

An Agent-Based Model on Task Allocation in Leaf-Cutter Ant Colony Settlement

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Abstract—We propose an agent-based model (ABM) to study the role of task allocation in young leaf-cutter ant colonies. Leaf-cutter ants are eusocial insects operating at the highest level of social organisation, which is evident in the obligate mutualistic interaction they have with their fungus garden. Previous studies used a system dynamics approach to model this mutualism, highlighting the importance of task allocation within the colony. However, they lack in explaining how this task allocation emerges. This research aims to provide a detailed investigation of the ecological processes that impact task allocation. It does so by investigating how leaf-cutter ants navigate task allocation during the critical early colony life stage and the stability dynamics that are ultimately responsible for the success of a colony using an ABM. In this model, we observe dynamics that are in agreement with observational studies and theory, such as an environmentally imposed carrying capacity and bistability regarding successful and unsuccessful colony settlement. Furthermore, stable task allocation emerges within successful colonies as a consequence of local rules. We also perform sensitivity analysis to understand better how different parameters affect the model's output. Our model yields insights into how simple local rules can give rise to collective behaviour in pursuit of a shared goal, in which individuals switch from in-nest to outside-nest tasks without central directives.

I. INTRODUCTION

Growth is intrinsic for all life forms and at levels varying from cellular to population. Similar to how cells grow in a multi-cellular organism resulting in a larger size of the organism, social insect colonies expand from a few individuals to a size of hundreds of thousands or even millions [1]. Thus, similarly to that for an individual organism, stability and success of growth for a colony are determined by resilient responses to the environmental defiance accompanied by a developmental trajectory, namely, intrinsic growth rates [2]. To ensure the resilience of responses to changes in the external conditions, social insects resort to an efficient allocation of their infertile workers to different tasks such as foraging, brood care, and nest defence, which individuals perform without centralised supervision or control. Existing literature connects the phenomenon of self-organised task allocation within social insects colonies to the ecological success of this life form [3], [4].

Stable at large colony sizes, population growth undergoes a critical transition with small colony size during the early life stages [2]. This transition involves improved efficiency in organisational structure, resulting in increased resilience

in reaction to environmental challenges and thus stabilization of growth. How social insects trade-off allocation to growth against functional maintenance and how self-organised task allocation of a colony enables them to achieve an equilibrium between the two components are two crucial questions in studying social insects at the early phase of colony growth.

The example of obligate mutualism between leaf-cutter ants and their fungus garden has offered social insect researchers a chance to proxy physiological maintenance of a colony to maintenance of fungus, which serves as a primary food source for the colony [2], [5]. This obligate mutualistic relationship between leaf-cutter ants and their fungus garden means that neither the fungus nor the ants can survive in the absence of the other. Thus, investigating how young leaf-cutter colonies with small population sizes transition from vulnerable to resilient, self-organised task allocation that balances work sustaining the nutritional state of the fungus and work enabling growth of the colony is of particular interest.

Formulated initially in the context of out-of-equilibrium systems in physics and chemistry, the term self-organisation refers to macroscopic pattern formation from processes at a microscopic level. It is now extended to other scientific fields, including ethology, to describe collective phenomena in social insects [6]. The theoretical literature on task allocation in social insects encompasses several self-organisation models that suggest different mechanisms for this phenomenon. However, it is essential to mention that while the terms “task allocation” and “division of labour” are frequently used interchangeably in social insect research, there is a scientific discourse on the terminology and hence what primary focus should be in this area of study [4]. Thus, although both terms attempt to describe the organisation of the social insect colonies, “division of labour” refers to individual specialization in performing a particular task and is substantially attributed to intrinsic factors such as genetics, morphology (caste polyethism) and hormones, as well as temporal forces (age or temporal polyethism). On the other hand, task allocation concerns processes of how a colony adjusts its allocation of workers to different tasks based on changing conditions [4].

This research focuses on task allocation considered in self-organisation models, which have been proposed in social insects research to study the dynamics of young leaf-cutter ant colonies. The main objectives of this paper are two-fold:

1. Investigate how leaf-cutter ants navigate their task allocation during the critical early colony life stage.
2. Consider stability dynamics that ultimately lead to survival throughout this process.

Given that self-organised task allocation is individual-centric and is accomplished without imposed directives, the modelling approach of choice is an agent-based model (ABM). This paper thus proposes an ABM that incorporates inter-individual interactions resulting from local rules and reactions to local environments. This approach allows studying the behavioural components to understand the mechanisms of the stabilization and growth in young leaf-cutter ant colonies.

The rest of this paper is organised as follows. Section II provides a detailed description of the model following the ODD+D protocol [7]. Section III summarises the results obtained from experiments and sensitivity analysis carried out in this research. The discussion Section IV firstly interprets the findings and considers the validity of the model, and, secondly, presents limitations and suggestions for future work.

II. MODEL DESCRIPTION

A. Overview

1) Purpose: This study aims to model the early stage colony of leaf-cutter ants and their mutualistic fungus garden. The growth, and thus ultimately survival, of a recently established colony, is highly dependent on the interplay between structural organisation within the ant colony and the nutritional state of the fungus [2]. The purpose of this model is to investigate the stability of the growth of an early-stage ant colony settlement and their mutualistic fungal partner in relation to the task allocation within the ant colony. Although up to 30 different tasks can be performed within the leaf-cutter colony [2], earlier research showed key dynamics of an efficient mutualistic relationship, and hence colony stability can be explained with just two primary tasks: foraging leaves for fungal growth and brood care ant for population growth [5]. The focus lies on the task allocation of the forager and caretaker tasks within the colony through local information indicative of task demand, hence the need for an agent-based modelling approach. Although this study is mainly concerned with the dynamics behind the obligate mutualism of leaf-cutter ants and their fungus, systems that rely on both caretakers (i.e. providing care for offspring) and foragers (i.e. providing resources/income) are not limited to the study of ecology. Hence, findings within this study may provide interesting analogies for human communities and societies.

2) Entities, state variables, and scales: The first entity we will consider is the fungus. The fungus can be regarded as a stationary resource for the larvae. Although the larvae are not explicitly modelled, the fungal biomass is the driver behind the population growth of the ants. Hence an important state variable is the fungus biomass, which can decrease either through natural decay or consumption and increase when the fungus is being fed. Additionally, a Boolean state variable keeps track of whether the fungus is alive or dead.

The essential agent entities are the ants. The state variables that all ants share are a unique identifier and location, which correspond to coordinates in a grid. The ant population consists of two tasks and various sub-tasks, each with its behaviour and state variables. The two tasks of the ant agents are caretaker and forager. Whereas the foragers can move and search for resources within the grid, the caretakers are stationary, located at a fixed center cell, representing the ant colony nest.

The caretaker is either dormant or feeding the larvae. Although no spatial components are modelled for the caretakers, a time delay is added to the larvae feeding task to represent general fungus maintenance and the duration of a round-trip from fungus to larvae. Hence, the state variables of a feeder include the time duration of this round-trip, as well as a memory of the fungal biomass before and after the round-trip. The state variables of a dormant caretaker include the time duration of its dormancy, as well as a memory of the fungal biomass before and after its dormant period.

Forager ants can be divided into three sub-tasks: exploring, recruiting, and harvesting. A detailed account of these sub-tasks is given in Sections II-A3 and II-B2. Although they can differ in sub-tasks, all foragers have the same state variables: a Boolean attribute indicating if they have a leaf or not, a tracker that counts the time duration of its trip, and an accumulator of the neighbour density at each time step.

The spatial components of the model are represented with the aforementioned grid, whose size of 50×50 cells has been chosen empirically to match the ant population size. Each cell may contain multiple entities, and moving to another neighbouring cell takes a precisely one-time step. Resources are represented via the entity of plants, which are uniformly distributed over the grid. The state variables of a plant are the number of leaves it has, which can be removed by the ants and regrows according to a fixed growth rate.

3) Process overview and scheduling: For scheduling in our model, time is considered to be discrete: events occur at distinct, separate points in time. At each time step, agents are activated synchronously in random order, with a different order each time step. After the agents have been activated, information about the current time step is gathered and saved by the data collector. A pseudo-code representation of the scheduling algorithm is shown in Algorithm 1.

Algorithm 1: Agent Scheduling

```

Input: Number of time steps  $N$ 
for  $t \leftarrow 1$  to  $N$  do
    Shuffle agents;
    foreach agent in agents do
        | Activate agent;
    end
    Collect data;
end

```

B. Design concepts

1) *Theoretical and empirical background:* Since this research focuses on the early colony expansion in leaf-cutter ants, a brief description of the biological background is in place. The process of obligate mutualism within a leaf-cutter ant colony can be simplified in terms of an interplay of ant' and fungus contributions to this mutualism. In particular, ants harvest leaves, which they use as fertiliser to grow a specific fungus. The cultivation process involves bringing fresh leaves to the fungus, tending it, and protecting it from pests. The fungus, in turn, serves as a primary nutritional source to the larvae, queen, and worker-population to restore energy [2]. Consequently, the increase in the ant population is provided by the fungus consumption, and the fungus growth is due to the foraging and tending efforts of ants.

At the system level, our model addresses a trade-off between allocating worker ants' efforts towards population growth as opposed to efforts in maintaining the nutritional state of the fungus at the early stage of colony expansion. Previous research has described this mutualistic relationship in terms of the system dynamics approach and found that internal organisation is essential in producing either stable growth or system collapse as an outcome of these dynamics [5]. While the model in the present research draws inspiration from the [5], it does not directly translate the ordinary differential equations (ODEs) proposed in it into an ABM. Specifically, since the modelling approach in [5] is primarily based on the analogy between biological and physical processes, the direct translation of this analogy to an ABM would be nontrivial.

Different types of leaf-cutter ants show varying categorisations of worker behaviour. However, [8] and [9] suggest the existence of three to four different major categories of tasks in the leaf-cutting ant *Acromyrmex subterraneus*. These studies agree that the main tasks of leaf-cutting ants can be broadly categorised as foraging, brood and queen care, and fungus care. Furthermore, [5] show that the key dynamics of early colony stability can be captured by generalising those into two activities: inside and outside of the nest. According to the model in [5], the former task includes taking care of queen and larvae, as well as tending the fungus garden, while the latter is primarily concerned with harvesting leaves for fungal growth.

In our model, on the other hand, we simplify the tasks of ants further by considering the only task for ants inside of the nest to be feeding fungus to larvae and keep the assumption for outside-nest activities congruent to [5]. Thus, we refer to the two tasks that an ant can take as foraging and caretaking. Likewise, we exclude energy expenditure resulting from performing tasks, which is captured by the system dynamics model in [5]. To do so, we assume that neither foragers nor caretakers feed on fungus, and only larvae are fed on fungus. These two assumptions allow us to capture the core dynamics of a mutualistic relationship: fungus needs ants to grow, and ants need fungus for the growth of their population. Hence, the focus lies on the two tasks of ants enabling this

dynamics, which we refer to as foragers and caretakers.

At the agents level, the model poses a problem of optimal self-organisation: how individuals settle on a certain task allocation that is efficient for the whole population from only having access to local information. There is a voluminous amount of literature on this problem concerning social insects, where much of the models in it can be grouped into three major classes: 1) response-threshold or signal-response dynamics models, 2) the foraging-for-work or spatial differentiation models, and 3) social interaction models [3]. The first two model classes focus primarily on temporal polyethism resulting in the “division of labour” in colonies. However, social interaction models aim to understand mechanisms of interaction among individual ants and between ants and their environment, which can arguably shed light on the emergence and evolution of collective behaviour such as task allocation [4]. Since we are interested in the phenomenon of individual ants switching tasks, which has been established by empirical literature [10], [11], the model we propose in this research is congruent with social interaction models. Yet, unlike social interaction models assuming that individual ants learn from direct interactions with nest-mates [12], [13], we assume no individual learning process in our model. Instead, we consider a mix of direct and indirect interactions among agents and between agents and environmental entities, which we elaborate on in Section II-B6. Moreover, for the decision-making process, we assume that agents use sensing, which is discussed in further detail in Section II-B4.

We now motivate the choice of decision models for the two main submodels in our model corresponding to the two considered tasks: foraging and caretaking. Carrying capacity is often explicitly modelled in population models such as in [5], yet, as we spatially model an environment in which ants forage, this carrying capacity is implicitly included in the limited availability of resources. Regarding the foraging strategy, ant species have been shown to use a number of different foraging recruitment mechanisms [14]. Most types of leaf-cutter ants adopt mass recruitment strategies using chemical trails, where ants that find a food source lay a trail of pheromones while returning to the nest, which recruits other forager ants to follow the set trail [15]–[17]. Foragers travelling along these trails repeatedly re-mark these pheromone trails as long as there are resources at that location [18]. Regarding the time frame of forager trips, it has been empirically observed in the leaf-cutting ant *Atta sexdens rubropilosa* that foragers randomly travel large distances until finding a resource, after which they return to the nest in a path with a significantly shorter distance [19].

Our foraging model is based on these findings from existing literature. Exploring forager ants perform a biased random walk until they find a plant, and returning foragers in our model take the shortest path back to the nest. Returning foragers will leave a pheromone among its path to alert other foragers about the possible location of a resource. The mass recruitment strategy is then completed by the ability of foragers to sense and follow pheromone trails to the plant.

These pheromone trails are re-marked by other returning foragers who found the same resource either through luck or following a pheromone trail. We note that our foraging model simplifies actual leaf-cutter ant foraging behaviour. That is, we do not model the selection of high-quality resources that is observed in many types of leaf-cutter ants [20].

The colony's nest is significantly simplified in our model to keep the model's complexity minimal. We do not model the spatial structure of the nest or the fungus garden — instead, we consider a single fungus, and the nest and fungus are located on a single cell in the center of the grid. Ants (both caretakers and foragers) can interact with the fungus when they are located in this cell. In turn, caretaker ants are static agents located at the nest. To represent the variety of tasks that worker ants perform in the nest in addition to feeding larvae (e.g. fungus garden care and maintenance, brood and queen care, and waste management [8]), we implement a dormancy state in which a caretaker is inactive for a certain period. Furthermore, we do not explicitly model the larvae or queens. Instead, feeding caretakers transfer some part of the fungus biomass to a reserve used to determine the number of larvae that metamorphose into ants. We assume no limit on the availability of larvae, as the queen egg production rate is shown to be an order of magnitude higher than offspring production [2].

A Moran process is used in the evolutionary game theory (EGT) literature in implementing reproduction and selection in constant populations with few offsprings and reproducing continuously [21]. We leverage the idea of an offspring strategy proportional to parental fitness from the Moran process to determine caretaker and forager proportion of ants newly joining population of working ants. We do so by assuming that the demand of those tasks determines the distribution of caretaking and foraging tasks for metamorphosed larvae in the recent time period, the detailed implementation of which can be found in Paragraph II-C4k. Moreover, we interpret this process as social learning in Section II-B3.

2) Individual decision-making: Both forager and caretaker ants are subjects of the individual decision-making process. The subject's decisions are influenced by objects available in their neighbourhood: pheromones and plants influence forager decisions, and the fungus influences caretaker decisions. While agents pursue the objective of finding a stable state of task division for which the colony survives, no explicit objective function is being optimised. Instead, foragers and caretakers have an individual fitness that indicates how well they perform their tasks. If an ants' perceived fitness is high, it is more likely to switch tasks, and if its perceived fitness is low, it is more likely to stay in its current task. This task switching mechanism is based on local information and will be explained in further detail in Sections II-B4 and II-C4.

A simplified overview of the decision-making tree of forager and caretaker ants is represented in Figure 1. For forager ants, space plays an important role in the decision process: most of their decision-making is based on what they observe in their neighbourhood. Foragers additionally use temporal

information about the average neighbour density during its foraging trip (further explanation of this process is given in Section II-B4 and Paragraph II-C4d).

Caretaker ants make decisions based on their perception of the fungus' health. While this is technically spatial data, it is different from how foragers use spatial data. As we do not model the spatial aspect of the nest, the caretakers and fungus always live on a single cell, and thus the caretakers always have access to fungus information.

3) Learning: Social learning refers to how individuals adjust behavioural choices by relying entirely on social information. In this context, given that the process of larvae metamorphosis into foragers and caretakers includes global information on the temporal demand of the two tasks, we can interpret it as an adaptation of the new generation of ants to the population fitness. Hence, the Moran process in our model can be viewed as social learning, despite not assuming individual choice.

4) Individual sensing: Both the forager and caretaker ants can use sensing to make decisions on whether it will change their task and sub-task, ultimately changing their behaviour. The sensing process is not erroneous, and there are no costs associated with gathering information.

A forager uses sensing during its trip in two ways: 1) decide if it will either explore, harvest, or recruit, and 2) gather information on if it should switch tasks and if it should draft a caretaker after the trip has finished. In the first case, the ant can sense the presence of a plant or pheromone in its immediate surroundings, which consists of their Moore neighbourhood. The sensing of a plant has priority, meaning the forager will prioritize leaf gathering and recruiting over following pheromone trails (harvesting).

In the second case, the foragers can determine the neighbour density within the Moore neighbourhood. Neighbour density is defined as the fraction of cells occupied by other foragers in its neighbourhood. It will collect this density for every time step during its trip. Additionally, it will keep track of the trip duration in terms of time steps. Using both the accumulated neighbour density values and trip duration, the forager has knowledge of the average neighbour density at the end of its trip, which it will use for its task-switching and drafting decision.

Caretakers can sense the fungus biomass. It measures the fungus biomass at two points in time and uses these measurements to decide how to act. If it measures a decrease in fungus biomass, it will go dormant, and if it measures an increase in fungus biomass, it will feed a part of the fungus to the larvae, allowing for larvae to mature and become ants.

5) Individual prediction: No individual prediction is used in the decision-making process.

6) Interaction: Direct interactions are present between both caretaker and forager ants, and the fungus. Caretakers interact with the fungus by taking some fungus biomass for feeding larvae, and foragers interact with the fungus by feeding it leaves and increasing its biomass. Foragers additionally interact directly with entities in two more ways: 1) they take leaves

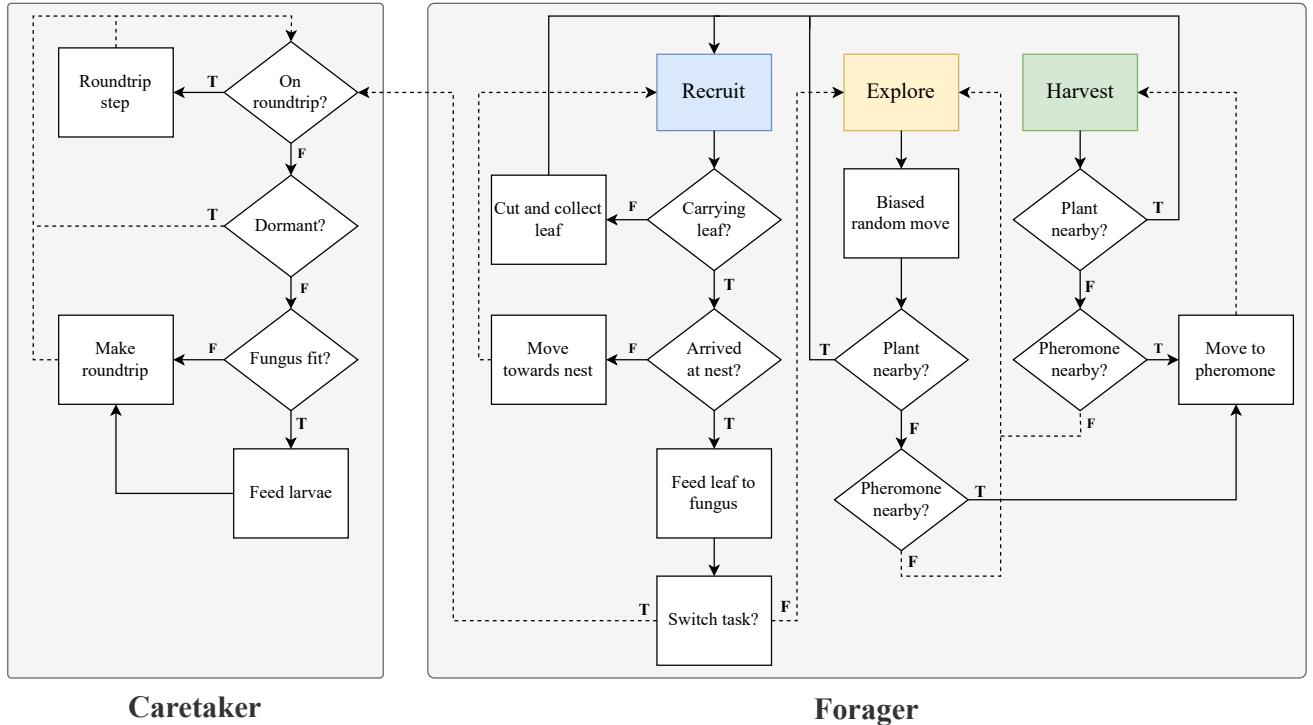


Fig. 1: Flow diagram of the possible decisions of the two types of ant agents in a single time step. The actions in the diagram are simplified as the goal of this figure is to represent the main decision tree for the two possible tasks of an ant agent: caretaker and forager. Solid lines represent transitions between choices in the current time step, while dashed lines indicate the transition to the next time step.

from plants, and 2) they may interact directly with caretakers if they choose to draft them to become a forager. Foragers also interact indirectly; they alert other foragers about potential plants through pheromones and extract leaves from plants. A leaf extracted by one forager is no longer available to other foragers. The interactions depend on the agent's location in relation to the agent or entity in question.

7) *Collectives:* Two separate collectives can be considered within the model: the collective of foragers and the collective of caretakers. Each collective works towards its own goals; the foragers feed the fungus while the caretakers feed the larvae. These collectives are imposed by the modeller, with the initial ant population being divided evenly among both collectives. However, the final division of the population among these two collectives does emerge from local information.

8) *Heterogeneity:* Ant agents are firstly heterogeneous in their task: forager or caretaker. Then, for each task, they differ in sub-task: foragers can be either exploring, harvesting, or recruiting, and caretakers can be dormant or feeding. Depending on which task they have, they are further heterogeneous in different ways. Foragers are heterogeneous in multiple state variables: observed neighbour density, trip duration, and whether they carry a leaf. Caretakers are heterogeneous in their dormancy status and round-trip length. The heterogeneity in the decision-making of the forager and caretaker ants is visible

in Figure 1.

9) *Stochasticity:* Stochasticity is present in multiple aspects of our model. First, it is used in the initialization of plant resources. The plants are randomly placed across the grid according to a uniform distribution. Second, ants die probabilistically. Exploring ants also move according to a biased random walk in which their next position is decided stochastically. Stochasticity is also used in the task allocation of new adults and in the task switching and drafting decisions that happen at the end of a forager's trip. Furthermore, when an exploring forager senses multiple pheromones in its neighbourhood, it will randomly choose one to move to. Finally, the length of a caretaker's dormancy and round-trip is randomly sampled from a uniform distribution.

10) *Observation:* Different measurements are collected for understanding and analysing the model: fungus biomass, number of ants, a fraction of forager ants, and a fraction of dormant caretakers. This data is either collected after every time step, or once at the end of a model run. The former collection method produces time series data which is used for intuiting and understanding dynamics. In contrast, the latter method is used for explaining the impact of different parameters using sensitivity analysis. We are further interested in measuring the emergent phenomena of colony death; what fraction of colonies, if any, die out for a given set of parameters.

C. Details

1) *Implementation details:* The model has been implemented in Python 3 using the Mesa ABM framework [22]. The source code is available on GitHub at <https://github.com/soudy/leafcutter-ants-fungi-mutualism-abm>.

2) Initialisation:

- **Environment:** A 50×50 multi-grid, i.e. a square grid with multiple agents allowed per cell.
- **Nest:** Occupies a single cell in the grid at (25, 25)
- **Ants:** Fixed even number of ants, all at the nest. There are equal numbers of foragers and caretakers. All foragers are initialised in the exploration state (i.e. as biased random walkers)
- **Fungus:** Located at the nest with a fixed initial biomass and zero energy in its energy buffer, i.e. it will grow in the next time step only if at least one forager brings a leaf to the nest
- **Plants:** A fixed number of plants are initialised at different points in the grid. The coordinates of each plant are independently chosen from a uniform distribution over the grid, excluding the nest cell. Every plant has the same number of leaves.

The choice of initial values are not based on real data for the purpose of capturing the qualitative behaviour as opposed to predictive validity.

3) Input data:

No external data is used as input.

4) Submodels:

a) *Ant death:* At every time step, an ant can die with a fixed probability given by the parameter d_A .

b) *Forager movement:* A forager ant executes spatial movement in different ways depending on its state:

- **Explore** The ant behaves like a biased random walker; the step is biased by letting the probability mass function (PMF) for the neighbourhood be proportional to the Manhattan distance from the previous position (Algorithm 2). This biases the random walk against the ant's previous position and minimizes the likelihood of returning to an already explored cell. So, the forager performs a biased random walk step at every time step until it comes across either a plant or a pheromone in its neighbourhood. If it finds a plant, it will go into the recruit state, and if it finds a pheromone, it will go into the harvest state.
- **Recruit** State reached when ant finds a plant and collects a leaf. Ant proceeds to follow the shortest path to the nest and adds a unit of pheromone on every traversed cell on the grid. The pheromone has a deterministic lifespan decided by the parameter T_p .
- **Harvest** State reached when ant finds a cell with a pheromone. The ant tries to follow a pheromone trail towards a potential plant. The ant scans its Moore neighbourhood for pheromones, and randomly chooses one of its neighbouring cells that have some non-zero pheromone and are farther from the nest than the ant's current position.

Algorithm 2: Biased Random Walk Step

```

Input: Current time step  $t$ , previous position  $\vec{p}_{t-1}$ 
if  $t = 0$  then
| Execute unbiased random walk step;
else
| neighbours  $\leftarrow$  Moore neighbourhood;
| distances  $\leftarrow$  manhattan-distance( $\vec{n}, \vec{p}_{t-1}$ ) for  $\vec{n}$ 
|   in neighbours;
| sum-of-distances  $\leftarrow \sum_{d \in \text{distances}} d$ ;
| probabilities  $\leftarrow$ 
|   distances/sum-of-distances;
|  $\vec{p} \leftarrow$  Choose from neighbours using the PMF
|   defined by probabilities;
| Move to  $\vec{p}$ ;
end

```

c) *Forager leaf cutting:* A forager will cut and collect a leaf when it is in explore or harvest mode and senses a plant in its neighbourhood. The plant entity's leaf state variable is decremented by one, and the ant's state variable corresponding to leaf carrying is updated.

d) *Forager neighbour sensing:* At every time step, a forager senses and remembers its neighbour density ρ_N . That is, it records the fraction of cells occupied by one or more other foragers (Figure 2). When the forager returns to the nest, it will use these collected neighbour densities to decide whether to switch task or not.

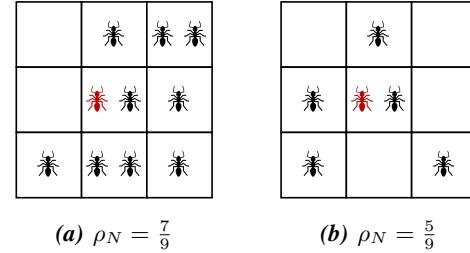


Fig. 2: Forager sensing: neighbour density (ρ_N) of a single time step.

e) *Forager nest return:* When a forager successfully returns to the nest after recruiting, it will first feed the leaf it harvested to the fungus:

$$E_F \leftarrow E_F + 1, \quad (1)$$

where E_F is the fungus energy at the current time step. Additionally, it decides if it will switch task and if it will draft a caretaker to become a forager. This decision is based on its average neighbour density (fitness):

$$\bar{\rho}_N = \frac{1}{t_{\text{trip}}} \sum_{i=1}^{t_{\text{trip}}} \rho_N^{(i)}, \quad (2)$$

where $t_{\text{trip}} = t_{\text{end}} - t_{\text{start}}$ is the duration of the foraging trip. Note that ρ_N is a fraction in $[0, 1]$, and thus $\bar{\rho}_N$ is also in $[0, 1]$.

TABLE I: Model parameters.

Symbol	Description	Type	Default Value	Scenario Range	Sobol' Scenario Range
$A(0)$	Initial ant population size	Integer	50	[1, 50]	-
$\pi_f(0)$	Initial fraction of foragers	Real	0.5	[0.1, 1]	-
$F(0)$	Initial fungus biomass	Real	50	[10, 50]	-
$P(0)$	Initial number of plants	Integer	64	[30, 200]	-
$P_L(0)$	Initial and maximum number of leaves on plant	Integer	100	[10, 200]	-
d_A	Death probability of ants	Real	0.01	[0, 0.02]	-
d_F	Decay rate of fungus	Real	0.005	[0.001, 0.02]	[0.001, 0.02]
T_p	Pheromone lifespan	Integer	30	[5, 100]	-
L_{growth}	Leaf regrowth rate	Real	0.5	[0.01, 1]	-
c_F	Leaf to fungus biomass conversion coefficient	Real	2	[1, 4]	[1, 4]
c_A	Fungus biomass to larvae energy conversion coefficient	Real	0.9	[0.2, 1.5]	[0.55, 1.25]
F_C	Amount of fungus biomass a single caretaker can carry	Real	1	[0.1, 2]	[0.5, 1.35]
K	Moran process memory	Integer	10	[1, 20]	-
μ_D	Mean ^a caretaker dormancy duration	Real	60	[30, 80]	-
μ_R	Mean ^a caretaker round-trip duration	Real	5	[5, 20]	[5, 12]

^aSamples are actually taken from $U(1, 2\mu)$, which has mean $\mu + 1/2$.

A forager will then switch task to caretaker with probability $\bar{\rho}_N$, and draft a caretaker to become a forager with probability $1 - \bar{\rho}_N$ (both events can happen in the same time step). Finally, the observed average neighbour density $\bar{\rho}_N$ is pushed to a queue whose size is given by parameter K , which will be used in the modified Moran process used for task allocation of new ants.

f) *Pheromone decay*: Pheromones decay at a fixed rate of one unit per time-step. If its lifespan hits zero, the pheromone disappears.

g) *Caretaker feeding and dormancy*: At the start of their existence, caretakers will go on a round-trip, whose length is sampled from $U(1, 2\mu_R)$, where μ_R is a parameter. When it goes on a round-trip, it records the current fungus biomass F_{start} . If a caretaker is currently on a round-trip, its current round-trip length is decremented. When its round-trip length hits zero, the caretaker again records the fungus biomass F_{end} . It will then calculate its individual fitness based on its perceived change in biomass:

$$\Delta F = F_{\text{end}} - F_{\text{start}}. \quad (3)$$

Then, if $\Delta F > 0$, the fungus is considered to be improving, and it will transfer a part of the fungus biomass to the larvae energy (“feeding”):

$$F \leftarrow F - F_C \quad (4)$$

$$E_L \leftarrow E_L + c_A F_C, \quad (5)$$

where F is the fungus biomass at the current time step, E_L is the larvae energy buffer, F_C is a parameter that determines how much fungus biomass a single caretaker can carry, and c_A is the fungus biomass to larvae energy conversion parameter. After feeding, the caretaker will go on a round-trip with length sampled from $U(1, 2\mu_R)$. If $\Delta F \leq 0$, the fungus is considered to be deteriorating, and the caretaker will go dormant for some length. The length of this dormancy is sampled from $U(1, 2\mu_D)$, where μ_D is a parameter.

h) *Fungus decay*: The fungus biomass is reduced by a fraction d_F :

$$F \leftarrow F - d_F F. \quad (6)$$

When $F < 5$, the fungus is considered dead, and ants can no longer feed the fungus or their larvae.

i) *Fungus energy conversion*: The energy (leaves) provided by foragers is converted into biomass according to parameter c_F :

$$F \leftarrow F + c_F E_F. \quad (7)$$

j) *Plant leaf regrowth*: All plants regrow their number of leaves every time step according to parameter L_{growth} :

$$P_L^{(i)} \leftarrow P_L^{(i)} + L_{\text{growth}}, \quad (8)$$

where $P_L^{(i)}$ is the amount of leaves on plant i .

k) *Larvae metamorphosis*: Ant population grows when caretakers transfer fungus biomass into the larvae energy buffer E_L . The amount of larvae energy required for a single larva to metamorphose into an adult ant is fixed at 1. Then, the number of larvae that metamorphose into adults is given by

$$n_A = \lfloor E_L \rfloor. \quad (9)$$

That is, if $E_L < 1$, no metamorphosis happens and no new ants emerge in the next time step. However, if $E_L \geq 1$, n_A larvae metamorphose into ants and the larvae energy gets updated accordingly:

$$E_L \leftarrow E_L - n_A. \quad (10)$$

The task of a new ant is probabilistically decided by a modified version of the Moran process. It gives the probability of an ant becoming a forager by averaging the last K average neighbour densities observed by returning foragers:

$$P(\text{forager}) = \frac{1}{K} \sum_{i=1}^K \bar{\rho}_N^{(i)}. \quad (11)$$

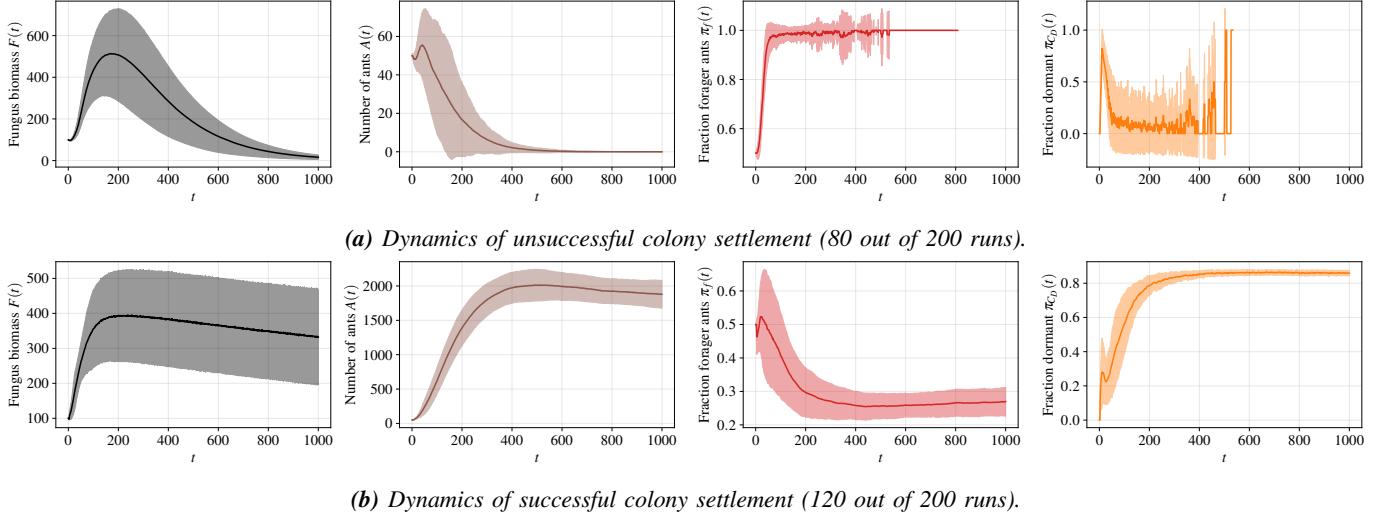


Fig. 3: Means of various measures from 200 simulation runs, separated based on if the colony was either successful or unsuccessful, with the latter case meaning (near) death of the colony and fungus. Envelopes represent the standard deviation. For the measures of the fraction of forager ants and fraction of dormant caretakers, the trailing zeroes have been removed to better show the dynamics before extinction.

Then, $P(\text{caretaker}) = 1 - P(\text{forager})$. If there are no neighbour densities observed yet, $P(\text{forager}) = P(\text{caretaker}) = 1/2$.

III. RESULTS

A. Experiments

1) *Principal Dynamics of Stability:* The aim of this first experiment is to show the principal dynamics of stability of the leaf-cutter ant colony as observed within the model's simulations. For this, a fixed parameter set is used (Table I), which are chosen based on the findings from the One-Factor-at-a-Time (OFAT) sensitivity analysis (Section III-B) and empirical observations of the model. As the focus of this study lies on the dynamics behind early-stage colony death or settlement, a simulation time of a 1000 time step was chosen, which is sufficient to show both these states. Figure 3 shows the successful and unsuccessful colony settlement of 200 runs separately, where an unsuccessful colony means that both the ant population and fungus have (nearly) died. The trajectories of the individual runs of this same experiment can be found in Figure 10 in Appendix A. The model shows bistability for the same parameter set, meaning that either it will go towards the state of death of a colony (unsuccessful) or colony settlement (successful). Thus, the random initialization of the environment and the stochastic processes within the model determine a colony's success or death.

The dynamics of unsuccessful colony settlement can be seen within Figure 3a. The decline within ant biomass starts early on within the simulations, which on average sets in around the first 50 time steps. The average ant biomass barely goes above the initial 50 ants, showing that an unsuccessful colony settlement has very little initial growth within the ant population. Whereas the ant biomass has already started declining very early on, the fungus biomass still has a sizable

growth phase, even succeeding the peak fungus biomass of a successful colony. This indicates that while ant biomass is on a decline, the forager ants are still capable of sustaining a growing fungus for a period of time.

This can be further explained by the increase of the fraction of foragers ants, with the average ant population consisting of 90% foragers within the first 50 time steps. Only when the ant population is too small, the foragers cannot sustain the fungus anymore. Due to the increase in foragers, there is a decrease in caretakers, which reduces the inflow of new ants, ultimately leading to colony death. The fraction of dormant caretakers within an unsuccessful colony shows somewhat chaotic behaviour due to the small number of caretakers within the population.

The dynamics of successful colony settlement can be seen within Figure 3b. This deviates from an unsuccessful colony settlement by having steady fungus biomass and ant biomass at the end of the simulations. The ant biomass shows a logistic increase towards an average population size of slightly below 2000 ants, reaching its peak at 500 time steps. The fungus biomass increases steadily initially, after which it slowly declines, reaching the peak fungus biomass of 400 at around 300 time steps. There is large variation between individual runs for this peak value, which can be most clearly seen in Figure 10 in Appendix A. Both the ant and fungus biomass show some sort of carrying capacity, where the environment imposes a natural limit on the growth of both the ants and fungus. It should be noted that the fungus biomass gradually declines, which leads to fungus death for longer simulations. This makes our model unsuitable for longer simulation past 1000 time steps.

The average fraction of foragers ants within a successful colony, after a small bump slightly above the initial fraction of

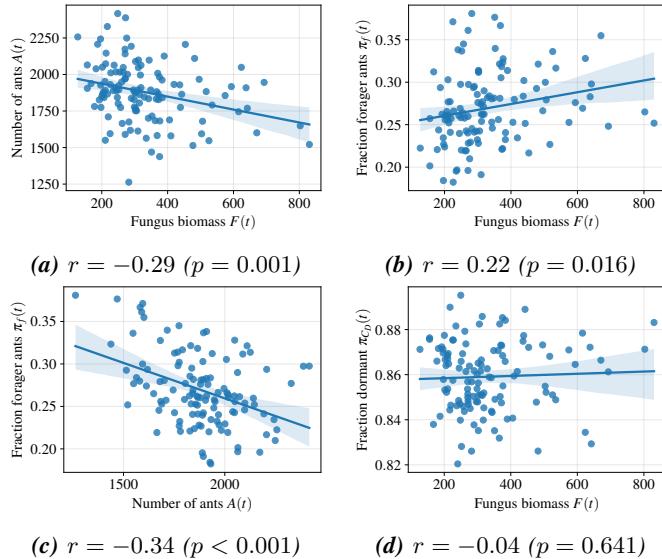


Fig. 4: Scatter plots between various measures, including a regression line and a 95%-bootstrap confidence interval of that regression. The data is from the last recorded value of the simulation ($t = 1000$) of the runs with successful colony settlement ($N = 120$).

0.5, steadily declines towards a population with approximately 25% foragers. As forager numbers diminish, the number of caretakers increases, ultimately leading to population growth. However, together with this increasing population size, the fraction of dormant caretakers increases as well, converging to an average of 85% of the caretakers being dormant.

Figure 4 is based on the final values (at $t = 1000$) from the runs with successful colony settlement, showing scatter plots between various pairs of measurements. Additionally, for these pairs of measurements, the Pearson correlation coefficient (r) is reported with a corresponding p -value. This p -value is an indication of the probability that uncorrelated data could produce as extreme of a Pearson correlation value [23]. Complementary to this figure is Figure 11 in Appendix A, in which the data distribution of these final values of both successful and unsuccessful colonies are displayed in histograms. The data using only the successful colonies show data distribution that is close to a normal distribution. In contrast, if the data from unsuccessful colonies is included, a bimodal distribution with a large peak at zero can be observed.

A negative correlation is found between the fungus biomass and the number of ants, with many runs with low fungal biomass and a large number of ants. The fraction of forager ants is positively correlated with the fungus biomass yet negatively correlated with the number of ants. This is intuitive with the model, as the forager's main task is to feed the fungus as opposed to feeding the larvae. Lastly, no significant correlation was found between the fraction of dormant caretakers and the fungus biomass.

2) *Resource Distribution:* The following experiment looks at the impact of different resource distributions on the dy-

namics of successful colonies, in particular task allocation. The model's environment is initialised with a fixed number of plants and leaves, with the plants randomly placed within the grid for each run. Hence, the total amount of initial resources within the system is determined by the product of the number of leaves and number of plants. While three different combinations of the number of plants and leaves are used, the amount of resources is fixed, but the resource distribution is changed. To provide some intuition, more plants with fewer leaves means that resources can be more easily found yet will be more quickly exhausted. Fewer plants with more leaves mean the ants have to travel further on average to find resources but can make longer use of the same plant. This experiment only focuses on the successful colonies hence runs with colony death are removed.

Figure 5 shows the results of three different parameter sets: Figure 5a considers 30 plants and 100 leaves, Figure 5b considers 60 plants and 50 leaves, and Figure 5c considers 120 plants with 25 leaves. As the number of plants is increased, with a subsequent lowering of the number of leaves, the final fraction of forager ants decreases. These differences were analysed by doing both an F -test to test differences in variances and subsequently a Welch-test to determine differences in sample mean. Both test results were corrected using Bonferroni correction. Between all parameter sets, the mean fractions of forager ants at the final time step were found to be significantly different (all $p < 0.0001$).

The average number of ants at the end of simulations with more plants and fewer leaves is relatively higher in comparison to simulations with fewer plants and more leaves. Additionally, there seems to be a lower average peak fungus biomass, with a somewhat steeper gradual decline. There are minimal differences in the dormant caretakers' fraction. Finally, we find that more colonies die out with fewer plants and more leaves — with 120 plants and 25 leaves, 35 out of 200 runs result in colony death, while with 30 plants and 100 leaves, over half (137 out of the 200) runs result in colony death.

B. Sensitivity analysis

In addition to experimental examination of the model behaviour, a sensitivity analysis on the input variables is conducted. The goal of the sensitivity analysis is threefold. Firstly, a local sensitivity analysis using the One-Factor-at-a-Time (OFAT) method is performed, to gain insights in how emergent phenomena, such as the bistability of survival, depend on input variables and how robust the model output is to initial conditions [24]. Secondly, a global sensitivity analysis — using the Sobol' method to estimate the first- and total-order indices — is realized to quantify the variability in model outcome caused by input parameters [25], [26]. Lastly, the OFAT is used to restrict the number of variable input parameters for the global sensitivity analysis, by observing which parameters have little effect on model output, and fixing these to their nominal value for further analyses.

1) *One-Factor-at-a-Time (OFAT):* For the local sensitivity analysis, a simple OFAT set-up is presented. For fifteen input

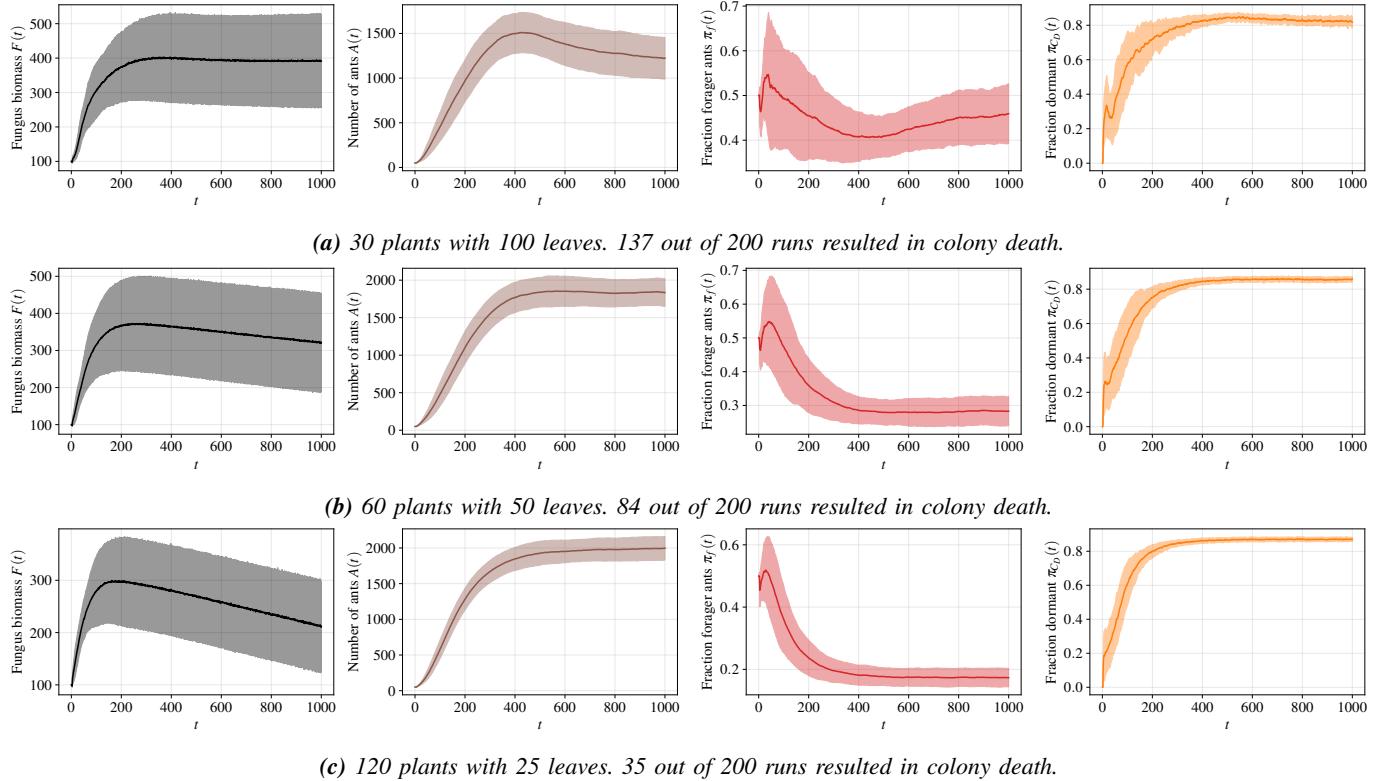


Fig. 5: The figure contains three different experiments, each with a different resource distribution in terms of plants and leaves. The total amount of available resources (plants * leaves) is the same for each experiment. Means of various measures are shown, with envelopes representing the standard deviation. Results are from 200 individual runs, without unsuccessful runs.

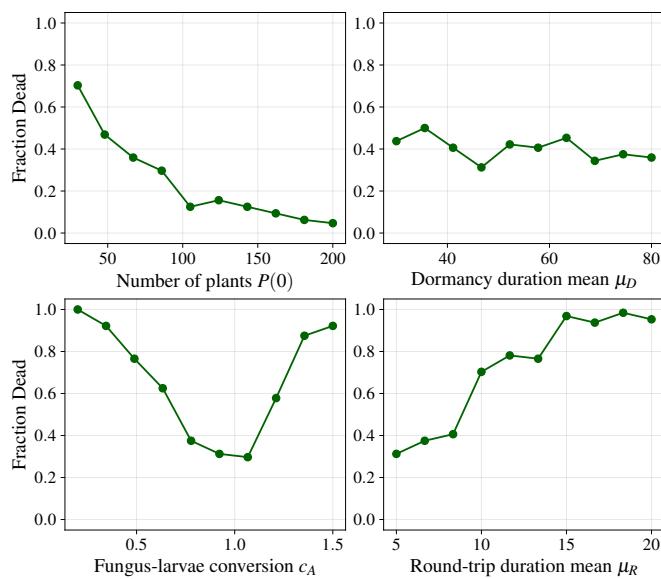


Fig. 6: Fraction of 64 runs resulting in unsuccessful colony, while varying the parameters according to OFAT. The figure shows four types of behaviour: a decrease in fraction dead, (top left), little/no effect (top right), a minimum (bottom left) and an increase in fraction dead as the parameter value increases (bottom right).

parameters, including all initial conditions, one factor is varied over ten equidistant points in a predefined range, while keeping all other input parameters at their nominal values (see also Table I). For each parameter setting the model is evaluated 64 times, producing the following output parameters after 1000 time steps: number of ants $A(t)$, fraction of ants that is forager $\pi_f(t)$, and fraction of caretakers that is dormant $\pi_{cD}(t)$. Note that the fungus biomass $F(t)$ is not included as model output here, since for the runs that do not result in successful colony settlement, the fungus is often still alive, although declining, after the maximum number of time steps. Subsequently, this model output cannot be accurately interpreted using OFAT in terms of our research.

Next to analysing sensitivity, the model evaluations are used to investigate influence of an input parameter on the bistability, by reporting the fraction of the 64 repetitions that do not result in successful colony settlement (defined as $A(t = 1000) = 0$). The full figure reporting these results for all input parameters can be found in Appendix B Figure 16, however four types of behaviour seen have been lifted out in Figure 6. Since we observe a bistability in successful/unsuccessful colony settlement, the OFAT results are presented with mean and standard deviation over all repetitions, as well as every single run, with minimum and maximum emphasized. As the results are extensive, we briefly summarize the main findings for

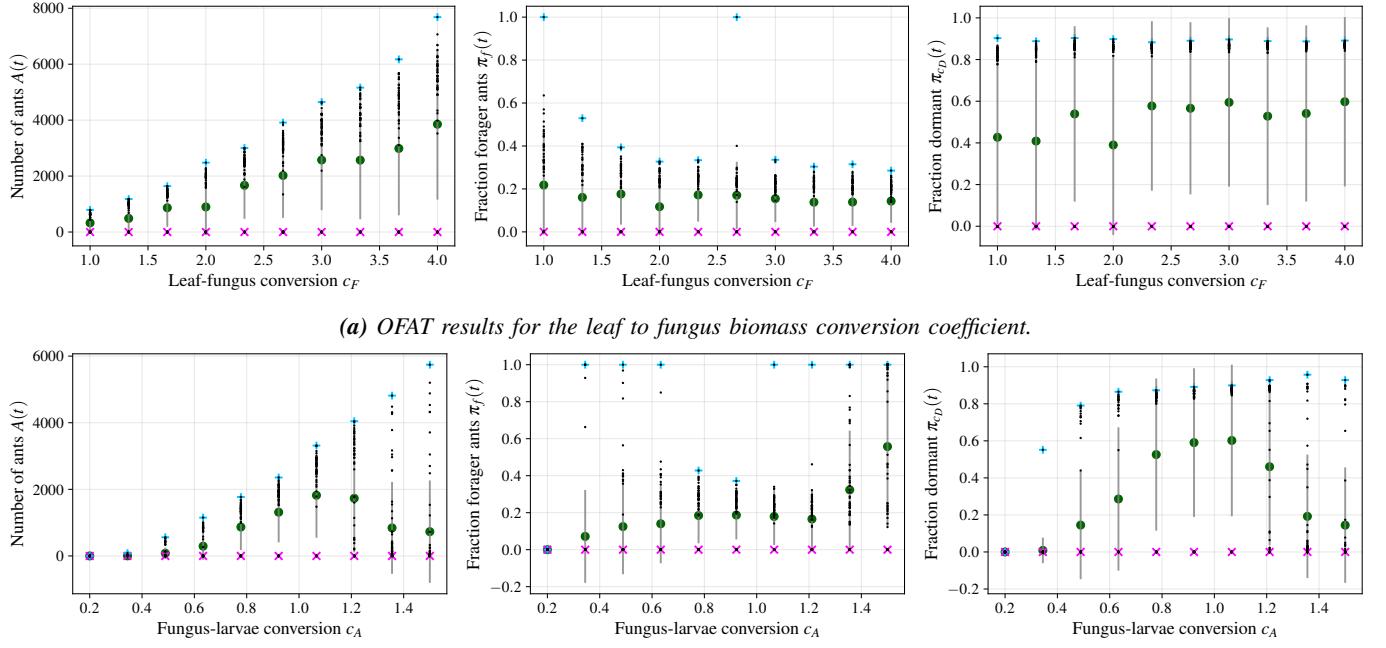


Fig. 7: OFAT results for two input variables, the leaf-fungus and fungus-larvae conversion coefficients, on three different output parameters, number of ants (left), fraction forager ants (middle), and fraction of caretakers dormant (right). The green dot represents mean over 64 runs, with standard deviation in grey. Individual runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

some input parameters, going into depth only for the more interesting parameters. For full results of the OFAT, including the initial conditions, the reader is referred to Figures 12 to 15 in Appendix B, where Figure 16 shows the fraction of repetitions resulting in an unsuccessful colony for all input parameters.

As can be seen in Figure 6, varying the input parameter that determines the mean of the dormant round-trip distribution, μ_D , has little effect on the fraction of runs resulting in successful colony settlement. The same holds for input parameters pheromone lifespan, Moran process memory, and leaf regrowth rate. To restrict the number of parameters for the Sobol' method, these four are fixed to their nominal values (see also Table I). As mentioned in results (Section III-A1), our fungus suffers from a gradual decline. Increasing or decreasing the probability of an ant dying at a time step destabilizes the system by introducing later-stage deaths. For this reason the value of ant-death probability is kept fixed at its nominal value, $d_A = 0.01$, for the Sobol' method. The fungus-larvae conversion coefficient, c_A , and the caretaker carrying amount, F_C , show a minimum in fraction of repetitions that result in early stage colony death, indicating where optimal values for these parameters lie (see also Figure 6). Deviating from these optima results almost surely in colony death. For this reason, the ranges included in the Sobol' sensitivity analysis have been restricted to minimise the number of colony deaths.

To illustrate interpretation of OFAT results, Figure 7 shows

the influence of varying the conversion coefficients, c_F and c_A , on three measures of model output. Note that model output is taken at $t = 1000$, which may not be enough time for some parameter values to ensure successful settlement of a colony, thus skewing results. This can for example be said when the fraction of foragers is reported as 1, since this behaviour generally shows imminent death of the colony.

Figure 7a shows effects of varying the leaf-to-fungus conversion coefficient. On the left, it can be seen that for the surviving runs, the number of ants increases with c_F , as does the variance between the runs. For each value of c_F , some runs do not result in successful settlement of the colony, however the fractions of colonies that survive in early stage is not much influenced by this input parameter. Additionally, this input parameter has little effect on the task allocation output measures, being the fraction of ants that is forager, π_f , and the fraction of caretakers that is dormant, π_D . For $\pi_f(t)$ it might be said that for lower values of the parameter, the fraction of foragers is slightly higher, most likely caused by a decrease in the total number of ants.

The other conversion coefficient, fungus-to-larvae, is represented in Figure 7b. For the surviving runs the number of ants initially increases with c_A , but for $c_A > 1.2$ it shows a decrease in the mean value and a larger variance in the number of ants for the surviving runs. The middle plot showing the fraction of foragers as model output, displays irregular output for the extreme values of c_A . As mentioned before,

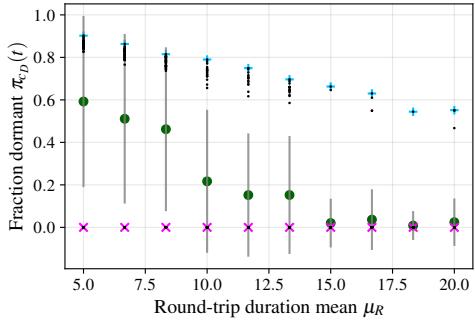


Fig. 8: OFAT results for the round-trip duration parameter μ_R with fraction of caretakers dormant as model output. The green dot represents mean over 64 runs, with standard deviation in grey. Single runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

a fraction of foragers near or equal to one usually indicates a colony's death, making it difficult to interpret these OFAT results. For this reason, the range of values included in the Sobol' sensitivity analysis is reduced to $[0.55, 1.25]$ for the parameter c_A .

Another parameter that exhibits interesting behaviour (Figure 15 in Appendix B) is the caretaker carrying amount, F_C , which shows an increase in number of ants as the value of the parameter increases, while the task allocation output variables are steady for the surviving colonies. The fungus decay rate parameter, d_F , acts conversely, decreasing the number of ants, as the value of the parameter increases. For all parameters, the fraction of caretakers that are dormant in runs with successful colony settlement seems to converge to the same value, around 0.85, except for the caretaker round-trip duration mean μ_R . In Figure 8 we see that, although many runs do not result in successful colony settlement, for the runs that do succeed ($\mu_R \in [5, 13]$), the fraction of dormant caretakers decreases as the value of μ_R increases. This could be caused simply by the fact more caretakers are needed or allowed as they take longer to feed fungus to larvae.

2) *Sobol' Sensitivity Analysis:* With Saltelli's extension of Sobol' sequences, a sample of length $N = 512$ is used for $d = 5$ input parameters, resulting in $N(d + 2) = 3584$ sets of parameter values [26], [27]. Each parameter setting is evaluated in the model ten times, giving a total of 35,840 model evaluations. For obtaining the sample of parameter settings and estimating the Sobol' sensitivity indices from model output, the Python package SALib [28] is used.

Figure 9 shows the first- and total-order sensitivity indices, S_i and S_{T_i} for three model output measures, with S_i (resp. S_{T_i}) corresponding to input parameters X_i , being fungus-larvae conversion c_A , fungus decay rate d_F , leaf-fungus conversion c_F , caretaker round-trip mean μ_R , or caretaker carrying amount F_C . The first-order sensitivity indices, S_i for an input parameter X_i measures the part of variance caused by X_i and includes only effects of the single parameter, and no interaction effects [24]. We see that for all three model

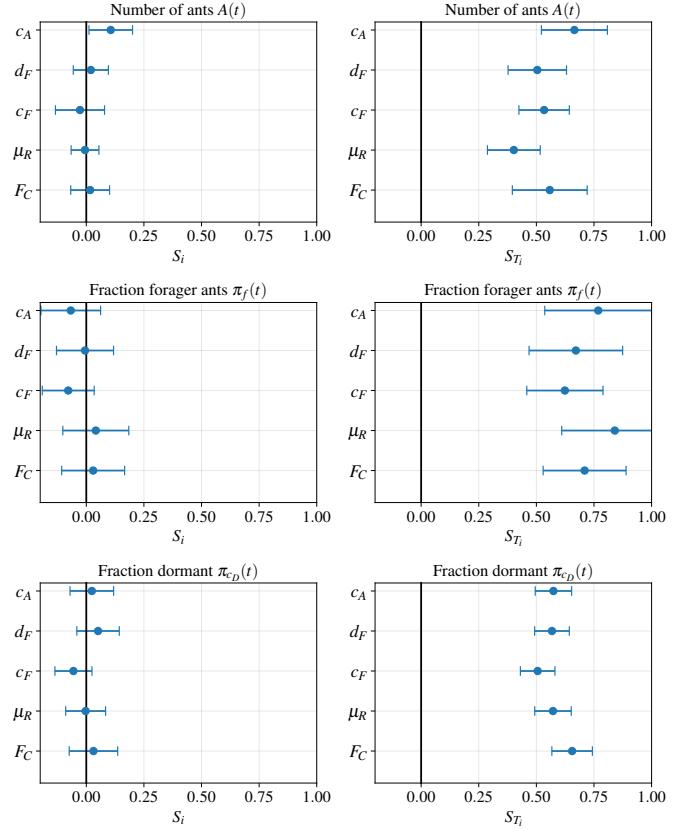


Fig. 9: Estimates of first- and total-order sensitivity indices of 5 input parameters (fungus-larvae conversion c_A , fungus decay rate d_F , leaf-fungus conversion c_F , caretaker round-trip mean μ_R , and caretaker carrying amount F_C), for three model output measures. Error bars indicate 95%-bootstrap confidence intervals. Black vertical line indicates the value of 0.

outputs, the first-order sensitivity indices are close to zero, or even negative. Negative sensitivity indices have no valid interpretation, but can be caused by numerical inaccuracy, e.g. the number of samples N being insufficient [24]. The sum of the first-order sensitivity indices for the three output values are 0.11 (number of ants), -0.08 (fraction forager), and 0.05 (fraction dormant), indicating that very little of the output variance can be explained by contributions of individual parameters.

From the total-order sensitivity indices it can be concluded that most the variance in model output is mainly caused by interaction effects between the parameters, since these indices include all first- and higher order interaction effects of an input parameter X_i [25]. The bootstrap confidence intervals mostly overlap, except for the total-order indices of $X_i = c_A$ and $X_i = \mu_R$, indicating that the fungus-larvae conversion parameter is more influential in the model output than the dormancy duration mean. Similarly, in fraction of caretaker ants that is dormant (π_{CD}), we see that the total-order index for parameter $X_i = F_C$ is higher than that of $X_i = c_F$, indicating

that the amount of fungus a caretaker can carry has more influence on the variance in fraction of ants that is dormant, than the leaf-fungus conversion coefficient. From a modelling perspective, this was reasonable to expect, since when a caretaker can carry less fungus, more caretakers might be necessary to feed enough fungus to larvae for metamorphosis into new ants.

It should be noted that results within this section come with a few uncertainties. The confidence intervals for the indices of fraction forager ants as model output are very wide, also indicating an inaccuracy in the method in explaining variance in this model output. Furthermore, it is important to mention that the Sobol' method comprises of a decomposition of variance, which might not be a good measure of variability (and thus sensitivity) in model output, if the distribution of output is skewed or includes outliers [24]. Since our model leads to bistability for most to all parameter settings included in the sensitivity analysis, the model produces a bimodal distribution of output (see also Figure 11). A high peak at zero, corresponding to unsuccessful colonies, causes higher variance for all three measures of model output. This makes the Sobol' method less suitable to explain sensitivity of input parameters for our model.

IV. DISCUSSION

This research set out to model the dynamics of leaf-cutter ants and their mutualistic fungus garden during the early stage of colony expansion. It does so by using an ABM to reproduce self-organisation arising from local rules, including spacial interactions and in which a heterogeneous population of ants is assumed. The two research objectives of this study are (1) to investigate how leaf-cutter ants manage their task allocation during the early stage of colony expansion and (2) to examine the dynamics of stability leading to survival throughout this process.

A. Model Dynamics and Validation

This section frames the experimental findings in terms of the two research objectives of this study while addressing the model validity. At the macro level, our leaf-cutter ant model can be described as bistable, where the colony's success is not easily guaranteed. This finding reflects those in [2] who observed high mortality in colonies of leaf-cutter ants species *Acromyrmex versicolor* in an experimental setting during the comparable period of colony settlement - from the appearance of workers in the nest to the maturity of a colony. While parameters throughout a set of simulations in this research remained the same, random initialisation of the environment and stochasticity within the model determined the eventual outcome of either unsuccessful or successful colony settlement. It also resulted in large variation in the outcomes of the measurements. Although the exact trigger to what causes either state is far from clear, we have observed general patterns within these two states of colony settlement.

First, the characteristics of successful colony settlement are discussed. This state starts with a rapid initial growth

phase of both the fungus and the ant population. Whereas the fungus grows linearly at first which eventually levels off, the ant population displays patterns similar to logistic growth. This also accords with earlier observations from numerical simulations in [5] and experimental data in [2] in terms of the initial behaviour. Both the fungus and ant population eventually reach a carrying capacity, as the environment limits how much the fungus can be fed, which in turn limits the growth of the ant population. Where exactly this carrying capacity lies differs, showing relatively large variance between simulations, in particular for the fungus biomass.

Focusing more closely on the dynamics of task allocation within successful colonies, generally, a small increase in the fraction of foragers at the start of the simulation can be observed, which afterwards rapidly decreases and converges. A potential reason for the initial increase in foragers could be the low perceived neighbour density of the foragers due to the small population and spread of abundant resources, which increases the demand for the forager task. After this initial slight increase in foragers, on average, the system converges towards a colony with more caretakers than foragers. Additionally, the fraction of dormant caretakers is rather high, with an average of 85% dormant caretakers. Whilst such a high proportion of inactive caretakers is not biologically meaningful, dormancy is considered in this research as a set of various tasks performed in the nest other than feeding larvae. The convergence towards a high proportion of dormant caretakers supports earlier empirical observations showing that as colonies grow, they re-allocate in-nest workers from brood rearing towards nest maintenance tasks in [2]. It is noteworthy here that the necessity of dormancy for caretakers arose from the process of verification by means of iterative face-validation. Specifically, previous model versions without dormancy allowed caretakers to continuously feed the larvae, quickly depleting the fungus. However, in reality, ants working in the nest have been observed to exhibit inactivity [29], and in-nest workers perform a variety of other tasks.

Second, the properties of unsuccessful colony settlement are considered. Whether a colony will be unsuccessful seems to be determined early on, with almost no initial increase in the ant population, setting in a rapid decline in the number of ants within the first 50 time steps. Interestingly, even with a dwindling ant population, efforts of the colony tend to go to feeding the fungus as opposed to feeding the larvae, resulting in an increase in the fungal biomass and further decrease of ant population. This behaviour is most likely not biologically plausible, as it has not been observed in the literature. While previous studies suggest that a small population of worker ants leads to the extinction of both ants and the fungus in a colony [5], the conditions for colony death in those studies also include a small proportion of foragers and loss of fungus [2], [5]. Given that, the present model behaviour might not correspond to what can be observed in nature.

A reason for this somewhat unnatural distribution of efforts within a dying colony can be found when looking at a fraction of foragers within the ant population. As the ant population

swiftly sets out on a decline, the fraction of forager ants within the population shoots up to close to 1. A small population size most likely reduces the perceived neighbour density of the foragers, causing a pull towards staying and becoming foragers within the colony. Yet, with a declining population and few caretakers to elicit population growth, the perceived neighbour density of the foragers still remains low, increasing forager task demand, despite the efforts of the foragers already there. This positive feedback loop caused by the local rules of the foragers is most likely the reason why the ant population decline is so rapid.

However, this does not explain why this positive feedback loop is or is not triggered in some runs, as all simulations start with the same small population. With the difference between simulations being the initialisation of the environment and stochastic dynamics, a strong hypothesis is that the unsuccessful colonies were unlucky to find resources. If a colony quickly establishes multiple pheromone trails towards resources early on, most foragers will follow the same trails as opposed to exploring, which increases the neighbour density and thus reduces the forager task demand, avoiding triggering the positive feedback loop. This hypothesis is further reinforced by experiments with resource distribution, which showed that simulations with fewer plants and more leaves per plant suffer from more extinctions, as resources were harder to find. Nevertheless, such model behaviour can suggest an important limitation corresponding to how local rules for the foragers are defined, which will be addressed in a later part.

Overall, in validating our model, we have compared the results to the findings in the empirical literature on leaf-cutter ants' early colony growth and general ant research. Thus, consistent with the literature [2], this research found bistability of success in colony settlement given the same initial condition. However, the characteristics of the unsuccessful colony settlements in this research do not match those observed in the previous studies. While small ant population appears to be linked to colony extinction for our model and earlier observations [5], the dominating forager proportion as opposed to hardly any caretakers seems not to be consistent with extinction patterns in the literature [2], [5]. At the micro level, this study broadly supports experimental observations of the ability of ants to switch from in-nest to outside-nest tasks without centralised control [30]–[32]. Furthermore, it is encouraging to compare the rising and stabilising proportion of dormancy as a set of tasks excluding larvae feeding with that of empirical research describing the same shift for in-nest workers [2] and the presence of inactive members as part of collective regulating activity as colony expands [29].

B. Limitations and Future Work

An important limitation of the research lies in the local rules of foragers. In particular, the local rules defined in the model trigger the positive feedback loop between the population size and proportion of foragers leading some colony settlements to reach zero in the number of ants. In the current implementation, the decision of forager whether to switch tasks or not

is primarily influenced by population size, which is notably detrimental in the case of small populations. Likewise, the way neighbourhood density is defined can lead to biased local information for foragers, which in turn can cause distorted foraging demand with the growth of population size. Another major source of weakness in this model is the consistent decline of the fungus over time. In particular, this problem introduces a limited time frame as well as a constrained parameter space, in which this declining fungus does not lead to colony death. The reasons for this model behaviour are not clear yet. Although a random activation in Mesa instead of simultaneous one might at least partially be responsible for exacerbating this process, further verification is strongly advised. Additionally, while the study provides an in-depth qualitative analysis of task allocation processes, it lacks a qualitative focus. Specifically, the research does not include time- and space calibration. It also does not consider the number of ants that is biologically viable for the beginning of the considered colony growth stage. This limitation hinders validation with data and deployment of the model.

A natural progression of this work is first to address the model shortcomings. Thus, local rules of the foragers can be improved by including information on resource availability, such as considering the neighbourhood density in terms of sensing other ants with leaves along their foraging trail. In tackling the problem of fungus decline, one can start with verifying the simultaneous activation in Mesa, and if it improves the model behaviour. Likewise, further modelling work will have to be conducted to determine how to time-calibrate the model, which will allow validating the model with observational data.

As noted in Section III-B2, the Sobol' method is limited in its application to our model output since it exhibits a bimodal distribution, for which variance might not be the best measure of variability [24]. Due to computational limitation, we didn't do sensitivity analysis on the fraction of repetitions with a successful settlement, as this requires the model output to be a proportion of colonies rather than a single colony. This could be included in future work to help explain what parameters are important in guaranteeing the survival of a colony.

As a potential direction for future research, the growth dynamics for ant colonies with more phases of life can be investigated. This can include the idea of elitism, which considers the specialization of individuals in a particular task with age. Another direction for future work can be modelling the energy of ants. This can be done by assuming energy depletion through activity, which would vary for different tasks and energy replenishment by feeding on fungus. Allowing ants to consume fungus can introduce new dynamics to the model.

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APPENDIX A
EXPERIMENT 1 INDIVIDUAL RUNS

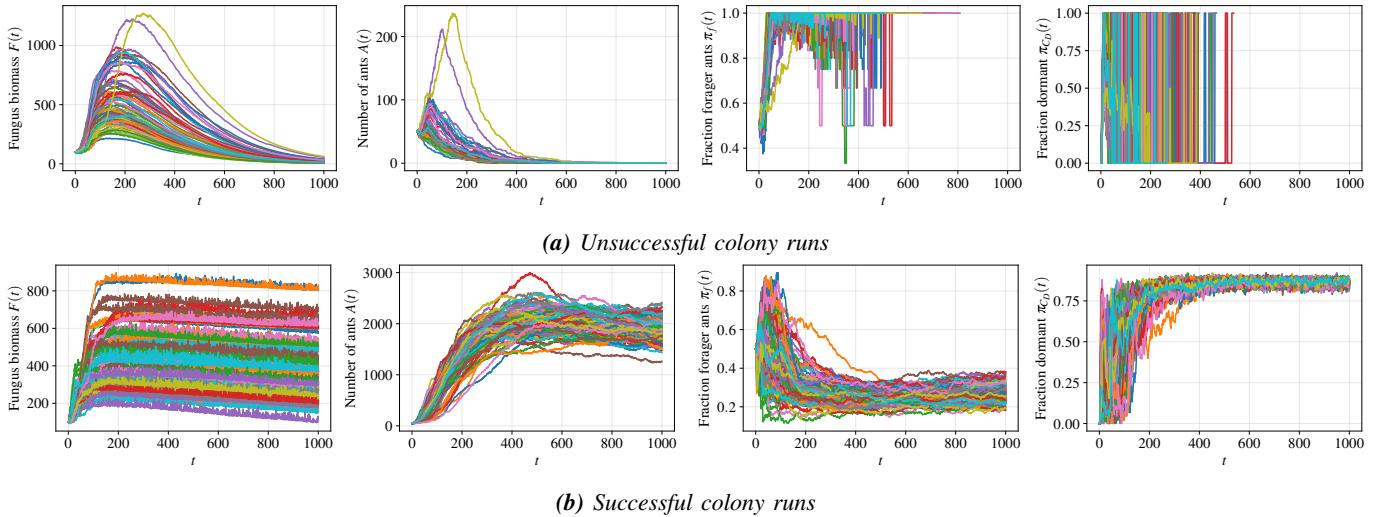


Fig. 10: Different measures of individual runs from experiments where colonies died out (a) and experiments where colonies survived (b).

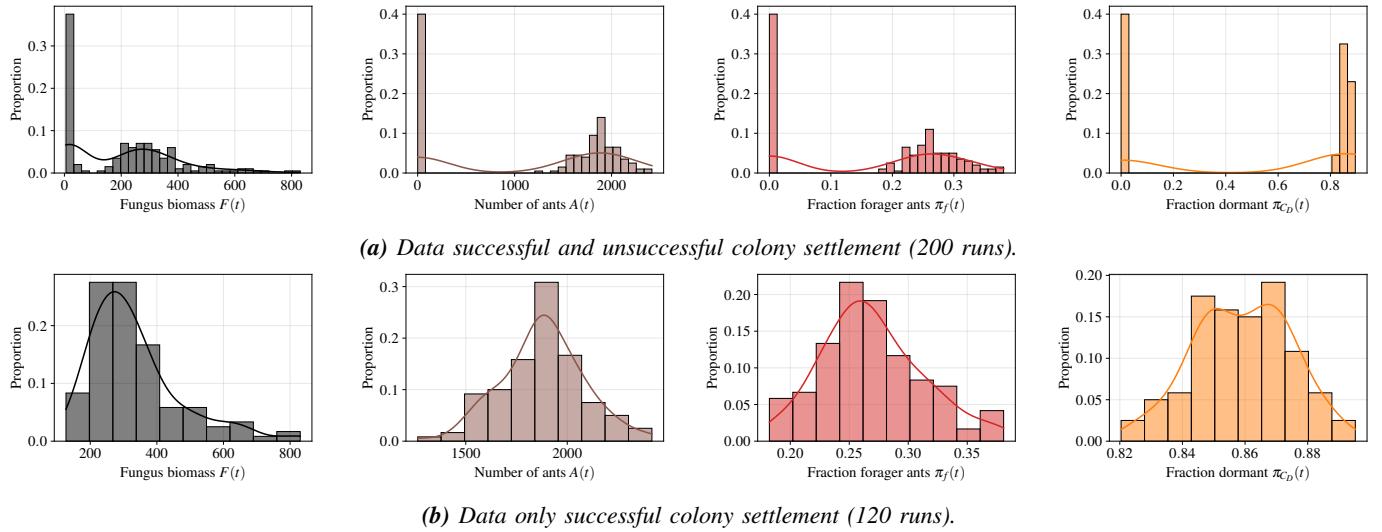


Fig. 11: Data distribution of the last recorded values ($t = 1000$), both with and without the runs with unsuccessfully colony settlement. In case of an unsuccessful colony settlement, the fraction of forager ants and fraction of dormant caretakers are set to zero after colony death.

APPENDIX B
SENSITIVITY ANALYSIS

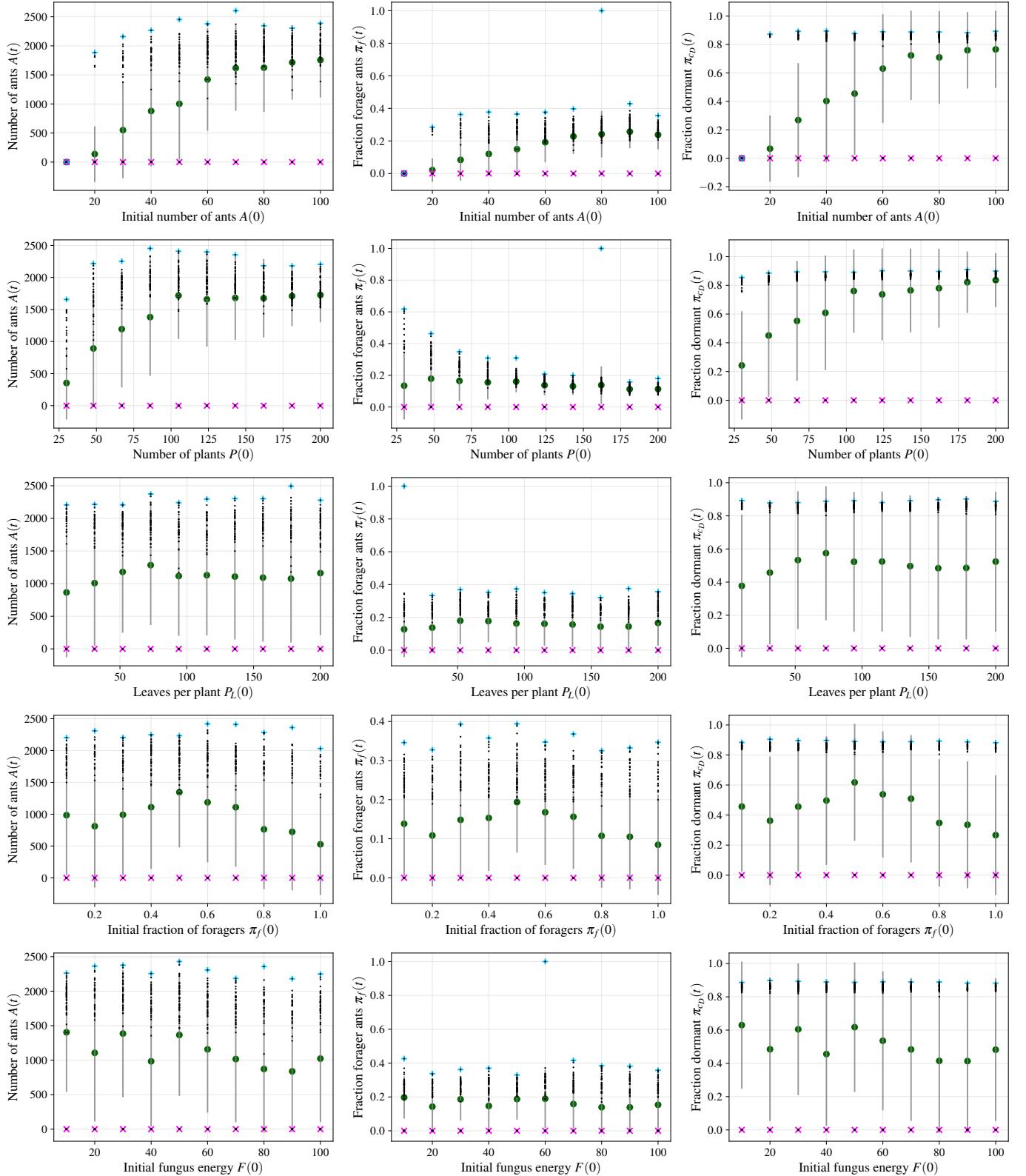


Fig. 12: OFAT results for parameters specifying initial condition, on three different output parameters, number of ants (left), fraction forager ants (middle), and fraction of caretakers dormant (right). The green dot represents mean over 64 runs, with standard deviation in grey. Individual runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

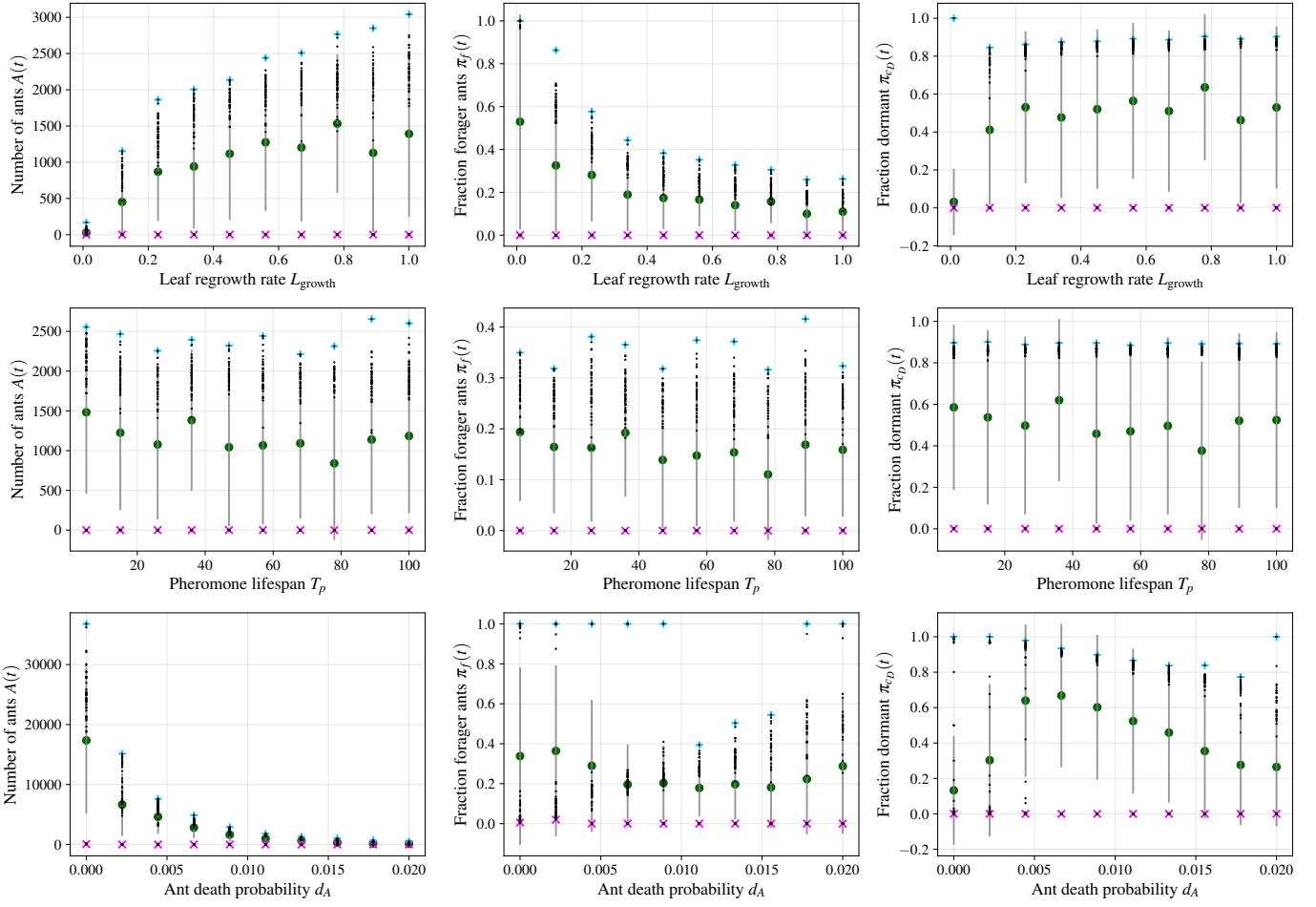


Fig. 13: OFAT results for input variables regarding ant biology and leaf regrowth rate, on three different output parameters, number of ants ($A(t)$), fraction forager ants ($\pi_f(t)$), and fraction of caretakers dormant ($\pi_D(t)$). The green dot represents mean over 64 runs, with standard deviation in grey. Individual runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

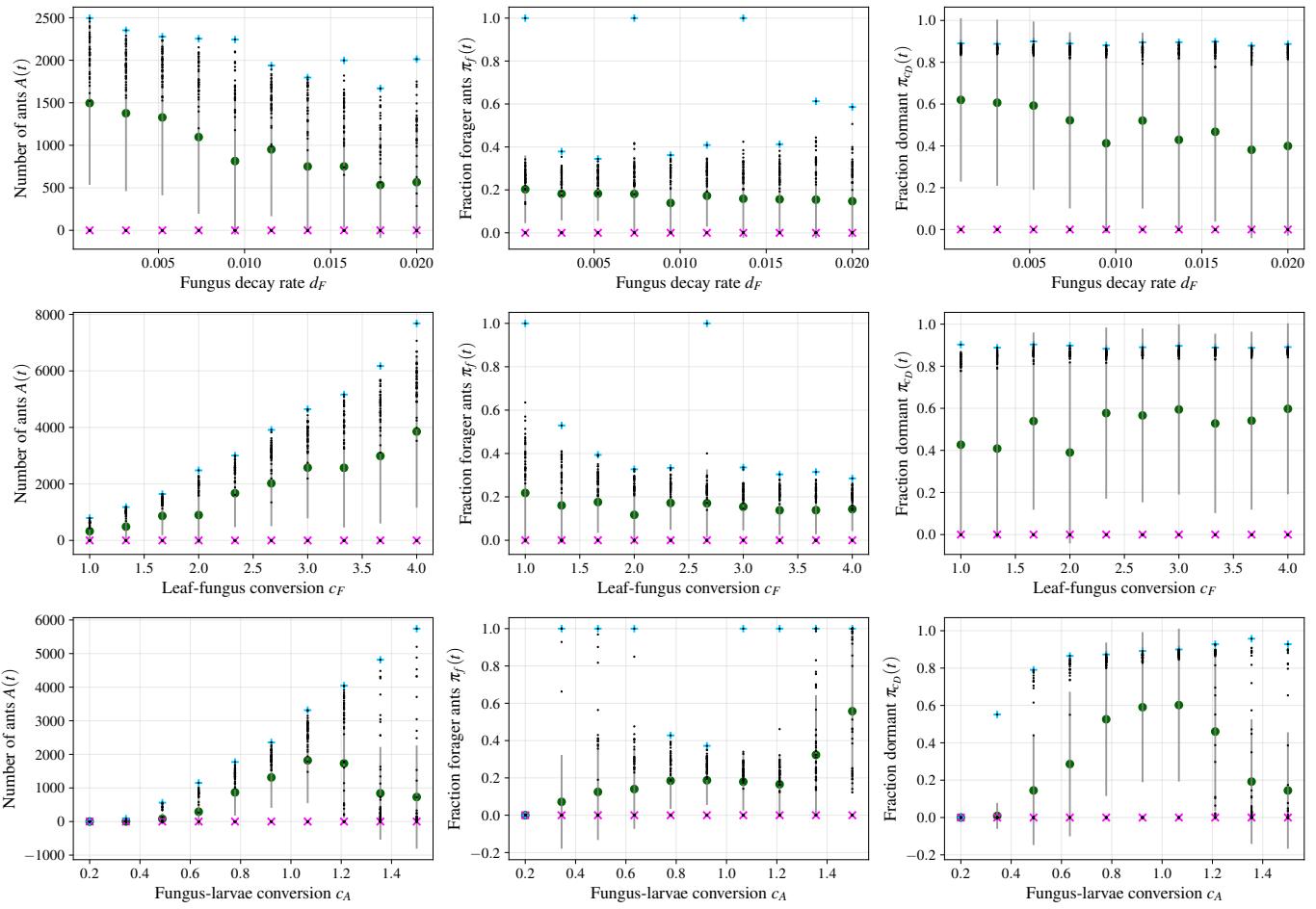


Fig. 14: OFAT results for input variables, the leaf-fungus and fungus-larvae conversion coefficients, on three different output parameters, number of ants (left), fraction forager ants (middle), and fraction of caretakers dormant (right). The green dot represents mean over 64 runs, with standard deviation in grey. Individual runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

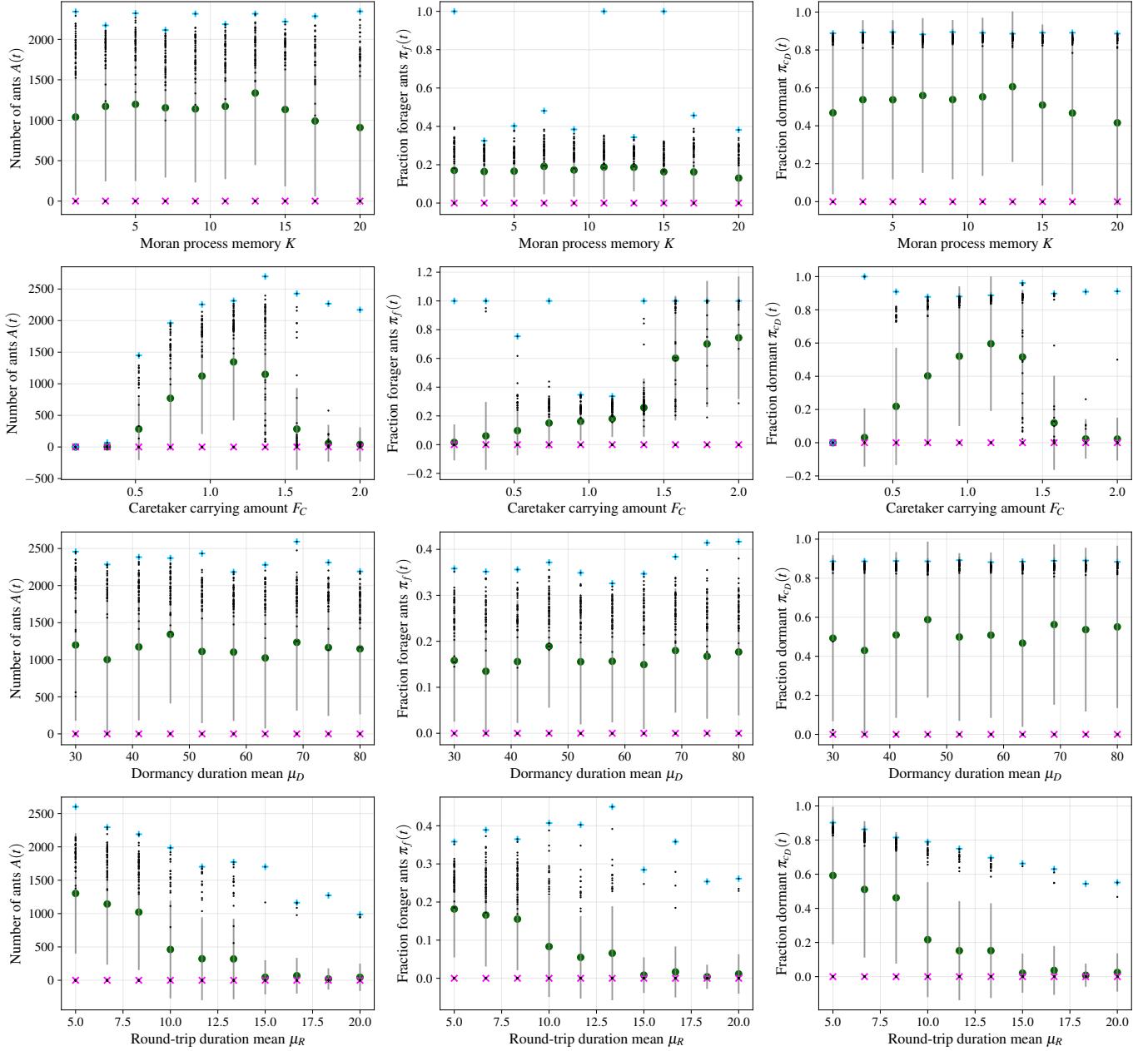


Fig. 15: OFAT results for input variables regarding caretaker ants, on three different output parameters, number of ants (left), fraction forager ants (middle), and fraction of caretakers dormant (right). The green dot represents mean over 64 runs, with standard deviation in grey. Individual runs are plotted as black dots, with minimum as a pink cross and maximum as blue plus.

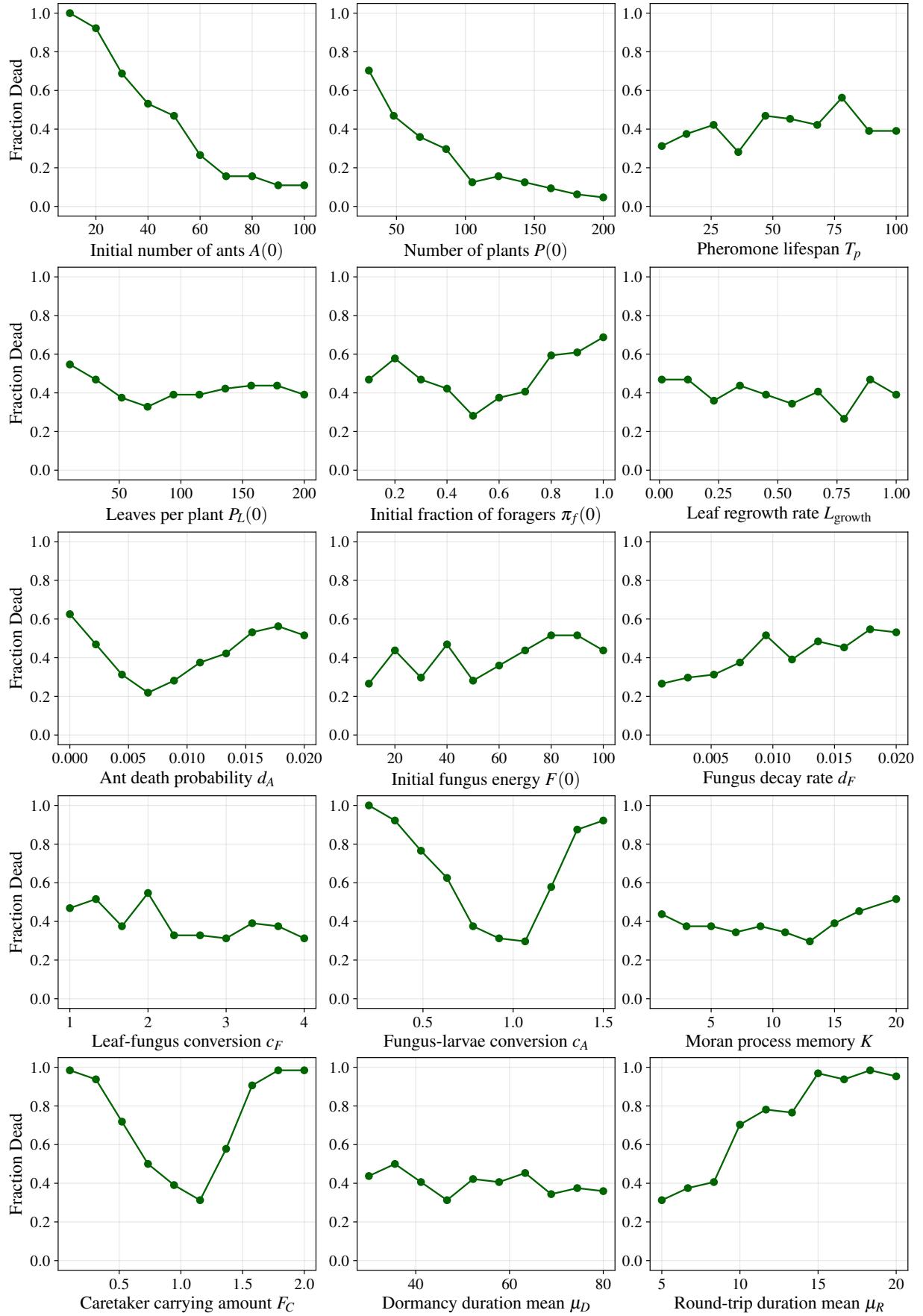


Fig. 16: Fraction of 64 runs resulting in unsuccessful colony settlement, while varying the input parameters according to OFAT.