The role of cognition and movement of seed-dispersing animals in shaping plant distributions

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Abstract | In the wild, an evolutionary play takes place in an unchanging setting, or so current hypotheses on the evolution of spatiotemporal cognition of animals implicitly assume. However, if plant-eating vagile animals are likely to have their spatiotemporal cognition shaped by the distribution of plant resources, their movement may shape the way resources are distributed as well, for example by dispersing seeds. Using an agent-based model simulating the foraging behaviour of a seed disperser endowed with spatiotemporal knowledge of resource distribution, I investigated whether resource spatiotemporal patterns could be influenced by the level of cognition involved in foraging. This level of cognition represented how well resource location and phenology were predicted by the agent. I showed that seed dispersers could shape the long-term distribution of resources by materialising the routes repeatedly used by the forager with the newly recruited trees. This stemmed from the conjunction of two forces: competition for space between trees and a seed-dispersing forager moving from tree to tree based on spatiotemporal memory. In turn, resource landscape modifications affected the benefits of spatiotemporal memory, hence the selection gradient that applies to cognition. This could create eco-evolutionary feedback loops between animal spatiotemporal cognition and the distribution patterns of plant resources. Altogether, the results emphasise that foraging cognition is a cause and a consequence of resource heterogeneity.

Keywords: Agent-based model - Feedback loop - Foraging - Frugivory - Memory - Movement - Phenology - Zoochory
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1

Contents

I Introduction

Hypotheses about the evolution of vagile plant-eating foragers' spatiotemporal cognition (i.e. the ability to process, integrate and utilise information on resource distribution and phenology) generally assume that foragers evolve in an unchanging environment (Rosati, 2017). However, while foragers' cognition is likely to be shaped by the distribution of resources (Boyer & Walsh, 2010; Bracis et al., 2015; Grove, 2013; Milton, 1981; Robira et al., 2021), the characteristics of the resources themselves could be the result of forager-induced selection (Lomáscolo & Schaefer, 2010; Rojas et al., 2021). In the tropical rainforests, for example, the cognition of frugivorous primates has probably been shaped by the challenge of the ephemerality and dispersion of their food (Milton, 1981; Trapanese et al., 2019a; Zuberbühler & Janmaat, 2010), supporting complex (Janmaat et al., 2013; Janson, 1998, 2016; Robira et al., in press; Teichroeb & Vining, 2019; Trapanese et al., 2019b) and versatile (Janmaat et al., 2006; Robira et al., 2023; Trapanese et al., 2022) movement heuristics. In turn, primates remember and forage for the most rewarding trees (Ban et al., 2014; Ban et al., 2016; Flörchinger et al., 2010). The latter are thus more likely to have their seeds dispersed, driving plant and landscape evolution (Chapman et al., 2013; Lambert & Garber, 1998).

The way seeds are dispersed contributes to the emerging pattern of resource distribution (Vittoz & Engler, 2007). Most of the world's plants (Tiffney & Mazer, 1995) and especially rainforest trees (Bagchi et al., 2011; Gottsberger & Silberbauer-Gottsberger, 1983) are dispersed by animals (zoochory). Compared to other modes of dispersal, such as wind (anemochory) or gravity (gravichory), zoochory induces a less patchy distribution of adult plants (Seidler & Plotkin, 2006; but see Hubbell, 1979). However, animal-dispersed fruit trees are still not homogeneously distributed (Hubbell, 1979). This is because although travelling long distances, animals may tend to revisit memorised sites regularly, if not exclusively (Addis et al., 2017; John et al., 2016). Furthermore, the imperfection and limited size of spatial memory (Fagan et al., 2013) is expected to lead to different movement patterns (Avgar et al., 2013), and therefore potentially to different patterns of resource distribution (Côrtes & Uriarte, 2013). By being affected by cognition and by affecting resource dispersal, animal movement could thus lead to eco-evolutionary feedback loops between animal cognition and resource dispersal (Borah & Beckman, 2022). In other words, foraging cognition could be both a cause and a consequence of resource heterogeneity.

To illustrate the possible retroactions between cognition and resource distribution, let's consider an extreme speculative scenario in which seed-dispersing frugivores are freely foraging (Figure 1). At start, assuming a random homogeneous distribution, long-term spatiotemporal memory can be advantageous and selected for (Bracis et al., 2015; Grove, 2013). Through zoochory, deliberate targeting of some resource patches over others may induce a change in resource distribution over time (e.g. increasing patchiness), eventually making cognition more and more advantageous (Boyer & Walsh, 2010; Bracis et al., 2015; Grove, 2013). Gradually, by repeatedly targeting the same trees, the routes used by the foragers may begin to materialise through the seeds scattered along the way. However, in doing so, foragers who can only passively follow these routes and have survived may also begin to become very efficient: they should not even have to bear the cost of high cognitive ability, putting them at an advantage over foragers who bear the burden of cognition (Burns et al., 2011; Raichle, 2006). While the pattern of resource distribution can be maintained because the routes are used equally by all foragers (but through two different mechanisms: long-term memory *vs* taxis, Benhamou & Bovet, 1992; Benhamou & Poucet, 1995), cognition could even start to be counter-selected.

While some facets of this scenario may be rooted in empirical evidence (e.g. with forest elephants, Blake et al., 2009; Blake & Inkamba-Nkulu, 2004; Campos-Arceiz & Blake, 2011), most of it remains

speculative. The aim of this study is to put such a scenario to the test. Using an agent-based model simulating the movement of seed-dispersing frugivores with different cognitive abilities, I sought to investigate (a) whether and how the spatial arrangement of resource varies with the cognitive level and movement behaviour of the simulated agents, and (b) whether and how this may in turn affect the selection pressure on the agents' cognition.

II   Material and Methods

II.1   Agent-based model

The main objective of the model was to simulate the foraging behaviour of a single agent in an environment that is dynamical both on the short term, through an interplay between resource growth and depletion, and on the long term, due to seed dispersal. For simplicity, I will refer to the agent as the forager, and to resource patches as fruit trees, but this model should find larger resonance. The model was implemented in the *C++* language in *R* software (v.4.2.1, R Core Team, 2022) based on the *Rcpp* package (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & François, 2011).

Environment

Spatial distribution   I modelled the environment as a flat square map of side 1000 arbitrary spatial units (su). Within this map, 1000 trees were initially homogeneously distributed (uniform distribution of their x and y coordinates, resulting in a Poisson distribution of tree density).

Resource growth   Time was cyclical, with a period of 365 arbitrary time units (tu). Each tree produced resource (fruit containing seeds) for 30 tu only once every period. Periods of productivity of each tree were randomly distributed (i.e. uniform distribution of the start date). Thus, resource was seasonal at the tree-level, but not at the map-level. Productivity was characterised by a triangular-shaped pattern of the quantity of food over time: at start of the productive period, food quantity started to increase linearly up to 1 arbitrary food unit (fu), mimicking progressive fruit ripening, and then decreased linearly to 0 fu, mimicking fruit rotting. The depletion of the food by the forager had no effect on this dynamic. Food could continue to ripen (though never to the same extent as if it had not been depleted) and rot. At a given time, the quantity of food available at a given tree thus depended on the productivity of the tree at that time, as well as the depletion history by the forager, creating a short-term dynamics of resource temporal distribution.

Seed dispersal   Trees reproduced by ingestion of ripe fruit by the forager and subsequent dispersal. Once the forager ate ripe fruit, seeds could be dispersed only one time up to 0.5 tu after ingestion. Dispersal occurred at a probability of 0.02 tu^{-1}, independent of the quantity of fruit ingested. This probability was considered low, to mimic the natural slow pace of land use changes. All fruit eaten did not mandatorily led to dispersal. Dispersal was eventually successful only if some space was left available for the new tree: no tree had to be at a distance less than 8.03 su. This number was obtained such that the cumulative (when non-overlapping) exclusive "lifespace" by trees (a circular area of radius the aforementioned distance) could reach 45% of the map area at most (but other percentages were tested, see Route formation as a product of two forces). If it happened that there was available space for the seedling to grow, then the seedling location was sampled in the available space along the linear path linking the previous and current locations. Otherwise, the seedling could not grow and died.
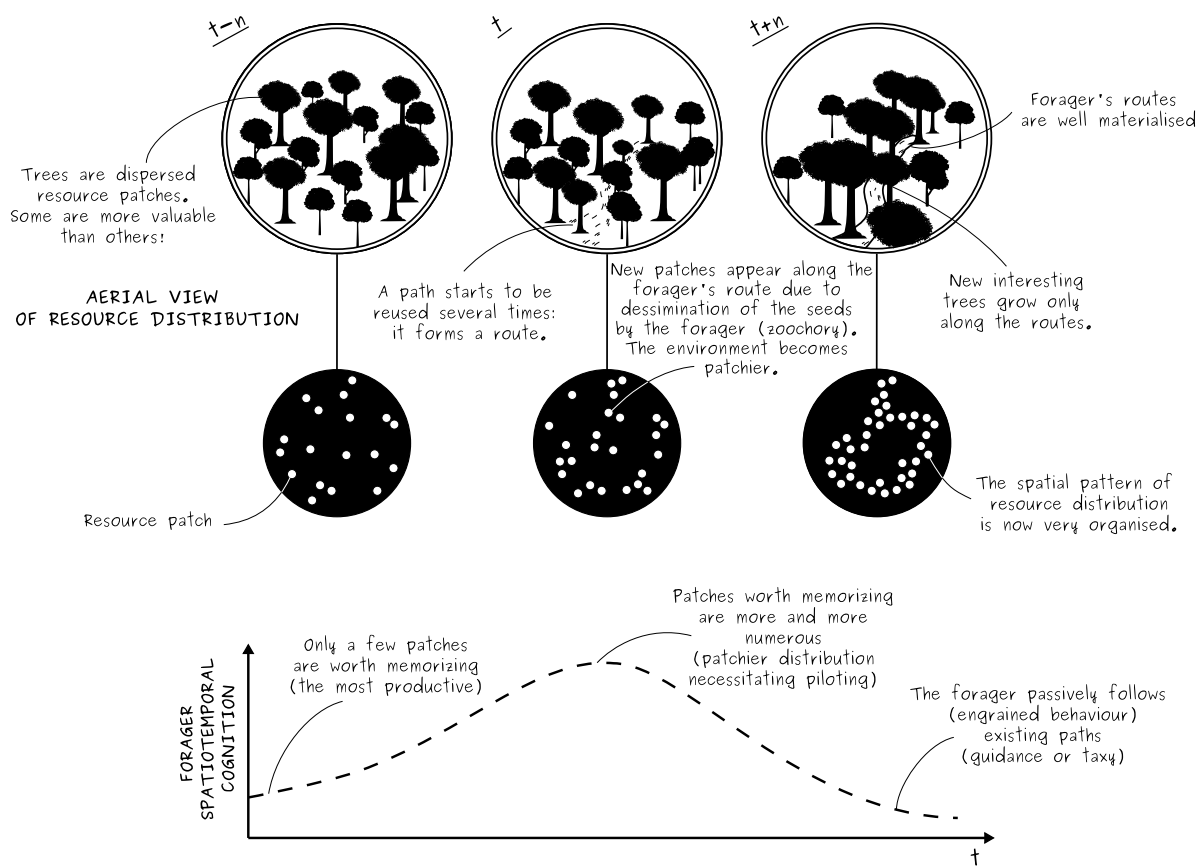
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Figure 1 – Theoretical expectations on eco-evolutionary feedback loops between animal spatiotemporal cognition and resource distribution

123   If the seedling was successfully dispersed and recruited, an old tree (already present in the map) was
124 randomly selected and died to keep density constant. The start date of fruiting of the newly recruited
125 tree was randomly sampled within a reduced Gaussian distribution (i.e. variance of one) centered on
126 the start date of fruiting of the parent tree. The location and fruiting time of the newly recruited tree
127 were memorised if it replaced a tree that was part of the forager's memory. The newly recruited tree
128 was considered as mature only the year after. Seed dispersal could thus induce a long-term dynamics
129 of resource spatial distribution and of the distribution of starting dates in the tree population.

Forager

Cognitive abilities

131   **Cognitive abilities**   The forager was endowed with a gradient of knowledge abilities: from no mem-
132 ory of the locations of trees (naive forager) and the timing of their period of productivity to perfect
133 omniscience (i.e. all tree locations are known) and prescience (i.e. all periods of productivity are known).
134 Otherwise, it only knew a certain proportion (fixed for the whole simulation) of tree locations and their
135 associated phenology (hereafter *spatiotemporal knowledge rate*). These trees were selected randomly
136 at the start of the simulation. When a tree was part of the forager's memory, the forager knew both
137 the spatial (location) and temporal (fruiting timing) attributes. Thus, it could not know only one or the
138 other.

Movement rules

139   **Movement rules**   The forager was initially randomly located within the map. It is fully aware of trees
140 present within sensory range fixed to 15.81 su. This actually corresponds to the average nearest-
141 neighbour distance which equates $\frac{1}{2\sqrt{\rho}}$, with ρ the density of trees (here 0.001) at start of the simula-
142 tion where trees are homogeneously distributed. It is also aware of trees that are part of its spatiotem-
143 poral long-term memory. To decide where to head next, the forager could either rely on its private
144 knowledge (sensory or memory) or not. If all trees within its private knowledge did not yield any fruit
145 (i.e., all having less than 0.001 fu), the forager was moving randomly. Random movements were per-
146 formed by randomly choosing a direction (uniform distribution of the heading angle), while the step
147 length was sampled within an exponential distribution of mean $\lambda_{step\,length}$ = 0.01. An exponential dis-
148 tribution of step lengths is indeed classically observed in nature (Benhamou, 2014). Otherwise, the
149 forager targeted the closest tree which maximised the ratio between the predicted food quantity at
150 the tree (which accounts for depletion history), and the distance to the tree. Nonetheless, the forager
151 avoided to target trees recently visited within the previous 2 tu to avoid targeting recently depleted
152 trees (Robira et al., 2021).
153   Once the target had been chosen (or random point, if none), the forager moved straight to the
154 first tree that should have been theoretically perceived *en route* to the initial destination point if any
155 (provided they were not recently visited), or the destination otherwise. When this destination was
156 reached, it then re-estimated the best tree to target and so on. After each moving bout time was
157 updated based on the distance travelled, knowing that the forager moved at a speed of 1000 su/tu.
158 Then, the resource quantity available at each tree was updated.
159   In case all trees were empty (no food available in the environment, considered if the sum of food
160 available was less than 1 fu), the forager entered a torpor period for 1 tu, and so on until food was
161 available again. This was done to avoid biasing measure of foraging efficiency in case the forager
162 could deplete entirely the environment while being unable to disperse to another area, as expected
163 in nature if this happens.

Table 1: Model parameters

Modelling entity	Parameter	Definition	Value	Unit
Environment	Map size	Length of a side of the square environmental map	1000	su
Environment	Quadrat size	Length of a side of a square quadrat to calculate Lloyd index of patchiness	50	su
Environment	Period length	Length of a period before a given tree starts producing again	365	tu
Environment	Number of periods	Number of periods before the simulation is ended	100	-
Environment	Number of trees	Number of trees hosted by the environment	1000	-
Environment	Fruiting length	Time duration of the fruiting period of each tree	30	tu
Environment	Maximum food yielded at a tree	Food quantity that a tree might yield at best (peak of the triangular-shaped food distribution)	1	fu
Environment	Space for tree	Space occupied by a tree and unavailable for others	45	% of map area
Agent	Speed	Speed at which the forager moves	1000	su/tu
Agent	Torpor time	Time duration for which the forager stops foraging in case no food is available in the environment	1	tu
Agent	Perceptual range	Distance at which the forager is aware of the environment	15.81	su
Agent	Knowledge rate	Proportion of trees of the environment for which the forager knows the location and prodution timing	(0, 0.25, 0.5, 0.75, 1)	-
Agent	No-return time	Time delay before a forager mentally decides to target a previously visited tree	2	tu
Agent	Dispersal time	Time duration during which seeds from a previously ingested fruit can be dispersed	0.5	tu
Agent	Probability of dispersal	Probability (per tu) that the seeds is actually dispersed	0.01	1/tu
Agent	lambda["step length"]	Average step length for random movements used to parameterise the exponential distribution	0.01	su

II.2 Analyses

Characterisation of tree distribution patterns

To assess whether different levels of cognition resulted in different organisations of the spatial distribution of trees at the end of the simulation, I focused on three metrics describing tree spatiotemporal patterns: the *patchiness*, the *alignment* and the *spatial autocorrelation of fruiting timing*.

Patchiness   Patchiness (i.e. the tendency of trees to aggregate into clusters) was measured using Lloyd's index of patchiness (Lloyd, 1967). This index is given by the following formula

$$P = N_{quadrat} \frac{\sum_i n_i(n_i-1)}{(\sum_i n_i)^2}$$

where n_i represents the number of trees in quadrat *i* and $N_{quadrat}$ the number of quadrats. The map was divided in 400 square quadrats of side 50 su. The quadrat size, provided sufficient length for biological relevance, little affects the measurement (Lloyd, 1967). Lower values indicate homogeneous distribution while larger values indicate heterogeneous and route distributions (see Appendix Material).

As the forager is set up to forage in a square map with reflective boundaries, seed dispersal may lead to the shrinkage of resource range towards the centre of the map (where recursions are inevitably higher), an artefact not of interest here. This would contribute to inflate measures of patchiness. I therefore calculated a measure of shrinkage *s* as one minus the area covered by the 95% of the Gaussian-based kernel distribution based on all tree locations divided by the map size. To account for variations in shrinkage in the different simulated scenarios (see Appendix Material), I corrected patchiness such as $P_c = P(1 - s)$.

Tree alignment   Routes are (curvi-)linear features. To assess the tendency of trees to form linear motifs, I quantified their alignment. For a given tree, alignment *a* was defined as one minus the minimum of the sine of the angles of the triangle formed by the tree of interest and the two closest trees. This varies from perfect alignment (value of 1), to no alignment (i.e., the minimum angle would be at worst 60° hence an alignment of ca. 0.134). Therefore, I used a corrected alignment a_c varying from 0 (no alignment) to 1 (perfect alignment) such as

$$a_c = \frac{a - (1 - sin(\pi/3))}{1 - (1 - sin(\pi/3))}$$

I defined the general alignement for a given environmental map as the opposite of the skewness of alignment values of all trees in the map. Positive values indicate the existence of linear motifs while negative values indicate no obvious linear motifs. Random distributions (homogeneous or heterogeneous) should show moderate positive values, while a route pattern should have a high positive value (see Appendix Material).

Spatial autocorrelation of fruiting timing   Spatial autocorrelation of fruiting timing (i.e. the tendency of fruiting date of trees to more closely match that of neighbours than of distant trees) was calculated as the Moran Index, *I* applied to the start of fruiting dates. Since the date of start of fruiting corresponds to a circular variable, I followed (Schmal et al., 2017) to adapt existing functions of the *ape* package (Paradis & Schliep, 2019) to circular variables. Moran's *I* was therefore defined as

$$I = \frac{1}{\sum_{ij} w_{ij}} \frac{\sum_{ij} w_{ij} d(t_i, \bar{t}) d(t_j, \bar{t})}{N^{-1} \sum_i d(t_i, \bar{t})^2}$$

where N is the number of trees, t is the fruiting date (in radian), $d(t_1, t_2) = atan2(sin(t_1 - t_2), cos(t_1 - t_2))$, $\bar{t} = atan2(1/N \sum_i sin(t_i), 1/N \sum_i cos(t_i))$. I used the inverse of the Euclidean distance between tree locations as weights. Values of C close to 0 indicate absence of spatial autocorrelation. Values close to -1 indicate negative spatial autocorrelation. Values close to 1 indicate positive spatial autocorrelation.

Routine emergence

For each simulation, I verified whether a routine behaviour emerged and paralleled the variations in tree distribution. I characterised routine holding on the notion of conditional entropy following (Riotte-Lambert et al., 2017) using the series of the id of trees targeted during five supplementary seasons in which dispersal could not occur. I computed the routine possibly up to only a first order conditional entropy, as computing routine indices is computationally demanding and a first order is expected to be the most informative to describe a perfect traplining behaviour (Riotte-Lambert et al., 2017). The routine index varies from 0 (no routine) to 1 (perfect traplining).

Research questions and associated scenarios

Q1. Does resource spatiotemporal distribution vary with cognition level?   To investigate whether different levels of cognition eventually led to different distribution patterns, I considered five forager types differing by the proportion of trees for which the location and phenology were known (from 0 to 100%, at a step of 20). For each forager, 200 simulations were performed for a given condition (i.e. knowledge rate), in which the forager foraged individually 100 seasonal periods.

Q2. Does resource distribution engineering favour some cognition levels?   To investigate whether the engineered distribution of trees could in turn affect the foraging benefits purported by cognition, I used the final tree distributions of simulations computed to answer question 1). For each of these tree distributions, in three different simulation runs, I let forage a forager endowed with no, intermediate (i.e. half of trees known), or full (all trees known, omniscience/prescience, hereafter only omniscience) spatiotemporal knowledge. In these simulations, no seed-dispersal could occur. I measured the foraging efficiency after the forager foraged for 20 full seasons and compared them across environments and forager abilities. Foraging efficiency was computed as the cumulated quantity of eaten food, over the cumulated distance travelled. I verified that at the end of the simulation that foraging efficiency stabilised, which meant that I reached a foraging equilibrium. I considered that foraging efficiency stabilised when the foraging efficiency sampled after each moving bout during the fourth and fifth quintile of simulation times did not differ of more than 5% (reference is the minimum efficiency in the fourth or the fifth quintile of simulation times). I repeated the simulations for a given condition (i.e. knowledge rate) 200 times.

Q3. Route formation as a product of two forces? Tree competition for space and forager movement step rule   During the model construction, I noticed that two mechanisms could amplify the phenomenon of route formation, in addition to the use of memory: space competition between trees and sequential targeting of all trees seen *en route* to the target. To better quantify the effect of those two forces, I considered two other sets of 200 simulations each.
 To assess the effect of competition for space between trees, I compared the final tree spatiotemporal patterns when an omniscient forager (all tree locations and phenology known) was let foraging in the

²⁴⁸ same setting as in question 1, with the only difference that the exclusive lifespace between trees
²⁴⁹ could be of 5 (small lifespace), 45 (intermediate lifespace) or 85% (large lifespace) of the map surface,
²⁵⁰ so that the radius of this exclusive circular lifespace was always inferior to the perception range (15.17
²⁵¹ su vs 15.81 su).
²⁵² To assess the effect of the movement rule of the forager on tree distribution patterns, I compared the
²⁵³ final tree spatiotemporal patterns when an omniscient forager was let foraging in the same setting as
²⁵⁴ in question 1) and while the stringency in skipping trees encountered *en route* varied. It could either
²⁵⁵ stop at all trees perceived on the way to the initial target (mimicking a "monitoring" behaviour, as in
²⁵⁶ all other simulations; small skipping stringency), stop only at trees currently fruiting (i.e., with at least
²⁵⁷ 0.001 fu, mimicking an opportunistic feeding only; intermediate skipping stringency) or move directly
²⁵⁸ to the target (large skipping stringency).

III Results

III.1 Resource distribution is affected by the forager's cognition

²⁶¹ Foragers' spatiotemporal knowledge rate affected the resource distribution emerging after it had been
²⁶² let foraging for a long time (Figure 2). Both the patchiness (the tendency of trees to be aggregated
²⁶³ into patches) and the alignment (the tendency of trees to form linear geometries) varied non-linearly
²⁶⁴ and oppositely with spatiotemporal knowledge rate. Patchiness abruptly increased and was max-
²⁶⁵ imised (1.258 times superior to that when a naive forager foraged) for low cognition (spatiotemporal
²⁶⁶ knowledge rate of 0.25). Conversely, alignment was minimised for this spatiotemnporal knowledge
²⁶⁷ (remaining equal to when a naive forager foraged). In both cases, higher cognition led to larger patch-
²⁶⁸ iness (1.158 to 1.202 times) and alignment (1.323 to 1.681 times) than when a naive forager foraged
²⁶⁹ (Figure 2).
²⁷⁰ Spatial autocorrelation in fruiting date (the tendency of trees to have fruiting dates closer/farther
²⁷¹ in time to their spatial neighbours) somehow followed the same trend as patchiness (Figure 2), but
²⁷² the variations were quantitatively extremely reduced and values remained close to 0 (i.e., no spatial
²⁷³ autocorrelation).
²⁷⁴ Overall, such a space engineering was paralleled with the emergence of routine behaviours, which
²⁷⁵ increased with spatiotemporal knowledge rate to saturate around 0.8 (Figure 2). This held when no
²⁷⁶ dispersal occurred (Figure A4).

III.2 Engineered patterns could affect the selection gradient on spatiotemporal cognition

²⁷⁹ On average, an "omniscient" forager (knowing all trees' locations and phenology patterns) was around
²⁸⁰ 1.316 times more efficient than an "intermediate" forager (knowing only 50% of them) or 3.666 times
²⁸¹ than a "null" forager (knowning none of them) (Figure 3). While the benefits of omniscience relatively
²⁸² to a null forager were rather constant (min-max = 3.582-3.737 times larger), the relative benefits of
²⁸³ intermediate memory varied a little with the resource distribution emerging from previous engineering
²⁸⁴ (Figure 3). Compared to when the foragers foraged in an environment previously shaped by a null
²⁸⁵ forager (left boxplots in Figure 3), the relative foraging efficiency of intermediate foragers compared
²⁸⁶ to null foragers increased of 5.7% and 7.91% when the foragers foraged in an environment previously
²⁸⁷ shaped by an intermediate or omniscient forager, respectively (middle and right boxplots in Figure 3).
²⁸⁸ Similarly, the relative foraging efficiency of intermediate foragers compared to omniscient foragers
²⁸⁹ increased of 10.31% and 9.62% when the forager foraged in an environment previously shaped by
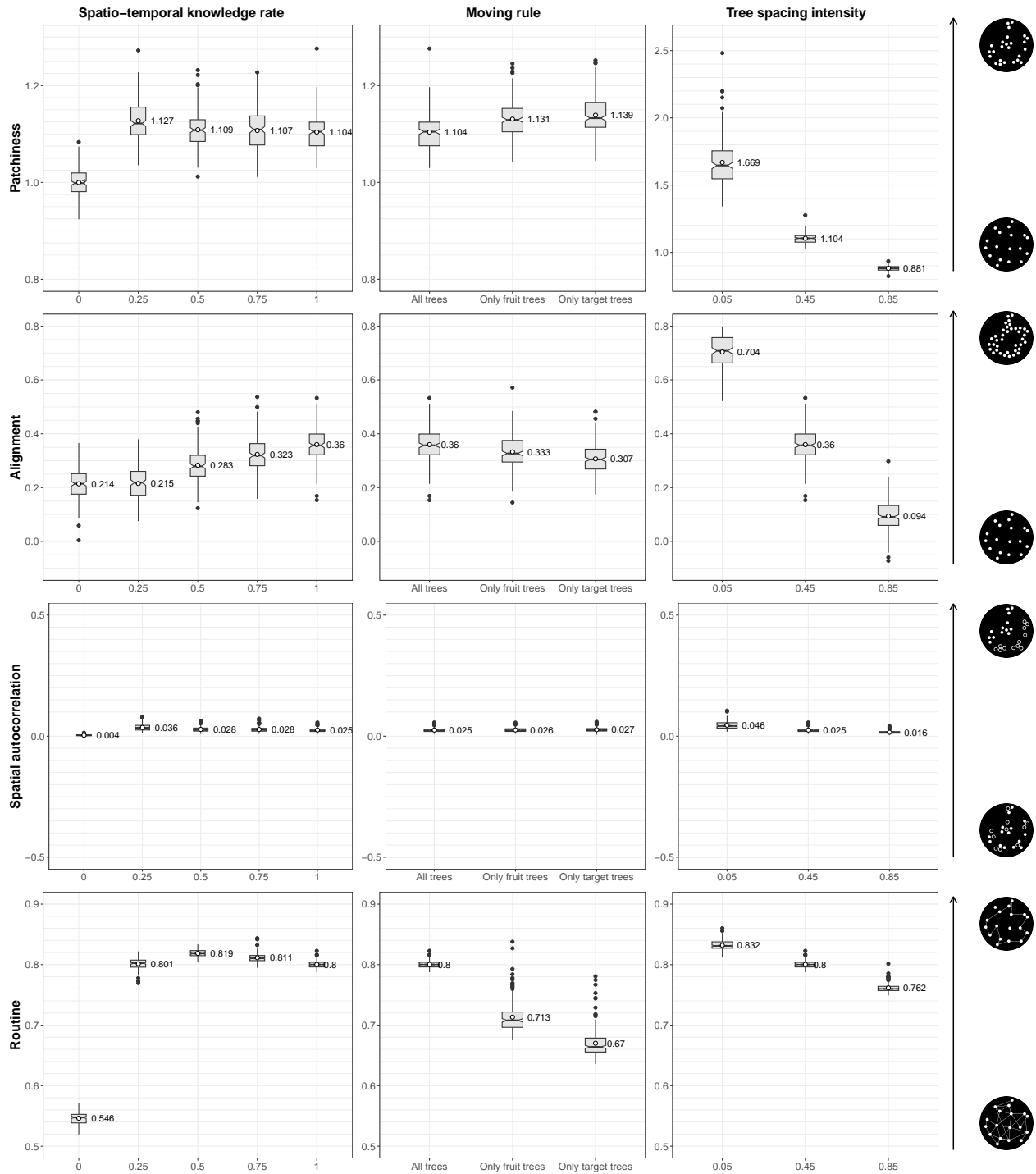
Figure 2 – Seed-dispersing foragers can shape resource distribution | The plots show the results of 200 simulations when a seed-dispersing forager with varying level of cognition (i.e. proportion of tree locations and associated phenology known), moving choice rules or space competition intensities between trees (the two latter being simulated with an omniscient forager; left to right) was let foraging for a long time. The resulting distribution pattern was assessed by its patchiness (the tendency of trees to be aggregated into patches; larger values indicate highly aggregated trees), its alignement (the tendency of trees to form linear geometries; larger values indicate the presence of linear geometries) and spatial autocorelation in fruiting date (the tendency of trees to have fruiting dates closer/farther in time to their spatial neighbours; values close to 0 indicate negative spatial autocorrelation, values close to 1 indicate no spatial autocorrelation, values above 1 indicate positive spatial autocorrelation). The emerging movement behaviour of the forager was described in terms of routine behaviour (the tendency of the forager to target trees in a predictible way; values close to 0 indicate no predictible movement, values close to 1 indicate highly predictible movements).
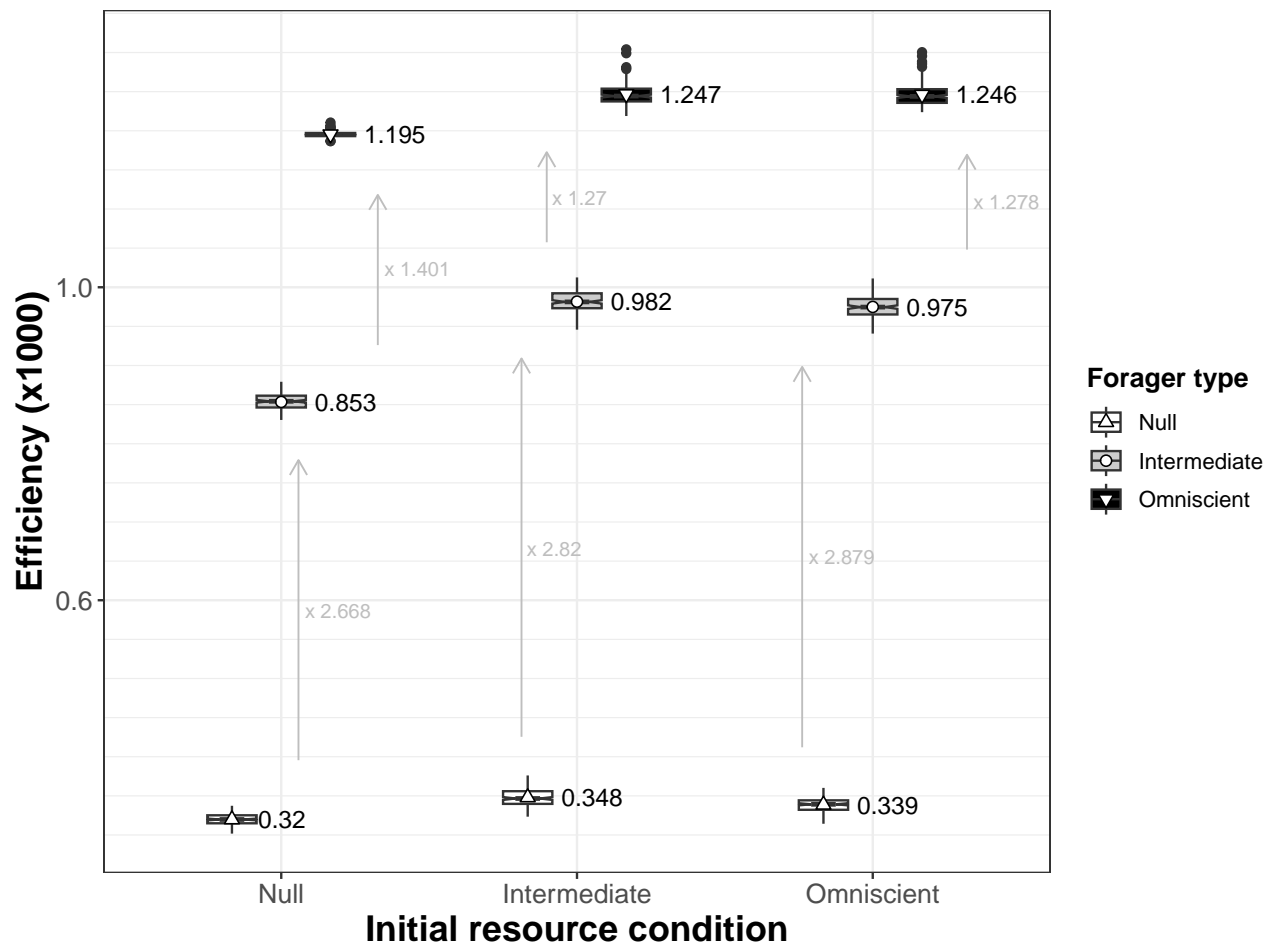
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Figure 3 – Relative foraging benefits of cognition are sensitive to the emerging resource distribution | The 'initial condition' of resource distribution was taken from the simulations in which a null, intermediate or omniscient forager was first let foraging. Then, those three forager types were let foraging (separately) without dispersal and foraging efficiency was measured (cumulated food eaten over cumulated travelled distance).

290 an intermediate or omniscient forager, respectively, compared to when the foragers foraged in an
291 environment previously shaped by a null forager.

III.3● Route formation is reinforced because of opportunistic stops and by low tree space competition

294 How a forager moved to the target affected the emerging resource pattern (Figure 2). In particular,
295 moving to all trees encountered *en route* to the target induced a 1.117 times lower patchiness than
296 only stopping to fruit trees and 1.128 times lower than moving only to the target. Resource alignment
297 was 1.081 and 1.172 times higher when the forager stopped at all trees rather than only stopped
298 fruiting trees or moved directly to the target (Figure 2). Both patchiness and alignment were con-
299 siderably reduced by competition for space between trees, with patchiness 1.643 and 2.134 times
300 larger when competition for space between trees was low compared to when it was intermediate or
301 high, and alignment being 2.04 and 7.814 times larger, respectively (Figure 2).
302   Spatial autocorrelation in fruiting date remained mostly unaffected by the forager movement rule or
303 competition for space between trees (Figure 2).
304   Variations in movement rules were paralleled by variations in routine behaviour, with foragers moving
305 to all trees being 1.122 and 1.194 times more routine than foragers stopping only to fruit trees or
306 their target, respectively. Competition for space between trees similarly affected the tendency of the
307 forager to engage in routine behaviour, with a larger routine when competition for space between
308 trees was low (Figure 2).

IV Discussion

310 The environment is shaped by the species that inhabit it. The destructive behaviour of some
311 animals when moving, such as forest elephants (Pringle, 2008; Vanleeuwe & Gautier-Hion,
312 1998), can lead to blatant changes, but more elusive - yet no less ecologically relevant - engineering
313 can also occur over longer time scales. Using an agent-based model, I have illustrated the role of vagile
314 animals in shaping the distribution of plants through zoochory. Based on a minimal set of realistic
315 assumptions, I showed how this slow process could affect resource distribution provided that the
316 seed-dispersing animal was endowed with cognitive abilities, which in turn shaped selection on these
317 abilities. Therefore, this study illustrates how foraging cognition is both a cause and a consequence
318 of resource heterogeneity.
319   As the breadth of knowledge increased, routine behaviour, the ability to repeatedly follow a fixed
320 sequence of movements, developed (routine index > 0.8, Riotte-Lambert et al., 2015). The model
321 evidenced that the emergence of such behaviour was associated with changes in the distribution of
322 resources, which tended to become more patchy, eventually forming linear features paralleling the
323 routes used. The agglomeration of seeds for cognitive foragers has been proposed theoretically (John
324 et al., 2016) and empirically (Fragoso et al., 2003), ultimately impacting the genetic structure and flow
325 of plant populations (Gelmi-Candusso et al., 2017). Here, the model highlighted how engineering
326 can go further by contributing to a more organised distribution of resources, with the emergence of
327 linear features likely to be associated with the foraging routes used due to cognition, as suggested
328 by forest elephant routes matching with fruit gradients in the forest (Blake et al., 2009). Indeed,
329 the non-linearity of the changes in patchiness and alignment with the cognition of the forager likely
330 corresponds to the formation of the routes themselves, with the "materialisation" first of the route
331 intersections (hence higher patchiness, lower alignment for low cognition), where most of the recur-

13

sions occur (Presotto et al., 2018), before more routes are used and formed when cognition increases. Long-distance travels through these routes may explain why animal-dispersed plant species are less aggregated than when other dispersal mechanisms are involved, such as gravichory, where dispersed seeds do not travel far from the parent tree (Seidler & Plotkin, 2006). This engineering remained yet limited because the resource patterns did not fully match the simulated route-based patterns (see Appendix). Furthermore, despite vertical inheritance of the parent tree phenology, seed dispersal was not sufficient to drive spatial autocorrelation in fruiting dates. This was not because the trees all ended up fruiting at the same time, as there was still ample variation in fruiting timing at the end of the simulations (see Appendix). Tree synchrony is an important tool that can be used by foragers to plan their movements efficiently (Janmaat et al., 2012). Given the climatic drivers of large-scale synchrony, the latter can be tracked by animals (Janmaat et al., 2006). A fine-scale synchrony is also observed in nature (Lamontagne & Boutin, 2007) and might as likely affect animal foraging success. While large-scale population trends in phenology might stem from genetic constraints (Chuine et al., 2000; Lyngdoh et al., 2012), the absence of emergence of spatial autocorrelation in fruiting date in this model (which considers vertical inheritance) may suggest a mainly non-genetic origin of these fine-scale variations in the absence of other dispersal modes (e.g. gravichory, leading to highly clustered patterns, Seidler & Plotkin, 2006). However, these conclusions may be challenged by more accurate modelling of movement behaviour, which may lead to different results (see below). Despite these limits, the observed spatial engineering could still be sufficient for the emergence of eco-evolutionary feedback loops between animal resources and animal movement (and cognition) (Riotte-Lambert & Matthiopoulos, 2020) due to the evidenced repercussions on foragers' foraging efficiency.

While the same individual might experience little change in resource distribution over its lifetime, the progressive engineering of resource distribution could overturn selection over generations. This model showed that changes in environmental conditions were likely to affect the benefits of memory, but not enough to completely overturn selection. Indeed, in all environment, memory was advantageous. The relative advantage of omniscience compared to no memory was nearly constant whatever the environment. Interestingly in contrast, the relative advantage of intermediate memory compare to no memory, was increased in engineered environments. The performance of these naive agents is clearly dependent on their sensory abilities (Grove, 2013). Although always superior to the randomly expected nearest neighbour distance, the sensory range modelled here may have been insufficient for simple movement strategies such as taxis to perform well. As much as memory could be favoured, the environment could also shape sensory abilities (LaScala-Gruenewald et al., 2019). Still, the changes in the relative efficiency of cognitive agents open the door to the possible emergence of evolutionary feedback loops if the costs of memory are no longer compensated, which should lead to a dynamic equilibrium (Beisner et al., 2003) due to the simultaneous changes in memory benefits (hence selection) with space engineering.

Space engineering was reinforced by the conjunction of two forces: the forager movement rules and competition for space between trees. Maximum resource engineering was achieved when the individual moved to all the trees it encountered along the way. At the other extreme, when the animal moved directly to the best target, engineering was reduced, following routine trends. Although more efficient, moving straight to the target is rarely observed in nature. Instead, animals tend to move along routes, sometimes bypassing or otherwise opportunistically inspecting trees without resources, fitting with a beacon-based navigation, where individuals move from beacon to beacon to reach a goal (Fagan et al., 2013; Warren, 2019). Such a movement strategy gives them the possibility to monitor the environment (de Guinea et al., 2019), allowing them to update personal information. As such, despite short-term costs due to detours, moving to all tress might provide long-term advantages. However, the simulated movement patterns remain extremely simplistic. Animal movement is in reality much more nuanced than in this modelling work. This could be important for seed acquisition

and deposition (Morales & Morán López, 2022). For example, this model considered directed movement supported by memory, which could alternate with random steps when memory was limited but independent of local cue feedback, as it would rather be expected for efficient foraging (Benhamou & Collet, 2015). Animal movement may indeed alternate between 'large-scale' directed relocation events and 'area-restricted' wandering searches of the tree in a non-random manner (Bartumeus et al., 2016). When and where area-restricted searches occur may further contribute to the emergent distribution of seed deposition (Russo et al., 2006; Westcott et al., 2005), provided that both seed deposition and foraging can occur simultaneously. Animals may yet be selective about where and when they defecate. The presence of latrines may contribute to shaping the distribution of resources too (Fragoso, 1997; Fuzessy et al., 2022b; Irwin et al., 2004; Pouvelle et al., 2009; Sakamoto & Takatsuki, 2015). Overall, as movement and/or dispersal scales with behaviour/personality (Brehm & Mortelliti, 2022; Zwolak, 2018; Zwolak & Sih, 2020), but also species and individual size (Jordano et al., 2007), a multi-individual and multi-species system could lead to a more complex multi-scale scaffolding than illustrated here. This could explain why the evolution of the cognitive machinery underpinning foraging might depend on the frugivore community composition (Robira & Perez-Lamarque, 2023).

In this scaffolding, the plant itself may also play a role. Not only are seed characteristics important in the dispersal process (Albert et al., 2015; Fuzessy et al., 2018), but the success of seedling germination is highly dependent on the conditions in which the seed is deposited, due to direct or indirect actions of conspecifics. This model took into account negative interactions between trees (e.g. competition for resource, Craine & Dybzinski, 2013, inducing an exclusive space use) and illustrated how this could act as a barrier to spatial engineering. Indeed, as competition for space between trees increased, both patchiness and alignment logically decreased. While the model effect was interpreted as a competition for space, this may also encompass other processes such as greater exposure of seeds to predation risk in the vicinity of adult plant conspecifics (Janzen, 1970). Conversely, facilitation could also occur, with the adult plants acting as a shelter for new seedlings (Callaway, 1995). This facilitation should thus increase clustering. While directly unmodelled here, in the quasi absence of competition for space, tree range was coherently drastically reduced (i.e. shrunk; Figure A3), with a tendency to agglomerate towards the centre of the map, where individual recurrences are likely to be most important. Therefore, the engineered patterns (e.g. from increased patchiness to route formation) may also depend on plant interactions, adding to the complexity of the system depicted.

The sessile lifestyle of plants may have created the illusion of residual fixity in the environmental conditions that shape the lives of frugivorous animals. While, in the absence of depletion, the resource spatial distribution is likely to remain the same in the short term, conferring the benefits of information retention in frugivores, resource spatial distribution can also change over longer periods of time. Selection could thus operate in two ways at two different evolutionary speeds: frugivores could play a key role in plant traits by actively selecting and dispersing their food over long time, while their traits could have been shaped by foraging on that primary food over shorter time. Considering the feedback loops between these different entities could be an important facet to make sense of still poorly understood patterns of co-evolution, such as the primates/angiosperms dyad (Fuzessy et al., 2023; Fuzessy et al., 2022a; Gómez & Verdú, 2012; Sussman, 1991).

V Acknowledgements

VI   Funding

VII   Declaration of conflict of interest

I declare having no conflict of interest.

VIII   Data and code availability

The code used to generate the data and perform the analyses is available at https://github.com/benjaminrobira/ModelZoochoryCognition. To fully reproduce the analysis, a singularity image (through which the model can be run and which was used to run the simulations on the HPC cluster) can be provided on request, as it is too large to store on git.

IX   Appendix

IX.1   Using patchiness and alignment to characterise spatial point patterns

I provide below evidence that the two metrics, namely *patchiness* and *alignment*, allows for distinguishing between homogeneous, heterogeneous and route point patterns. In both the low (100 trees) and high (1000 trees) density, I considered 1/10 of the number of trees as the number of clusters for the heterogeneous distribution (i.e. 10 clusters at low density, 100 at high density). Around these clusters of strictly equivalent size, trees were distributed according to a Gaussian distribution (both for the *x* and *y* axis) of variance 50 su. The distribution resembling a route network was obtained by modelling one (low density) to ten (high density) correlated random walks of 100 steps ("simm.crw" function of the *adehabitatLT* package, Calenge (2006), with a scaling parameter, to determine step length, of 20 su, and a concentration parameter, relative to the correlation in heading, of 0.9). I calculated the two metrics on 200 distributions.

Homogeneous distributions are identified by a low patchiness and a low alignment. Heterogeneous distributions are identified by an intermediate patchiness and a low alignment. Finally route point distributions are evidenced by a high patchiness and a high alignment (Figure A2). This pattern is robust to density variations, although absolute differences in the indices shrink with density increase (Figure A2).

IX.2   Variations in resource range shrinkage intensity

Shrinkage was affected by the forager's cognition, peaking at low cognition (Figure A3a). Shrinkage was also driven by the forager limiting visits to tree encountered *en route*, with a maximum reached when the forager discarded all of these trees and moved directly to the target (Figure A3b). Finally, shrinkage was removed when the competition for space between trees was high (Figure A3c).

IX.3   Variations in routine behaviour when no dispersal occurs

In the absence of seed dispersal (scenarios in Q2 were used), routine behaviour still increased (and saturated) with more advanced cognition, whatever the environment (i.e. the engineering level, Figure A4).

IX.4   Variations in fruiting dates

I quantified the variation in fruiting dates as one minus the length of the mean vector of fruiting dates (Batschelet, 1981) in either the initial or final conditions. It varies from 0 (no variation; all fruiting dates are the same) to 1 (extensive variation; fruiting dates are uniformly distributed). At the beginning or end of the simulations, the variation in fruiting dates was considerable, regardless of the scenario tested (Figure A5).
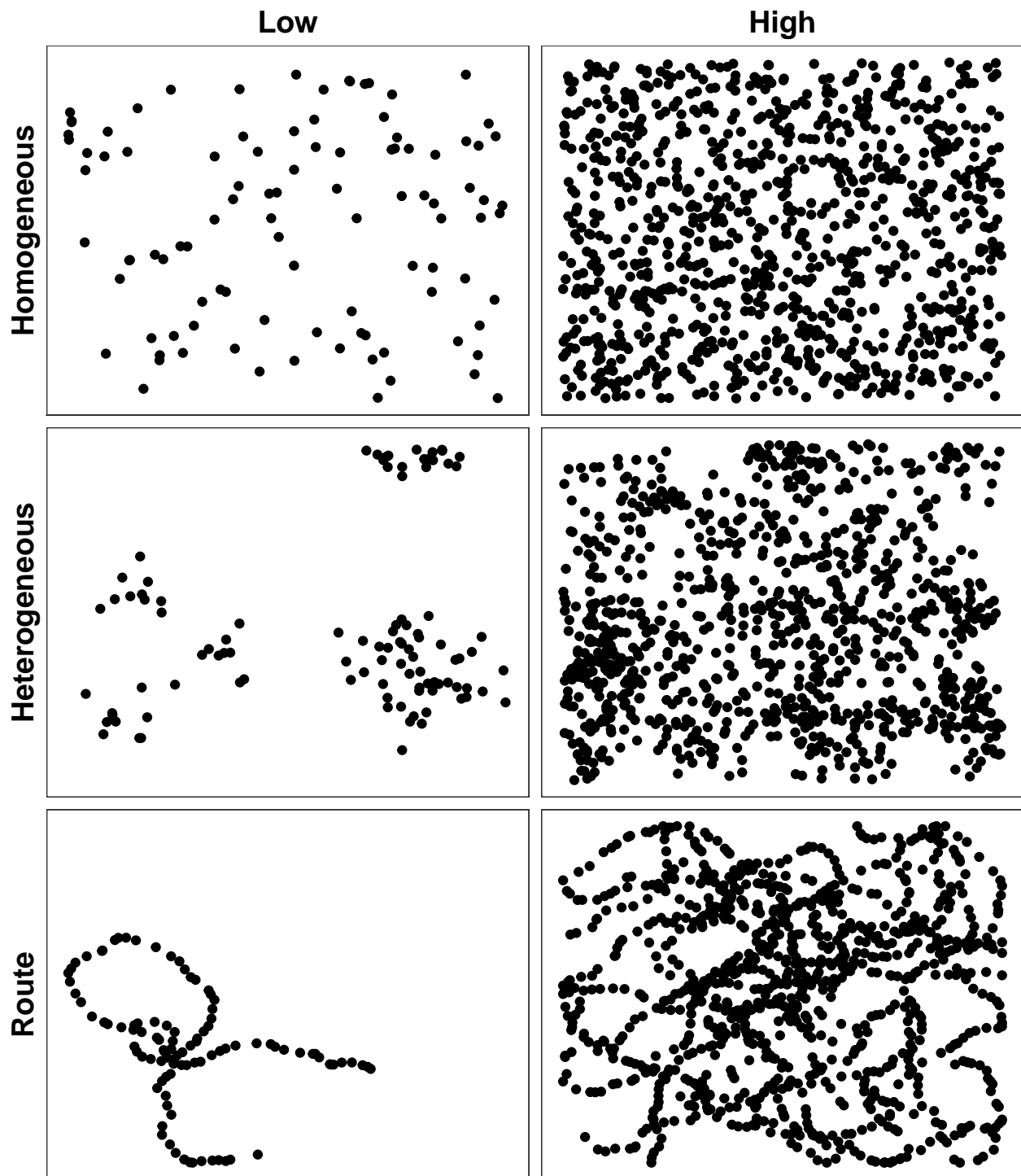
Figure A1 – Simulated spatial distributions to investigate metrics value | Distribution: Homo. = homogeneous, Hetero. = Heterogeneous, Route = Route network-like. Tree population size: Low = 100 trees, High = 1000 trees, within a square map of side length 1000 su.
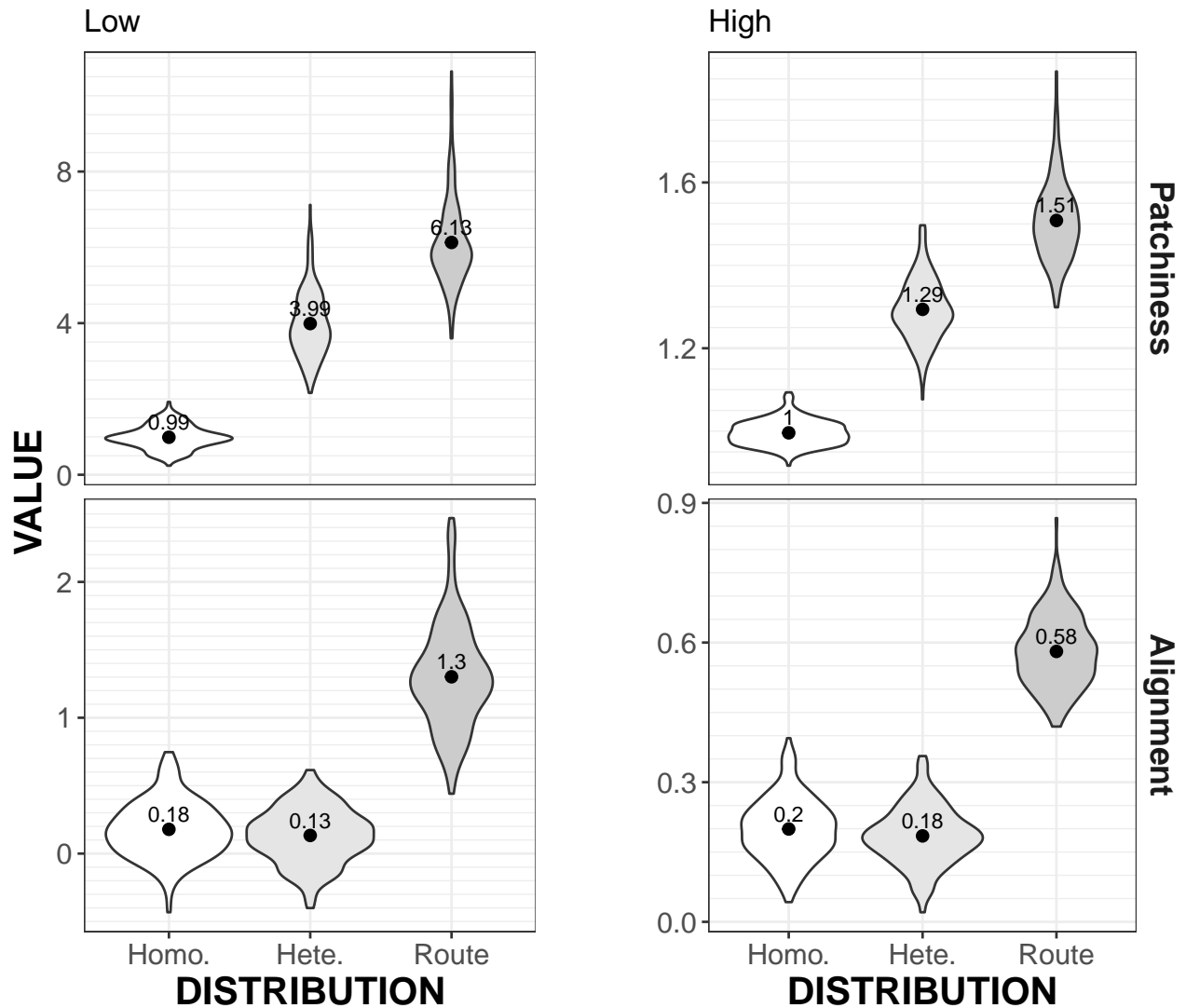
Figure A2 – Patchiness and alignment allow for identifying spatial distributions at low (100 trees) or high (1000 trees) tree population size | Results are based from simulated data following a homogeneous (Homo.), heterogeneous (Hetero.) or route network-like (Route) distribution. The mean value is depicted by the black dot and the text. The shape of the distribution is depicted by the contour of the violins.
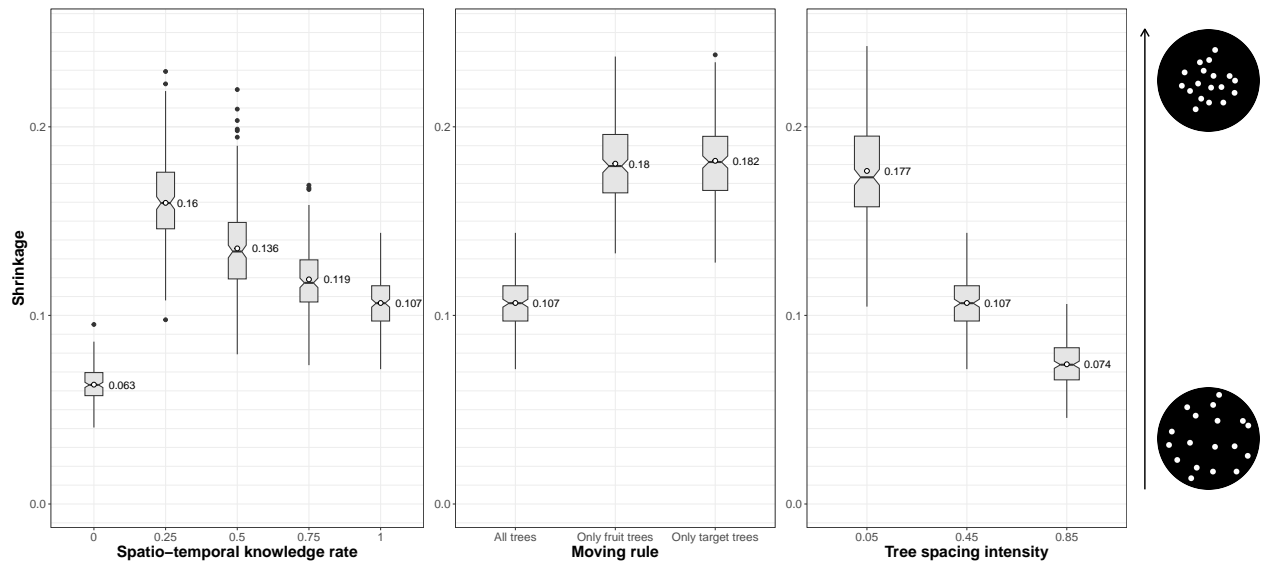
Figure A3 – Shrinkage of resource range is driven by cognition, the forager's movement rules and competition for space between trees.
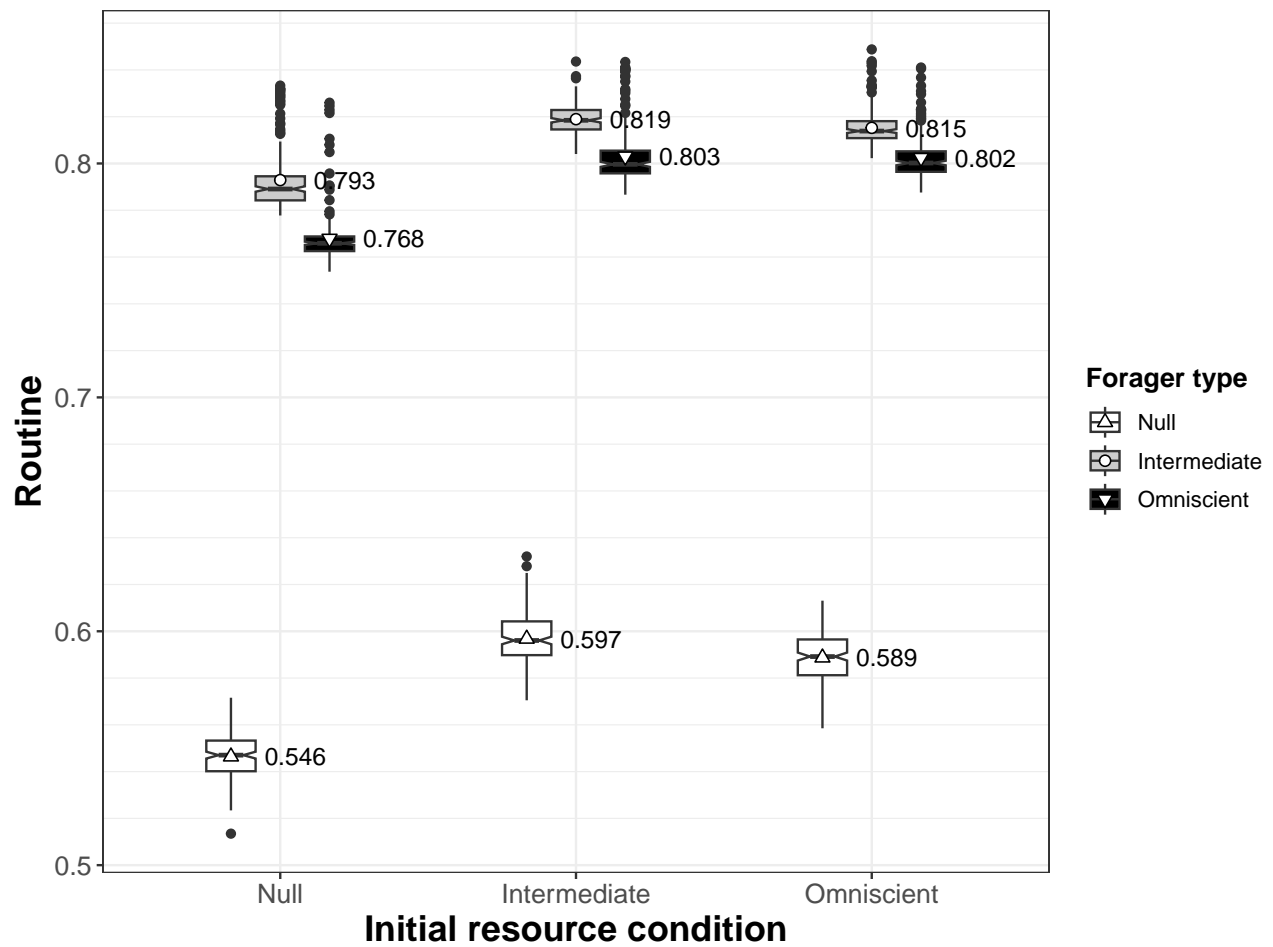
Figure A4 – Routine emerges when cognition is high, independent of environment engineering | The 'initial condition' of resource distribution was taken from the simulations in which a null, intermediate or omniscient forager was first let foraging. Then, those three forager types were let foraging (separately) without dispersal and routine behaviour was quantified (the tendency of the forager to target trees in a predictible way; values close to 0 indicate no predictible movement, values close to 1 indicate highly predictible movements).
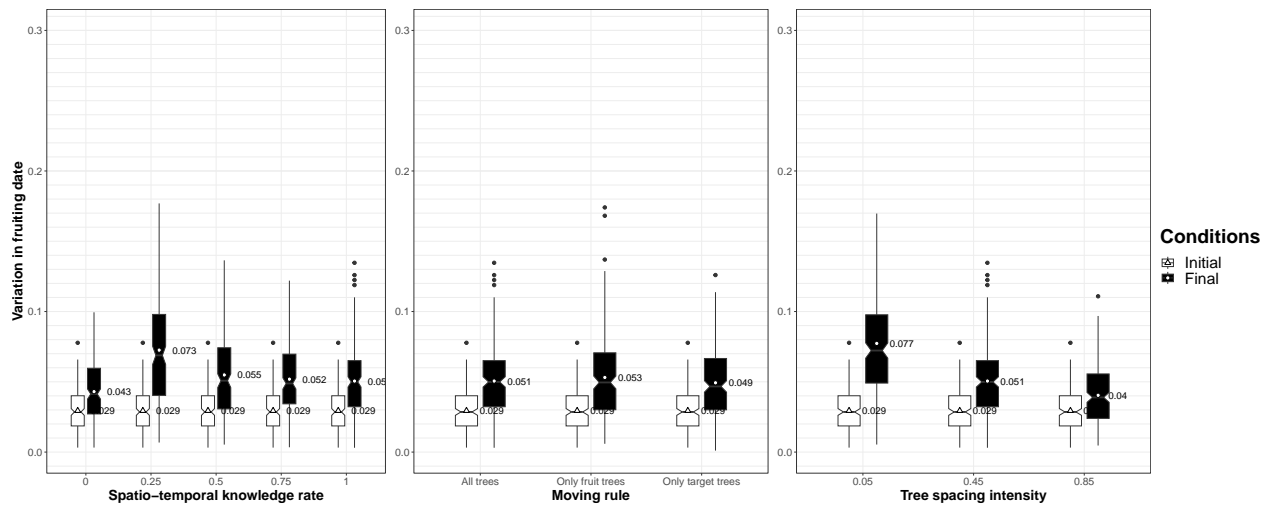
Figure A5 – Variation in fruiting dates at the beginning of the simulation ('initial' condition) or at the end ('final' condition) | The plots show the results of 200 simulations when a seed-dispersing forager with varying level of cognition (i.e. proportion of tree locations and associated phenology known), moving choice rules or space competition intensities between trees (the two latter being simulated with an omniscient forager; left to right) was let foraging for a long time. The index of variation in fruiting dates ranges from 0 (no variation) to 1 (extensive variation).

References

Addis, C. R., et al. (2017). *Causes and consequences of movement: The interaction between foraging and landscape patterns* (Doctoral dissertation).

Albert, A., Auffret, A. G., Cosyns, E., Cousins, S. A. O., D'hondt, B., Eichberg, C., Eycott, A. E., Heinken, T., Hoffmann, M., Jaroszewicz, B., Malo, J. E., Mårell, A., Mouissie, M., Pakeman, R. J., Picard, M., Plue, J., Poschlod, P., Provoost, S., Schulze, K. A., & Baltzinger, C. (2015). Seed dispersal by ungulates as an ecological filter: A trait-based meta-analysis. *Oikos*, *124*(9), 1109–1120. https://doi.org/https://doi.org/10.1111/oik.02512

Avgar, T., Deardon, R., & Fryxell, J. M. (2013). An empirically parameterized individual based model of animal movement, perception, and memory. *Ecological Modelling*, *251*, 158–172. https://doi.org/10.1016/j.ecolmodel.2012.12.002

Bagchi, R., Henrys, P. A., Brown, P. E., Burslem, D. F., Diggle, P. J., Gunatilleke, C. V., Gunatilleke, I. A., Kassim, A. R., Law, R., Noor, S., & Valencia, R. L. (2011). Spatial patterns reveal negative density dependence and habitat associations in tropical trees. *Ecology*, *92*(9), 1723–1729. https://doi.org/10.1890/11-0335.1

Ban, S. D., Boesch, C., & Janmaat, K. R. (2014). Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition*, *17*(6), 1353–1364. https://doi.org/10.1007/s10071-014-0771-y

Ban, S. D., Boesch, C., N'Guessan, A., N'Goran, E. K., Tako, A., & Janmaat, K. R. (2016). Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits. *Animal Behaviour*, *118*, 135–147. https://doi.org/10.1016/j.anbehav.2016.05.014

Bartumeus, F., Campos, D., Ryu, W. S., Lloret-Cabot, R., Méndez, V., & Catalan, J. (2016). Foraging success under uncertainty: search tradeoffs and optimal space use. *Ecology Letters*, *19*(11), 1299–1313. https://doi.org/10.1111/ele.12660

Batschelet, E. (1981). *Circular Statistics in Biology*. Academic Press.

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, *1*(7), 376–382.

Benhamou, S. (2014). Of scales and stationarity in animal movements. *Ecology Letters*, *17*(3), 261–272. https://doi.org/10.1111/ele.12225

Benhamou, S., & Bovet, P. (1992). Distinguishing between elementary orientation mechanisms by means of path analysis. *Animal Behaviour*, *43*(3), 371–377.

Benhamou, S., & Collet, J. (2015). Ultimate failure of the lévy foraging hypothesis: Two-scale searching strategies outperform scale-free ones even when prey are scarce and cryptic. *Journal of theoretical biology*, *387*, 221–227.

Benhamou, S., & Poucet, B. (1995). A comparative analysis of spatial memory processes. *Behavioural Processes*, *35*(1-3), 113–126.

Blake, S., Deem, S. L., Mossimbo, E., Maisels, F., & Walsh, P. (2009). Forest elephants: Tree planters of the congop. *Biotropica*, *41*(4), 459–468. https://doi.org/10.1111/j.1744-7429.2009.00512.x

Blake, S., & Inkamba-Nkulu, C. (2004). Fruit, minerals, and forest elephant trails: Do all roads lead to Rome? *Biotropica*, *36*(3), 392–401. https://doi.org/10.1111/j.1744-7429.2004.tb00332.x

Borah, B., & Beckman, N. G. (2022). Studying seed dispersal through the lens of movement ecology. *Oikos*, *2022*(2).

Boyer, D., & Walsh, P. D. (2010). Modelling the mobility of living organisms in heterogeneous landscapes: Does memory improve foraging success? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *368*(1933), 5645–5659. https://doi.org/10.1098/rsta.2010.0275

Bracis, C., Gurarie, E., Van Moorter, B., & Goodwin, R. A. (2015). Memory effects on movement behavior in animal foraging. *PLoS ONE*, *10*(8), e0136057. https://doi.org/10.1371/journal.pone.0136057

Brehm, A. M., & Mortelliti, A. (2022). Small mammal personalities generate context dependence in the seed dispersal mutualism. *Proceedings of the National Academy of Sciences*, *119*(15), e2113870119. https://doi.org/10.1073/pnas.2113870119

Burns, J. G., Foucaud, J., & Mery, F. (2011). Costs of memory: Lessons from 'mini'brains. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707), 923–929.

Calenge, C. (2006). The package adehabitat for the r software: Tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 1035.

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, *61*, 306–349.

Campos-Arceiz, A., & Blake, S. (2011). Megagardeners of the forest - the role of elephants in seed dispersal. *Acta Oecologica*, *37*(6), 542–553. https://doi.org/10.1016/j.actao.2011.01.014

Chapman, C. A., Bonnell, T. R., Gogarten, J. F., Lambert, J. E., Omeja, P. A., Twinomugisha, D., Wasserman, M. D., & Rothman, J. M. (2013). Are primates ecosystem engineers? *International Journal of Primatology*, *34*(1), 1–14. https://doi.org/10.1007/s10764-012-9645-9

Chuine, I., Belmonte, J., & Mignot, A. (2000). A modelling analysis of the genetic variation of phenology between tree populations. *Journal of Ecology*, *88*(4), 561–570. Retrieved June 21, 2023, from http://www.jstor.org/stable/2648589

Côrtes, M. C., & Uriarte, M. (2013). Integrating frugivory and animal movement: A review of the evidence and implications for scaling seed dispersal. *Biological Reviews*, *88*(2), 255–272.

Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, *27*(4), 833–840. https://doi.org/https://doi.org/10.1111/1365-2435.12081

de Guinea, M., Estrada, A., Nekaris, K. A.-I., & Van Belle, S. (2019). Arboreal route navigation in a Neotropical mammal: Energetic implications associated with tree monitoring and landscape attributes. *Movement Ecology*, *7*(1), 1–12. https://doi.org/10.1186/s40462-019-0187-z

Eddelbuettel, D. (2013). *Seamless R and C++ integration with Rcpp* [ISBN 978-1-4614-6867-7]. Springer. https://doi.org/10.1007/978-1-4614-6868-4

Eddelbuettel, D., & Balamuta, J. J. (2018). Extending extitR with extitC++: A Brief Introduction to extitRcpp. *The American Statistician*, *72*(1), 28–36. https://doi.org/10.1080/00031305.2017.1375990

Eddelbuettel, D., & François, R. (2011). Rcpp: Seamless R and C++ integration. *Journal of Statistical Software*, *40*(8), 1–18. https://doi.org/10.18637/jss.v040.i08

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., Ladage, L., Schlägel, U. E., Tang, W. W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*(10), 1316–1329. https://doi.org/10.1111/ele.12165

Flörchinger, M., Braun, J., Böhning-Gaese, K., & Schaefer, H. M. (2010). Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia*, *164*(1), 151–161. https://doi.org/10.1007/s00442-010-1655-8

Fragoso, J. M. V. (1997). Tapir-generated seed shadows: Scale-dependent patchiness in the amazon rain forest. *Journal of Ecology*, *85*(4), 519–529.

Fragoso, J. M. V., Silvius, K. M., & Correa, J. A. (2003). Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology*, *84*(8), 1998–2006. https://doi.org/https://doi.org/10.1890/01-0621

Fuzessy, L., Balbuena, J. A., Nevo, O., Tonos, J., Papinot, B., Park, D., Sol, D., Valenta, K., Razafindratsima, O., & Verdu, M. (2023). Friends or foes? plant-animal coevolutionary history is driven by both mutualistic and antagonistic interactions.

Fuzessy, L., Silveira, F. A., Culot, L., Jordano, P., & Verdú, M. (2022a). Phylogenetic congruence between Neotropical primates and plants is driven by frugivory. *Ecology Letters*, *25*(2), 320–329. https ://doi.org/10.1111/ele.13918

Fuzessy, L., Sobral, G., & Culot, L. (2022b). Linking howler monkey ranging and defecation patterns to primary and secondary seed dispersal. *American Journal of Primatology*, *84*(2), e23354. htt ps://doi.org/https://doi.org/10.1002/ajp.23354

Fuzessy, L. F., Janson, C., & Silveira, F. A. (2018). Effects of seed size and frugivory degree on dispersal by neotropical frugivores. *Acta Oecologica*, *93*, 41–47.

Gelmi-Candusso, T. A., Heymann, E. W., & Heer, K. (2017). Effects of zoochory on the spatial genetic structure of plant populations. *Molecular Ecology*, *26*(21), 5896–5910. https://doi.org/https: //doi.org/10.1111/mec.14351

Gómez, J. M., & Verdú, M. (2012). Mutualism with plants drives primate diversification. *Systematic Biology*, *61*(4), 567–577. https://doi.org/10.1093/sysbio/syr127

Gottsberger, G., & Silberbauer-Gottsberger, I. L. S. E. (1983). Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbd natuwiss. ver. Hamburg*, *7*, 315–352.

Grove, M. (2013). The evolution of spatial memory. *Mathematical Biosciences*, *242*(1), 25–32. https: //doi.org/10.1016/j.mbs.2012.11.011

Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest: That tropical trees are clumped, not spaced, alters conceptions of the organization and dynamics. *Science*, *203*(4387), 1299–1309.

Irwin, M. T., Samonds, K. E., Raharison, J.-L., & Wright, P. C. (2004). Lemur Latrines: Observations of Latrine Behavior in Wild Primates and Possible Ecological Significance. *Journal of Mammalogy*, *85*(3), 420–427. https://doi.org/10.1644/1383937

Janmaat, K. R., Ban, S. D., & Boesch, C. (2013). Taï chimpanzees use botanical skills to discover fruit: What we can learn from their mistakes. *Animal Cognition*, *16*(6), 851–860. https://doi.org/10 .1007/s10071-013-0617-z

Janmaat, K. R., Byrne, R. W., & Zuberbühler, K. (2006). Primates take weather into account when searching for fruits. *Current Biology*, *16*(12), 1232–1237. https://doi.org/10.1016/j.cub.2006 .04.031

Janmaat, K. R., Chapman, C. A., Meijer, R., & Zuberbühler, K. (2012). The use of fruiting synchrony by foraging mangabey monkeys: A 'simple tool' to find fruit. *Animal Cognition*, *15*(1), 83–96. https://doi.org/10.1007/s10071-011-0435-0

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, Cebus apella. *Animal Behaviour*, *55*(5), 1229–1243. https://doi.org/10.1006/anbe.1997.0688

Janson, C. H. (2016). Capuchins, space, time and memory: An experimental test of what-where-when memory in wild monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1840), 20161432. https://doi.org/10.1098/rspb.2016.1432

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*(940), 501–528.

John, E. A., Francesca, S., Burman, O. H. P., Anna, W., & Pike, T. W. (2016). Plant ecology meets animal cognition: impacts of animal memory on seed dispersal. *Plant Ecology*, *217*, 1441–1456. http s://doi.org/10.1007/s11258-016-0652-3

Jordano, P., García, C., Godoy, J. A., & García-Castaño, J. L. (2007). Differential contribution of fru-givores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences*, *104*(9), 3278–3282. https://doi.org/10.1073/pnas.0606793104

Lambert, J. E., & Garber, P. A. (1998). Evolutionary and ecological implications of primate seed disper-sal. *American Journal of primatology*, *45*(1), 9–28.

Lamontagne, J. M., & Boutin, S. (2007). Local-scale synchrony and variability in mast seed production patterns of picea glauca. *Journal of Ecology*, *95*(5), 991–1000.

LaScala-Gruenewald, D. E., Mehta, R. S., Liu, Y., & Denny, M. W. (2019). Sensory perception plays a larger role in foraging efficiency than heavy-tailed movement strategies. *Ecological Modelling*, *404*, 69–82. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2019.02.015

Lloyd, M. (1967). Mean crowding. *The Journal of Animal Ecology*, 1–30. https://doi.org/https://doi.org/10.2307/3012

Lomáscolo, S. B., & Schaefer, H. M. (2010). Signal convergence in fruits: A result of selection by frugivores? *Journal of Evolutionary Biology*, *23*(3), 614–624. https://doi.org/10.1111/j.1420-9101.2010.01931.x

Lyngdoh, N., Gunaga, R., Joshi, G., Vasudeva, R., Ravikanth, G., & Shaanker, R. U. (2012). Influence of geographic distance and genetic dissimilarity among clones on flowering synchrony in a teak (*Tectona grandis Linn. f*) clonal seed orchard. *Silvae Genetica*, *61*(1-6), 10–18.

Milton, K. (1981). Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development. *American Anthropologist*, *83*(3), 534–548. https://doi.org/10.1525/aa.1981.83.3.02a00020

Morales, J. M., & Morán López, T. (2022). Mechanistic models of seed dispersal by animals. *Oikos*, *2022*(2). https://doi.org/https://doi.org/10.1111/oik.08328

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.

Pouvelle, S., Jouard, S., Feer, F., Tully, T., & Ponge, J.-F. (2009). The latrine effect: Impact of howler monkeys on the distribution of small seeds in a tropical rain-forest soil. *Journal of Tropical Ecology*, *25*(3), 239–248. https://doi.org/10.1017/S0266467409005987

Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O., Spagnoletti, N., Madden, M., & Izar, P. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, *21*(3), 393–405. https://doi.org/10.1007/s10071-018-1176-0

Pringle, R. M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, *89*(1), 26–33. https://doi.org/10.1890/07-0776.1

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/

Raichle, M. E. (2006). The brain's dark energy. *Science-New York Then Washington-*, *314*(5803), 1249.

Riotte-Lambert, L., Benhamou, S., & Chamaillé-Jammes, S. (2015). How memory-based movement leads to nonterritorial spatial segregation. *American Naturalist*, *185*(4), E103–E116. https://doi.org/10.1086/680009

Riotte-Lambert, L., Benhamou, S., & Chamaillé-Jammes, S. (2017). From randomness to traplining: a framework for the study of routine movement behavior. *Behavioral Ecology*, *28*(1), 280–287. https://doi.org/10.1093/beheco/arw154

Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology and Evolution*, *35*(2), 163–174. https://doi.org/10.1016/j.tree.2019.09.009

Robira, B., Benhamou, S., Bayanga, E. O., Breuer, T., & Masi, S. (in press). How do primates decide where to feed? insights from wild western gorillas. *Animal behaviour*.

Robira, B., Benhamou, S., Fuh, T. N., & Masi, S. (2023). Do seasonal frugivory and cognition shape foraging movements in wild western gorillas? In *Movement ecology of afrotropical forest mammals* (pp. 151–170). Springer.

Robira, B., Benhamou, S., Masi, S., Llaurens, V., & Riotte-Lambert, L. (2021). Foraging efficiency in temporally predictable environments: Is a long-term temporal memory really advantageous? *Royal Society Open Science*, *8*(9), 210809. https://doi.org/10.1098/rsos.210809

Robira, B., & Perez-Lamarque, B. (2023). Primate sympatry shapes the evolution of their brain architecture. *Peer Community Journal*, *3*.

Rojas, T. N., Bruzzone, O. A., Zampini, I. C., Isla, M. I., & Blendinger, P. G. (2021). A combination of rules govern fruit trait preference by frugivorous bat and bird species: Nutrients, defence and size. *Animal Behaviour*, *176*, 111–123.

Rosati, A. G. (2017). Foraging cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Russo, S. E., Portnoy, S., & Augspurger, C. K. (2006). Incorporating animal behaviour into seed dispersal models: Implications for seed shadows. *Ecology*, *87*(12), 3160–3174. https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[3160:IABISD]2.0.CO;2

Sakamoto, Y., & Takatsuki, S. (2015). Seeds Recovered from the Droppings at Latrines of the Raccoon Dog (*Nyctereutes procyonoides viverrinus*): The Possibility of Seed Dispersal. *Zoological Science*, *32*(2), 157–162. https://doi.org/10.2108/zs140107

Schmal, C., Myung, J., Herzel, H., & Bordyugov, G. (2017). Moran's i quantifies spatio-temporal pattern formation in neural imaging data. *Bioinformatics*, *33*(19), 3072–3079.

Seidler, T. G., & Plotkin, J. B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, *4*(11), 2132–2137. https://doi.org/10.1371/journal.pbio.0040344

Sussman, R. W. (1991). Primate origins and the evolution of angiosperms. *American Journal of Primatology*, *23*(4), 209–223. https://doi.org/10.1002/ajp.1350230402

Teichroeb, J. A., & Vining, A. Q. (2019). Navigation strategies in three nocturnal lemur species: diet predicts heuristic use and degree of exploratory behavior. *Animal Cognition*, *22*(3), 343–354. https://doi.org/10.1007/s10071-019-01247-4

Tiffney, B. H., & Mazer, S. J. (1995). Angiosperm growth habit, dispersal and diversification reconsidered. *Evolutionary Ecology*, *9*, 93–117.

Trapanese, C., Meunier, H., & Masi, S. (2019a). What, where and when: spatial foraging decisions in primates. *Biological Reviews*, *94*(2), 483–502. https://doi.org/10.1111/brv.12462

Trapanese, C., Meunier, H., & Masi, S. (2022). Do primates flexibly use spatio-temporal cues when foraging? *Quarterly Journal of Experimental Psychology*, *75*(2), 232–244. https://doi.org/10.1177/1747021820970724

Trapanese, C., Robira, B., Tonachella, G., Di Gristina, S., Meunier, H., & Masi, S. (2019b). Where and what? Frugivory is associated with more efficient foraging in three semi-free ranging primate species. *Royal Society Open Science*, *6*(5), 181722. https://doi.org/10.1098/rsos.181722

Vanleeuwe, H., & Gautier-Hion, A. (1998). Forest elephant paths and movements at the Odzala National Park, Congo: The role of clearings and Marantaceae forests. *African Journal of Ecology*, *36*(2), 174–182. https://doi.org/10.1046/j.1365-2028.1998.00123.x

Vittoz, P., & Engler, R. (2007). Seed dispersal distances: A typology based on dispersal modes and plant traits. *Botanica Helvetica*, *117*(2), 109–124. https://doi.org/10.1007/s00035-007-0797-8

Warren, W. H. (2019). Non-euclidean navigation. *Journal of Experimental Biology*, *222*.

Westcott, D. A., Bentrupperbäumer, J., Bradford, M. G., & McKeown, A. (2005). Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, *146*, 57–67.

Zuberbühler, K., & Janmaat, K. (2010). Foraging cognition in non-human primates. *Primate neuroethology*, 64–83.

Zwolak, R. (2018). How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews*, *93*(2), 897–913. https://doi.org/https://doi.org/10.1111/brv.12377

700   Zwolak, R., & Sih, A. (2020). Animal personalities and seed dispersal: A conceptual review. *Functional*
701   *Ecology*, *34*(7), 1294–1310. https://doi.org/https://doi.org/10.1111/1365-2435.13583