LINKING RESOURCE ABUNDANCE AND ENVIRONMENTAL STOCHASTICITY WITH ANIMAL SPACE USE USING CONTINUOUS-TIME STOCHASTIC PROCESSES

by

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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:

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submitted by Stefano Mezzini in partial fulfillment of the requirements of the degree of Master of Science.

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Abstract

281/350 words

The ability to move allows animals to access more resources and decrease the risk of mortality or injury from various threats, including predation and competition. However, most motile animals depend on movement to achieve an energetic balance, survive, and reproduce. Animals' spatial needs depend on a multidute of factors, including resource abundance, competitive pressure, predation, weather, and climate. The effects of many of these factors have been studied extensively, but the effects of environmental heterogeneity and unpredictability remain largely understudied. This thesis aims to quantify how resource abundance and environmental variation affect animals' spatial needs using theoretical arguments, computational simulations, and a large animal movement dataset of over 1500 individuals from more than 75 species. To this end, this thesis will produce a new global measure of environmental variance which will be used to quantify the effect of environmental heterogeneity and stochasticity on animals' spatial needs while accounting for spatiotemporal trends and correlations within populations and species. The animals' movement will be modeled using continuous-time stochastic movement models. The effects of environmental variance on animal's spatial needs will be estimated using hierarchical generalized additive models that account for common trends between taxonomic groups and populations. The work will be carried out within a framework that recognizes the value of different forms of knowledge, including Traditional Indigenous Knowledge, and it will incorporate Traditional Indigenous Knowledge when possible. Overall, I expect spatial needs to be lower in areas with higher resource abundance and lower environmental variance. However, I also expect the effects of resource abundance and environmental variance to depend on the species and ecosystems of interest. Thus, the average trends between species may not be representative of individual populations and species.

Lay Summary

Many factors affect how much space animals need to survive and reproduce. The effects of many factors have been studied extensively, such as resource abundance, competitive pressure, predation, weather, and climate. However, the effects of environmental heterogeneity and unpredictability remain understudied. This thesis aims to quantify how resource abundance and environmental variation affect animals' spatial needs using a large animal movement dataset. This thesis will produce a global measure of environmental variance which will be used to quantify the effect of such variance on animals' spatial needs while accounting for spatiotemporal trends and correlations within populations and species. The work will be carried out while recognizing the value of different forms of knowledge, including Traditional Indigenous Knowledge. I expect spatial needs to be lower in areas with higher resource abundance and lower environmental variance, although this will likely depend on the species and ecosystems of interest.

Foreword

Two-eyed seeing: Recognizing Traditional Indigenous Knowledge

The lands managed and protected by Indigenous Peoples are often markedly different from those inhabited by urban societies. While recognizing that there is great diversity between Indigenous Peoples (as well as other colonized Peoples), it is important to recognize that many hold great knowledge on how to live sustainably, safeguard environments, and protect biodiversity (Schuster *et al.*, 2019), and have been doing so for millennia. Yet, their leaders and representatives are seldom included in conservation-related decision-making. Instead, many Western institutions often dismiss, ignore, and contradict the ancestral and traditional Knowledge of Indigenous and colonized Peoples (Kimmerer, 2020; Smith, 2021). The development of Western science is frequently assumed to clash with the (often sacred) Knowledge many colonized People hold. Western science is often viewed as more objective, methodical, and unbiased than traditional Knowledge, and as such Western institutions and people often consider it to be superior to Indigenous Knowledge (Smith, 2021). However, it is common for Western institutions to (reluctantly) reach similar, if not identical, conclusions as those held by Indigenous people (Kimmerer, 2020; Smith, 2021; Bennett *et al.*, 2021). The refusal to recognize traditional Knowledge and cooperate with non-Western institutions often results in a loss of time, resources, and funds to the Western institutions and severe damage to the Land the institution operated on, as well as to the people who's ancestors inhabited the region for millennia (Smith, 2021). The development of Western science at the exclusion of Indigenous Peoples perpetuates colonialism and brings harm all parties involved.

The concept of *two-eye 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). One possibility, however, is to use Traditional Knowledge to create properly informed Bayesian priors (Bolstad & Curran, 2017). The validity of the priors can be ensured using prior predictive modeling (McElreath, 2016) to select priors that align with the Traditional Knowledge. This practice is not new (Girondot & Rizzo, 2015; Bélisle *et al.*, 2018), but it is rarely used, despite it aligning well with the philosophy of Bayesian statistics.

Although this project does not focus on Indigenous Knowledge or Data, I intend to carryout the work with an anti-imperial and anti-colonial stance, to combat problematic and questionable practices and views (rather than risking perpetuating them). 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 (including Westbank First Nation) to offer help in related fields 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). Regardless of whether collaborations will be possible, I will actively work on removing any form of colonial bias in my work and perspectives while also combating colonialism, imperialism, and other forms of oppression.

Contents

List of Tables

List of Figures

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

I would like to thank 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 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

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

1 Chapter 1: Literature review and quantitative predictions

1.1 Home ranges as proxies for animals' needs

The ability to move provides animals with the capacity to respond rapidly and continuously to heterogeneous and changing environments. Animals may move to search for resources (e.g., as food, nutrients, water, heat, a new den or nesting spot), a mate, or a new group. Movement also allows animals to escape predation or dangerous competition, and it allows them to defend resources and territory, too. Thus, we can estimate changes in animals' movement and space use as a proxy for many needs, rather than measuring changes in the various individual needs (Nathan *et al.*, 2008).

In this context, the concept of a home range (HR) has a long history in ecological research as an indicator of the space an animal requires to satisfy its essential requirements during a period of time (Burt, 1943, see figure 1). These include both energetic needs and reproductive needs (which are not limited to finding a mate, since offspring require energy a safe location to develop in, too), but exploratory movement outside the habitual HR are generally excluded. However, for an animal to have what we may consider a HR, the animal must remain in a stable "home" area for long periods of time (Noonan *et al.*, 2019). That is, the animal must be range-resident and the HR must have a stable centroid. Stable centroids may be concrete locations such as the dens or nests of central place foragers (*sensu* Orians, 1979), or they may be abstract points such as the center of an individual's foraging grounds. Thus, animals with an unstable centroid would not be appropriate for HR analysis. In addition, while an individual's HR may change over time (e.g., following a forest fire or a flood), it should remain stable during the period of observation. Ideally, properties of the HR (e.g., range size and structure) are representative of any new HR the animal will move to if the current one becomes inhospitable. For instance, an animal with a HR area of 1 km^2 would be expected to occupy a comparably sized area if it were displaced by a fire, assuming that the new habitat is sufficiently similar. Similarly, the movement of the individual within the HR (e.g., range crossing time τ_p, directional persistence τ_v) are also expected to be representative. Nomadic (e.g., Morato *et al.*, 2016; Nandintsetseg *et al.*, 2019) or migrating (e.g., Jonzén *et al.*, 2006; Abrahms *et al.*, 2019; Geremia

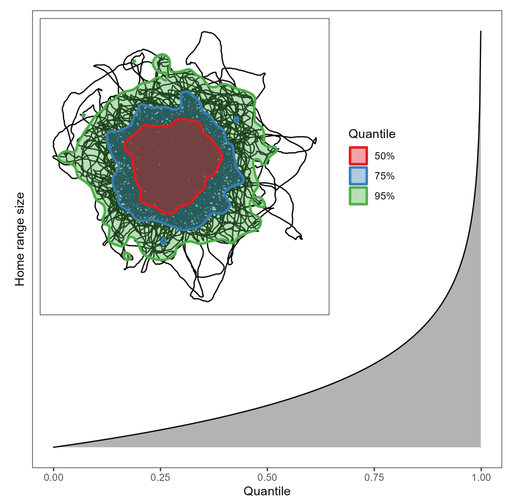

Figure 1: Inset: Simulated movement of an animal with a stationary home range centroid. The colored areas indicate the home range estimates for different quantiles. The red area indicates the core home range (50%), while the blue and green areas indicate the 75% and 95% home ranges, respectively. Main figure: Home range area as a function of utilization quantile. Note that as the quantile approaches 1, home range size approaches infinity, since if the animal was to move for an infinite amount of time, it would cover all possible space.

et al., 2019) animals are thus generally not considered range resident, and tracking periods should be long enough to provide a representative sample of the animal's spatial needs.

In the case of a species or population where spatial needs change over the animals' lifetimes (figure 2), one may define HR as a function of the animal's life stages (with distinct discrete HRs) or as a function of age (so HR changes smoothly). In either case, the accuracy of the estimate will depend strongly on the length of the observation period as well as the measurement frequency (Noonan *et al.*, 2019). Data from a portion of an animal's life may be sufficient if it is representative the animal's movement or if inference is limited to the period(s) for which data is available.

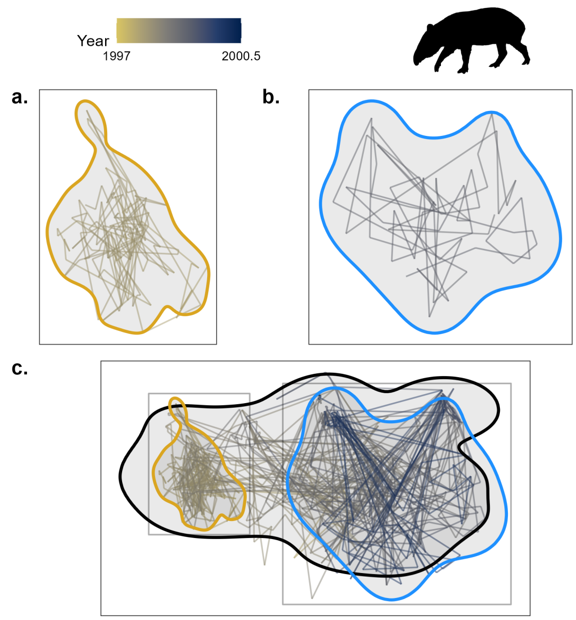

Figure 2: Movement of a tapir during a monitoring period of approximately 3 years (1997-07-10 to 2000-06-08) used in the work by Medici *et al.* (*in press*). Different subsamples may result in different estimates of home range size and centroid (a, b; each span 100 days), so neither subsample is necessarily representative of the space the animal used over the entire monitoring period (c).

There are many factors which may affect animal's spatial requirements and how they use their HR (*sensu* Nathan *et al.*, 2008). In particular, resource abundance is often assumed to be inversely proportional to HR size (or some function of it), such that regions with higher abundance correspond to smaller spatial needs, since animals do not have to range over extensive areas to meet the energetic requirements. However, the effect of many other factors likely depends on how an animal responds to them. For instance, competition may push individuals to explore other areas and expand their HR (Jetz *et al.*, 2004), but strong and consistent competition paired with territorial defense (e.g., wolves, Rich *et al.*, 2012; feral cats, Bengsen *et al.*, 2016; capuchin monkeys, Tórrez-Herrera, Davis & Crofoot, 2020) may also prevent them from doing so. Similarly, predation may force animals to move more frequently to escape predators, or it may prevent them from venturing too far from the safety of their den (the HR's centroid) too often (Suraci *et al.*, 2022). Patch quality, size, fragmentation, and heterogeneity may cause animals to explore more patches if some are of low value, too small, too disconnected, or too variable (Fahrig *et al.*, 2019), but high diversity may also decrease HR size (Fox, 1981; Lucherini & Lovari, 1996). Similarly, patch connectivity and ease of movement may widen HRs by decreasing the energetic cost of movement and favoring exploration (Dickie *et al.*, 2022), or they may shrink HRs by decreasing the energetic cost of movement while increasing encounter rates with resources (Visser & Kiørboe, 2006; Bartumeus *et al.*, 2008; Martinez-Garcia *et al.*, 2020). However, not all animals take advantage of linear features or higher predictability in human-altered habitats. Noonan *et al.* (2021) found that giant anteaters (*Myrmecophaga tridactyla*) in Brazil did not use roads to reduce movement costs or increase movement speed. Instead, roads increased anteater mortality because the animals were attracted to the high-quality foraging found on roadside habitat. Similarly, Medici *et al.* (in press) found that the movement of tapirs (*Tapirus terrestris*) was unaffected by anthropogenic activity or habitat type.

The effects of resource abundance on animals' spatial needs have been studied by many in the last century. Multiple general hypotheses have been postulated based on (relatively) small-scale empirical studies (e.g., Burt, 1943; Southwood, 1977; Lindstedt & Boyce, 1985; Grant, 1993; Lucherini & Lovari, 1996; Nilsen, Herfindal & Linnell, 2005; Bengsen *et al.*, 2016), and supported (or questioned) by more recent work with larger, higher-resolution datasets (e.g., Jonzén *et al.*, 2006; Wolkovich *et al.*, 2012; Falcón-Cortés *et al.*, 2021; Dickie *et al.*, 2022; Nathan *et al.*, 2022) and simulations (Blackwell, 2007; Quaglietta, Porto & Ford, 2019; Tucker *et al.*, 2021). Recently, the amount of movement data which can be modeled at once has increased due to improvements in the quality and affordability of tracking equipment (Rutz & Hays, 2009), together with growing propensity (and requirements) to share data openly on various open data platforms such as Movebank (Kranstauber *et al.*, 2011; Kays *et al.*, 2022; but see Roche *et al.*, 2015), as well as the development of high-level modeling software (Bürkner, 2017, 2018; Wood, 2017; e.g., R Core Team, 2021). The abundance of data and statistical software allows researchers build on current knowledge by building increasingly complex hypotheses and models and testing them empirically and quantitatively.

While it is understood that an animal's spatial use strongly depends on the amount of resources and energy the animal can obtain from their habitat, estimates are often restricted to single populations or at most single species. To my knowledge, there are currently no large-scale estimations of vertebrate (or mammalian) space use as a function of resource availability. Additionally, little attention is often given to the stochasticity of resource availability or, more generally, habitat heterogeneity *and* stochasticity (but see Lucherini & Lovari, 1996; Nilsen *et al.*, 2005; Rizzuto *et al.*, 2021). This thesis aims to disentangle the effects of resource abundance and environmental stochasticity on animal space use using statistical models which are based on continuous-time stochastic processes and are insensitive to sampling frequency and spatiotemporal or taxonomic autocorrelation in the data. Findings from this thesis will provide information on how stochasticity has shaped the ecology and evolution of terrestrial mammals and how terrestrial mammals are currently adapting to heterogeneous and changing environments.

1.2 Effects of resource availability and productivity on spatial needs

Environmental productivity is tightly linked to the amount of space that animals need to cover to obtain the resources they needed to survive and reproduce (Lucherini & Lovari, 1996; Relyea, Lawrence & Demarais, 2000). While animals' needs vary greatly between taxonomic groups, some needs are essential for most species for survival and reproduction, such as energetic needs (e.g., food, water; see Baldwin & Bywater, 1984), habitat needs (e.g., dens, trees, tall grass, breeding grounds, protection from predators and competitors; see **refs?**), and maintaining a thermoregulatory balance. The size of a home range, is hypothesized to be proportional to resource abundance (Burt, 1943), such that spatial needs increase when resources are low, but the relationship is likely not monotonic nor linear, since larger home ranges can result in higher rates of competition and are harder to defend (Grant, 1993; Jetz *et al.*, 2004).

The favorableness of a patch or habitat often depends on a variety of factors, including resource availability, competitive pressure, and predation risk. Let the random variable[1] R indicate the amount of *resources* in a particular patch, and let S be the random variable indicating whether or not a patch visit is *successful*. For simplicity, we can let S follow a Bernoulli distribution with probability of success p (which we can write as $S \sim Ber(p)$). Next, let

$$U = R \cdot S \tag{1}$$

indicate the resources an animal can *use* during a visit. Following this simple model, a patch visit can result in two possible outcomes: if the visit is successful ($S = 1$), an animal can use the entirety of the resource ($U = R \cdot 1 = R$), but if it

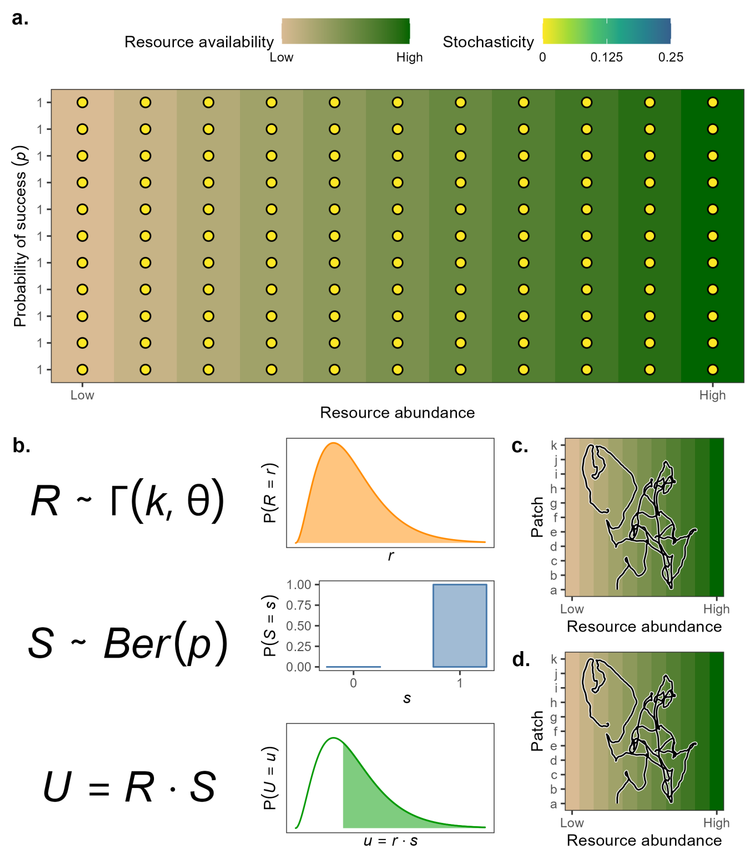

Figure 3: Fictitious example of variation in resource abundance in a heterogeneous but fully predictable environment. (a.) Complete predictability results in guaranteed successes (dots) during each foraging attempt. (b.) Arbitrary definition of R as following a Gamma distribution with shape k and scale θ, while S follows a Bernoulli distribution with probability of success $p = 1$, since successes always occur (i.e., $P(S = 0) = 0$ implies $S = 1$). Thus, $U = R \cdot S = R$, so U follows the same distribution as R. The shaded green area indicates the probability of obtaining an arbitrarily sufficient amount of resources to survive and reproduce. (c.) Since foraging attempts are guaranteed to be successful, the amount of usable resources will equal the resource abundance. (d.) Since $U = R$, the expected (i.e., average) amount of usable resources is equal to the expected resource abundance.

[1] In statistics, random variables indicate random (i.e., unknown) quantities and are indicated with capital letters (e.g., R, S, U). Known values, such as realizations (i.e., known observations) of random variables, are indicated with lower-case letters (e.g., r, s, u). Using this notation we can write the statement "the probability of random variable R taking the value r" as $P(R = r)$.

is unsuccessful ($S = 0$) the animal is unable to access any of the resource ($U = R \cdot 0 = 0$).

If we start by considering the simplistic, though admittedly unlikely, scenario where patches are fully predictable and free of disturbance and competition, such that the animal can access the patches' resources during any visit, i.e., $p = P(S = 1) = 1$. In heterogeneous regions with no stochasticity (figure 3a-b), the favorableness of a location will depend strongly on R, so regions with higher R should be preferred (figure 3c). Since all patch visits in fully predictable regions are successful, animals can expect U to be equal to R, since $U = R \cdot S = R \cdot 1 = R$ (figure 3d), which implies that $\mathbb{E}(U) = \mathbb{E}(R\,S) = \mathbb{E}(R)$. Since $U = R$, animals can choose their home ranges based on R directly, without having to account for any spatiotemporal stochasticity. Therefore, animals in such regions are likely to maximize fitness and minimize movement costs by spending large amounts of time in highly productive regions, with occasional exploratory movements to different patches. This model is quite simplistic, but its simplicity makes it easy to fit and conceptualize, and it provides a null model against which comparisons can be made. In other words, although it is unlikely for a region to be fully predictable, this model may provide acceptable results when environmental variance is low and has little effect on animal fitness, such as is areas where the variation in U, $\mathbb{V}(U)$, is low relative to its expected value, $\mathbb{E}(U)$, such that the costs of moving to another favorable area are low or the chances of encountering prey are high. Mathematically, we can say that this simple model may be acceptable when the coefficient of variation, $\sqrt{\mathbb{V}(R)}/\mathbb{E}(R)$, is low. Additionally, this model may be the only option when data availability is too low to produce appreciable measures of stochasticity or there is no way to estimate it.

1.3 Effects of environmental variance on spatial needs

There are many sources of environmental change over both time and space. Some are due to repetitive, predictable, or even well-known patterns (such as daily or seasonal changes in temperature and precipitation or the location of different patches), while others are due to infrequent, unpredictable, or poorly-understood events (such as forest fires, the arrival of new competitors, or human activity). In this thesis, I will refer to predictable or known changes in space and time as environmental **heterogeneity** (defined as $\mathbb{V}(R)$; see the orange distribution in figure 5), while I will use the term **stochasticity** specifically for unpredictable (spatiotemporal) variation (defined as $\mathbb{V}(S)$; see the blue distribution in figure 5)[2]. For example, the location of (high-yield) apple trees trees in an orchard and the time at which they produce fruit may be heterogeneous, but predictable. In contrast, the yield produced during a given year is unpredictable (i.e., stochastic). Environmental sources of *heterogeneity* also include any known spatial variation in patch quality and size, and predictable daily or seasonal changes in temperature throughout the day, while environmental sources

[2]Note that both sources of variation, $\mathbb{V}(R)$ and $\mathbb{V}(S)$ affect the variation in usable resource, $\mathbb{V}(U)$, which is represented in the green distribution in figure 5.

of *stochasticity*, include changes in temperature ranges, precipitation, and the frequency of extreme events due to climate change (IPCC, 2018; Noonan *et al.*, 2018). Unpredictable events such as forest fires, floods, and earthquakes also constitute sources of stochasticity.

Generally, events are predictable when (1) they occur with a probability density that is approximately constant over time and space, (2) they occur frequently within an organism's generation time or lifespan, and (3) they occur frequently enough to be expected as normal (e.g., rain in rainforests).[3] When an event occurs fairly frequently (e.g., approximately $0.3 \lesssim p \lesssim 0.5$), animals may begin to expect the event to occur and consider it normality (figure 5a), as long as the change in frequency and magnitude is sufficiently gradual. For instance, Lamont *et al.* (2020) found that serotiny (the storage of seeds in closed cones or fruits which open following a fire) is common in plant populations which suffer fires at least once per lifespan, on average. However, the trait becomes less common if the fires become so common that plants survive more often as resprouters than by producing seeds. If a dangerous event such as fires becomes more frequent, unpredictable, or severe, organisms may store resources in favorable times and locations so they can resist more adverse times, and mobile animals may move to avoid avoid such events altogether (Southwood, 1977; Lindstedt & Boyce, 1985). However, variety in fires may increase environmental heterogeneity and promote biodiversity (Fuhlendorf & Engle, 2004), particularly shortly after fires occur and when fires produce heterogeneous burns (Tingley *et al.*, 2016), but the effects of fire can differ between ecosystems (Koerner & Collins, 2013).

The timescale over which an event is (un)predictable will also play a key role in determining how species respond, or not, to stochasticity. Adverse events which occur frequently during an organism's generation time or lifespan (e.g., at least twice, on average) may be considered as threats worth preparing for. Stochastic and destructive events which happen frequently can become part of an organism's habitat and life history, so organisms may either adapt to their occurrence and even learn to predict them (Foley, Pettorelli & Foley, 2008), or they may avoid the risk altogether by moving to a new habitat (Southwood, 1977). If habitats are (or become) unfavorable, animals may move to a new habitat, migrate seasonally (Geremia *et al.*, 2019), or simply prefer nomadism over range residency (e.g., Nandintsetseg *et al.*, 2019). It is unclear when animals switch from range residency to nomadism (or vice-versa), but understanding the connection between the two types of movement is important for quantifying the effect of spatiotemporal stochasticity on animal's spatial needs. From a quantitative perspective, the switch is related to an animal's positional autocorrelation over time (also known as home range crossing time, here indicate as τ_p). Animals without a constant home home range (i.e., without a constant centroid) will spend more time away from the overall mean position, so the

[3] The variance of a Bernoulli random variable Y is maximized when $P(Y = 1) = p = 0.5 \implies \mathbb{V}(Y) = p\,(1 - p) = 0.25$, and minimized when the event occurs almost never ($p \approx 0$) or or almost always ($p \approx 1$), since now $\mathbb{V}(Y) \approx 0(1 - 0) = 1(1 - 1) = 0$. Thus, events which occur extremely rarely, such as meteor impacts, are predictably infrequent and often assumed not to occur.

time required to crossing their entire range time will be large (i.e., on the order of the animal's lifespan).

Adverse events which are too infrequent (e.g., $p \lesssim 0.1$) may not be perceived as a reoccurring threat, so organisms may be unable to adapt appropriately. Instead, highly infrequent events are more likely to perceived as an oddity rather than something worth preparing for. In contrast, highly stochastic events (e.g., $p \approx 0.5$ or if p changes unpredictably) may be perceived as a threat, but organisms may be unable to predict their occurrence, since it would require refined cognitive abilities. For a species or population to adapt to an event, the event must thus occur with sufficient frequency and for a sufficiently long period of time.

What an animal perceives as a stochastic process depends on the stochasticity of the process relative to the animal's size, current age (or average lifespan), and adaptability. Generally, small, short-lived, or young organisms will tend to be more sensitive to small-scale (spatial) or short-term (temporal) changes (Southwood, 1977). Smaller organisms (e.g., mice) are more likely to be be severely impacted by a stochastic event than larger ones (e.g. elephants), since larger organisms can have bigger energy reserves (Lindstedt & Boyce, 1985), can move longer distances over short periods of time (Hirt *et al.*, 2017), and tend to have longer lifespans, generation times, and developmental periods (Brown *et al.*, 2004), which allow them to develop or memory about the frequency and severity of such events (Foley *et al.*, 2008; Polansky, Kilian & Wittemyer, 2015). However, the short generation time and high fertility of smaller *r-selected* species (Pianka, 1970; Brown *et al.*, 2004) can allow them to develop traits that increase the chances of survival following an extreme event. Additionally, the effects of size and lifespan on sensitivity are likely nonlinear and correlated, since smaller animals tend to have shorter lives (and vice-versa), and small animals also tend to have lower metabolic rates, which often limit their movement speed, home ranges, and how the animals interact with their ecosystem (Brown *et al.*, 2004). Thus, processes will have stronger impacts on smaller animals than on bigger ones: The grazing pattern of

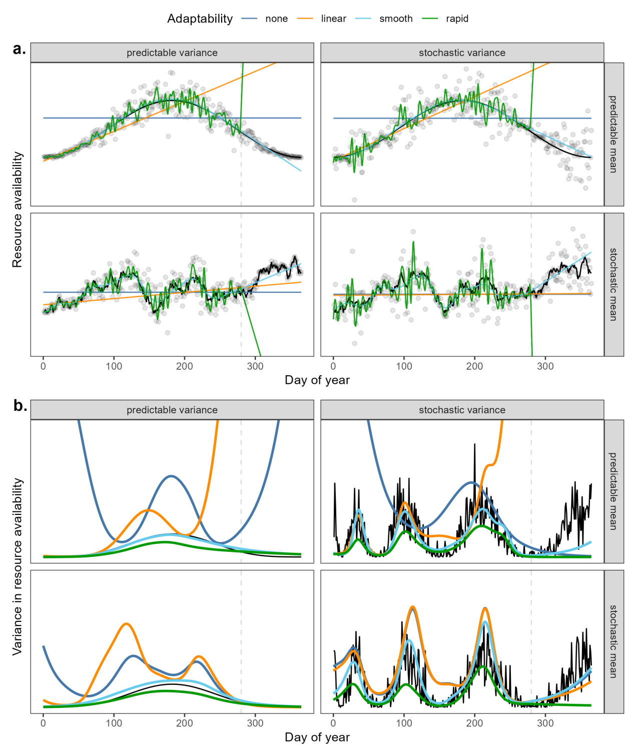

Figure 4: Fictitious changes in resource abundance mean (a) and variance (b) over the course of a year. The true trends are indicated by the black line, while the colored lines indicate the estimates perceived based on different levels of adaptability. The dashed vertical line indicates the hypothetical current date, such that any data to the right of the line is unknown to the animals, so estimates on the right of the dashed line are extrapolations. The data were simulated using Gaussian noise to ensure mean-variance independence and modeled using Generalized Additive Models with an identity link function to allow linear responses.

a bison (*Bison bison*) drastically alters the habitat of most crawling insects, but other grazing mammals would not pay attention to changes in grass length at the same spatial or temporal resolution. Similarly, the timing and quantity of yearly snowfall would be a somewhat predictable and expected event for most adult moose (*Alces alces*), but it may be a shock for many adult zooplankton or a new-born wolf (*Canis lupus*). What one animal may perceive as a single stochastic event (or cycle) may be considered as a series of short and highly stochastic events by another animal.

Figure 4 illustrates the perceived resource availability mean and variance by animals with four different levels of adaptability and how they may predict the mean and variance to change in the future (after the vertical grey line). In the extreme (and likely fictitious) case where an animal does not adapt to the environment (dark blue), it cannot react to or predict changes in mean resource abundance, and thus the perceived variance is inflated whenever the resource abundance does not match the overall mean. Environments appear highly unpredictable to such animals. Animals which can only perceive simple, linear changes in mean resource abundance (orange) perform better as long as resources continue to change linearly in the same direction (i.e. increasing or decreasing). However, they may be surprised when the trend's direction changes, as indicated by the rapid increase in variance in the top rows of figure 4b. Animals which are able to adapt smoothly (light blue) can predict changes in mean without a significant bias in estimated variance, as long as the process is not highly stochastic (unsurprisingly, see the bottom rows of figure 4). Finally, animals which adapt rapidly to changing environments may be most able to take advantage of frequent environmental changes, but they may be unable to produce reasonable predictions based on memory (*sensu* Fagan *et al.*, 2013; Abrahms *et al.*, 2019). Instead, they depend on constant information and only predict on the most recent information (as indicated by the deviations from the data when predicting into the future).

1.3.1 The temporal scale of stochastic events

An animal's ability to alter its behavior (including its movement) in response to environmental conditions is essential in stochastic or changing landscapes. Whether the changes be due to highly variable but (potentially) predictable changes such as the seasons and the weather, or whether they be due to more stochastic events (e.g., natural events such as fires or floods, but also anthropogenic events like oil spills; see Matkin *et al.*, 2008), an animal's ability to adapt increases its odds of survival. Generally, temporal variation is more likely to promote plasticity over diversity, since adaptability will likely offer better odds of survival than temporally static diversity in a population or species (Bell *et al.*, 1993). Rickbeil *et al.* (2019) showed that the yearly migration of elk (*Cervus canadensis*) depends on variable environmental events and cues such as available forage biomass, hunting pressure, snow fall, and snow melt. Birds have also shown to change their

their migration as the climate changes, including large-scale, trans-Saharian migrants (Jonzén *et al.*, 2006). And while genetic diversity and polymorphisms also increase the odds of survival for a species (Cavedon *et al.*, 2022), this project will focus strictly on animal behavior.

In an environment that changes over time, organisms which depend on mutable cycles such as changes in temperature, precipitation, and resource availability are more likely to respond to environmental changes than organisms which depend purely on deterministic cycles (e.g., photoperiod). While this thesis focuses on the movement and spatial use of animals, the adaptability (or lack thereof) of non-animal organisms is also crucial. The ability of most animals to rely on visual cues and move accordingly greatly increases their adaptability and plasticity, particularly for those animals that are able to move large distances over short periods of time (e.g., flying birds and large vertebrates). Although this project will focus on vertebrate animals, such changes are important to consider because the ability of a specialist or obligate symbiont to shift its home range or adapt will likely depend strongly on its associate's ability to move or adapt, too.

1.3.2 Spatial needs in stochastic environments

In areas where animals are not guaranteed that the resources they find during one visit will be there the next time (figure 5a), stochasticity will have an appreciable effect on the location's favourableness. Patches with low or high p will be most predictable, since successes can be expected to be very rare (if $p \approx 0$) or very common (if $p \approx 1$). In contrast, patches will be most stochastic when the probabilities of success and failure are approximately the same (i.e., $p \approx 1 - p \implies p \approx 0.5$, see figure 5b). In stochastic habitats, $\mathbb{E}(U)$ will depend on $\mathbb{E}(S)$ as well as $\mathbb{E}(R)$, since S is no longer constant (figure 5c). Now, expected usable resources become

$$\mathbb{E}(U) = \mathbb{E}(R\,S), \tag{2}$$

or

$$\mathbb{E}(U) = \mathbb{E}(R)\,\mathbb{E}(S) \tag{3}$$

if R and S are independent. This model can be applied to all mobile animals, including herbivores, carnivores, and omnivores. In the case of herbivores, p may indicate the chance of finding good forage, which may be absent if regeneration times are long, if competitors have already exhausted the resource, or following a fire. For carnivores, p may indicate the chance of feeding on prey, which may depend on encountering and killing some first (Suraci *et al.*, 2022). However, since R is not limited to energetic resources, p may also indicate the chance of finding water or also a suitable location for a den or nest.

While resource availability is often considered in conservation decision-making (**refs?**), an environment's heterogeneity (i.e., diversity), stochasticity (i.e., unpredictability), and how the two change over time are rarely accounted for. In addition, environmental stochasticity, including extreme events, can reduce a landscape's energetic balance (Chevin, Lande & Mace, 2010), which, in turn, decreases animals' fitness. Therefore, I expect animals living in unpredictable environments to require more space than those in stable environments. Although this hypothesis is supported by a few recent studies (Morellet *et al.*, 2013; Nandintsetseg *et al.*, 2019; Riotte-Lambert & Matthiopoulos, 2020), many of them are limited in their analytical depth and geographic and taxonomic scales, so the extent to which these preliminary findings can be generalized is still very limited. There thus remains a need for developing a more complete understanding of how animals' spatial needs change with environmental stochasticity. These stresses are compounded by climate change, which exposes species to increasingly common stochastic events (IPCC, 2018; Noonan *et al.*, 2018). Furthermore, anthropogenic structures reduce the habitat available to terrestrial species (Wilson *et al.*, 2016), who struggle to move in fragmented (Fahrig, 2007), human-dominated landscapes (Tucker *et al.*, 2018). As the impacts of habitat loss and climate change will worsen in the future (Hansen *et al.*, 2013; IPCC, 2018), it is imperative that we better understand spatial requirements of taxa to protect wildlife existence and bio-

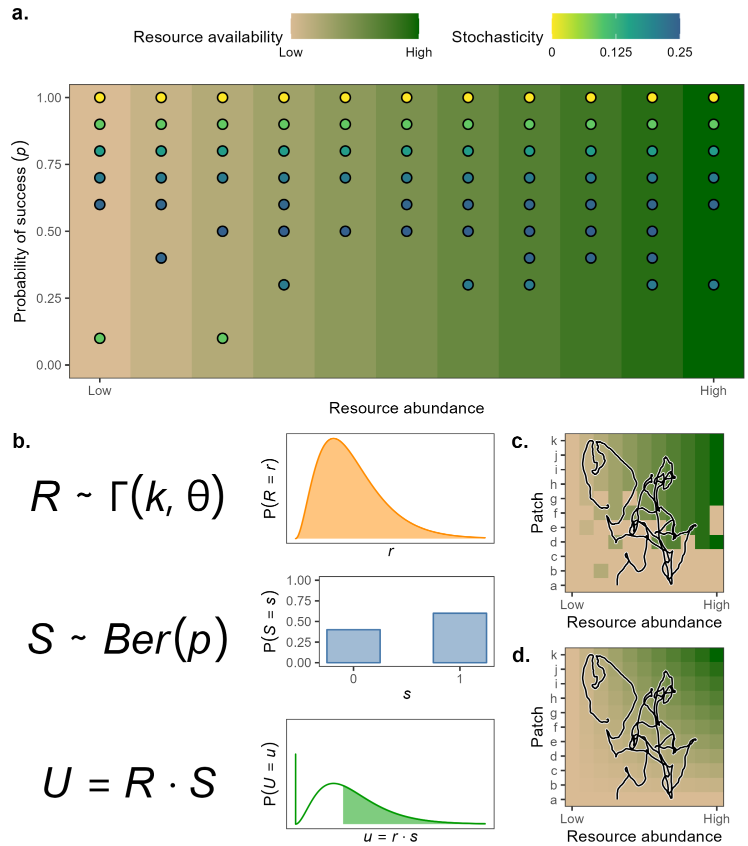

Figure 5: Fictitious example of variation in resource abundance in a heterogeneous and stochastic environment. (a.) Foraging successes (dots) can vary due to various reasons, including differences in competition, predation, and resource-specific trends. Successes most stochastic when the probability of success is approximately 0.5, while they are least stochastic (i.e., most predictable) when they are guaranteed to occur ($p = 1$) or guaranteed to fail ($p = 0$). (b.) Arbitrary definition of R as following a Gamma distribution with shape k and scale θ, while S follows a Bernoulli distribution with probability of success $p = 0.6$, so successes are not always guaranteed. (c.) Animals living in such an environment cannot always expect each foraging attemp to be successful. Thus, resources may not be accessible even though they are abundant. (d.) Expected resource availability, $\mathbb{E}(U)$, is highest in areas with high resource abundance and high probability of success. When possible, animals are likely to rely mostly on predictable, resource-rich areas (top right). Alternatively, they may prefer predictable areas with lower resource abundance (top left) or adapt to high-risk, high-reward areas (bottom right).

diversity. Environmental safeguarding is also essential for Reconciliation with Indigenous People in Canada (Truth and Reconciliation Commission of Canada, 2015).

1.4 Interaction effects of resource availability and stochasticity

In the previous section, I mentioned that a model which does not account for environmental variance may be acceptable when $\sqrt{\mathbb{V}(R)}/\mathbb{E}(R)$ is low, as in the case of a habitat with high R and $p \approx 1$. However, since maximum resource abundance is constrained by environmental stochasticity (Chevin *et al.*, 2010) and resources can be depleted or rendered inaccessible by other individuals (Grant, 1993; Jetz *et al.*, 2004), $\mathbb{E}(R)$ does not provide a sufficiently complete picture of resource availability in an environment. Thus, the effect of $\mathbb{V}(R)$ should be included when possible, even when $p \approx 1$ or $p \approx 0$.

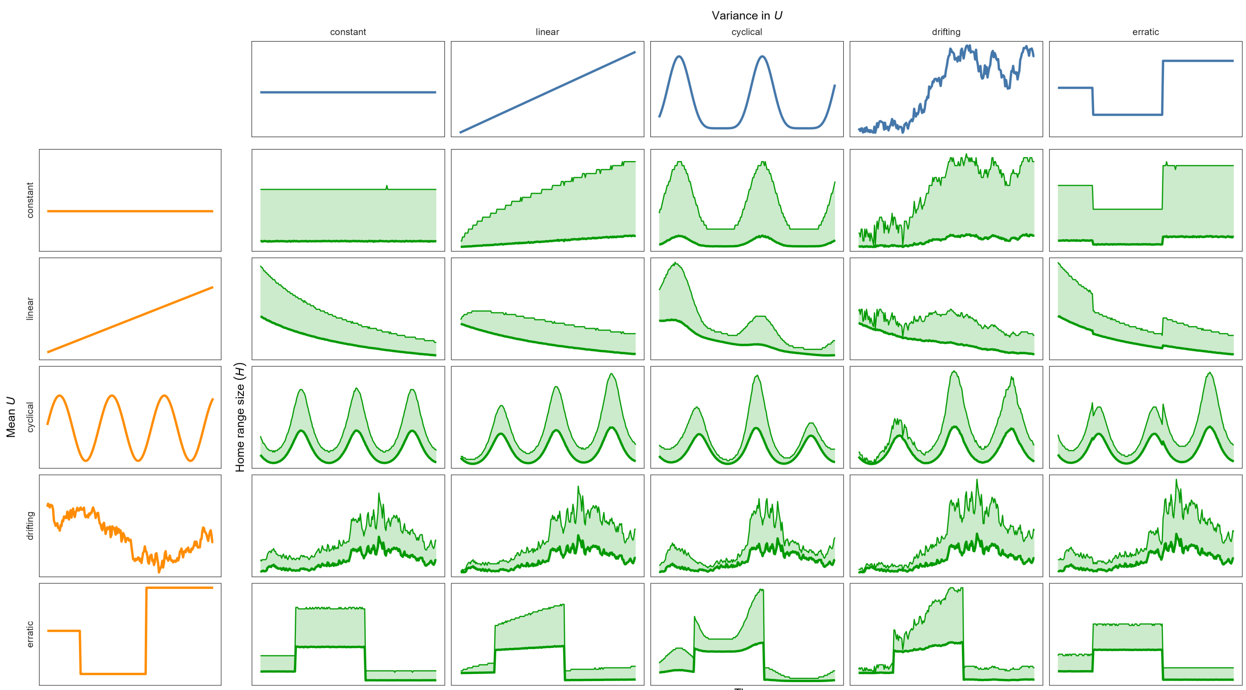

Figure 6: Simulated spatial requirements for animals living in habitats where resource availability vary with constant, linearly increasing, cyclical, drifting, or erratic means and variances. The thick line indicates the mean spatial requirement needed for survival, while the thin line indicates the 95% quantile. The thick line can also be interpreted as the animal's core home range, while thin line can be interpreted as the requirements needed for a 95% chance of survival, which would be similar to the animals' 95% home range. Changes in $\mathbb{V}(R)$ have greater impacts when $\mathbb{E}(R)$ or $\mathbb{V}(R)$ are low.

Let H indicate the size of an animal's HR.[4] As explained above, H will be higher in regions with lower $\mathbb{E}(U)$ or higher $\mathbb{V}(U)$. Figure 6 presents various scenarios with different trends in $\mathbb{E}(U)$ and $\mathbb{V}(U)$. Although some of these scenarios may seem overly simplistic, they can help us understand the complex interaction effects of $\mathbb{E}(U)$ and $\mathbb{V}(U)$. In regions where U has constant mean and variance, H remains approximately constant, although small oscillations are possible, since $\mathbb{V}(U) \neq 0$ and thus the environment is still stochastic. When

[4] We can consider specific utilization quantiles of the HR, such as the core HR, $H_{50\%}$, or the 95% HR, $H_{95\%}$, but for simplicity I will refer to the entirety of the HR with H. Statistically, we can imagine H as having a probability distribution with support over the interval from zero (not included) to infinity (also not included), which we can indicate with the notation $H \in (0, \infty)$.

$\mathbb{E}(U)$ changes over time but $\mathbb{V}(U)$ remains constant, it is easy to see that H decreases as $\mathbb{E}(U)$ increases, with changes in $\mathbb{E}(U)$ having larger effects when $\mathbb{E}(U)$ is low and smaller effects when $\mathbb{E}(U)$ is already large. This is best visualized in the scenario in which $\mathbb{E}(U)$ is increasing linearly while $\mathbb{V}(U)$ is constant, since decrease in core HR ($H_{50\%}$) and 95% HR ($H_{95\%}$) is decreases over time. Additionally, as $\mathbb{E}(U)$ increases, the difference between $H_{50\%}$ and $H_{95\%}$ also decreases. Thus, $H_{95\%}$ is more sensitive to changes in $\mathbb{E}(U)$ than $H_{50\%}$. $H_{95\%}$ is also more sensitive to changes in $\mathbb{V}(U)$, since changes in $\mathbb{V}(U)$ cause greater oscillations in $H_{95\%}$ than in $H_{50\%}$.

Not all 25 scenarios depicted in figure 6 may be realistic, but the trends in $\mathbb{E}(U)$ and $\mathbb{V}(U)$ are useful examples that can be thought of as simplified scenarios. $\mathbb{E}(U)$ and $\mathbb{V}(U)$ may be (approximately) constant in highly homogeneous environments, or environments where resources are sufficiently available that changes in $\mathbb{E}(U)$ and $\mathbb{V}(U)$ remain undetected. Although it is impossible for $\mathbb{E}(U)$ and $\mathbb{V}(U)$ to increase linearly continuously, such increases may be possible for short periods of time (followed by periods of no change or decrease). Additionally, these examples are important because they demonstrate the relationships between H, $\mathbb{E}(U)$, and $\mathbb{V}(U)$ in a (relatively) simple scenario. Cyclical oscillations in $\mathbb{E}(U)$ and $\mathbb{V}(U)$ may occur in urban environments (Péron *et al.*, 2017) and as temperatures fluctuate daily and seasonally (Geremia *et al.*, 2019), while $\mathbb{E}(U)$ and $\mathbb{V}(U)$ may drift randomly in highly complex environments with an abundance of competitors, threats, and stochasticity, such as a habitat with a high degree of human alteration and activity. Finally, erratic changes in $\mathbb{E}(U)$ and $\mathbb{V}(U)$ may occur in environments where changes are very sudden, such as fire-prone or floor-prone areas, or habitats with drastic human alteration (e.g., a forest which is clear-cut for mining purposes with a subsequent artificial re-forestation). However, if highly stochastic or erratic changes occur frequently, animals are most likely to perceive them as a smooth transition rather a series of small, sudden, changes. Estimating the true trend would often require an excessively high cognitive capacity and an equally unlikely abundance of information. Additionally, although changes in $\mathbb{E}(U)$ are not due to $\mathbb{V}(U)$, but often distinguishing between the two is not easy (Steixner-Kumar & Gläscher, 2020).

1.5 Thesis structure and aims

This thesis aims to quantify how animal's movement and use of space are affected by the abundance of resources (e.g., food, water, breeding grounds) and environmental 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 environmental stochasticity and its effects; (iii) estimating between-species trends using models that are robust to commonly-found issues (e.g., correlations within species); and (iv) understanding how Traditional Indigenous Knowledge can be integrated into large-scale ecological research and conservation planning within a framework that acknowledges both Traditional Indigenous Knowledge and Western science (Kutz & Tomaselli, 2019). The present section provides the framework 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 stand alone, together they provide convergent evidence towards the role of stochasticity in shaping animal space use.

To address these over-arching objections, in **Chapter 2**, I will produce a global raster of a new environmental stochasticity index, and new quantitative methods for animal movement. This metric will then serve as the basis for my subsequent investigation into the relationship between environmental stochasticity and animal movement.

In **Chapter 3**, I will use simulation studies and an unprecedented and conservation-relevant animal tracking dataset (>1500 animals, 77 globally-distributed species) to investigate how animal spatial needs change with environmental stochasticity.

Chapter 4 summarizes the work presented in this thesis and demonstrates its significance within the larger picture of movement ecology, conservation, and quantitative zoology.

Chapters 5-8 contain various supporting information, namely links to the code and data used in this thesis (**Chapter 5**), a table of all abbreviations used in the thesis (**Chapter 6**), a table of all mathematical notations and symbols used in the thesis (**Chapter 7**), and the tentative timeline (**Chapter 8**), which will not be present in the final version of the thesis.

Appendix 1 contains details on further original work. These published works are included as appendix material as I have made substantial contributions, but I am not the lead author.

ADD ONE SENTENCE ON WHAT THIS BRINGS TO THE BIG PICTURE QUESTION.

2 Chapter 2: A new measure of environmental variance

Whether an animal is affected by or can perceive environmental variance depends strongly on the spatiotemporal scale of the process(es) involved. Organisms are most affected by stochastic events and processes which occur on time scales which are in the order of the organisms' life spans or generation times (Southwood, 1977). Weekly heavy rains which alter a lake's salinity are more likely to affect an individual than a multi-centennial drought, and the high salinity that follows the drought may be perceived as the (stressful) standard by individuals which were born during or following the drought. In contrast, organisms can adapt to unpredictable heavy rains if they occur on a daily frequency. However, stochastic processes and events which occur on time scales that are longer than an organism's lifespan may still cause significant effects on a population's fitness and stability. Droughts which occur on the time scale of centuries or millennia (Haig *et al.*, 2013) are unlikely to affect organisms directly, but such events could still alter the population's habitat or breeding grounds enough to cause a population collapse or prevent individuals from reproducing in their habitual breeding region (or reproduce altogether).

Thus, the scale at which we quantify variance should depend on the spatiotemporal scale and sensitivity of the animals being studied. Since this project focuses on medium to large animals, I will focus on processes and events which occur on the temporal scale of hours to decades and spatial scale of meters to kilometers. I will assume small-scale variances such as heterogeneity in grass density at the centimeter scale or fluctuations in temperature over the span of a few minutes have little to no (measurable) effect on the spatial needs of the animals which I will be studying. Even if such small-scale variances had an effect, such an effect would be hard to detect or quantify because: (1) the effect size would be small (so large amounts of data would be necessary for an appreciable result), and (2) the uncertainty in the tracking data limits the precision at which one is able to detect changes in movement in response to such small variation (figure 7). Thus, it seems reasonable to quantify environmental variance at the scale of minutes to days and meters to kilometers.

To my knowledge, there currently is no large-scale measurement of environmental variance. Producing a worldwide raster of such a measure would allow researchers to estimate the spatiotemporal variance of an animal's habitat and better understand not only how heterogeneity and unpredictability affect its home range, but also when and why animals decide to migrate or become nomadic, and many other behaviors or decisions, such as the timing of reproduction, when animals decide to defend territory and resources, and more. Some measures of environmental productivity and heterogeneity already exist, such as the machine learning human footprint index (ml-HFI) produced by Keys, Barnes & Carter (2021) and the Normalized Difference Vegetation Index (NDVI, Pettorelli *et al.*, 2011). However, none of these indices provides a comprehensive measure of environmental variance over the years. For instance, the ml-HFI is a temporally static raster, so it prevents us from accounting for temporal changes in anthropogenic habitat alteration, and neither the ml-HFI and the NDVI account for the frequency of events.

A measure of environmental variance should thus account for the spatiotemporal variance in frequent events (e.g., precipitation) and continuous processes (e.g., temperature) as well as the frequency of extreme and rare events (e.g., fires, cyclones). How the frequency and average intensity of events are estimated depends on the event(s) considered. Processes for which we have an abundance of global-scale data, such as daily air temperature and precipitation can be included as raw data, and their variances can be estimated using smooth location-scale models, such as GAMs with appropriate conditional distributions (i.e., Gaussian location-scale for temperature and Gamma location-scale for precipitation; see Stasinopoulos & Rigby, 2007; Umlauf, Klein & Zeileis, 2018). In contrast, the frequency of rare events should be modeled with more smooth (i.e., less flexible) models, since the low data availability does not allow us to use models with high degrees of freedom (i.e., very wiggly predictors; see Simpson, 2018).

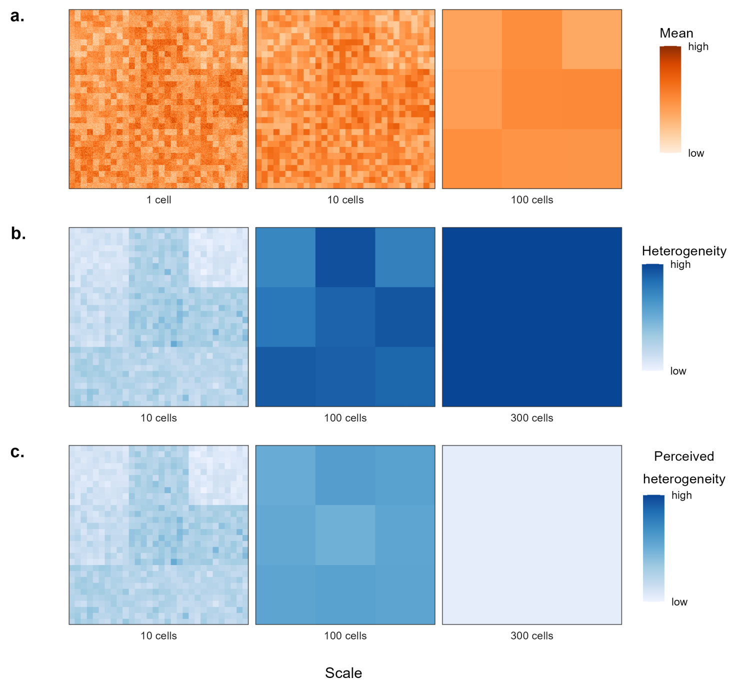

Figure 7: (a.) Fictitious means of an arbitrary random variable (e.g., resource abundance, productivity, temperature, precipitation) in a two-dimensional space. The mean value varies within small-scale patches (left), between small-scale patches (center) and large scale-patches (right). Thus, the perceived means depend on the spatial scale at which the observer can detect differences. (b.) Environmental heterogeneity detected at different degrees of precision. Wider regions have a wider range of means, which results in higher heterogeneity. Thus, each cell in the left panel represents the heterogeneity of the 100 pixels in the cell, while the cells in the central panel indicate the heterogeneity in the 10,000 cells in each of the larger cells, and the right panel indicates the heterogeneity in all 90,000 pixels. (c.) Fictitious, scale-dependent, perceived heterogeneity. The left panel is calculated as in row (b), while heterogeneity in the central and right panels are calculated on the means in the central and right panels in row (a), respectively. Perceived heterogeneity is lower than true heterogeneity because heterogeneity is lost when averaging values.

2.1 Quantifying environmental variance

Let Z indicate the measure of environmental variance used in this thesis. Z should contain information on a multitude of sources of environmental variance, including daily, seasonal, and spatial variance (e.g., changes in temperature, precipitation, and photoperiod, NDVI), inter-annual variance (e.g., climatic oscillations such as the El Niño-Souther Oscillation, see Rasmusson & Wallace, 1983; and anthropogenic climate change, see

IPCC, 2018), and the frequency of extreme events, such as fires, floods, and droughts. The variation from most sources can be modeled using a Generalized Additive Model (GAM, see Wood, 2011; Wood, 2017) for location and scale (GAMLS, see Stasinopoulos & Rigby, 2007) with an appropriate distribution.[5] Similarly, the frequency of extreme events can be estimated from the estimated probability of occurrence of the event. We can estimate such probability using a piece-wise exponential additive model (PAM; see Bender & Scheipl, 2018), which is a GAM for time-to-event data.

Since each source of variation will affect animals to different degrees and will have different units (e.g., °C, milliliters, hours) or no units (e.g., NDVI, frequency of events), and different ranges (e.g., $(-\infty, \infty)$ for temperature, $[0, \infty)$ for precipitation, $[0, 1]$ for fraction of daylight, and $[-1, 1]$ for NDVI), it would not be appropriate to define Z as the sum of each variance. Instead, a weighted average of the (scaled) variances or coefficients of variation (i.e., standard deviation over mean) may be more appropriate. Weights and scaling could be informed by an algorithm similar to a principal components analysis (PCA) that varies over time and space. However, the more abstract Z is, the less interpretable it becomes, so results based on Z should be interpreted carefully since a different set of variables or different weights may result in different conclusions. Therefore, although using few sources of variance will fail to account for some factors, the results may be easier to understand and apply. This would particularly be the case if few variables accounted for most environmental variance.

Since the variance of a process has a lower limit (0) but does not necessarily have an upper limit, it seems reasonable to model Z using a Gamma distribution for the model residuals. Estimating $\mathbb{E}(Z)$ over time and space will require various measures of spatiotemporal heterogeneity and stochasticity. The measure should vary over time and space, such that: (1) $\mathbb{E}(Z)$ changes over time, (2) individual location can have different values of $\mathbb{E}(Z)$, and (3) the change in $\mathbb{E}(Z)$ over time can also differ between habitats, since it may change faster in some habitats than others, and the shape and direction of the change may also differ between locations. Thus, the model used to estimate environmental variance should have 3 main terms: (1) a term for the global average over time (t), (2) a term for the global average over space (longitude, s_x, and latitude, s_y), and (3) an interaction term of space and time that allows locations to deviate from the global average temporal and spatial trends:

[5]For example, temperature (measured in °C) could be modeled using a Gaussian distribution since it can take both positive and negative values, while precipitation is strictly positive and continuous, so a Gamma distribution would be appropriate. A beta distribution could be used to model the proportion of a day with light (e.g., hours of sunlight divided by 24, which would result in a proportion in the interval $[0, 1]$) and NDVI (Pettorelli *et al.*, 2011), since it can easily be transformed from the interval $[-1, 1]$ to $[0, 1]$ using the function $g(x) = (x + 1)/2$. Note that it is acceptable to transform the models' responses (light per day and NDVI) since both transformations ($f(x) = x/24$ and $g(x) = (x + 1)/2$) are linear (i.e. only comprised of addition and multiplication), so Jensen's inequality (Jensen, 1906) does not apply here.

$$\mathbb{E}(Z) = f_1(t) + f_2(s_1, s_2) + f_3(t, s_1, s_2) \tag{4}$$

The terms should be smooth and sufficiently complex to maximize model flexibility, but the wiggliness should also be penalized to avoiding over-fitting the data (Simpson, 2018). Thus, it seems appropriate to estimate the average Z over space and time using a GAM, which can be fit easily using the `mgcv` (Wood, 2017) package for `R` (R Core Team, 2021). The smooth of time, $f_1(t)$ could be modeled with a thin-plate spline smooth (Wood, 2003; Simpson, 2018), while the two-dimensional spatial term, $f_2(s_1, s_2)$, should use a two-dimensional spline. While splines on the sphere (Wahba, 1981) would provide a good approximation for the shape of the earth, Z will likely be constrained to terrestrial or freshwater habitats, so Duchon splines are a better alternative (Duchon, 1977). Duchon splines are well-behaved as they move away from the support of the data, so they are less likely to produce questionable edge behavior. Finally, the interaction term $f_3(t, s_1, s_2)$ can be modeled as the tensor interaction product (Wood, Scheipl & Faraway, 2013) of time and space, with a thin-plate spline smooth for time and a Duchon spline for space. To reduce computation time, the GAM will be fit using the `bam()` function from the `mgcv` package, which fits models similarly to `mgcv::gam()` but is specific for fitting models to very large datasets. `bam()` allows model fitting using fast restricted maximum likelihood and discretized covariates (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017; Li & Wood, 2020), with no appreciable loss to model fit.

3 Chapter 3: Movement analyses

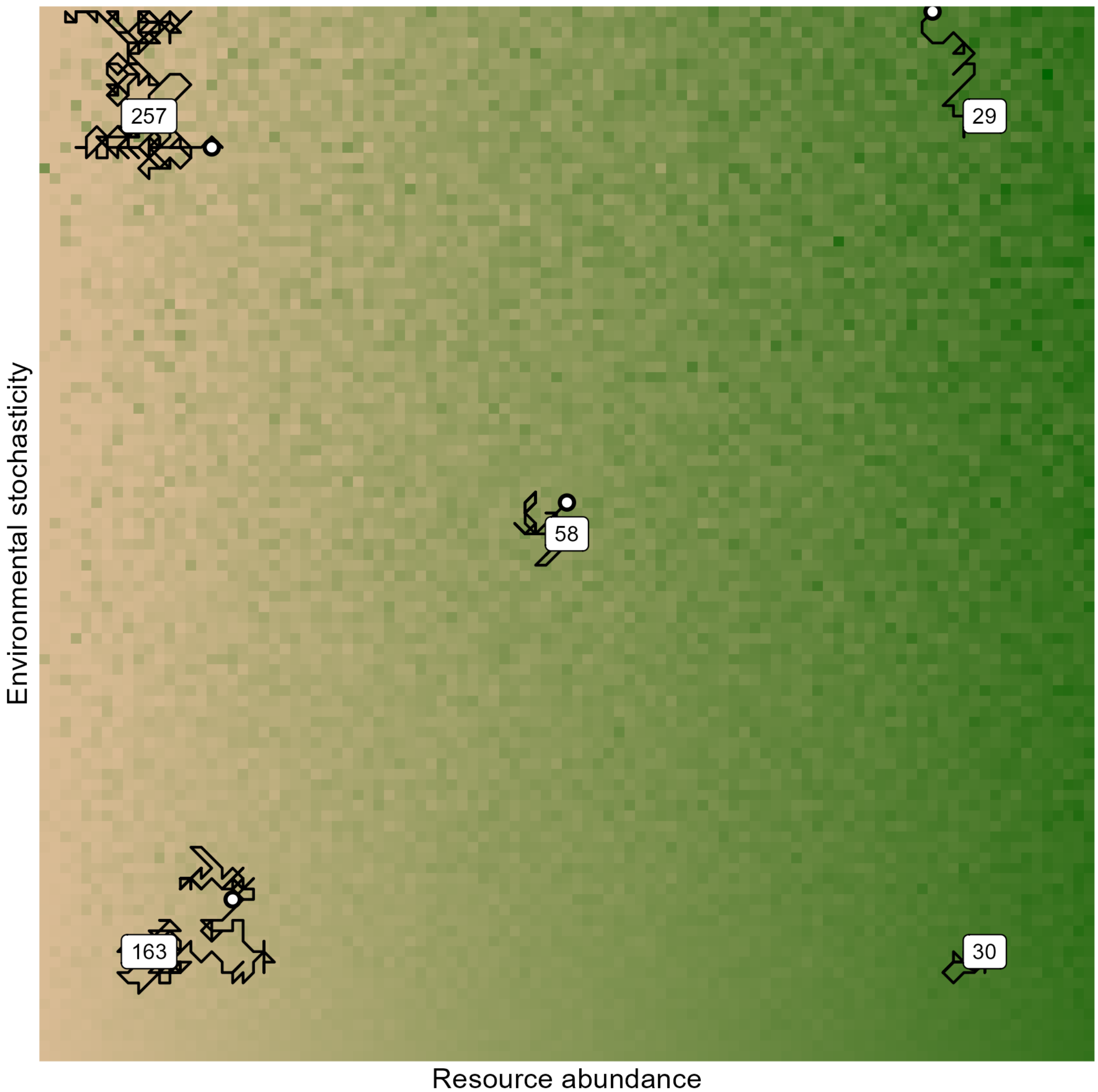

Figure 8: Simulations depicting the effects of resource availability and stochasticity on spatial needs. Animals moved from the circles to nearby tiles until satiated. The labels indicate how many steps animals took to reach satiety. Note the higher spatial needs of animals in more unpredictable or resource-scarce environments. Resources were generated using a gamma random variable parameterized by independent mean and variance paramters, which represented the resource abundance and environmental stochasticity, respectively, even though the two are likely correlated in nature.

3.1 Movement simulations

- Inform priors and simulation distributions using Indigenous Traditional Knowledge

3.2 Movement analysis

The increase in movement data availability allows researchers to produce more powerful results, but the high-frequency sampling often results in non-independence between temporally consecutive data. Additionally, high-frequency data is more likely to be sampled at irregular intervals. Thus, many commonly-used home range estimation methods (e.g., minimum convex polygon, kernel density estimation) cannot be used with such datasets because they assume data points to be approximately independent and at regular time intervals. While one could coarsen data to larger, regular intervals at the expense of data frequency, this nullifies great part of the benefits achieved with recent improvements in tracking technologies. Thus, it is increasingly more important to model animal movement data using models that (1) do not assume data is regularly sampled, and (2) account for the spatiotemporal autocorrelation within the data. Continuous-time models such as Ornstein-Uhlenbeck (OU) and OU foraging (OUF) models relax the assumption of spatiotemporal independence by accounting for positional autocorrelation (OU and OUF models) and directional (i.e., velocity) autocorrelation (OUF models only), which allows them to estimate the animal's average home range crossing time (OU and OUF) and the animal's average directional persistence (OUF only). Péron *et al.* (2017) provide additional information OU and OUF models and how to interpret them while also demonstrating how to use high-frequency movement data can help detect small-scale cycles, such as patterns that occur daily or weekly.

4 Chapter 4: Summary

- why is this work important?
- so what?
- now what?

5 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-masters. The repository currently does not include the animal movement data that will be used, which is available on Movebank and will be linked in future R scripts in the repository. The tapir movement data used for figure 2 is available in the `data` folder at https://github.com/StefanoMezzini/tapirs.

All scripts include comments to help people replicate the analysis, but they do assume some basic knowledge of `R` (including referring to help files and vignettes). Comments and requests regarding the project can be placed in the repository as issues.

6 List of abbreviations used

Abbreviation	Phrase
CTMM	Continuous-time movement model
GAM	Generalized additive model
GAMLS	Generalized additive model for location and scale
HGAM	Hierarchical generalized additive model
ml-HFI	Machine learning human footprint index
NDVI	Normalized difference vegetation index
PAM	Piecewise exponential additive model
PCA	Principal components analysis

7 List of notations and symbols used

Symbol	Meaning
$c \in (a, b]$	c is in the interval from a (not included) to b (included)
$c \propto k$	c is proportional to k
$\mathbb{E}(\cdot)$	Expectation, mean
F	Favorableness or value of a region
H	Home range, spatial needs, required area
$P(A)$	Probability of event A, e.g., $A =$ successful foraging
R	Resources
τ_p	Positional autocorrelation, mean reversion to HR center, range crossing time
τ_v	Velocity autocorrelation, directional persistance
$\mathbb{V}(\cdot)$	Variance

8 Project timeline

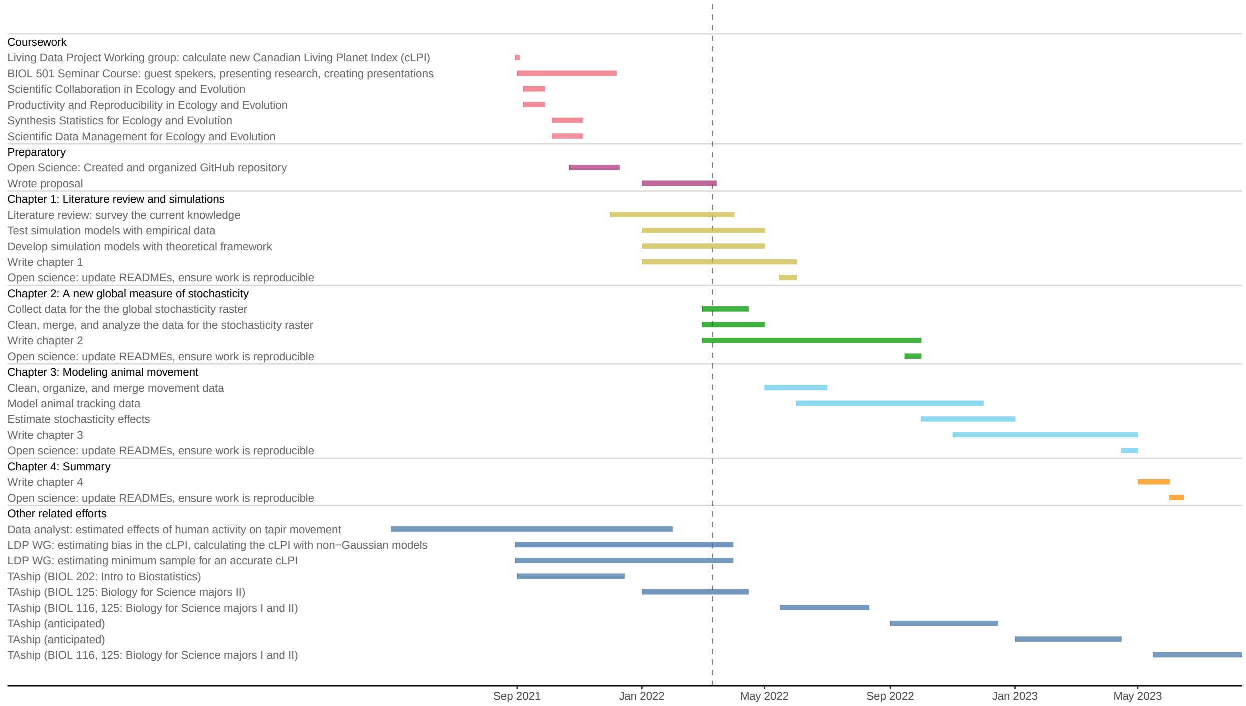

Figure 9: Visual representation of the estimated timeline for my Master's project.

8.1 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.

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Appendix 1: Manuscripts contributed to during the degree

LIMNOLOGY and OCEANOGRAPHY

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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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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/services/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 km^2), although White Bear Lake is deeper (Z_{max} = 15 vs. 8 m) and drains a larger area (172 vs. 60 km^2) 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 ± 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 ($\mu g \cdot L^{-1}$)	2048±38	2533±116
TP ($\mu g \cdot L^{-1}$)	27.50±9.57	14.46±10.41
TOC ($mg \cdot L^{-1}$)	26.75±0.44	35.03±1.97
Chl *a* ($\mu g \cdot L^{-1}$)	9.44±4.41	8.40±7.79
Salinity ($g \cdot L^{-1}$)	1.07±0.03	1.84±0.06
pH	8.58±0.14	8.72±0.07
Secchi depth (m)	1.84±1.36	2.58±1.07

(*Fraxinus pennsylvanica*), white birch (*Betula papyrifera*), and Manitoba maple (*Acer negundo*; Henderson et al. 2002), ~ 21–27% cover by other water bodies, ~ 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 ~ 7.6 m depth (49°49.455′N, 102°18.882′W) and was ~ 57 cm in length, while the White Bear Lake core was taken at ~ 9.2 m depth (49°49.455′N, 102°18.882′W) and was ~ 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 ($g\ cm^{-2}\ yr^{-1}$) 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 ($\delta^{15}N$, $\delta^{13}C$) 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 N_2, 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 N_2 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 indictors 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 *tidyr* 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.

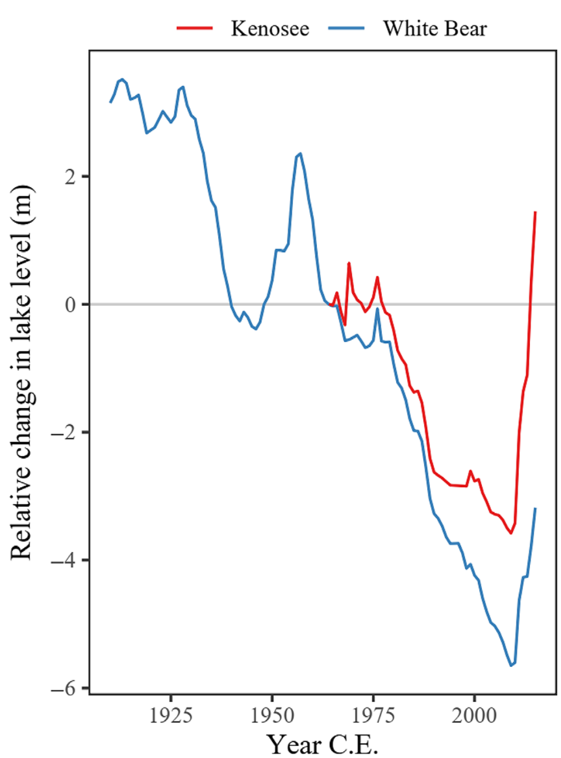

Fig. 2. Water levels of Kenosee Lake (red) and White Bear Lake (blue) relative to their levels in 1964. Data from 1964 to 2015 were obtained from the Government of Canada Water Office; data prior to 1964 for White Bear Lake were obtained from estimates from Cullimore and Griffin (1979).

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 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 ~75% and ~55% of their present depth, respectively, with only very recent increases toward historical benchmarks (Fig. 2).

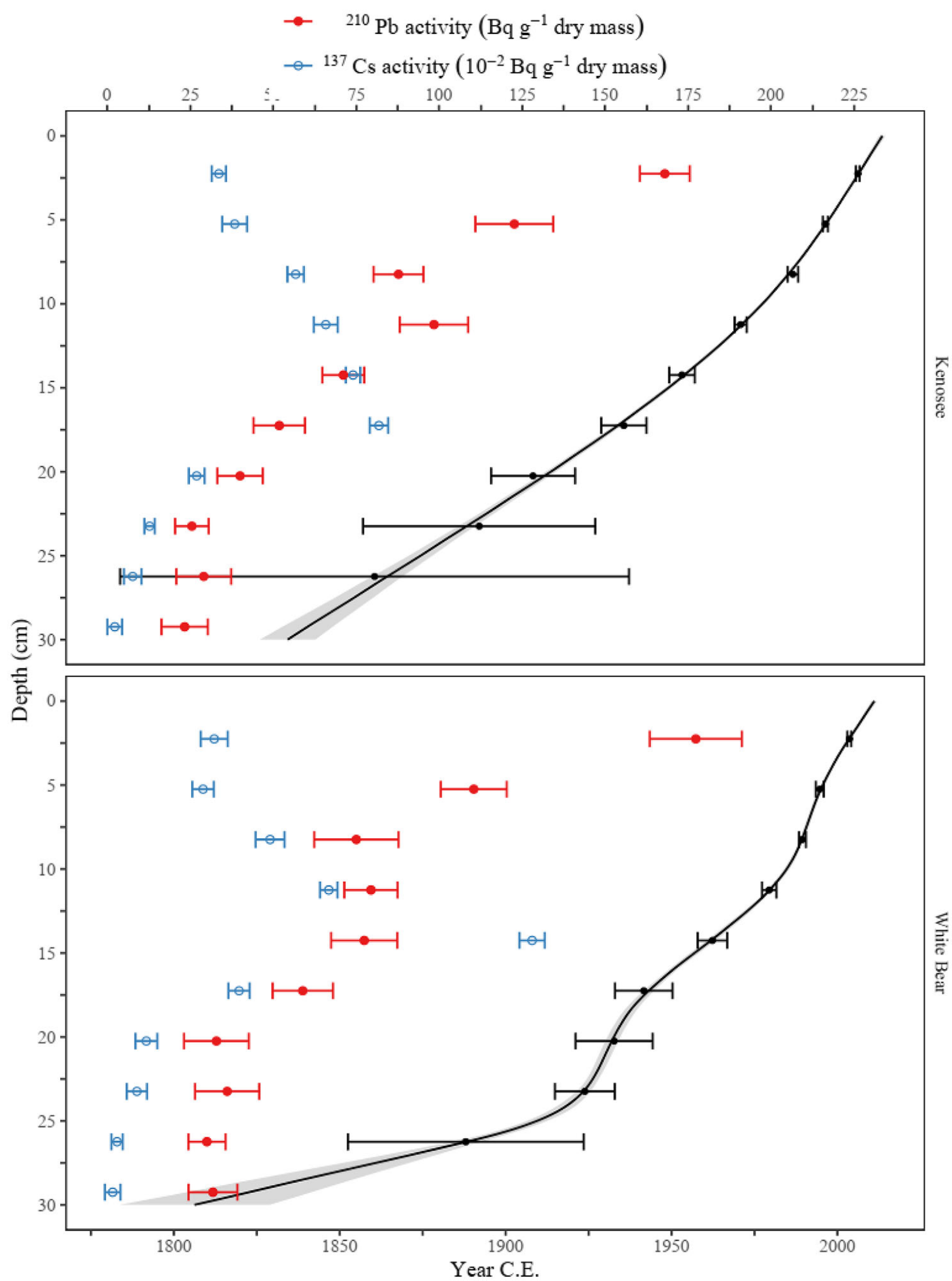

Fig. 3. Activities of ^{210}Pb and ^{137}Cs with associated error estimates (1 σ) by core depth for Kenosee Lake and White Bear Lake. Age-depth relationships were estimated using SCAMs (shape-constrained additive models)-based CRS (constant rate of supply) models of ^{210}Pb activity in each core. Inferred dates are also presented with error ranges (1 σ) 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 $\delta^{13}C$ values were relatively stable and elevated at both sites before ~ 2000 (~ 15‰), after which isotope values declined to ~ −22.5‰ in both lakes (Fig. 4). In contrast, trends in $\delta^{15}N$ were markedly different between lakes. In Kenosee Lake, $\delta^{15}N$ ratios decreased from ~ 6‰ to ~ 4‰ after approximately 1925 before returning to more enriched values after ~ 1960 (Fig. 4), whereas in White Bear Lake, $\delta^{15}N$ ratios continue to decline after ~ 1960 with depletions to ~ 2‰ 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

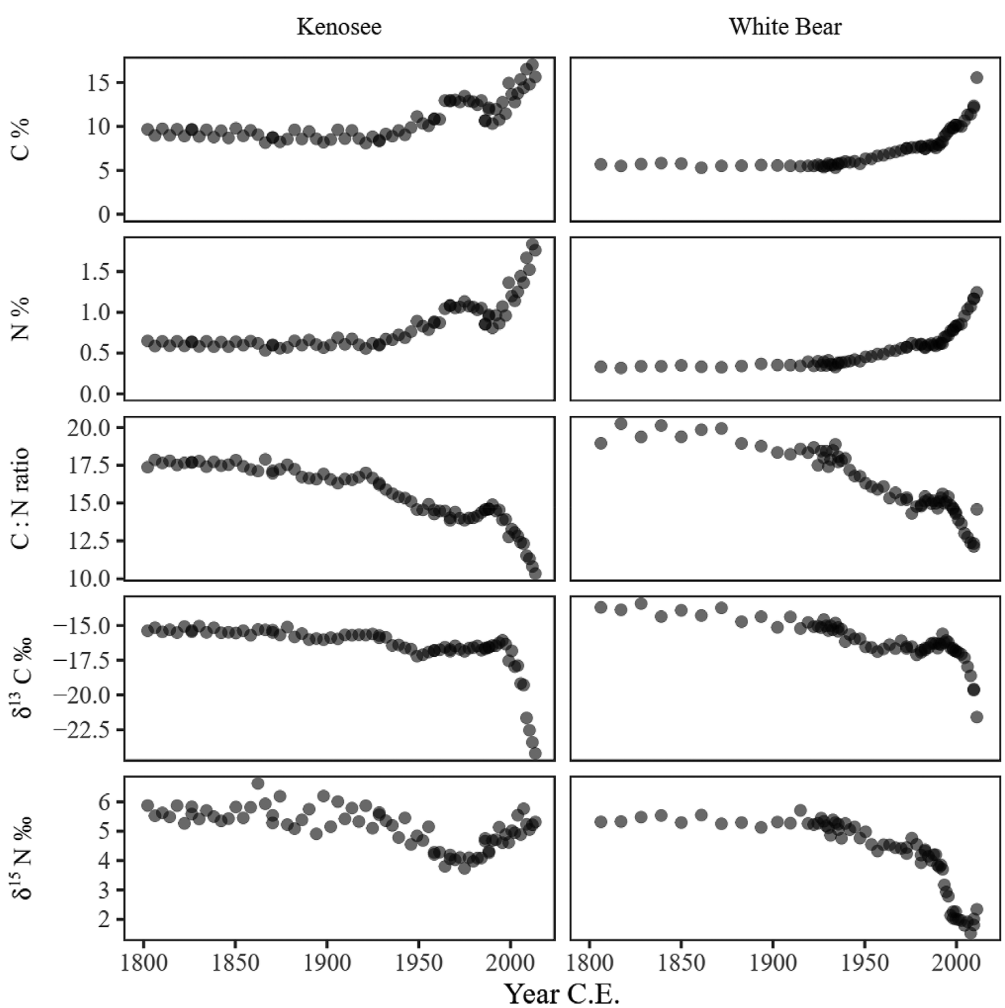

Fig. 4. Carbon (C%) and nitrogen (N%) content, C : N ratios, and stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ (‰) plotted by year for Kenosee Lake and White Bear Lake.

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

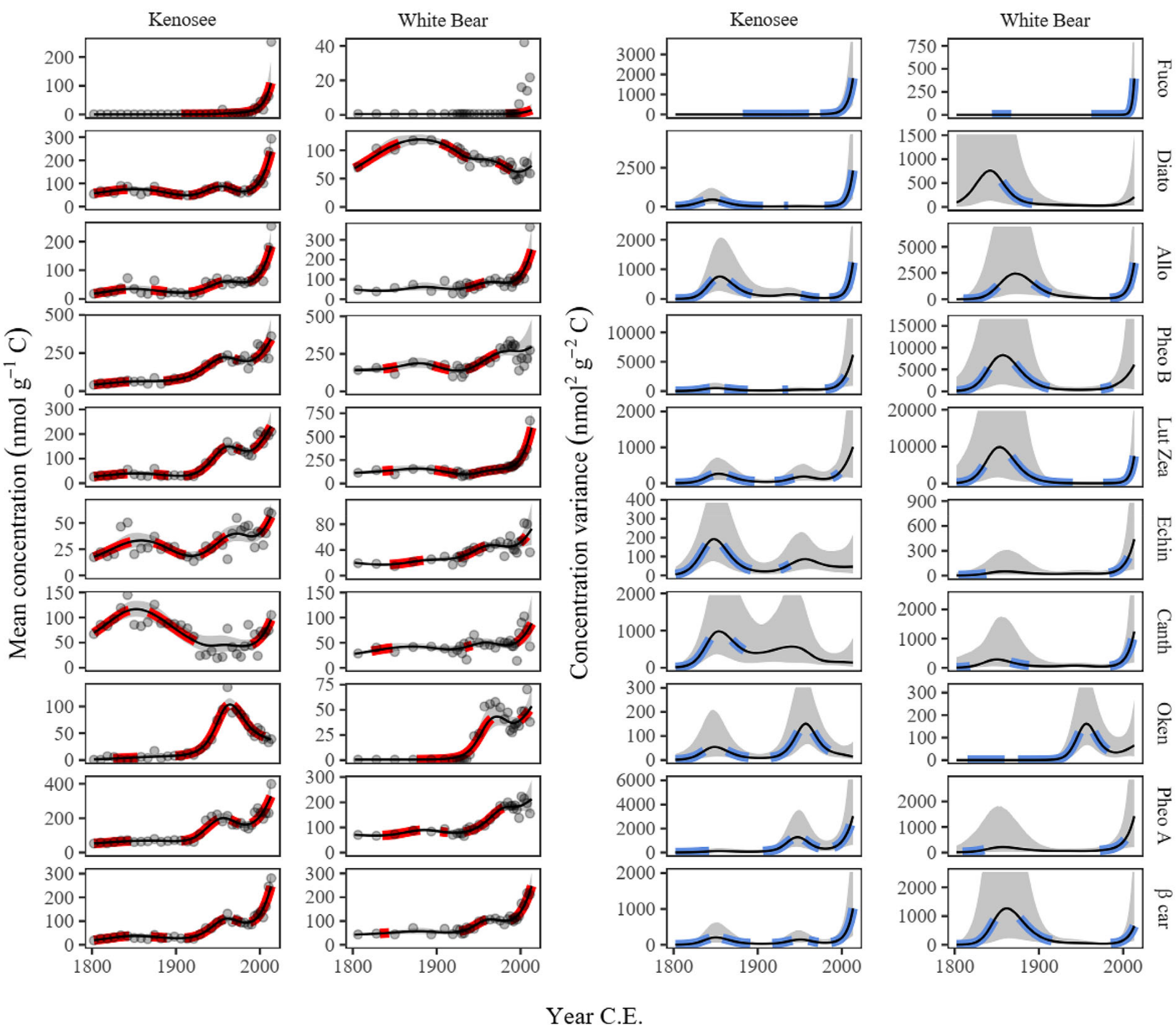

Fig. 5. Mean concentrations (left) and concentration variances (right) of fossil pigments by year in sediments from Kenosee Lake and White Bear Lake. Pigment mean concentrations and concentration variances are fitted with hierarchical generalized additive models (HGAMs). In all plots, solid lines are 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 N_2-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

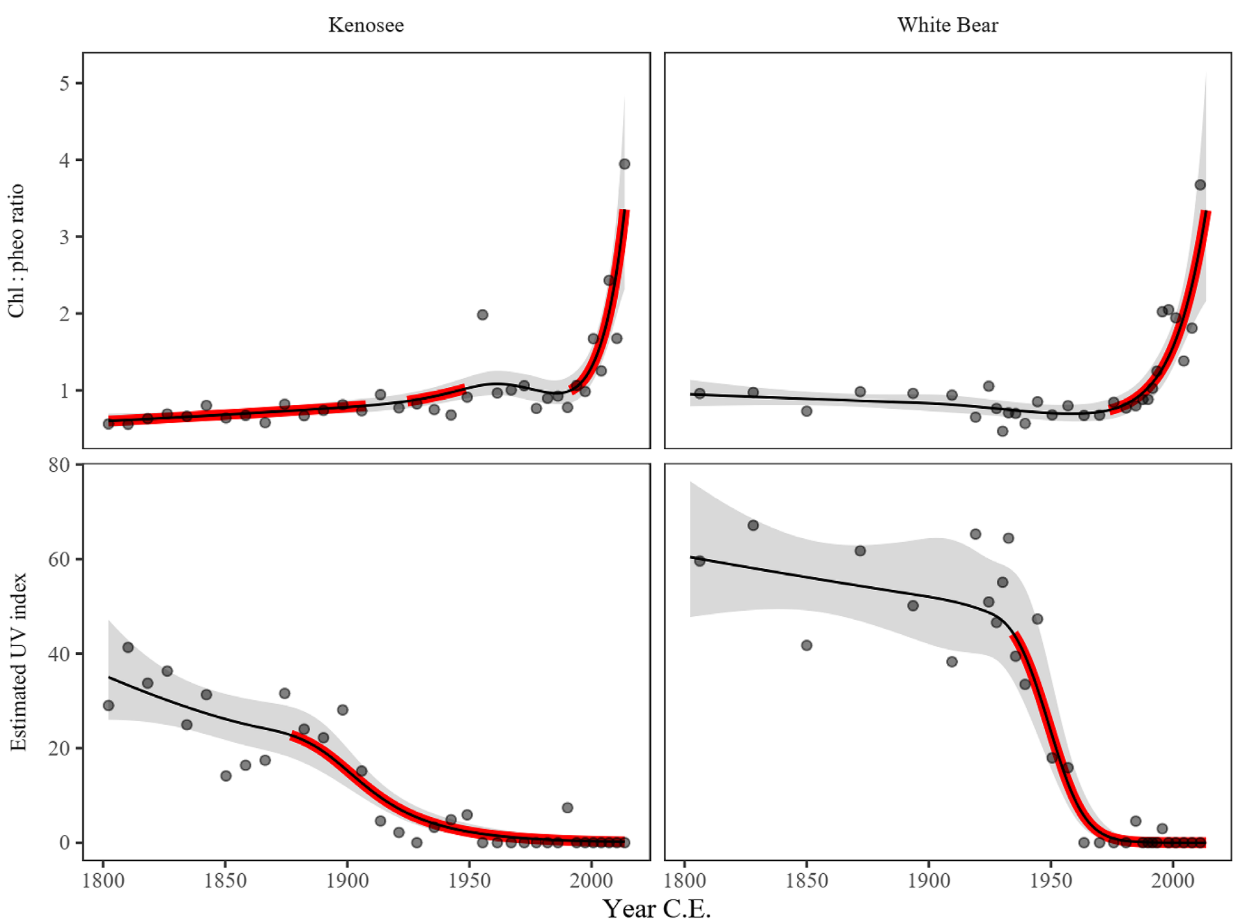

Fig. 6. Precursory Chl *a* to derivative pheophytin *a* (Chl : pheo) ratios and estimated UV index values plotted by year for Kenosee Lake and White Bear Lake. In all plots, solid lines are the fitted model trends, gray shading represents 95% trend confidence intervals, and emboldened sections represent 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 $-60\ \mathrm{cm\ yr^{-1}}$ (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 $\sim$ 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 $\sim$ 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 $\sim$ 1930 and $\sim$ 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 $\sim$ 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 $\sim$ 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 $\sim$ 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 $\sim$ 20–25) to those associated with autochthonous organic matter (C : N $\sim$ 8–12; Gu et al. 2006; Woodward et al. 2012). Depleted δ^{13}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 CO_2 from respired 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 δ^{15}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 δ^{15}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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 ($\sim$ 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 $\sim$ 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 $\sim$ 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 $\sim$ 1930 and $\sim$ 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 $\sim$ 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 hyposaline (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 evaporations 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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Conflict of Interest

None declared.

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Movement ecology of vulnerable lowland tapirs across a gradient of human disturbance

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Running head: Lowland tapir space use

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Statement on human or animal subjects: 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).

Abstract

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. 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 a gradient of human disturbance within three biomes in southern Brazil: the Pantanal, Cerrado, and Atlantic Forest.

From these data we found that the mean home range size across all monitored tapirs was 8.31 km^2 (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.

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. 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

Introduction

While agriculture, urbanisation, and transportation infrastructure are critical to human socio-economic improvement (Esfahani and Ramírez 2003), the associated habitat transformations represent a major threat to species survival (Fahrig 1997; Venter et al. 2006; Powers and Jetz 2019). Of particular concern is the impact of human activities on animal movement and space use (Allen and Singh 2016; Tucker et al. 2018; Doherty et al. 2021). Animal movement governs how individuals, populations, and species interact with each other and the environment (Schick et al. 2008; Martinez-Garcia et al. 2020; He et al. 2021) and mediates key ecological processes (Bauer and Hoye 2014). 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 (Brooks et al. 2002; Cardinale et al. 2012; Hooper et al. 2012). This has spurred substantial changes in animal movement behaviour across the globe (Fahrig 2007; Tucker et al. 2018; Doherty et al. 2021), with potential consequences including reduced fitness and survival, altered predator-prey dynamics, reduced seed dispersal, genetic isolation and local extinction (Fahrig 2007; Dickie et al. 2017; Cosgrove et al. 2018; Tucker et al. 2021).

Notably, human disturbance has been shown to have differential effects across species (Toews et al. 2018; Doherty et al. 2021), even for closely related taxa occupying the same habitat (Thatte et al. 2020). Responses to human activities are thus largely context specific (Doherty et al. 2021) and cannot be expected to be consistent across taxa. For instance, while Wall et al. (2021) found a tendency for African elephants (*Loxodonta spp.*) to exhibit reduced movement in human modified landscapes, Morato et al. (2016) 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 a gradient of 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 meters in length and weigh up to 250kg (Medici 2011). While lowland tapirs are distributed throughout South America (Gardner 2008), their populations have suffered severe reductions, with local and regional extirpations, and are currently classified as vulnerable to extinction (Varela et al. 2019). Although the incorporation of information on animal movement is a key component in designing effective conservation and recovery strategies (Allen and Singh 2016), currently, very little is known about the movement ecology of tapirs (but see Noss et al. 2003; Tobler 2008; Fleming et al. 2019). 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 (Calder 1983; Noonan et al. 2020), making them more susceptible to anthropogenic impacts than smaller bodied species (Tucker et al. 2018; Hill et al. 2020). 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 (Lucherini and Lovari 1996; Relyea et al. 2000; Nilsen et al. 2005). 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 (Doherty et al. 2021) 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 km^2 composed by a mosaic of mature and secondary deciduous forest, surrounded by the Paranapanema River in the south, and by a matrix of cattle ranches and agriculture, mostly sugar cane, in the remaining borders (Uezu et al. 2008). Its average annual temperature is 22°C and annual rainfall is 1347 mm (Faria and Pires 2006). 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 (Salis et al. 1995). In fact, the semi-deciduous forests of the "Planalto Forest" are similar to those occurring within or on the edges of the Cerrado (Salis et al. 1995).

Pantanal

Baía das Pedras Ranch, a private property of 145 km^2, 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 (Calheiros and Fonseca Júnior 1996).

Cerrado

The study site in the Cerrado biome is a 2200 km^2 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°60'S, 53°83'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.

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 (Quse et al. 2014). Animals were anesthetized mostly using a combination of butorphanol, medetomidine and ketamine, as described by Medici et al. (2014) and Fernandes-Santos et al. (2020). 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 hours at dawn (04:00-07:00 h) and 3 hours at dusk (17:00-20:00 h). These periods are the two main peaks of tapir activity (Medici 2011). Each tapir was located every 30 minutes 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 Supplementary 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.

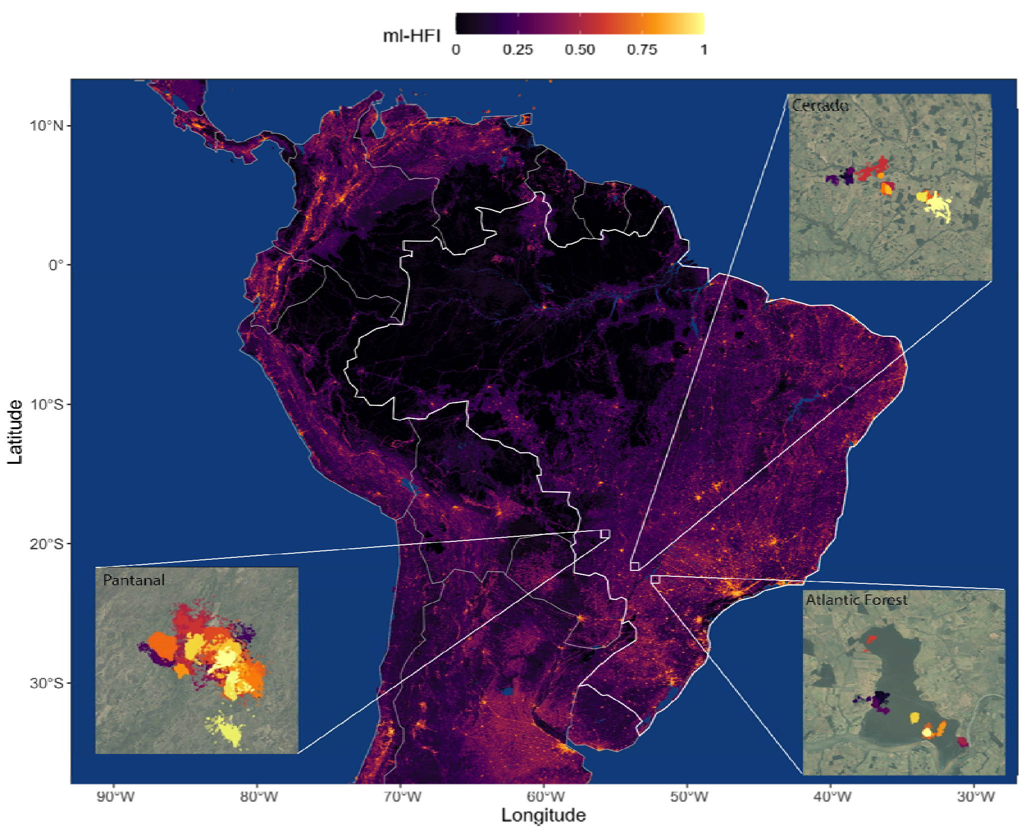

Figure 1: *Location of the tree study sites (Pantanal, Cerrado, Atlantic Forest) over a raster of machine-learning-based human footprint index (ml-HFI), an index of human pressure on the landscape that is derived from remotely sensed surface imagery and ranges on a scale between 0 (no human impact), and 1 (high human impact).*

Data analysis

Initial exploratory analyses were carried out in ctmmweb (version 0.2.11, Calabrese et al. 2021). All formal statistical analysis and plotting were performed using R (version 4.0.5, R Core Team 2021), with the packages ctmm (version 0.6.1, Calabrese et al. 2016), mgcv (version 1.8-36, Wood 2017), ggplot2 (version 3.3.4, Wickham 2016), ggmap (version 3.0.0, Kahle and Wickham 2013). The furrr package (version 0.2.2, Vaughan and Dancho 2021) was used for parallel computation on Windows machines. All R code can be found in the GitHub repository at https://github.com/StefanoMezzini/tapirs.

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 (Fleming et al. 2020). Data cleaning and calibration were carried out using the methods implemented in the ctmm R package. For this process, location estimates collected via VHF telemetry were assumed to be free from any meaningful measurement error 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. 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 ($\geq$ 1m/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, Fleming et al. 2019) 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, Fleming et al. 2014, Blackwell et al. 2016) and they account for spatio-temporal autocorrelation in the data (when necessary), so they are robust to irregular or frequent sampling frequency (Fleming et al. 2018). 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) (Fleming and Calabrese 2017), and average daily movement speed (in km/day) using continuous-time speed and distance (CTSD) estimation (Noonan et al. 2019).

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 (Fleming et al. 2021), whereas other movement metrics were analysed using the meta-regression model implemented in the R package metafor (Viechtbauer 2010). This allowed for uncertainty in each individual estimate to be propagated into the population level estimate when making comparisons, minimising the risk of spurious significance.

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 (Faria and Pires 2006). 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. Similarly, the HR sizes and average daily speeds were regressed against their HR's average machine-learning-based human footprint index (ml-HFI) (Keys et al. 2021) to test whether human activity significantly altered the animals' behavior. The 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 (Wood 2017) and Residual Maximum Likelihood (REML), and the best model was selected using AIC.

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 km^2 and 29.7 km^2 (Fig. 3a). Tapirs had HR crossing times of 0.72 days on average (95% CI: 0.35 - 1.10), ranging from 0.05 to 12.8 days (Fig. 3b), and a mean velocity autocorrelation timescale of 0.44 hours (95% CI: 0.39 - 0.49), ranging from 0.17 to 1.88 hours (Fig. 3c). We estimated that tapirs had mean movement speeds of 11.2 km/day (95% CI: 10.2 - 12.1), 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: 9.52 km/day, 95% CI: 7.94 - 11.4;
, Fig. 4b).

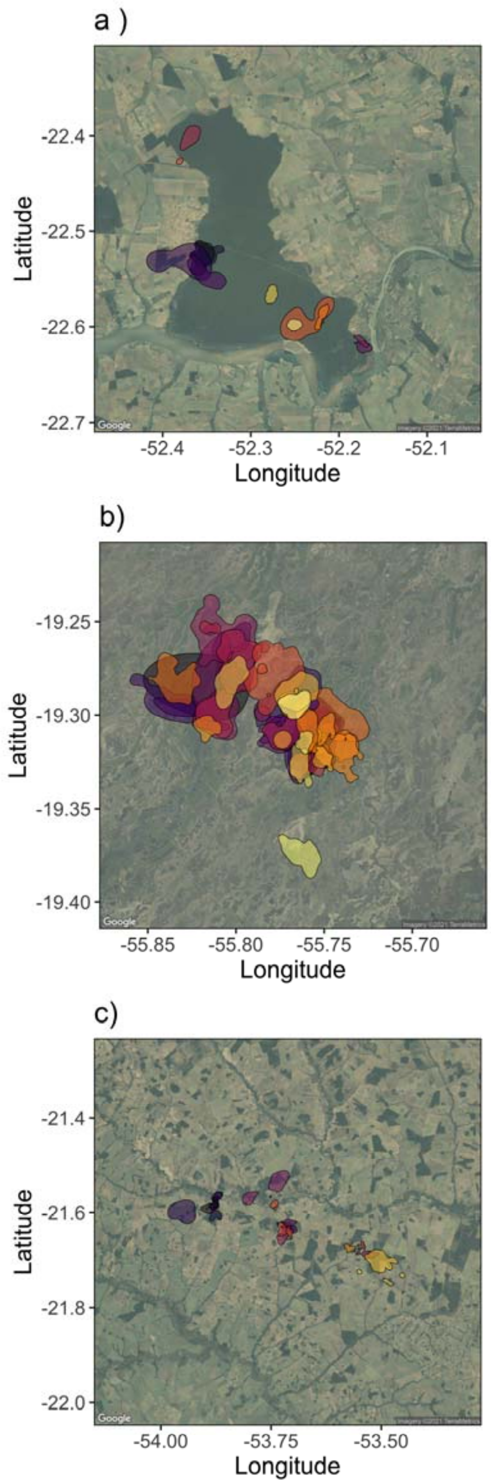

Figure 2: *Autocorrelated kernel density estimates of each tapir's 95% home range in each of the three regions: a) Atlantic Forest, b) Pantanal, and c) Cerrado.*

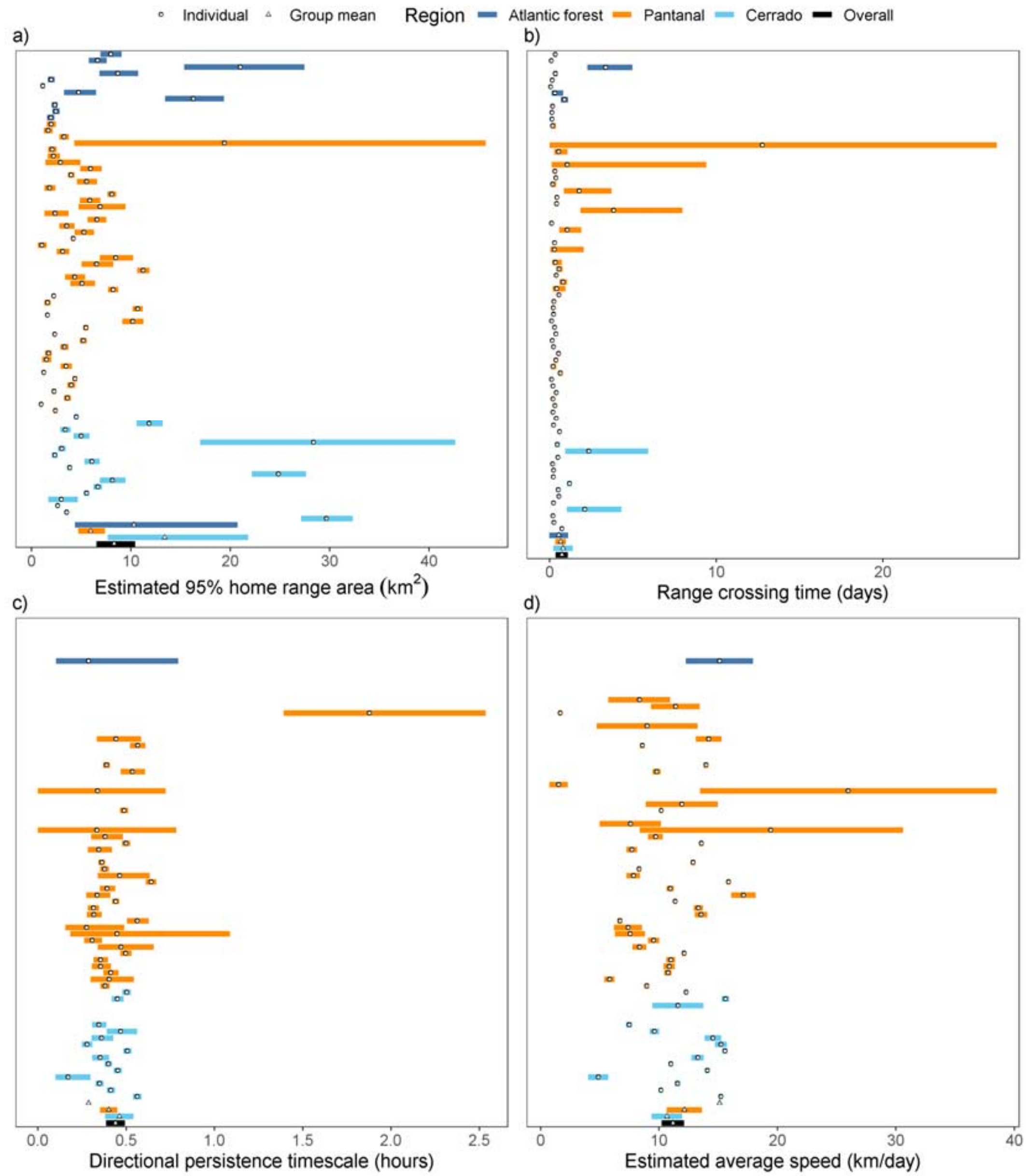

Figure 3: *Parameter estimates from each tapir's movement model (circles) and group means (triangles), with 95% confidence intervals. Individuals with a movement model that does not allow for inferences in movement speed are left blank.*

There was no evidence that home range sizes differed between sexes (males: 5.43 km^2, 95% CI: 3.84 - 7.68; females: 6.27 km^2, 95% CI: 4.64 - 8.48; $p = 0.541$, Fig. 4c) nor between age groups (adults: 5.47 km^2, 95% CI: 4.21 - 7.1; sub-adults: 7.01 km^2, 95% CI: 4.63 - 10.6; $p = 0.324$, Fig. 4d).

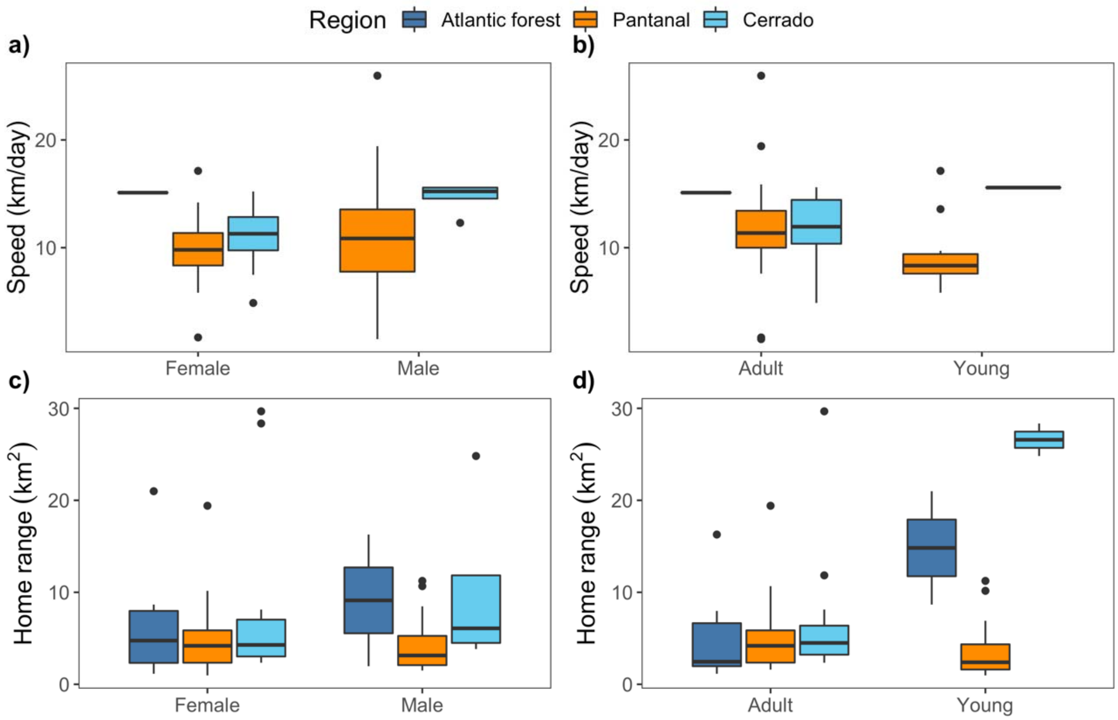

Figure 4: *Boxplots of daily average speed (a, b) and estimated home range size (c, d) by sex and age group. We note that estimation of movement speeds for adult females was only possible for a single tapir in the Atlantic Forest. In addition, we could only estimate speed for a single young tapir in the Cerrado.*

Variation in movement across biomes and gradients of 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, = 0.477; 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 ( ) was significantly lower for animals who had a higher amount of forested area (Fig. 5b) or water (Fig. 5c) 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.

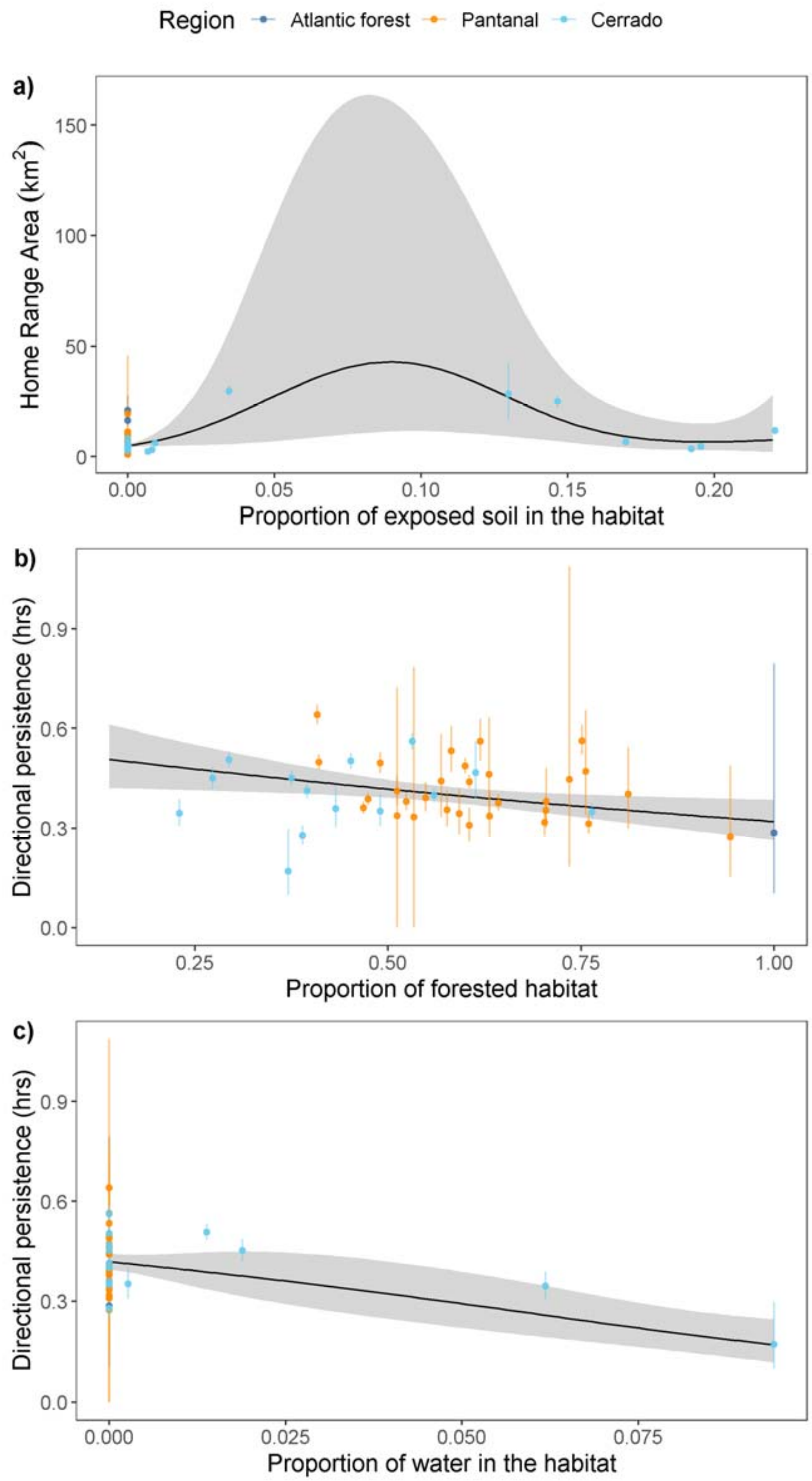

Figure 5: *Effect of habitat types on lowland tapir space use and movement. The vertical error-bars indicate the 95% confidence intervals for the movement parameter estimates. Panel a) depicts the estimated mean effect of exposed soil on the tapirs' estimated home range area. The effects of b) forested area or c) water in a tapir's home range on its estimated directional persistence are also shown.*

HFI had no significant effect on lowland tapir home range size (p-value = 0.90; Fig. 6a), nor average daily movement speed (p-value = 0.53; Fig. 6b), nor directional persistence (p-value = 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 13.19 km/day (95% CI: 7.82 - 22.1) with a directional persistence of 0.355 hours (95% CI: 0.160 - 0.784), 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 - 14.3) and an average speed of 10.43 km/day (95% CI: 8.27 - 13.2) with a directional persistence of 0.478 hours (95% CI: 0.335 - 0.683).

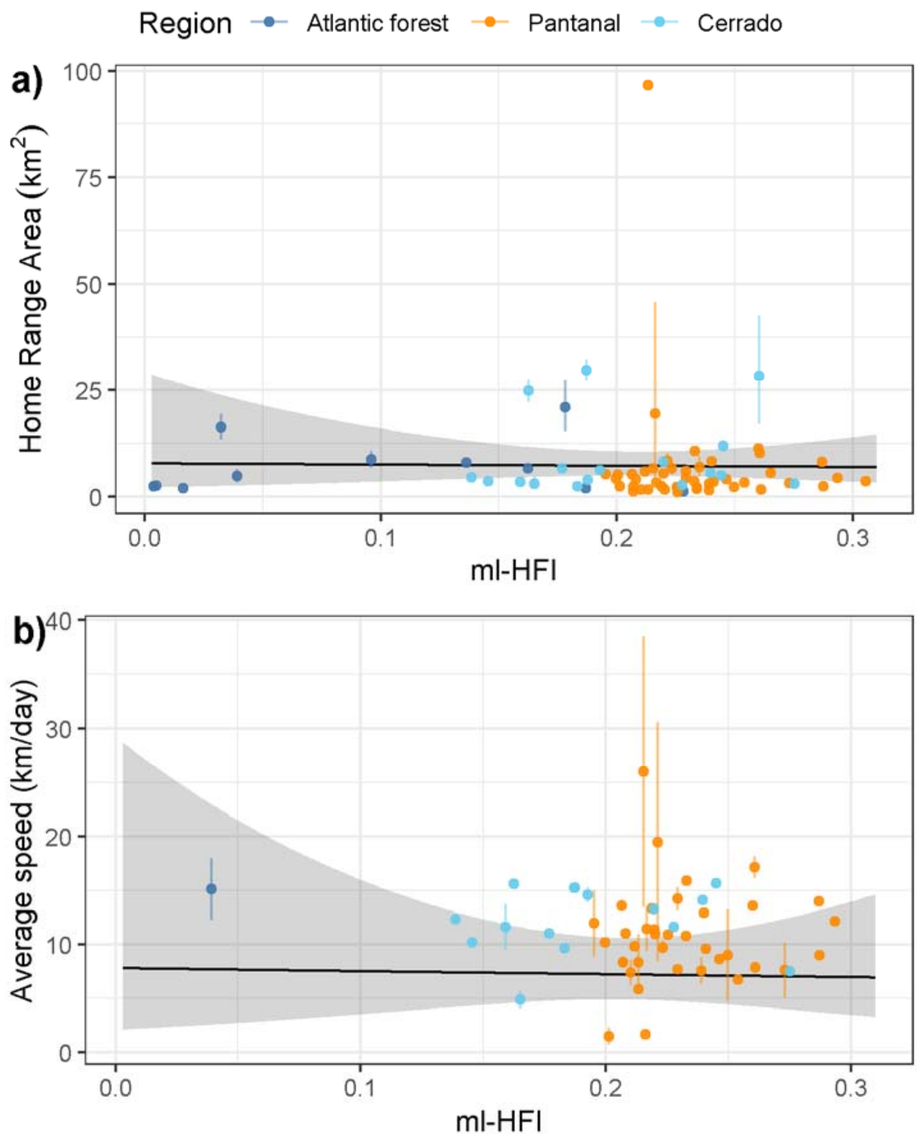

Figure 6: *Estimated mean effect of machine-learning-based human footprint index (ml-HFI) on the tapirs' estimated home range area and estimated average daily speed. The vertical segments indicate the 95% confidence intervals for the movement parameter estimates.*

Discussion

Understanding individual movement and space use requirements is a key step in conservation planning (Allen and Singh 2016). Prior to the present study, very little was known about the movement ecology of tapirs despite their vulnerable status and declining population sizes (Varela et al. 2019). 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 (Tucker et al. 2018; Doherty et al. 2021), 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 (Morato et al. 2016; see also 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 (Tobler 2008). 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 (Fleming et al. 2014) showed that tapir movement was extremely consistent over time (see also Fleming et al. 2019). 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 (Alho 2008). 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 (Marengo et al. 2015).

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 (Dickie et al. 2017), with potential implications for foraging efficiency and encounter rates (Visser and Kiørboe 2006; Bartumeus et al. 2008; Martinez-Garcia et al. 2020). Nonetheless, these differences did not translate into patterns in tapir home range sizes and mean daily movement speeds.

Lowland tapir movement across a gradient of 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 (Doherty et al. 2021), human impacts on the landscape also had no measurable effect on tapir movement. Tapirs inhabiting the Atlantic Forest, the most disturbed biome with only 12.4% of habitat remaining (SOS Mata Atlântica 2008), had home range sizes that were comparable in size to tapirs inhabiting the Cerrado, a biome that has lost almost 50% of its natural area (Machado et al. 2004; Ministério da Agricultura 2021), 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 (Medici et al. 2007), 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 (Hill et al. 2019). Mortality at this scale is expected to impose strong selection pressure on animal populations (Oro et al. 2013; Swaddle et al. 2015). As genotypic adaptation takes generations to occur (Barnosky and Kraatz 2007), behavioral plasticity provides the most immediate response to the pressures of Human Induced Rapid Environmental Change (HIREC, Sih et al. 2011). 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 (Rosenheim and Tabashnik 1991; Sih et al. 2011; Montgomery et al. 2020) that take years to reach sexual maturity and have long inter-generational intervals (Medici 2011). 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 (Medici 2019; Abra et al. 2020), pesticide and environmental pollutants (Medici et al. 2014; Fernandes-Santos et al. 2020; Medici et al. 2021) and poaching (Sanches et al. 2011). Human modified habitats thus risk being ecological traps (Schlaepfer et al. 2002) 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 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.

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Appendix S1

In this appendix we provide supporting information on all of the analyses presented in the main text.

Home range estimates and data collection methods

The tapir location data included in this study were collected over 22 years using a mix of VHF and GPS tracking. As these two data types resulted in different sampling frequencies, it was possible for differences in autocorrelation to drive differences in the estimated home range areas (Noonan et al. 2019). We therefore carried out a supporting analysis to ensure that there was no relationship between data collection methods and the estimated home range estimates. We found that there was no significant difference in the home range estimates between individuals who were monitored using GPS collars, VHF tracking, or a mixture of the two (GPS as the control, p-values: 0.495 for GPS and VHF, 0.739 for VHF only, see Fig. S1).

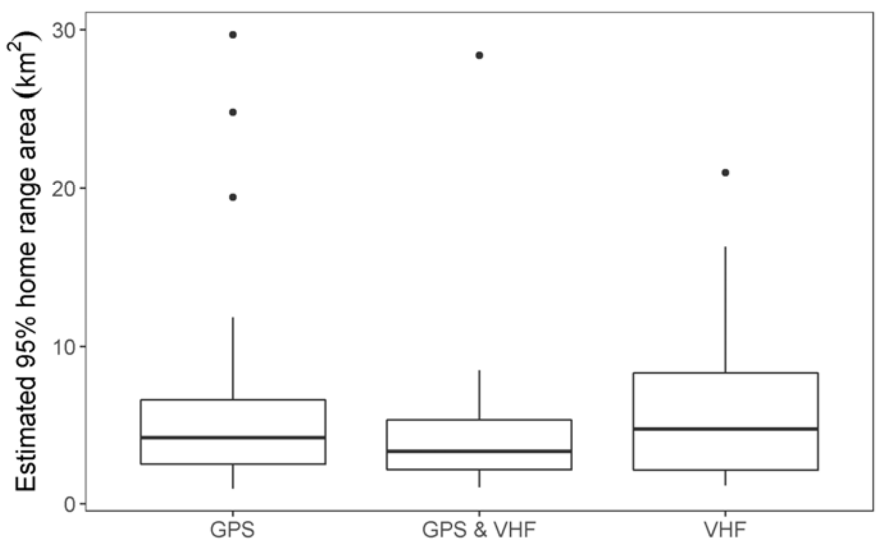

Figure S1: *Estimated 95% home range area by tracking method. Tapirs were monitored using GPS collars, Very High Frequency (VHF) tracking, or both.*

These findings suggest that any of the results presented in the main text are robust to inter-individual differences in data collection.

Habitat composition

Here we show how the habitat composition differed between each of the three study areas. In addition, we show how the proportion of each land use type within the home range of each tapir.

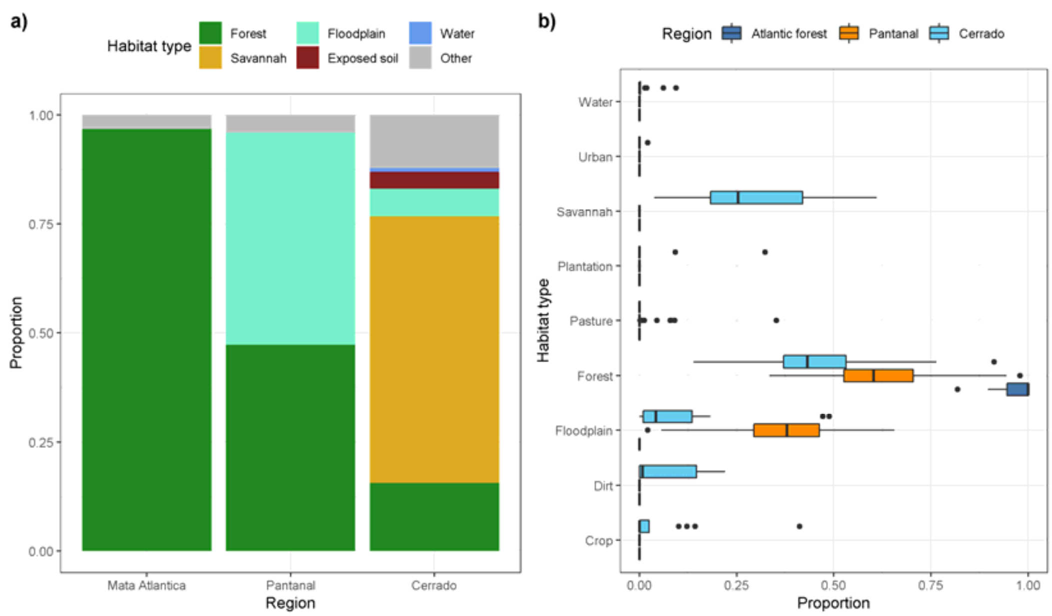

Figure S2: *Figure depicting a) the proportion of habitat type in each of the three study areas, and b) the proportion of each land use type within the home range of each tapir.*

Influence of outliers

As noted in the main text, HFI had no significant effect on lowland tapir home range size, nor average daily movement speed, nor directional persistence. These findings were consistent before and after removing outliers (p-value = 0.596, ; p-value = 0.188, , respectively, Fig. S3).

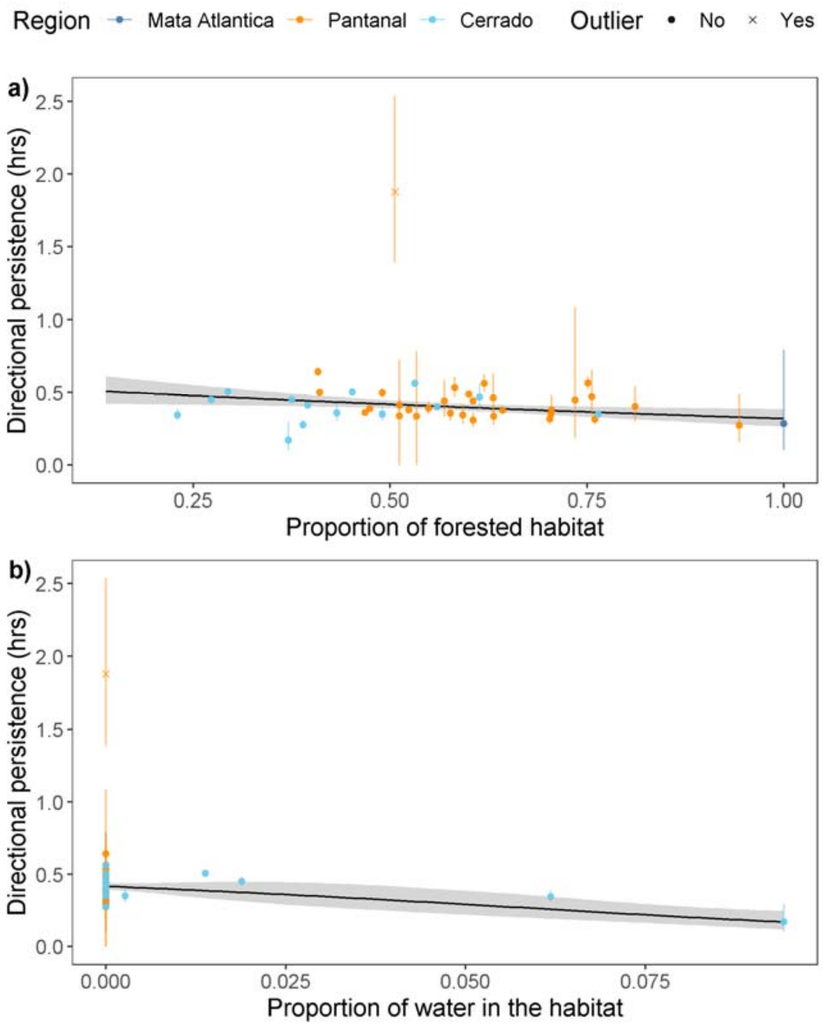

Figure S3: *Effect of forested area or water in a tapir's home range on its estimated directional persistence. The point indicated as an outlier was removed from the dataset for the purpose of the regression.*