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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 , γ , 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 γ 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 β prevented a zero denominator (Table 1).

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

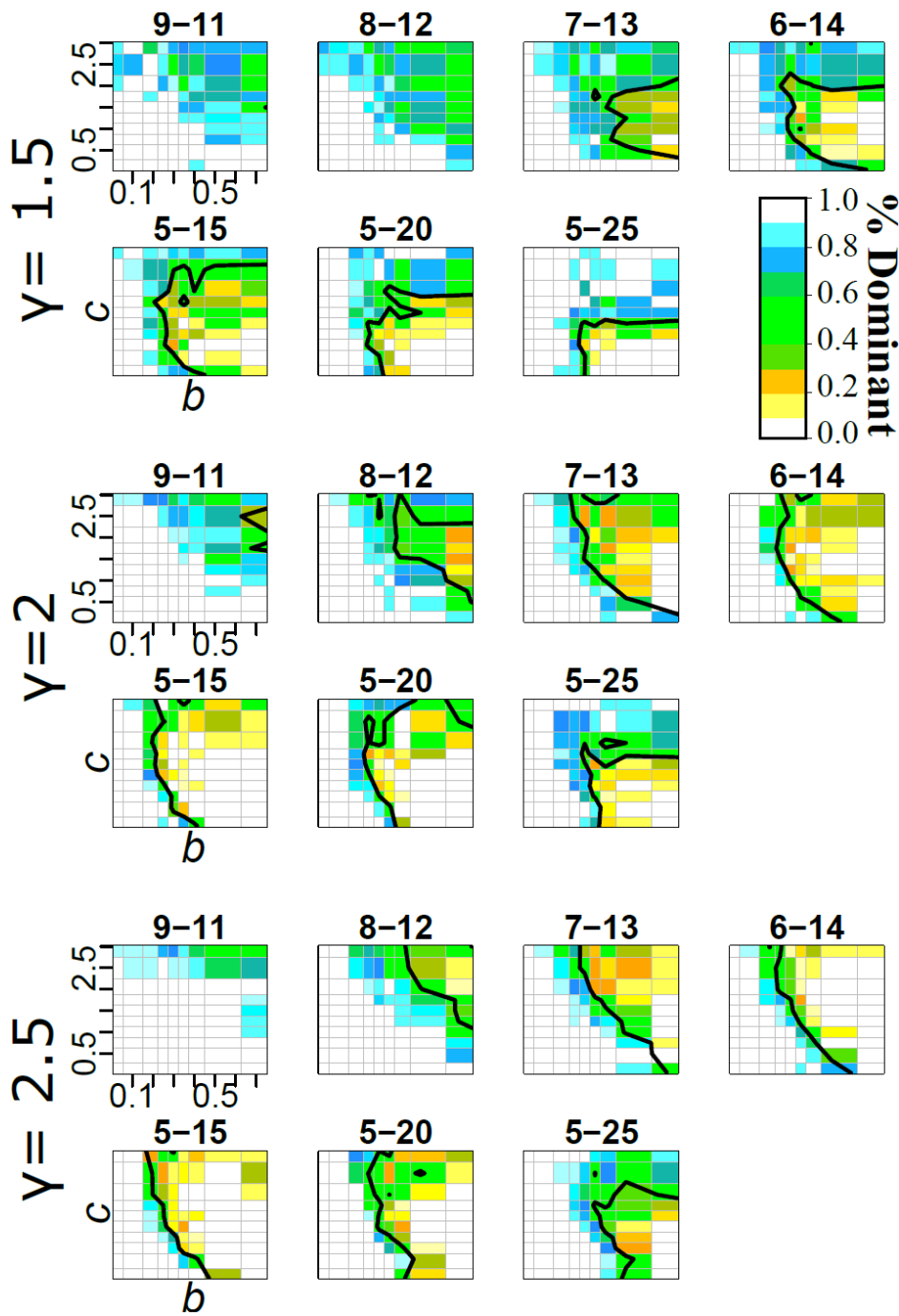
205 Lastly, as the difference in movement threshold increased, the range of conditions that enabled
206 coexistence increased (Fig. 1&2; ANOVA in Table S1), irrespective of whether $A_1^* < A_2^*$ or $A_1^* > A_2^*$.
207 The only exception was when $A_1^* < A_2^*$ and $\gamma=1.5$ (ANOVA in Table S1). 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

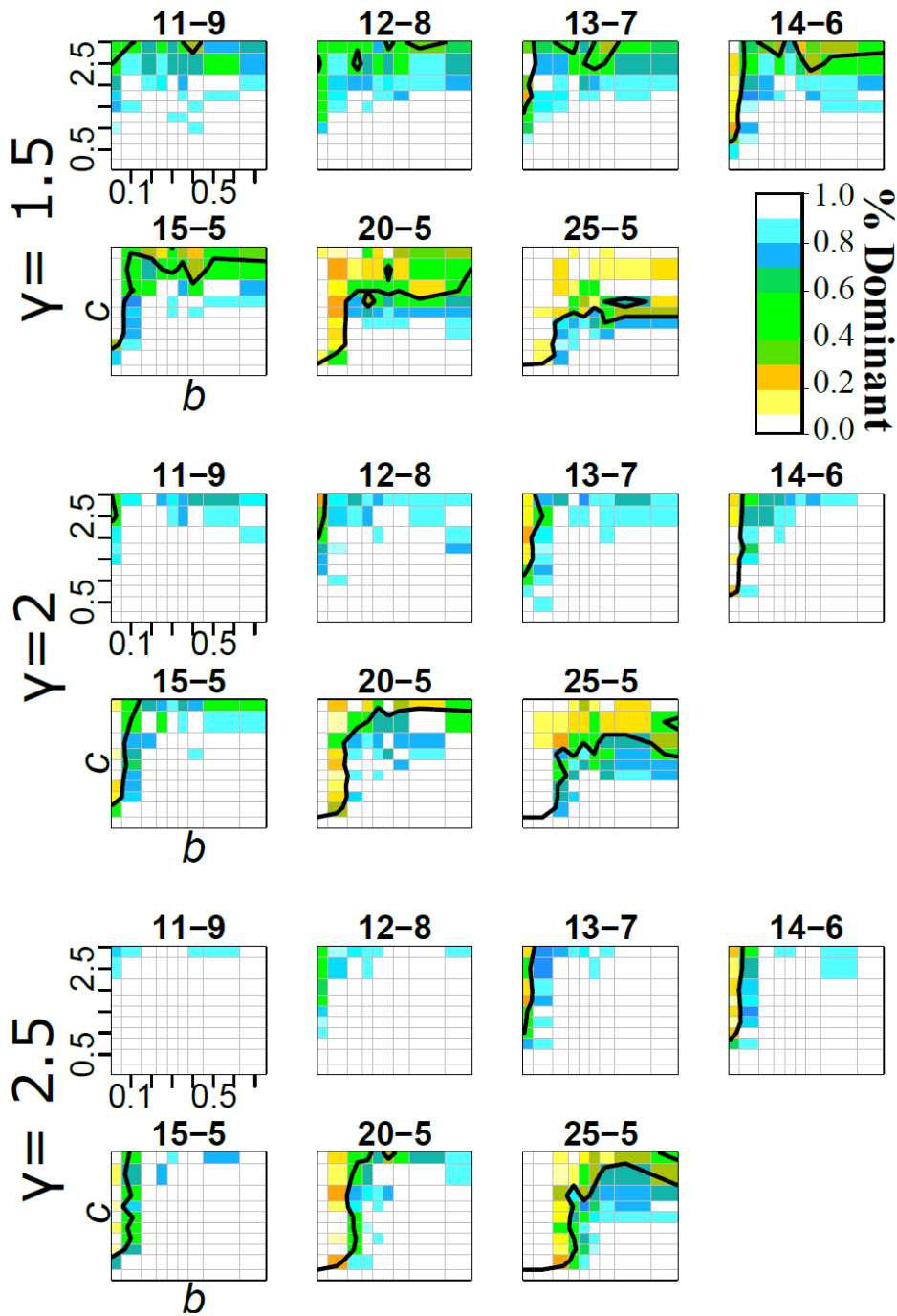
213 Fig. 1: Coexistence outcome when the movement threshold of the dominant species A_1^* was lower
 214 than the threshold of the subordinate species A_2^* . This situation mimicked the occurrence of a
 215 tradeoff between discovery and dominance, as per the current coexistence theory. In each panel, 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^* . γ 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 γ , 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 γ , 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 γ 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 γ 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.

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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
γ	Yield	1.5 – 2.5
c	Cost of movement	0 – 3
Parameters for the spatial reaction norms		
A^*	Threshold of resource density that triggers movement	5 – 25
σ	Scale parameter for the decision to leave	0.1
D	Diffusion coefficient	10
b	Efficiency of the step selection	0 – 0.8
β	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 γ 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.

	Coefficient	SE	df	F	P-value
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.