

How resource abundance and resource stochasticity affect organisms' range  
sizes

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## <sup>1</sup> Abstract

<sup>2</sup> **Background:** From megafauna to amoebas, the amount of space heterotrophic organisms  
<sup>3</sup> use is thought to be tightly linked to the availability of resources within their habitats,  
<sup>4</sup> such that organisms living in productive habitats generally require less space than those  
<sup>5</sup> in resource-poor habitats. This hypothesis has widespread empirical support, but existing  
<sup>6</sup> studies have focused primarily on responses to spatiotemporal changes in mean resources,  
<sup>7</sup> while responses to unpredictable changes in resources (i.e., variance in resources or resource  
<sup>8</sup> stochasticity) are still largely unknown. Since organisms adjust to variable environmental  
<sup>9</sup> conditions, failing to consider the effects of resource unpredictability can result in an in-  
<sup>10</sup> sufficient understanding of an organism's range size. **Methods:** We leverage the available  
<sup>11</sup> literature to provide a unifying framework and hypothesis for the effects of resource abun-  
<sup>12</sup> dance and stochasticity on organisms' range sizes. We then use simulated movement data  
<sup>13</sup> to demonstrate how the combined effects of resource abundance and stochasticity interact  
<sup>14</sup> to shape predictable patterns in range size. Finally, we test the hypothesis using real-world  
<sup>15</sup> tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado. **Results:**  
<sup>16</sup> Organisms' range sizes decrease nonlinearly with resource abundance and increase nonlin-  
<sup>17</sup> early with resource stochasticity, and the effects of resource stochasticity depend strongly  
<sup>18</sup> on resource abundance. Additionally, the distribution and predictability of resources can  
<sup>19</sup> exacerbate the effects of other drivers of movement, such as resource depletion, competition,  
<sup>20</sup> and predation. **Conclusions:** Accounting for resource abundance and stochasticity is cru-  
<sup>21</sup> cial for understanding the movement behavior of free-ranging organisms. Failing to account  
<sup>22</sup> for resource stochasticity can lead to an incomplete and incorrect understanding of how and  
<sup>23</sup> why organisms move, particularly during periods of rapid change.

<sup>24</sup> **Background**

<sup>25</sup> The amount of resources an organism is able to access is a strong determinant of its fitness.  
<sup>26</sup> Resource limitations can cause individuals to experience a negative energetic balance, which  
<sup>27</sup> can then result in lower fitness [1,2], altered physiology [2–5], lower chance of reproduction  
<sup>28</sup> [2,6–8], and even death [9,10]. Thus, many organisms adapt their behaviors and/or physiol-  
<sup>29</sup> ogy in response to changes in local resource abundance to ensure their needs are met [e.g.,  
<sup>30</sup> soil amoebae *Dictyostelium spp.*: 11, plants: 12, and animals: 13].

<sup>31</sup> While there are many ways that individuals can respond to resource availability, move-  
<sup>32</sup> ment represents one of the most readily available traits that motile species can adjust [14–16].  
<sup>33</sup> The relationship between organisms' movement and resource abundance has long been of in-  
<sup>34</sup> terest to biologists. In his seminal paper, Burt [17] considered the search for food as the  
<sup>35</sup> primary driver for movement within an organism's home range. Three decades after, South-  
<sup>36</sup> wood [18] suggested that change in resource abundance drives how organisms decide where  
<sup>37</sup> to live and when to reproduce. Two years later, Harestad and Bunnel [13] proposed that the  
<sup>38</sup> simplest relationship between resource abundance and an organism's home-range size is

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

<sup>39</sup> where  $H$  is the organism's home-range size,  $C$  is the organism's resource consumption rate  
<sup>40</sup> ( $\text{kcal day}^{-1}$ ), and  $R$  is the resources the organism can access ( $\text{kcal day}^{-1} \text{ unit area}^{-1}$ ).  
<sup>41</sup> Harestad and Bunnel's model is simple to conceptualize, and it allows for testable predictions,  
<sup>42</sup> but few studies are structured around a set of theoretical expectations such as Harestad  
<sup>43</sup> and Bunnel's hypothesis. Many researchers have since demonstrated that organisms adapt  
<sup>44</sup> their range sizes in response to resource abundance, but results are typically reported as  
<sup>45</sup> independent, novel findings. Perhaps more problematic is the fact that, while much work has  
<sup>46</sup> been done on estimating organisms' responses to changes in mean resource abundance, there  
<sup>47</sup> is little information on how organisms respond to unpredictable changes in resources [i.e.,

48 resource stochasticity, but see: 19,20–22]. Thus, there remains a need for a clear, unifying  
49 hypothesis of the effects of both resource abundance and stochasticity on organisms’ range  
50 sizes.

51 Here, we refer to a location’s average amount of resources as “resource abundance”, while  
52 we use the phrase “resource stochasticity” to indicate the variability in resources after ac-  
53 counting for changes in the mean. We argue that, on its own, a habitat’s resource abundance  
54 is not sufficient to assess the habitat’s quality, nor make predictions about how much space  
55 an organism might use. To see this, consider, for instance, a herbivore grazing in a grassland  
56 with relatively low but constant forage availability (i.e., low mean and variance). The ani-  
57 mal may require a large but constant home range size as it moves between patches in search  
58 of food. If, instead, it lived in a desert with equally scarce forage but rare, sudden, and  
59 strong pulses of resources (i.e., low long-term mean and high stochasticity), it may switch  
60 between dispersal in search for high-resource patches and short-term range residency within  
61 patches [*sensu* 15,see 23,24,25]. Previous studies suggest that resource stochasticity may  
62 decrease organisms’ fitness and landscapes’ energetic balances [e.g., 26], but there is still  
63 limited empirical evidence to support this hypothesis [but see: 21,27,28].

64 In this paper, we illustrate how an organism’s range size can be expected to depend on  
65 both the abundance and unpredictability of resources. First, we set the theoretical back-  
66 ground necessary for the successive sections by introducing key concepts and notation. Next,  
67 we provide a review of the effects of resource abundance on range sizes while suggesting a  
68 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource  
69 stochasticity on organisms’ range sizes while suggesting a second simple and unifying hy-  
70 pothesis. Subsequently, we support the hypothesis using quantitative, simulated responses  
71 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate  
72 how this framework can be used in practice to describe the movement ecology of a lowland  
73 tapir (*Tapirus terrestris*) from the Brazilian Cerrado [29].

<sup>74</sup> **Resources as a random variable**

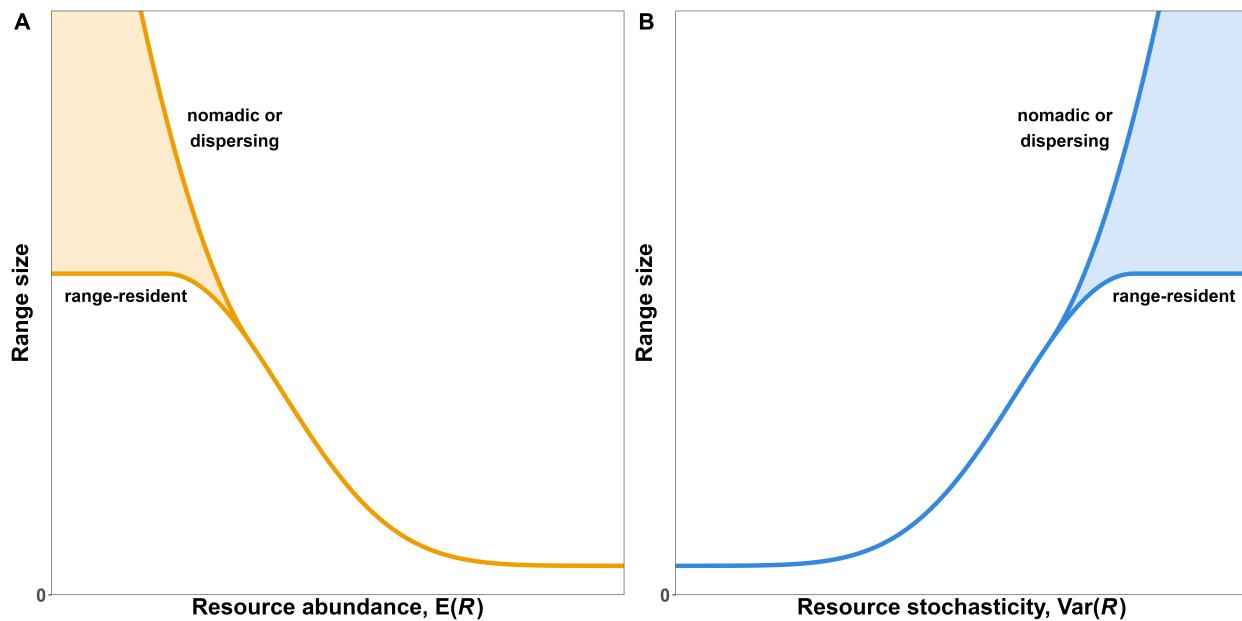
<sup>75</sup> Resources (e.g., food, water, shelter, heat) are often unpredictable (and difficult to quantify),  
<sup>76</sup> since they depend on various factors which cannot be accounted for easily, including climate  
<sup>77</sup> [7,30,31], weather [31,32], competitive pressure [33,34], and differences in energetics at among  
<sup>78</sup> individuals [7] and species [35]. Thus, it is possible to treat the amount of resources  $R$  at a  
<sup>79</sup> given point in time ( $t$ ) and space (location vector  $\vec{u}$ ) as a random variable, denoted as  $R(t, \vec{u})$ .  
<sup>80</sup> Treating resources as a random variable allows us to leverage techniques from probability  
<sup>81</sup> theory and statistics, such as the expectation of a random variable (i.e., its mean) and its  
<sup>82</sup> variance around the mean. We indicate the expected value and variance of random variable  
<sup>83</sup>  $R$  using  $E(R)$  and  $\text{Var}(R)$ , respectively, and we use  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  to indicate them  
<sup>84</sup> as functions of time ( $t$ ) and space ( $\vec{u}$ ). Appendix A defines and expands on the concepts  
<sup>85</sup> of probability distributions, expected value, variance, and provides examples of them for  
<sup>86</sup> Gamma and Beta distributions.

<sup>87</sup> **Effects of resource abundance,  $E(R)$**

<sup>88</sup> While organisms' needs vary greatly between taxonomic groups, some needs are essential  
<sup>89</sup> for the growth, survival, and reproduction of most organisms. All heterotrophic organisms  
<sup>90</sup> require sources of chemical energy (i.e., food), water, and various limiting nutrients [36–38].  
<sup>91</sup> As the abundance of essential resources fluctuates, motile organisms can move to new loca-  
<sup>92</sup> tions or 'patches' to meet their requirements [15,39], but movement also increases energetic  
<sup>93</sup> needs [40].

<sup>94</sup> When  $E(R)$  is high, we expect organisms' ranges to be relatively small and near the  
<sup>95</sup> smallest amount of space required to survive [see fig. 1A as well as: 27,28,41]. Like Harestad  
<sup>96</sup> and Bunnel [13], we also expect organisms' range sizes to increase nonlinearly as  $E(R)$   
<sup>97</sup> decreases, but we highlight that organisms may adopt different behaviors at low values of  
<sup>98</sup>  $E(R)$ . These behaviors include maximal home range expansion [home range size is limited by

vagility, habitat structure, competition, and predation, e.g., 33,34,42,43], migration [44–46], and nomadism [23,25,47,48]. It is unclear when organisms switch from range residency to migration or nomadism (or vice-versa), but understanding the gradient among these types of movement is necessary for quantifying the effect of resource abundance on organisms' range size and movement behavior [mammals: 49, moose, *Alces alces*: 23, eagles, *Haliaeetus leucocephalus*: 24,50, lesser flamingos, *Phoeniconaias minor*: 51].



**Figure 1:** Hypothesized range size of an organism as a function of (A) resource abundance and (B) resource stochasticity. We expect low values of  $E(R)$  and large values of  $\text{Var}(R)$  to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory. As  $E(R)$  increases or  $\text{Var}(R)$  decreases, range size should decrease nonlinearly until it reaches the minimum amount of space required by the organism to survive.

Note that the relationship between range size and both  $E(R)$  and  $\text{Var}(R)$  cannot be of the form  $H = \beta_0 + \beta_1 E(R) + \beta_2 \text{Var}(R)$  because it would require range size to be negative for high values of  $E(R)$  or low values of  $\text{Var}(R)$ .

Overall, the hypothesis that range size decreases with resource abundance,  $E(R)$ , is commonly accepted and well supported, but many studies assume a linear relationship [e.g., 21,41,52–54]. This is problematic because, conceptually, the relationship between range size and  $E(R)$  must be nonlinear, since: (1) there is an upper limit to how much space an organism is able to explore in its finite lifetime and (2) the minimum amount of space it requires to survive is necessarily greater than zero [see 27,28,55,56,57, and contrast them to

the earlier references that assume a linear relationship between  $H$  and  $R$ ]. Consequently, we suggest analysts use models that account for this nonlinearity when estimating the effects of resource abundance on range size. While the relationship may be approximately linear for some range of  $E(R)$ , this assumption often does not hold for low or high values of  $E(R)$  [e.g., 52]. Additionally, identifying inflection points in nonlinear relationships can help understand the pressures and limitations of increasing range size.

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

Assuming resource stochasticity is constant over time and space can be a useful simplification of relatively stable environments or when information on how  $E(R)$  changes is limited and estimating changes in  $\text{Var}(R)$  is unreasonable. However, such an assumption is likely not realistic, since  $\text{Var}(R)$  often differ across space and over time. Generally, bounded quantities have correlated means and variances, as in the case of random variables that are strictly positive (e.g., Gamma and Poisson) or fully bounded (e.g., Beta). For example, prey abundance in a given area over time may approximately follow a Poisson distribution, which implies that the mean and variance will be approximately equal. When prey are scarce, the variance will also be low, and when prey are abundant the variance will also be high. This occurs because the behavior, fitness, and predator-prey dynamics of many prey are more stochastic than those of few prey [58]. Similarly, in the case of fully bounded random variables, the variance is generally lowest when the mean is near either boundary. For example, successful predation events are predictably scarce if the probability of capture is near 0, predictably common if the probability is near 1, and most stochastic if the probability is near 0.5 [i.e., as far as possible from both 0 and 1; see [59]]. See Appendix A for more information.

Recognizing changes in  $\text{Var}(R)$  helps account for the residual, fine-scale variation in  $R$  after accounting for trends in the large-scale average  $R$  [e.g., variations in plant phenology between years after accounting for mean seasonal trends, see 60]. However, when both  $E(R)$  and  $\text{Var}(R)$  change over time (fig. A2), disentangling changes in  $E(R)$  and  $\text{Var}(R)$  is

137 not simple [61]. Statistically, this confound occurs because the more change one attributes  
138 to  $\mu(t, \vec{u})$  (i.e., the wigglier it is), the smaller  $\sigma^2(t, \vec{u})$  becomes. Conversely, the smoother  
139  $\mu(t, \vec{u})$  is, the larger  $\sigma^2(t, \vec{u})$  becomes. Biologically, it is important because an organism's  
140 perception scale determines whether it attributes a change in  $R$  to a trend in  $E(R)$  or as  
141 a stochastic event [i.e., due to  $\text{Var}(R)$ ; see [60]]. An organism's perception of changes in  
142  $R$  will also depend strongly on the its cognitive capacities and memory [9,62–65]. Whether  
143 an organism is able to predict trends in  $\sigma^2(t, \vec{u})$  or not, environmental variability is thought  
144 to reduce a landscape's energetic balance [26], which, in turn, decreases organisms' fitness  
145 [e.g., 10] and increases their range size. While this behavioral response occurs with both  
146 predictable and unpredictable stochasticity, extreme and rare events are more likely to have  
147 a stronger effect due to their unpredictability and magnitude [66,67]. A few recent studies  
148 support these hypotheses [22,26,31,48,68], but many of them are limited in geographic and  
149 taxonomic scales or fail to account for nonlinear relationships, so the extent to which these  
150 preliminary findings can be generalized is currently unknown. Thus, there remains a need  
151 for developing a more complete understanding of how organisms' range sizes changes with  
152 environmental stochasticity.

153 Similarly to  $E(R)$ , we hypothesize  $\text{Var}(R)$  has a nonlinear effect on an organism's range  
154 size. When  $\text{Var}(R)$  is low enough that  $R$  is relatively predictable, we expect organisms to  
155 be range-resident with small home ranges, and we do not expect small changes in  $\text{Var}(R)$  to  
156 have a noticeable effect. As resources become increasingly unpredictable, we expect home  
157 range size to increase progressively faster (fig. 1B) because: (1) as  $\text{Var}(R)$  increases, the  
158 chances of finding low  $R$  increase superlinearly, (2) the added movement required to search  
159 for food increases organisms' energetic requirements, and (3) stochasticity reduces an or-  
160 ganism's ability to specialize and reduce competition for  $R$  [69]. If resources remain highly  
161 unpredictable over long periods of time (e.g., multiple lifespans), organisms may evolve or  
162 develop new and consistent behaviors (e.g, nomadism) or adaptations (e.g., increased fat  
163 storage or food caching) to buffer themselves against times of unpredictably low  $R$ . Con-

164 versely, if changes in  $\sigma^2(t, \vec{u})$  are sufficiently predictable, organisms may learn to anticipate  
165 and prepare for times of greater stochasticity by pre-emptively caching food, reducing  
166 energetic needs, migrating, or relying on alternative food sources [e.g., 70].

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

168 We have provided the case for why both  $E(R)$  and  $\text{Var}(R)$  should be expected to affect  
169 organisms' range size, but we presented the two parameters as independent drivers of move-  
170 ment. However, organisms may respond to changes in  $\sigma^2(t, \vec{u})$  more when resources are  
171 scarce than when they are abundant. Consequently, an organism's movement behavior is  
172 likely to be a function of not only the marginal effects of  $E(R)$  and  $\text{Var}(R)$  but also their  
173 interactive effects. A highly unpredictable habitat may be very inhospitable if resources  
174 are poor, but  $\text{Var}(R)$  may have little effect if resources are stochastic but always abundant.  
175 Thus, we expect  $\text{Var}(R)$  to have a stronger effect on range size when  $E(R)$  is low, and less of  
176 an effect when  $E(R)$  is high. We explore this interaction effect more in the following section.

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

178 To evaluate our hypothesis of how organisms' range sizes are affected by  $E(R)$ ,  $\text{Var}(R)$ , and  
179 the interaction effect of  $E(R)$  and  $\text{Var}(R)$ , we present the results from a series of quantitative  
180 simulations. To start, we used the `ctmm` package [71] for R [72] to generate 200 tracks (see Ap-  
181 pendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement model  
182 [IOU model, see 73]. The IOU model's correlated velocity produced tracks with directional  
183 persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF)  
184 models, IOU models do not produce spatially stationary movement, so the organism is not  
185 range-resident. Consequently, each track is spatially unrestricted and can be interpreted as  
186 purely exploratory or memoryless movement.

187 Each of the 200 tracks were placed on a grid with common starting point  $\langle 0, 0 \rangle$  (fig. B1).  
188 Each time the simulated individual moved to a new cell, it collected  $R$  resources sampled

189 from a Gamma distribution. The mean and variance of the distribution were defined by a  
 190 series of deterministic functions  $\mu(t)$  and  $\sigma^2(t)$  (orange and blue lines in fig. 3). The value  
 191 of  $t$  was constant within each set of 200 tracks, so the distribution  $R$  was sampled from  
 192 was independent of both the organism's location and its time spent moving. Tracks were  
 193 truncated once the organism reached satiety, and the organism was given enough time to  
 194 return to  $\langle 0, 0 \rangle$  independently from the following track (section 2.1 of Appendix B). Finally,  
 195 we fit an OUF movement model [74] to the set of tracks to calculate the 95% Gaussian  
 196 home-range size using the formula

$$\hat{H}_{95\%} = -2 \log(1 - 0.95) \pi \hat{\varsigma}^2,$$

197 where  $\hat{\varsigma}^2$  is the positional variance estimated by the movement model.

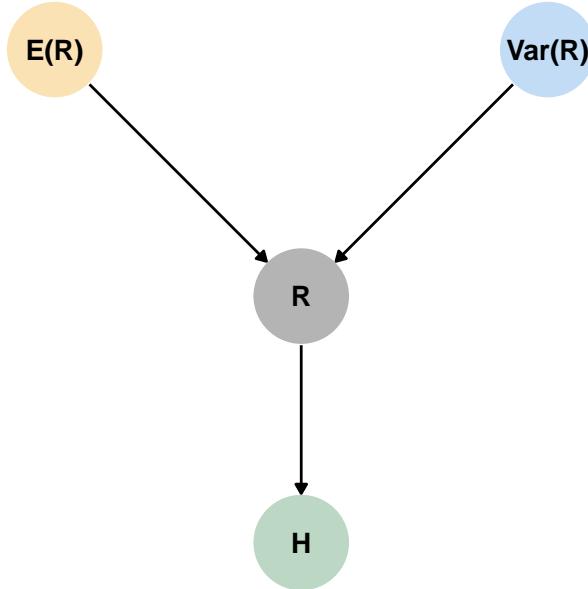
198 We designed the simulations to estimate the effects of  $E(R)$  and  $\text{Var}(R)$  in simplistic  
 199 environments where organisms could only respond by searching for longer periods of time.  
 200 Consequently, we made the following assumptions:

- 201 1) Environments are homogeneous for a given  $t$ . Given  $t$ ,  $E(R) = \mu(t)$  and  $\text{Var}(R) = \sigma^2(t)$   
 202 are constant over space and within each set of 200 tracks, but  $R$  is random and follows  
 203 a  $\text{Gamma}(\mu(t), \sigma^2(t))$  distribution.
- 204 2) There are no external pressures on the simulated organism. Resources do not deplete,  
 205 and there is no competition nor predator avoidance.
- 206 3) The organism has a fixed daily energetic requirement that is independent of movement  
 207 rates, and it cannot alter its metabolism or physiology. Additionally, the organism  
 208 does not have energetic reserves, so excess resources cannot be carried over to the next  
 209 track or  $t$ .
- 210 4) The organism is range-resident and can only respond to changes in  $E(R)$  and  $\text{Var}(R)$   
 211 by altering its home-range size. The organism does not disperse or abandon a range.
- 212 5) The organism's movement is simplistic. The organism's movement speed and direction

213        are stochastic and independent of  $E(R)$  and  $\text{Var}(R)$ .

- 214     6) The organism has no perceptive range or memory. It is unable to detect, learn, or  
215        predict where resources are abundant (high  $E(R)$ ) or reliable (low  $\text{Var}(R)$ ) over time  
216        or space.
- 217     7) Animals only move to search for food or return to the center of their home-range after  
218        reaching satiety.

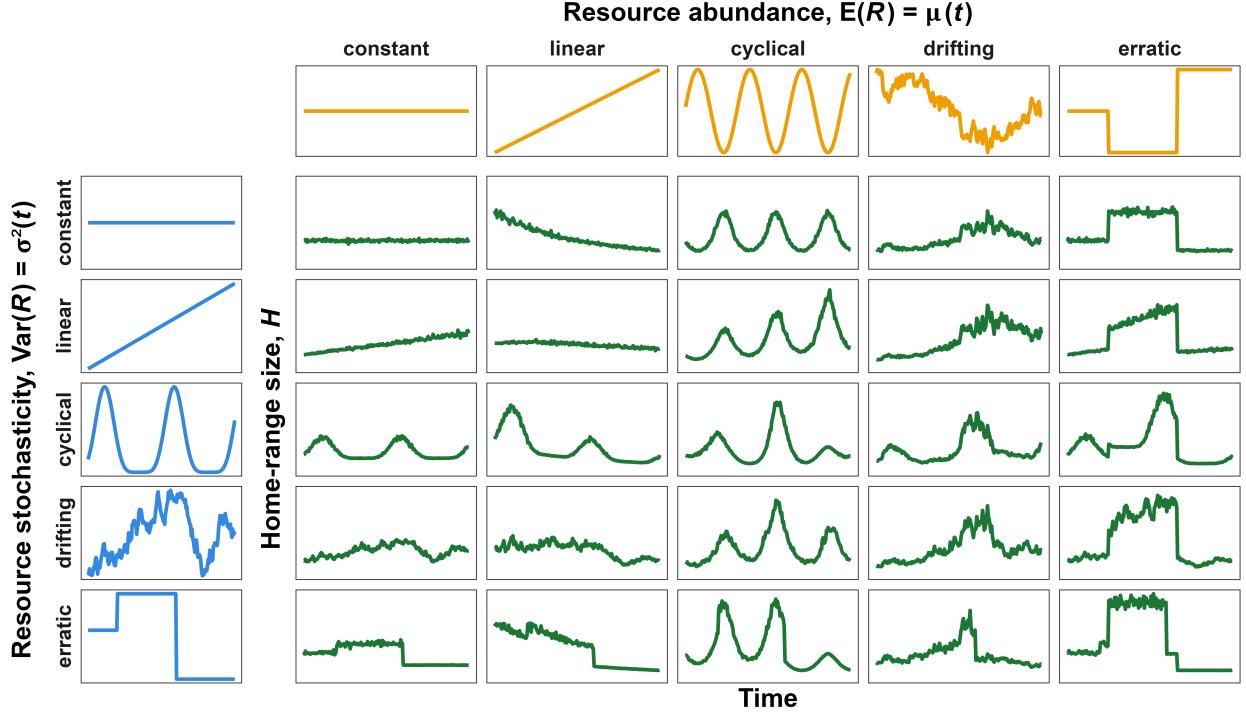
219        Based on the assumptions above, we constructed the following causal model for the  
220        simulated effects of  $E(R)$  and  $\text{Var}(R)$  on  $H$  [see fig. 2 and 75]:  $E(R)$  and  $\text{Var}(R)$  were  
221        determined independently of each other, but they jointly determined the distribution of  $R$ ,  
222        which, in turn, determined the distribution of  $H$ . Additional information is provided in  
223        Appendix B.



**Figure 2:** Directed acyclical graph assumed for inferring the causal effects of  $E(R)$  and  $\text{Var}(R)$  on the distributions of  $R$  and  $H$  in the simulations.

224        Fig. 3 shows how simulated home-range size,  $H$ , responded to changes in  $\mu(t)$  and  $\sigma^2(t)$   
225        in scenarios where both functions can remain constant, increase linearly, oscillate cyclically,  
226        drift stochastically, or change erratically. The top row (constant  $\text{Var}(R)$ ) shows how  $H$  varies  
227        for different trends in  $\mu(t)$  while  $\text{Var}(R)$  remains constant (like in fig. A1). As  $E(R)$  increases

228 at a constant slope (linear  $\mu(t)$ ),  $H$  decreases nonlinearly, with larger changes when  $E(R)$   
 229 is low, until it approaches the minimum size required by the organism. Also note how the  
 230 noise in the green lines also decreases as  $E(R)$  increases.



**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 (but homogeneous over space for a given  $t$ ). 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.

231 The leftmost column of fig. 3 (constant  $E(R)$ ) illustrates the effects of  $\text{Var}(R)$  on  $H$   
 232 while  $E(R)$  remains constant. Overall, both mean  $H$  and the variance around it increase  
 233 with  $\sigma^2(t)$  (most visible with constant  $E(R)$  and linear  $\text{Var}(R)$ ). Similarly to resource-poor  
 234 periods, times of greater stochasticity require the organism to move over larger areas for  
 235 longer periods of time. Additionally, the greater uncertainty in how much time and space  
 236 the organism will require to reach satiety, or indeed whether an organism living in highly  
 237 stochastic environments can even reach satiety within a finite amount of time.

238 The remaining panels in fig. 3 illustrate how  $E(R)$  and  $\text{Var}(R)$  jointly affect  $H$  and  
 239 how unintuitive the effects can be. Since  $E(R)$  and  $\text{Var}(R)$  have opposite effects on  $H$ ,  
 240 disentangling the effects can be particularly difficult when both parameters change in a

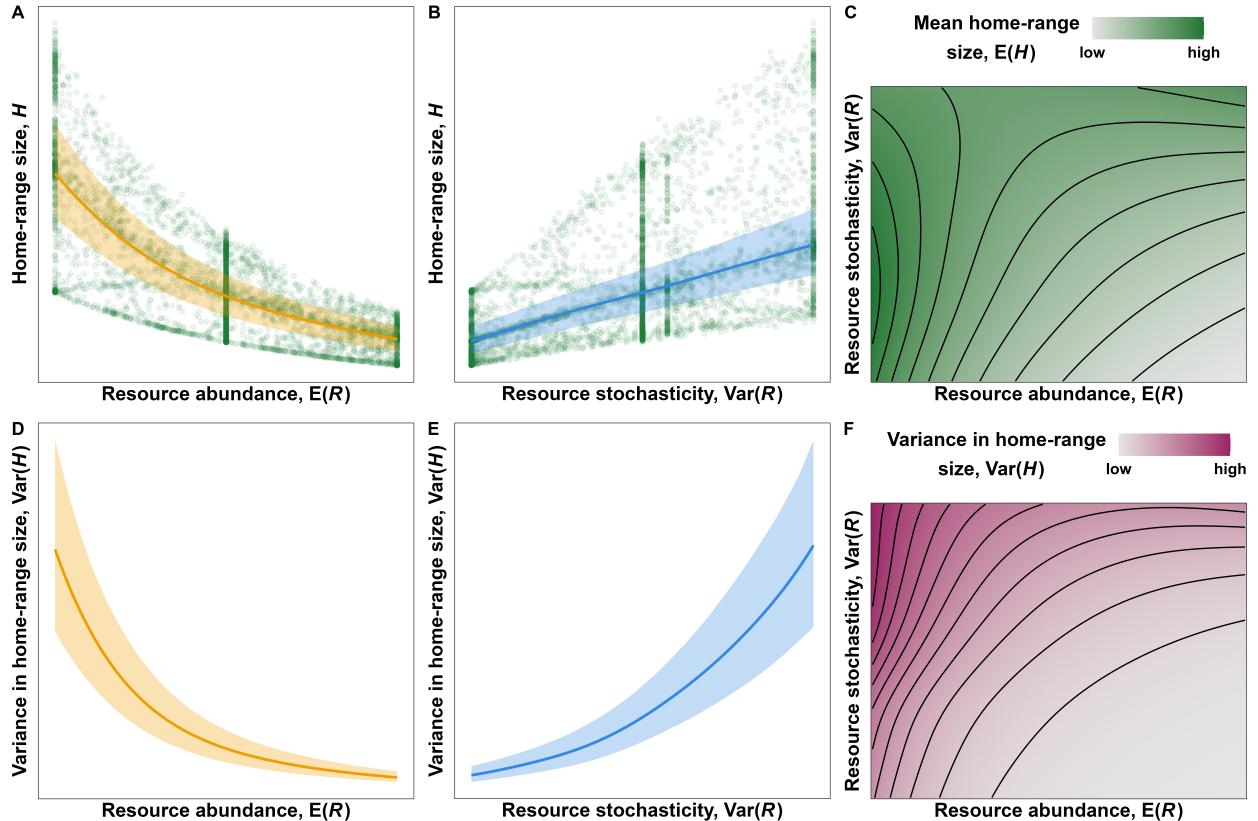
241 correlated manner (e.g., linear  $E(R)$  and  $\text{Var}(R)$ ). When both  $E(R)$  and  $\text{Var}(R)$  increase  
242 linearly,  $H$  initially increases since the effect of  $\text{Var}(R)$  is stronger, but then decreases as the  
243 effect of  $E(R)$  begins to dominate. Difficulties in disentangling the two effects are explored  
244 in greater depth in the case study in the following section.

245 Although the temporal trends in fig. 3 are complex and the effects of  $E(R)$  and  $\text{Var}(R)$   
246 can be hard to disentangle, two simple relationships emerge when  $H$  is shown as a function of  
247 either  $E(R)$  or  $\text{Var}(R)$ , rather than time:  $H$  decreases nonlinearly with  $E(R)$  and increases  
248 with  $\text{Var}(R)$  (panels A and B of fig. 4). The estimated relationships thus follow the hypothesis  
249 we presented in fig. 1, although we found that the effect of  $\text{Var}(R)$  at average  $E(R)$  was linear  
250 with a slight sublinear saturation at high values of  $\text{Var}(R)$ . However, notice that the effect of  
251  $\text{Var}(R)$  on  $E(H)$  depends strongly on  $E(R)$  (panel C): When  $E(R)$  is low,  $E(H)$  is high and  
252  $\text{Var}(R)$  does not have a strong effect, but when  $E(R)$  is high the effect of  $\text{Var}(R)$  on  $E(H)$   
253 is exponential. Similarly,  $E(H)$  decreases exponentially with  $E(R)$  except when  $\text{Var}(R)$  is  
254 very high.

255 As expected by the changes in the spread of the points in panels A and B of fig. 4, the  
256 variance in  $H$ ,  $\text{Var}(H)$ , also depends on  $E(R)$  and  $\text{Var}(R)$  (fig. 4D-F). Since we modeled  
257  $H$  using a Gamma family of distributions, we expected  $\text{Var}(H)$  to increase with  $E(H)$ , but  
258 the location-scale model removes the assumption of a constant mean-variance relationship  
259 (i.e., constant coefficient of variation,  $\frac{\mu(t)}{\sigma^2(t)}$ ). This allowed us to show that the effect of  $R$  on  
260  $\text{Var}(H)$  is much stronger than the effect of  $R$  on  $E(H)$ . Consequences of these effects are  
261 explored in the discussion section.

## 262 A case study on a lowland tapir in the Brazilian Cerrado

263 The simulations in the section above support the hypothesis we presented in the background  
264 section, but they are based on assumptions that are often not met in real natural environ-  
265 ments. Organisms live in spatiotemporally heterogeneous and dynamic environments that  
266 promote the use of perceptual ranges, navigation, and memory. Together, these abilities



**Figure 4:** Effects of  $E(R)$  and  $\text{Var}(R)$  on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of  $\text{Var}(R)$  on  $E(H)$  is sublinear (panel B), the effect of  $\text{Var}(R)$  is superlinear for high values of  $E(R)$  (panel C). The relationships were estimated using a Generalized Additive Model for Location and Scale with a Gamma location-scale family of distributions (`mgcv::gammals`). Credible intervals were calculated using 10,000 samples from the posterior distribution while assuming multivariate Gaussian coefficients. Additional details on the model structure are provided in Appendix B.

267 result in selective space use that depends on resource availability [14] and resource depletion  
268 [15].

269 In this section, we test the hypothesis using empirical tracking data on a lowland tapir  
270 from the Brazilian Cerrado along with empirical estimates of  $E(R)$  and  $\text{Var}(R)$ . We measure  
271  $R$  using Normalized Difference Vegetation Index [NDVI, see 76], a remote-sensed measure  
272 of landscape greenness, as a proxy for forage abundance. Appendix C contains additional  
273 information on how we modeled NDVI and the tapir’s movement using continuous-time  
274 movement models [71,77] and autocorrelated kernel density estimation [78–80].

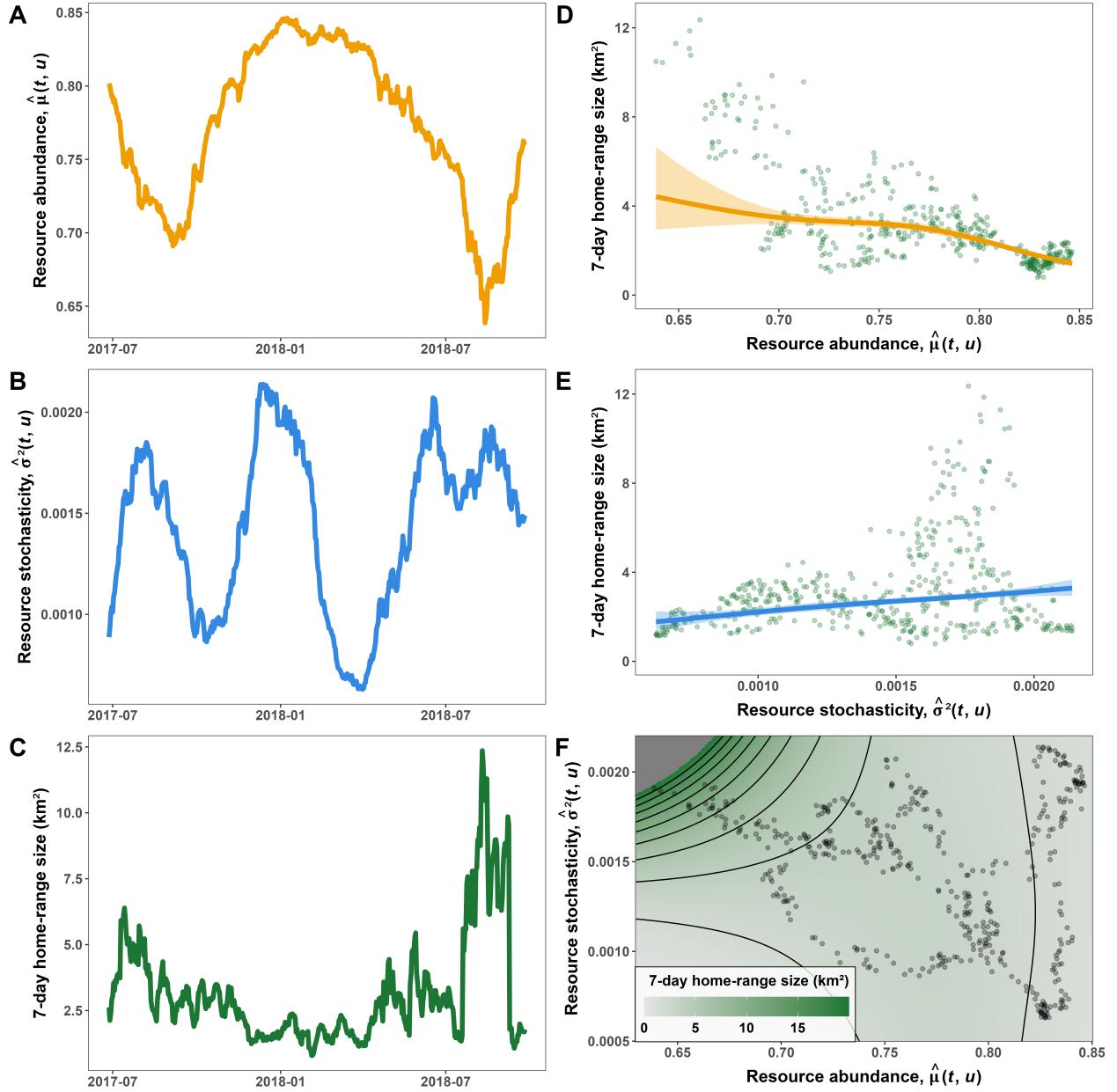
275 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapted its 7-day home-range  
276 size to spatiotemporal changes in estimated  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  (telemetry data from the  
277 individual labelled as “Anna” in the dataset from [29]). Panels A and B show the changes in  
278 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during  
279 the tracking period. The mean and variance in NDVI were estimated using a Generalized  
280 Additive Model for Location and Scale [GAMLS, 81] with a Beta family of distributions  
281 (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in the tapir’s 7-day  
282 home range over time. All 457 of the 7-day windows had a minimum effective sample size  
283 of 7 range crossings [range: 7.7 – 69.6, see 82], and 92% had resolvable (i.e., non-NA) home  
284 range crossing times, all of which were below 17 hours. Note how the tapir uses more space  
285 during periods of lower NDVI (e.g., August 2017) and less space during periods with high  
286 NDVI (January 2018). Additionally, when resources are scarce and highly unpredictable  
287 (August 2018), the tapir uses up to 5 times more space than when resources are abundant  
288 and predictable (e.g., January 2018). Finally, panels D and E show the estimated (marginal)  
289 effects of  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  on the tapir’s 7-day home-range size. Since  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$   
290 are correlated (panel F) and spatiotemporally autocorrelated (panels A, B, and F), the effects  
291 of  $R$  on  $H$  should be modeled carefully. To avoid over-fitting the model, we constrained  
292 the smooth effects of  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  and their interaction effect to a small basis size  
293 ( $k = 3$ ). Additional information is provided in appendix C. The results presented in panels

<sup>294</sup> D-F of fig. 5 match our findings from the simulations (fig. 4A-C): The tapir's 7-day home  
<sup>295</sup> range decreases with  $\hat{\mu}(t, \vec{u})$  and increases with  $\hat{\sigma}^2(t, \vec{u})$ , and the effect of  $\hat{\mu}(t, \vec{u})$  depends on  
<sup>296</sup>  $\hat{\sigma}^2(t, \vec{u})$ , and vice-versa. Alone,  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  cause the tapir to double her home range  
<sup>297</sup> (panels D and E), but together they result in an approximate 15-fold change in home-range  
<sup>298</sup> size (observed range: 0.8 to 12.4 km<sup>2</sup>; see panel F). Additionally, note how high NDVI values  
<sup>299</sup> ( $\hat{\mu}(t, \vec{u}) > 0.8$ ) cause  $\hat{\sigma}^2(t, \vec{u})$  to have little to no effect on home-range size, as indicated by the  
<sup>300</sup> vertical contour line in panel F. Similar conclusions can be drawn for the animal's diffusion  
<sup>301</sup> (i.e., area covered per unit time), which is a more appropriate measure of space use when  
<sup>302</sup> animals are not range resident [82].

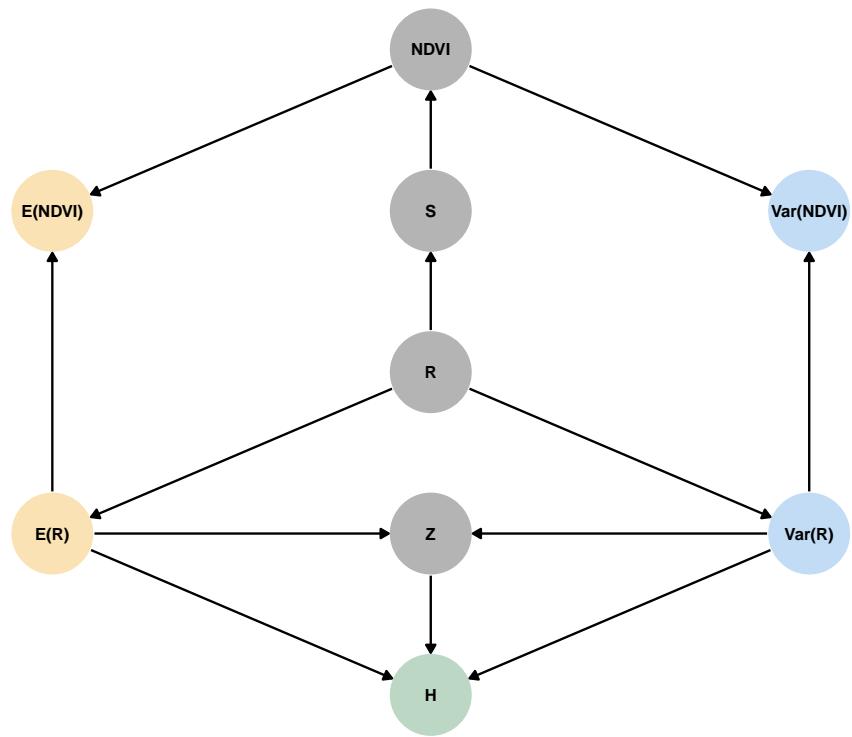
<sup>303</sup> Quantifying the direct effects of  $E(R)$  and  $\text{Var}(R)$  on  $H$  using empirical data is more  
<sup>304</sup> complex than with simulated data, and it requires a different causal framework, particularly  
<sup>305</sup> in the case of observational studies (as opposed to experimentally-controlled studies; see  
<sup>306</sup> fig. 6). Unlike with the simulations,  $E(R)$  and  $\text{Var}(R)$  are not controlled variables and instead  
<sup>307</sup> depend on the distribution of  $R$ , which depends on a variety of other factors (that we exclude  
<sup>308</sup> from the figure for simplicity). Both  $E(R)$  and  $\text{Var}(R)$  then impact  $H$  as well as habitat-level  
<sup>309</sup> variables (e.g., competition, predation, etc.; indicated as  $Z$ ) that also affect  $H$ . Additionally,  
<sup>310</sup> estimating  $R$  via a proxy (NDVI) adds satellite-level noise and confounds [e.g., saturation,  
<sup>311</sup> cloud cover, spatiotemporal averaging – indicated as  $S$ , see 83,84,85]. However,  $E(R)$  and  
<sup>312</sup>  $\text{Var}(R)$  can be correlated to  $E(\text{NDVI})$  and  $\text{Var}(\text{NDVI})$ , respectively, provided that analysts  
<sup>313</sup> use models that are sufficiently smooth and flexible at the relevant spatiotemporal scale [86].  
<sup>314</sup> We discuss this in further detail in the section below on the strengths and limitations of the  
<sup>315</sup> empirical approach.

## <sup>316</sup> Discussion

<sup>317</sup> The amount of space organisms use is determined by a multitude of factors [16], but the  
<sup>318</sup> search for resources is often a main driver of how much and where organisms move. This  
<sup>319</sup> paper builds on earlier theoretical work [13,e.g., 18,19] and presents a unifying hypothesis



**Figure 5:** Effects of estimated  $\mu(t, \bar{u})$  and  $\sigma^2(t, \bar{u})$  on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time,  $\hat{\mu}(t, \bar{u})$ , estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources over time,  $\hat{\sigma}^2(t, \bar{u})$ , estimated as the average variance in NDVI at the locations visited by the tapir during a seven-day period. (C) Seven-day 95% home range estimated using Autocorrelated Kernel Density Estimation. (D, E) Estimated marginal effects of  $\hat{\mu}(t, \bar{u})$  and  $\hat{\sigma}^2(t, \bar{u})$  on home-range size. The model accounted for the marginal effects of  $\hat{\mu}(t, \bar{u})$ ,  $\hat{\sigma}^2(t, \bar{u})$ , and their interaction effect. (F) Estimated home-range size in response to changes in both  $\hat{\mu}(t, \bar{u})$  and  $\hat{\sigma}^2(t, \bar{u})$ . Note how the effect of  $\hat{\sigma}^2(t, \bar{u})$  is more pronounced when  $\hat{\mu}(t, \bar{u})$  is low. See Appendix C for additional information. The tapir movement data corresponds to the individual named “Anna” from the Cerrado sample of Medici *et al.* [29].



**Figure 6:** Directed Acyclical Graph assumed for inferring the causal effects of  $E(R)$  and  $Var(R)$  on  $H$ , where NDVI was used as a proxy for  $R$ .  $Z$  and  $S$  indicate confounds that result from habitat-level variables (e.g., competition, predation, etc.) and satellite-level variables (e.g., noise, cloud cover).

320 that describes the effects of resource abundance and stochasticity on organisms' range sizes.  
321 We use quantitative simulations and an empirical case study to support the hypothesis and  
322 show that it provides a simple framework for understanding how motile organisms adapt  
323 their movement in dynamic environments. Separately, resource abundance and stochasticity  
324 have simple but opposing effects on organisms' range sizes:  $H$  decreases with  $E(R)$  and  
325 increases with  $\text{Var}(R)$ . Together, the degree to which  $E(R)$  affects  $H$  depends on  $\text{Var}(R)$ ,  
326 and vice-versa, so organisms' responses to resource dynamics can be complex. The simulated  
327 and empirical results suggest qualitatively similar marginal effects of  $E(R)$  and  $\text{Var}(R)$ , but  
328 there are differences in the estimated interactive effects. In the simulated data,  $\text{Var}(R)$  has  
329 little effect when  $E(R)$  is low and a strong effect when  $E(R)$  is high, while the opposite  
330 is true for the empirical data. This difference is due to two reasons. Firstly, the shape  
331 and symmetry of bounded distributions such as Gamma ( $R > 0$ ) and Beta ( $0 < R < 1$ )  
332 distributions depend on both  $E(R)$  and  $\text{Var}(R)$  (figs. A3, A4), but  $\text{Var}(R)$  does not affect the  
333 shape of a Gamma distribution as much if  $E(R)$  is low (fig. B3). Secondly, and perhaps more  
334 interestingly, the simulation approach does not account for real-world adaptations to  $E(R)$   
335 and  $\text{Var}(R)$  such as selective space use, which are included (but not explicitly accounted for)  
336 in the empirical approach. Below we discuss the strengths and limitations of each approach.

### 337 **Strengths and limitations of the simulation-based approach**

338 Our simulations are based on a simplistic environment with many assumptions that allowed  
339 us to estimate how resource abundance and stochasticity affect organisms' home-range sizes  
340 if organisms can only respond to changes by adapting the amount of time spent searching for  
341 food (with no energetic cost to movement). The use of continuous-time movement models  
342 coupled with few drivers of movement supported realistic data that could be explained by  
343 straightforward causal models. The absence of confounding variables (e.g., predator avoidance,  
344 territoriality, competition, landscape connectivity; see fig. 2) or sample size limitation  
345 allowed us to ensure estimates were accurate and robust (sensitivity analysis available in

<sup>346</sup> Appendix B).

<sup>347</sup> Deviations from the simulations offer a means of detecting when the underlying assumptions  
<sup>348</sup> are inappropriate and how additional factors may affect organisms' responses to changes  
<sup>349</sup> in  $E(R)$  and  $\text{Var}(R)$ . For example, energetic costs of movement are often non-negligible and  
<sup>350</sup> depend on organism size [40], movement speed [40], and ambient temperature [1,87]. In addition,  
<sup>351</sup> an organism may alter its movement behavior, physiology, and energetic needs to buffer  
<sup>352</sup> itself against changes in  $E(R)$  and  $\text{Var}(R)$  by using space selectively [68,88–90] and adapting  
<sup>353</sup> their behavior and physiology over time [18,69]. Before or during periods of scarcity, organisms  
<sup>354</sup> may cache resources [91], build up fat reserves [45], enter states of dormancy [92–94],  
<sup>355</sup> or even pause fetal growth [7]. However, organisms may be unable to respond to changes  
<sup>356</sup> in  $E(R)$  and  $\text{Var}(R)$  optimally due to various reasons, including limited perceptive range  
<sup>357</sup> [61], lack of experience [9,47,63–65,95], avoidance of competitors and predators [14,96], or a  
<sup>358</sup> physiology that is not amenable to things like hibernation or fat storage. Thus, organisms  
<sup>359</sup> may relocate their range to a sub-optimal location [33,34,97,98], which may exacerbate the  
<sup>360</sup> effects of  $E(R)$  and  $\text{Var}(R)$  on both mean range size and the variance around it.

### <sup>361</sup> Strengths and limitations of the empirical approach

<sup>362</sup> There are two main advantages of taking an empirical approach. Firstly, modeling real-world  
<sup>363</sup> animal movement data can produce scale-appropriate and easily interpretable estimates.  
<sup>364</sup> Secondly, empirical data contain information on the effects of  $E(R)$ ,  $\text{Var}(R)$ , and confounding  
<sup>365</sup> variables without having to design complex and time-consuming simulations. However, it  
<sup>366</sup> is not always possible to quantify confounding variables. For example, while there may be  
<sup>367</sup> some appropriate proxies of competition, such as density of competitors, these variables may  
<sup>368</sup> be hard to quantify, and they may not account for the confounding effects appropriately  
<sup>369</sup> (i.e., the presence of competitors may not reflect competitive pressure). This is problematic  
<sup>370</sup> if one is interested in estimating the direct causal effect of  $E(R)$  and  $\text{Var}(R)$ , which requires  
<sup>371</sup> removing any non-negligible confounding effects [75].

372     Similarly, if  $R$  non-measurable (as is often the case),  $R$  must be estimated with proxies  
373     such as NDVI [76], which may introduce complexities. While  $R$  and NDVI are correlated  
374     for many species [e.g., 45,46,95,99–101], the relationship between the two can be weak [84],  
375     satellite-dependent [85], and nonlinear [83,85]. This complexity can introduce two sources  
376     of bias: ecosystem-level biases (indicated as  $Z$  in the directed acyclical graph in fig. 6)  
377     and satellite-level confounding variables ( $S$  in fig. 6). Examples of ecosystem-level biases  
378     are the effects of competition, predation, habitat connectivity, and movement costs, all of  
379     which can depend on habitat quality, and, consequently, be correlated nonlinearly to  $R$   
380     and NDVI [35,102]. Resource-rich patches can attract larger amounts of competitors [14]  
381     and predators [20], which may, in turn, increase pressures from competition and predation  
382     [15,39]. However, such pressures may result in both an expansion of the range [35,102] or  
383     a contraction, since larger ranges can be harder to defend and result in higher movement  
384     costs [35,103] and encounter rates [104]. Satellite-level confounds include information loss  
385     due to coarse spatiotemporal resolution [83,85], satellite-level error [83,85,105], and other  
386     limitations of remote sensing (e.g., inability to quantify specific resources or small-scale  
387     resource depletion). However, nonlinear models such as Generalized Additive Models [106]  
388     can help account for preferences for intermediate values of remotely-sensed  $R$  [e.g., young  
389     grass rather than mature grasslands, see 85].

## 390     **Conclusions**

391     The work presented here provides a unifying framework for viewing movement as a response  
392     to resource abundance and stochasticity. We provide a sensible and unifying hypothesis  
393     of the effects of  $E(R)$  and  $\text{Var}(R)$  on organisms' range sizes and movement behavior. We  
394     demonstrate that organisms' range sizes decrease with resource abundance, increase with  
395     resource stochasticity, and that the effects of  $\text{Var}(R)$  can depend strongly on  $E(R)$ .

396     Recent advances in computational power have greatly increased analysts' ability to fit  
397     computationally demanding models [107,108] that allow biologists to move beyond only

398 considering changes in mean conditions. By accounting for changes in stochasticity, we can  
 399 start developing a more comprehensive understanding of how organisms adapt to the dynamic  
 400 environments organisms live in, including recent changes in climate [109] and increases in  
 401 the frequency and intensity of extreme events [66,67,110–112].

402 **List of abbreviations**

| <b>Abbreviation</b>     | <b>Definition</b>  |
|-------------------------|--|
| $H$                     | Range size   |
| $\hat{H}_{95\%}$        | Estimated 95% home range size                              |
| $C$                     | Resource consumption rate                                  |
| $R$                     | Resources  |
| $t$                     | Moment in time   |
| $\vec{u}$               | Location in space (vector of coordinates)                  |
| $E(R)$                  | Resource abundance   |
| $\mu(t)$                | Resource abundance as a function of time                   |
| $\mu(t, \vec{u})$       | Resource abundance as a function of time and space         |
| $\text{Var}(R)$         | Resource stochasticity                                     |
| $\sigma^2(t)$           | Resource stochasticity as a function of time               |
| $\sigma^2(t, \vec{u})$  | Resource stochasticity as a function of time and space     |
| $\hat{\varsigma}^2$     | Estimated positional variance                              |
| $\Gamma(\mu, \sigma^2)$ | Gamma distribution with mean $\mu$ and variance $\sigma^2$ |
| NDVI                    | Normalized Difference Vegetation Index                     |
| GAMLS                   | Generalized Additive Model for Location and Scale          |

<sup>404</sup> **Declarations**

<sup>405</sup> **Ethics approval and consent to participate**

<sup>406</sup> Not applicable.

<sup>407</sup> **Consent for publication**

<sup>408</sup> Not applicable.

<sup>409</sup> **Availability of data and materials**

<sup>410</sup> All code and data used for this manuscript is available on GitHub at <https://github.com/QuantitativeEcologyLab/hr-resource-stoch>, with the exception of two simulated datasets  
<sup>411</sup> that were greater than 100 MB and the tapir data. The simulated data can be produced  
<sup>412</sup> by running the scripts in the repository, while the tapir data is available at <https://github.com/StefanoMezzini/tapirs>.  
<sup>413</sup>  
<sup>414</sup>

<sup>415</sup> **Competing interests**

<sup>416</sup> The authors declare that they have no competing interests.

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<sup>422</sup> **Authors' contributions**

<sup>423</sup> SM performed the literature review, designed the simulations, analyzed the data, and wrote  
<sup>424</sup> the manuscript. CHF contributed to the analyses. EPM provided the tapir telemetry data.

<sup>425</sup> MJN conceived the project idea and provided support throughout the analyses. All authors  
<sup>426</sup> contributed to the writing and read and approved the final manuscript.

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