

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

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## <sup>1</sup> Abstract

<sup>2</sup> The amount of space organisms use is thought to be tightly linked to the availability of  
<sup>3</sup> resources within their habitats, such that organisms living in productive habitats generally  
<sup>4</sup> require less space than those in resource-poor habitats. This hypothesis has widespread em-  
<sup>5</sup> pirical support, but existing studies have focused primarily on responses to the *mean* amount  
<sup>6</sup> of resources, while responses to the variance around the mean are still largely unknown. This  
<sup>7</sup> is not a trivial oversight. Organisms adjust to variable environmental conditions, so failing  
<sup>8</sup> to consider the effects of resource (un)predictability can result in a limited understanding  
<sup>9</sup> of organisms' space-use requirements, challenging ecological theory and applied conservation  
<sup>10</sup> alike. In this study, we first review the literature of studies that estimate organisms' space-  
<sup>11</sup> use requirements as a function of resource abundance. We then leverage this information to  
<sup>12</sup> provide a unifying framework and hypotheses for the effect of mean *and* variance in resources  
<sup>13</sup> on organisms' space use. Next, we use simulated movement data to demonstrate how the  
<sup>14</sup> combined effects of mean and variance in resource abundance interact to shape predictable  
<sup>15</sup> patterns in space use. Finally, we use real-world tracking data on a lowland tapir (*Tapirus*  
<sup>16</sup> *terrestris*) from the Brazilian Cerrado to show how this framework can be applied to better  
<sup>17</sup> understand the movement ecology of free-ranging animals. Results from the simulations and  
<sup>18</sup> empirical examples are presented using a fully transparent approach that allows researchers  
<sup>19</sup> to apply the framework to their own data and inform area-based conservation efforts.

<sup>20</sup> **Key words:** energetics, energetic landscape, environmental stochasticity, space use, spatial  
<sup>21</sup> needs, ctmm.

## **22 Introduction**

23 The amount of resources an organism is able to access is a strong determinant of its odds  
24 of survival and reproduction. Resource limitations can cause individuals to experience a  
25 negative energetic balance, which can then result in lower fitness (Le Bot et al. 2019; Hou  
26 et al. 2020), altered physiology (Wessling et al. 2018; Le Bot et al. 2019; Rocha et al. 2021;  
27 Dai Pra et al. 2022), lower chance of reproduction (Douglas and Pearce-Higgins 2014; Le  
28 Bot et al. 2019; Schmidt et al. 2020; Stefanescu et al. 2021), and even death (Foley et  
29 al. 2008; Berger et al. 2018), along with changes to community structure (Burson et al.  
30 2018; Ghislandi et al. 2018; Haney and Siepielski 2018; Riotte-Lambert and Matthiopoulos  
31 2020). Thus, many organisms will adapt their behaviors in response to changes in local  
32 resource abundance to ensure their needs are met. Some species may respond to fluctuations  
33 in resource abundance by, if possible, switching to other food sources (Le Bot et al. 2019;  
34 Steinmetz et al. 2021), reducing energetic costs by lowering body heat (Schmidt et al.  
35 2020), or entering hibernation or torpor (Boyles et al. 2020; Mohr et al. 2020; Fjelldal et  
36 al. 2021). However, movement represents one of the most readily available behaviors that  
37 species can adjust, whether this be by modifying their home range (Lucherini and Lovari  
38 1996; Relyea et al. 2000; Arechavala-Lopez et al. 2019; Bista et al. 2022; Bradsworth  
39 et al. 2022; Yu et al. 2022), migrating (Middleton et al. 2018; Geremia et al. 2019),  
40 moving nomadically (Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019), or dispersing  
41 (framework: Southwood 1977; amphibians: Cayuela et al. 2020; Wheat et al. 2017; birds:  
42 Pretorius et al. 2020; mammals: Singh et al. 2012).

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

<sup>48</sup> Bunnel (1979) proposed that the simplest relationship between resource abundance and an  
<sup>49</sup> organism's home-range size is

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

<sup>50</sup> where  $H$  is the organism's **home-range size**,  $C$  is the organism's resource consumption  
<sup>51</sup> ( $\text{kcal day}^{-1}$ ), and  $R$  is the **resources** the organism can access ( $\text{kcal day}^{-1} \text{ unit area}^{-1}$ ).  
<sup>52</sup> Harestad and Bunnel's model is simple to conceptualize and allows for testable predictions,  
<sup>53</sup> but an organism's values of  $C$  and  $R$  likely depend on numerous factors, such as competition,  
<sup>54</sup> metabolic rate, diet, and body weight (Harvey and Clutton-Brock 1981, 1981; Gittleman and  
<sup>55</sup> Harvey 1982; Lindstedt et al. 1986; Reiss 1988; Jetz et al. 2004; Boratyński 2020; Noonan  
<sup>56</sup> et al. 2020). While many researchers have since demonstrated that organisms adapt their  
<sup>57</sup> home ranges in response to resources abundance, few studies build upon others' previous  
<sup>58</sup> work. Instead, results are typically reported as independent, novel findings. Consequently,  
<sup>59</sup> we currently lack a unifying framework for quantifying the effects of resource abundance  
<sup>60</sup> on organisms' space-use requirements. In addition, while much work has been done on  
<sup>61</sup> estimating organisms' responses to average resource abundance, there is little information  
<sup>62</sup> on how they respond to unpredictable changes in resources.

<sup>63</sup> Here, we refer to a location's average amount of resources as **resource abundance**, while  
<sup>64</sup> we use the phrase **resource stochasticity** to indicate the variability in resource abundance  
<sup>65</sup> due to unpredictable causes. We argue that, on its own, a habitat's long-term resource  
<sup>66</sup> abundance is not sufficient to assess the habitat's quality, nor make predictions about how  
<sup>67</sup> much space an organism might use. For instance, a grassland with relatively low but constant  
<sup>68</sup> forage availability will require drastically different behaviors and adaptations from a desert  
<sup>69</sup> location with equally scarce forage but rare, sudden, and strong pulses of resources. In  
<sup>70</sup> the grassland, an animal may require a large but constant home range as it moves between  
<sup>71</sup> locations in search of food (*sensu* Teitelbaum and Mueller 2019), while an animal in the  
<sup>72</sup> desert may switch between dispersal as it searches for high-resource patches and short-term

73 range residency until the local resources are depleted. Although it may be possible for both  
74 habitats to have the same long-term average resource abundance, the differences in resource  
75 unpredictability result in substantially different movement and life history strategies being  
76 selected for. Although it is generally expected that resource unpredictability will decrease  
77 organisms' fitness and a landscape's energetic balance (Chevin et al. 2010), there is limited  
78 empirical evidence to support this hypothesis (but see: Herfindal et al. 2005; Nilsen et al.  
79 2005; Rizzuto et al. 2021).

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

## 92 Resources as a random variable

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

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

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

### 118 Effects of resource abundance, $E(R)$

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

125 locations in search of resources, but they must also account for a higher metabolism and  
 126 movement costs (Taylor et al. 1982). The hypothesis that space-use requirements decrease  
 127 with resource abundance,  $E(R)$ , is commonly accepted and well supported, but many studies  
 128 assume a linear relationship (e.g., Harestad and Bunnel 1979; Relyea et al. 2000; McClintic et  
 129 al. 2014; Rizzuto et al. 2021; Bista et al. 2022; Bradsworth et al. 2022). This is problematic  
 130 because a linear relationship can lead to questionable estimates and problematic biases, such  
 131 as negative or excessively small home ranges (e.g., figure 2 in the work of Bista et al. 2022).  
 132 Conceptually, the relationship between space-use requirements and  $E(R)$  must be nonlinear,  
 133 since there are limits to how much space an organism is able to explore in its lifetime as well  
 134 as the minimum amount of space it requires to survive (which is necessarily greater than  
 135 zero – see fig. 1 as well as: Lucherini and Lovari 1996; Herfindal et al. 2005; Nilsen et al.  
 136 2005; Simcharoen et al. 2014; Watson 2020; and contrast them to estimates based on linear  
 137 models, e.g.: Relyea et al. 2000; Rizzuto et al. 2021; Bista et al. 2022).

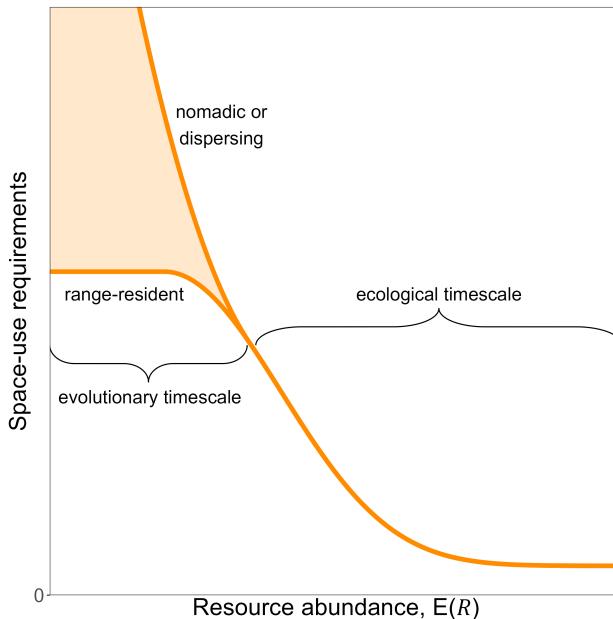


Figure 1: Hypothesized space-use requirements of an organism as a function of resource abundance ( $E(R)$ ). We expect low values of  $E(R)$  to result in high space-use requirements as organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident 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  $E(R)$ .

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

<sup>140</sup> et al. 2005; Nilsen et al. 2005). However, as  $E(R)$  decreases, we expect organisms' spatial  
<sup>141</sup> requirements to increase nonlinearly, since low values of  $E(R)$  force organisms to expand their  
<sup>142</sup> home ranges (Lucherini and Lovari 1996; Relyea et al. 2000; Herfindal et al. 2005; Nilsen  
<sup>143</sup> et al. 2005; Bista et al. 2022), migrate to better locations (Samarra et al. 2017; Middleton  
<sup>144</sup> et al. 2018; Geremia et al. 2019), or move nomadically (Singh et al. 2012; Polansky et al.  
<sup>145</sup> 2015; Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019). It is unclear when organisms  
<sup>146</sup> switch from range residency to migration or nomadism (or vice-versa), but understanding  
<sup>147</sup> the connection between these types of movement is important for quantifying the effect of  
<sup>148</sup> resource abundance on organisms' space-use requirements and when an organism may choose  
<sup>149</sup> to migrate or disperse rather than remaining range-resident (mammals: Teitelbaum et al.  
<sup>150</sup> 2015; moose, *Alces alces*: Singh et al. 2012; eagles, *Haliaeetus leucocephalus*: Wheat et al.  
<sup>151</sup> 2017; Poessel et al. 2022; lesser flamingos, *Phoeniconaias minor*: Pretorius et al. 2020).  
<sup>152</sup> Still, large-scale changes in movement behavior (such as species-wide shifts to dispersal,  
<sup>153</sup> migration, or nomadism) are more likely to occur over evolutionary timescales than over  
<sup>154</sup> an organism's lifespan. For instance, larger home ranges requires greater vagility, which,  
<sup>155</sup> in turn, is facilitated by morphological features such as hinged joints and elongated limbs  
<sup>156</sup> (Andersson 2004; Jetz et al. 2004; Samuels et al. 2013; Hirt et al. 2017).

<sup>157</sup> It is also worth noting that high  $E(R)$  does not necessarily imply that organisms  
<sup>158</sup> have access to high amounts of resources, as predator avoidance and competition within an  
<sup>159</sup> organism's habitat will decrease the proportion of  $R$  it is able to access. Thus, organisms  
<sup>160</sup> in habitats with strong competitive pressure and predation may require larger home ranges  
<sup>161</sup> (Jetz et al. 2004; Prox and Farine 2020), but larger home ranges can be harder to defend and  
<sup>162</sup> also result in higher rates of competition and movement costs (Grant 1993; Jetz et al. 2004;  
<sup>163</sup> but also see Dickie et al. 2022). Additionally, persistent territorial defense from competitors  
<sup>164</sup> may prevent organisms from using space freely and as necessary (wolves, *Canis lupus*: Rich  
<sup>165</sup> et al. 2012; feral cats, *Felis catus*: Bengsen et al. 2016; Capuchin monkeys, *Cebus capucinus*:  
<sup>166</sup> Tórrez-Herrera et al. 2020), so the effect of  $E(R)$  on space use may vary between individuals,

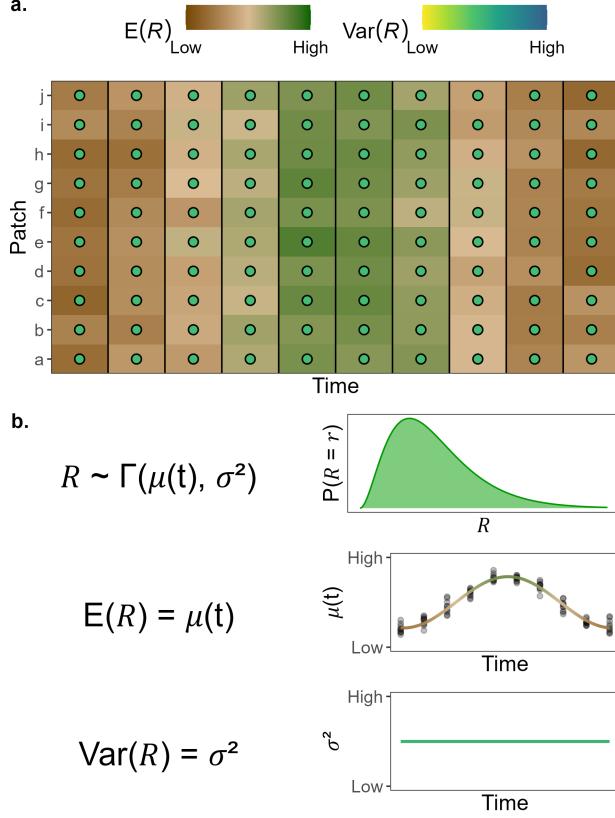


Figure 2: Fictitious example of variation in resources in a heterogeneous environment with constant variance (after accounting for changes in the mean). (a.) Resources ( $R$ , brown-green fill) vary over time and space with a constant the variance (dot color). (b.) Arbitrary definition of  $R$  as following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

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

Consider the scenario where the average in resource abundance,  $E(R)$ , changes over time but  $\text{Var}(R) = \sigma^2 > 0$  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

<sup>179</sup> where  $R$  is high if  $E(R)$  does not vary predictably over space.

<sup>180</sup> 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,  $E(R)$  will vary over time, and organisms' behaviors will change in response.

<sup>189</sup> **Effects of resource stochasticity,  $\text{Var}(R)$**

<sup>190</sup> 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  $E(R)$ , while  $\text{Var}(R)$  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,  $\text{Var}(R)$  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.

205 2020; Severson et al. 2021), and other extreme events (Logares and Nuñez 2012; Anderson  
 206 et al. 2017).

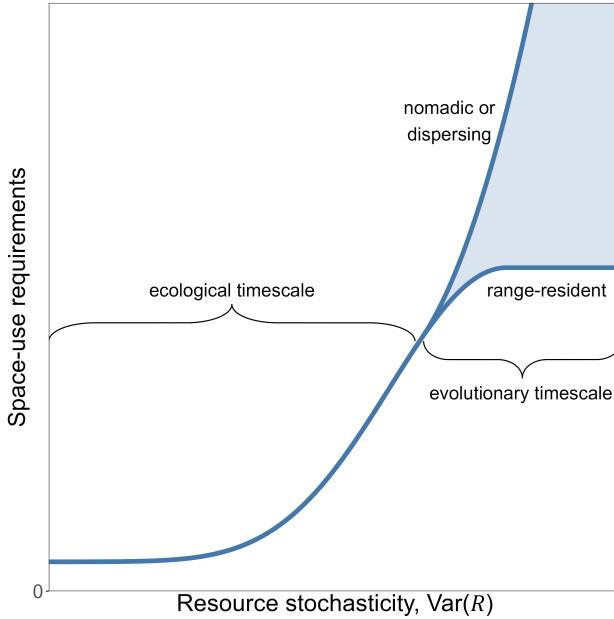


Figure 3: Hypothesized space-use requirements of an organism as a function of resource stochasticity ( $\text{Var}(R)$ ). We expect low values of  $\text{Var}(R)$  to result in low space-use requirements as organisms are able to depend on relatively predictable resources. As  $\text{Var}(R)$  increases, 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  $\text{Var}(R)$  and space-use requirements cannot be linear because it would require space-use requirements to be negative for low values of  $\text{Var}(R)$ .

207 Environmental variability can reduce a landscape's energetic balance (Chevin et al. 2010),  
 208 which, in turn, decreases organisms' fitness (Berger et al. 2018) and increases their space-  
 209 use requirements. While this is true for both predictable and unpredictable stochasticity,  
 210 extreme and rare events are more likely to have a stronger effect. A few recent studies  
 211 support these hypotheses (Chevin et al. 2010; Morellet et al. 2013; Nandintsetseg et al.  
 212 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic  
 213 and taxonomic scales, so the extent to which these preliminary findings can be generalized is  
 214 still very limited. Thus, there remains a need for developing a more complete understanding  
 215 of how organisms' space-use requirements change with environmental stochasticity.

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

(fig. 3) because: (1) as  $\text{Var}(R)$  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-emptively 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  $E(R)$  and  $\text{Var}(R)$  change over time. We can then define  $\text{Var}(R)$  as a function of time using the same notation as we did for  $E(R)$ , i.e.,  $\text{Var}(R|t) = \sigma^2(t)$  (fig. 4). When both  $E(R)$  and  $\text{Var}(R)$  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  $\text{Var}(R)$ . Biologically, this is important because some organisms may perceive changes in  $R$  as a change in  $E(R)$ , 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  $E(R)$  and  $\text{Var}(R)$  is not easy (Steixner-Kumar and Gläscher 2020), especially if  $E(R)$  and  $\text{Var}(R)$  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  $\text{Var}(R)$  is arguably as important as the effect of  $E(R)$  in determining how said organism will respond to changes in  $R$  and consequently adapt its space use.

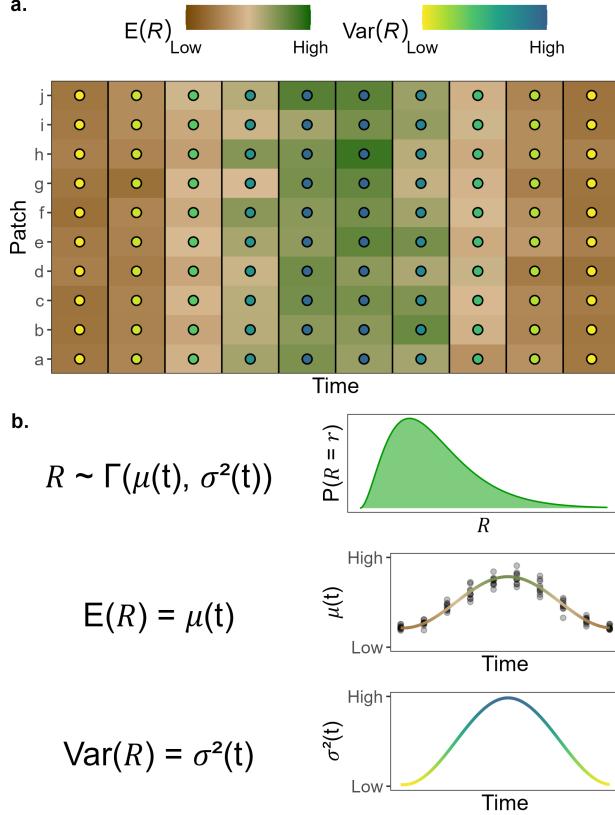


Figure 4: Fictitious example of variation in resources in a heterogeneous environment with changing variance (even after accounting for changes in the mean). (a.) Although resources ( $R$ , brown-green fill) varies over time and space, the variance (dot color) is lowest at the beginning and end of the observational period and highest when  $E(R)$  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 realizations of  $R$  in panel a.

## 245 Interactive effects of $E(R)$ and $\text{Var}(R)$

246 We have provided the case for why both  $E(R)$  and  $\text{Var}(R)$  affect organisms' space-use require-  
 247 ments, but we presented the two parameters as independent drivers of movement. However,  
 248 in the more realistic scenario where both  $E(R)$  and  $\text{Var}(R)$  fluctuate over time, organ-  
 249 isms may respond to changes in  $\text{Var}(R)$  more when resources are scarce than when they are  
 250 abundant. Consequently, models estimating the effects of  $R$  on organism's movement should  
 251 account for not only the effects of  $E(R)$  and  $\text{Var}(R)$  separately, but also their interactive  
 252 effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but  
 253  $\text{Var}(R)$  may have little effect if resources are stochastic but always abundant. Thus, we  
 254 expect  $\text{Var}(R)$  to have a stronger effect on space-use requirements when  $E(R)$  is low, and  
 255 less of an effect when  $E(R)$  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 over 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  $\text{Var}(R)$  or simply spatial changes in  $E(R)$  (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  $E(R)$  and  $\text{Var}(R)$  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  $E(R)$ , such as seasonal trends in  $\mu(t)$ , and stochasticity ( $\text{Var}(R)$ ). The need to account for changes in both  $E(R)$  and  $\text{Var}(R)$  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  $E(R)$  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  $E(R)$ . Therefore, it may

not be sufficient to account for the effects of  $E(R)$  and  $\text{Var}(R)$ ; 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  $E(R)$  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  $E(R)$  and  $\text{Var}(R)$  allows one to separate the two seasonal cycles and produce more consistent results.

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

To support our hypothesis of how organisms' space use is affected by  $E(R)$ ,  $\text{Var}(R)$ , and the interaction effect of  $E(R)$  and  $\text{Var}(R)$ , 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

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

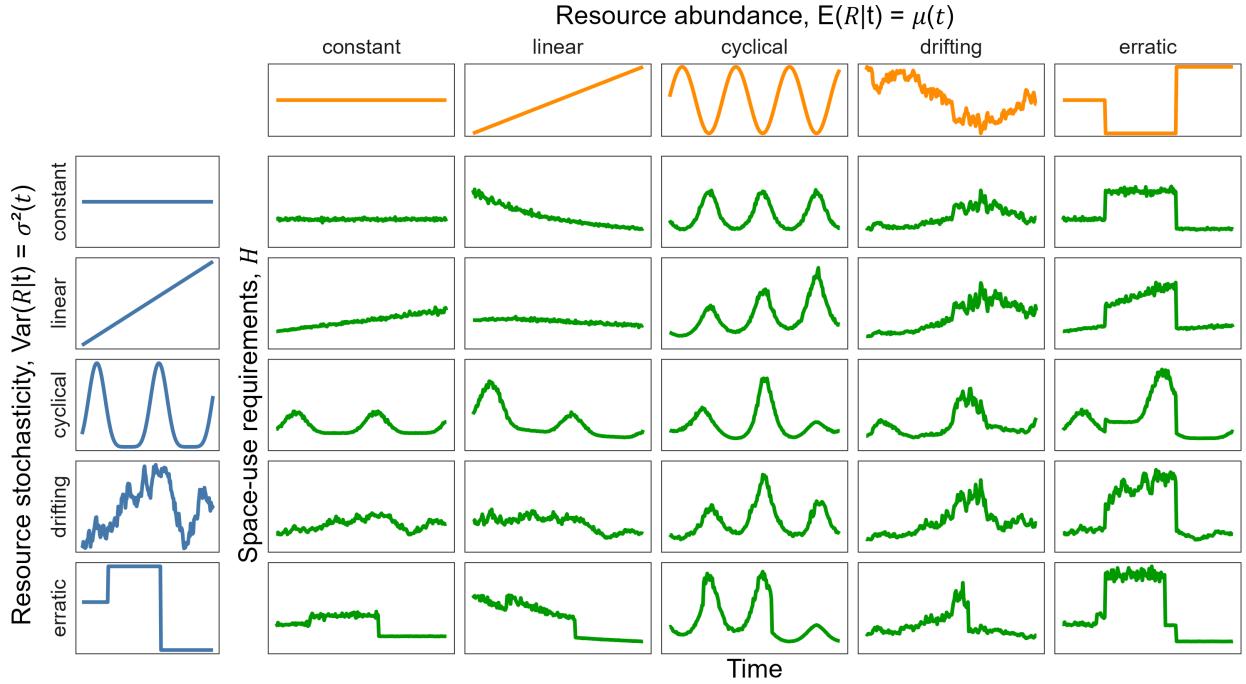


Figure 5: Simulated home range sizes,  $H$ , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how  $H$  decreases nonlinearly as  $\mu(t)$  increases and increases nonlinearily 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.

314 Fig. 5 shows how the simulated space-use requirements changed in response to  $\mu(t)$  and  
 315  $\sigma^2(t)$ . The top row (constant  $\text{Var}(R)$ ) shows how space-use requirements vary for different  
 316 trends in  $\mu(t)$  while  $\text{Var}(R)$  remains constant (like in fig. 2). As  $E(R)$  increases at a constant  
 317 slope (linear  $\mu(t)$ ) the space-use requirements decrease nonlinearly, with larger changes when  
 318  $E(R)$  is low, until home-range size approaches the minimum size required by the organism.  
 319 As described in the section on the effects of resource abundance, the nonlinear decrease is  
 320 because changes in  $\mu(t)$  have a larger effect when  $E(R)$  is low (e.g., Lucherini and Lovari  
 321 1996; Herfindal et al. 2005; Nilsen et al. 2005).

322 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  $E(R)$  (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  $E(R)$ ) illustrates the effects of  $\text{Var}(R)$  on the simulated space-use requirements while  $E(R)$  remains constant. Overall, both mean  $H$  and the variance around it increase with  $\sigma^2(t)$  (most visible with constant  $E(R)$  and linear  $\text{Var}(R)$ ). 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  $\text{Var}(R)$  depends on  $E(R)$  (and vice-versa) as well as how complex the relationship can be. Since  $E(R)$  and  $\text{Var}(R)$  have opposite effects on  $H$ , disentangling the effects can be particularly difficult when both parameters change in a correlated manner (e.g., linear  $E(R)$  and  $\text{Var}(R)$ ). When both  $E(R)$  and  $\text{Var}(R)$  increase linearly,  $H$  initially increases since the effect of  $\text{Var}(R)$  is stronger, but then decreases as the effect of  $E(R)$  begins to dominate. However, when  $\mu(t)$  and  $\sigma^2(t)$

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

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

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

movement was simulated to be range resident within an homogeneous environment. Since real-world landscapes are spatially heterogeneous in both  $E(R)$  and  $\text{Var}(R)$ , 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  $E(R)$  and  $\text{Var}(R)$ , since the simulated organisms cannot select for areas of higher  $E(R)$  or lower  $\text{Var}(R)$ . Additionally, the simulations also ignore how competition, movement costs, predation, and other factors may affect the effects of  $E(R)$  and  $\text{Var}(R)$  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.

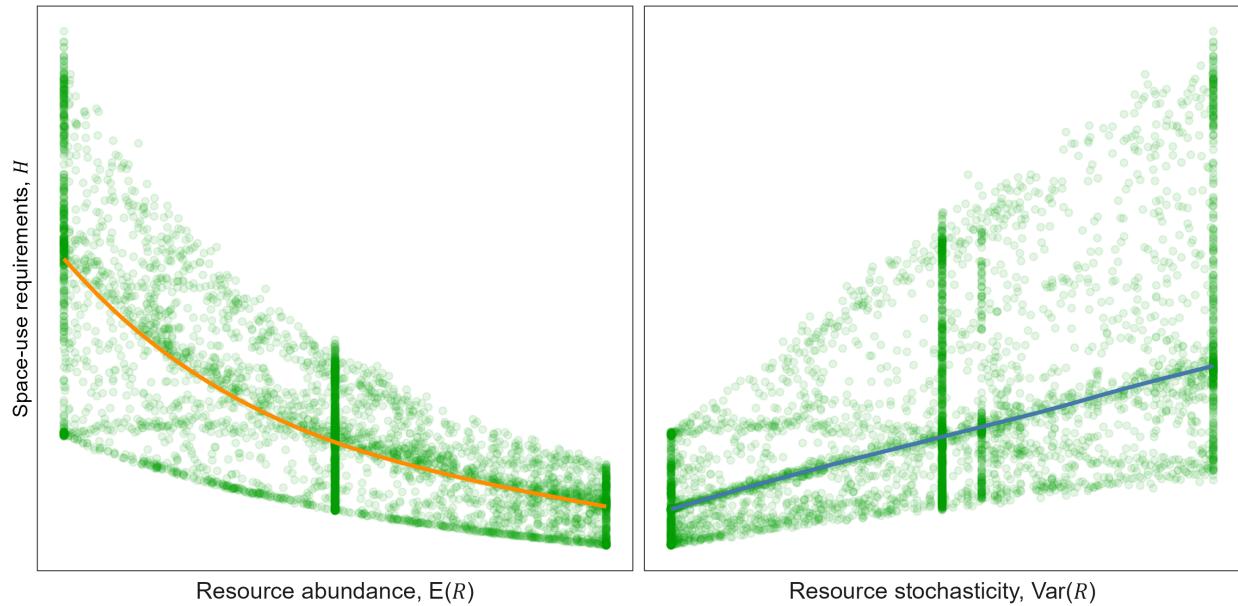


Figure 6: Effects of  $E(R)$  and  $\text{Var}(R)$  on simulated spatial requirements with 95% credible intervals for the mean (overlapping the line). Credible intervals were calculated assuming a gaussian posterior distribution on the link scale. The relationships were estimated using a Generalized 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  $E(R)$  and  $\text{Var}(R)$  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  $E(R)$  increases and the increase in  $H$  as  $\text{Var}(R)$  increases. Additionally, note how the variance in space-use requirements strongly increases with mean space-use requirements.

### 386 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

390 from the Brazilian Cerrado. Appendix 3 contains additional information on how NDVI  
391 was modeled along with details on the continuous-time movement models (Noonan et al.  
392 2019a; Fleming and Calabrese 2021) and autocorrelated kernel density estimation (Noonan  
393 et al. 2019b; Alston et al. 2022; Silva et al. 2022) used to quantify the tapir’s space-use  
394 requirements.

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

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

416 **Modeling  $R$**

417 Location-scale models (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) are  
418 a class of statistical models that allow us to estimate changes in a random variable's mean  
419 (i.e. its location) and variance (which depends on its scale) while allowing the mean-variance  
420 relationship to vary. `mgcv` (Wood 2017) is a commonly used package for R (R Core Team  
421 2022) that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and Gener-  
422 alized Additive Models (GAMs, see Wood 2017), including hierarchical and location-scale  
423 GLMs and GAMs. Currently, the `mgcv` package allows one to fit location-scale models with  
424 various families of distributions, including Gaussian (i.e., normal), gamma, and Tweedie  
425 location-scale families.

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

432 The Gamma location-scale family is best for strictly positive responses, such as areas  
433 (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto  
434 et al. 2021), total biomass, or energetic intake. The Tweedie location-scale family is similar  
435 to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-  
436 trivial amount of zeros, such as daily precipitation or prey density (but see zero-inflated  
437 distributions: Zuur et al. 2009). In this paper, we estimate  $R$  by modeling NDVI using `mgcv`  
438 and a beta location-scale family (not available in `mgcv` at the time of publication). If one  
439 is interested in families of distributions which are not available in `mgcv`, we suggest using  
440 the `brms` package (Bürkner 2017), which allows full control over all of a family's parameters  
441 via a fully Bayesian approach (as opposed to `mgcv`'s Empirical Bayes method – see Bürkner  
442 2018).

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

#### 456 **Estimating $R$ using NDVI**

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

$$\nu_{[0,1]} = \frac{\nu + 1}{2}, \quad (2)$$

460 where  $\nu$  indicates the NDVI value in  $[-1, 1]$  and  $\nu_{[0,1]}$  is the scaled NDVI value (see Denny  
 461 2017 for more information on transforming response data). In this case, we can define  $R$  as  
 462 following a beta distribution with mean and variance that depend on time using the notation  
 463  $B(\mu(t), \sigma^2(t))$ . We use this parameterization here for ease of explanation, but note that beta  
 464 distributions are generally parameterized using the shape parameters  $\alpha$  and  $\beta$  such that the  
 465 mean is

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

466 while the variance is

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

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

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

469 Consequently, we have

$$E(\nu|t) = 2\mu(t) - 1. \quad (6)$$

470 and

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

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

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

475 As discussed in the previous section, the first step to modeling  $H$  is to choose an appropriate  
476 family of distributions. Since  $H$  is strictly positive and continuous, a Gamma family seems  
477 the most appropriate among the distributions currently offered by the `mgcv` package (Wood  
478 2017), but the Tweedie family would also be appropriate if the variance does not scale with  
479 the squared mean.

480 As with the simulated effects of  $\mu(t)$  and  $\sigma^2(t)$  on  $H$  (fig. 6), a location-scale Gamma  
481 model is likely required. If there is not sufficient data to fit a location-scale model (which is  
482 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  $\text{Var}(R)$  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.

#### 489 The effects of $E(R)$ and $\text{Var}(R)$ on a lowland tapir's space-use requirements

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

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

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

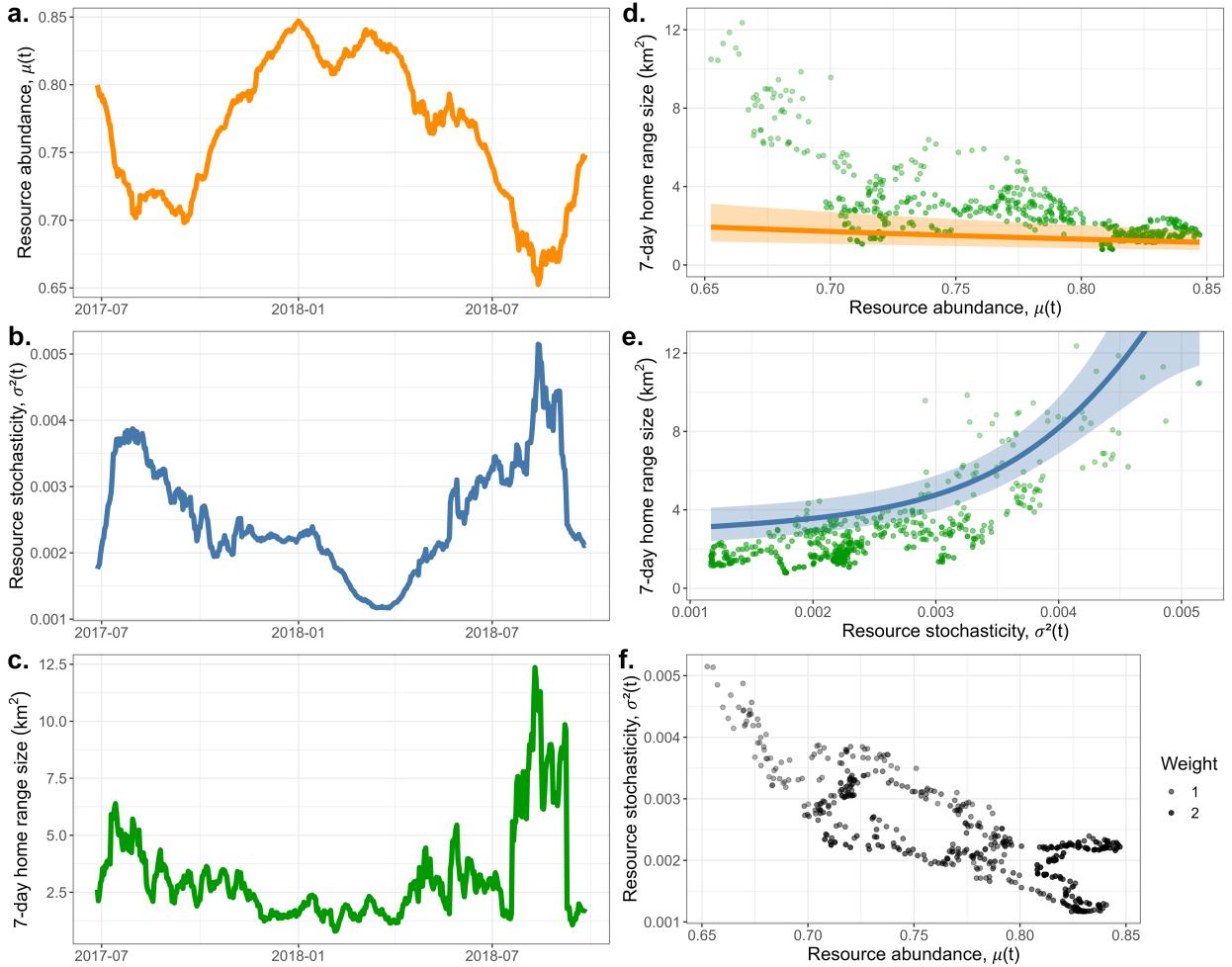


Figure 7: Seven-day home-range size of a lowland tapir (*Tapirus terrestris*) in response to changes in mean and variance in resources. (a.) Trends in resource abundance over time,  $\mu(t)$ , estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (b.) Variance in resources over time,  $\sigma^2(t)$ , estimated 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  $E(R)$  and  $\text{Var}(R)$  are highly correlated. Consequently, while estimating the effects of  $E(R)$  and  $\text{Var}(R)$  via separate models would allow result in a closer fit, the estimated effects would be inappropriate because they do not disentangle the effects of  $E(R)$  and  $\text{Var}(R)$ . 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).

514 **Discussion**

515 **Adaptations to changes in  $E(R)$  and  $\text{Var}(R)$**

516 The spatiotemporal scale over which an event occurs is a main determinant of whether an  
517 organism will be able to predict the event and how it will respond to it (or fail to do so).  
518 Events that occur at the scale of the organism (i.e. approximately one or more times per  
519 generation and on the spatial scale of the organism's spatial range, see Frankham and Brook  
520 2004) are more likely to be perceived as a threat or boon worth preparing for (Foley et  
521 al. 2008; Berger et al. 2018; Geremia et al. 2019). Consequently, organisms with long  
522 generations (e.g., elephants, *Loxodonta sp.*) or large spatial ranges (e.g., migratory birds)  
523 are more likely to experience stochastic events and thus are also more likely to respond to and  
524 prepare for them. Animals may adapt by adjusting the timing of reproduction (Southwood  
525 1977; Boersma et al. 2021) and torpor or hibernation (Inouye et al. 2000; Goldberg and  
526 Conway 2021), or storing large amounts of energy (Lindstedt and Boyce 1985) through fat  
527 storage (Armitage et al. 2003; Nespolo et al. 2022) or resource caching (Post et al. 2006).  
528 Alternatively, animals may alter their movement and travel long distances over short periods  
529 of time (Jetz et al. 2004; Hirt et al. 2017), whether this be for migration (Mueller et al.  
530 2013; Geremia et al. 2019) or nomadism (Teitelbaum et al. 2015; Nandintsetseg et al. 2019;  
531 Teitelbaum and Mueller 2019). Over the years, animals may also develop more complex  
532 cognitive abilities (Brown et al. 2004), including the development of memory (Foley et al.  
533 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et al. 2019; Geremia et al. 2019;  
534 Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Steixner-Kumar and Gläscher  
535 2020; Falcón-Cortés et al. 2021; Cavedon et al. 2022; Ranc et al. 2022), which is required  
536 for migration (Mueller et al. 2013; Middleton et al. 2018; Abrahms et al. 2019; Geremia  
537 et al. 2019; Merkle et al. 2019; Rickbeil et al. 2019; but see: Cuadrado 2021; Stefanescu  
538 et al. 2021). However, adapting to changes in environmental cues rather than relying on  
539 memory alone (Jonzén et al. 2006; Büntgen et al. 2017; Rickbeil et al. 2019; Severson et al.

540 2021), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et  
541 al. 2019).

542 In contrast, individuals with short lifespans are less likely to experience stochastic events  
543 and develop memory about them. However, the short generation time and high reproductive  
544 rate of r-selected species (as opposed to k-selected species, see Pianka 1970; Brown et al.  
545 2004) may promote other traits that increase survival following extreme events. Examples in-  
546 clude higher population size, dispersal, higher genetic diversity, and complex group dynamics  
547 (e.g., Cuadrado 2021; Stefanescu et al. 2021). Events that occur over large spatiotemporal  
548 scales can thus promote slow, large-scale changes through the adaptation, natural selection,  
549 and evolution of the species (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et  
550 al. 2017; Grant et al. 2017), which is more likely to adapt if starting populations are large  
551 with high genetic diversity and short generations, as in the case of r-selected species (but see  
552 Leung 2022). Of course, an organism with a lifespan shorter than a year will be unable to  
553 experience the cyclical nature of the seasons, and an organism with a lifespan of a few weeks  
554 or days may not even experience substantial changes in weather other than daily cycles and  
555 some weather stochasticity. Still, a population may respond to spatiotemporal cycles in  
556  $E(R)$  and  $\text{Var}(R)$  by adapting the group's reproduction timing and migration (e.g., painted  
557 lady butterflies: Cuadrado 2021; Stefanescu et al. 2021).

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

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

## 581 Applications for conservation

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

592 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  $\text{Var}(R)$ , 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 (Mukuka 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  $E(R)$  and  $\text{Var}(R)$ , 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

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

## 629 Conclusion

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

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649 **Code and data availability**

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

653 **Conflict of interest**

654 The authors declare there are no conflicts of interest.

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