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# Movement-based coexistence does not always require a functional trade-off

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Running title: Movement-based coexistence beyond functional tradeoffs

**Abstract** : The theory for species coexistence in metacommunities largely ignores small-scale, station-keeping movements such as when animals forage inside their home range. At this scale, there are numerous examples of positive correlations across species between traits that the current theory would expect to correlate negatively instead. The current theory indeed emphasizes functional tradeoffs, such as the colonization-competition or dominance-discovery tradeoff. Using simulations, I generated a counter-example to formally demonstrate that these functional tradeoffs are not a necessary condition for species coexistence. First, I reformulated the tradeoffs in the context of animal movement ecology. In a spatial grid representing the potential home range of the study individuals, I modelled the patch depletion and renewal cycles, and the associated movement decisions, using spatial reaction norms incorporated into a spatially-explicit, two-consumer one-resource Lotka-Volterra model. I made these reaction norms species-specific, so that some species allocated more time to exploring for resource while others allocated more time to exploiting known resource. Under this time allocation tradeoff, I generated the desired example in which coexistence happened irrespective of the direction of the covariation between traits. More generally, under the time allocation tradeoff hypothesis, the species-specific space use patterns constituted true functional traits and captured an otherwise neglected aspect of the ecological niche.

**Additional Keywords:** Discovery-dominance tradeoff; Competition-colonization tradeoff; Exploration-exploitation dilemma; Producer-scrounger game; Optimal foraging; Giving-up density; Mixed-species flocks

# 1 Introduction

2 In animals, variation between species in space use can be sufficient to enable the coexistence of  
3 species that exploit the same resource and have the same predators (Hubbell, 2001; Leibold et al.,  
4 2004; Qi et al., 2022; Shoemaker and Melbourne, 2016; Zhang et al., 2022). However, most  
5 researchers analyze this movement-based coexistence mechanisms at the metacommunity level,  
6 where movements correspond to dispersal between distinct population units. Here I am interested in  
7 the role of small-scale, station-keeping movements, such as when animals forage through their home  
8 range. At this scale, the discovery-dominance tradeoff hypothesis (Adler et al., 2007; Parr and Gibb,  
9 2012 and references therein), inspired by the producer-scrounger game theory (Barnard and Sibly,  
10 1981) and the colonization-competition tradeoff theory in metacommunity ecology (Cadotte et al.,  
11 2006; Ferzoco and McCauley, 2022; Leibold et al., 2004), posits that a functional tradeoff must occur  
12 between different aspects of foraging performance in a dynamic field of resource. Typically, a  
13 tradeoff is assumed between the rate at which new resource items are discovered (associated with  
14 movement rates), and the dominance over these items (associated with competitive ability). More  
15 precisely, dominance can correspond to a superior ability to interfere with competitors (Parr and  
16 Gibb, 2012) or a superior rate of resource exploitation (Qi et al., 2022). This concept has been quite  
17 influential in the community ecology literature, leading some authors to consider that the lack of  
18 negative covariation between discovery and dominance constituted evidence that niche-based  
19 coexistence mechanisms prevailed (Adler et al., 2007).

20 Indeed, there is not much evidence that discovery and dominance are negatively correlated among  
21 coexisting species in animal guilds. Instead, a recurrent observation is that, in each guild, some  
22 species performed consistently best at all tasks while other species performed consistently worst. For  
23 example, in meta-analyses of ant communities, the species that found resource items first were the  
24 best, not the worst, at exploiting these items or defending them against competitors (Adler et al.,  
25 2007; Parr and Gibb, 2012). In a guild of avian scavengers, the largest, most dominant species (*Gyps*

26 *fulvus*) arrived first, not last, at carcasses (Cortés-Avizanda et al., 2012). In mixed-species groups of  
27 the two oxpecker birds *Buphagus* sp., the largest, most dominant species left giraffe hosts first, not  
28 last, which implied that the dominant species adopted a “cream-skimming” tactic with frequent  
29 discovery of new hosts (Péron et al., 2019). In ant-following insectivorous passerines of the  
30 Neotropics, large, dominant species were more attractive to potential flock mates than small  
31 subordinate species (Martínez et al., 2018), which suggested that the dominant species were the  
32 ones discovering the most or best resource. In other guilds, dominance and discovery were  
33 uncorrelated; typically one species would move more than others, without appearing significantly  
34 less dominant. For example, amongst the ungulates of Kruger NP (South Africa), wildebeests  
35 (*Connochaetes taurinus*) concentrated within a few grazing “arenas” for prolonged periods, while co-  
36 occurring zebras (*Equus quagga*) used more arenas but exploited them for briefer periods (Owen-  
37 Smith et al., 2015). In Ankarafantsika Ampijoroa NP (Madagascar), the lemur *Avahi occidentalis*  
38 travelled an order or magnitude more than the similarly-sized *Lepilemur edwardsi* (Warren and  
39 Crompton, 1997).

40 In summary, in many animal guilds, the expected negative covariation between discovery and  
41 dominance was at best lacking, and oftentimes actually inversed. With that in mind, my objective  
42 was to demonstrate that the lack of this negative correlation was still compatible with movement-  
43 based coexistence, albeit via another mechanism than the discovery-dominance tradeoff. In other  
44 words, the lack of functional tradeoff does not constitute sufficient evidence to refute movement-  
45 based coexistence and support niche-based coexistence instead. For this demonstration, I generated  
46 a counter-example in silica.

47 I built my model onto the common observation that, in a dynamic field of resource, species and  
48 individuals need to divide their time between the search for resource items and the exploitation of  
49 resource items (e.g., Berger-Tal et al., 2014). At any time, they can choose to leave the current  
50 resource item, even before it is depleted, in order to try and find a better resource item elsewhere

51 (Bedoya-Perez et al., 2013 and references therein). Inversely, when exploring, at any time they can  
52 choose to stop and settle, with limited information as to whether they have found the best location  
53 yet. In the current era of animal movement tracking, several authors have called for better theory  
54 regarding the role of these small movement decisions in species coexistence (Schlägel et al., 2020).  
55 Indeed, individuals and species could, and do, exhibit consistent biases when making these decisions  
56 (Spiegel et al., 2017). Yet, coexistence researchers have so far largely ignored the station-keeping  
57 movements associated with these decisions. For example, Qi et al. (2022) considered movement into  
58 a new resource category as permanent, and Zhang et al. (2022) allowed a single movement per  
59 generation time.

60 I developed a spatially-explicit version of the Lotka-Volterra model for two consumers and one  
61 resource, with spatial reaction norms describing station-keeping movement decisions in the field of  
62 resource. A single parameter controlled the rate of movement and thereby the rate at which  
63 resource patches could be discovered. To generate the desired counter-example that supported the  
64 claim in the paper's title, I started by designing a pair of consumers that were unable to coexist if  
65 their movement rates were identical. There was thus one dominant species and one subordinate  
66 species. Only the dominant species survived if movement was impossible. Then I progressively  
67 increased the difference in movement rates between the species, in both directions: either the  
68 dominant moved more or the dominant moved less than the subordinate. I expected that  
69 coexistence would ensue irrespective of the direction of the difference in movement rates. In  
70 addition, I expected that the coexistence outcome would be increasingly resilient to changes in other  
71 parameters, i.e., the parameter space for coexistence would increase in size, as the difference in  
72 movement rates between species increased. Lastly, the model featured a step selection function,  
73 which I used to investigate the effect of varying the discovery rate for a given movement rate,  
74 thereby deciphering the two mechanisms.

## 75 **Material and methods**

76 **Base model: the two-consumer one-resource Lotka-Volterra system of differential**  
 77 **equations**

78 This classic yet parameter-rich model describes density-dependent population dynamics and links the  
 79 population growth of the consumers to the consumption of resource (MacArthur and Levins, 1967). I  
 80 used the time-discretized version without resource partitioning, to separate the exploitation process  
 81 from the interference process (Eq. 1; Table 1).

Eq. 1	$\left\{ \begin{array}{l} \text{(Species } s) \quad \Delta N_s(t) = \frac{\overbrace{rA(t)N_s(t)}^{\text{growth}}}{h + A(t)} - \overbrace{m_0 N_s(t)}^{\text{DI mortality}} - \overbrace{\sum_{s'=1}^2 m_{s' \rightarrow s} N_s(t) N_{s'}(t)}^{\text{DD mortality}} \\ \text{(Resource)} \quad \Delta A(t) = \underbrace{g_1 A(t)}_{\text{renewal}} - \underbrace{g_2 A(t)}_{\text{loss}} - \underbrace{\sum_{s=1}^2 \frac{1}{\gamma} \cdot \frac{rA(t)N_s(t)}{h + A(t)}}_{\text{consumption}} \end{array} \right.$
-------	---

82  $N_s$  denoted the population abundance of species  $s$  and  $A$  denoted the resource abundance. The  
 83 parameters  $r$ ,  $\gamma$ ,  $h$ , and  $m_0$  roughly represent the trophic niche, i.e., the way species exploit resource  
 84 and die from predation. I assumed these four parameters to be the same in both species. More  
 85 precisely,  $r$  was the population growth rate of the consumers. The yield  $\gamma$  quantified the rate at  
 86 which the consumers transformed the resource into population growth, and in turn the intensity of  
 87 exploitation competition within and between species.  $h$  was the half-saturation coefficient  
 88 corresponding to the value of resource density which gave half the maximum per capita growth rate,  
 89 following the formula of Holling's (1959) type II functional response. The density-independent (DI)  
 90 mortality rate  $m_0$  represented the baseline mortality without competition. Lastly, in addition to the  
 91 resource that got consumed, a proportion  $g_2$  of the resource was lost to decay at each interval. On  
 92 the other hand, the resource renewed at rate  $g_1$ .

93 To introduce species-specificity in dominance, I used the density-dependent (DD) mortality  
 94 component. This component simulated the ability for individuals to restrict the demographic  
 95 performance of their competitors by means other than the consumption of resource, i.e.,  
 96 interference competition. Both conspecifics (parameters  $m_{1 \rightarrow 1}$ , and  $m_{2 \rightarrow 2}$ ) and heterospecifics

97 ( $m_{1\rightarrow 2}$  and  $m_{2\rightarrow 1}$ ) could interfere. To make species 1 dominant over species 2 as explained above, I  
98 imposed that  $m_{1\rightarrow 2} > m_{2\rightarrow 2}$ .

### 99 **Different timescales for movement and reproduction**

100 I divided the annual breeding cycle into intervals, so that the movements corresponded to foraging  
101 decisions instead of dispersal decisions. Precisely, I implemented 10 intervals (which in terms of  
102 computing time amounted to about 1 month). Movement and mortality occurred at the interval level  
103 whereas breeding occurred at the annual level. I introduced a latent individual attribute, the energy  
104 level, to make the link between the performance at the interval scale and at the annual scale. The  
105 energy level could represent, e.g., the fat store of geese (Drent and Daan, 1980). At each interval, I  
106 applied a binomial survival model whose success rate depended on the individual energy level. At the  
107 end of each year, I drew the number of offspring from a Poisson distribution whose mean depended  
108 on the current energy level of the individual.

109 The offspring began with energy level  $e_0$ . Individuals accrued energy over each interval as a function  
110 of the resource density at their current location. As such, in Eq. 1, I replaced the population  
111 abundance  $N_s$  by the population energy level  $E_s$ , which was the sum of the individual energy levels  
112 (Eq. 2 in the next section), and I distributed the energy gains or losses evenly across the individuals in  
113 each grid cell (Eq. 4). Finally, breeding incurred a cost that I deducted from the energy level of the  
114 parent (Table 1).

### 115 **Spatially-explicit version of the Lotka-Volterra model**

116 The spatialized version of Eq. 1 (still without movement at this stage) is Eq. 2, where the indexes  $(i,j)$   
117 denote the grid cell coordinates and where I replaced the population abundances  $N$  with the energy  
118 levels  $E$  as explained above. Also, in the resource renewal term, I used  $A(0)$  instead of  $A(t)$ , so that  
119 the resource renewal term represented the local abiotic constraints on primary productivity. This  
120 way, some locations would always renew faster than others.

Eq. 2	$\left\{ \begin{array}{l} \text{(Species } s) \quad \Delta E_{i,j}^{(s)}(t) = \frac{\overbrace{rA_{i,j}(t)E_{i,j}^{(s)}(t)}^{\text{growth}}}{h + A_{i,j}(t)} - \overbrace{m_0 E_{i,j}^{(s)}(t)}^{\text{DI mortality}} - \overbrace{\sum_{s'=1}^2 m_{s' \rightarrow s} E_{i,j}^{(s)}(t) E_{i,j}^{(s')}(t)}^{\text{DD mortality}} \\ \text{(Resource)} \quad \Delta A_{i,j}(t) = \frac{\overbrace{g_1 A_{i,j}(0)}^{\text{renewal}}}{\text{renewal}} - \frac{\overbrace{g_2 A_{i,j}(t)}^{\text{loss}}}{\text{loss}} - \underbrace{\sum_{s=1}^2 \frac{1}{\gamma} \cdot \frac{rA_{i,j}(t)E_{i,j}^{(s)}(t)}{h + A_{i,j}(t)}}_{\text{consumption}} \end{array} \right.$
-------	--

121 Next, I made the individuals move.  $(i_k(t), j_k(t))$  denoted the current location of individual  $k$  in the  
 122 grid cell at time  $t$ . I drew the movement status  $\delta_k(t)$  from a Bernoulli trial of which the success rate  
 123 depended on the difference between the resource abundance at the current location,  $A_{i_k(t), j_k(t)}(t)$ ,  
 124 and the species-specific threshold of resource abundance that triggered movement,  $A_{s_k}^*$  (Eq.3; Table  
 125 1) where  $s_k$  denoted the species of individual  $k$ .

Eq. 3	$\delta_k(t) \sim \text{Bernoulli} \left( 1 - \text{logit}^{-1} \left( \frac{A_{i_k(t), j_k(t)}(t) - A_{s_k}^*}{\sigma} \right) \right)$
-------	--

126 The parameter  $A_{s_k}^*$  is sometimes referred to as the “giving-up density of resource” (Bedoya-Perez et  
 127 al., 2013, and references therein). It is in some way akin to the amount of resource that the focal  
 128 species would leave unused in a monospecific population (Qi et al., 2022; Tilman, 1982), hence the  
 129 choice of a similar notation. If individual  $k$  moved, it lost a species-specific amount of energy, the cost  
 130 of movement, denoted  $c_{s_k}$  (Eq. 4).

Eq. 4	$e_k(t + \Delta t) = e_k(t) + \frac{\Delta E_{i_k(t), j_k(t)}^{s_k}(t)}{N_{i_k(t), j_k(t)}^{s_k}(t)} - \delta_k(t) \cdot c_{s_k}$
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131 Like in Eq. 3,  $(i_k(t), j_k(t))$  was the location of individual  $k$  at time  $t$ .

132 When an individual moved, it then had to choose its next location. I computed the movement kernel  
 133  $\mathcal{K}$  describing the probability to go to new location  $(u, v)$  when the current location was  $(i, j)$ .  $\mathcal{K}$  was  
 134 comprised of a diffusion term and a step selection term (Eq. 5). The diffusion term corresponded to  
 135 Brownian motion and represented on the one hand the temporal autocorrelation in the movement  
 136 track and on the other hand the tendency to ignore the information about resource distribution. The  
 137 step selection term on the contrary represented the tendency to preferentially move into the best



138 resource patch. The step selection efficiency parameter  $b$  controlled the relative importance of step  
 139 selection relative to diffusion (Duffy, 2011; Zhang et al., 2022). If  $b = 0$  then there was no step  
 140 selection at all. The larger  $b$  was, the more the movement was dominated by step selection as  
 141 opposed to diffusion. The scaling parameter  $\beta$  prevented a zero denominator (Table 1).

Eq. 5	$\mathcal{K}(u, v i, j) = \frac{\kappa(u, v i, j)}{\int_{u,v} \kappa(u, v i, j) du dv} \text{ with } \kappa(u, v i, j) = \exp \left[ \frac{\overbrace{(x_u - x_i)^2 + (y_v - y_j)^2}^{\text{Diffusion}}}{D} + b \cdot \frac{\overbrace{A_{u,v} - A_{i,j}}^{\text{Step selection}}}{A_{i,j} + \beta} \right]$
-------	--

142 The time dependency is omitted in Eq. 5 for the sake of clarity.

143 Finally, I updated the energy level at the previous and current locations:  $E_{i_k(t+\Delta t), j_k(t+\Delta t)}^{(s_k)}(t + \Delta t) =$   
 144  $E_{i_k(t+\Delta t), j_k(t+\Delta t)}^{(s_k)}(t) + e_k(t + \Delta t)$  and  $E_{i_k(t), j_k(t)}^{(s_k)}(t + \Delta t) = E_{i_k(t), j_k(t)}^{(s_k)}(t) - e_k(t + \Delta t)$ .

145 The R code to run that model is provided in Appendix S1.

## 146 Parameterization

147 My objective was to generate a counter-example that supported the claim that a tradeoff between  
 148 dominance and discovery was not a necessary condition for movement-based coexistence. For this  
 149 purpose, I selected the following parameter values. The grid always contained 400 resource patches,  
 150 each year contained 10 intervals (out of convenience with respect to the computing time). The initial  
 151 field of resource  $A(0)$  varied over space between 0 and 30 arbitrary units of energy with a Moran  
 152 index of spatial autocorrelation of 0.5 on average. 100 individuals of each species were released at  
 153 random locations (uniform) at time  $t=0$ . The relationship between individual fitness and individual  
 154 energy level followed the curve  $S(e) = \text{Min}(0.95, \text{logit}^{-1}(-2 + 0.5 \cdot e))$  for the survival  
 155 probability and  $F(e) = \text{Max}(0, -2 \cdot (1 - \exp(-2 \cdot e)))$  for fecundity. The annual survival  
 156 probability thus varied between 0 and 0.6 and the annual fecundity rate varied between 0 and 2.5  
 157 offspring per year, which corresponded to recorded values in passerines for example. I then  
 158 temporarily set the density-dependence coefficients to be equal:  $m_0 = m_{1 \rightarrow 1} = m_{2 \rightarrow 2} = m_{1 \rightarrow 2} =$

159  $m_{2 \rightarrow 1} = 0.025$ , and I temporarily imposed different movement rates:  $A_1^* = 5$ , and  $A_2^* = 15$ . I then  
160 fine-tuned the other parameters so that the resource depletion/renewal cycles lasted 5 time  
161 intervals or more and the species coexisted for at least 50 years, yielding the values in Table 1. Then,  
162 for the final scenario onto which the simulation was built, I made the interactions coefficients to  
163 differ:  $m_{1 \rightarrow 2} = 0.075$  and  $m_{2 \rightarrow 1} = 0.025$  and I set the movement thresholds to be equal:  $A_1^* = A_2^* =$   
164 10. With this parameterization, species 1 excluded species 2. Species 1 is hereafter referred to as  
165 dominant and species 2 as subordinate.

### 166 **Increasing the difference between the species-specific movement thresholds $A_1^*$ and $A_2^*$**

167 To induce coexistence, departing from  $A_1^* = A_2^* = 10$ , I progressively increased the difference  
168 between  $A_1^*$  and  $A_2^*$ , in both directions. The cases where  $A_1^* < A_2^*$  mimicked a discovery-dominance  
169 tradeoff, whereas the cases where  $A_1^* > A_2^*$  corresponded to a positive correlation between  
170 discovery and dominance that contradicted the discovery-dominance tradeoff hypothesis and was  
171 instead compatible with the time allocation tradeoff hypothesis. I recorded the change in  
172 coexistence outcome after 50 years. Based on the time allocation tradeoff hypothesis, I predicted  
173 that coexistence would occur both when  $A_1^* > A_2^*$  and  $A_1^* < A_2^*$ .

174 As a sensitivity analysis, I computed the range of values of the step selection efficiency parameter  $b$ ,  
175 the cost of movement  $c$ , and the yield  $\gamma$  that enabled coexistence. In particular, tuning the parameter  
176  $b$  made it possible to change the rate at which resource was discovered for a given movement rate,  
177 and thereby decipher the effect of discovery *per se* from the effect of the giving-up density.  $c$  and  $\gamma$   
178 represented the environment, such as the habitat fragmentation and the resource quality, thereby  
179 making it possible to investigate the resilience of the coexistence outcome to environmental change.  
180 I ran the simulation 10 times for each of 3,024 combinations of  $A_1^*$ ,  $A_2^*$ ,  $b$ ,  $c$ , and  $\gamma$ . I predicted that as  
181 the difference between  $A_1^*$  and  $A_2^*$  increased, the species would coexist over an increasingly large  
182 range of combinations of  $b$ ,  $c$ , and  $\gamma$ , irrespective of whether  $A_1^* > A_2^*$  or  $A_1^* < A_2^*$ .

## 183 **Results**

184 Irrespective of whether  $A_1^* > A_2^*$  or  $A_1^* < A_2^*$ , there always existed a range of combinations of  $b$ ,  $c$ ,  
185 and  $\gamma$  that made coexistence possible (Figs. 1&2). By contrast, if  $A_1^* = A_2^*$  the scenario was designed  
186 to prevent coexistence. In other words, in the study system, coexistence between otherwise  
187 incompatible species was made possible by the difference in movement rates between species,  
188 irrespective of the direction of that difference.

189 However, the parameter space for coexistence (combinations of  $b$ ,  $c$ , and  $\gamma$  that enabled coexistence)  
190 was on average 29% larger when  $A_1^* < A_2^*$  (discovery-dominance tradeoff) than  $A_1^* > A_2^*$  (time  
191 allocation tradeoff) (Fig. 1 vs. 2, Table S1: ANOVA P-value  $< 0.001$ ). The coexistence outcome was thus  
192 overall more resilient under the discovery-dominance tradeoff than time allocation tradeoff.

193 In addition to the parameter space for coexistence, the specific values of parameters that enabled  
194 coexistence also depended on the direction of the covariation. When  $A_1^* > A_2^*$ , coexistence required  
195 a more challenging environment than when  $A_1^* < A_2^*$ : either a lower  $b$  (harder to find resource),  
196 higher  $c$  (costlier movement) or lower  $\gamma$  (less energy per unit of resource) (Fig. 1 vs 2). These results  
197 indicated that the time allocation tradeoff was a less robust coexistence mechanism than the  
198 discovery-dominance tradeoff – which does not mean that it is less likely to operate in real life  
199 situations (cf. discussion).

200 Increasing the parameter  $b$  and thereby increasing the discovery rate for a given movement rate  
201 helped the most mobile species (the one with highest movement threshold), irrespective of whether  
202 the most mobile species was the dominant ( $A_1^* > A_2^*$ ) or the subordinate species ( $A_1^* < A_2^*$ ) (Fig. 1 vs  
203 2: x-axis of each panel). This result confirmed that coexistence was not dependent on a tradeoff  
204 between discovery and dominance.

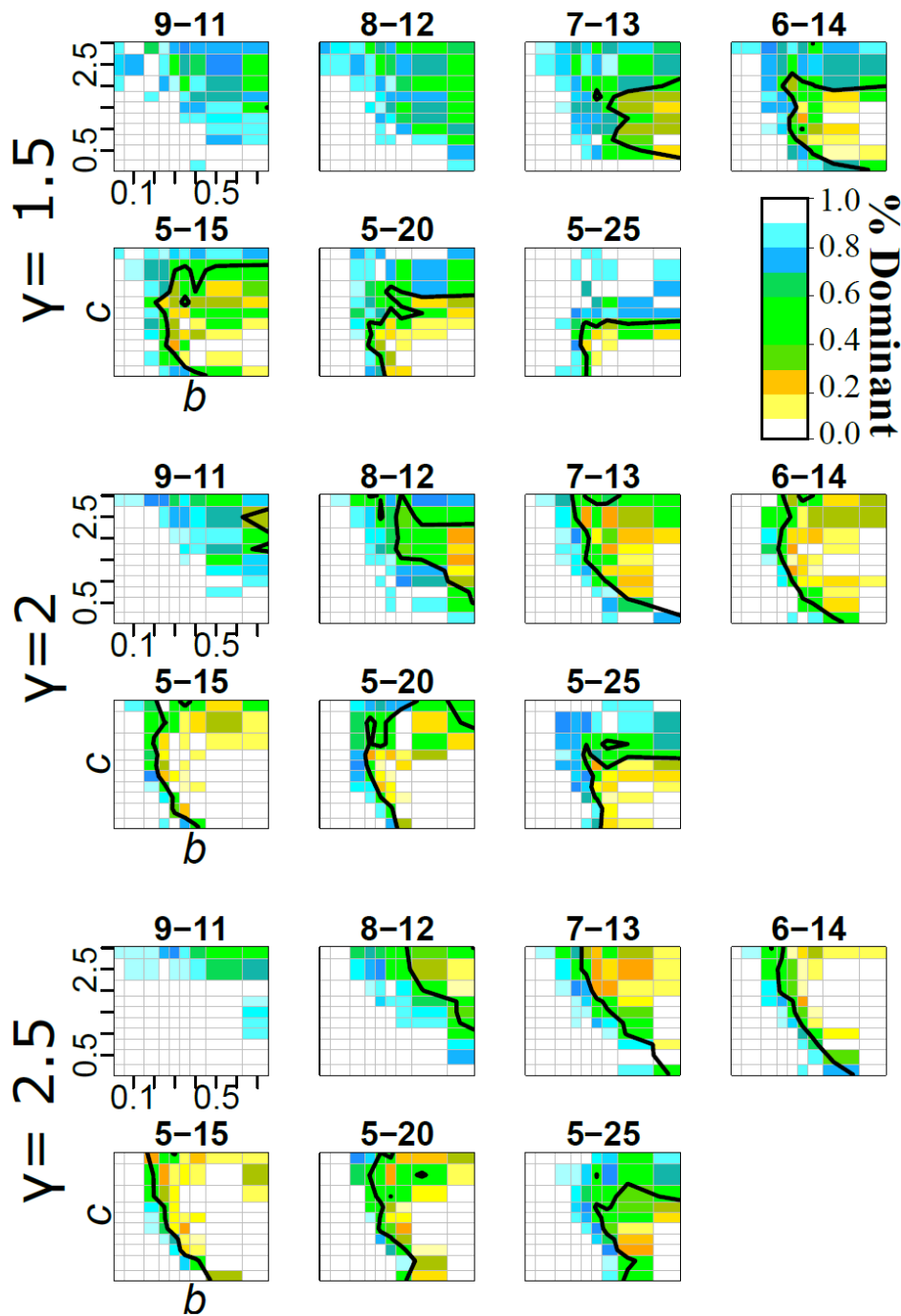
205 Lastly, as the difference in movement threshold increased, the range of conditions that enabled  
206 coexistence increased (Fig. 1&2; ANOVA in Table S1), irrespective of whether  $A_1^* < A_2^*$  or  $A_1^* > A_2^*$ .  
207 The only exception was when  $A_1^* < A_2^*$  and  $\gamma=1.5$  (ANOVA in Table S1). Indeed, for  $\gamma = 1.5$ , the range  
208 of  $b$  and  $c$  values that enabled coexistence actually decreased for the largest difference (Fig. 1: “5-25”

209 and “25-5”), in a way that suggested an upper limit to the value of the movement thresholds  $A_1^*$  and  
210  $A_2^*$ . This upper limit is expectedly controlled by the resource parameters  $g_1$  and  $g_2$ .

211

212

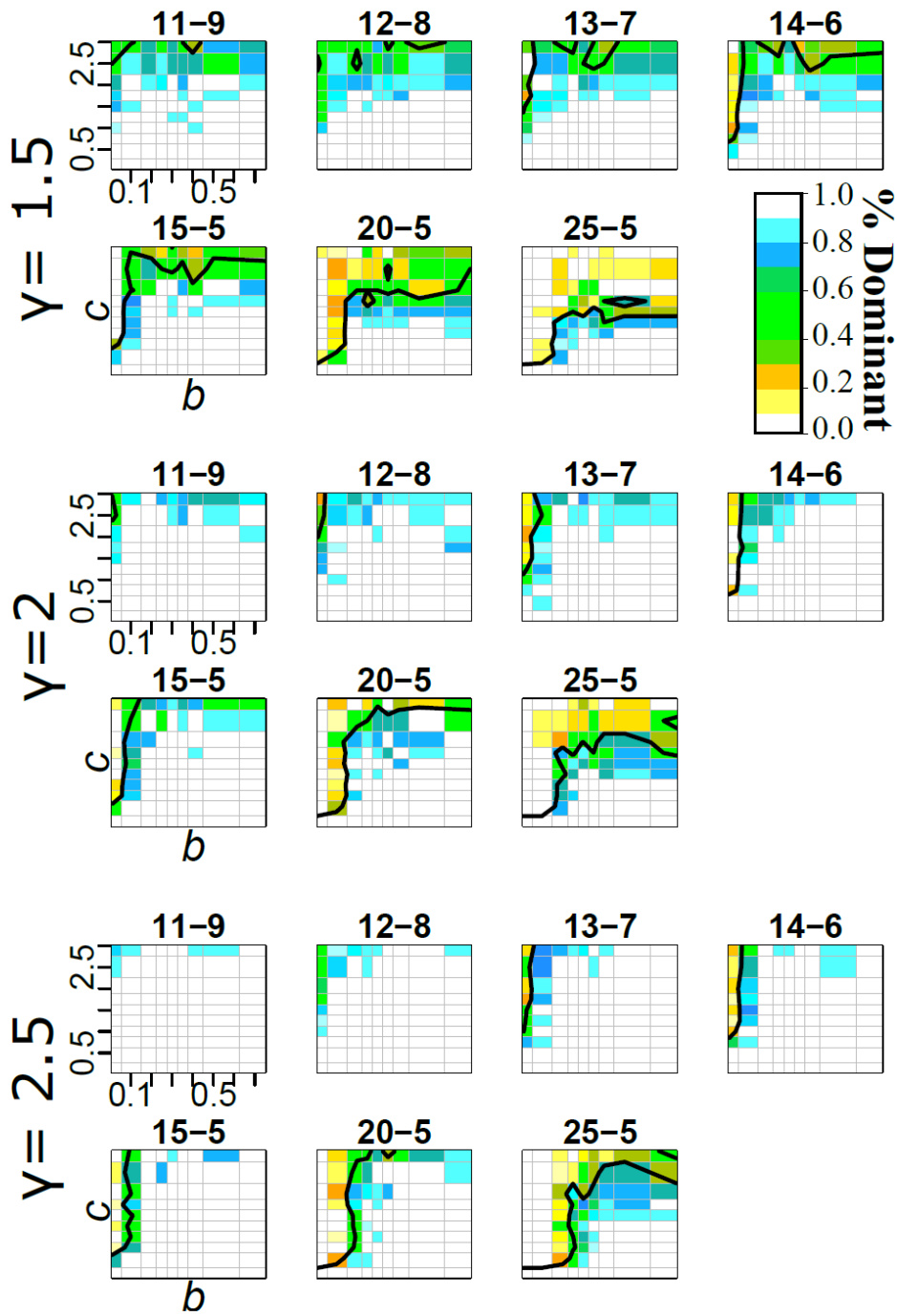
213 Fig. 1: Coexistence outcome when the movement threshold of the dominant species  $A_1^*$  was lower  
 214 than the threshold of the subordinate species  $A_2^*$ . This situation mimicked the occurrence of a  
 215 tradeoff between discovery and dominance, as per the current coexistence theory. In each panel, the  
 216 x-axis corresponds to the efficiency of step selection  $b$ , the y-axis corresponds to the cost of  
 217 movement  $c$ , and the header gives the values of  $A_1^*$  and  $A_2^*$ .  $\gamma$  was the yield (Eq. 1; Table 1). The color  
 218 scale represents the average over 10 simulations of the coexistence outcome after 50 years: white:  
 219 at least one species went extinct; blue: the dominant species was more numerous than the  
 220 subordinate; yellow: the subordinate species was more numerous. The black lines separate the  
 221 parameter space dominated by each species.



222

223

224 Fig. 2: Coexistence outcome when the movement threshold of the dominant species  $A_1^*$  was higher  
 225 than the threshold of the subordinate species  $A_2^*$ . This situation was incompatible with a tradeoff  
 226 between discovery and dominance and instead mimicked a time allocation tradeoff, between the  
 227 time spent exploiting resource and the time spent looking for resource. Legend as in Fig. 1.



228

229

## 230 Discussion

231 Using a counter-example that I generated with a modified Lotka-Volterra model, I demonstrated that  
232 movement-based coexistence does not require that dominance and discovery are negatively  
233 correlated between species, as assumed by the dominance-discovery tradeoff hypothesis. Some  
234 authors, after observing the lack of negative covariation ( $A_1^* > A_2^*$  in the notation of the present  
235 study), concluded that some cryptic trophic differences existed instead, e.g., microhabitat  
236 specialization. Based on my results, the lack of negative covariation is however not sufficient to  
237 conclude that niche-based coexistence mechanisms prevail.

238 In my model, coexistence could effectively proceed from a time allocation tradeoff between the time  
239 spent looking for resource and the time spent exploiting the resource. This time allocation tradeoff  
240 has previously been referred to as the “exploration-exploitation dilemma” (Berger-Tal et al., 2014,  
241 and references therein). Its importance for species coexistence has to my knowledge largely been  
242 ignored so far. Based on my results, species could theoretically specialize on either exploration or  
243 exploitation. Such specialization would not compulsorily need much morphological adaptation, and  
244 could mostly involve decisions and behavioral syndromes. However, my model does not make any  
245 assumption regarding the cause of species-specificity in movement rates and foraging behavior. The  
246 model is compatible with the occurrence of morphological differences that allow some species to  
247 overcome the physical limitations of others, e.g., the depth at which individuals can dig, or their  
248 dexterity.

249 To make a link with a recurrent topic in the recent movement ecology literature, one could verbally  
250 reframe the model in the present study in terms of memory effects (Gautestad, 2011; Ranc et al.,  
251 2021). In my model, the species with the highest movement threshold indeed tended to revisit  
252 known locations within the current grid cell, and could therefore be labelled as memory-reliant. The  
253 species with the lowest movement threshold could on the other hand easily be labelled as  
254 exploration-prone. However, the memory framework strongly implies a role for cognitive

255 development and cognitive performance (Gopnik, 2020), which my model does not require.

256 Nevertheless, my results confirm that spatial memory can promote coexistence with competitors  
257 that lack spatial memory.

258 I made no claim regarding whether the time allocation tradeoff plays a large or small role in nature,  
259 compared to the previously-described niche-based mechanisms and to the dominance-discovery  
260 tradeoff. Indeed, in the sensitivity analysis to variation in  $b$ ,  $c$ , and  $\gamma$ , the conditions for coexistence  
261 were more restrictive under the time allocation tradeoff than under the discovery-dominance  
262 tradeoff. This could be interpreted as evidence that the time allocation tradeoff is less likely to occur  
263 than the discovery-dominance tradeoff. However, this is not my interpretation. Actually, even if  
264 coexistence is harder to achieve and maintain under the time allocation tradeoff than the discovery-  
265 dominance tradeoff, the conditions for the time allocation tradeoff might still be more frequently  
266 met than the conditions for the discovery-dominance tradeoff. As a matter of fact, the numerous  
267 examples listed in the introduction suggested that the conditions for the discovery-dominance  
268 tradeoff are rarely met in real-life animal guilds. By contrast, the time allocation tradeoff does not  
269 need any morphological or physiological differences between species, and can operate based on  
270 decisions alone, which makes for relatively easy to meet conditions.

271 The full exploration of the parameter space was beyond the scope of the present study, and would  
272 represent a challenge with such a parameter-rich model. I acknowledge that the number of  
273 parameters represented a major drawback of my modeling framework. However, I had two reasons  
274 to work with that many parameters. First, the two-species one-resource Lotka-Volterra structure (Eq.  
275 1) made it possible to fully separate niche exploitation (population growth  $r$ , half-saturation  
276 coefficient  $h$ , yield  $\gamma$ , and density-independent mortality  $m_0$ ) from dominance (density-dependent  
277 mortality parameters  $m_{S \rightarrow S'}$ ). Second, I needed the individual-based stochastic component to  
278 reproduce the spatial reaction norms that are routinely observed in movement ecology studies, i.e.,  
279 the giving-up density of resource and the step selection function. These key components allowed me



280 to transform the Lotka-Volterra equation into a model of station-keeping movements and their  
281 demographic implications. Another potential benefit of using a complex model was that, in the  
282 future, the same modeling framework could be extended with components representing other  
283 coexistence mechanisms, to explore their relative contributions. For example,  $r$  or  $\gamma$  could be used to  
284 introduce some species-specificity in exploitation competition, in order to reproduce the mechanism  
285 that e.g., Qi et al. (2022) focused on. Temporal and spatial fluctuations in abiotic factors such as  
286 droughts (Duffy, 2011) could be incorporated via  $A(t)$ ,  $g_1$  or  $g_2$ . Species-specificity in predation rate  
287 (Weterings et al., 2019) could be represented via the  $m$ -parameters and their spatial variation. A  
288 second field of resource could be incorporated to represent the availability of suboptimal resource  
289 and the partition of resource space.

#### 290 **Differences in movement rates without trophic differences**

291 The working hypothesis in this study is that species that have the exact same trophic relationships  
292 exhibit different movement ecologies. This hypothesis might not be completely intuitive to some  
293 readers, because species that have the same trophic relationships would expectedly respond to the  
294 same constraints emerging from the same distributions of resource and risks. In addition, the stakes  
295 involved in small movement decisions are small, and at the same time these decisions proceed from  
296 the instant processing of numerous, potentially contradictory stimuli, combined with long-term goals  
297 and individual strategies. The resulting movement patterns are therefore sometimes quite  
298 idiosyncratic, which could hinder the ability to develop distinctive, species-specific time allocation  
299 tactics. That said, empirically, coexisting species have been observed to exhibit species-specific  
300 signatures in their movement tracks. The most obvious of these signatures are the home range size  
301 and average speed, which for example depend on the species-specific body mass (Brown and West,  
302 2000). Coexisting species may also vary in more subtle statistics like the average residence time,  
303 revisitation frequency, periodic patterns of space use, and the response to perturbations and  
304 resource depletion (Linder et al., 2022; Owen-Smith et al., 2015; Péron et al., 2018). Early movement  
305 ecologists had also identified that night- and day-active species could coexist without either

306 partitioning the resource or relying on a discovery-dominance tradeoff, which they termed “temporal  
307 partitioning” (Kotler et al., 1993; Kronfeld-Schor and Dayan, 2003). In addition, single loci have been  
308 uncovered that control consistent individual variation in movement rates within some invertebrate  
309 species (Zhang et al., 2022; Zheng et al., 2009), and within at least one vertebrate species (Ophir et  
310 al., 2008). This genetic control of movement rates could conceivably operate across species as well.  
311 Variation in morphology between species can also influence and respond to variation in movement  
312 rates. For example, the cost of movement increases with the wing loading in birds and bats (Alerstam  
313 et al., 2003; Hedenström and Johansson, 2015), suggesting different rate of fidelity to foraging sites  
314 (Franklin et al., 2017). Theoretical works also suggest an evolutionary feedback between the  
315 movement rates and the efficiency of step selection (Duffy, 2011; Zhang et al., 2022 and references  
316 therein), which could favor the evolution of hard-wired behavioral syndromes and represent another  
317 way for systematic differences in movement rates to emerge. Time allocation tactics may also be  
318 positively reinforced by learning (Gopnik, 2020), at least in cognitively advanced species,  
319 representing another proximate pathway for species-specificity in time allocation to occur. Lastly, the  
320 optimal giving-up density of resource ( $A^*$  in the present study) varies with the species-specific  
321 sensitivity to risk (Brown, 1988; Charnov, 1976). Species with different paces of life should thus  
322 exhibit different movement thresholds even if they forage on the exact same resource and share the  
323 same predators, as has been observed when species differ in their susceptibility to a shared predator  
324 (Weterings et al., 2019).

### 325 **Implications for functional trait analysis**

326 Under the time allocation tradeoff hypothesis, in order to fully describe the ecological niche of a  
327 species, one would need to document its movement rates, i.e., its position on what could be termed  
328 the time allocation continuum, by opposition to the niche continuum which classically describes the  
329 dominance of the species in a given niche (Leibold et al., 2004). At one end of the time allocation  
330 continuum, one would find the “roamers” (Zhang et al., 2022) or “cream-skimmers” (Qi et al., 2022).  
331 At the other end of the continuum would lie the “dwellers” or “crumb-pickers”. Like traditional

332 functional traits, the position of a species on the time allocation continuum would both depend on  
333 and influence the environment. For example, in an Italian study area, the coexistence of chamois  
334 (*Rupicapra rupicapra*), a subordinate-dweller, and red deer (*Cervus elaphus*), a dominant-roamer,  
335 and the risk that they would overgraze their shared resource, interacted with the landscape  
336 configuration and the way it restricted the movements of the red deer (Ferretti et al., 2015). In the  
337 present analysis, the sensitivity analysis to  $b$ ,  $c$  and  $\gamma$  also indicated that the resilience of the  
338 coexistence outcome to stationary changes in the environment would depend on the positions of the  
339 species on both the niche continuum and the time allocation continuum.

340 These considerations call for the increased use of movement data in trait-based community ecology  
341 (Luck et al., 2012; Schlägel et al., 2020; Schleuning et al., 2023). Documenting the position of an  
342 animal species on the time allocation continuum however requires methods that allow comparisons  
343 across individuals and species, which is not always straightforward due to the discrete nature of  
344 movement tracking datasets (Péron, 2019; Péron et al., 2017, and references therein).

345

346 **Data availability:** This paper does not use data

347 **Author contributions:** G.P. conceived the ideas; G.P. led the experimental procedures; and G.P. led  
348 the writing.

## References

- Adler, F.R., LeBrun, E.G., Feener Jr., D.H., 2007. Maintaining Diversity in an Ant Community: Modeling, Extending, and Testing the Dominance-Discovery Trade-Off. *The American Naturalist* 169, 323–333. <https://doi.org/10.1086/510759>
- Alerstam, T., Hedenstrom, A., Akesson, S., 2003. Long-distance migration: evolution and determinants. *Oikos* 103, 247–260. <https://doi.org/10.1034/j.1600-0706.2003.12559.x>
- Barnard, C.J., Sibly, R.M., 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29, 543–550. [https://doi.org/10.1016/S0003-3472\(81\)80117-0](https://doi.org/10.1016/S0003-3472(81)80117-0)
- Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A., McArthur, C., Banks, P.B., 2013. A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology* 67, 1541–1553. <https://doi.org/10.1007/s00265-013-1609-3>
- Berger-Tal, O., Nathan, J., Meron, E., Saltz, D., 2014. The Exploration-Exploitation Dilemma: A Multidisciplinary Framework. *PLOS ONE* 9, e95693. <https://doi.org/10.1371/JOURNAL.PONE.0095693>
- Brown, J.H., West, G.B., 2000. *Scaling in Biology*, Santa Fe Institute Studies in the Sciences of Complexity. Oxford University Press, Oxford.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22, 37–47.
- Cadotte, M.W., Mai, D.V., Jantz, S., Collins, M.D., Keele, M., Drake, J.A., 2006. On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage. *The American Naturalist* 168, 704–709. <https://doi.org/10.1086/508296>
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9, 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
- Cortés-Avizanda, A., Jovani, R., Carrete, M., Donazar, J.A., 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93, 2570–2579. <https://doi.org/10.1890/12-0221.1>
- Drent, R.H., Daan, S., 1980. The Prudent Parent: Energetic Adjustments in Avian Breeding. *Ardea* 55, 225–252. <https://doi.org/10.5253/arde.v68.p225>
- Duffy, K.J., 2011. Simulations to investigate animal movement effects on population dynamics. *Natural Resource Modeling* 24, 48–60. <https://doi.org/10.1111/j.1939-7445.2010.00082.x>
- Ferretti, F., Corazza, M., Campana, I., Pietrocini, V., Brunetti, C., Scornavacca, D., Lovari, S., 2015. Competition between wild herbivores: Reintroduced red deer and Apennine chamois. *Behavioral Ecology* 26. <https://doi.org/10.1093/beheco/aru226>
- Ferzoco, I.M.C., McCauley, S.J., 2022. Breaking down the components of the competition-colonization trade-off: New insights into its role in diverse systems. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.13845>
- Franklin, D.C., Legge, S., Skroblin, A., Heathcote, J., Maute, K., Schaefer, D.J., Garnett, S.T., 2017. Wings of tropical finches: interspecific differences in shape are consistent with levels of mobility, but moult and feather fault patterns are more complex. *Emu - Austral Ornithology* 117, 370–381. <https://doi.org/10.1080/01584197.2017.1361790>
- Gautestad, A.O., 2011. Memory matters: influence from a cognitive map on animal space use. *Journal of theoretical biology* 287, 26–36. <https://doi.org/10.1016/j.jtbi.2011.07.010>
- Gopnik, A., 2020. Childhood as a solution to explore–exploit tensions. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375. <https://doi.org/10.1098/rstb.2019.0502>
- Hedenström, A., Johansson, L.C., 2015. Bat flight: aerodynamics, kinematics and flight morphology. *Journal of Experimental Biology* 218, 653–663. <https://doi.org/10.1242/jeb.031203>

- Holling, C.S., 1959. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *The Canadian Entomologist* 91, 293–320.  
<https://doi.org/10.4039/Ent91293-5>
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kotler, B.P., Brown, J.S., Subach, A., 1993. Mechanisms of Species Coexistence of Optimal Foragers: Temporal Partitioning by Two Species of Sand Dune Gerbils. *Oikos* 67, 548–556.  
<https://doi.org/10.2307/3545367>
- Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of Time as an Ecological Resource. *Annual Review Of Ecology Evolution And Systematics* 34, 153–181.  
<https://doi.org/10.1146/annurev.ecolsys.34.011802.132435>
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7, 601–613.  
<https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Linder, A.C., Lyhne, H., Laubek, B., Bruhn, D., Pertoldi, C., 2022. Modeling Species-Specific Collision Risk of Birds with Wind Turbines: A Behavioral Approach. *Symmetry* 14, 2493.  
<https://doi.org/10.3390/sym14122493>
- Luck, G.W., Lavorel, S., McIntyre, S., Lumb, K., 2012. Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology* 81, 1065–1076. <https://doi.org/10.1111/j.1365-2656.2012.01974.x>
- Macarthur, R., Levins, R., 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101, 377–385. <https://doi.org/10.1086/282505>
- Martínez, A.E., Pollock, H.S., Kelley, J.P., Tarwater, C.E., 2018. Social information cascades influence the formation of mixed-species foraging aggregations of ant-following birds in the Neotropics. *Animal Behaviour* 135, 25–35. <https://doi.org/10.1016/j.anbehav.2017.10.024>
- Ophir, A.G., Wolff, J.O., Phelps, S.M., 2008. Variation in neural V1aR predicts sexual fidelity and space use among male prairie voles in semi-natural settings. *Proceedings of the National Academy of Sciences of the United States of America* 105, 1249–1254.  
<https://doi.org/10.1073/PNAS.0709116105>
- Owen-Smith, N., Martin, J., Yoganand, K., 2015. Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere* 6, art152.  
<https://doi.org/10.1890/ES14-00487.1>
- Parr, C.L., Gibb, H., 2012. The discovery–dominance trade-off is the exception, rather than the rule. *Journal of Animal Ecology* 81, 233–241. <https://doi.org/10.1111/j.1365-2656.2011.01899.x>
- Péron, G., 2019. The time frame of home-range studies: from function to utilization. *Biological Reviews* 94, 1974–1982. <https://doi.org/10.1111/brv.12545>
- Péron, G., Bonenfant, C., Gagnon, R., Mabika, C.T., 2019. The two oxpecker species reveal the role of movement rates and foraging intensity in species coexistence. *Biology Letters* 15, 20190548.  
<https://doi.org/10.1098/rsbl.2019.0548>
- Péron, G., Duparc, A., Garel, M., Marchand, P., Morellet, N., Saïd, S., Loison, A., 2018. Circadian periodicity in space use by ungulates of temperate regions: How much, when and why? *Journal of Animal Ecology* 87, 1299–1308. <https://doi.org/10.1111/1365-2656.12857>
- Péron, G., Fleming, C.H., de Paula, R.C., Mitchell, N., Strohbach, M., Leimgruber, P., Calabrese, J.M., 2017. Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients. *Ecological Monographs* 87, 442–456.  
<https://doi.org/10.1002/ecm.1260>
- Qi, M., DeMalach, N., Dong, Y., Zhang, H., Sun, T., 2022. Coexistence under hierarchical resource exploitation: the role of R\*-preemption tradeoff. *The American Naturalist* 200.  
<https://doi.org/10.1086/720269>

- Ranc, N., Moorcroft, P.R., Ossi, F., Cagnacci, F., 2021. Experimental evidence of memory-based foraging decisions in a large wild mammal. *Proceedings of the National Academy of Sciences* 118, e2014856118. <https://doi.org/10.1073/pnas.2014856118>
- Schlägel, U.E., Grimm, V., Blaum, N., Colangeli, P., Dammhahn, M., Eccard, J.A., Hausmann, S.L., Herde, A., Hofer, H., Joshi, J., Kramer-Schadt, S., Litwin, M., Lozada-Gobilard, S.D., Müller, M.E.H., Müller, T., Nathan, R., Petermann, J.S., Pirhofer-Walzl, K., Radchuk, V., Rillig, M.C., Roeleke, M., Schäfer, M., Scherer, C., Schiro, G., Scholz, C., Teckentrup, L., Tiedemann, R., Ullmann, W., Voigt, C.C., Weithoff, G., Jeltsch, F., 2020. Movement-mediated community assembly and coexistence. *Biological Reviews* 95, 1073–1096. <https://doi.org/10.1111/brv.12600>
- Schleuning, M., García, D., Tobias, J.A., 2023. Animal functional traits: Towards a trait-based ecology for whole ecosystems. *Functional Ecology* 37, 4–12. <https://doi.org/10.1111/1365-2435.14246>
- Shoemaker, L.G., Melbourne, B.A., 2016. Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* 97, 2436–2446. <https://doi.org/10.1002/ecy.1454>
- Spiegel, O., Leu, S.T., Bull, C.M., Sih, A., 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters* 20, 3–18. <https://doi.org/10.1111/ele.12708>
- Tilman, D., 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Warren, R.D., Crompton, R.H., 1997. Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. *American Journal of Physical Anthropology* 104, 471–486. [https://doi.org/10.1002/\(SICI\)1096-8644\(199712\)104:4<471::AID-AJPA4>3.0.CO;2-V](https://doi.org/10.1002/(SICI)1096-8644(199712)104:4<471::AID-AJPA4>3.0.CO;2-V)
- Weterings, M.J.A., Ewert, S.P., Peereboom, J.N., Kuipers, H.J., Kuijper, D.P.J., Prins, H.H.T., Jansen, P.A., van Langevelde, F., van Wieren, S.E., 2019. Implications of shared predation for space use in two sympatric leporids. *Ecology and Evolution* 9, 3457–3469. <https://doi.org/10.1002/ece3.4980>
- Zhang, B., Lam, K.Y., Ni, W.M., Signorelli, R., Collins, K.M., Fu, Z., Zhai, L., Lou, Y., DeAngelis, D.L., Hastings, A., 2022. Directed movement changes coexistence outcomes in heterogeneous environments. *Ecology Letters* 25, 366–377. <https://doi.org/10.1111/ele.13925>
- Zheng, C.Z., Ovaskainen, O., Hanski, I., 2009. Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364, 1519–1532. <https://doi.org/10.1098/rstb.2009.0005>

## Tables

Table 1: Notation and biological meaning of the model parameters. Parameters whose effect on the coexistence outcome was assessed are in bold and I give the bracket of values that I considered. The other parameters were fixed at the specified values. The energy and time units are arbitrary and the distance unit is the width of one grid cell.

Variable	Meaning	Value
Parameters for the Lotka-Volterra frame		
$g_1$	Resource renewal rate	0.15
$g_2$	Resource loss rate	0.03
$h$	Half-saturation coefficient	18
$e_0$	Starting energy level	9
$B$	Cost of breeding	4.5
$r$	Asymptotic growth rate	2
$m_0$	Density-independent mortality rate	0.025
$m_{1 \rightarrow 2}$	Interference coefficient of species 1 on 2	0.075
$m_{2 \rightarrow 1}$	Interference coefficient of species 2 on 1	0.025
$m_{1 \rightarrow 1}$ and $m_{2 \rightarrow 2}$	Intra-specific interference coefficients	0.025
$\gamma$	<b>Yield</b>	<b>1.5 – 2.5</b>
$c$	<b>Cost of movement</b>	<b>0 – 3</b>
Parameters for the spatial reaction norms		
$A^*$	<b>Threshold of resource density that triggers movement</b>	<b>5 – 25</b>
$\sigma$	Scale parameter for the decision to leave	0.1
$D$	Diffusion coefficient	10
$b$	<b>Efficiency of the step selection</b>	<b>0 – 0.8</b>
$\beta$	Constant to ensure that the denominator stays positive in the step selection function	0.5

## Supplementary material

Appendix S1: R script containing the functions to reproduce the simulations

Table S1: Linear model of the size of the parameter space that allowed coexistence. Coexistence is the fact that no species is rarer than 5% after 50 years, and the size of the parameter space is the proportion of  $b$ ,  $c$ , and  $\gamma$  values that allowed coexistence (shaded surface in Fig. 1). Estimates are given on the natural scale for interpretability but the ANOVA was performed after logit-transformation of the response proportion.

	<b>Coefficient</b>	<b>SE</b>	<b>df</b>	<b>F</b>	<b>P-value</b>
Intercept ( $a_1 < a_2$ and $\gamma = 1.5$ )	0.686	0.049	34		
$ a_1 - a_2 $	-0.009	0.004	1	10.8	0.002
$a_1 > a_2$ vs. $a_1 < a_2$	-0.290	0.049	1	49.7	<0.001
$\gamma = 2$ vs. 1.5	-0.233	0.060	2	21.3	<0.001
$\gamma = 2.5$ vs. 1.5	-0.390	0.060			
$ a_1 - a_2  * a_1 > a_2$ vs. $a_1 < a_2$	0.011	0.004	1	6.2	0.018
$ a_1 - a_2  * \gamma = 2$ vs. 1.5	0.013	0.005	2	6.4	0.004
$ a_1 - a_2  * \gamma = 2.5$ vs. 1.5	0.019	0.005			

Appendix S1: R code. To be provided upon acceptance of the article.