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2 **Eco-evolutionary feedback loops between**  
3 **animal cognition, movement and resource**  
4 **distribution**

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**Abstract** | Cognition can shape the movement of animals such as for frugivores. As frugivores can be involved in the life cycle of plants, for example in seed dispersal (i.e. zoochory), their cognition could also shape resource distribution patterns. As resource distribution patterns are known to affect the benefits of cognition, this could create eco-evolutionary feedback loops between animal cognition and the spatio-temporal patterns of resources. Using an agent-based model simulating the foraging behaviour of a frugivorous seed disperser endowed with spatio-temporal knowledge of resource distribution, we investigated whether resource spatio-temporal 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. We showed that ... sentence on the consequence of cognitive foraging on resource distribution

This stems from the conjunction of two forces: competition for space between trees and a seed-dispersal forager moving from tree to tree based on spatio-temporal memory. The engineering of the resource landscape was eventually beneficial/detrimental to the forager. . .

Altogether, this study highlights. . .

🔑 **Keywords:** Agent-based model - Cognition - Foraging - Frugivory - Movement - Phenology - Seed dispersal

📊 **Word Count:** 3100

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[TO BE UPDATED]

Introduce with:

In the theatre of the rainforest, an evolutionary play takes place in an unchanging setting, or so current hypotheses on the evolution of foragers' cognition assume (Rosati, 2017). If the protagonists, the foragers, are likely to have their cognition shaped by the distribution of resources (Grove, 2013; Robira et al., 2021), the characteristics of the resources themselves could be the result of forager-induced selection (Chapman et al., 2013; John et al., 2016; Lomáscolo & Schaefer, 2010). For example, fruit-eating primates tend to forage on trees that produce the highest quality fruit (e.g. the sweetest fruit, Ban et al., 2014; Ban et al., 2016) and in the greatest quantity (Flörchinger et al., 2010). Therefore, the evolutionary history of resources and associated foragers, as in the angiosperms/primates dyad, may be joint (Fuzessy et al., 2022; Gómez & Verdú, 2012; Lim et al., 2021; Sussman, 1991).

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>

Flörchinger, M., Braun, J., Böhning-Gaese, K., & Schaefer, H. M. (2010). Fruit size, crop mass, and plant height explain differential fruit choice of primates

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

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>

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>

Lim, J. Y., Wasserman, M. D., Veen, J., Després-Einspenner, M. L., & Kissling, W. D. (2021). Ecological and evolutionary significance of primates' most consumed plant families. *Proceedings of the Royal Society B: Biological Sciences*, 288 (1953). <https://doi.org/10.1098/rspb.2021.0737>

§1) The effect of resource distribution on foragers' cognition -> Cognition enhances foraging movement

-> Cognition is promoted by specific spatial distribution.

-> Fix setting (only short term dynamism - because fix during an individual lifetime), but in reality, interaction is two ways

§2) possible consequence of forager on resource distribution -> It can affect the spatial distribution:

The dispersal way is affecting the distribution.

Pooping areas preference -> spatial aggregation

The use of memory is associated to the emergence of route, as suggested from theoretical (Louise) to empirical evidence.

Route distribution: elephants' route are following gradient. What comes first, following or gradient born from route?

-> It can affect the temporal distribution:

Note biblio: seed dispersal and personality

<https://www.pnas.org/doi/full/10.1073/pnas.2113870119>

<https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.13583>

seed dispersal and animal behaviour

<https://link.springer.com/article/10.1007/s00442-005-0178-1>

seed dispersal animal cognition

<https://link.springer.com/article/10.1007/s11258-016-0652-3>

<https://onlinelibrary.wiley.com/doi/full/10.1111/j.1469-185X.2012.00250.x>

<https://onlinelibrary.wiley.com/doi/full/10.1111/brev.12377>

<https://repositories.lib.utexas.edu/bitstream/handle/2152/68127/ADDIS-DISSERTATI>

ON-2017.pdf?sequence=1

A la mobilité du frugivore s'oppose la sessilité des ressources.

The two-way interaction between frugivore and fruit plants therefore [questionne, necessite une meilleure comprehension] of their joint history [REF].

Primates, for instance, have boomed in the late

-> the possible joint history, ref to fuzessy -> question ISS

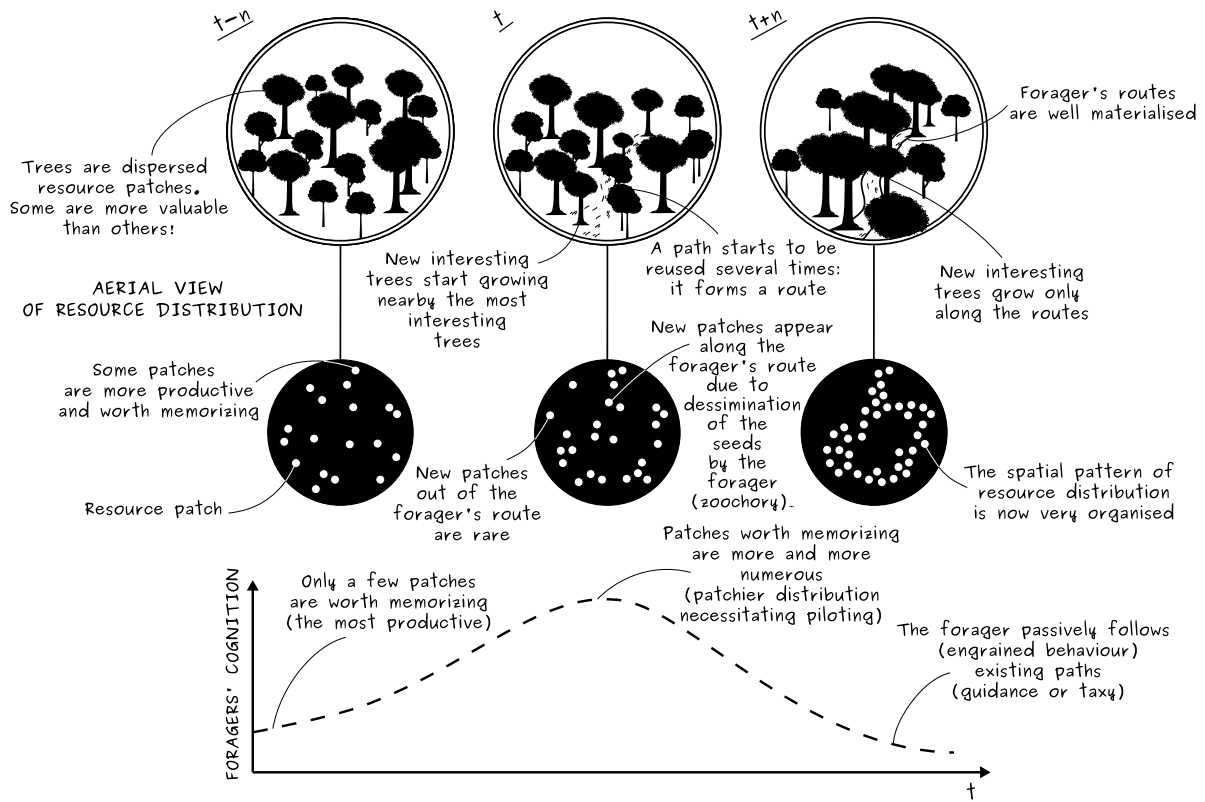
In the case of retroaction between frugivore movement, cognition and resource distribution, an extreme scenario is illustrated in Figure 1. Initially, assuming a parcimonious homogeneous distribution, long-term spatio-temporal memory is only marginally advantageous [REF]. As it is nonetheless, cognition should be selected. Through zoochory, deliberate targeting of some resource patches over others should initiate a change in resource distribution (e.g. increasing patchiness), eventually making cognition more and more advantageous. Over time, by repeatedly targeting the same trees, the routes used by the foragers may begin to materialise due to the seeds scattered along the way. However, in doing so, foragers who can only passively follow these routes may also start to become very efficient: they should not even have to bear the cost of high cognitive abilities, putting them at an advantage over foragers bearing the burden of cognition [REF]. While the pattern of resource distribution can be maintained, given that the routes are equally used by all foragers (yet because of two different proximal mechanisms: long-term memory vs. taxis), cognition could even start to be counter-selected. However, in the absence of concrete evidence, such a scenario remains a fable. In this study, we propose to provide a basis for discussing its realism, based on computer simulations that mimic the foraging behaviour of an agent endowed with spatio-temporal knowledge of resource spatial distribution and phenology and the role of seed-disperser.

## 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 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, we will refer to the agent as the forager, and to resource patches as trees, but this model should find larger resonance. The model was implemented in the *Rcpp* language in *R* software (v.4.2.1, R Core Team, 2020) based on the *Rcpp* package (Eddelbuettel, 2013; Eddelbuettel & Balamuta,

Eco-evolutionary feedbacks:  
From the environment to cognition  
and back



**Figure 1** – Theoretical expectations on eco-evolutionary feedback loops between animal movement cognition and resource distribution

2018; Eddelbuettel & François, 2011).

## Environment

**Spatial distribution** We 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 could produce resource (fruit containing seeds) for 30 tu only once every period. Thus, resource was seasonal at the tree-level, but not at the map-level. Periods of productivity of each tree were randomly distributed (i.e. uniform distribution of the start date). Productivity was characterised by a triangular-shaped pattern of the quantity of food along 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. 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 agent, creating a short-term dynamics of resource temporal distribution.

**Seed dispersal** Trees could reproduce and disperse via fruit eaten by the agent. Once the agent ate on ripe fruit, seeds could be dispersed once up to 0.5 tu after ingestion, with a probability of  $0.02 \text{ tu}^{-1}$ , independent of the quantity of fruit ingested, for simplicity. Thus, all fruit eaten did not mandatorily led to dispersal. Dispersal was eventually successful only if some space was left available for the new tree. This means that no tree had to be at a distance lower than 14.27 su. This number was obtained such as the exclusive “lifespace” by trees (a circular area of radius the aforementioned distance) was equal to 80% of the map area. 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 target. Otherwise, the seedling could not grow and died.

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

## Agent

**Cognitive abilities** The forager was endowed with a gradient of knowledge abilities: from no memory of the locations of trees (naive forager) and the timing of their period of productivity to perfect omniscience (i.e. all tree locations are known) and prescience (i.e. all periods of productivity are known). In case a tree was part of the forager’s memory, the forager knew

both the spatial (location) and temporal (fruiting timing) attributes. Thus, it could not know only one or the other. In case of partial knowledge, known trees were randomly selected at start.

**Moving rules** The forager was initially randomly located within the map. It is fully aware of trees present within sensory range fixed to 15.81 su. This actually corresponds to the average nearest-neighbour distance which equates  $1/(2\sqrt{\rho})$ , with  $\rho$  the density of trees (here 0.001) at start of the simulation where trees are homogeneously distributed. It is also aware of trees part of its spatio-temporal long-term memory. To decide where to head next, the forager could either rely on its private knowledge (sensory or memory) or not. If all trees within its private knowledge did not yield any fruit (i.e., all having less than 0.001 fu), the forager was moving randomly. Random movements were performed by randomly choosing a direction (uniform distribution of the heading angle), while the step length was sampled within an exponential distribution of mean  $\lambda_{steplength} = 0.01$ . An exponential distribution of step lengths is indeed classically observed in nature [REF]. Otherwise, the agent targeted the closest tree which maximised the ratio between the predicted food quantity at the tree (which accounts for depletion history), and the distance to the tree. Nonetheless, the forager avoided to target trees recently visited within the previous 2 tu to avoid targeting recently depleted trees (Robira et al., 2021).

Once the target had been chosen (or random point, if none), the forager moved straight to the first tree that should have been theoretically perceived *en route* to the initial destination point if any (provided they were not recently visited), or the destination otherwise. When this destination is reached, it then re-estimated the best tree to target and so on. Such a movement roughly mimics a beacon/landmark-based navigation, where individuals move from beacon to beacon to reach a target [REF] and frames coherently with the tendency of individuals to monitor resource state while moving [REF]. After each moving bout time was updated based on the distance travelled, knowing that the forager moved at a speed of 1000 su/tu. Then, the resource quantity available at each tree was updated.

In case all trees were empty (no food available in the environment, considered if sum of food available was less than 1 fu), the forager entered a torpor period for 1 tu, and so on until food was available again. This was done to avoid biasing measure of foraging efficiency in case the forager could deplete entirely the environment while being unable to disperse to another area, as expected 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	0.00045	% 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 and can harvest food at no moving cost	15.81	su
Agent	Knowledge rate	Proportion of trees of the environment for which the forager knows the location and production 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	"tu" <sup>-1</sup>
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 organisation of the spatial distribution of trees at the end of the simulation we focused on three metrics describing the tree spatio-temporal 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

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

where  $n_i$  represents the number of trees in quadrat  $i$  and  $N_{\text{quadrat}}$  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).

**Tree alignment** Routes are (curvi-)linear features. To assess the tendency of trees to form linear pattern, we 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 two closest trees. This varies from perfect alignment (value of 1), to no alignment (i.e., the minimum angle would be at worse  $60^\circ$  hence an alignment of ca. 0.134). Therefore, we use a corrected alignment  $a_c$  varying from 0 (no alignment) to 1 (perfect alignment) such as

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

We used the opposite of the skewness of alignment values of all trees to describe the whole distribution. Positive values indicate the existence of linear motifs while negative values indicate no obvious linear patterns. In the simulated conditions, random distributions (homogeneous or heterogeneous) should highlight moderate positive values (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 Geary Index,  $C$  [REF] applied to the start of fruiting dates. Since the date of start of fruiting corresponds to a circular variable, we followed [https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5870747/] to adapt existing functions of the *ape* package (Paradis & Schliep, 2019) to circular variables. Geary’s  $C$  was therefore defined as

$$C = \frac{(N-1) \sum_i \sum_j w_{ij} d(t_i, t_j)^2}{2 \sum_{i,j} w_{ij} \sum_i d(x_i, \bar{t})^2}$$

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

### **Does resource spatio-temporal distribution vary with cognition level?**

To investigate whether different levels of cognition eventually led to different distribution patterns, we considered five forager types differing by the proportion of trees for which the location and phenology was known (from 0 to 100%, at a step of 20, henceforth *spatio-temporal knowledge rate*). Each forager was first let foraging individually for 100 seasonal periods. We repeated the simulations for a given condition (i.e. knowledge rate) 100 times.

For each simulation, we verified whether a routine behaviour emerged and paralleled the variations in tree distribution. We characterised routine holding on the notion of conditional entropy following [REF Riotte-Lambert] using the series of tree id targeted during five supplementary season periods in which dispersal could not occur. The routine index varies from 0 (no routine) to 1 (perfect traplining).

### **Does resource distribution engineering favour some cognition levels?**

To investigate whether the engineered distribution of trees could in turn affect the foraging benefices purported by cognition, we considered the final tree distributions of simulations computed to answer question 1). For each of these tree distributions, in three different simulation runs, we let forage a forager endowed with no, intermediate (i.e. half of trees known), or full (all trees known) spatio-temporal knowledge. In these simulations, no seed-dispersal could occur. We measured the foraging efficiency after the forager foraged for 20 full seasons and compared them across environments and agent abilities. Foraging efficiency was computed as the cumulated quantity of eaten food, over the cumulated distance travelled. We verified that at the end of the simulation that foraging efficiency stabilised, which meant that we reached a foraging equilibrium. We 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 statistically differed of more than 5% (reference is the minimum efficiency in the fourth or the fifth quintile). Distributions of foraging efficiency measures were compared with Student tests (“t.test” function). We repeated the simulations for a given conditions (i.e. knowledge rate) 100 times.

### **Route formation as a product of two forces: tree competition for space and agents’ movement step rule**

During the model construction, we noticed that routes eventually appeared with the implementation of two mechanisms: 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, we considered two other sets of 100 simulations each.

To assess the effect of competition for space between trees, we compared the final tree spatio-temporal patterns when a perfectly knowledgeable agent (all tree locations and phenology

known) was let foraging in the same setting as in question 1), with the only difference that the exclusive lifespace between trees could vary be of 5 (small lifespace), 45 (intermediate lifespace) or 85% (large lifespace) of the map surface, so that the radius of this exclusive circular lifespace was at best slightly superior to the perception range (15.17 su vs 15.81 su).

To assess the effect of the movement tactic of the forager on tree distribution patterns, we compared the final tree spatio-temporal patterns when an omniscient agent was let foraging in the same setting as in question 1) and while the stringency in skipping trees encountered *en route* varied. It could either stop at all trees perceived on the way to the initial target (mimicking a “monitoring” behaviour, as in all other simulations; small skipping stringency), stop only at trees currently fruiting (i.e., with at least 0.001 fu, mimicking an opportunistic feeding only; intermediate skipping stringency) or move directly to the target (large skipping stringency).

### III Results

[TO BE UPDATED]

**Resource distribution varies with the cognition of the seed-disperser forager**

**Cognitive foraging efficiency is (not? -> awaiting results) affected by tree distribution engineering**

**Route pattern emerges...**

### IV Discussion

The environment is shaped by the species that inhabit it. The destructive behaviour of some animals, such as forest elephants [REF], can lead to blatant changes. But more elusive - but no less ecologically relevant - engineering can also occur over longer time scales. Using an agent-based model, we have illustrated the role of frugivores in shaping the distribution of fruit plants through zoochory. We showed that...

[TO BE UPDATED]

### V Acknowledgements

Simulations were ran on the HPC cluster of the Edmund Mach Foundation. We thank Louise Riotte-Lambert and Kavel Ozturk for discussion on the model.

### VI Funding

B.R. was supported by the Gordon and Betty Moore Foundation.

## **VII** Declaration of conflict of interest

We declare having no conflict of interest.

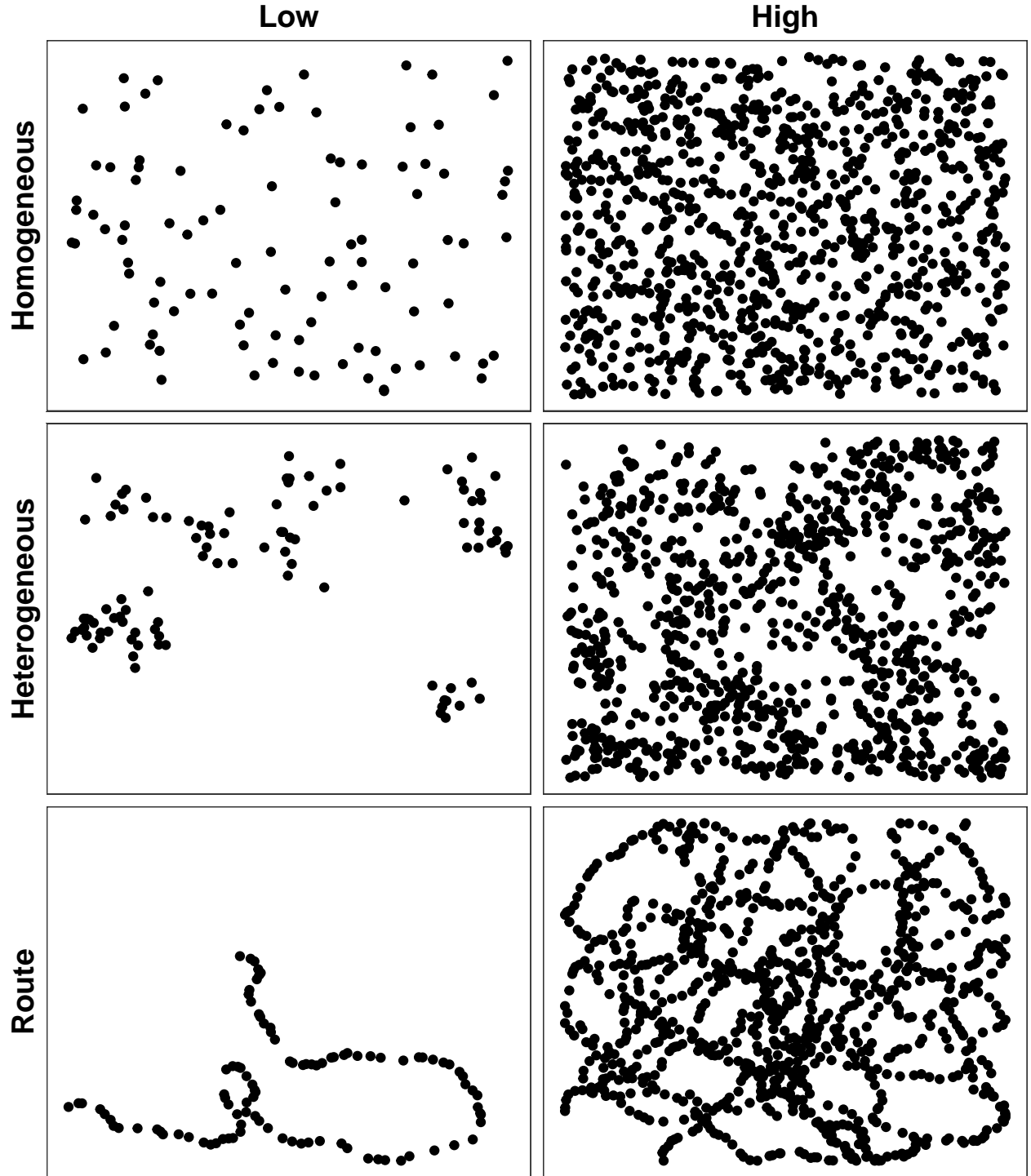
## **VIII** Data and code availability

The code used to generate the data and perform the analyses is available at XXXX. We provide it with the singularity image, which would allow the user to access the computing environment used to run the simulations in the first place.

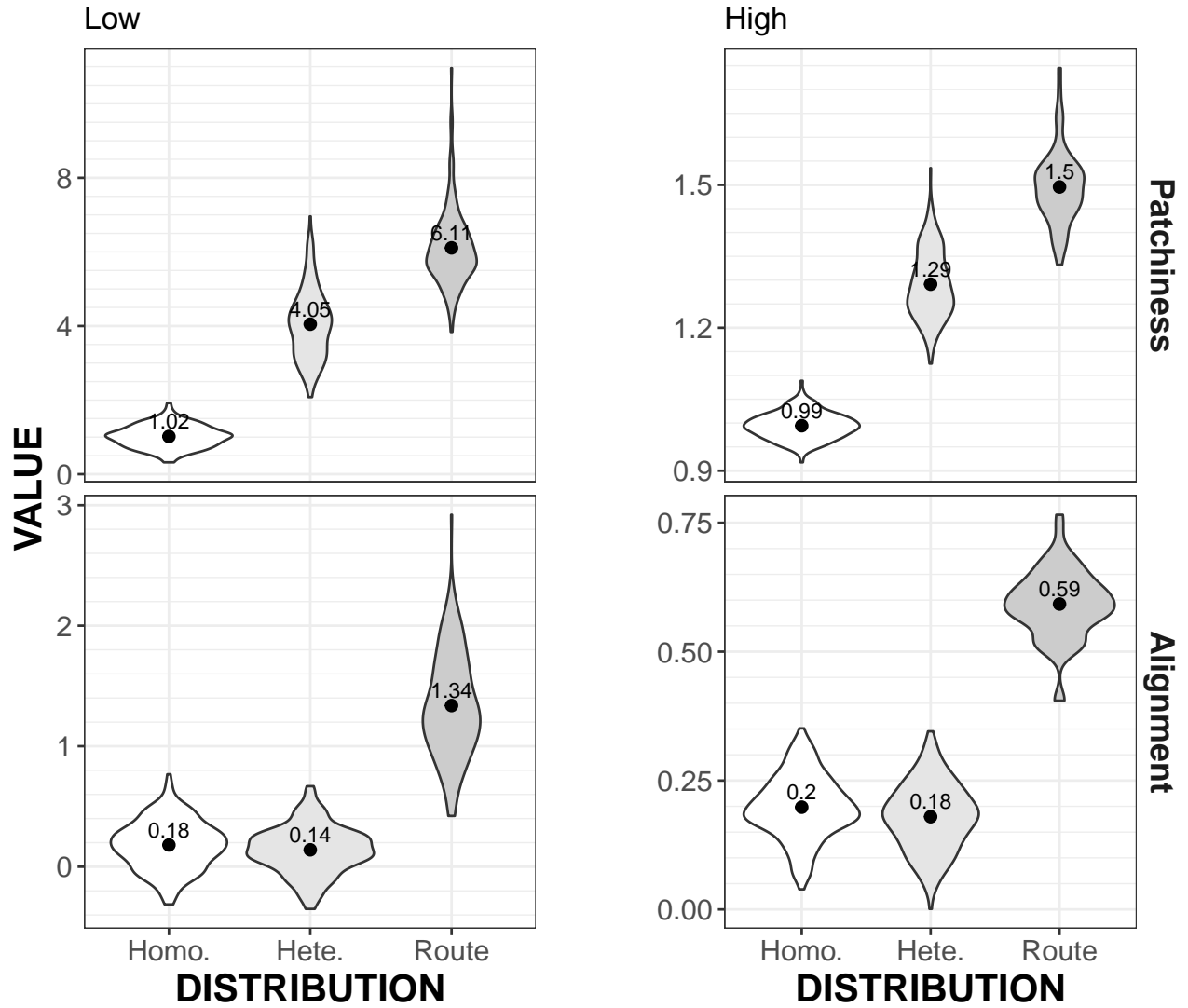
## IX.1 • Using patchiness and alignment to characterise spatial point patterns

We 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 and high density, we 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). We calculated the two metrics on 200 distributions. Note that, because we are in “perfect” conditions, we considered a neighbourhood for the alignment of 0 su, implying that the calculation was based on the triangle formed with the two closest trees for each tree.

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 organisation is 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).



**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 allows 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 half-violin plot, right to raw jittered data.



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