

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

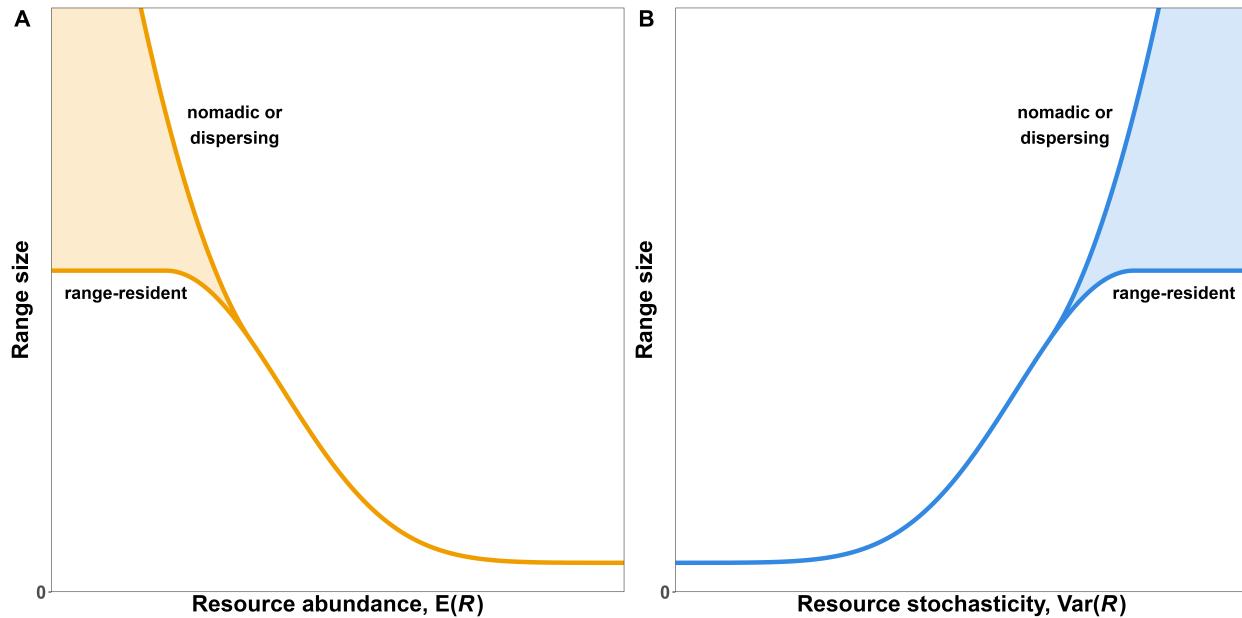
<sup>75</sup> Resources (e.g., food, water, shelter, heat) are often unpredictable (and difficult to quantify),  
<sup>76</sup> since they depend on various factors which cannot be accounted for easily, including climate  
<sup>77</sup> [7,30,31], weather [31,32], competitive pressure [33,34], and differences in energetics at among  
<sup>78</sup> individuals [7] and species [35]. Thus, we can treat the amount of resources  $R$  at a given  
<sup>79</sup> 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 [33,home range size is limited

99 by vagility, habitat structure, competition, and predation, e.g., 34,42,43], migration [44–46],  
 100 and nomadism [23,25,47,48]. It is unclear when organisms switch from range residency to  
 101 migration or nomadism (or vice-versa), but understanding the gradient among these types  
 102 of movement is necessary for quantifying the effect of resource abundance on organisms'  
 103 range size and movement behavior [mammals: 49, moose, *Alces alces*: 23, eagles, *Haliaeetus*  
 104 *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 non-linearly until it reaches the minimum amount of space required by the organism to survive. While our hypotheses imply that small-scale changes in range size can occur over ecological timescales (i.e., within an individual's lifetime), we suggest that large-scale (i.e., population-level and species-level) shifts to range residency and nomadism or frequent dispersal (or vice-versa) are more likely to occur within evolutionary timescales.

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

105 Overall, the hypothesis that range size decreases with resource abundance,  $E(R)$ , is  
 106 commonly accepted and well supported, but many studies assume a linear relationship [e.g.,  
 107 21,41,52–54]. This is problematic because, conceptually, the relationship between range size  
 108 and  $E(R)$  must be nonlinear, since: (1) there is an upper limit to how much space an  
 109 organism is able to explore in its finite lifetime and (2) the minimum amount of space it

110 requires to survive is necessarily greater than zero [see 27,28,55,56,57, and contrast them to  
111 the earlier references that assume a linear relationship between  $H$  and  $R$ ]. Consequently, we  
112 suggest analysts use models that account for this nonlinearity when estimating the effects of  
113 resource abundance on range size. While the relationship may be approximately linear for  
114 some range of  $E(R)$ , this assumption often does not hold for low or high values of  $E(R)$  [e.g.,  
115 52]. Additionally, identifying inflection points in nonlinear relationships can help understand  
116 the pressures and limitations of increasing range size.

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

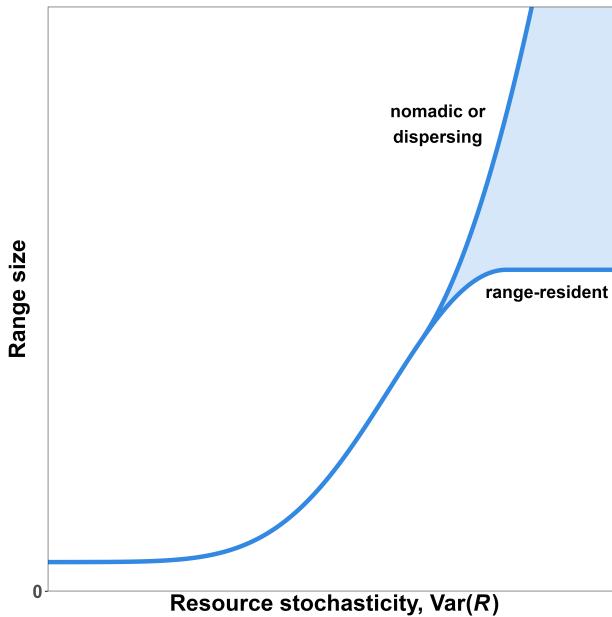
118 Assuming resource stochasticity is constant over time and space can be a useful simplification  
119 of relatively stable environments or when information on how  $E(R)$  changes is limited and  
120 estimating changes in  $\text{Var}(R)$  is unreasonable. However, such an assumption is likely not  
121 realistic, since  $\text{Var}(R)$  often differ across space and over time. Generally, bounded quantities  
122 have correlated means and variances, as in the case of random variables that are strictly pos-  
123 itive (e.g., Gamma and Poisson) or fully bounded (e.g., Beta). For example, prey abundance  
124 in a given area over time may approximately follow a Poisson distribution, which implies  
125 that the mean and variance will be approximately equal. When prey are scarce (e.g., a mean  
126 of 10), the variance will also be low, and when prey are abundant (e.g., a mean of 300)  
127 the variance will also be high. This occurs because the behavior, fitness, and predator-prey  
128 dynamics of ~300 prey are more stochastic than those of 10 prey [58]. Similarly, in the  
129 case of fully bounded random variables, the variance is generally lowest when the mean is  
130 near either boundary. For example, successful predation events are predictably scarce if the  
131 probability of capture is near 0, predictably common if the probability is near 1, and most  
132 stochastic if the probability is near 0.5 [i.e., as far as possible from both 0 and 1; see [59]].  
133 See Appendix A for more information.

134 Recognizing changes in  $\text{Var}(R)$  helps account for the residual, fine-scale variation in  $R$   
135 after accounting for trends in the large-scale average  $R$  [e.g., variations in plant phenology

136 between years after accounting for mean seasonal trends, see 60]. However, when both  
137  $E(R)$  and  $\text{Var}(R)$  change over time (fig. A2), disentangling changes in  $E(R)$  and  $\text{Var}(R)$  is  
138 not simple [61]. Statistically, this confound occurs because the more change one attributes  
139 to  $\mu(t, \vec{u})$  (i.e., the wigglier it is), the smaller  $\sigma^2(t, \vec{u})$  becomes. Conversely, the smoother  
140  $\mu(t, \vec{u})$  is, the larger  $\sigma^2(t, \vec{u})$  becomes. Biologically, it is important because an organism's  
141 perception scale determines whether it attributes a change in  $R$  to a trend in  $E(R)$  or as  
142 a stochastic event [i.e., due to  $\text{Var}(R)$ ; see [60]]. An organism's perception of changes in  
143  $R$  will also depend strongly on its cognitive capacities and memory [9,62–65]. Whether  
144 an organism is able to predict trends in  $\sigma^2(t, \vec{u})$  or not, environmental variability is thought  
145 to reduce a landscape's energetic balance [26], which, in turn, decreases organisms' fitness  
146 [e.g., 10] and increases their range size. While this behavioral response occurs with both  
147 predictable and unpredictable stochasticity, extreme and rare events are more likely to have  
148 a stronger effect due to their unpredictability and magnitude [66,67]. A few recent studies  
149 support these hypotheses [22,26,31,48,68], but many of them are limited in geographic and  
150 taxonomic scales or fail to account for nonlinear relationships, so the extent to which these  
151 preliminary findings can be generalized is currently unknown. Thus, there remains a need  
152 for developing a more complete understanding of how organisms' range sizes changes with  
153 environmental stochasticity.

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

163 develop new and consistent behaviors (e.g., nomadism) or adaptations (e.g., increased fat  
 164 storage or food caching) to buffer themselves against times of unpredictably low  $R$ . Con-  
 165 versely, if changes in  $\sigma^2(t, \vec{u})$  are sufficiently predictable, organisms may learn to anticipate  
 166 and prepare for times of greater stochasticity by pre-emptively caching food, reducing  
 167 energetic needs, migrating, or relying on alternative food sources [e.g., 70].



**Figure 2:** Hypothesized range size of an organism as a function of resource stochasticity,  $\text{Var}(R)$ . We expect low values of  $\text{Var}(R)$  to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As  $\text{Var}(R)$  increases, range size should increase nonlinearly, whether this results in an expansion of the home range (in the case of range-resident organisms) or a switch to a larger range via dispersal, nomadism, or migration. Note that the relationship between  $\text{Var}(R)$  and range size cannot be linear because it would require range size to be negative for low values of  $\text{Var}(R)$ .

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

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

176 Thus, we expect  $\text{Var}(R)$  to have a stronger effect on range size when  $E(R)$  is low, and less of  
177 an effect when  $E(R)$  is high. We explore this interaction effect more in the following section.

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

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

188 Each of the 200 tracks were placed on a grid with common starting point  $\langle 0, 0 \rangle$  (fig. B1).  
189 Each time the simulated individual moved to a new cell, it collected  $R$  resources sampled  
190 from a Gamma distribution. The mean and variance of the distribution were defined by a  
191 series of deterministic functions  $\mu(t)$  and  $\sigma^2(t)$  (orange and blue lines in fig. 3). The value  
192 of  $t$  was constant within each set of 200 tracks, so the distribution  $R$  was sampled from  
193 was independent of both the organism's location and its time spent moving. Tracks were  
194 truncated once the organism reached satiety, and the organism was given enough time to  
195 return to  $\langle 0, 0 \rangle$  independently from the following track (section 2.1 of Appendix B). Finally,  
196 we fit an OUF movement model [74] to the set of tracks to calculate the 95% Gaussian  
197 home-range size using the formula

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

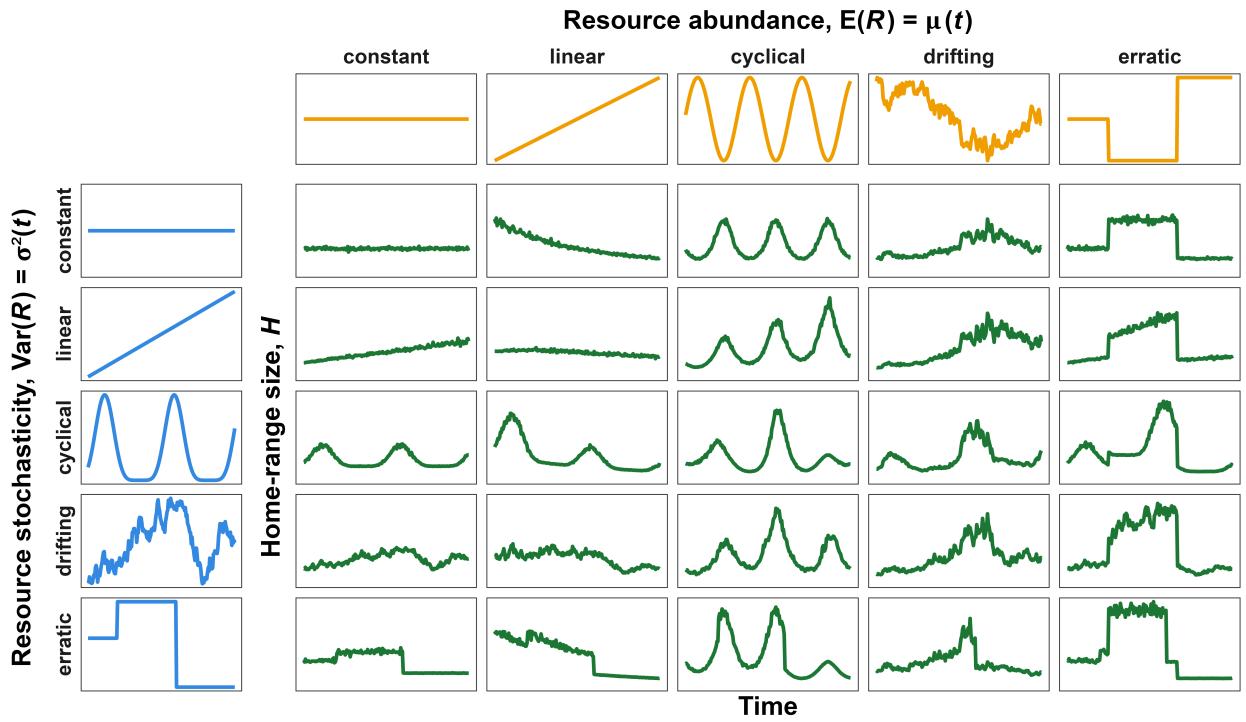
198 where  $\hat{\varsigma}^2$  is the positional variance estimated by the movement model.

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

- 202 1) Environments are homogeneous for a given  $t$ . Given  $t$ ,  $E(R) = \mu(t)$  and  $\text{Var}(R) = \sigma^2(t)$   
203 are constant over space and within each set of 200 tracks, but  $R$  is random and follows  
204 a  $\text{Gamma}(\mu(t), \sigma^2(t))$  distribution.
- 205 2) There are no external pressures on the simulated organism. Resources do not deplete,  
206 and there is no competition nor predator avoidance.
- 207 3) The organism has a fixed daily energetic requirement that is independent of movement  
208 rates, and it cannot alter its metabolism or physiology. Additionally, the organism  
209 does not have energetic reserves, so excess resources cannot be carried over to the next  
210 track or  $t$ .
- 211 4) The organism is range-resident and can only respond to changes in  $E(R)$  and  $\text{Var}(R)$   
212 by altering its home-range size. The organism does not disperse or abandon a range.
- 213 5) The organism's movement is simplistic. The organism's movement speed and direction  
214 are stochastic and independent of  $E(R)$  and  $\text{Var}(R)$ .
- 215 6) The organism has no perceptive range or memory. It is unable to detect, learn, or  
216 predict where resources are abundant (high  $E(R)$ ) or reliable (low  $\text{Var}(R)$ ) over time  
217 or space.
- 218 7) Animals only move to search for food or return to the center of their home-range after  
219 reaching satiety.

220 Additional information is provided in Appendix B, including the directed acyclical graph  
221 [see fig. B6 and 75] we used to infer causal mechanisms of changes in  $H$  and estimate the  
222 direct effects of  $E(R)$  and  $\text{Var}(R)$  on  $H$  (contrast the graph with fig. C3 and the empirical  
223 case study below).

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,



**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.

drift stochastically, or change erratically. The top row (constant  $\text{Var}(R)$ ) shows how  $H$  varies 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  $\mu(t)$ ),  $H$  decreases nonlinearly, with larger changes when  $E(R)$  is low, until it approaches the minimum size required by the organism. Also note how the noise in the green lines also decreases as  $E(R)$  increases.

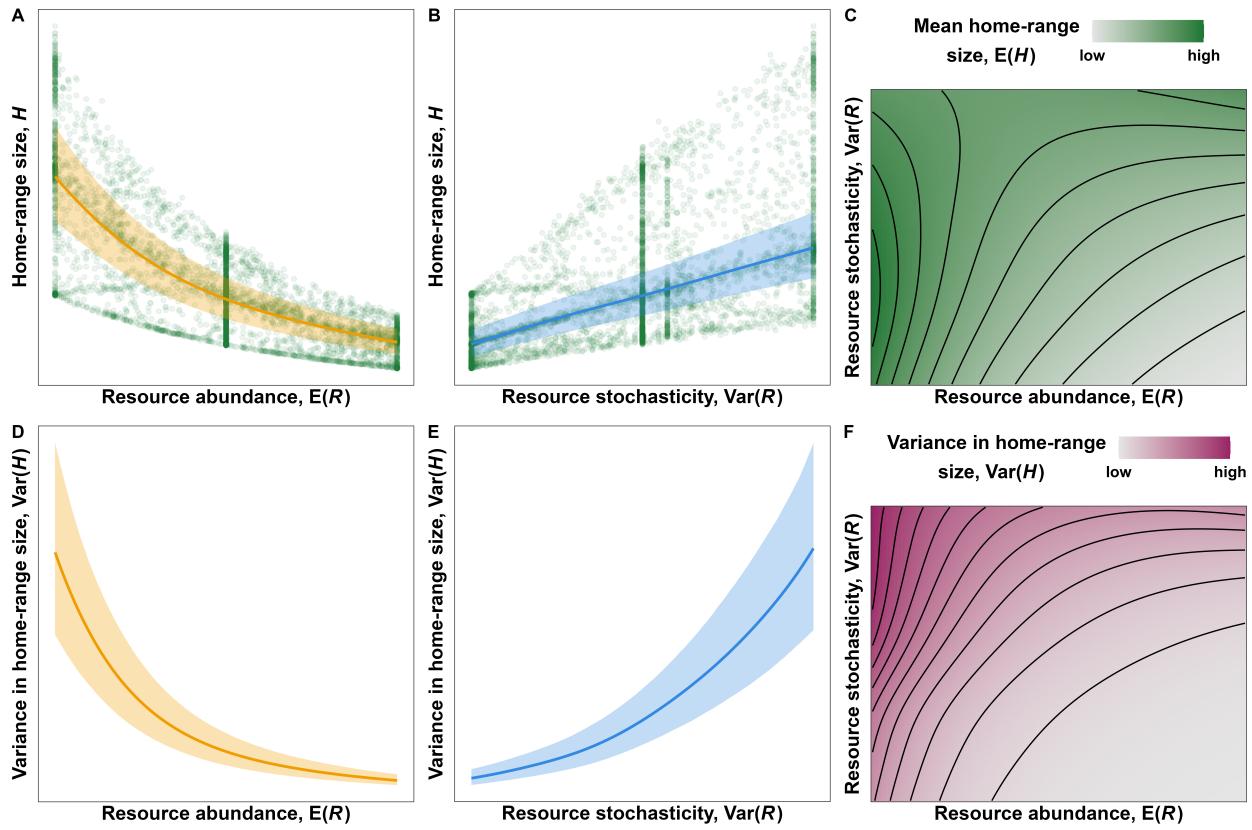
The leftmost column of fig. 3 (constant  $E(R)$ ) illustrates the effects of  $\text{Var}(R)$  on  $H$  while  $E(R)$  remains constant. Overall, both mean  $H$  and the variance around it increase with  $\sigma^2(t)$  (most visible with constant  $E(R)$  and linear  $\text{Var}(R)$ ). Similarly to resource-poor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

The remaining panels in fig. 3 illustrate how  $E(R)$  and  $\text{Var}(R)$  jointly affect  $H$  and how unintuitive the effects can be. Since  $E(R)$  and  $\text{Var}(R)$  have opposite effects on  $H$ , disentangling the effects can be particularly difficult when both parameters change in a correlated manner (e.g., linear  $E(R)$  and  $\text{Var}(R)$ ). When both  $E(R)$  and  $\text{Var}(R)$  increase linearly,  $H$  initially increases since the effect of  $\text{Var}(R)$  is stronger, but then decreases as the effect of  $E(R)$  begins to dominate. Difficulties in disentangling the two effects are explored in greater depth in the case study in the following section.

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 simple relationships emerge when  $H$  is shown as a function of either  $E(R)$  or  $\text{Var}(R)$ , rather than time:  $H$  decreases nonlinearly with  $E(R)$  and increases with  $\text{Var}(R)$  (panels A and B of fig. 4). The estimated relationships thus follow the hypotheses we presented in fig. 1, although we found that the effect of  $\text{Var}(R)$  at average  $E(R)$  was linear with a slight sublinear saturation at high values of  $\text{Var}(R)$ . However, notice that the effect of  $\text{Var}(R)$  on  $E(H)$  depends strongly on  $E(R)$  (panel C): When  $E(R)$  is low,  $E(H)$  is high and  $\text{Var}(R)$  does not have a strong effect, but when  $E(R)$  is high the effect of

253  $\text{Var}(R)$  on  $E(H)$  is exponential. Similarly,  $E(H)$  decreases exponentially with  $E(R)$  except  
 254 when  $\text{Var}(R)$  is 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.



**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.

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

263 The simulations in the section above support the hypotheses we presented in the background  
264 section, but they are based on assumptions that are often not met in real natural environments.  
265 Organisms live in spatiotemporally heterogeneous and dynamic environments that  
266 promote the use of perceptual ranges, navigation, and memory. Together, these abilities  
267 result in selective space use that depends on resource availability [14] and resource depletion  
268 [15].

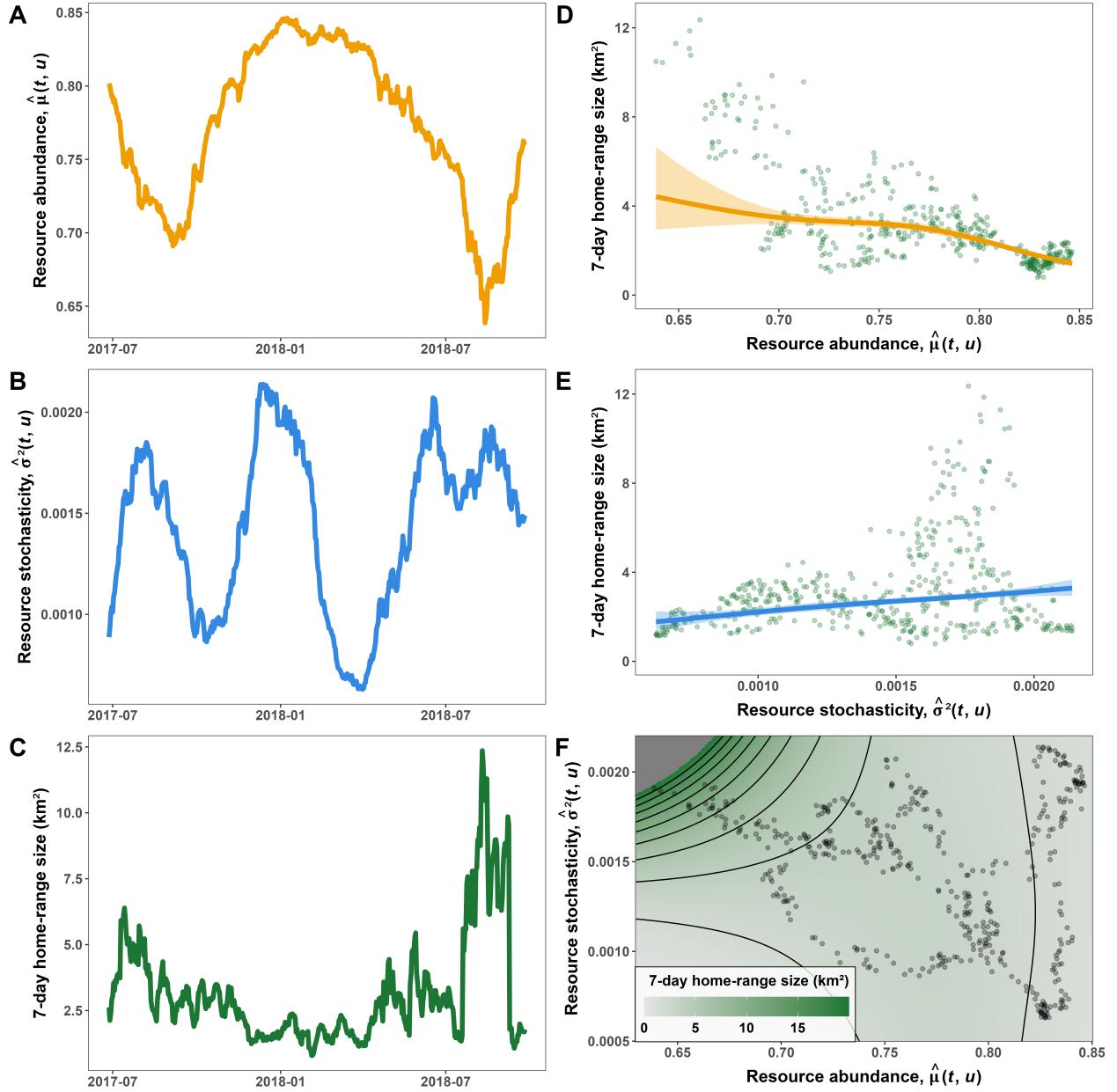
269 In this section, we test the hypotheses using empirical tracking data on a lowland tapir  
270 from the Brazilian Cerrado along with empirical estimates of  $E(R)$  and  $\text{Var}(R)$ . We measure  
271  $R$  using Normalized Difference Vegetation Index [NDVI, see 76], a remote-sensed measure  
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 adapts 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  
282 7-day home range over time. Note how the tapir uses more space during periods of lower  
283 NDVI (e.g., August 2017) and less space during periods with high NDVI (January 2018).  
284 Additionally, when resources are scarce and highly unpredictable (August 2018), the tapir  
285 uses up to 5 times more space than when resources are abundant and predictable (e.g.,  
286 January 2018). Finally, panels D and E show the estimated (marginal) effects of  $\hat{\mu}(t, \vec{u})$  and  
287  $\hat{\sigma}^2(t, \vec{u})$  on the tapir’s 7-day home-range size. Since  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  are correlated (panel

288 F) and spatiotemporally autocorrelated (panels A, B, and F), the effects of  $R$  on  $H$  should  
289 be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects  
290 of  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  and their interaction effect to a small basis size ( $k = 3$ ). Additional  
291 information is provided in appendix C. The results presented in panels D-F of fig. 5 match  
292 our findings from the simulations (Fig. 4A-C): The tapir's 7-day home range decreases  
293 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  $\hat{\sigma}^2(t, \vec{u})$ , and  
294 vice-versa. Alone,  $\hat{\mu}(t, \vec{u})$  and  $\hat{\sigma}^2(t, \vec{u})$  cause the tapir to double her home range (panels  
295 D and E), but together they result in an approximate 15-fold change in home-range size  
296 (observed range: 0.8 to 12.4 km<sup>2</sup>; see panel F). Additionally, note how high NDVI values  
297 ( $\hat{\mu}(t, \vec{u}) > 0.8$ ) cause  $\hat{\sigma}^2(t, \vec{u})$  to have little to no effect on home-range size, as indicated by  
298 the vertical contour line in panel F.

## 299 Discussion

300 The amount of space organisms use is determined by a multitude of factors [16], but the  
301 search for resources is often a main driver of how much and where organisms move. This  
302 paper builds on earlier theoretical work [13,e.g., 18,19] and presents two hypotheses that  
303 describe the effects of resource abundance and stochasticity on organisms' range sizes. We  
304 use quantitative simulations and an empirical case study to support the hypotheses and  
305 show that, together, they provide a simple framework for understanding how motile organ-  
306 isms adapt their movement in dynamic environments. Separately, resource abundance and  
307 stochasticity have simple but opposing effects on organisms' range sizes:  $H$  decreases with  
308  $E(R)$  and increases with  $\text{Var}(R)$ . Together, the degree to which  $E(R)$  affects  $H$  depends on  
309  $\text{Var}(R)$ , and vice-versa, so organisms' responses to resource dynamics can be complex. The  
310 simulated and empirical results suggest qualitatively similar marginal effects of  $E(R)$  and  
311  $\text{Var}(R)$ , but there are differences in the estimated interactive effects. In the simulated data,  
312  $\text{Var}(R)$  has little effect when  $E(R)$  is low and a strong effect when  $E(R)$  is high, while the op-  
313 posite is true for the empirical data. This difference is due to two reasons. Firstly, the shape



**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.* [27].

314 and symmetry of bounded distributions such as Gamma ( $R > 0$ ) and Beta ( $0 < R < 1$ ) dis-  
315 tributions depend on both  $E(R)$  and  $\text{Var}(R)$  (figs. A3, A4), but  $\text{Var}(R)$  does not affect the  
316 shape of a Gamma distribution as much if  $E(R)$  is low (fig. B3). Secondly, and perhaps more  
317 interestingly, the simulation approach does not account for real-world adaptations to  $E(R)$   
318 and  $\text{Var}(R)$  such as selective space use, which are included (but not explicitly accounted for)  
319 in the empirical approach. Below we discuss the strengths and limitations of each approach.

### 320 Strengths and limitations of the simulation-based approach

321 Our simulations are based on a simplistic environment with many assumptions that allowed  
322 us to estimate how resource abundance and stochasticity affect organisms' home-range sizes  
323 if organisms can only respond to changes by adapting the amount of time spent searching for  
324 food (with no energetic cost to movement). The use of continuous-time movement models  
325 coupled with few drivers of movement supported realistic data that could be explained by  
326 straightforward causal models. The absence of confounding variables (e.g., predator avoid-  
327 ance, territoriality, competition, landscape connectivity) or sample size limitation allowed  
328 us to ensure estimates were accurate and robust (sensitivity analysis available in Appendix  
329 B).

330 Deviations from the simulations offer a means of detecting when the underlying assump-  
331 tions are inappropriate and how additional factors may affect organisms' responses to changes  
332 in  $E(R)$  and  $\text{Var}(R)$ . For example, energetic costs of movement are often non-negligible and  
333 depend on organism size [40], movement speed [40], and ambient temperature [1,82]. In addi-  
334 tion, an organism may alter its movement behavior, physiology, and energetic needs to buffer  
335 itself against changes in  $E(R)$  and  $\text{Var}(R)$  by using space selectively [68,83–85] and adapting  
336 their behavior and physiology over time [18,69]. Before or during periods of scarcity, organ-  
337 isms may cache resources [86], build up fat reserves [45], enter states of dormancy [87–89],  
338 or even pause fetal growth [7]. However, organisms may be unable to respond to changes  
339 in  $E(R)$  and  $\text{Var}(R)$  optimally due to various reasons, including limited perceptive range

[61], lack of experience [9,47,63–65,90], avoidance of competitors and predators [14,91], or a physiology that is not amenable to things like hibernation or fat storage. Thus, organisms may relocate their range to a sub-optimal location [33,34,92,93], which may exacerbate the effects of  $E(R)$  and  $\text{Var}(R)$  on both mean range size and the variance around it.

#### **Strengths and limitations of the empirical approach**

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

Similarly, if  $R$  non-measurable (as is often the case),  $R$  must be estimated with proxies such as NDVI [76], which may introduce complexities. While  $R$  and NDVI are correlated for many species [e.g., 45,46,90,94–96], the relationship between the two can be weak [97], satellite-dependent [98], and nonlinear [98,99]. This complexity can introduce two sources of bias: ecosystem-level biases (indicated as  $Z$  in the directed acyclical graph in fig. C3) and satellite-level confounding variables ( $S$  in fig. C3). Examples of ecosystem-level biases are the effects of competition, predation, habitat connectivity, and movement costs, all of which can depend on habitat quality, and, consequently, be correlated nonlinearly to  $R$  and NDVI [35,100]. Resource-rich patches can attract larger amounts of competitors [14] and predators [20], which may, in turn, increase pressures from competition and predation [15,39]. However, such pressures may result in both an expansion of the range [35,100] or

366 a contraction, since larger ranges can be harder to defend and result in higher movement  
367 costs [35,101] and encounter rates [102]. Satellite-level confounds include information loss  
368 due to coarse spatiotemporal resolution [98,99], satellite-level error [98,99,103], and other  
369 limitations of remote sensing (e.g., inability to quantify specific resources or small-scale  
370 resource depletion). However, nonlinear models such as Generalized Additive Models [104]  
371 can help account for preferences for intermediate values of remotely-sensed  $R$  [e.g., young  
372 grass rather than mature grasslands, see 98].

## 373 Conclusions

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

379 Recent advances in computational power have greatly increased analysts' ability to fit  
380 computationally demanding models [105,106] that allow biologists to move beyond only  
381 considering changes in mean conditions. By accounting for changes in stochasticity, we can  
382 start developing a more comprehensive understanding of how organisms adapt to the dynamic  
383 environments organisms live in, including recent changes in climate [107] and increases in  
384 the frequency and intensity of extreme events [66,67,108–110].

<sup>385</sup> **List of abbreviations**

| Abbreviation            | Definition   |
|-------------------------|--|
| $H$                     | 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   |
| <sup>386</sup> $\mu(t)$ | 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     |
| $\hat{\zeta}^2$         | 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>387</sup> **Declarations**

<sup>388</sup> **Ethics approval and consent to participate**

<sup>389</sup> Not applicable.

<sup>390</sup> **Consent for publication**

<sup>391</sup> Not applicable.

392 **Availability of data and materials**

393 All code and data used for this manuscript is available on GitHub at <https://github.com/>  
394 QuantitativeEcologyLab/hr-resource-stoch, with the exception of two simulated datasets  
395 that were greater than 100 MB and the tapir data. The simulated data can be produced  
396 by running the scripts in the repository, while the tapir data is available at <https://github.com/StefanoMezzini/tapirs>.  
397

398 **Competing interests**

399 The authors declare that they have no competing interests.

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405 **Authors' contributions**

406 SM performed the literature review, designed the simulations, analyzed the data, and wrote  
407 the manuscript. CHF contributed to the analyses. EPM provided the tapir telemetry data.  
408 MJN conceived the project idea and provided support throughout the analyses. All authors  
409 contributed to the writing and read and approved the final manuscript.

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