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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-scrrounger 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*

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

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

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

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

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

## **Material and methods**

## Base model: the two-consumer one-resource Lotka-Volterra system of differential equations

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

Eq. 1	$\left\{ \begin{array}{l} \text{(Species } s) \quad \Delta N_s(t) = \underbrace{\frac{rA(t)N_s(t)}{h + A(t)}}_{\text{growth}} - \underbrace{\overline{m_0 N_s(t)}}_{\text{DI mortality}} - \underbrace{\sum_{s'=1}^2 m_{s' \rightarrow s} N_s(t) N_{s'}(t)}_{\text{DD mortality}} \\ \text{(Resource)} \quad \Delta A(t) = \underbrace{g_1 A(t)}_{\text{renewal}} - \underbrace{g_2 A(t)}_{\text{loss}} - \underbrace{\sum_{s=1}^2 \frac{1}{\gamma} \cdot \frac{rA(t)N_s(t)}{h + A(t)}}_{\text{consumption}} \end{array} \right.$
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$N_s$  denoted the population abundance of species  $s$  and  $A$  denoted the resource abundance. The parameters  $r$ ,  $\gamma$ ,  $h$ , and  $m_0$  roughly represent the trophic niche, i.e., the way species exploit resource and die from predation. I assumed these four parameters to be the same in both species. More precisely,  $r$  was the population growth rate of the consumers. The yield  $\gamma$  quantified the rate at which the consumers transformed the resource into population growth, and in turn the intensity of exploitation competition within and between species.  $h$  was the half-saturation coefficient corresponding to the value of resource density which gave half the maximum per capita growth rate, following the formula of Holling's (1959) type II functional response. The density-independent (DI) mortality rate  $m_0$  represented the baseline mortality without competition. Lastly, in addition to the resource that got consumed, a proportion  $g_2$  of the resource was lost to decay at each interval. On the other hand, the resource renewed at rate  $g_1$ .

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

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

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

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

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

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

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

Eq. 2	$\begin{cases} (Species\ s) & \Delta E_{i,j}^{(s)}(t) = \frac{\overbrace{rA_{i,j}(t)E_{i,j}^{(s)}(t)}^{growth}}{h + A_{i,j}(t)} - \overbrace{m_0E_{i,j}^{(s)}(t)}^{DI\ mortality} - \overbrace{\sum_{s'=1}^2 m_{s' \rightarrow s} E_{i,j}^{(s)}(t)E_{i,j}^{(s')}(t)}^{DD\ mortality} \\ (Resource) & \Delta A_{i,j}(t) = \underbrace{g_1A_{i,j}(0)}_{renewal} - \underbrace{g_2A_{i,j}(t)}_{loss} - \underbrace{\sum_{s=1}^2 \frac{1}{\gamma} \cdot \frac{rA_{i,j}(t)E_{i,j}^{(s)}(t)}{h + A_{i,j}(t)}}_{consumption} \end{cases}$
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Next, I made the individuals move.  $(i_k(t), j_k(t))$  denoted the current location of individual  $k$  in the grid cell at time  $t$ . I drew the movement status  $\delta_k(t)$  from a Bernoulli trial of which the success rate depended on the difference between the resource abundance at the current location,  $A_{i_k(t), j_k(t)}(t)$ , and the species-specific threshold of resource abundance that triggered movement,  $A_{s_k}^*$  (Eq.3; Table 1) where  $s_k$  denoted the species of individual  $k$ .

Eq. 3	$\delta_k(t) \sim Bernoulli \left( 1 - \text{logit}^{-1} \left( \frac{A_{i_k(t), j_k(t)}(t) - A_{s_k}^*}{\sigma} \right) \right)$
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The parameter  $A_{s_k}^*$  is sometimes referred to as the “giving-up density of resource” (Bedoya-Perez et al., 2013, and references therein). It is in some way akin to the amount of resource that the focal species would leave unused in a monospecific population (Qi et al., 2022; Tilman, 1982), hence the choice of a similar notation. If individual  $k$  moved, it lost a species-specific amount of energy, the cost 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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Like in Eq. 3,  $(i_k(t), j_k(t))$  was the location of individual  $k$  at time  $t$ .

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



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

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

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

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

## Parameterization

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

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

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

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

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

## **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 (Fig. 1). By contrast, if  $A_1^* = A_2^*$  the scenario was designed to  
186 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, 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). 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: x-  
203 axis of each panel). This result confirmed that coexistence was not dependent on a tradeoff between  
204 discovery and dominance.

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

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

## 211 **Discussion**

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

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

230 To make a link with a recurrent topic in the recent movement ecology literature, one could verbally  
231 reframe the model in the present study in terms of memory effects (Gautestad, 2011; Ranc et al.,  
232 2021). In my model, the species with the highest movement threshold indeed tended to revisit  
233 known locations within the current grid cell, and could therefore be labelled as memory-reliant. The

234 species with the lowest movement threshold could on the other hand easily be labelled as  
235 exploration-prone. However, the memory framework strongly implies a role for cognitive  
236 development and cognitive performance (Gopnik, 2020), which my model does not require.  
237 Nevertheless, my results confirm that spatial memory can promote coexistence with competitors  
238 that lack spatial memory.

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

252 The full exploration of the parameter space was beyond the scope of the present study, and would  
253 represent a challenge with such a parameter-rich model. I acknowledge that the number of  
254 parameters represented a major drawback of my modeling framework. However, I had two reasons  
255 to work with that many parameters. First, the two-species one-resource Lotka-Volterra structure (Eq.  
256 1) made it possible to fully separate niche exploitation (population growth  $r$ , half-saturation  
257 coefficient  $h$ , yield  $\gamma$ , and density-independent mortality  $m_0$ ) from dominance (density-dependent  
258 mortality parameters  $m_{S \rightarrow S'}$ ). Second, I needed the individual-based stochastic component to

reproduce the spatial reaction norms that are routinely observed in movement ecology studies, i.e., the giving-up density of resource and the step selection function. These key components allowed me to transform the Lotka-Volterra equation into a model of station-keeping movements and their demographic implications. Another potential benefit of using a complex model was that, in the future, the same modeling framework could be extended with components representing other coexistence mechanisms, to explore their relative contributions. For example,  $r$  or  $\gamma$  could be used to introduce some species-specificity in exploitation competition, in order to reproduce the mechanism that e.g., Qi et al. (2022) focused on. Temporal and spatial fluctuations in abiotic factors such as droughts (Duffy, 2011) could be incorporated via  $A(0)$ ,  $g_1$  or  $g_2$ . Species-specificity in predation rate (Weterings et al., 2019) could be represented via the  $m$ -parameters and their spatial variation. A second field of resource could be incorporated to represent the availability of suboptimal resource and the partition of resource space.

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

The working hypothesis in this study is that species that have the exact same trophic relationships exhibit different movement ecologies. This hypothesis might not be completely intuitive to some readers, because species that have the same trophic relationships would expectedly respond to the same constraints emerging from the same distributions of resource and risks. In addition, the stakes involved in small movement decisions are small, and at the same time these decisions proceed from the instant processing of numerous, potentially contradictory stimuli, combined with long-term goals and individual strategies. The resulting movement patterns are therefore sometimes quite idiosyncratic, which could hinder the ability to develop distinctive, species-specific time allocation tactics. That said, empirically, coexisting species have been observed to exhibit species-specific signatures in their movement tracks. The most obvious of these signatures are the home range size and average speed, which for example depend on the species-specific body mass (Brown and West, 2000). Coexisting species may also vary in more subtle statistics like the average residence time, revisitation frequency, periodic patterns of space use, and the response to perturbations and

resource depletion (Linder et al., 2022; Owen-Smith et al., 2015; Péron et al., 2018). Early movement ecologists had also identified that night- and day-active species could coexist without either partitioning the resource or relying on a discovery-dominance tradeoff, which they termed “temporal partitioning” (Kotler et al., 1993; Kronfeld-Schor and Dayan, 2003). In addition, single loci have been uncovered that control consistent individual variation in movement rates within some invertebrate species (Zhang et al., 2022; Zheng et al., 2009), and within at least one vertebrate species (Ophir et al., 2008). This genetic control of movement rates could conceivably operate across species as well. Variation in morphology between species can also influence and respond to variation in movement rates. For example, the cost of movement increases with the wing loading in birds and bats (Alerstam et al., 2003; Hedenström and Johansson, 2015), suggesting different rate of fidelity to foraging sites (Franklin et al., 2017). Theoretical works also suggest an evolutionary feedback between the movement rates and the efficiency of step selection (Duffy, 2011; Zhang et al., 2022 and references therein), which could favor the evolution of hard-wired behavioral syndromes and represent another way for systematic differences in movement rates to emerge. Time allocation tactics may also be positively reinforced by learning (Gopnik, 2020), at least in cognitively advanced species, representing another proximate pathway for species-specificity in time allocation to occur. Lastly, the optimal giving-up density of resource ( $A^*$  in the present study) varies with the species-specific sensitivity to risk (Brown, 1988; Charnov, 1976). Species with different paces of life should thus exhibit different movement thresholds even if they forage on the exact same resource and share the same predators, as has been observed when species differ in their susceptibility to a shared predator (Weterings et al., 2019).

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

Under the time allocation tradeoff hypothesis, in order to fully describe the ecological niche of a species, one would need to document its movement rates, i.e., its position on what could be termed the time allocation continuum, by opposition to the niche continuum which classically describes the dominance of the species in a given niche (Leibold et al., 2004). At one end of the time allocation

continuum, one would find the “roamers” (Zhang et al., 2022) or “cream-skimmers” (Qi et al., 2022). At the other end of the continuum would lie the “dwellers” or “crumb-pickers”. Like traditional functional traits, the position of a species on the time allocation continuum would both depend on and influence the environment. For example, in an Italian study area, the coexistence of chamois (*Rupicapra rupicapra*), a subordinate-dweller, and red deer (*Cervus elaphus*), a dominant-roamer, and the risk that they would overgraze their shared resource, interacted with the landscape configuration and the way it restricted the movements of the red deer (Ferretti et al., 2015). In the present analysis, the sensitivity analysis to  $b$ ,  $c$  and  $\gamma$  also indicated that the resilience of the coexistence outcome to stationary changes in the environment would depend on the positions of the species on both the niche continuum and the time allocation continuum.

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

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

**Author contributions:** G.P. conceived the ideas; G.P. led the experimental procedures; and G.P. led 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
$\gamma$	<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

## Figure legends

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

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

## 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.

	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.