stable trends of vertebrate population abundance since 1970, on average (+6% (C-LPI) and -4% (CSI), owing to differences among data selection). The dataset underlying the C-LPI, largely publicly available via the LPI database ([livingplanetindex.org](#)) and continuously augmented, now incorporates thousands of time series from more than 900 vertebrate species, representing 50.9% of native vertebrate species in Canada ([CESCC 2016](#)). [Marconi et al. \(2021\)](#) analyzed the taxonomic and spatial representation of the dataset behind the indicator and showed that Canadian birds are better represented in comparison to other taxonomic groups. However, it is also important to know whether species currently included in the C-LPI database are representative of the distributions of biological and ecological traits observed in the broader set of vertebrate species that occur in Canada.

The biases in available data broadly reflect the biases in biodiversity research more generally ([Donaldson et al. 2016](#), [Troudet et al. 2017](#)). Monitoring is important ([Tittensor et al. 2014](#)), and additional data collection is key to establishing accurate trends in currently monitored species. However, it seems unlikely that there will be sufficient data to provide us with an unbiased picture of biodiversity trends overall, at least in the short-term, despite calls to address data gaps (e.g., [Leung et al. 2022b](#); [Murali et al. 2022](#)). In the meantime, intrinsic (biological) and extrinsic (ecological) traits may provide information on species' vulnerability to anthropogenic threats and therefore on their predicted population trends and risk of extinction (see [Chichorro et al. 2019](#) for a comprehensive review). Without insight into some of the characteristics of the species that are not

currently monitored (i.e., insight into data gaps), however, we may be wrongly estimating the direction and magnitude of temporal trends in population abundance.

Here we analyze the representation of species-specific biotic variables for vertebrates within the C-LPI compared to native vertebrate species lacking LPI data to assess whether the current dataset is representative of the distribution of life history characteristics of Canadian wildlife. Importantly, the alignment of biotic traits for vertebrates within the C-LPI, compared to those lacking LPI data, will help to identify biases in the underlying data that may affect the utility of the C-LPI at a national level, particularly as an ecological indicator to track progress towards biodiversity goals. In addition to assessing the distribution of common biotic variables among taxa, we collated data for a variety of supplementary biotic variables that we are making publicly available for future analyses.

Methods

Species list

Canadian Living Planet Index

We used the data underlying the C-LPI ([WWF-Canada 2020](#)). These data are also included within the global LPI Data Portal ([livingplanetindex.org/data_portal](#); except records that were provided to the LPI team under the agreement they would be kept confidential, e.g., data for sensitive populations or at-risk species), a repository that contains thousands of records depicting temporal changes in vertebrate abundance. The data have been collated from a variety of sources, including peer-reviewed publications, government databases, and grey literature. The criteria for inclusion within the dataset are as follows: (i) the data have been collected using comparable methods for at least two years for the same population (aligns with the global LPI and CSI methodology, the C-LPI methodology has recently been improved to limit inclusion to populations that have at least three years of data collection); (ii) data are specific to units of population size, either a direct measure such as population counts, densities, or indices, or a reliable proxy such as breeding pairs, nests, tracks, capture per unit effort or measures of biomass for a single species; and (iii) the source is referenced and traceable ([Collen et al. 2009](#)). Species classified as “presumed extirpated”, “probably extirpated” or “not applicable” by the Wild Species Report ([CESCC 2016](#)) have been excluded from the dataset. The latter category includes exotic species, hybrids, or species occurring infrequently and unpredictably in Canada. Non-native species are excluded from the dataset. These criteria resulted in a final subset of 906 vertebrate species that commonly occur in Canada.

Native Canadian vertebrates

Species listed within the 2015 Wild Species Reports ([CESCC 2016](#)) were compiled into a complementary dataset to compare traits of species within the C-LPI (dataset: C-LPI), to the broader group of native vertebrates found in Canada (dataset: C-Vertebrates) and those lacking LPI data (dataset: C-Vertebrates Only). Species were sorted according to binomial scientific name. We included native Canadian species with applicable conservation status (i.e., exotic species, hybrids, and accidental species under the NatureServe rank of “not applicable” were excluded). Discrepancies in nomenclature between the C-LPI taxonomic authorities and Wild Species Reports ([CESCC 2016](#)) necessitated evaluation of 58 species, which were resolved for comparison using the *taxize* R package ([Chamberlain et al. 2020](#)). For some species, we matched those that had synonymous binomial scientific names; others were resolved to address discrepancies between North American (greater species specificity) and global (where species are sometimes lumped together) nomenclature. In total, there are 1,779 extant, native vertebrate species in Canada—more than half of which (n = 906) have population trend data within the broader C-LPI dataset.

Biotic variables

Abiotic and biotic species trait data (i.e., life history characteristics, habitats and threats) were extracted from a variety of publicly accessible online databases for birds ([Table S1](#); Myhrvold et al. 2015; Sheard et al. 2020), fishes ([Table S2](#); Froese and Pauly 2016), mammals ([Table S3](#); Wilman et al. 2014; Myhrvold et al. 2015), and amphibians and reptiles ([Table S4](#); Myhrvold et al. 2015; Oliveira et al. 2017; Santini et al. 2018; Grubler 2020). Data extraction was conducted separately for each taxon, given differences among ideal databases, common variables, and units reported across taxonomic groups. For instance, length was typically recorded for fishes and herpetofauna (Froese and Pauly 2016, Santini et al. 2018), while mass was more commonly reported for birds and mammals (Myhrvold et al. 2015). For each taxonomic group, variables with sufficient data were mapped onto species from the C-LPI according to binomial scientific name using the *traitdata* (RS-eco 2021; birds, mammals, herpetofauna), *squamata* (Grubler 2020; herpetofauna), and *fishbase* (Boettiger et al. 2012; fishes) R packages—creating multi-variable datasets that are now publicly available for future analyses. The code and extracted data for Canadian vertebrates can be found online (Currie et al. 2022). Note that only body size, lifespan, and trophic level were included in our analysis as they had broad taxonomic coverage, but additional traits with sufficient species coverage were also extracted for public interest and use. Moreover, the available code can be adapted to extract additional traits of interest from the available databases. Details on data extraction for biotic variables with sufficient species coverage, by taxon, are found below.

Birds

Five biotic variables were selected for inclusion within the C-LPI Bird Trait database ([Table S1](#)), based upon data availability. Using the R package *traitdata* (RS-eco 2021), adult body mass, lifespan (maximum longevity), and mean longevity were extracted from the Amniote database (Myhrvold et al. 2015). Data on body mass were also available from the EltonTraits database (Wilman et al. 2014), but the Amniote database (Myhrvold et al. 2015) was selected as the primary source given the quality of its metadata (i.e., more extensive). Average values per species were calculated for each biotic variable. In addition, hand-wing index (i.e., a measure of wing aspect ratio and a proxy for dispersal ability) and dietary guild were extracted from the Global Hand-Wing Index repository (Sheard et al. 2020). Dietary guild categories were aligned to trophic level categorization (carnivore, omnivore, and herbivore). One species (turkey vulture, *Cathartes aura*) was assigned to the carnivore category as it almost exclusively feeds on carrion.

Fishes

Data were extracted from FishBase (Froese and Pauly 2016) using the R package *rfishbase* (Boettiger et al. 2012). Fourteen biotic variables were selected for inclusion within the C-LPI Fishes Trait database ([Table S2](#)), including length, weight, and lifespan. Average values per species were calculated for each biotic variable.

Mammals

Gestation period and lifespan (maximum longevity) were retrieved from the Amniote database (Myhrvold et al. 2015) using the R package *traitdata* (RS-eco 2021), while body size and diet were extracted from EltonTraits (Wilman et al. 2014). In total, four biotic variables were selected for inclusion within the C-LPI Mammal Trait database, including body mass, trophic level, gestation period, and lifespan ([Table S3](#)). Mammal trophic level was calculated using diet composition, where herbivore was defined as species associated with an entirely vegetarian diet (e.g., plants, seeds, nectar, and fruit), carnivores were classified as species that consume other animals, and omnivores included species with mixed diets.

iv. Amphibians & Reptiles

Seven biotic variables were selected for inclusion within the C-LPI Amphibian and Reptile Trait database (**Table S4**), including variables related to body size, diet, and reproduction. Data were extracted from AmphiBIO (Oliveira et al. 2017), the Amniote database (Myhrvold et al. 2015, Meiri 2018; Santini et al. 2018, Atwood et al. 2020), and SquamataBase (Grubler 2020) using *traitdata* (RS-eco 2021) and *squamatabase* (Grubler 2020) R packages. Trait data that were comparable across datasets (e.g., body mass) were hierarchically extracted. For example, body mass was first extracted from AmphiBIO (Oliveira et al. 2017), then from the amniote life history database (Myhrvold et al. 2015) for species that lacked data in AmphiBIO. Because multiple entries were available per species within the amphibian allometry database (Santini et al. 2018), values with the highest sample sizes were selected for inclusion. Amphibians and reptiles were grouped together as herpetofauna to improve sample size for analysis.

We also endeavored to extract of abiotic variables for this analysis—including species' geographic ranges and average topographic and climate variables within those ranges. However, due to a lack of data coverage, we did not include these variables within our analysis. Nevertheless, the code and associated data can be found online.

Analyzing the representation of biotic variables

Three biotic variables with sufficient cross-taxon information were selected from the taxon-specific datasets to create a more fulsome cross-taxon database. The selection of traits was dependent upon a combination of (i) data availability within and across taxa and (ii) considerations on the available evidence of relationships between a trait and population declines and (or) extinction risk. For instance, call frequency and positioning are traits used to evaluate amphibian tolerance to anthropogenic pressures (e.g., Liu et al. 2021) but are not applicable biotic traits for fishes.

Furthermore, biodiversity loss is not random (Dirzo et al. 2014) and functional traits, specifically, covary with patterns in biodiversity trends (Munstermann et al. 2021; Dirzo et al. 2014; Lee and Jetz 2010). Trait diversity can therefore result in a biased impact on ecosystem functioning (Diaz et al. 2006). For instance, body size is often a predictor of species loss, with large-bodied species particularly vulnerable (e.g., Dirzo et al. 2014; Seguin et al. 2014; Cardillo et al. 2005; Solan et al. 2004; Bennett and Owens 1997), though there has been mixed evidence dependent on taxonomic group (e.g., Chichorro et al. 2019; Kopf et al. 2016). Etard et al. (2020) found that while traits for mammals and birds are generally well-studied, there are gaps in information associated with reptiles and amphibians, making cross-taxon analyses more difficult. Moreover, a recent meta-analysis evaluating species traits and extinction risk identified body size as the most studied biotic trait, followed by fecundity and diet (Chichorro et al. 2019). Yet, while fecundity was often investigated, it was infrequently linked to patterns in biodiversity trends. Alternatively, longevity was less frequently studied, but had the second-highest biotic variable significance (following body size). Lifespan was also found to be an important predictor of extinction risk for freshwater megafauna (He et al. 2020). Likewise, we selected body size, longevity, and trophic level (i.e., diet) for our analysis based on the availability of information within and across taxonomic groups, as well as the evidence pertaining to relationship among these traits and biodiversity trends. While continuous traits are preferred for evaluating functional diversity (Laureto et al. 2015), the categorical trait of trophic level was applied to assess trends across taxonomic groups, based on the taxon-specific databases available.

Continuous variables of body size and lifespan were log-transformed, while trophic level included three categorical levels (herbivore, omnivore, carnivore). The overarching cross-taxon C-LPI Trait Database included 836 species, while the broader C-Vertebrate Trait Database included 1679 species.

Shapiro–Wilk tests were used to assess assumptions of normality for the continuous variables of body size and lifespan for species included within the C-LPI trait database and for other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only) ([Fig. S1](#)). Given that the data generally exhibited skewed distributions, we applied two-sample nonparametric Kolmogorov–Smirnov (KS) tests to evaluate differences between the distribution of traits for species in the C-LPI Trait database and the C-Vertebrate (Only) Trait database. The widely used, asymptotic KS test measures distributional differences between two samples and has previously been applied to compare relationships among biotic variables (e.g., [Adjeroud et al. 2007](#); [Langlois et al. 2012](#); [Cornwell et al. 2014](#)). Importantly, we also assessed the percent overlap among distributions for continuous variables to evaluate the degree of differences in the distributions. These statistical tests were accompanied by a resampling approach to estimate differences in trait distributions between species in the C-LPI and C-Vertebrates (Only) datasets (see more below). We assessed the difference in categorical distribution of trophic level using Pearson’s χ^2 tests. Fisher’s exact test was used to validate small-sized samples that ran into computational errors during the application of Pearson’s χ^2 test ([Kim 2017](#)). All tests were performed for each biotic variable at the taxonomic level (i.e., birds, mammals, fish, amphibians and reptiles), and with all species combined.

Completeness of variables in our dataset ranged between 35.0% and 87.8%. Consequently, we also reran the analysis with a more complete dataset, imputing missing biotic trait values via nonparametric imputation using the Random Forest approach ([Stekhoven and Buehlmann 2012](#)) and an algorithm known as missForest ([Stekhoven 2013](#)). This approach helped to identify important predictors of body size, lifespan, and trophic level using the additional biotic trait information that was extracted for each taxonomic group. The Random Forest approach permits biotic trait data imputation (i.e., estimation of missing data with complex relationships among multiple variables; e.g., [Debastiani et al. 2021](#)) and can deal with both continuous and categorical data to develop a more complete dataset for analysis ([Stekhoven and Buehlmann 2012](#)).

To supplement our analysis of the two continuous traits (body size and lifespan), we applied a nonparametric bootstrapping approach to generate 95% compatibility intervals (95% CIs) on the median difference between datasets (i.e., the effect size; [Cohen 1994](#); [Ho et al. 2019](#)). Bootstrapping was done via randomized resampling with replacement ($n = 5000$ iterations) of the C-LPI and C-Vertebrate (Only) subsets of species-specific trait values to generate resamples equal in size to the original subsets. In addition, bootstrapping was performed twice: once using an unstratified approach in which all species were treated as a single sample without consideration for taxonomic representation and once using taxon-specific resampling in which data were sampled proportionally for each of the four vertebrate groups under consideration. We include the median and corresponding 95% CI on the difference between subsets for each of trait comparisons as a data-centered complement, and present Gardner–Altman estimation plots of these effects in the Supplementary Material.

Analyses and visualization were conducted using R statistical software (v. 4.1.1; R Core Team 2021), making use of the *missforest* ([Stekhoven 2013](#)), *tidyverse* ([Wickham et al. 2019](#)), *dabestr* ([Ho et al. 2019](#)), *ggpubr* ([Kassambara 2020](#)), *effectsize* ([Ben-Schachar et al. 2020](#)), *data.table* ([Dowle and Srinivasan 2021](#)), and *traitdata* ([RS-eco 2021](#)) packages.

All compiled trait data and associated code for this analysis are available through a Figshare repository ([Currie et al. 2022](#)).

Results

Dataset description

While the C-LPI contains data for 50.9% (906/1779) of native vertebrate species in Canada, not all of these species had available trait data (**Table 1**). In total, 49.8% (836/1679) of Canadian vertebrates with data for at least one biotic variable were included within the C-LPI Trait database, resulting in a trait database covering 92.3% of species (836 of 906) included in the C-LPI. Overall, birds tended to have the best data coverage in terms of both population time series and traits, with over 85% of species with trait data included within the C-LPI Trait database (**Fig. 1**). Birds were the best represented, while the representation of fish trait data was more variable; only 35.0% (352/1007) of fishes with available trait information were included within the C-LPI Trait database relative to the broader C-Vertebrates Trait database. In total, 629 species within the C-LPI Trait database, and 883 native Canadian vertebrate species lacking LPI data (C-Vertebrates Only) had trait data for all three biotic variables. Impressively, 94.4% (1679/1779) of native Canadian vertebrates were included in the analysis.

Representation of biotic variables

The distribution of body size, lifespan, and trophic level for species within the C-LPI were largely overlapping (> 64%) with the distribution of biotic variables for native Canadian vertebrate species lacking LPI data (C-Vertebrates Only) (**Fig. 2**; **Table S5**) and the broader vertebrate subphylum (>82%) nationally (i.e., including LPI species) (**Table S6**; **Fig. S7**). Despite the broad overlap, differences between distributions were found for body size (KS test statistic D: 0.23, $p: < 2.2 \times 10^{-16}$), lifespan (KS test statistic D: 0.20, $p: 3.1 \times 10^{-7}$), and trophic level ($\chi^2: 28.96$, df:2, $p: 5.1 \times 10^{-7}$), largely due to differences among fish distributions (**Table S5**)—the taxonomic group that contributed the most data yet had the poorest overlap in distributions (< 54%). Overall, there were a greater number of fishes with large body sizes (**Fig. 3**; average log body size: 3.93; average body size: 50.91) and long lifespans (**Fig. 4**; average log lifespan: 2.93; average lifespan: 18.73) compared to species lacking LPI data (average log body size: 3.56; average body size: 35.12; average log lifespan: 2.58; average lifespan: 13.20). Amphibians and reptiles exhibited the largest overlap in distributions for body size and lifespan among datasets (>67%), while fishes exhibited the poorest overlap (<54%). Although differences among trophic levels were detected when taxonomic groups were combined (**Table S5**; **Fig. 2**), there were fewer differences among datasets within each taxonomic group (**Fig. 5**). In addition, relationships among biotic variables were similar for species within the C-LPI and those lacking LPI data (C-Vertebrates Only) and appeared to be correlated (**Fig. S2**).

Table 1. Data availability for assessing the representation of species included within the Canadian Living Planet Index (C-LPI), including proportion of vertebrates within Canada, and the relative representation of biotic traits.

Data Availability	Birds	Fish	Herps	Mammals	All
C-LPI (Representation in C-LPI, %)	388 (42.8)	370 (40.8)	47 (5.2)	101 (11.1)	906
C-Vertebrates (Representation in C-Vertebrates, %)	453 (25.5)	1044 (58.7)	88 (4.9)	194 (10.9)	1779
Species representation (%)	85.7	35.4	53.4	52.1	50.9
C-LPI Trait Database (Representation in C-LPI Trait Database, %)	344 (41.1)	352 (42.1)	46 (5.5)	94 (11.2)	836
C-Vertebrates Trait Database (Representation in C-Vertebrates Trait Database, %)	404 (24.1)	1007 (60.0)	86 (5.1)	182 (10.8)	1679
Species trait representation (%)	85.1	35.0	53.5	51.6	49.8
C-Vertebrates Only Trait Database (Representation in C-Vertebrates Only Trait Database, %)	60 (7.1)	655 (77.7)	40 (4.7)	88 (10.4)	843

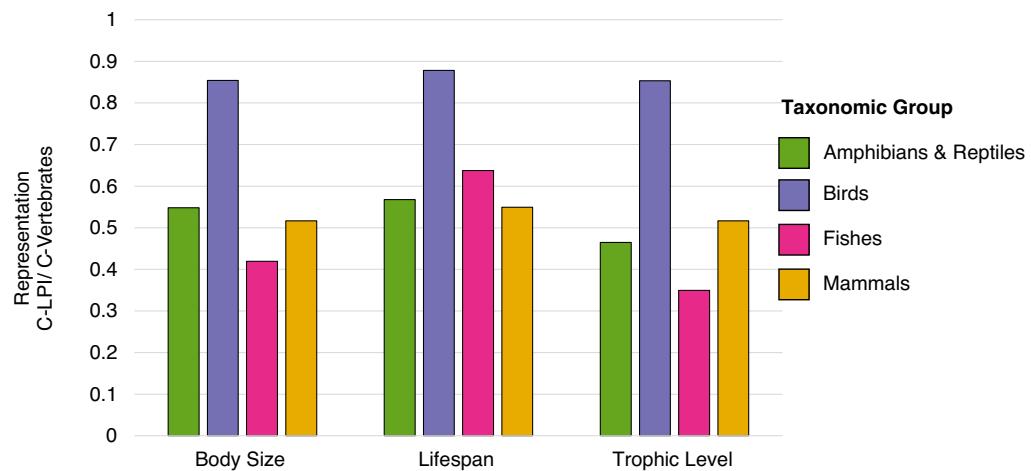


Fig. 1. Data availability for assessing the distribution of species traits. Bars depict the representation of species with trait data in the Canadian Living Planet Index, relative to the number of species with trait data for the broader vertebrate subphylum in Canada (C-Vertebrates).

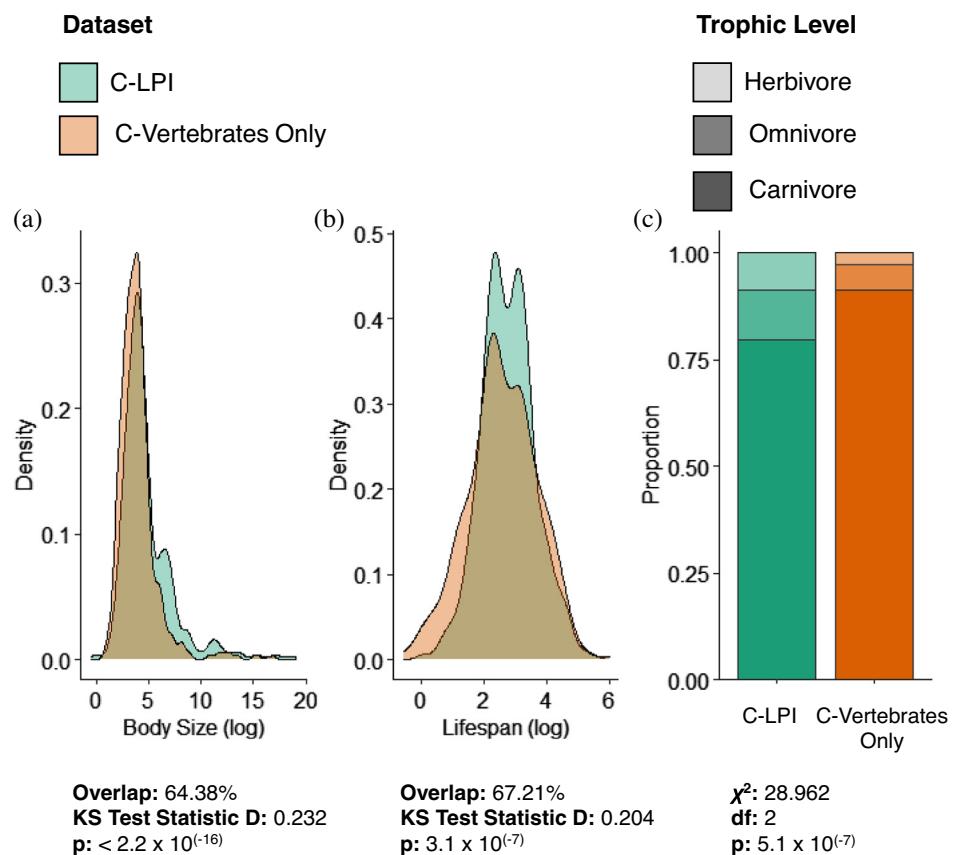


Fig. 2. Comparing distributions of (a) body size, (b) lifespan, and (c) trophic level for species included within the Canadian Living Planet Index (C-LPI) Trait database, compared to other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only).

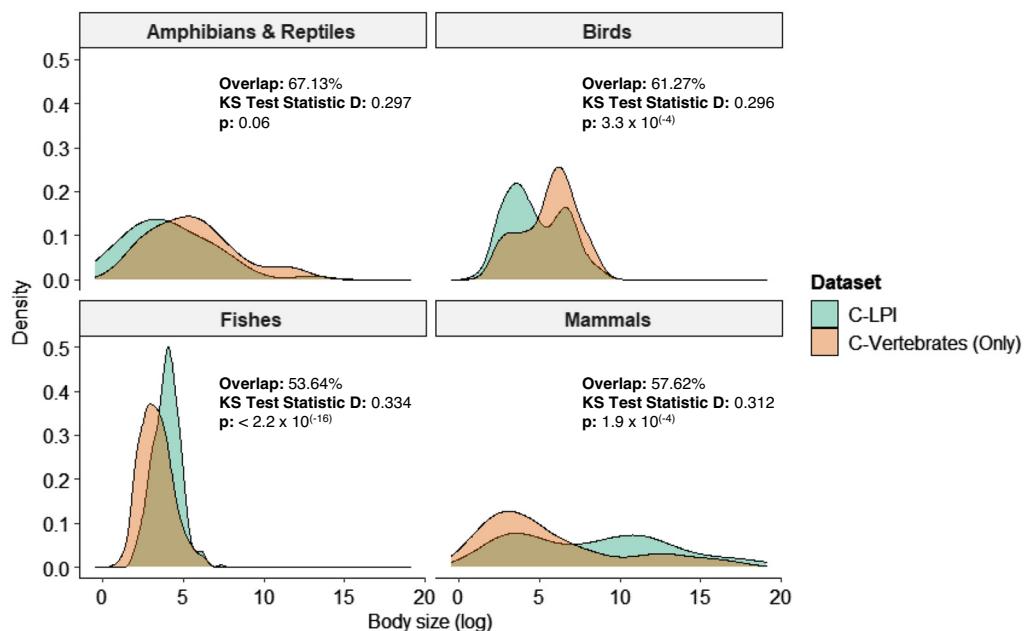


Fig. 3. Comparing distributions of bird, fish, herpetofauna, and mammal body size for species included within the Canadian Living Planet Index (C-LPI) Trait database, compared to other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only).

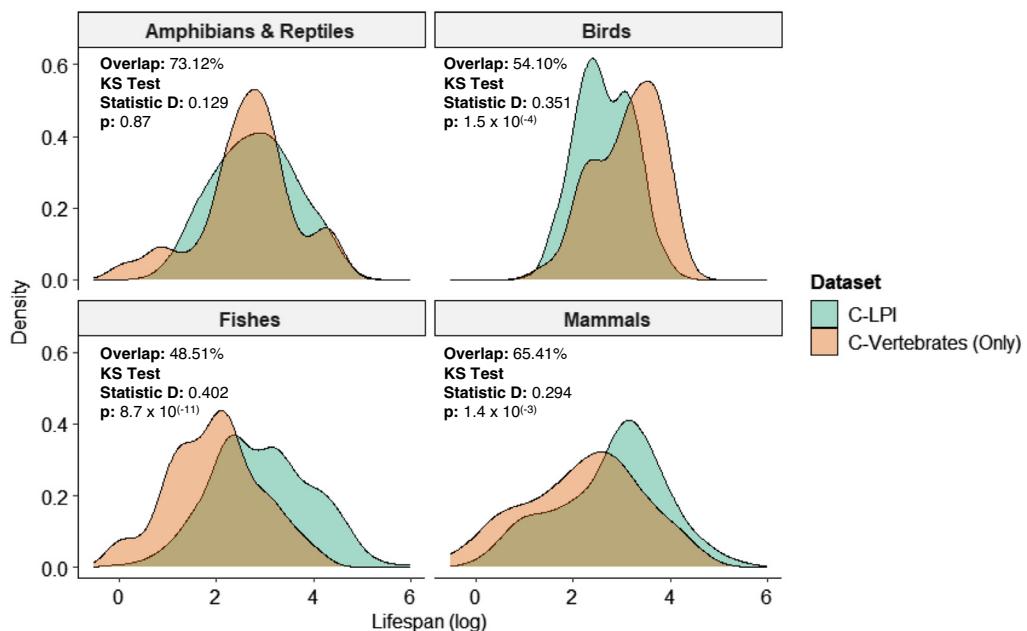


Fig. 4. Comparing distributions of bird, fish, herpetofauna, and mammal lifespan for species included within the Canadian Living Planet Index (C-LPI) Trait database, compared to other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only).

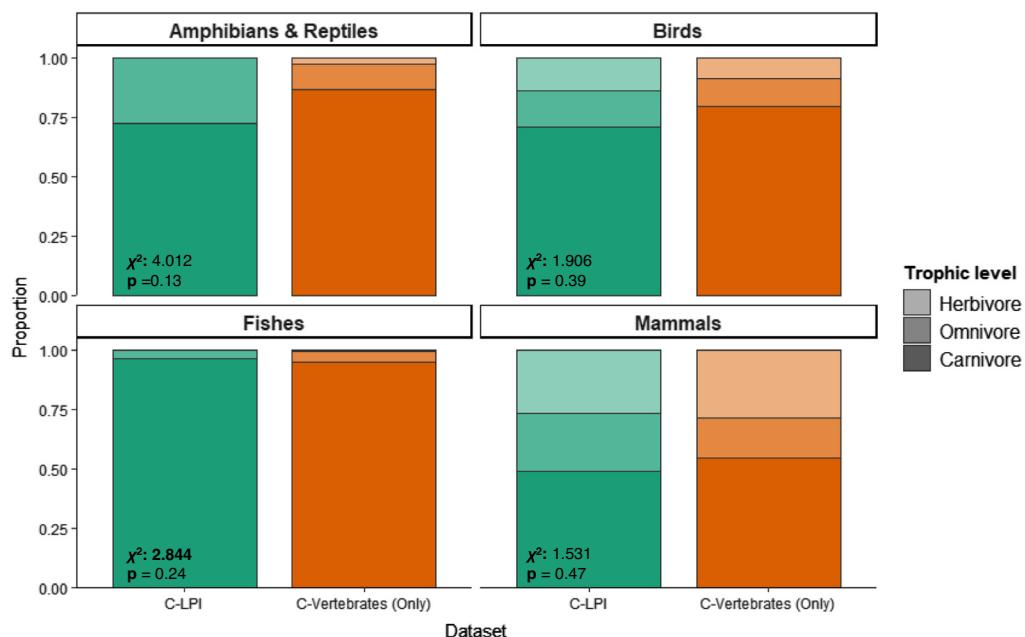


Fig. 5. Comparing distributions of bird, fish, herpetofauna, and mammal trophic level for species included within the Canadian Living Planet Index (C-LPI) Trait database, compared to other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only).

Although the distribution of biotic variables for species within the C-LPI generally overlapped with species lacking LPI data (C-Vertebrates Only), we were able to pinpoint traits within taxonomic groups that may help to improve coverage across Canada. For instance, the C-LPI should work to incorporate temporal population estimates data for large birds and small fishes (Fig. 3)—which correlate to long-lived birds and fishes with short lifespans (Fig. 4)—in addition to carnivorous amphibians and reptiles (Fig. 5). These results are reinforced through a bootstrapping approach (i.e., repeated resampling with replacement to generate samples of the same size as the reference) that depicted considerable overlap between the bootstrapped datasets, yet small differences among distributions were detected when assessing all species combined for body size (median difference between groups = -0.72, 95% CI = -0.87, -0.56; Fig. S3) and lifespan (median difference between groups = -0.45, 95% CI = -0.64, -0.27; Fig. S4). Likewise, some differences among distributions were also apparent when evaluating individual taxonomic groups, particularly for fishes (Fig. S5 and Fig. S6).

Fishes also had the poorest overlap in biotic traits when comparing the C-LPI to the broader vertebrate subphylum nationally (Table S6). Conversely, the overlap in body size (Fig. S8) and lifespan (Fig. S9) for birds improved largely due to bird data representation (i.e., sample size among datasets). Interestingly, trophic level representation among species in the C-LPI relative to the broader vertebrate subphylum nationally was nearly identical for birds, fishes and mammals (Fig. S10).

When imputing values to increase dataset coverage (and minimize biases resulting from the removal of species due to a lack of biotic trait data), the number of species in the C-LPI trait database grew from 836 to 850 species, while the number of species in the C-Vertebrates Only database grew from 843 to 852 species. Consequently, only a handful of additional species were added to the analysis, but the data coverage for biotic variables increased dramatically, particularly for fishes (Fig. S11). When using imputed data to enhance coverage of biotic variables, the distribution of body size,

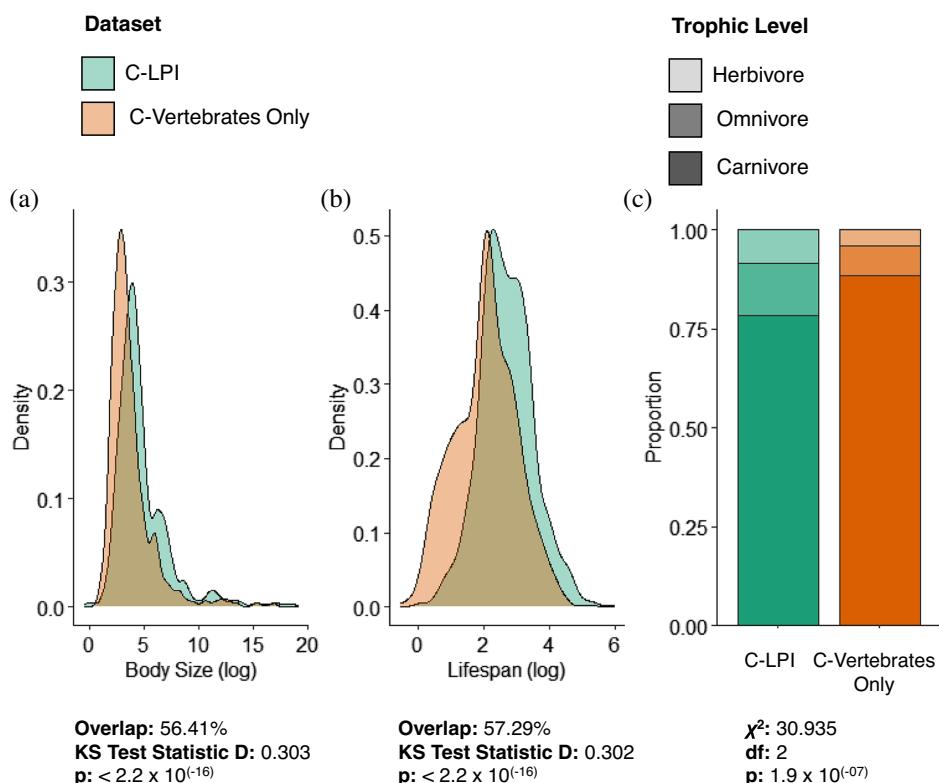


Fig. 6. Comparing distributions of (a) body size, (b) lifespan, and (c) trophic level for species included within the Canadian Living Planet IndexTrait database, compared to other native Canadian vertebrate species lacking LPI data (C-Vertebrates Only) using imputed data.

lifespan, and trophic level for species within the C-LPI exhibited slightly less overlap (>56% using imputed data compared to >64% for the original database) with the distribution of biotic variables for native Canadian vertebrate species lacking LPI data (C-Vertebrates Only) (Fig. 6). When imputing data, greater differences among distributions were found for all three biotic variables and despite improved data coverage, fishes still exhibited the smallest overlap in distributions relative to other taxonomic groups.

Discussion

Dataset description

The analysis presented here included at least some data for over 95% of native Canadian vertebrates, boasting impressive data coverage. However, data coverage for individual traits varied. In these instances, taxonomic biases known to exist within published biodiversity data may have been inherited within the compiled datasets for this analysis—including, for example, threatened species (Donaldson et al. 2016) or those with public appeal (e.g., charismatic species; Troudet et al. 2017). Birds were the best represented taxonomic group for each of the three biotic variables considered, largely attributable to the high representation of this taxonomic group within the dataset itself (Marconi et al. 2021). By contrast, the representation of trait data was more variable for fishes, where species with publicly available trait data ranged from 322 (of 1044 native species) for lifespan, to 792 for body size, and to 1018 for trophic level. The availability of this information for Canadian species is

consistent with data availability for other studies using Fishbase, which found fewer entries of lifespan and mortality, yet more data for growth parameters (Thorson et al. 2014). Importantly, while there now exists a plethora of publicly available information regarding species-specific life history characteristics on a global scale (e.g., Myhrvold et al. 2015; Froese and Pauly 2016), the information is not always accurate or precise (Thorson et al. 2014), and thus any subsequent analyses, such as the one presented here, would inherit the biases within the datasets used, including biases related to representation—the very component that we endeavored to assess. Similarly, while the imputed dataset helped to enhance biotic trait coverage, the overlap in distributions declined compared to the nonimputed dataset, and it's possible that biases were introduced, consequently affecting the results of the analysis.

Representation of biotic variables

Effective evidence-based wildlife management requires that conclusions and conservation decisions are informed by analyses of representative datasets and, where the data are not fully representative, recognition that such underlying biases may impact conservation approaches. Consequently, the interpretation of indicators is inherently tied to considerations of data representation. In the context of the C-LPI, the species and population time series underlying the index must be representative of the diversity of Canadian vertebrates to be an effective biodiversity indicator. Yet, despite boasting some of the best representation of species included within a national-scale abundance indicator, trends for approximately half of native Canadian vertebrates are lacking within the current dataset (Marconi et al. 2021). By evaluating and integrating the distribution of biotic traits for species within the C-LPI, compared to native Canadian vertebrate species lacking LPI data, we can target data gaps and recognize underlying data biases for more informed reporting of average trends in population abundance nationwide.

While the distributions of biotic variables from species within the C-LPI overlap with the distributions of those for native Canadian vertebrate species lacking LPI data, reinforcing the utility of the C-LPI at a national level, some notable discrepancies—and potential biases—nevertheless exist. For instance, the body size of fishes within the C-LPI skewed larger relative to the broader group of fishes in Canada. Most temporal population trend data for fishes were derived from marine Research Vessel Trawl Surveys conducted by Fisheries and Oceans (DFO) Canada (e.g., DFO 2020a, 2020b, 2020c), resulting in a bias towards marine over freshwater species and towards commercially important species. Although DFO trawl data date back to the 1940s, stratified random sampling for temporal evaluation of biological information was introduced in the 1970s, resulting in substantial temporal data coverage within Canada's Exclusive Economic Zone (Smith and Somerton 1981). Annual Research Vessel surveys on both Pacific and Atlantic coasts are conducted using trawls (i.e., standardized equipment for comparison), that are more tailored to sampling groundfishes, which include the greatest number and highest proportion of stocks classified as critical (ECCC 2021). Moreover, the primary purpose of these trawls is to gain species-specific information as a key component for science-based stock assessments for proper management of marine fisheries—often targeting larger fishes (Pauly et al. 2002). Consequently, this bias noted within the C-LPI is not particularly surprising. In fact, it is in many ways important that the data in body size skews towards large-bodied marine fishes compared to small-bodied species, as Canadian fishes are frequently threatened with overexploitation (Currie and Marconi 2020), less likely to receive legal protections under the *Species at Risk Act* (Mooers et al. 2007; Findlay et al. 2009), and large fishes are under greater threat of global extinction (Olden et al. 2007).

While there was large overlap in biotic traits between datasets, our results indicate that monitoring and data collection should target temporal abundance trends for small fishes and mammals and large birds, which are correlated with short and long lifespans, respectively. In addition, efforts should be made to enhance the representation of carnivorous herpetofauna, particularly reptiles, which

represent 70% of carnivorous herpetofauna not included within the C-LPI. Globally, abundance studies for reptiles are comparatively scarce ([Saha et al. 2018](#)). This additional data collection would further enhance the representation of biotic traits within the C-LPI, ensuring that it is as representative as possible, while recognizing that temporal population trend data likely does not exist for all vertebrate species in Canada. The number of species within the C-LPI doubled over the decade between the first national Living Planet Report Canada in 2007 ([WWF-Canada et al. 2007](#)) and the landmark update in 2017 ([WWF-Canada 2017](#)), owing to dedicated data collection efforts in recent years ([Marconi et al. 2021](#)). However, despite concerted efforts since, few additional species with publicly available temporal abundance data have been added to the C-LPI database ([WWF-Canada 2020](#)). Thus, targeted monitoring programs may be required for missing species and specific biotic traits to further enhance representation in the absence of publicly available abundance data.

This work builds upon the taxonomic and spatial representation of the dataset analyzed in [Marconi et al. \(2021\)](#), which has been used to assess threats to at-risk vertebrates in Canada and potential management actions for their recovery ([Currie and Marconi 2020](#)). Moreover, variations on the approach outlined in this analysis could be useful for evaluating a representative sample of vertebrates needed for calculating an LPI at national and (or) regional scales beyond Canada—a frequent question that has yet to be remedied, though studies are underway (Pata et al., A sampled approach to the Living Planet Index; in preparation).

Moving forward

The broad alignment of biotic traits uncovered through the analysis helps to reinforce the value of the C-LPI at a national level—including its use as an ecological indicator to track progress towards biodiversity goals, and as a tool for communication and policy. The C-LPI database is sufficiently representative of the biotic traits of Canadian vertebrates to produce representative indicators. Nevertheless, there are a variety of additional considerations, analyses, and data collection needed to further strengthen the applicability, accuracy, and precision of the indicator. We support calls for greater monitoring to address data gaps and ensure adequate representation of biodiversity within indicators ([Leung et al. 2022b; Murali et al. 2022](#)). Based on our analysis, data monitoring and collection in Canada could be targeted towards small fishes and mammals and large birds (correlating to short and long lifespans, respectively), in addition to carnivorous reptiles. The LPI (and derived indicators such as the C-LPI and CSI) are meant to reveal high-level, long-term trends in biodiversity. While full species representation may not be possible, targeted data monitoring and collection may serve to strengthen the indicator and its use for policy and communication.

From an indicator perspective, the C-LPI (and CSI) and current analysis are specific to native vertebrate species, which represent a small proportion of the 80 000 known species in Canada ([CESCC 2016](#)); thus, a more fulsome account of biodiversity trends may be needed to detect changes at multiple taxonomic and temporal levels, particularly as there is concern regarding population declines of invertebrates ([Sánchez-Bayo and Wyckhuys 2019](#)). Yet, despite recognition of the importance of monitoring vertebrate and invertebrate abundance as part of the Post-2020 Global Biodiversity Framework ([Williams et al. 2020](#)), data and capacity deficiencies for the diverse assemblage of invertebrates, plants, and fungi remain—so resourcing and monitoring should be prioritized accordingly ([Hochkirch et al. 2020](#)). Similarly, while enhanced representation of species strengthens the accuracy of the indicator, improving the geographic coverage of data collection to ensure that population trends wholly reflect patterns at a national scale will be critical in addressing geographic biases. [Buschke et al. \(2021\)](#) highlighted the usefulness of randomization null models for improving accuracy and presenting uncertainty around the LPI, which may be useful for overcoming random population fluctuations that can bias quantitative estimates. [Leung et al. \(2020\)](#) proposed investigating clusters of extreme decline or increase from the LPI to inform decision-makers and prioritize conservation

efforts, as averages tend to mask important trends. Yet moving beyond the use of the LPI as a biodiversity indicator to action, bending the curve of biodiversity loss (Mace et al. 2018) requires an integrated strategy underpinned by immediate effort and unprecedented ambition (Leclère et al. 2020).

Acknowledgements

We are grateful to the Living Data Project, led by Professor Diane Srivastava (UBC), for financially supporting our working group. We also thank Dr. Gracielle Higino for her help in organizing and facilitating the working group, and Francis Banville for his participation. We are grateful to Dr. Sally Otto and Dr. Xavier Harrison for their statistical expertise and guidance in strengthening the manuscript. The data used in our analyses have been collected by countless researchers and field technicians, so we thank them for sharing their hard-earned data and making this work possible. We acknowledge that Canada is colonized land; data have been collected on the traditional, ancestral, treaty, and unceded territories of many Indigenous Peoples, often without consultation or consent. Reconciliation requires that we progress in a way that respects Indigenous connections to these lands, with a shared sense of responsibility for the wildlife that call them home.

Author contribution statement

Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Visualization, Validation: JC, SAB, SE, KH, GX, NM, XW, AB, JBB, LG, VM, LM, SM, PP, RF

Funding acquisition, Project Administration, Supervision, Resources: JBB, VM, JC, LM, RF

Competing interest statement

The authors declare there are no competing interests.

Funding statement

This manuscript is a product of virtual working group supported by the Living Data Project (LDP), an initiative of the Canadian Institute of Ecology and Evolution. The LDP is funded by a Collaborative Research and Training Experience (CREATE) grant from the Natural Science and Engineering Research Council of Canada. We thank WWF-Canada and Environment and Climate Change Canada for enabling the creation of the dataset used in this manuscript over the years.

Data availability statement

All compiled trait data and associated code for this analysis are available from figshare at: doi.org/10.6084/m9.figshare.c.5901434.v3.

Supplementary material

The following Supplementary Material is available with the article through the journal website at doi:[10.1139/facets-2022-0063](https://doi.org/10.1139/facets-2022-0063).

Supplementary Material 1

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How climate change and population growth will shape attendance and human-wildlife interactions at British Columbia parks

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Words in the abstract: 195

Number of figures: 5

Words in main text: 4582

Number of tables: 0

Number of references: 66

Supplementary material: 0

Abstract

Protected areas are important for ecological conservation while simultaneously supporting culturally, and economically valuable tourism. However, excessive guest volumes strain operations and risk human-wildlife conflict, threatening the sustainability of nature-based tourism. Thus, park managers need to know what factors underpin attendance and how these might interact to shape future attendance. Using a decade of attendance records from 249 provincial parks, in British Columbia (BC), Canada, as well as 12 years of human-wildlife interactions (HWI) records at five national parks in BC, we modelled the impacts of weather conditions and population growth interact on park attendance and HWIs. We paired these models with climate change and population growth scenarios to generate projections of how attendance and HWIs will change throughout the century. Climate change is projected to result in more precipitation and higher temperatures, and, over this same time span, BC's population is expected to grow substantially. Based on the observed relationship between attendance and weather, parks should anticipate a marked rise in visitors and HWIs especially during their respective peak seasons. These projections provide park managers with the information required for proactive management, ultimately contributing to the sustainability of recreation and tourism in protected areas.

Keywords: Ecotourism; Human-wildlife conflict; Conservation; Recreation; Sustainability

1 **Introduction**

2 Conservation, tourism, and outdoor recreation have developed a long history of working in
3 tandem through protected areas toward mutually beneficial outcomes (Stronza et al., 2019).
4 Protected areas are essential for conservation: they play an important role in protecting local
5 flora and fauna, and they promote high species richness and biodiversity (Bass et al., 2010; C.
6 Chen et al., 2022; Gray et al., 2016; Margules & Pressey, 2000; Thomas & Gillingham, 2015). In
7 turn, many protected areas serve as culturally and economically important tourism and recreation
8 sites, offering significant economic value by way of employment (Eagles, 2002), GDP
9 contribution (Buckley, 2018), and the bolstering of local economies (Sangpikul, 2017; Taylor et
10 al., 2003). Indeed, the mental health benefits of visiting protected areas alone have been valued
11 at US\$6 trillion (Buckley et al., 2019). Yet, even though biodiverse protected areas can reinforce
12 tourism benefits and vice versa (Stronza et al., 2019), nearly 40% of protected areas worldwide
13 are operating under severe human pressure (Jones et al., 2018).

14 Guest volume is a pressing issue for park managers, as it strains operations and reduces
15 the quality of the visitor experience (Manning, 2001; Prakash et al., 2019). The presence and
16 behaviour of humans in protected areas can negatively impact wildlife through increased
17 zoonotic disease transmission (Charron, 2002; Monahan et al., 2009), a loss of biodiversity
18 (Nyhus, 2016), altered spatiotemporal patterns in habitat use, including habitat loss through
19 avoidance, behavioural change (e.g., conditioning, tolerance, predator shield; Lopez Gutierrez et
20 al., 2020; Prockto et al., 2023), and changes in energetics (Corradini et al., 2021; Gaynor et al.,
21 2018; Larson et al., 2016; Reed & Merenlender, 2008; Rogala et al., 2011; Sarmento & Berger,
22 2017; Whittington et al., 2022). Human sourced food and salts also act as attractants for many

23 species, generating human-wildlife-interactions (HWIs) that can result in the destruction of
24 individual animals (Hebblewhite et al., 2003; Vayro et al., 2023). Beyond the impacts on
25 wildlife, HWIs also pose a risk of physical endangerment to park visitors, property damage, and
26 a loss of recreational opportunities (Nyhus, 2016). As protected areas receive more guests, these
27 issues become amplified and HWIs become difficult to avoid, resulting in more frequent and
28 severe conflict (Cui et al., 2021; Geng, 2021). The managers of protected areas thus often find
29 themselves on the frontlines of socioecologically challenging human-wildlife-conflict issues. If
30 HWIs cannot be managed effectively, protected areas may face consequences that threaten their
31 ability to support both species conservation and the tourism and recreation industries (Rastogi et
32 al., 2015).

33 Because guest volume is a key driver of HWIs (Cui et al., 2021; Geng, 2021), it is
34 important to understand the factors that shape attendance, as well as how these might alter future
35 attendance. Attendance varies predictably with season and is sensitive to weather, as prevailing
36 weather conditions have a strong impact on the appeal of visiting a protected area and the types
37 of outdoor activities that park-goers participate in (Albano et al., 2013; Fisichelli et al., 2015;
38 Hadwen et al., 2011; Hewer et al., 2016). Protected areas thus have busy seasons, transitory
39 ‘shoulder’ seasons, and off seasons (Butler, 2001), which are primarily determined by
40 temperature and precipitation (Hewer et al., 2016), in combination with the activities available
41 within the protected area. For instance, areas known for skiing will be busiest in the winter, while
42 those used mainly for day hiking or swimming will be busiest in the summer. However, as
43 weather conditions are altered by climate change, such seasonal activities, could be jeopardised
44 and attendance rates may vary considerably (Nyaupane & Chhetri, 2009). The magnitude of
45 these changes will likely be compounded by population growth, since protected areas are likely

46 to experience a greater demand for outdoor recreation and tourism as the human population rise
47 (Balmford et al., 2009). It is thus essential to understand how climate change and population
48 growth will interact to shape visitor counts, HWI rates, and the sustainability of recreation and
49 tourism in protected areas.

50 The aim of this study is to provide an assessment of the impacts of future climate change
51 and population growth on park tourism in British Columbia, Canada. The Canadian province of
52 British Columbia (BC) is well known for its iconic outdoor recreation industry, which attracts
53 local and international tourists alike and contributes more than US\$11 billion in economic value
54 to British Columbians annually (Lloyd-Smith, 2021). Consequently, population growth and
55 climate change are likely to have a profound impact on the province's income and the
56 sustainability of outdoor recreation and nature-based tourism. All provincially protected areas in
57 British Columbia are managed by BC Parks, a governmental organisation that oversees more
58 than 1,000 protected areas, including conservancies, ecological reserves, and provincial parks
59 (BC Government News, 2021) under the dual mandate of conserving ecological diversity while
60 simultaneously promoting nature-based recreation. The recent growth in the popularity of
61 outdoor recreation and nature-based tourism has caused a rapid rise in provincial park visitors
62 (BC Parks, 2018), which, in turn, has been challenging park operations throughout Canada. In
63 Banff National Park, for instance, interactions with black bears (*Ursus americanus*) attracted to
64 the food brought in by park visitors results in high levels of management-induced bear mortality
65 and relocations (Hebblewhite et al., 2003). Similarly, high densities of visitors in BC's Cathedral
66 Provincial Park have been spurring an increase in mountain goat (*Oreamnos americanus*)
67 interactions, with reports of goats showing threat displays and forcing hikers off of trails (Balyx,
68 2022; Vayro et al., 2023).

69 While increasing guest volume and HWIs challenge the sustainability of tourism and
70 recreation in BC's parks, there has been no investigation into the potential drivers of these trends,
71 nor whether they might be expected to continue. Like other northern regions, BC's climate is
72 expected to get warmer and wetter over the coming century (T. Wang et al., 2016), which will
73 likely have pronounced impacts on its tourism industry (Gilani & Innes, 2020). Indeed, previous
74 work has suggested that nature-based tourism in Northern regions is likely to benefit from a
75 warming climate (Steiger et al., 2023). Alongside this trend, BC's population has nearly doubled
76 since 1980 (Government of British Columbia, 2022) and is presumed to continue growing
77 rapidly. BC's protected areas are therefore likely to experience notable changes in attendance
78 rates and HWI occurrence through the century as the climate changes and the population grows.
79 Our research will serve as a foundation for understanding and minimizing issues of over-
80 crowding and human-wildlife conflict, thereby contributing to sustainable tourism within
81 Canada's most biodiverse province.

82

83 **Methods**

84 **Empirical Data**

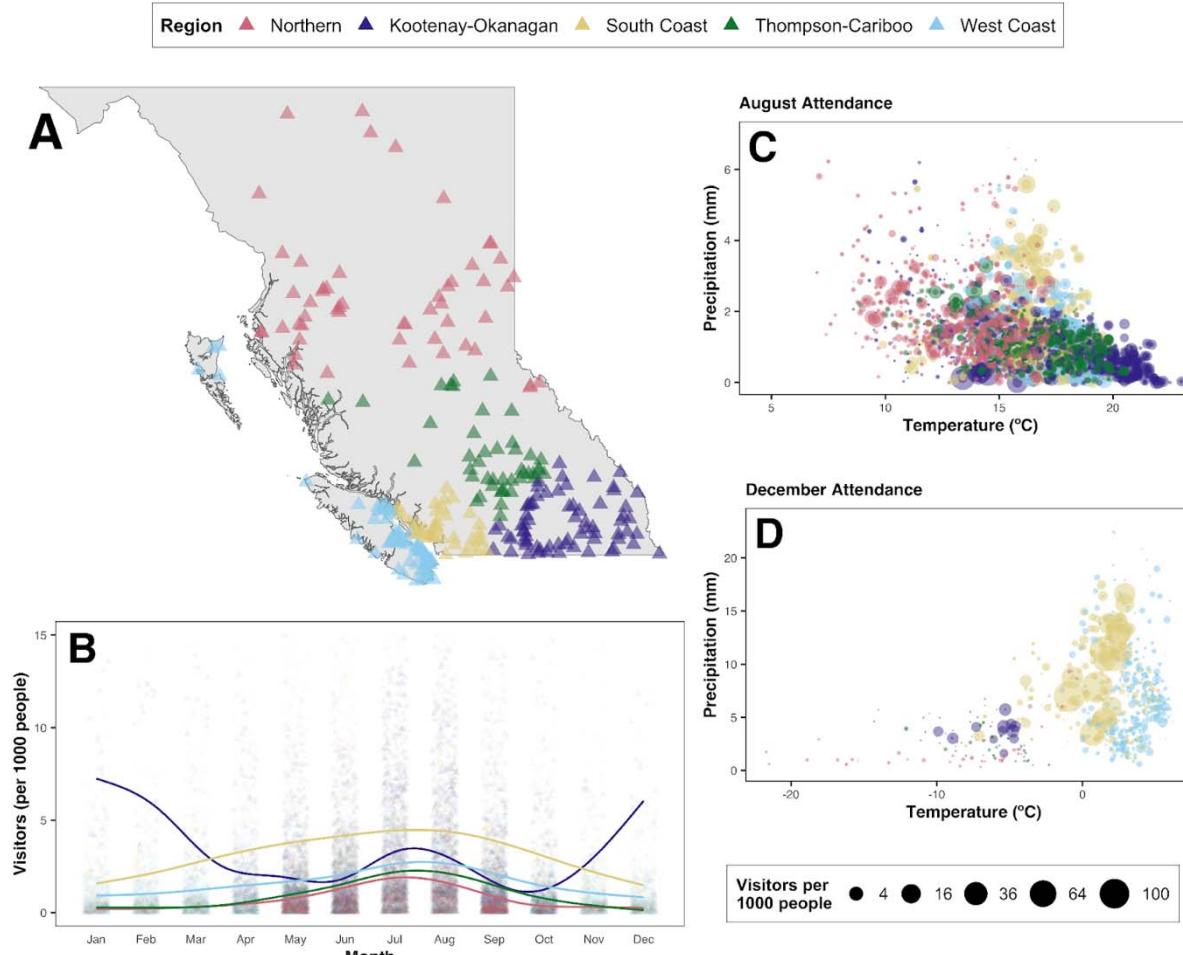
85 To understand drivers of park attendance, we analyzed nearly 13 years (January 2010 to August
86 2022) of day-use attendance records from 249 parks spanning all five of BC Parks' management
87 regions: Northern, South Coast, West Coast, Thompson-Cariboo, and Kootenay-Okanagan (Fig.
88 1A). While records of camping were also available for these parks, campsites within the province
89 are limited and generally reserved months in advance and are thus unlikely to reflect decisions
90 based on short-term weather conditions. We thus focused solely on trends in day-use attendance.
91 Attendance records were obtained directly from BC Parks. These data were collected by BC

92 Parks operators using a standardised protocol that estimates visitor counts based on vehicle
93 counts, with buses estimated as 40 visitors and regular vehicles counted as 3.5 visitors. These
94 counts were then totalled for each month and then standardised to ‘visitors per 1,000 people’
95 based on BC population data obtained from Statistics Canada (Statistics Canada, 2019).
96 Instances of missing visitor counts for a month could not be assumed to indicate no park visitors,
97 and so were treated as NA values. The resulting dataset consisted of 16,469 monthly attendance
98 records, detailing an estimated 41,341,600 individual visits to parks in BC.

99 To characterise trends in HWIs, human-wildlife coexistence incidents data were obtained
100 from the Government of Canada’s Open Government database. The Open Data Record dataset is
101 compiled by the Parks Canada Agency and contains records of human-wildlife coexistence
102 incidents from January 2010 to December 2021 for thirty-five national parks and historic sites.
103 Of the 9 incident types in the dataset, we focused solely on records that were classified as
104 ‘Human Wildlife Interactions’ within the five national parks in British Columbia (i.e., Glacier
105 National Park of Canada, Kootenay National Park of Canada, Mount Revelstoke National Park
106 of Canada, Pacific Rim National Park Reserve of Canada, and Yoho National Park of Canada).
107 The individual HWI records were converted to total monthly counts prior to analysis. The
108 resulting dataset consisted of 460 monthly total HWI records describing 4,782 instances of HWI
109 over 136 months (12 years).

110 Data were cleaned, modelled, and visualized in R (version 4.2.2, R Core Team, 2022).
111 Historical and projected climate data (temperature, precipitation) were obtained from the open-
112 source climatenaR R package that accesses data from the ClimateNA software (T. Wang et al.,
113 2016). As the climatenaR package requires the location and elevation data of the study sites, the

114 coordinates for each park were obtained from Google maps, while the associated Digital
115 Elevation Model (DEM) was acquired using the elevatr package (Hollister et al., 2021).



116

117 **Figure 1. Visualisation of park attendance records.** (A) shows the geographic distribution of parks included in
118 this analysis ($n = 249$), coloured by management region. (B) illustrates average seasonal trends for each region from
119 2010 to 2019. Points represent total monthly visitors, while the smooth lines are average trends across each
120 respective region. (C) demonstrates the relationship between attendance (represented by the size of the points) and
121 weather for August. (D) shows the same relationship but for the month of December. Note that these figures are
122 purely for visualization of the trend lines and do not reflect the interactions later accounted for by our model.
123

124 Modelling Park Attendance and HWIs

125 To estimate the effects of weather on park attendance, we fit a Hierarchical Generalized Additive
126 Model (HGAM; Pedersen et al., 2019; Wood, 2011) with a gamma distribution and a log link
127 function data using the mgcv R package (version 1.8-41, Wood, 2017). The gamma distribution

128 and log link were selected because the response variable, attendance (visitors per 1,000 people),
129 was continuous and strictly positive. The predictor variables included in this model were smooth
130 terms of month, average monthly temperature ($^{\circ}\text{C}$), and average monthly precipitation (mm). We
131 also included tensor interaction terms between month and temperature, month and precipitation,
132 and temperature and precipitation, as the effect of temperature and precipitation depends on the
133 month (e.g., people may avoid hiking on a cold and rainy summer day, but they will enjoy skiing
134 with crisp and snowy weather). This model structure allowed us to tease apart the effects of
135 weather on attendance from the seasonal cycle. A cyclic cubic spline was used to account for the
136 cyclical nature of the response variable over the seasons (Fig. 1B). In addition, park ID was
137 included as a random effect to account for differences between parks.

138 To estimate the effects of weather on HWIs, we fit an HGAM with a Poisson distribution
139 and a log link function using the mgcv package. The Poisson distribution and log link function
140 were selected because the response variable was strictly positive count data. The HWI model
141 included smooth predictors of month, average monthly temperature ($^{\circ}\text{C}$), and average monthly
142 precipitation (mm). Similarly with our attendance model, we also included tensor interaction
143 terms between month and temperature, month and precipitation, and temperature and
144 precipitation, as the effect of temperature and precipitation depends on the month. Here again,
145 this model structure allowed us to tease apart the effects of weather on HWIs from the seasonal
146 cycle. As with our attendance model, we also included interactions between month and
147 temperature, month and precipitation, and temperature and precipitation. Again, a cyclic cubic
148 spline was used to account for the cyclical nature of the month term, and park was included as a
149 random effect to account for differences between parks.

150

151 **Projections Under Climate Change and Population Growth Scenarios**

152 Using the HGAMs, we projected day-use attendance and HWI rates for the current century based
153 on the combined effects of future climate change and population growth. As future climate
154 depends heavily on many unpredictable factors, including global economics and politics,
155 technological improvements, pollution, and energy and land use (van Vuuren et al., 2011), we
156 produced predictions for each of the Intergovernmental Panel on Climate Change (IPCC)'s
157 Shared Socioeconomic Pathways (SSPs; see Chen et al., 2021): SSP 1-2.6 (sustainability), SSP
158 2-4.5 ('middle of the road'), SSP 3-7.0 (global inequality), and SSP 5-8.5 (continued fossil-
159 fueled based development). Under each of these scenarios, climate change is expected to result in
160 higher temperatures and more precipitation in BC, though the magnitude of these changes is
161 scenario-specific (Wang et al., 2016). As noted above, projected climate data were obtained from
162 the open source ClimateNA software (Wang et al., 2016) via the climatenaR R package.

163 It is largely assumed that BC's population will continue to rise. Statistics Canada
164 (Statistics Canada, 2019) predicts BC population growth rates under 9 scenarios (high growth,
165 low growth, medium growth 1 through 5, slow aging, and fast aging) for three years: 2022-2023,
166 2032-2033, and 2042-2043. We extrapolated growth rates between these decades and beyond to
167 2100 using a generalized linear mixed-effect model via the R package lme4 (version 1.1-31,
168 Bates et al., 2015). Again, this model had a gamma distribution and a log link function.
169 According to our population growth model, BC's population is expected to increase under all
170 population growth scenarios (see Supplementary Material). We focused primarily on the high
171 and low growth scenarios, but projections for all 9 population growth scenarios are openly
172 available on our GitHub repository (link below).

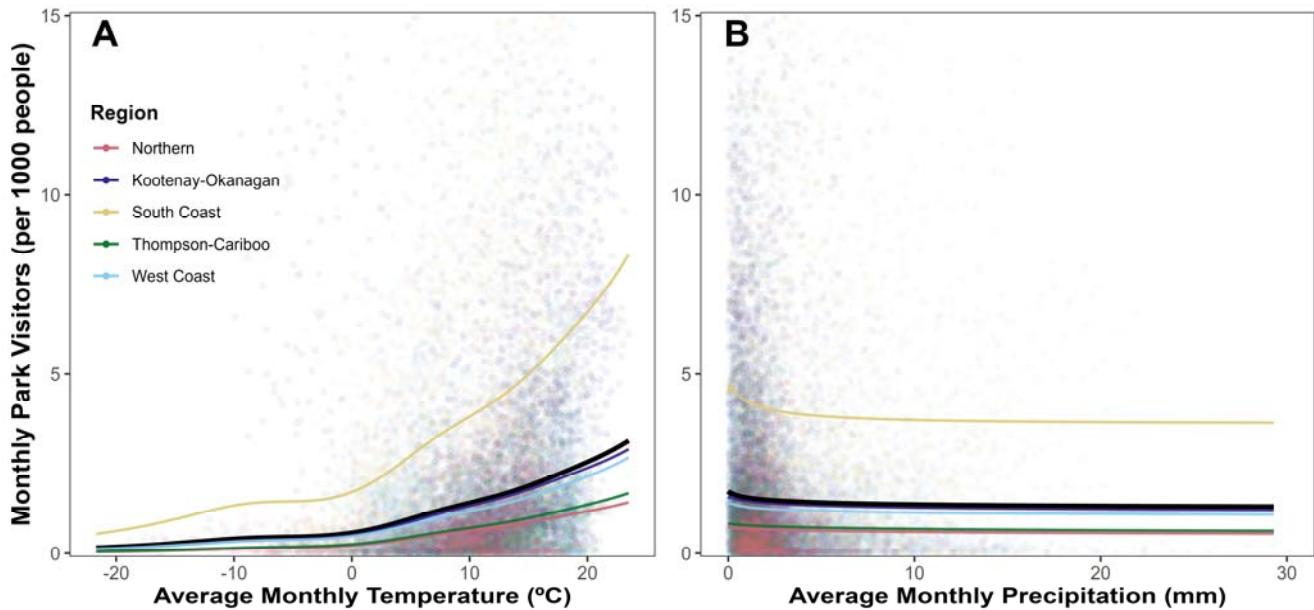
173 All the data, R scripts, supporting figures, and supplementary material are openly
174 available at https://github.com/QuantitativeEcologyLab/BCParks_Attendance.

175

176 **Results**

177 **Weather, Seasons, and Park Attendance**

178 Overall, we found that prevailing weather conditions and season had substantial impacts on park
179 attendance. Attendance was positively correlated with temperature (Fig. 2A), with summer (June
180 through August) being the peak season for most regions (Fig. 1B). There was also a negative
181 relationship between park attendance and precipitation, with heavier rains tending to result in
182 lower attendance, although the effect of precipitation was much weaker than the effect of
183 temperature trends varied (Fig. 2B). Importantly though, the relationship between attendance and
184 weather changed based on the seasonal context, and park attendance was impacted by both the
185 marginal and interaction effects of temperature, precipitation, and time of year. For instance,
186 parks tended to receive fewer visitors in unusually warm summers, but they received more
187 visitors during unusually warm winters (see e.g., Fig. 1C, and 1D).



188

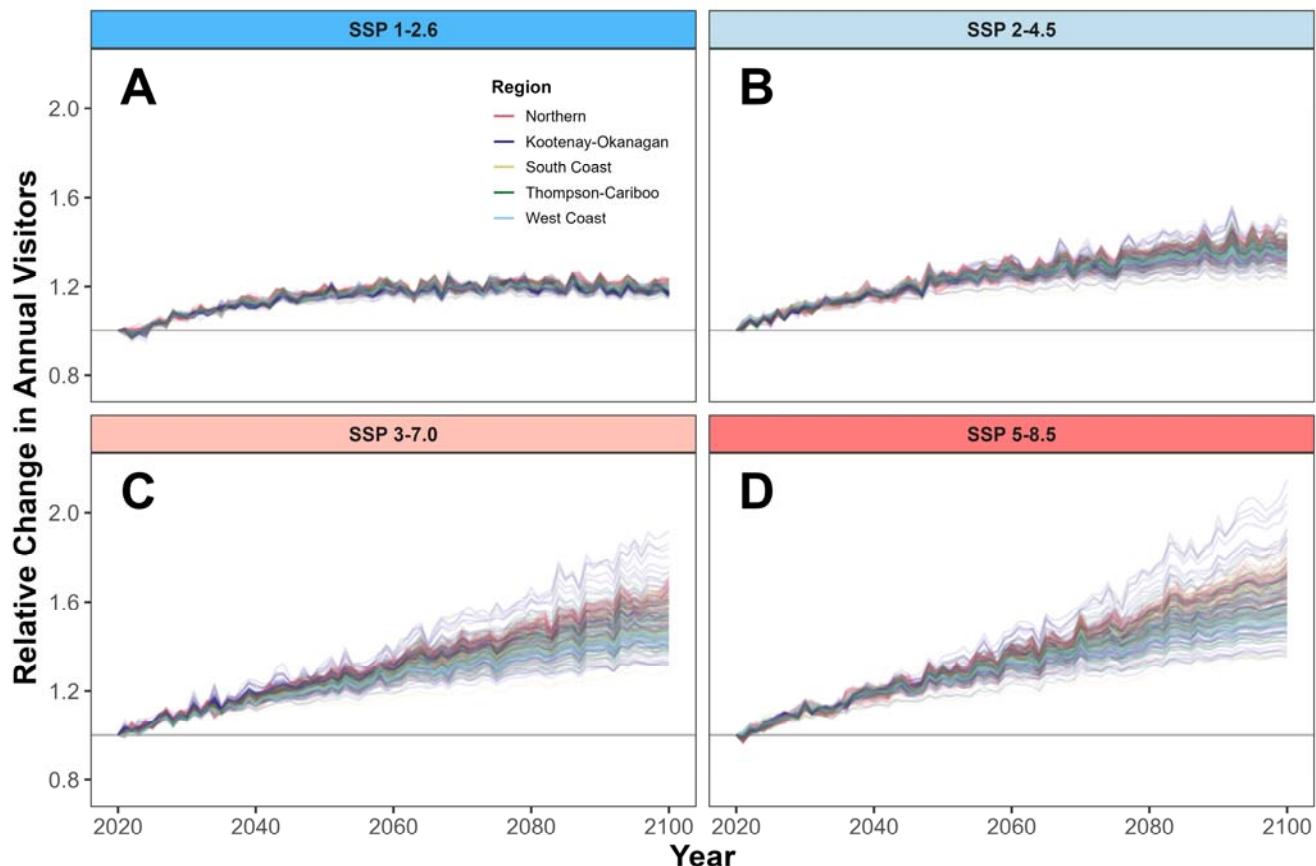
189 **Figure 2. Relationship between BC Parks attendance and weather.** Observations are represented by points, while
190 the coloured lines show the model-predicted trends in regional attendance. (A) shows a positive, non-linear
191 relationship between the number of visitors and average monthly temperature overall, although regions differ in
192 exact trends. (B) shows that increasing precipitation generally has a negative, though relatively weak impact on
193 attendance.

194

195 Climate Change and Projected Attendance

196 Due to the strong relationships between park attendance and weather conditions, visitation was
197 generally projected to increase under each of the climate change scenarios (Fig. 3). However, the
198 magnitude of increase differed strongly between scenarios. Under SSP 1-2.6 (the more optimal
199 pathway), attendance rates were little changed, with only a ca. 20% increase in attendance. In

200 contrast, attendance was projected to nearly double under the most drastic scenario (SSP 5-8.5).



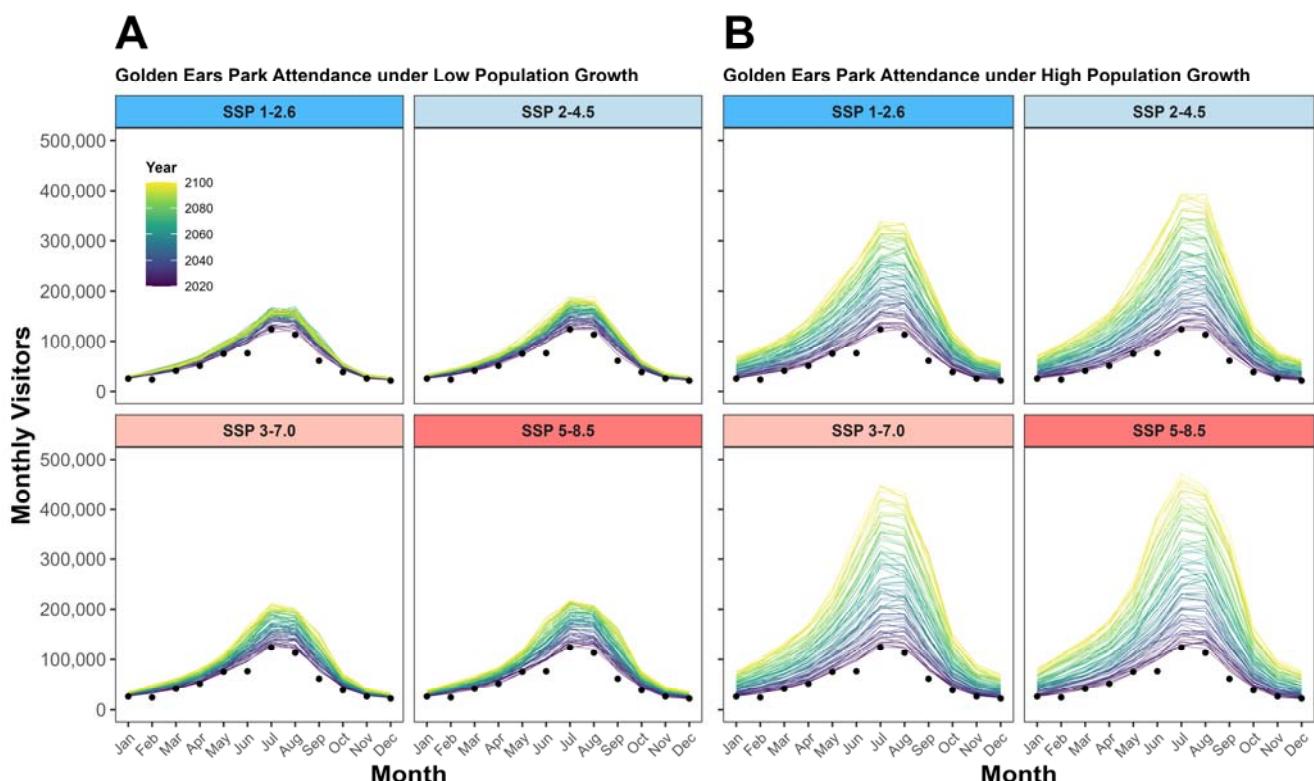
201

202 **Figure 3. Attendance projections for 249 parks.** Each line represents one park's change in visitors relative to 2020.
203 Projection lines are coloured by region and are presented for the four climate change scenarios corresponding to
204 each Shared Socioeconomic Pathway (SSP) hypothesized by the IPCC. The horizontal grey line at 1 indicates no
205 relative change in attendance. These panels exclusively show the effect of climate change on park attendance; the
206 effect of population growth is not visualized here.
207

208 Case Study: Golden Ears Park

209 The results presented above serve as an overview of day-use park attendance in the upcoming
210 century. Notably though, the values shown in figure 3 are on a relative scale, and the absolute
211 number of visitors will also depend on population growth. To examine how the model projected
212 seasonal trends under different combinations of climate change and population growth, we
213 investigated Golden Ears Park as a case study. Our projections suggest that, under any
214 combination of scenarios, Golden Ears Park will experience a substantial rise in visitors moving

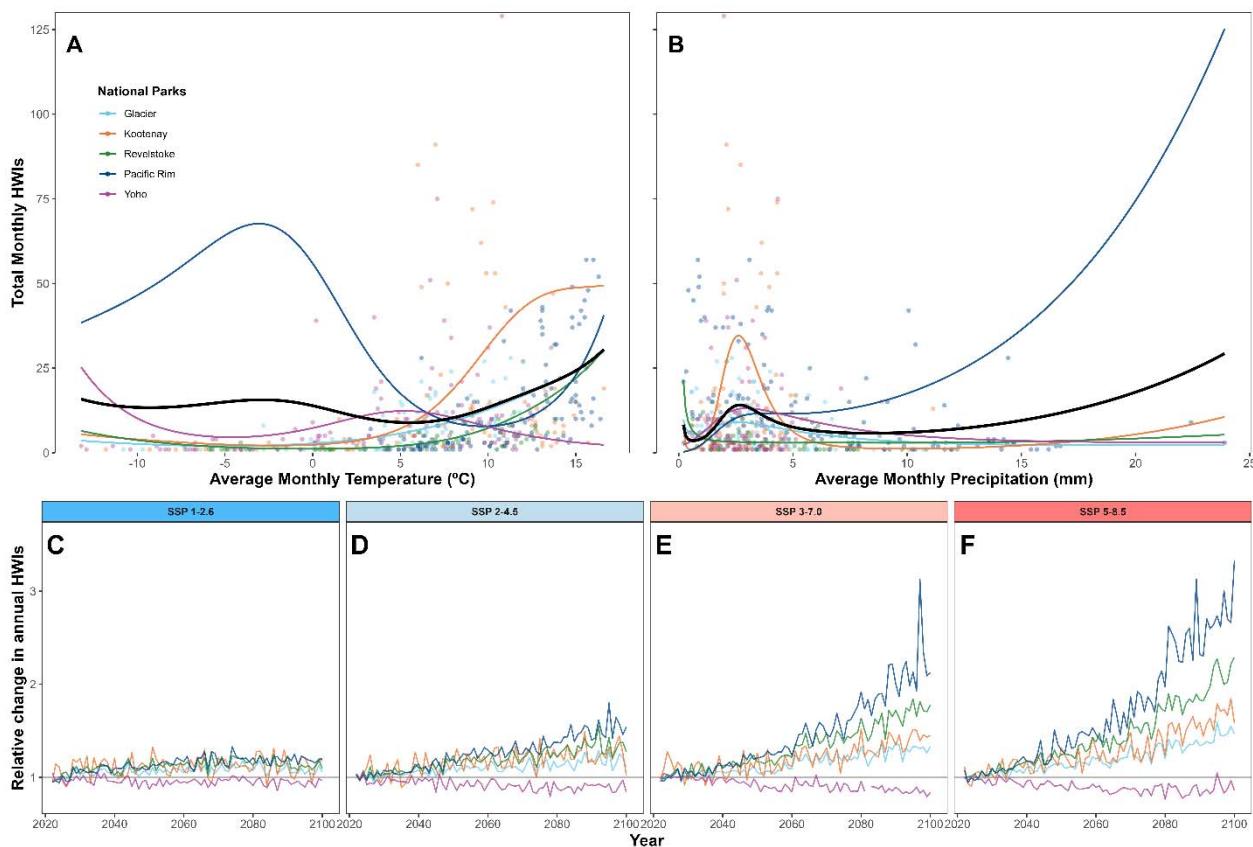
215 forward (Fig. 4). Consistent with the general trends described above, the lower-emissions climate
216 scenarios (SSP 1-2.6 and 2-4.5) were projected to lead to fewer visitors than the higher-emissions
217 scenarios (SSP 3-7.0 and 5-8.5). Not only did our models project substantially busier peak
218 seasons, but it appears that shoulder seasons will quickly approach and succeed attendance rates
219 comparable to that of the current peak season. High levels of population growth further amplified
220 the effects of climate change on park attendance (Fig. 4B). While we only present results for
221 Golden Ears Park here, similar patterns were observed across all 249 parks (Supplementary
222 Material).



224 **Figure 4. Attendance projections for Golden Ears Park under different population growth and climate change**
225 **scenarios.** Average historical attendance from 2010 to 2019 is represented by black points. Projections are coloured
226 according to year, ranging from 2020 to 2100. Attendance rates depend on the climate change scenario (facets; SSP
227 1-2.6, SSP 2-4.5, SSP 3-7.0, and SSP 5-8.5) and the population growth scenario. (A) shows projected attendance
228 when BC is under a low population growth scenario, and (B) shows projected attendance for a high population
229 growth scenario.
230

231 **The Future of Human-Wildlife-Interactions**

232 When modelling HWIs, we found that the same weather conditions that drove more people to
233 visit parks also resulted in greater HWI rates. The number of HWIs was positively correlated
234 with temperature (Fig. 5A), and there was also a negative (albeit weaker) relationship between
235 HWIs and precipitation (Fig. 5B). Consequently, HWIs were projected to increase under all four
236 climate change scenarios we investigated (Fig. 5C-F). As with park attendance, we found
237 markedly different outcomes depending on which climate change scenario we assumed would
238 occur. Under the lower emissions scenarios like SSPs 1-2.6, our model projected a minor (ca.
239 10%) increase in HWIs. In contrast, the 'worst-case' climate change scenario (SSP 5-8.5) is
240 expected to result in a substantial increase in the number of HWIs, though projected trends still
241 differ between parks.



242
243 **Figure 5. Effects of temperature and precipitation on human-wildlife interactions and projections for the**
244 **current century in BC national parks.** The top row shows the relationship between the number of human-wildlife

245 interactions (HWIs) and average monthly (A) temperature and (B) precipitation. Observed HWIs are represented by
246 points, while thin coloured lines show park specific trends and overall trends are represented by thick, black lines.
247 The bottom row depicts the projected relative change in HWIs for these parks. Each line represents one park's
248 annual change in HWIs relative to 2022 for the four climate change scenarios. The horizontal grey line at 1 indicates
249 no relative change in annual HWIs.
250

251 **Discussion**

252 This study sought to model and project trends in attendance and human-wildlife-interactions in
253 British Columbia's protected areas through to the end of the next century. This work allows park
254 managers to make proactive management decisions that will help ensure the sustainability of
255 nature-based tourism within the province. Our findings are consistent with recent work by
256 (Steiger et al., 2023), who found that nature-based tourism in Northern regions, such as British
257 Columbia, is likely to benefit from a warming climate. Notably though, increased attendance is
258 not necessarily a beneficial outcome, as high volumes of guests can strain operations (Manning,
259 2001) and negatively impact wildlife (Cui et al., 2021; Geng, 2021). Indeed, we found that the
260 same weather conditions that drove more people to visit parks also resulted in more HWIs,
261 highlighting the intrinsic relationship between weather, park attendance, and HWIs. If not
262 properly managed for, climate change-driven increases in attendance and HWIs risk challenging
263 the sustainability of nature-based tourism within British Columbia's network of protected areas.

264 The tight correlation between attendance and weather was not surprising. It is well
265 recognised that weather shapes the appeal of visiting a protected area and the types of outdoor
266 activities that park-goers will participate in (Albano et al., 2013; Fisichelli et al., 2015; Hadwen
267 et al., 2011; Hewer et al., 2016). Importantly, however, we were able to tease apart the effects of
268 weather from the seasonal cycle (Hadwen et al., 2011) and leverage these relationships to project
269 attendance and HWIs through to the end of the century. While there is debate as to which climate
270 change scenario is considered the most likely outcome based on past and current trends

271 (Hausfather & Peters, 2020; Schwalm et al., 2020), the goal of our work was not to assess the
272 probability of each pathway, so we provide predictions for each of the SSPs. It is also important
273 to note that we projected total expected HWIs across all species, yet there will likely be
274 interspecific differences in HWIs. Black bears and mountain goats, for instance, are often
275 attracted towards people and HWIs may increase for these species if animals are rewarded with
276 resources or predator shields (Balyx, 2022; Hebblewhite et al., 2003). Other species such as
277 wolves (*Canis lupus*) or caribou (*Rangifer tarandus tarandus*) tend to avoid or change their
278 behaviour in areas where humans recreate (Gill et al., under review; Rogala et al., 2011), which
279 would result in a reduction in HWIs with rising park attendance. Future research should aim to
280 identify the effects of increasing visitor volumes across species (e.g., Procko et al., 2023).

281 Rising attendance rates and HWIs have the potential to severely disrupt the day-to-day
282 operations of protected areas, particularly in the case of highly crowded parks, and threaten the
283 sustainability of nature-based tourism (Stem et al., 2003; Stronza et al., 2019). While increasing
284 the number of parking spaces, trails, campsites, and guest facilities may mitigate operational
285 challenges caused by overcrowding, these solutions can result in a loss of conservation value in
286 parks (Jones et al., 2018; Sarmento & Berger, 2017; Stronza et al., 2019), violating the dual
287 mandate that BC Parks and similar organizations operate under. To mitigate these challenges, we
288 recommend that park managers make proactive decisions based on projections such as those
289 presented here, in order to be better prepared for the increase in attendance and HWIs they are
290 likely to experience over the coming decades. In the near term, an increase in staff may help
291 alleviate the pressure of additional visitors (including substantial increases during shoulder
292 seasons). Longer term, however, managers should carefully evaluate their seasonal carrying
293 capacities (Manning, 2001) and consider imposing guest limits. Yet rather than taking a one-size-

294 fits-all approach, managers should make decisions on a park-by-park basis (Baker, 1992), and
295 actively consider how higher attendance rates will affect each unique park and what further
296 action must be taken to comply with BC Parks' dual mandate. To assist in understanding
297 individual park trends, we generated detailed projections for all 249 parks (available in our
298 public GitHub repository; see the data availability statement).

299 Though our models were able to accurately capture trends in the historical data, there are
300 many consequences of climate change that could influence attendance but are not accounted for
301 in our predictions. For instance, our model did not account for thermal thresholds at which
302 people might lose interest in visiting a park, whether it be because temperatures are too high or
303 too low (Fisichelli et al., 2015). However, research by (Hewer et al., 2016) suggests that parks
304 may still experience a rise in annual visitors despite exceeding a maximum thermal threshold.
305 Extreme climatic events such as heat domes, wildfires, and flash floods also have the potential to
306 severely disrupt tourism and recreation in protected areas (Nyaupane & Chhetri, 2009). Although
307 it was beyond the scope of this study to make predictions about the future occurrence of natural
308 disasters, the frequency of these events is expected to increase in the current century (X. Wang et
309 al., 2015), so managers should strategize methods of managing protected areas based on parks'
310 unique attributes (Baker, 1992). Additionally, it is worth noting that our projections were based
311 on average monthly predictions of future temperature and precipitation. Consequently, our
312 predictions do not account for weather variations within months, including short-term extreme
313 weather events. Changes in snow cover (and changes in the frequency of avalanches) are also
314 expected to affect park attendance, but we did not include snow data in the present study due to a
315 lack of snow cover projection models.

316 In addition to extreme weather events, climate change is also predicted to have ecological
317 consequences that could affect park attendance. Wildlife is a major attraction for some BC Parks,
318 and peak seasons at these parks align with the timing of annual ecological events. For instance,
319 Rathtrevor Beach Park is often attended for bird-watching opportunities when seabirds gather to
320 feed on spawning herrings in spring and Brant geese migrate in late winter (BC Parks, 2023b). In
321 contrast, the busiest season at Kokanee Creek Park is mid-August to mid-September, as this is
322 when visitors visit the park to see salmon spawning in the channels (BC Parks, 2023a). As the
323 climate changes, wildlife may shift the timing of reproduction or migration (Cadahía et al., 2017;
324 Matthysen et al., 2011; Moyes et al., 2010), which will likely change the timing of peak months.
325 Further research might thus explore local phenology in response to climate change to predict the
326 future peak seasons in parks with wildlife attractions.

327

328 Conclusion

329 This study provides insight into the patterns of park attendance and HWIs during the coming
330 century, along with a valuable framework for modelling and predicting the two. We have
331 demonstrated that both park attendance and HWI frequency will increase in the next few
332 decades, regardless of which climate change or population growth scenarios occur.
333 Consequently, proactive management is urgently required by BC Parks. Without adequate
334 planning, human-wildlife conflict will likely escalate, which will challenge BC Parks' dual
335 mandate and render recreation in these parks unsustainable. Park managers should use these
336 findings to plan for more visitors and avoid cases of human-wildlife conflict, ultimately
337 sustaining the viability of nature-based tourism.

338

339 **Funding details:** This work was supported by an NSERC Discovery Grant RGPIN-2021-02758,
340 the Canadian Foundation for Innovation, as well as the BC Parks Living Labs funding program.

341 **Disclosure statement:** Authors declare that they have no competing interests.

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353 Michael Noonan is a quantitative ecologist and head of the Quantitative Ecology Lab at the
354 University of British Columbia Okanagan. Noonan's research is focused on protecting vulnerable
355 species by using data-driven approaches to ensure that the evidence used to support evidence-
356 based conservation is both accurate and reliable.

357 **Data availability:** The data and R scripts used to carry out this study are openly available on
358 GitHub at https://github.com/QuantitativeEcologyLab/BCParks_Attendance.

359

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