

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

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## **1 Abstract**

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

<sup>17</sup> **Introduction**

<sup>18</sup> The amount of resources an organism is able to access is a strong determinant of its odds  
<sup>19</sup> of survival and reproduction. Resource limitations can cause individuals to experience a  
<sup>20</sup> negative energetic balance, which can then result in lower fitness (Le Bot et al. 2019; Hou  
<sup>21</sup> et al. 2020), altered physiology (Wessling et al. 2018; Le Bot et al. 2019; Rocha et al. 2021;  
<sup>22</sup> Dai Pra et al. 2022), lower chance of reproduction (Douglas and Pearce-Higgins 2014; Le  
<sup>23</sup> Bot et al. 2019; Schmidt et al. 2020; Stefanescu et al. 2021), and even death (Foley et  
<sup>24</sup> al. 2008; Berger et al. 2018), along with changes to community structure (Burson et al.  
<sup>25</sup> 2018; Ghislandi et al. 2018; Haney and Siepielski 2018; Riotte-Lambert and Matthiopoulos  
<sup>26</sup> 2020). Thus, many organisms will adapt their behaviors in response to changes in local  
<sup>27</sup> resource abundance to ensure their needs are met. Some species may respond to fluctuations  
<sup>28</sup> in resource abundance by, if possible, switching to other food sources (Le Bot et al. 2019;  
<sup>29</sup> Steinmetz et al. 2021), reducing energetic costs by lowering body heat (Schmidt et al.  
<sup>30</sup> 2020), or entering hibernation or torpor (Boyles et al. 2020; Mohr et al. 2020; Fjelldal et  
<sup>31</sup> al. 2021). However, movement represents one of the most readily available behaviors that  
<sup>32</sup> species can adjust, whether this be by modifying their home range (Lucherini and Lovari  
<sup>33</sup> 1996; Relyea et al. 2000; Arechavala-Lopez et al. 2019; Hirt et al. 2021; Bista et al. 2022;  
<sup>34</sup> Bradsworth et al. 2022; Yu et al. 2022), migrating (Middleton et al. 2018; Geremia et al.  
<sup>35</sup> 2019), moving nomadically (Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019), or  
<sup>36</sup> dispersing (framework: Southwood 1977; amphibians: Cayuela et al. 2020; Wheat et al.  
<sup>37</sup> 2017; birds: Pretorius et al. 2020; mammals: Singh et al. 2012).

<sup>38</sup> The relationship between organisms' movement and resource abundance has been of  
<sup>39</sup> interest to biologists for nearly a century. Burt (1943) considered the search for food as  
<sup>40</sup> the primary driver for movement within an organism's home range. Three decades after,  
<sup>41</sup> Southwood (1977) suggested that change in resource abundance is a strong determinant of  
<sup>42</sup> how organisms decide where to live and when to reproduce. Two years later, Harestad and

<sup>43</sup> Bunnel (1979) proposed that the simplest relationship between resource abundance and an  
<sup>44</sup> organism's home-range size is

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

<sup>45</sup> where  $H$  is the organism's home-range size,  $C$  is the organism's resource consumption (kcal  
<sup>46</sup> day<sup>-1</sup>), and  $R$  is the resources the organism can access (kcal day<sup>-1</sup> unit area<sup>-1</sup>). Harestad  
<sup>47</sup> and Bunnel's model is simple to conceptualize and allows for testable predictions, but an  
<sup>48</sup> organism's values of  $C$  and  $R$  likely depend on numerous factors, such as competition,  
<sup>49</sup> metabolic rate, diet, and body weight (Harvey and Clutton-Brock 1981, 1981; Gittleman and  
<sup>50</sup> Harvey 1982; Lindstedt et al. 1986; Reiss 1988; Jetz et al. 2004; Boratyński 2020; Noonan  
<sup>51</sup> et al. 2020). While many researchers have since demonstrated that organisms adapt their  
<sup>52</sup> home ranges in response to resources abundance, few studies build upon others' previous  
<sup>53</sup> work. Instead, results are typically reported as independent, novel findings. Consequently,  
<sup>54</sup> we currently lack a unifying framework for quantifying the effects of resource abundance  
<sup>55</sup> on organisms' space-use requirements. In addition, while much work has been done on  
<sup>56</sup> estimating organisms' responses to average resource abundance, there is little information  
<sup>57</sup> on how they respond to unpredictable changes in resources.

<sup>58</sup> Here, we refer to a location's average amount of resources as resource abundance, while  
<sup>59</sup> we use the phrase resource stochasticity to indicate the variability in resource abundance  
<sup>60</sup> due to unpredictable causes. We argue that, on its own, a habitat's long-term resource  
<sup>61</sup> abundance is not sufficient to assess the habitat's quality, nor make predictions about how  
<sup>62</sup> much space an organism might use. For instance, a grassland with relatively low but constant  
<sup>63</sup> forage availability will require drastically different behaviors and adaptations from a desert  
<sup>64</sup> location with equally scarce forage but rare, sudden, and strong pulses of resources. In  
<sup>65</sup> the grassland, an animal may require a large but constant home range as it moves between  
<sup>66</sup> locations in search of food (*sensu* Teitelbaum and Mueller 2019), while an animal in the  
<sup>67</sup> desert may switch between dispersal as it searches for high-resource patches and short-term

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

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

## 87 Resources as a random variable

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

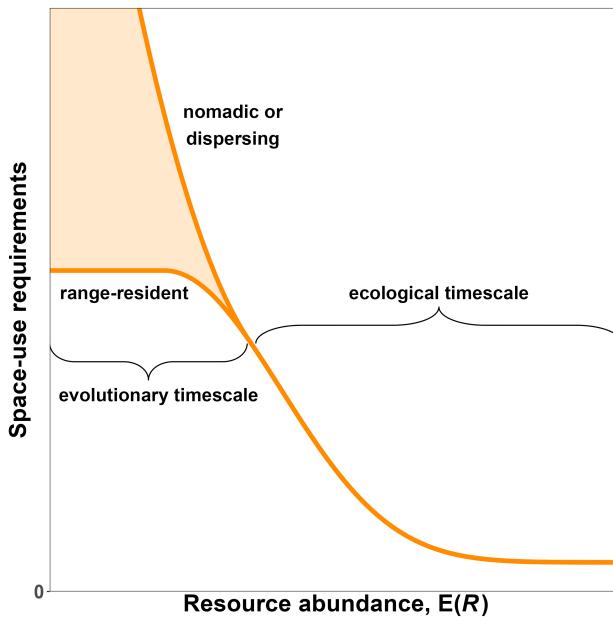
94 and Boyce 1985; Morellet et al. 2013; Schmidt et al. 2020), weather (Morellet et al. 2013;  
95 Fjelldal et al. 2021), competitive pressure (Rich et al. 2012; Tórrez-Herrera et al. 2020),  
96 and differences in energetics at the individual (Schmidt et al. 2020) and species level (Jetz  
97 et al.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

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

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

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

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

160 et al. 2012; feral cats, *Felis catus*: Bengsen et al. 2016; Capuchin monkeys, *Cebus capucinus*:  
161 Tórrez-Herrera et al. 2020), so the effect of  $E(R)$  on space use may vary between individuals,  
162 species, and locations. Still, these pressures simply alter the intensity with which organisms  
163 respond to  $E(R)$  but not the shape of the relationship, since each of these cases fall along  
164 different parts of the continuum in  $E(R)$  shown in fig. 1.

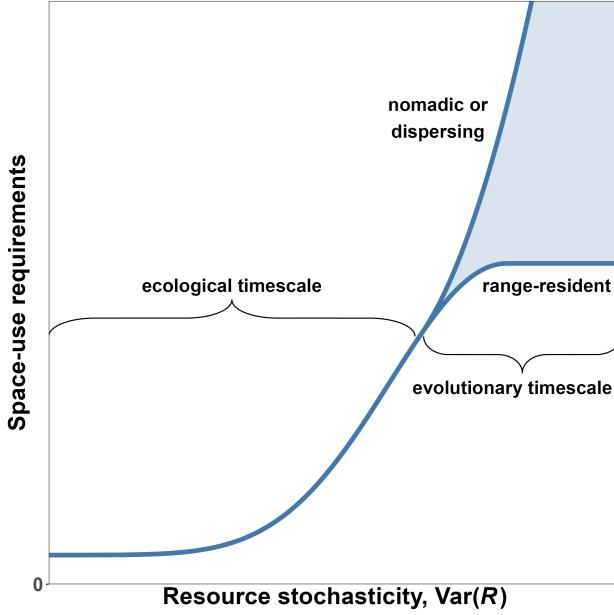
165 Consider the scenario where the average in resource abundance,  $E(R)$ , changes over time  
166 but  $\text{Var}(R) = \sigma^2 > 0$  is constant over time and space (see fig. A1). We can use the notation  
167  $R \sim \Gamma(\mu(t), \sigma^2)$  to indicate that  $R$  follows a Gamma distribution with a mean  $\mu(t)$  that  
168 changes over time (i.e., it is a function of time) while the variance is constant (fig. A2).  
169 Since  $R$  is spatiotemporally random, an organism that moves in the landscape will not find  
170 the same  $R$  at different time points or throughout the habitat. However, if  $\mu(t)$  changes  
171 repetitively and regularly over time (e.g. peaks each spring and is lowest in winter), an  
172 organism may learn to predict times of high or low  $R$  (Samarra et al. 2017; Abrahms et al.  
173 2019; Geremia et al. 2019; e.g., Falcón-Cortés et al. 2021), but it will not be able to predict  
174 where  $R$  is high if  $E(R)$  does not vary predictably over space.

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

<sup>184</sup> **Effects of resource stochasticity,  $\text{Var}(R)$**

<sup>185</sup> Although the effect of  $R$  on organisms' space-use requirements is often recognized and ac-  
<sup>186</sup> counted for in ecology (Burt 1943; Southwood 1977; Lucherini and Lovari 1996; Relyea et  
<sup>187</sup> al. 2000; Nilsen et al. 2005; Williams-Guillen et al. 2006; Rickbeil et al. 2019), most of  
<sup>188</sup> the focus has been on the effects of  $E(R)$ , while  $\text{Var}(R)$  has received far less attention (but  
<sup>189</sup> see Nilsen et al. 2005; Di Stefano et al. 2011; Rizzuto et al. 2021; Seigle-Ferrand et al.  
<sup>190</sup> 2021). However,  $\text{Var}(R)$  can fluctuate temporally (and spatially) due to many important  
<sup>191</sup> drivers, including repetitive and predictable patterns as well as more stochastic ones. For  
<sup>192</sup> example, since berries are scarce outside the growing season, the variance in berries will also  
<sup>193</sup> be low. But during the growing season, both the average number of berries and the vari-  
<sup>194</sup> ance in berries are higher, since a bear may explore a location before fruiting time or after  
<sup>195</sup> competitors ate all the berries. In contrast, other sources of stochasticity can be much less  
<sup>196</sup> predictable, such as the arrival of new competitors (Alexander et al. 2015), the emergence  
<sup>197</sup> of new diseases (Hollings et al. 2014), droughts (Foley et al. 2008; Haig et al. 2013), fires  
<sup>198</sup> (Jolly et al. 2022), floods (Ramos Pereira et al. 2013), changes in climate and phenology  
<sup>199</sup> (Inouye et al. 2000; Jonzén et al. 2006; Grant et al. 2017; Berger et al. 2018; Woolway et al.  
<sup>200</sup> 2020; Severson et al. 2021), and other extreme events (Logares and Nuñez 2012; Anderson  
<sup>201</sup> et al. 2017).

<sup>202</sup> Environmental variability can reduce a landscape's energetic balance (Chevin et al. 2010),  
<sup>203</sup> which, in turn, decreases organisms' fitness (Berger et al. 2018) and increases their space-  
<sup>204</sup> use requirements. While this is true for both predictable and unpredictable stochasticity,  
<sup>205</sup> extreme and rare events are more likely to have a stronger effect. A few recent studies  
<sup>206</sup> support these hypotheses (Chevin et al. 2010; Morellet et al. 2013; Nandintsetseg et al.  
<sup>207</sup> 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic  
<sup>208</sup> and taxonomic scales, so the extent to which these preliminary findings can be generalized is  
<sup>209</sup> still very limited. Thus, there remains a need for developing a more complete understanding  
<sup>210</sup> of how organisms' space-use requirements change with environmental stochasticity.



**Figure 2:** 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  $\text{Var}(R)$ .

211      Similar to the effect of  $E(R)$ , we expect  $\text{Var}(R)$  to have a nonlinear effect on organisms'  
 212    space-use requirements. When  $\text{Var}(R)$  is low enough that  $R$  is relatively predictable, we  
 213    do not expect changes in  $\text{Var}(R)$  to have a noticeable effect, but as resources become in-  
 214    creasingly unpredictable, we expect space-use requirements to increase progressively faster  
 215    (fig. 2) because: (1) as  $\text{Var}(R)$  increases the chances of finding low  $R$  increase superlinearly,  
 216    (2) stochastic environments tend to be less productive (Chevin et al. 2010), and (3) the  
 217    added movement required to search for food increases organisms' energetic requirements. If  
 218    resources remain highly unpredictable over long periods of time (e.g., multiple lifespans),  
 219    organisms may evolve or develop new behaviors (such as nomadism, dispersal, and migra-  
 220    tion) or adaptations (such as increased fat storage or food caching). If changes in  $\sigma^2(t)$  are  
 221    sufficiently predictable, organisms may learn to anticipate and prepare for periods of greater  
 222    stochasticity by pre-emptively caching food or migrating, or relying on alternative food  
 223    sources during stochastic events (e.g., after the arrival of competitors).

Like the scenario illustrated in fig. A1, 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. A2). 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.

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

We have provided the case for why both  $E(R)$  and  $\text{Var}(R)$  affect organisms' space-use requirements, but we presented the two parameters as independent drivers of movement. However, in the more realistic scenario where both  $E(R)$  and  $\text{Var}(R)$  fluctuate over time, organisms may respond to changes in  $\text{Var}(R)$  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  $E(R)$  and  $\text{Var}(R)$  separately, but also their interactive effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but  $\text{Var}(R)$  may have little effect if resources are stochastic but always abundant. Thus, we expect  $\text{Var}(R)$  to have a stronger effect on space-use requirements when  $E(R)$  is low, and

250 less of an effect when  $E(R)$  is high.

251 Rizzuto et al. (2021) found that the space-use requirements of snowshoe hares (*Lepus*  
252 *americanus*) increased with average carbon to nitrogen ratio (C:N, a measure of N scarcity)  
253 in lowbush blueberry as well as the coefficient of variation (the standard deviation divided  
254 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'  
255 space-use requirements since the coefficient of variation is a function of both  $\mu(t)$  and  $\sigma^2(t)$ ,  
256 so the effects of the two variables are confounded. Similarly, Mueller et al. (2011) suggested  
257 that ecosystem variability (measured as spatial semivariance in NDVI) causes ungulates to  
258 move more and adopt more nomadic behaviors, but it is hard to determine whether the higher  
259 semivariances in NDVI are due to an increase in  $Var(R)$  or simply spatial changes in  $E(R)$   
260 (e.g., increased seasonality or continentality). Likewise, Herfindal et al. (2005) found that  
261 the home ranges of Canadian lynx (*Lynx canadensis*) decreased with seasonality, but this  
262 may be an artifact of a lower  $\mu(t)$  in highly seasonal environments, rather than stochasticity  
263 in  $R$ . A subsequent analysis by Nilsen et al. (2005) of the lynx data of Herfindal et al.  
264 (2005) along with data on wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), and coyotes (*Canis*  
265 *latrans*) found that carnivores respond differently to seasonality, which suggests that different  
266 species may have different perceptions of the changes in  $R$  over the seasons. Collectively,  
267 these studies provide support towards the effects of both  $E(R)$  and  $Var(R)$  on organisms'  
268 space-use requirements, but the lack of a unifying framework across these studies makes it  
269 challenging to synthesize their findings. Thus, it is important to disentangle the effects of  
270 changes in  $E(R)$ , such as seasonal trends in  $\mu(t)$ , and stochasticity ( $Var(R)$ ). The need to  
271 account for changes in both  $E(R)$  and  $Var(R)$  is compounded by recent changes in climate,  
272 which expose species to novel situations and increasingly common and extreme stochastic  
273 events (Noonan et al. 2018; Yao et al. 2022; Intergovernmental Panel On Climate Change  
274 2023).

275 Nilsen et al. (2005) also show that the effect of  $E(R)$  on the home-range size of wolves  
276 and fishers (*Martes pennanti*) depends on seasonality (and vice-versa), since organisms in

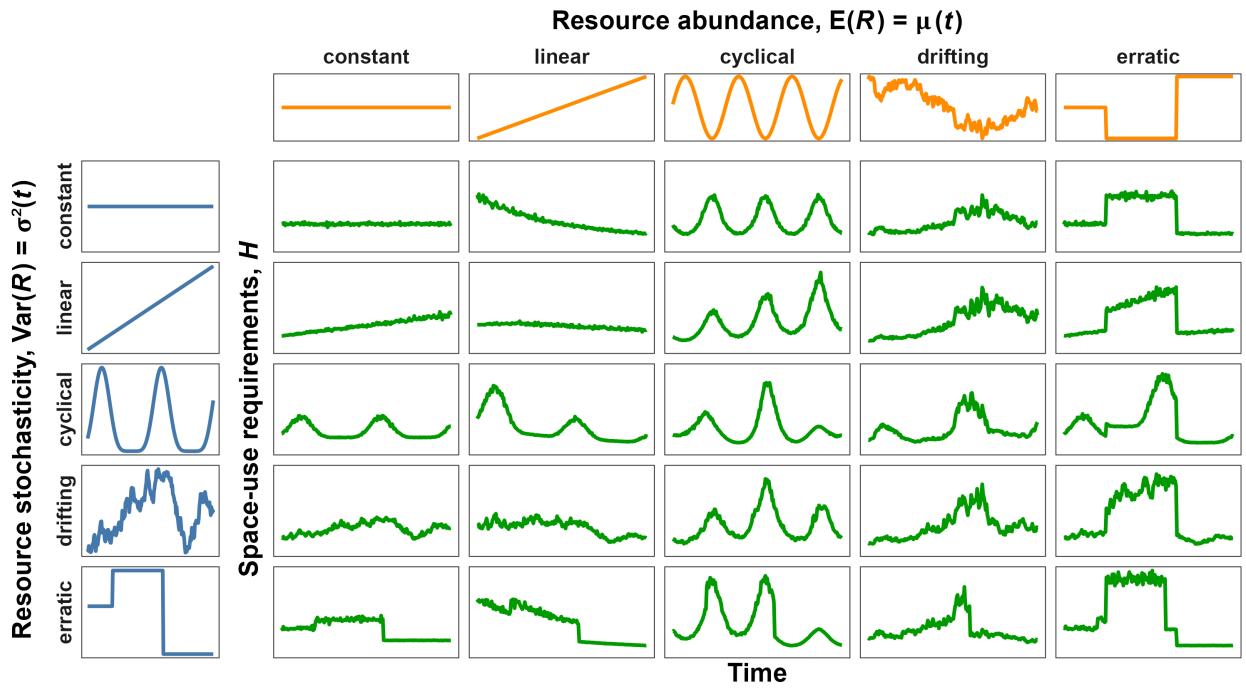
habitats with high and low seasonality had opposite responses to  $E(R)$ . Therefore, it may not be sufficient to account for the effects of  $E(R)$  and  $\text{Var}(R)$ ; models may also need a term for interaction between the two. This may be because organisms respond strongly to  $\sigma^2(t)$  when  $\mu(t)$  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. 3). 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 B.



**Figure 3:** 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. 3 shows how the simulated space-use requirements changed in response to  $\mu(t)$  and  $\sigma^2(t)$ . The top row (constant  $\text{Var}(R)$ ) shows how space-use requirements vary for different trends in  $\mu(t)$  while  $\text{Var}(R)$  remains constant (like in fig. A1). 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

316 1996; Herfindal et al. 2005; Nilsen et al. 2005).

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

331 The leftmost column of fig. 3 (constant  $E(R)$ ) illustrates the effects of  $\text{Var}(R)$  on the  
332 simulated space-use requirements while  $E(R)$  remains constant. Overall, both mean  $H$  and  
333 the variance around it increase with  $\sigma^2(t)$  (most visible with constant  $E(R)$  and linear  
334  $\text{Var}(R)$ ). This is because, similarly to resource-poor periods, times of greater stochasticity  
335 require the organism to move over larger areas for longer periods of time. This results in a  
336 greater uncertainty in how much time and space the organism will require to reach satiety, or  
337 indeed whether an organism living in highly stochastic environments can even reach satiety  
338 within a finite amount of time.

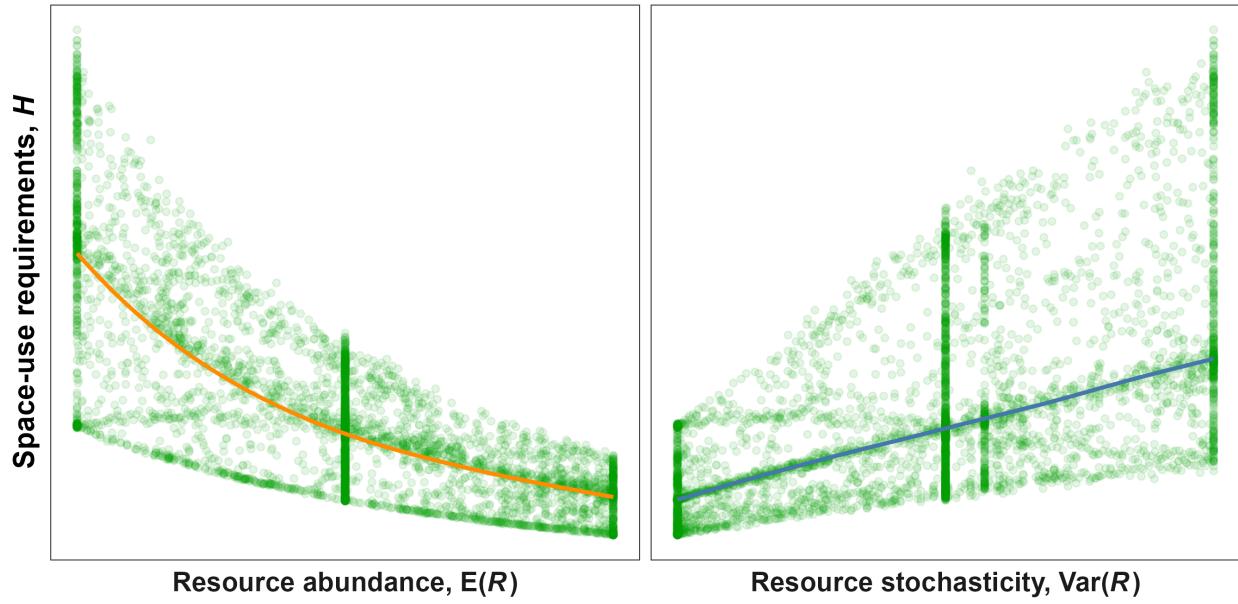
339 The remaining panels in fig. 3 illustrate how the effect of  $\text{Var}(R)$  depends on  $E(R)$   
340 (and vice-versa) as well as how complex the relationship can be. Since  $E(R)$  and  $\text{Var}(R)$   
341 have opposite effects on  $H$ , disentangling the effects can be particularly difficult when both  
342 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  $\sigma^2(t)$  follow fairly different trends (e.g., cyclical  $E(R)$  and linear  $\text{Var}(R)$ ), it is easy to see how an increase in  $\text{Var}(R)$  amplifies the effects of  $E(R)$ . In contrast, the effect of  $\text{Var}(R)$  is stronger when  $E(R)$  is low (e.g., linear  $E(R)$  with cyclical  $\text{Var}(R)$ ). Thus,  $H$  is largest when  $E(R)$  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 panel with cyclical  $E(R)$  and  $\text{Var}(R)$  as well as Lai et al. 2017).

Not all 25 scenarios depicted in fig. 3 may be realistic, but the trends in  $E(R)$  and  $\text{Var}(R)$ , and their impacts on space use are useful examples that can be thought of as simplified scenarios.  $E(R)$  and  $\text{Var}(R)$  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  $E(R)$  and  $\text{Var}(R)$  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  $E(R)$  and  $\text{Var}(R)$  may drift randomly in highly complex environments which are too hard to predict. Finally, erratic changes in  $E(R)$  and  $\text{Var}(R)$  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. 3 are complex and the effects of  $E(R)$  and  $\text{Var}(R)$  can be hard to disentangle, two surprisingly simple relationships emerge when home-range size is shown as a function of either  $E(R)$  or  $\text{Var}(R)$ , rather than time. Both  $E(R)$  and  $\text{Var}(R)$  affect space-use requirements precisely as we hypothesized (fig. 4). We believe the approximately linear effect of  $\text{Var}(R)$  on  $H$  is mainly due to two factors. Firstly,  $H$  scales superlinearly with

370 the standard deviation in  $R$  (as  $\sqrt{\text{Var}(R)}$  is on the same scale as  $E(R)$ ; not shown), which  
 371 would necessarily imply that  $H$  increases sublinearly with  $\text{Var}(R)$ . Secondly, the organism's  
 372 movement was simulated to be range resident within an homogeneous environment. Since  
 373 real-world landscapes are spatially heterogeneous in both  $E(R)$  and  $\text{Var}(R)$ , organisms may  
 374 choose to shift their home range to a new area following a stochastic event that caused  $\mu(t)$   
 375 to decrease, such as a fire or a flood. Thus, we hypothesize that our simulations may be  
 376 underestimating organisms' responses to spatiotemporal changes in  $E(R)$  and  $\text{Var}(R)$ , since  
 377 the simulated organisms cannot select for areas of higher  $E(R)$  or lower  $\text{Var}(R)$ . Additionally,  
 378 the simulations also ignore how competition, movement costs, predation, and other factors  
 379 may affect the effects of  $E(R)$  and  $\text{Var}(R)$  on  $H$ . While these are definitely important effects  
 380 that should be accounted for (Jetz et al. 2004), doing so was beyond the scope of this paper.



**Figure 4:** 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.

## **381 Applying the framework**

382 In this section, we show how this framework can be applied to better understand the move-  
383 ment ecology of free-ranging organisms via remote sensing data such as NDVI (Pettorelli  
384 et al. 2011). To illustrate the methods, we use empirical tracking data on a lowland tapir  
385 from the Brazilian Cerrado. Appendix C contains additional information on how NDVI  
386 was modeled along with details on the continuous-time movement models (Noonan et al.  
387 2019a; Fleming and Calabrese 2021) and autocorrelated kernel density estimation (Noonan  
388 et al. 2019b; Alston et al. 2022; Silva et al. 2022) used to quantify the tapir’s space-use  
389 requirements.

390 The hypotheses we present here allow researchers to combine otherwise complicated find-  
391 ings (e.g., fig. 3) and generalize results to a single, common set of functions. We expect the  
392 two hypotheses we present here (figs. 1 and 2) to be applicable to all motile organisms,  
393 once differences in size, metabolic needs, and diet are accounted for. In this subsection,  
394 we illustrate how researchers can leverage these hypotheses using their own data to build  
395 on previous work rather than listing the results as new findings. Additionally, the analyses  
396 can be expanded to the population or species level with the use of Hierarchical Generalized  
397 Additive Models (HGAMs) with individual-level intercepts and smooth terms (see models  
398 “GS” and “GI” in Pedersen et al. 2019). Such models would allow one to test whether  
399 members of the same population or species respond similarly to  $E(R)$  and  $\text{Var}(R)$  while also  
400 quantifying any deviation from the hypothesized behavior. Individuals and populations that  
401 were once thought to have different space-use requirements due to differences in behavior  
402 may instead be simply responding to different local conditions along the functions in figs. 1  
403 and 2 (e.g., Singh et al. 2012). In the following sections, we illustrate how one can apply  
404 this framework to empirical data.

405 We start by providing examples and considerations on how one may model  $R$  and the  
406 effects of  $E(R)$  and  $\text{Var}(R)$  on organisms’ space-use requirements. Next, we apply the

407 methods to the tapir's GPS tracking data and use NDVI as a proxy for  $R$ . Finally, we  
408 offer suggestions on how this approach can be used to inform conservation-related decisions,  
409 including assessing habitat quality and estimating organisms' space-use requirements under  
410 different scenarios.

411 **Modeling  $R$**

412 Location-scale models (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) are  
413 a class of statistical models that allow us to estimate changes in a random variable's mean  
414 (i.e. its location) and variance (which depends on its scale) while allowing the mean-variance  
415 relationship to vary. `mgcv` (Wood 2017) is a commonly used package for R (R Core Team  
416 2022) that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and Gener-  
417 alized Additive Models (GAMs, see Wood 2017), including hierarchical and location-scale  
418 GLMs and GAMs. Currently, the `mgcv` package allows one to fit location-scale models with  
419 various families of distributions, including Gaussian (i.e., normal), gamma, and Tweedie  
420 location-scale families.

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

427 The Gamma location-scale family is best for strictly positive responses, such as areas  
428 (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto  
429 et al. 2021), total biomass, or energetic intake. The Tweedie location-scale family is similar  
430 to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-  
431 trivial amount of zeros, such as daily precipitation or prey density (but see zero-inflated  
432 distributions: Zuur et al. 2009). In this paper, we estimate  $R$  by modeling NDVI using `mgcv`

433 and a beta location-scale family (not available in `mgcv` at the time of publication). If one  
434 is interested in families of distributions which are not available in `mgcv`, we suggest using  
435 the `brms` package (Bürkner 2017), which allows full control over all of a family's parameters  
436 via a fully Bayesian approach (as opposed to `mgcv`'s Empirical Bayes method – see Bürkner  
437 2018).

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

## 451 Estimating $R$ using NDVI

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

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

455 where  $\nu$  indicates the NDVI value in  $[-1, 1]$  and  $\nu_{[0,1]}$  is the scaled NDVI value (see Denny  
456 2017 for more information on transforming response data). In this case, we can define  $R$  as

457 following a beta distribution with mean and variance that depend on time using the notation  
 458  $B(\mu(t), \sigma^2(t))$ . We use this parameterization here for ease of explanation, but note that beta  
 459 distributions are generally parameterized using the shape parameters  $\alpha$  and  $\beta$  such that the  
 460 mean is

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

461 while the variance is

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

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

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

464 Consequently, we have

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

465 and

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

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

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

470 As discussed in the previous section, the first step to modeling  $H$  is to choose an appropriate  
 471 family of distributions. Since  $H$  is strictly positive and continuous, a Gamma family seems  
 472 the most appropriate among the distributions currently offered by the `mgcv` package (Wood  
 473 2017), but the Tweedie family would also be appropriate if the variance does not scale with

474 the squared mean.

475 As with the simulated effects of  $\mu(t)$  and  $\sigma^2(t)$  on  $H$  (fig. 4), a location-scale Gamma  
476 model is likely required. If there is not sufficient data to fit a location-scale model (which is  
477 not the case here), a simple Gamma model may be sufficient, but we suggest selecting the  
478 best family of distributions using an information criterion such as the Akaike Information  
479 Criterion (Akaike 1974). Due to potential correlation between  $E(R)$  and  $\text{Var}(R)$  in a small  
480 and autocorrelated sample, the relationship between  $R$  and  $H$  should be modeled carefully  
481 and with parsimony. Below, we present an empirical example using GPS tracking data from  
482 a lowland tapir (*Tapirus terrestris*) and satellite-derived NDVI. Additional information can  
483 be found in Appendix C.

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

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

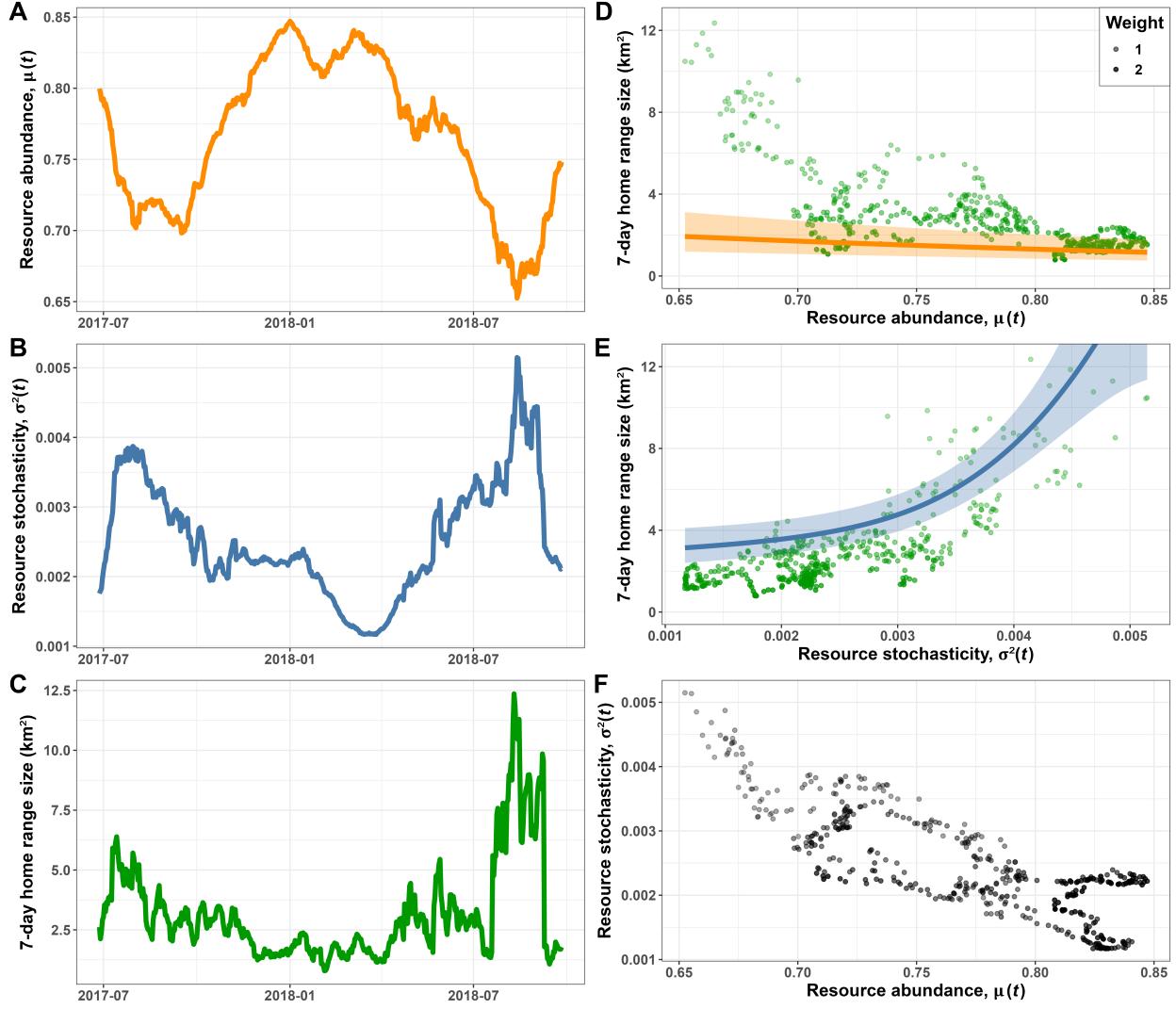
498 Modeling the tapir's space use as a function of resource abundance alone would result  
499 in an excessively strong estimated effect and a worse model fit ( $\Delta\text{AIC} \approx 87$ , see Appendix

500 C). By including the effect of  $\sigma^2(t)$  in the model along with that of  $\mu(t)$ , we show that the  
501 tapir responds to both resource abundance and stochasticity. While the tracking period may  
502 be too short to see the effects of  $E(R)$  clearly, it should also be noted that the Cerrado is  
503 relatively rich in vegetation throughout the entire year (fig. 5A), and thus the tapir does  
504 not experience resource scarcity during the tracking period. Consequently, this example  
505 demonstrates two points central to this paper. Firstly, even animals in resource-rich regions  
506 such as the Brazilian Cerrado adapt their behavior in response to reosurce stochasticity.  
507 Secondly, trends in mean resources alone are not sufficient to explain the tapir's space use,  
508 and the stochasticity in  $R$  is an important driver of the tapir's movement.

## 509 Discussion

### 510 Adaptations to changes in $E(R)$ and $\text{Var}(R)$

511 The spatiotemporal scale over which an event occurs is a main determinant of whether an  
512 organism will be able to predict the event and how it will respond to it (or fail to do so).  
513 Events that occur at the scale of the organism (i.e. approximately one or more times per  
514 generation and on the spatial scale of the organism's spatial range, see Frankham and Brook  
515 2004) are more likely to be perceived as a threat or boon worth preparing for (Foley et  
516 al. 2008; Berger et al. 2018; Geremia et al. 2019). Consequently, organisms with long  
517 generations (e.g., elephants, *Loxodonta sp.*) or large spatial ranges (e.g., migratory birds)  
518 are more likely to experience stochastic events and thus are also more likely to respond to and  
519 prepare for them. Animals may adapt by adjusting the timing of reproduction (Southwood  
520 1977; Boersma et al. 2021) and torpor or hibernation (Inouye et al. 2000; Goldberg and  
521 Conway 2021), or storing large amounts of energy (Lindstedt and Boyce 1985) through fat  
522 storage (Armitage et al. 2003; Nespolo et al. 2022) or resource caching (Post et al. 2006).  
523 Alternatively, animals may alter their movement and travel long distances over short periods  
524 of time (Jetz et al. 2004; Hirt et al. 2017), whether this be for migration (Mueller et al.



**Figure 5:** 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 C for additional information. The tapir movement data corresponds to the individual named “Anna” from the Cerrado sample of Medici *et al.* (2022).

525 2013; Geremia et al. 2019) or nomadism (Teitelbaum et al. 2015; Nandintsetseg et al. 2019;  
526 Teitelbaum and Mueller 2019). Over the years, animals may also develop more complex  
527 cognitive abilities (Brown et al. 2004), including the development of memory (Foley et al.  
528 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et al. 2019; Geremia et al. 2019;  
529 Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Steixner-Kumar and Gläscher  
530 2020; Falcón-Cortés et al. 2021; Cavedon et al. 2022; Ranc et al. 2022), which is required  
531 for migration (Mueller et al. 2013; Middleton et al. 2018; Abrahms et al. 2019; Geremia  
532 et al. 2019; Merkle et al. 2019; Rickbeil et al. 2019; but see: Cuadrado 2021; Stefanescu  
533 et al. 2021). However, adapting to changes in environmental cues rather than relying on  
534 memory alone (Jonzén et al. 2006; Büntgen et al. 2017; Rickbeil et al. 2019; Severson et al.  
535 2021), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et  
536 al. 2019).

537 In contrast, individuals with short lifespans are less likely to experience stochastic events  
538 and develop memory about them. However, the short generation time and high reproductive  
539 rate of r-selected species (as opposed to k-selected species, see Pianka 1970; Brown et al.  
540 2004) may promote other traits that increase survival following extreme events. Examples in-  
541 clude higher population size, dispersal, higher genetic diversity, and complex group dynamics  
542 (e.g., Cuadrado 2021; Stefanescu et al. 2021). Events that occur over large spatiotemporal  
543 scales can thus promote slow, large-scale changes through the adaptation, natural selection,  
544 and evolution of the species (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et  
545 al. 2017; Grant et al. 2017), which is more likely to adapt if starting populations are large  
546 with high genetic diversity and short generations, as in the case of r-selected species (but see  
547 Leung 2022). Of course, an organism with a lifespan shorter than a year will be unable to  
548 experience the cyclical nature of the seasons, and an organism with a lifespan of a few weeks  
549 or days may not even experience substantial changes in weather other than daily cycles and  
550 some weather stochasticity. Still, a population may respond to spatiotemporal cycles in  
551  $E(R)$  and  $\text{Var}(R)$  by adapting the group's reproduction timing and migration (e.g., painted

552 lady butterflies: Cuadrado 2021; Stefanescu et al. 2021).

553 A population's fitness and chances of survival in a changing environment depend strongly  
554 on its adaptability and responsiveness to change (Riotte-Lambert and Matthiopoulos 2020),  
555 and its ability to recognize cues that precede extreme events or periods of scarcity or abun-  
556 dance can have appreciable effects on its members' chances of survival and reproduction.  
557 For example, ungulates' ability to time their yearly migrations on available forage biomass,  
558 snow fall, snow melt, and hunting pressure allow them to adapt to changes in both  $E(R)$  and  
559  $\text{Var}(R)$ , while their spatial memory (Falcón-Cortés et al. 2021; Ranc et al. 2022) allows them  
560 to optimize their large-scale movement by reducing the amount of time and energy spent  
561 exploring. Similarly, the ability of trans-Saharan migrant birds to adapt their migration  
562 timing based on environmental cues allows them to account for differences in  $\mu(t)$  between  
563 years (Jonzén et al. 2006). However, relying too strongly on short-term changes rather than  
564 depending on long-term memory can also cause animals to fail to find crucial resources dur-  
565 ing unpredictable times (whooping cranes: Mueller et al. 2013; Foley et al. 2008; elephants:  
566 Polansky et al. 2015; whales: Abrahms et al. 2019). Instead, if anomalies occur repeatedly  
567 over time, organisms may adapt to a higher  $\sigma^2(t)$  or shift their ranges altogether (terrestrial  
568 animals: Chen et al. 2011; Büntgen et al. 2017; ungulates: Severson et al. 2021), including  
569 migratory animals (Jonzén et al. 2006). Still, while range shifts can help species overcome  
570 changes in the long-term trends in  $\mu(t)$  and  $\sigma^2(t)$ , including changes in phenology (Severson  
571 et al. 2021), they can also result in phenological mismatches (Lameris et al. 2018) and add  
572 pressure to the species that already live in the habitat (e.g., Wallingford et al. 2020; but see  
573 Shepard et al. 2022), including specialists and obligate symbionts that may be unable to  
574 shift their range, since it is determined by their food sources' and associates' ability to move  
575 and adapt, too.

576 **Applications for conservation**

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

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

598 Ignoring the effects of recent and predicted increases in  $\text{Var}(R)$ , including an increase  
599 in the intensity and frequency of extreme events (Yao et al. 2022; Intergovernmental Panel  
600 On Climate Change 2023), has the potential to greatly hinder future conservation efforts.  
601 Since not accounting for an increase in  $\sigma^2(t)$  will result in an under-estimation of animals'  
602 space-use requirements, protected areas which were designated based on the area's  $\mu(t)$  but

603 not  $\sigma^2(t)$  will likely be insufficient in both size and resources in the future, which may lead to  
604 decreases in the fitness and size of a population while also increasing the risk of population  
605 collapse and human-wildlife conflict (Mukaka et al. 2019). This is particularly the case  
606 in resource-poor, stochastic regions, where animals are forced to endure longer and more  
607 unpredictable searches, which results in a larger variance in space-use requirements.

608 It is also worth noting that carnivores may be more susceptible to changes in  $E(R)$  and  
609  $\text{Var}(R)$ , and that this susceptibility is likely amplified further at higher trophic levels. While  
610 primary consumers can rely on relatively predictable and static resources that can be esti-  
611 mated easily via remote sensing measures such as NDVI, the fine-scale location of secondary  
612 consumers' resources may not correlate as strongly with measures of habitat productivity. In  
613 fact, primary consumers' ability to move makes their location and abundance more stochas-  
614 tic than those of plants. Consequently, the abundance of primary consumers may correlate  
615 with productivity weakly or at a temporal lag (e.g., Geremia et al. 2019). Thus, primary  
616 consumers' delayed responses to fluctuations in  $E(R)$  and  $\text{Var}(R)$  may result in an increase  
617 in secondary consumers' resource stochasticity, which would also be perceived with a delay.  
618 Similar hypotheses can be formulated for higher trophic levels but with amplified temporal  
619 lags, since each trophic level adds another layer of uncertainty and delayed response, which  
620 together increase the unpredictability on how carnivores indirectly respond to changes in  
621 primary productivity. However, the effect is likely less pronounced for omnivores and other  
622 diet generalists, as they may have the ability to switch to more abundant and less stochastic  
623 resources.

## 624 Conclusion

625 The work presented here provides a unifying framework for viewing movement as a function  
626 of resource abundance and stochasticity. We provide realistic and flexible hypotheses of  
627 the effects of  $E(R)$  and  $\text{Var}(R)$  on organisms' space-use requirements and movement behav-  
628 ior. We demonstrate that organisms' space-use requirements respond nonlinearly to both

629 resource abundance and stochasticity, and we demonstrate the importance of accounting  
630 for  $\text{Var}(R)$  besides  $\text{E}(R)$ . We also provide a moving window approach that allows one to  
631 model movement continuously rather than imposing arbitrary thresholds between different  
632 periods or types of behaviors, including temporal changes in space-use requirements and  
633 shifts between range-residency and nomadism. The methods presented here can be applied  
634 to assess the current and future quality of protected areas while also estimating the amount  
635 of space organisms currently need and will need in the future under different climate change  
636 scenarios.

### 637 **Conflict of interest**

638 The authors declare there are no conflicts of interest.

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