How resource abundance and stochasticity affect organisms' space-use requirements

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Abstract

The amount of space organisms use is thought to be tightly linked to the availability of resources within their habitats, such that organisms living in productive habitats generally require less space than those in resource-poor habitats. This hypothesis has widespread empirical support, but existing studies have focused primarily on responses to the *mean* amount of resources, while responses to the variance around the mean are still largely unknown. This is not a trivial oversight. Organisms adjust to variable environmental conditions, so failing to consider the effects of resource (un)predictability can result in a limited understanding of organisms' space-use requirements, challenging ecological theory and applied conservation alike. In this study, we first review the literature of studies that estimate organisms' space-use requirements as a function of resource abundance. We then leverage this information to provide a unifying framework and hypotheses for the effect of mean *and* variance in resources on organisms' space use. Next, we use simulated movement data to demonstrate how the combined effects of mean and variance in resource abundance interact to shape predictable patterns in space use. Finally, we use real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado to show how this framework can be applied to better understand the movement ecology of free-ranging animals. Results from the simulations and empirical examples are presented using a fully transparent approach that allows researchers to apply the framework to their own data and inform area-based conservation efforts.

Key words: energetics, energetic landscape, environmental stochasticity, space use, spatial needs, `ctmm`.

Introduction

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

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

Bunnel (1979) proposed that the simplest relationship between resource abundance and an organism's home-range size is

$$H = C/R, \tag{1}$$

where H is the organism's **home-range size**, C is the organism's resource consumption (kcal day^{-1}), and R is the **resources** the organism can access (kcal day^{-1} unit area^{-1}). Harestad and Bunnel's model is simple to conceptualize and allows for testable predictions, but an organism's values of C and R likely depend on numerous factors, such as competition, metabolic rate, diet, and body weight (Harvey and Clutton-Brock 1981, 1981; Gittleman and Harvey 1982; Lindstedt et al. 1986; Reiss 1988; Jetz et al. 2004; Boratyński 2020; Noonan et al. 2020). While many researchers have since demonstrated that organisms adapt their home ranges in response to resources abundance, few studies build upon others' previous work. Instead, results are typically reported as independent, novel findings. Consequently, we currently lack a unifying framework for quantifying the effects of resource abundance on organisms' space-use requirements. In addition, while much work has been done on estimating organisms' responses to average resource abundance, there is little information on how they respond to unpredictable changes in resources.

Here, we refer to a location's average amount of resources as **resource abundance**, while we use the phrase **resource stochasticity** to indicate the variability in resource abundance due to unpredictable causes. We argue that, on its own, a habitat's long-term resource abundance is not sufficient to assess the habitat's quality, nor make predictions about how much space an organism might use. For instance, a grassland with relatively low but constant forage availability will require drastically different behaviors and adaptations from a desert location with equally scarce forage but rare, sudden, and strong pulses of resources. In the grassland, an animal may require a large but constant home range as it moves between locations in search of food (*sensu* Teitelbaum and Mueller 2019), while an animal in the desert may switch between dispersal as it searches for high-resource patches and short-term

range residency until the local resources are depleted. Although it may be possible for both habitats to have the same long-term average resource abundance, the differences in resource unpredictability result in substantially different movement and life history strategies being selected for. Although it is generally expected that resource unpredictability will decrease organisms' fitness and a landscape's energetic balance (Chevin et al. 2010), there is limited empirical evidence to support this hypothesis (but see: Herfindal et al. 2005; Nilsen et al. 2005; Rizzuto et al. 2021).

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

Resources as a random variable

In statistics, **random variables** indicate random (i.e., unknown) quantities and are indicated with capital letters (e.g., R). Known values, such as realizations of random variables (i.e., known observations or instances), are indicated with lower-case letters (e.g., r). Using this notation, we can write the statement "the probability of random variable R taking the value r" as $P(R = r)$. Resources are often unpredictable (and difficult to quantify), since they depend on various factors which cannot be accounted for easily, including climate

(Lindstedt and Boyce 1985; Morellet et al. 2013; Schmidt et al. 2020), weather (Morellet et al. 2013; Fjelldal et al. 2021), competitive pressure (Rich et al. 2012; Tórrez-Herrera et al. 2020), and differences in energetics at the individual (Schmidt et al. 2020) and species level (Jetz et al. 2004). Thus, we can let the random variable R indicate the amount of resources at a given point in space and time. Quantifying resources as a numerical random variable, as opposed to using *ad hoc* qualitative descriptions, provides us with the capacity to leverage techniques from probability theory and statistics.

In this section, we simulate R using a Gamma distribution with time-dependent (but spatially homogeneous) mean $\mu(t)$ and variance $\sigma^2(t)$, which we write as $R \sim \Gamma(\mu(t), \sigma^2(t))$. Although Gamma distributions are more often parameterized using parameters shape and scale ($k > 0$ and $\theta > 0$) or shape and rate ($\alpha > 0$ and $\beta = 1/\theta > 0$), we use $\mathrm{E}(R) = k\theta$ and $\mathrm{Var}(R) = k\theta^2$ to facilitate visualizing the simulations. However, note that $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ are not independent because the variance depends strongly on the mean (and vice-versa). As the mean approaches zero (from the positive side, which we write as $\mathrm{E}(R) \to 0^+$) the variance also does: $\mathrm{E}(R) \to 0^+ \iff k\theta \to 0^+ \iff k\theta^2 = 0^+ \iff \mathrm{Var}(R) = 0^+$. This assumption also holds biologically, since resources tend to be less variable when they are less abundant. We assume readers are familiar with the concepts of: random variables, probability distributions, expected value of a random variable, and variance of a random variable, but we define and explain each of the four concepts in Appendix 1.

Effects of resource abundance, $\mathbf{E}(R)$

While organisms' needs vary greatly between taxonomic groups, some needs are essential for most species for survival and reproduction. All heterotrophic organisms require sources of chemical energy (i.e., food), water, and various limiting nutrients to survive, grow, and reproduce (Harvey and Clutton-Brock 1981; Baldwin and Bywater 1984; Reich 2001). Failing to acquire sufficient resources can result in lower fitness, behavioral changes, physiological changes or damage, inability to reproduce, and death. Motile organisms can move to new

locations in search of resources, but they must also account for a higher metabolism and movement costs (Taylor et al. 1982). The hypothesis that space-use requirements decrease with resource abundance, E(R), is commonly accepted and well supported, but many studies assume a linear relationship (e.g., Harestad and Bunnel 1979; Relyea et al. 2000; McClintic et al. 2014; Rizzuto et al. 2021; Bista et al. 2022; Bradsworth et al. 2022). This is problematic because a linear relationship can lead to questionable estimates and problematic biases, such as negative or excessively small home ranges (e.g., figure 2 in the work of Bista et al. 2022). Conceptually, the relationship between space-use requirements and E(R) must be nonlinear, since there are limits to how much space an organism is able to explore in its lifetime as well as the minimum amount of space it requires to survive (which is necessarily greater than zero – see fig. 1 as well as: Lucherini and Lovari 1996; Herfindal et al. 2005; Nilsen et al. 2005; Simcharoen et al. 2014; Watson 2020; and contrast them to estimates based on linear models, e.g.: Relyea et al. 2000; Rizzuto et al. 2021; Bista et al. 2022).

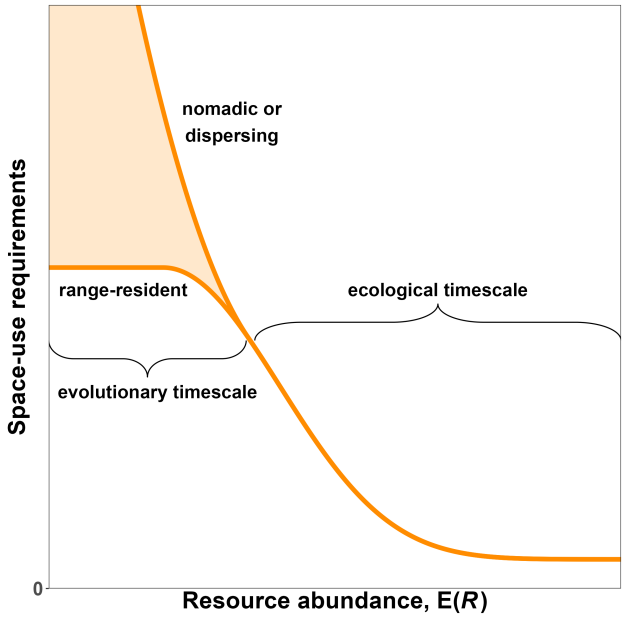

Figure 1: Hypothesized space-use requirements of an organism as a function of resource abundance (E(R)). We expect low values of E(R) to result in high space-use requirements as organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident or nomadic. As E(R) increases, space-use requirements should decrease nonlinearly until they reach the minimum amount of space required by the organism to survive. Note that the relationship between E(R) and space-use requirements cannot be linear because it would require space-use requirements to be negative for high values of E(R).

When E(R) is high, we expect organisms' spatial requirements to be relatively small and near the smallest amount of space required to survive (e.g., Relyea et al. 2000; Herfindal

et al. 2005; Nilsen et al. 2005). However, as E(R) decreases, we expect organisms' spatial requirements to increase nonlinearly, since low values of E(R) force organisms to expand their home ranges (Lucherini and Lovari 1996; Relyea et al. 2000; Herfindal et al. 2005; Nilsen et al. 2005; Bista et al. 2022), migrate to better locations (Samarra et al. 2017; Middleton et al. 2018; Geremia et al. 2019), or move nomadically (Singh et al. 2012; Polansky et al. 2015; Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019). It is unclear when organisms switch from range residency to migration or nomadism (or vice-versa), but understanding the connection between these types of movement is important for quantifying the effect of resource abundance on organisms' space-use requirements and when an organism may choose to migrate or disperse rather than remaining range-resident (mammals: Teitelbaum et al. 2015; moose, *Alces alces*: Singh et al. 2012; eagles, *Haliaeetus leucocephalus*: Wheat et al. 2017; Poessel et al. 2022; lesser flamingos, *Phoeniconaias minor*: Pretorius et al. 2020). Still, large-scale changes in movement behavior (such as species-wide shifts to dispersal, migration, or nomadism) are more likely to occur over evolutionary timescales than over an organism's lifespan. For instance, larger home ranges requires greater vagility, which, in turn, is facilitated by morphological features such as hinged joints and elongated limbs (Andersson 2004; Jetz et al. 2004; Samuels et al. 2013; Hirt et al. 2017).

It is also worth noting that high E(R) does not does not necessarily imply that organisms have access to high amounts of resources, as predator avoidance and competition within an organism's habitat will decrease the proportion of R it is able to access. Thus, organisms in habitats with strong competitive pressure and predation may require larger home ranges (Jetz et al. 2004; Prox and Farine 2020), but larger home ranges can be harder to defend and also result in higher rates of competition and movement costs (Grant 1993; Jetz et al. 2004; but also see Dickie et al. 2022). Additionally, persistent territorial defense from competitors may prevent organisms from using space freely and as necessary (wolves, *Canis lupus*: Rich et al. 2012; feral cats, *Felis catus*: Bengsen et al. 2016; Capuchin monkeys, *Cebus capucinus*: Tórrez-Herrera et al. 2020), so the effect of E(R) on space use may vary between individuals,

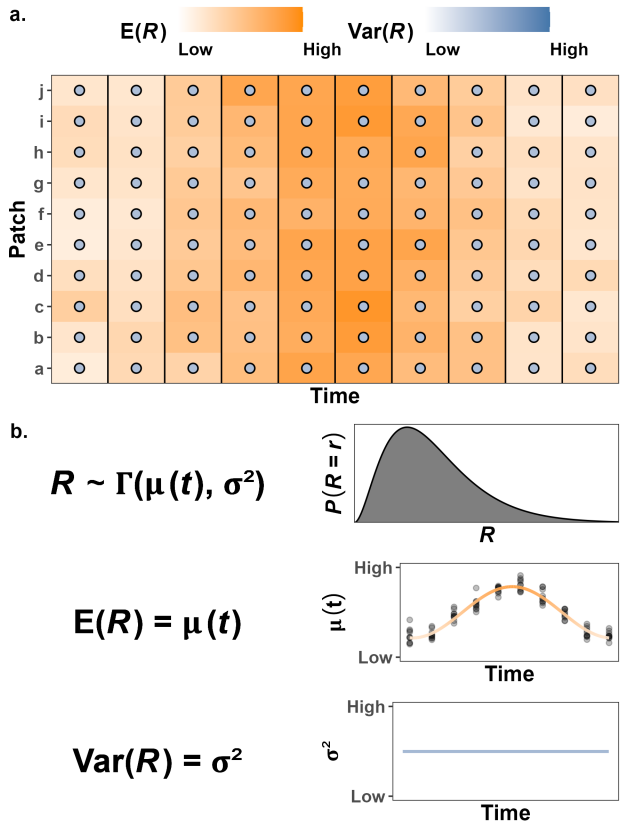

Figure 2: Fictitious example of variation in resources in a heterogeneous environment with constant variance (after accounting for changes in the mean). (a.) Resources (R, brown-green fill) vary over time and space with a constant the variance (dot color). (b.) Arbitrary definition of R as following a Gamma distribution with time-varying mean $\mu(t)$ and constant variance $\mathrm{Var}(R) = \sigma^2$. The points in the central panel indicate the ralizations of R in panel a.

species, and locations. Still, these pressures simply alter the intensity with which organisms respond to $\mathrm{E}(R)$ but not the shape of the relationship, since each of these cases fall along different parts of the continuum in $\mathrm{E}(R)$ shown in fig. 1.

Consider the scenario where the average in resource abundance, $\mathrm{E}(R)$, changes over time but $\mathrm{Var}(R) = \sigma^2 > 0$ is constant over time and space (see fig. 2a). We can use the notation $R \sim \Gamma(\mu(t), \sigma^2)$ to indicate that R follows a Gamma distribution with a mean $\mu(t)$ that changes over time (i.e., it is a function of time) while the variance is constant (fig. 2b). Since R is spatiotemporally random, an organism that moves in the landscape will not find the same R at different time points or throughout the habitat. However, if $\mu(t)$ changes repetitively and regularly over time (e.g. peaks each spring and is lowest in winter), an organism may learn to predict times of high or low R (Samarra et al. 2017; Abrahms et al. 2019; Geremia et al. 2019; e.g., Falcón-Cortés et al. 2021), but it will not be able to predict

where R is high if $\mathrm{E}(R)$ does not vary predictably over space.

This model is somewhat simplistic, but its simplicity makes it easy to fit and conceptualize. Such a model may be appropriate in regions where variability does not change noticeably spatiotemporally, or when data availability is too low to produce appreciable measures of changes in variance. Examples of temporally homogeneous habitats include regions where productivity remains fairly predictable throughout the year (e.g., equatorial rain forests or highly homogeneous deserts). When productivity is approximately stable over long periods of time, it may be possible to further simplify the model by assuming a constant mean, but this is likely rarely the case. Most often, $\mathrm{E}(R)$ will vary over time, and organisms' behaviors will change in response.

Effects of resource stochasticity, $\mathbf{Var}(R)$

Although the effect of R on organisms' space-use requirements is often recognized and accounted for in ecology (Burt 1943; Southwood 1977; Lucherini and Lovari 1996; Relyea et al. 2000; Nilsen et al. 2005; Williams-Guillen et al. 2006; Rickbeil et al. 2019), most of the focus has been on the effects of $\mathrm{E}(R)$, while $\mathrm{Var}(R)$ has received far less attention (but see Nilsen et al. 2005; Di Stefano et al. 2011; Rizzuto et al. 2021; Seigle-Ferrand et al. 2021). However, $\mathrm{Var}(R)$ can fluctuate temporally (and spatially) due to many important drivers, including repetitive and predictable patterns as well as more stochastic ones. For example, since berries are scarce outside the growing season, the variance in berries will also be low. But during the growing season, both the average number of berries and the variance in berries are higher, since a bear may explore a location before fruiting time or after competitors ate all the berries. In contrast, other sources of stochasticity can be much less predictable, such as the arrival of new competitors (Alexander et al. 2015), the emergence of new diseases (Hollings et al. 2014), droughts (Foley et al. 2008; Haig et al. 2013), fires (Jolly et al. 2022), floods (Ramos Pereira et al. 2013), changes in climate and phenology (Inouye et al. 2000; Jonzén et al. 2006; Grant et al. 2017; Berger et al. 2018; Woolway et al.

2020; Severson et al. 2021), and other extreme events (Logares and Nuñez 2012; Anderson et al. 2017).

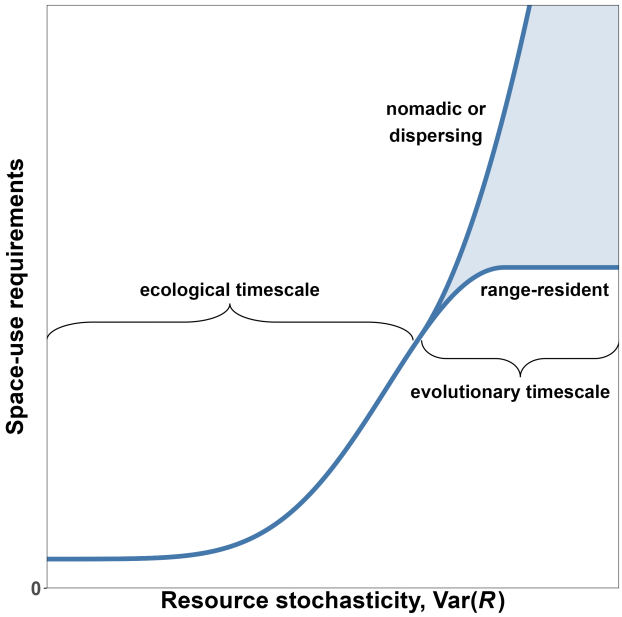

Figure 3: Hypothesized space-use requirements of an organism as a function of resource stochasticity (Var(R)). We expect low values of Var(R) to result in low space-use requirements as organisms are able to depend on relatively predictable resources. As Var(R) increases, space-use requirements should increase nonlinearly, whether this results in an expansion of the home range (in the case of range-resident organisms) or a switch to dispersal, nomadism, or migration. Note that the relationship between Var(R) and space-use requirements cannot be linear because it would require space-use requirements to be negative for low values of Var(R).

Environmental variability can reduce a landscape's energetic balance (Chevin et al. 2010), which, in turn, decreases organisms' fitness (Berger et al. 2018) and increases their space-use requirements. While this is true for both predictable and unpredictable stochasticity, extreme and rare events are more likely to have a stronger effect. A few recent studies support these hypotheses (Chevin et al. 2010; Morellet et al. 2013; Nandintsetseg et al. 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic and taxonomic scales, so the extent to which these preliminary findings can be generalized is still very limited. Thus, there remains a need for developing a more complete understanding of how organisms' space-use requirements change with environmental stochasticity.

Similar to the effect of E(R), we expect Var(R) to have a nonlinear effect on organisms' space-use requirements. When Var(R) is low enough that R is relatively predictable, we do not expect changes in Var(R) to have a noticeable effect, but as resources become increasingly unpredictable, we expect space-use requirements to increase progressively faster

(fig. 3) because: (1) as $\mathrm{Var}(R)$ increases the chances of finding low R increase superlinearly, (2) stochastic environments tend to be less productive (Chevin et al. 2010), and (3) the added movement required to search for food increases organisms' energetic requirements. If resources remain highly unpredictable over long periods of time (e.g., multiple lifespans), organisms may evolve or develop new behaviors (such as nomadism, dispersal, and migration) or adaptations (such as increased fat storage or food caching). If changes in $\sigma^2(t)$ are sufficiently predictable, organisms may learn to anticipate and prepare for periods of greater stochasticity by pre-preemptively caching food or migrating, or relying on alternative food sources during stochastic events (e.g., after the arrival of competitors).

Like the scenario illustrated in fig. 2, we can imagine an environment where both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ change over time. We can then define $\mathrm{Var}(R)$ as a function of time using the same notation as we did for $\mathrm{E}(R)$, i.e., $\mathrm{Var}(R|t) = \sigma^2(t)$ (fig. 4). When both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ change over time, predicting R becomes more complex. Statistically, this is because $\sigma^2(t)$ decreases as we allow $\mu(t)$ to change more over time and explain a greater proportion of $\mathrm{Var}(R)$. Biologically, this is important because some organisms may perceive changes in R as a change in $\mathrm{E}(R)$, while others may perceive the change as a stochastic event. An organism's perception of changes in R will depend strongly on the organism's cognitive capacities, including its memory and lifespan (Foley et al. 2008; Fagan et al. 2013; Mueller et al. 2013; Abrahms et al. 2019; Falcón-Cortés et al. 2021). The ability to predict trends in $\mu(t)$ and $\sigma^2(t)$ requires organisms have high cognitive capacity, since distinguishing between changes in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ is not easy (Steixner-Kumar and Gläscher 2020), especially if $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ are not independent, as in the case of $R \sim \Gamma(\mu(t), \sigma^2(t))$. Regardless of whether an organism is capable of predicting changes in $\sigma^2(t)$, the effect of $\mathrm{Var}(R)$ is arguably as important as the effect of $\mathrm{E}(R)$ in determining how said organism will respond to changes in R and consequently adapt its space use.

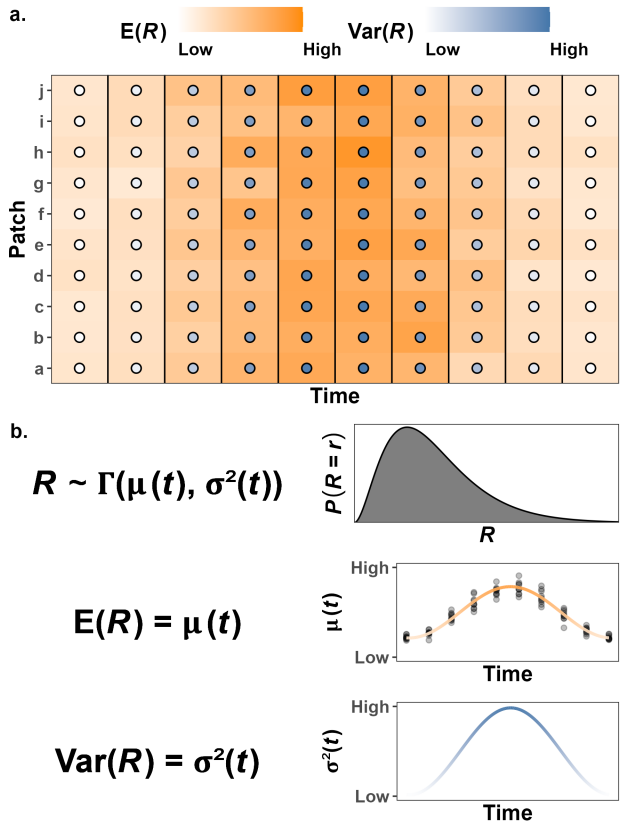

Figure 4: Fictitious example of variation in resources in a heterogeneous environment with changing variance (even after accounting for changes in the mean). (a.) Although resources (R, brown-green fill) varies over time and space, the variance (dot color) is lowest at the beginning and end of the observational period and highest when $\mathrm{E}(R)$ peaks. (b.) Arbitrary definition of R as following a Gamma distribution with time-varying mean $\mu(t)$ and variance $\sigma^2(t)$. The points in the central panel indicate the ralizations of R in panel a.

Interactive effects of $\mathbf{E}(R)$ and $\mathbf{Var}(R)$

We have provided the case for why both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ affect organisms' space-use requirements, but we presented the two parameters as independent drivers of movement. However, in the more realistic scenario where both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ fluctuate over time, organisms may respond to changes in $\mathrm{Var}(R)$ more when resources are scarce than when they are abundant. Consequently, models estimating the effects of R on organism's movement should account for not only the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ separately, but also their interactive effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but $\mathrm{Var}(R)$ may have little effect if resources are stochastic but always abundant. Thus, we expect $\mathrm{Var}(R)$ to have a stronger effect on space-use requirements when $\mathrm{E}(R)$ is low, and less of an effect when $\mathrm{E}(R)$ is high.

Rizzuto et al. (2021) found that the space-use requirements of snowshoe hares (*Lepus americanus*) increased with average carbon to nitrogen ratio (C:N, a measure of N scarcity) in lowbush blueberry as well as the coefficient of variation (the standard deviation divided by the mean, $\frac{\sqrt{\sigma^2(t)}}{\mu(t)}$) in C:N. However, it is hard to determine how $\sigma^2(t)$ affected the hares' space-use requirements since the coefficient of variation is a function of both $\mu(t)$ and $\sigma^2(t)$, so the effects of the two variables are confounded. Similarly, Mueller et al. (2011) suggested that ecosystem variability (measured as spatial semivariance in NDVI) causes ungulates to move more and adopt more nomadic behaviors, but it is hard to determine whether the higher semivariances in NDVI are due to an increase in $\mathrm{Var}(R)$ or simply spatial changes in $\mathrm{E}(R)$ (e.g., increased seasonality or continentality). Likewise, Herfindal et al. (2005) found that the home ranges of Canadian lynx (*Lynx canadensis*) decreased with seasonality, but this may be an artifact of a lower $\mu(t)$ in highly seasonal environments, rather than stochasticity in R. A subsequent analysis by Nilsen et al. (2005) of the lynx data of Herfindal et al. (2005) along with data on wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) found that carnivores respond differently to seasonality, which suggests that different species may have different perceptions of the changes in R over the seasons. Collectively, these studies provide support towards the effects of both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ on organisms' space-use requirements, but the lack of a unifying framework across these studies makes it challenging to synthesize their findings. Thus, it is important to disentangle the effects of changes in $\mathrm{E}(R)$, such as seasonal trends in $\mu(t)$, and stochasticity ($\mathrm{Var}(R)$). The need to account for changes in both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ is compounded by recent changes in climate, which expose species to novel situations and increasingly common and extreme stochastic events (Noonan et al. 2018; Yao et al. 2022; Intergovernmental Panel On Climate Change 2023).

Nilsen et al. (2005) also show that the effect of $\mathrm{E}(R)$ on the home-range size of wolves and fishers (*Martes pennanti*) depends on seasonality (and vice-versa), since organisms in habitats with high and low seasonality had opposite responses to $\mathrm{E}(R)$. Therefore, it may

not be sufficient to account for the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$; models may also need a term for interaction between the two. This may be because organisms respond strongly to $\sigma^2(t)$ when $\mu(t)$ is low, but they may not respond if $\mu(t)$ is sufficiently high. However, it does not explain why organisms may respond to $\mathrm{E}(R)$ in opposite ways in different habitats. Instead, we suspect this inconsistency is because Nilsen et al. (2005) do not distinguish between changes in $\mu(t)$ and $\sigma^2(t)$ between seasons, so the effects of the two are confounded in the seasonality term. Distinguishing between changes in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ allows one to separate the two seasonal cycles and produce more consistent results.

Simulating responses to $\mathbf{E}(R)$ and $\mathbf{Var}(R)$

To support our hypothesis of how organisms' space use is affected by $\mathrm{E}(R)$, $\mathrm{Var}(R)$, and the interaction effect of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, we present the results from a series of quantitative simulations. To start, we used the `ctmm` package (Fleming and Calabrese 2021) for `R` (R Core Team 2022) to generate 200 tracks (see Appendices 2 for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement model [IOU model; Gurarie et al. (2017)]. The IOU model's correlated velocity produces realistic tracks with directional persistence despite the tracks being discrete samples of continuous-time movement processes. However, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF) models, IOU models do not assume the movement process is spatially stationary, so the organism is not assumed to be range-resident. Consequently, each track is spatially unrestricted and can be interpreted as purely exploratory movement.

Each of the 200 tracks were placed on a raster with common starting point $\langle 0, 0\rangle$ and sufficient time between tracks to be independent of one another (other than the starting point). Each time the track moved to a new cell, the organism collected resources R sampled from a Gamma distribution. The mean and variance of the distribution were defined by deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 5). Note that t was constant within each set of 200 tracks, so the time spent moving by the organism in each

track did not affect the distribution R was sampled from. Tracks were truncated once the organism reached satiety, and the organism was given enough time to return to $\langle 0, 0 \rangle$ with no correlation to the following track. Finally, each set of 200 truncated tracks was modeled using an OUF model and Autocorrelated Kernel Density Estimate to estimate the 95% utilization distribution. Additional information is provided in Appendix 2.

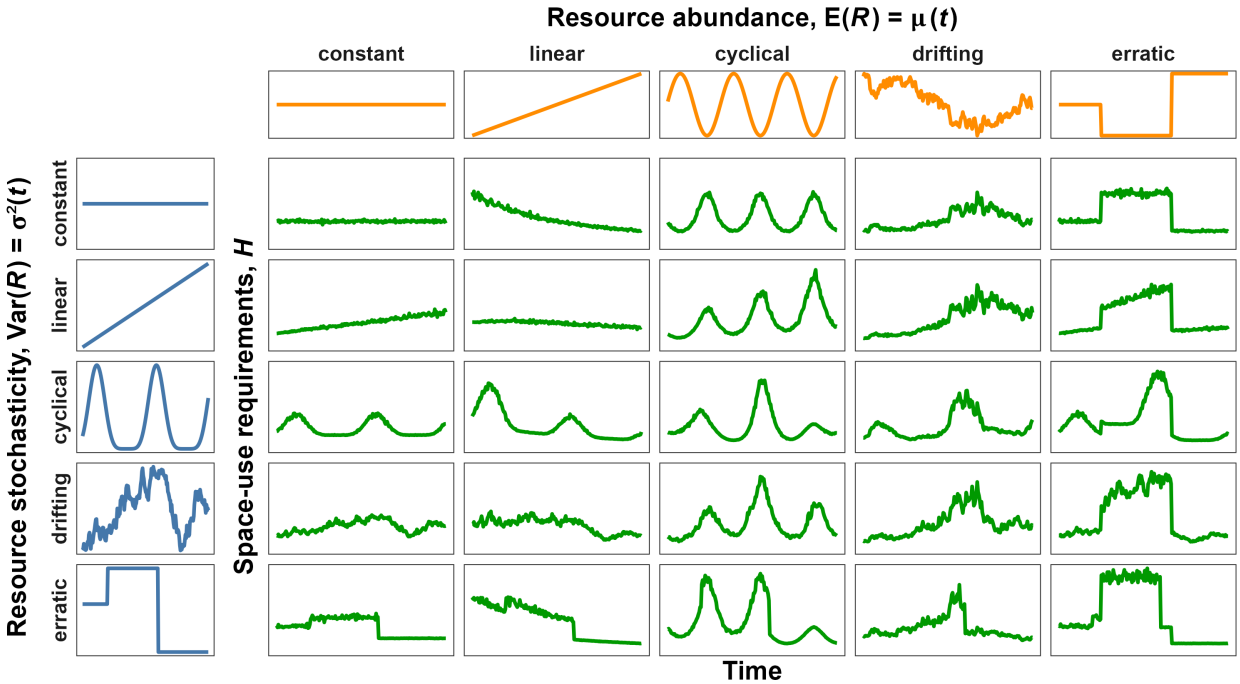

Figure 5: Simulated home range sizes, H, of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how H decreases nonlinearly as $\mu(t)$ increases and increases nonlinearly as $\sigma^2(t)$ increases. Additionally, the variance in H is higher when $\mu(t)$ is lower or $\sigma^2(t)$ is higher, and changes in $\sigma^2(t)$ have greater impacts when $\mu(t)$ is low.

Fig. 5 shows how the simulated space-use requirements changed in response to $\mu(t)$ and $\sigma^2(t)$. The top row (constant Var(R)) shows how space-use requirements vary for different trends in $\mu(t)$ while Var(R) remains constant (like in fig. 2). As E(R) increases at a constant slope (linear $\mu(t)$) the space-use requirements decrease nonlinearly, with larger changes when E(R) is low, until home-range size approaches the minimum size required by the organism. As described in the section on the effects of resource abundance, the nonlinear decrease is because changes in $\mu(t)$ have a larger effect when E(R) is low (e.g., Lucherini and Lovari 1996; Herfindal et al. 2005; Nilsen et al. 2005).

In regions where the $\mu(t)$ changes over time (e.g., seasonal changes – see cyclical E(R)

and Lai et al. 2017), organisms should have access to sufficient space to fulfill their needs during periods of scarcity, whether the space available is sufficiently large year-round or it changes seasonally with the expected changes in $\mu(t)$ (e.g., winter park closures). However, estimates of spatial requirements based on estimated changes in $\mu(t)$ should be interpreted carefully, since model error and unforeseeable decreases in $\mathrm{E}(R)$ (such as following fires or floods) may increase organisms' space-use requirements suddenly and unpredictably. Thus, it is best to include a "buffer" area so the available space is larger than the estimated space-use requirements. This is particularly the case in environments where resource abundance changes unpredictably (drifting $\mu(t)$), since accurate long-term estimates and predictions of $\mu(t)$ may be hard to produce, if not impossible. In cases where $\mu(t)$ is highly unpredictable, organisms should have enough space to collect resources during times of greatest predicted scarcity, particularly if the changes in resource abundance occur rapidly, often, or for long periods of time (erratic $\mu(t)$).

The leftmost column of fig. 5 (constant $\mathrm{E}(R)$) illustrates the effects of $\mathrm{Var}(R)$ on the simulated space-use requirements while $\mathrm{E}(R)$ remains constant. Overall, both mean H and the variance around it increase with $\sigma^2(t)$ (most visible with constant $\mathrm{E}(R)$ and linear $\mathrm{Var}(R)$). This is because, similarly to resource-poor periods, times of greater stochasticity require the organism to move over larger areas for longer periods of time. This results in a greater uncertainty in how much time and space the organism will require to reach satiety, or indeed whether an organism living in highly stochastic environments can even reach satiety within a finite amount of time.

The remaining panels in fig. 5 illustrate how the effect of $\mathrm{Var}(R)$ depends on $\mathrm{E}(R)$ (and vice-versa) as well as how complex the relationship can be. Since $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ have opposite effects on H, disentangling the effects can be particularly difficult when both parameters change in a correlated manner (e.g., linear $\mathrm{E}(R)$ and $\mathrm{Var}(R)$). When both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ increase linearly, H initially increases since the effect of $\mathrm{Var}(R)$ is stronger, but then decreases as the effect of $\mathrm{E}(R)$ begins to dominate. However, when $\mu(t)$ and $\sigma^2(t)$

follow fairly different trends (e.g., cyclical $\mathrm{E}(R)$ and linear $\mathrm{Var}(R)$), it is easy to see how an increase in $\mathrm{Var}(R)$ amplifies the effects of $\mathrm{E}(R)$. In contrast, the effect of $\mathrm{Var}(R)$ is stronger when $\mathrm{E}(R)$ is low (e.g., linear $\mathrm{E}(R)$ with cyclical $\mathrm{Var}(R)$). Thus, H is largest when $\mathrm{E}(R)$ is low and $\mathrm{Var}(R)$ is high, and it is smallest when $\mathrm{E}(R)$ is high and $\mathrm{Var}(R)$ is low (see the panel with cyclical $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ as well as Lai et al. 2017).

Not all 25 scenarios depicted in fig. 5 may be realistic, but the trends in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, and their impacts on space use are useful examples that can be thought of as simplified scenarios. $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ may be assumed to be (approximately) constant in highly homogeneous environments. Although it is impossible for $\mu(t)$ and $\sigma^2(t)$ to increase linearly forever, these examples are useful to demonstrate that linear changes in $\mu(t)$ and $\sigma^2(t)$ affect H nonlinearly. Cyclical oscillations in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ may occur in urban environments as human activity changes within and between days (Péron et al. 2017; Ikeda et al. 2022) and as temperatures fluctuate daily and seasonally (Geremia et al. 2019; Alston et al. 2020), while $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ may drift randomly in highly complex environments which are too hard to predict. Finally, erratic changes in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ may occur in environments where changes are very sudden, such as areas prone to fires or floods, as well as habitats with drastic human alteration (e.g., a forest which is clear-cut with a subsequent artificial re-forestation). However, if stochastic changes are sufficiently small and frequent, organisms may perceive them as continuous and smooth changes rather a series of small and sudden changes.

Although the temporal trends in fig. 5 are complex and the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ can be hard to disentangle, two surprisingly simple relationships emerge when home-range size is shown as a function of either $\mathrm{E}(R)$ or $\mathrm{Var}(R)$, rather than time. Both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ affect space-use requirements precisely as we hypothesized (fig. 6). We believe the approximately linear effect of $\mathrm{Var}(R)$ on H is mainly due to two factors. Firstly, H scales superlinearly with the standard deviation in R (as $\sqrt{\mathrm{Var}(R)}$ is on the same scale as $\mathrm{E}(R)$; not shown), which would necessarily imply that H increases *sub*linearly with $\mathrm{Var}(R)$. Secondly, the organism's

movement was simulated to be range resident within an homogeneous environment. Since real-world landscapes are spatially heterogeneous in both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, organisms may choose to shift their home range to a new area following a stochastic event that caused $\mu(t)$ to decrease, such as a fire or a flood. Thus, we hypothesize that our simulations may be underestimating organisms' responses to spatiotemporal changes in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, since the simulated organisms cannot select for areas of higher $\mathrm{E}(R)$ or lower $\mathrm{Var}(R)$. Additionally, the simulations also ignore how competition, movement costs, predation, and other factors may affect the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ on H. While these are definitely important effects that should be accounted for (Jetz et al. 2004), doing so was beyond the scope of this paper.

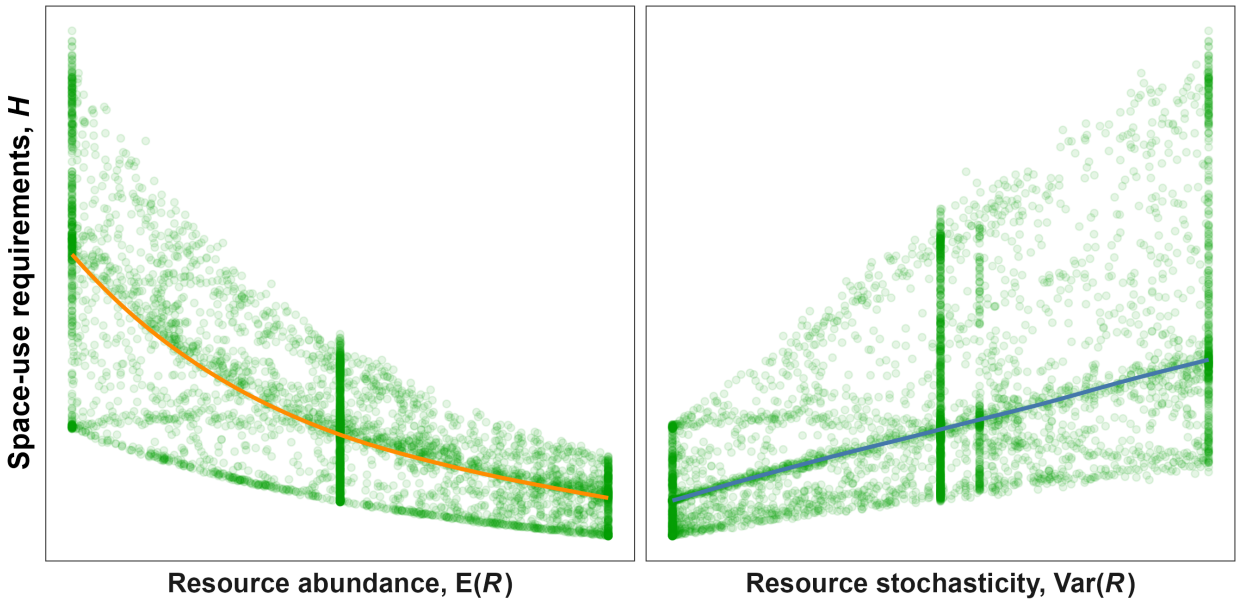

Figure 6: Effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ on simulated spatial requirements with 95% credible intervals for the mean (overlapping the line). Credible intervals were calculated assuming a gaussian posterior distribution on the link scale. The relationships were estimated using a Generalized Additive Model for Location and Scale (GAMLS; Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) with a Gamma location-scale family of distributions (`mgcv::gammals`). The model accounted for the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ and the interaction effects between the two on both the location (i.e., mean) of H and its scale parameter. Note the nonlinear decrease in H as $\mathrm{E}(R)$ increases and the increase in H as $\mathrm{Var}(R)$ increases. Additionally, note how the variance in space-use requirements strongly increases with mean space-use requirements.

Applying the framework

In this section, we show how this framework can be applied to better understand the movement ecology of free-ranging organisms via remote sensing data such as NDVI (Pettorelli et al. 2011). To illustrate the methods, we use empirical tracking data on a lowland tapir

from the Brazilian Cerrado. Appendix 3 contains additional information on how NDVI was modeled along with details on the continuous-time movement models (Noonan et al. 2019*a*; Fleming and Calabrese 2021) and autocorrelated kernel density estimation (Noonan et al. 2019*b*; Alston et al. 2022; Silva et al. 2022) used to quantify the tapir's space-use requirements.

The hypotheses we present here allow researchers to combine otherwise complicated findings (e.g., fig. 5) and generalize results to a single, common set of functions. We expect the two hypotheses we present here (figs. 1 and 3) to be applicable to all motile organisms, once differences in size, metabolic needs, and diet are accounted for. In this subsection, we illustrate how researchers can leverage these hypotheses using their own data to build on previous work rather than listing the results as new findings. Additionally, the analyses can be expanded to the population or species level with the use of Hierarchical Generalized Additive Models (HGAMs) with individual-level intercepts and smooth terms (see models "GS" and "GI" in Pedersen et al. 2019). Such models would allow one to test whether members of the same population or species respond similarly to $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ while also quantifying any deviation from the hypothesized behavior. Individuals and populations that were once thought to have different space-use requirements due to differences in behavior may instead be simply responding to different local conditions along the functions in figs. 1 and 3 (e.g., Singh et al. 2012). In the following sections, we illustrate how one can apply this framework to empirical data.

We start by providing examples and considerations on how one may model R and the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ on organisms' space-use requirements. Next, we apply the methods to the tapir's GPS tracking data and use NDVI as a proxy for R. Finally, we offer suggestions on how this approach can be used to inform conservation-related decisions, including assessing habitat quality and estimating organisms' space-use requirements under different scenarios.

Modeling R

Location-scale models (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) are a class of statistical models that allow us to estimate changes in a random variable's mean (i.e. its location) and variance (which depends on its scale) while allowing the mean-variance relationship to vary. `mgcv` (Wood 2017) is a commonly used package for `R` (R Core Team 2022) that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and Generalized Additive Models (GAMs, see Wood 2017), including hierarchical and location-scale GLMs and GAMs. Currently, the `mgcv` package allows one to fit location-scale models with various families of distributions, including Gaussian (i.e., normal), gamma, and Tweedie location-scale families.

The Gaussian location-scale family of distributions is very flexible, since the mean and variance parameters are assumed to be independent, and the response can be either positive or negative. However, the distribution's flexibility can also result in unreliable estimates for non-Gaussian responses, such as strictly positive data (e.g. available biomass), count data (e.g., number of prey), proportions (e.g., percentage of forested habitat), and bounded ratios (e.g., NDVI, see Pettorelli et al. 2011).

The Gamma location-scale family is best for strictly positive responses, such as areas (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto et al. 2021), total biomass, or energetic intake. The Tweedie location-scale family is similar to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-trivial amount of zeros, such as daily precipitation or prey density (but see zero-inflated distributions: Zuur et al. 2009). In this paper, we estimate R by modeling NDVI using `mgcv` and a beta location-scale family (not available in `mgcv` at the time of publication). If one is interested in families of distributions which are not available in `mgcv`, we suggest using the `brms` package (Bürkner 2017), which allows full control over all of a family's parameters via a fully Bayesian approach (as opposed to `mgcv`'s Empirical Bayes method – see Bürkner 2018).

Modeling the mean and variance terms of R should be done carefully. Since trends in both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ can be spatiotemporally nonlinear and non-monotonic, we suggest using a GAM rather than a GLM. However, the complexity of the spatiotemporal terms should be chosen carefully, particularly for the mean's terms. An excessively wiggly $\hat{\mu}(t)$ will cause $\sigma^2(t)$ to be under-estimated, while an excessively smooth $\hat{\mu}(t)$ will cause $\sigma^2(t)$ to be over-estimated. Although there is no error-proof system, choosing the complexity of the terms based on the organism's ability to detect change and adapt is a reasonable starting point. Additionally, setting the basis dimension (`k`) of the scale terms to be half or less than that of the mean terms and using restricted marginal likelihood (Wood 2011) should provide reasonably accurate results. We suggest starting with low values of `k` and adjusting `k` based on the trends in the residuals. Note that since R is likely spatiotemporally autocorrelated, it may be easy to overfit the model. Simpson (2018) provides a useful introduction to GAMs for biological time series.

Estimating R using NDVI

Since there is no commonly-used distribution with a support over the interval $[-1, 1]$, we use beta distribution after scaling NDVI to the interval $[0, 1]$ by applying the **linear transformation**

$$\nu_{[0,1]} = \frac{\nu + 1}{2}, \tag{2}$$

where ν indicates the NDVI value in $[-1, 1]$ and $\nu_{[0,1]}$ is the scaled NDVI value (see Denny 2017 for more information on transforming response data). In this case, we can define R as following a beta distribution with mean and variance that depend on time using the notation $B(\mu(t), \sigma^2(t))$. We use this parameterization here for ease of explanation, but note that beta distributions are generally parameterized using the shape parameters α and β such that the mean is

$$\mathrm{E}(R) = \frac{\alpha}{\alpha + \beta} \tag{3}$$

while the variance is

$$\mathrm{Var}(R) = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}. \tag{4}$$

We can easily convert $\mu(t)$ and $\sigma^2(t)$ back to mean and variance in NDVI using the inverse of equation (2):

$$\nu = 2\nu_{[0,1]} - 1. \tag{5}$$

Consequently, we have

$$\mathrm{E}(\nu|t) = 2\mu(t) - 1. \tag{6}$$

and

$$\mathrm{Var}(\nu|t) = 2^2\sigma^2(t) + 0 = 4\sigma^2(t). \tag{7}$$

Particular attention should be be given when deciding what distribution to use and how to estimate means and variances in R. Improper models and simulations of resource abundance can fail to produce robust, sensible, and accurate estimates of R.

Modeling the effects of $\mathbf{E}(R)$ and $\mathbf{Var}(R)$ on space-use requirements

As discussed in the previous section, the first step to modeling H is to choose an appropriate family of distributions. Since H is strictly positive and continuous, a Gamma family seems the most appropriate among the distributions currently offered by the `mgcv` package (Wood 2017), but the Tweedie family would also be appropriate if the variance does not scale with the squared mean.

As with the simulated effects of $\mu(t)$ and $\sigma^2(t)$ on H (fig. 6), a location-scale Gamma model is likely required. If there is not sufficient data to fit a location-scale model (which is not the case here), a simple Gamma model may be sufficient, but we suggest selecting the

best family of distributions using an information criterion such as the Akaike Information Criterion (Akaike 1974). Due to potential correlation between E(R) and Var(R) in a small and autocorrelated sample, the relationship between R and H should be modeled carefully and with parsimony. Below, we present an empirical example using GPS tracking data from a lowland tapir (*Tapirus terrestris*) and satellite-derived NDVI. Additional information can be found in Appendix 3.

The effects of E(R) and Var(R) on a lowland tapir's space-use requirements

Fig. 7 illustrates how a tapir in the Brazilian Cerrado (data from Medici et al. 2022) adapts its spatial needs to changes in E(R) and Var(R). Panels **a** and **b** show the changes in seven-day average mean and variance in NDVI, respectively, experienced by the tapir during the tracking period. Panel **c** shows the changes in the tapir's 7-day home range over time. Note how the tapir uses more space during periods of lower NDVI (e.g., August 2017) and less space during periods with high NDVI (January 2018). Additionally, when resources are scarce and highly unpredictable (August 2018), the tapir uses up to 5 times more space than when resources are abundant and predictable (e.g., January 2018). Finally, panels **d** and **e** show the estimated (marginal) effects of $\mu(t)$ and $\sigma^2(t)$ on the tapir's space use. Simce $\mu(t)$ and $\sigma^2(t)$ are strongly correlated (panel **f**) and (spatio)temporally autocorrelated (panels **a** and **b**), the effects of R on H should be modeled carefully. To avoid over-fitting the model, we constrain the smooth effects of $\mu(t)$ and $\sigma^2(t)$ using a shape-constrained additive models (SCAM) with monotone deceasing and increasing P-splines for $\mu(t)$ and $\sigma^2(t)$, respectively.

Modeling the tapir's space use as a function of resource abundance alone would result in an excessively strong estimated effect and an worse model fit (ΔAIC ≈ 87). By including the effect of $\sigma^2(t)$ in the model along with that of $\mu(t)$, we show that the tapir responds to both resource abundance and stochasticity. While the tracking period may be too short to see the effects of E(R) clearly, it should also be noted that the Cerrado is relatively rich in vegetation throughout the entire year (fig. 7a), and thus the tapir does not experience resource scarcity

during the tracking period. Consequently, this example demonstrates two points central to this paper. Firstly, even animals in resource-rich regions such as the Brazilian Cerrado adapt their behavior in response to reosurce stochasticity. Secondly, trends in mean resources alone are not sufficient to explain the tapir's space use, and the stochasticity in R is an important driver of the tapir's movement.

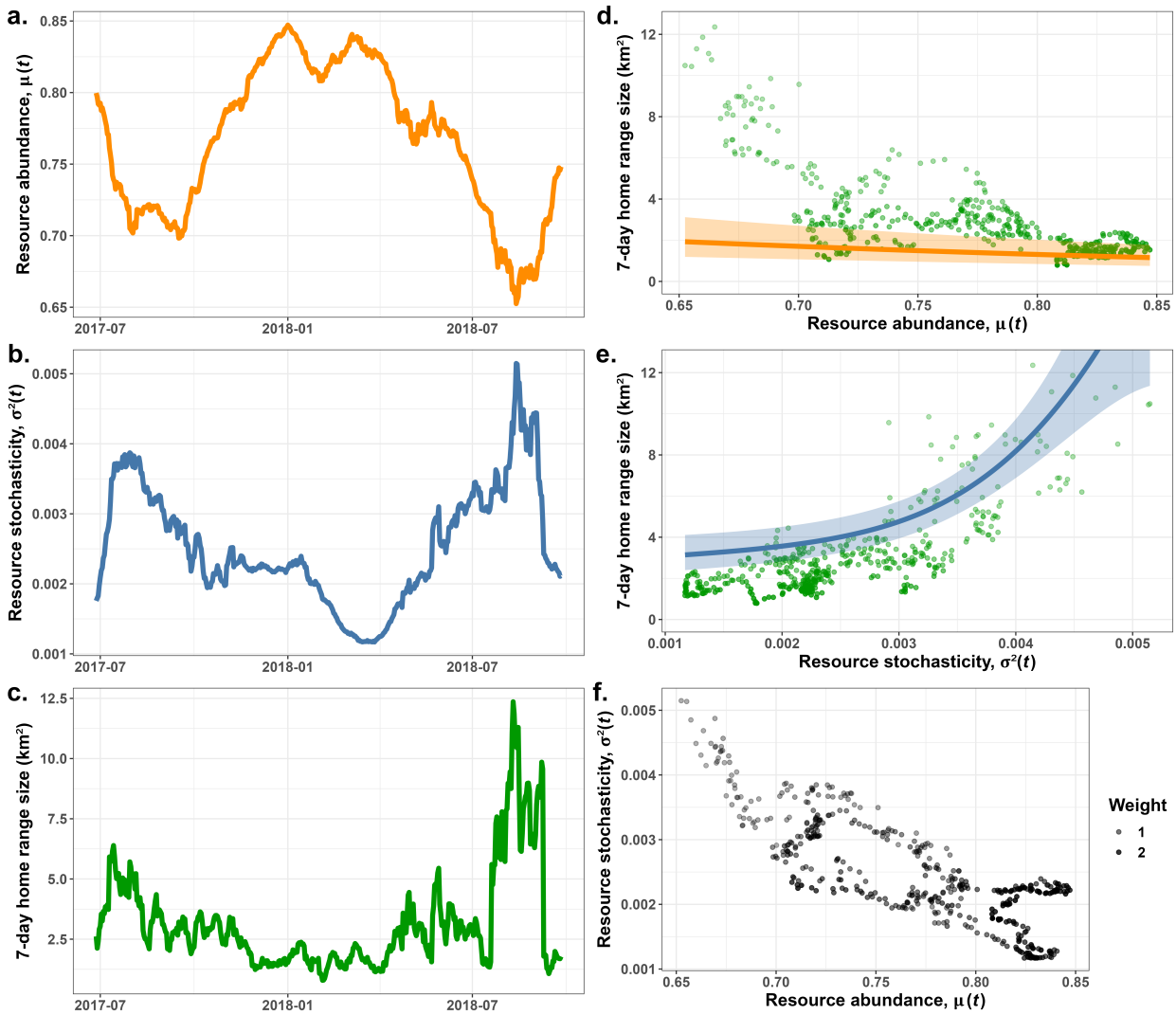

Figure 7: Seven-day home-range size of a lowland tapir (*Tapirus terrestris*) in response to changes in mean and variance in resources. (a.) Trends in resource abundance over time, $\mu(t)$, esimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (b.) Varince in resources over time, $\sigma^2(t)$, esimated as the average variance in NDVI at the locations visited by the tapir during a seven-day period. (c.) Estimated seven-day home range based on the 95% utilization quantiles. (d., e.) Estimated marginal effects of $\mu(t)$ and $\sigma^2(t)$ on home-range size. The model accounted for the marginal effects of $\mu(t)$ and $\sigma^2(t)$ and their interaction on mean space-use requirements and the variance around them. (f.) The effect of $\mu(t)$ does not follow the data closely because $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ are highly correlated. Consequently, while estimating the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ via separate models would allow result in a closer fit, the estimated effects would be inappropriate because they do not disentangle the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$. See Appendix 3 for additional information. The tapir movement data corresponds to the individual named "Anna" from the Cerrado sample of Medici *et al.* (2022).

Discussion

Adaptations to changes in $\mathbf{E}(R)$ and $\mathbf{Var}(R)$

The spatiotemporal scale over which an event occurs is a main determinant of whether an organism will be able to predict the event and how it will respond to it (or fail to do so). Events that occur at the scale of the organism (i.e. approximately one or more times per generation and on the spatial scale of the organism's spatial range, see Frankham and Brook 2004) are more likely to be perceived as a threat or boon worth preparing for (Foley et al. 2008; Berger et al. 2018; Geremia et al. 2019). Consequently, organisms with long generations (e.g., elephants, *Loxodonta sp.*) or large spatial ranges (e.g., migratory birds) are more likely to experience stochastic events and thus are also more likely to respond to and prepare for them. Animals may adapt by adjusting the timing of reproduction (Southwood 1977; Boersma et al. 2021) and torpor or hibernation (Inouye et al. 2000; Goldberg and Conway 2021), or storing large amounts of energy (Lindstedt and Boyce 1985) through fat storage (Armitage et al. 2003; Nespolo et al. 2022) or resource caching (Post et al. 2006). Alternatively, animals may alter their movement and travel long distances over short periods of time (Jetz et al. 2004; Hirt et al. 2017), whether this be for migration (Mueller et al. 2013; Geremia et al. 2019) or nomadism (Teitelbaum et al. 2015; Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019). Over the years, animals may also develop more complex cognitive abilities (Brown et al. 2004), including the development of memory (Foley et al. 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et al. 2019; Geremia et al. 2019; Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Steixner-Kumar and Gläscher 2020; Falcón-Cortés et al. 2021; Cavedon et al. 2022; Ranc et al. 2022), which is required for migration (Mueller et al. 2013; Middleton et al. 2018; Abrahms et al. 2019; Geremia et al. 2019; Merkle et al. 2019; Rickbeil et al. 2019; but see: Cuadrado 2021; Stefanescu et al. 2021). However, adapting to changes in environmental cues rather than relying on memory alone (Jonzén et al. 2006; Büntgen et al. 2017; Rickbeil et al. 2019; Severson et al.

2021), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et al. 2019).

In contrast, individuals with short lifespans are less likely to experience stochastic events and develop memory about them. However, the short generation time and high reproductive rate of r-selected species (as opposed to k-selected species, see Pianka 1970; Brown et al. 2004) may promote other traits that increase survival following extreme events. Examples include higher population size, dispersal, higher genetic diversity, and complex group dynamics (e.g., Cuadrado 2021; Stefanescu et al. 2021). Events that occur over large spatiotemporal scales can thus promote slow, large-scale changes through the adaptation, natural selection, and evolution of the species (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et al. 2017; Grant et al. 2017), which is more likely to adapt if starting populations are large with high genetic diversity and short generations, as in the case of r-selected species (but see Leung 2022). Of course, an organism with a lifespan shorter than a year will be unable to experience the cyclical nature of the seasons, and an organism with a lifespan of a few weeks or days may not even experience substantial changes in weather other than daily cycles and some weather stochasticity. Still, a population may respond to spatiotemporal cycles in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ by adapting the group's reproduction timing and migration (e.g., painted lady butterflies: Cuadrado 2021; Stefanescu et al. 2021).

A population's fitness and chances of survival in a changing environment depend strongly on its adaptability and responsiveness to change (Riotte-Lambert and Matthiopoulos 2020), and its ability to recognize cues that precede extreme events or periods of scarcity or abundance can have appreciable effects on its members' chances of survival and reproduction. For example, ungulates' ability to time their yearly migrations on available forage biomass, snow fall, snow melt, and hunting pressure allow them to adapt to changes in both $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, while their spatial memory (Falcón-Cortés et al. 2021; Ranc et al. 2022) allows them to optimize their large-scale movement by reducing the amount of time and energy spent exploring. Similarly, the ability of trans-Saharan migrant birds to adapt their migration

timing based on environmental cues allows them to account for differences in $\mu(t)$ between years (Jonzén et al. 2006). However, relying too strongly on short-term changes rather than depending on long-term memory can also cause animals to fail to find crucial resources during unpredictable times (whooping cranes: Mueller et al. 2013; Foley et al. 2008; elephants: Polansky et al. 2015; whales: Abrahms et al. 2019). Instead, if anomalies occur repeatedly over time, organisms may adapt to a higher $\sigma^2(t)$ or shift their ranges altogether (terrestrial animals: Chen et al. 2011; Büntgen et al. 2017; ungulates: Severson et al. 2021), including migratory animals (Jonzén et al. 2006). Still, while range shifts can help species overcome changes in the long-term trends in $\mu(t)$ and $\sigma^2(t)$, including changes in phenology (Severson et al. 2021), they can also result in phenological mismatches (Lameris et al. 2018) and add pressure to the species that already live in the habitat (e.g., Wallingford et al. 2020; but see Shepard et al. 2022), including specialists and obligate symbionts that may be unable to shift their range, since it is determined by their food sources' and associates' ability to move and adapt, too.

Applications for conservation

Technical advancements from the last few decades have allowed scientists to collect increasingly larger amounts of data at finer and finer scales (Nathan et al. 2022), but little attention has been paid to estimating the effects of environmental stochasticity on organisms' behaviors. In these times of great change and climatic uncertainty (Abrahms 2021; Intergovernmental Panel On Climate Change 2023), it is increasingly important to recognize how environmental stochasticity affects organisms' behaviors and shapes ecosystems. Accounting for changes in both resource abundance and resource stochasticity is crucial when assessing whether the quality of protected areas is sufficiently high to sustain biodiversity long term. Protecting areas with high resource abundance and low resource stochasticity will reduce animals' spatial requirements.

The designation of high-quality habitats is a central concern of many conservation initia-

tives. This framework allows consultants and conservation managers to quantify the quality of a habitat based on its resource abundance and stochasticity as well as the amount of space animals would need in the habitat. With the methods presented in this paper, one can (1) assess the quality of current protected areas, (2) predict whether or not the areas will be able to sustain current populations in future decades, and (3) evaluate the quality of new potential conservation areas. In light of the UN's objective to conserve 30% of global landmasses and waters by 2030 (IPBES 2019), the framework and methods presented here provide useful metrics for evaluating whether protected areas will have sufficient quality and long-term stability to support species under various possible climate change scenarios (Intergovernmental Panel On Climate Change 2023).

Ignoring the effects of recent and predicted increases in $\mathrm{Var}(R)$, including an increase in the intensity and frequency of extreme events (Yao et al. 2022; Intergovernmental Panel On Climate Change 2023), has the potential to greatly hinder future conservation efforts. Since not accounting for an increase in $\sigma^2(t)$ will result in an under-estimation of animals' space-use requirements, protected areas which were designated based on the area's $\mu(t)$ but not $\sigma^2(t)$ will likely be insufficient in both size and resources in the future, which may lead to decreases in the fitness and size of a population while also increasing the risk of population collapse and human-wildlife conflict (Mukeka et al. 2019). This is particularly the case in resource-poor, stochastic regions, where animals are forced to endure longer and more unpredictable searches, which results in a larger variance in space-use requirements.

It is also worth noting that carnivores may be more susceptible to changes in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$, and that this susceptibility is likely amplified further at higher trophic levels. While primary consumers can rely on relatively predictable and static resources that can be estimated easily via remote sensing measures such as NDVI, the fine-scale location of secondary consumers' resources may not correlate as strongly with measures of habitat productivity. In fact, primary consumers' ability to move makes their location and abundance more stochastic than those of plants. Consequently, the abundance of primary consumers may correlate

with productivity weakly or at a temporal lag (e.g., Geremia et al. 2019). Thus, primary consumers' delayed responses to fluctuations in $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ may result in an increase in secondary consumers' resource stochasticity, which would also be perceived with a delay. Similar hypotheses can be formulated for higher trophic levels but with amplified temporal lags, since each trophic level adds another layer of uncertainty and delayed response, which together increase the unpredictability on how carnivores indirectly respond to changes in primary productivity. However, the effect is likely less pronounced for omnivores and other diet generalists, as they may have the ability to switch to more abundant and less stochastic resources.

Conclusion

The work presented here provides a unifying framework for viewing movement as a function of resource abundance and stochasticity. We provide realistic and flexible hypotheses of the effects of $\mathrm{E}(R)$ and $\mathrm{Var}(R)$ on organisms' space-use requirements and movement behavior. We demonstrate that organisms' space-use requirements respond nonlinearly to both resource abundance and stochasticity, and we demonstrate the importance of accounting for $\mathrm{Var}(R)$ besides $\mathrm{E}(R)$. We also provide a moving window approach that allows one to model movement continuously rather than imposing arbitrary thresholds between different periods or types of behaviors, including temporal changes in space-use requirements and shifts between range-residency and nomadism. The methods presented here can be applied to assess the current and future quality of protected areas while also estimating the amount of space organisms currently need and will need in the future under different climate change scenarios.

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Code and data availability

All code and data used for this manuscript is available on GitHub at https://github.com/QuantitativeEcologyLab/hr-resource-stoch, with the exception of the tapir data, which is available at https://github.com/StefanoMezzini/tapirs.

Conflict of interest

The authors declare there are no conflicts of interest.

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