A computational model of ant nest morphogenesis

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Abstract

The nests of social insects are not only impressive because of their sheer complexity, but also because they are built from much smaller agents whose work is not centrally coordinated. A central question is therefore how this coordination can lead to such large scale structures. In this paper we present an individual based nest construction model from experimentally inspired rules. The coordination of the building process is achieved through three main ingredients: 1) stigmergy, which implies that the local configuration of the structure is the stimulus which determines how to continue, 2) body template, where the interaction between the ant's body and the growing structure determines the proportions of the emerging pattern, and 3) a construction "pheromone", a chemical compound capable of triggering building actions. Our simulations show that this simple set of coordination rules can reproduce the key features observed experimentally in the ant *Lasius niger*, notably the emergence of mushroom-like pillars and layered structures. A sensitivity analysis on the evaporation rate of the construction pheromone shows that a large range of architectures, from dynamic multilayered nests to compact sponge-like structures, can be produced with the same behavioural rules by simply modifying evaporation rate. We discuss the relevance of these results with respect to the variety of nest architectures found in social insects.

Figure 1: Examples of nest architectures built by ant colonies. (a) Detail of a nest in wood pulp sculpted by the ant *Lasius fuliginosus*. (b) Detail of the nest structure built by the ant *Lasius pallitarsis* ©Alex Wild. (c) A closer look on the walls and vertical passages connecting chambers inside a nest built by the ant *Lasius niger*.

Introduction

The nest architectures of social insects (ants, termites, some bees and wasps species) are among the most impressive and complex artifacts built by animals with the notable exception of man (Theraulaz et al., 1998; Turner, 2000a,b). All along the evolution of social insects, there has been a whole set of innovations in terms of architectural designs and construction techniques that proved to be very efficient to solve a large number of problems such as controlling the temperature inside the nest, ensuring the gas exchanges with the outside environment (Bollazzi and Roces, 2007) or adapting the nest structure when colony size is growing (Hansell, 2005). More than fifty years after Pierre-Paul Grassé has introduced stigmergy as a basic principle for the coordination of work in these societies, we are still very far from having a full understanding of the mechanisms that shape architecture and functional designs of the nests (Grassé, 1959). While being extremely simple, stigmergy is able to give rise to complex self-organised patterns (Deneubourg, 1977; Bonabeau et al., 1998). Moreover stigmergy is often combined with environmental templates that modulate the expression of individual building rules, thus increasing the range of potential architectures (Jost et al., 2007). Other factors are also likely to play a key role in nest morphogenesis such as building pheromones. Such pheromones have been identified in termites (Bruinsma, 1979) and are likely to exist in some ant species (our unpublished data).

In this paper we present an individual-based model of ant nest construction based on a detailed analysis of individual building behaviours that take into account the logistic constraints imposed by the architecture on the movement of ants. With this model we investigate the role played by the building pheromone on the resulting shape of the nest.

The paper is organised as follows: in section two we introduce the experimental results and describe the individual building rules in the ant *Lasius niger*. In section 3, we present an overview of the 3D agent-based model. In section 4, we report simulation results that illustrate the impact of evaporation rate of building pheromone on the resulting nest architectures. Finally, in section 5, we establish comparisons with related work and draw some conclusions and directions for future work.

Construction mechanisms at the individual level

We performed a series of experiments to investigate the mechanisms involved in nest construction in the ant *Lasius niger*. These experiments showed that the deposition of material in a particular place stimulates the ants to accumulate more material in that same place, thus creating a positive feed-back. Experiments also revealed that the workers add a chemical signal (a building pheromone) to the building material. The main action of this chemical signal is to attract ants, but there are also indications that it stimulates the deposition of building material.

There was no particular effect of this signal on the extraction of building material, but it was noticed that ants prefer to dig where they have already dug, forming a type of quarry. This may be simply due to physical constraints, in the sense that it is much harder for an ant to extract a pellet from a place where the soil has been solidly packed, compared to a place where the soil surface has been broken (as by a previously digging ant).

The consequence of all these behaviours is the formation of pillars. Once pillars have been erected and have reached a critical height, the workers start to build a canopy on the sides. The height at which the ants attach the pellets on the pillars corresponds approximately to the mean body length of an ant worker. The workers therefore use their body as a kind of template to decide at which height they will stop to increase the size of an existing pillar and start to build a roof from that pillar.

Behaviour-based model of nest construction

We developed a spatially explicit individual-based model in a discrete 3D cubic-lattice in which we have incorporated the behavioral rules characterized by the experiments

General principles

The model is stochastic: ant workers are represented by agents whose behavioural rules are modelled according to probabilities to perform simple elementary actions. Moreover, the process is Markovian: the probability of performing a given action is only depending on the current state of the environment around the agent (spatial configuration, quantity and age of the building pheromone, number of

empty cells below). Indeed, agents are memoryless and tireless.

Following Ladley and Bullock's work (2005), our model takes into account the geometric constraints: each pellet of building material occupies a single cell and the ants are represented by agents that move randomly in a three-dimensional discrete cubic lattice ($200 \times 200 \times 200$ voxels). Each agent occupies a single cell and their movements are constrained by the structures they build: they cannot walk through the built structures. The layers on the bottom and on the sides of the lattice act as borders. Ants simply bounce on the floor and walls when they come into contact. We choose a discrete time step approach. At each step, the system is updated: agents move, then, if they are not already transporting building material, they can pick up a pellet, else drop it, or simply continue their walk without doing anything else. Each agent can only perceive the first twenty six neighbouring cells that surround the place where it is located at a given moment (cell c). We denote these twenty-six 3D-neighbours by $V_{26,c}$, and the influent neighbourhood for certain behavioural rules may be restricted as detailed below.

Behavioural rules of an ant

Motion The motion of ants is a constrained random walk, which means that they stay in contact with the outer surface of the architecture. The building pheromone that will be introduced in dropped pellets doesn't affect their motion: ants are not attracted or repelled by it.

Ants may only move to adjacent locations, i.e. the six orthogonal cells. We call $V_{6,c}$ this reduced neighbourhood around the cube c. A worker cannot walk through an occupied cell (clay, floor, wall or another worker): only empty cells of $V_{6,c}$ are really available for moving. The second constraint prevents flying ants: they must stay in contact with the surface of the structure. Thus, only adjacent locations, which have at least one $V_{6,c}$ neighbour cell occupied by clay, floor or walls, are available for moving. The algorithmic description of the motion rule is summarized below (Algorithm 1).

Picking-up rule A worker can only pick up a pellet when it stands atop it. If it does, it takes the location of the pellet.

To compute the picking-up probability, the worker simply considers the bottom layer of cells in its neighbourhood. We call $V_{8,c}$ the eight horizontal neighbours of the cell she is standing on. The probability to pick-up the block she is standing on is not influenced by the presence of pheromone in the material but it slightly decreases as the quantity of building material in this bottom layer increases. This is a simple consequence of the fact that it is much more difficult for an ant to extract a pellet when the ground is packed more solidly. The corresponding picking up probability is shown in Figure 2 (a).

Algorithm 1 Motion rule – The algorithm used to simulate the workers' random walk. To simulate agents' diffusion, one agent performs *nbMove* elementary moves each time step. c_w is the cube with the worker w. $V_{6,w}$ is the list of the six neighbours of w that share a face with it. We denote by A_w the list of the accessible immediate neighbours of w and by Random the random drawing in a discrete set of cells.

```
1: // The worker is in c_w.
2: for all step ∈ {1; nbMove} do
3:     A_w = EMPTY LIST
4:     for all c_i ∈ V_6,w do
5:         if (c_i == empty) and (one of V_6,c_i is full )
           // The cube c_i is accessible.
            then
6:             A_w ← concat(A_w, c_i)
7:         end if
8:     end for
       // A_w contains all the accessible adjacent neighbours
       of w.
       // Random choice of c_r ∈ A_w.
9:     c_r = Random(A_w)
10:    c_w ← c_r
11: end for
```

The algorithmic description of the picking up rule is summarized below (Algorithm 2).

Building rule A worker drops its pellet at its current location, provided there exists a cell in the neighbourhood $V_{26,c}$ where it can move after dropping. This building behaviour is also conditioned by physical constraints, which means that a building pellet can be added to the previous structure only if at least one of its faces is in contact with another pellet located in the neighbourhood (pellets do not stick together by the cube's corners or edges).

Since we found experimental evidence that clay which has been previously manipulated by workers stimulates the dropping behaviour, we implement a building pheromone. The building pheromone contained in a pellet is renewed each time a pellet has been picked-up and dropped. It does not diffuse to adjacent cells but still undergoes an exponential decay (at some rate), so it directly delivers a local signal about the time elapsed since the pellet was deposited. The probability to drop a pellet or add it to an existing structure is enhanced by the number of pellets previously dropped in the neighbourhood but it decreases with time.

Since we found also experimental evidence that ants use their body as a kind of template to build the canopies on top of the pillars and prefer to drop their load at some height (standing upright along the pillar), we also include a modulation of the dropping probability when a worker is moving over a vertical surface. In those situations, when the potential dropping site has h empty cells below it, the behavioural
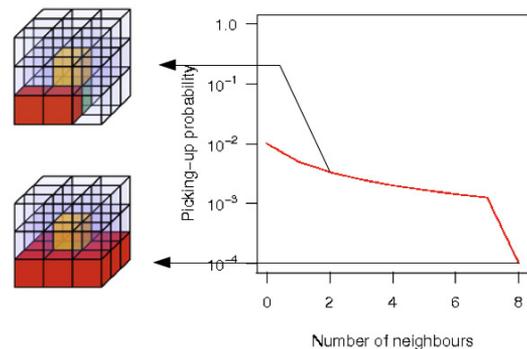
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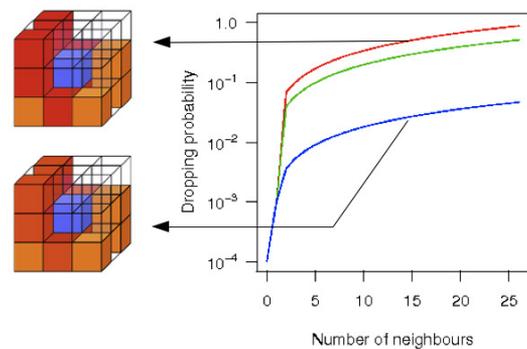
b

Figure 2: Probabilistic building rules implemented in the model. (a) Picking-up probability as a function of the number of cells containing clay in the bottom layer. The shown curve is implemented as a two-parameter function of the number of neighbours n, taking the value $spontPick$ for $n = 0$, $spontPick/100$ for $n = 8$ and $spontPick/(amplifPick \cdot n)$ for $1 \leq n \leq 7$. (b) Dropping probability as a function of the local density (number of neighbouring cells containing clay, n) and of the age of the latest dropped pellet in the neighbourhood. It takes the values $spontDrop$ for $n = 0$ and $(drop1 + amplifDrop \cdot (n - 1)) \cdot \exp(-(time - latestDropTime) \cdot evap)$ for $1 \leq n \leq 26$, where $time$ is the current time. For parameter values and explanations see Table 1. The red, green and blue lines mark the probabilities where the last dropped pellet is younger to older respectively.

Algorithm 2 Picking-up rule – The algorithm used to estimate the granularity around the worker w currently located in the cube c_w. We denote by $t_{w,p}$ the target cube for the picking up. Here, the rule $H_{p,1}$ is that $t_{w,p}$ is underneath c_w. $V_{8,t_{w,p}}$ is the list of the influent neighbours of $t_{w,p}$. The variable $n_{w,p}$ counts the number of full neighbours. $p_{w,n}$ is the associated picking up probability. Uniform denotes a random number in $[0;1[$.

1: $n_{w,p} = 0$
2: **for all** $c_i \in V_{8,t_{w,p}}$ **do**
3:    **if** c_i == full **then**
4:       $n_{w,p} \leftarrow n_{w,p} + 1$
5:    **end if**
6: **end for**
   // Calculate the picking up probability, associated to $n_{w,p}$.
7: $p_{w,p} \leftarrow f(n_{w,p})$ // According to a decreasing amplification curve, see figure 2 (a).
8: **if** $p_{w,p} <$ Uniform **then**
9:    // Pick-up $t_{w,p}$.
10:    // Move to $t_{w,p}$.
11: **end if**

Algorithm 3 Building rule – The algorithm used to estimate the local density around the worker w which is located in the cube c_w. The influent neighbours are V_{26,c_w}. The variable $n_{w,d}$ allows to count the number of full neighbours. $ageOf(c_i)$ corresponds to the date of dropping the pellet c_i. We define by $latestDropAge$ the date of the latest dropped pellet in V_{26,c_w}. Uniform denotes a random number in $[0;1[$.

1: $n_{w,d} = 0$
2: $latestDropAge = 0$
3: **for all** $c_i \in V_{26,c_w}$ **do**
4:    **if** c_i == full **then**
5:       $n_{w,d} \leftarrow n_{w,d} + 1$
6:       **if** $latestDropAge < ageOf(c_i)$ **then**
7:          $latestDropAge = ageOf(c_i)$
8:       **end if**
9:    **end if**
10: **end for**
   // Calculate the dropping probability, associated to $n_{w,d}$ and $latestDropAge$.
11: $p_{w,d} \leftarrow f(n_{w,d}, latestDropAge)$ // According to the increasing curve shown in figure 2 (b).
12: **if** $p_{w,d} <$ Uniform **then**
13:    // Drop in c_w.
14:    $ageOf(c_w) =$ currentStep
15:    // Use OneMove (Algorithm 1) with $nbMove = 1$ to escape from c_w.
16: **end if**

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algorithm includes a multiplication factor of the dropping probability, $p_{w,d}(h)$, according to the equation

$$p_{w,d}(h) = p_{w,d} \cdot \frac{h^n}{\bar{h}^n + h^n} \qquad (1)$$

with $\bar{h}$ being the mean length of an ant.

The algorithmic description of the building rule is summarised above (Algorithm 3).

Simulation results

We implemented the three behavioural rules in the model and we run the simulations with the parameters values given in table 1. The 3D cubic lattice ($200 \times 200 \times 200$) was initialised with 20 bottom layers uniformly filled with pellet and 1000 workers randomly placed on the surface. The maximum value of the spontaneous picking-up probability is reached when the eight horizontal neighbours on the bottom layer are empty. This is fixed in the picking-up probability function by the parameter $spontPick$ which we set to 10^{-2}. The decrease in picking-up rate, specified by parameter $amplifPick$, is set to 1.

The spontaneous dropping probability $spontDrop$, when there is only one pellet in its $V_{26,c}$ neighbourhood, is fixed at 10^{-4}. In case of one additional neighbouring cell we set the dropping probability to $drop1 = 10^{-3}$ (Fig 2). Dropping probability then increases continuously with the number of pellets in $V_{26,c}$ to the maximum value of $drop26 = 0.9$. The evaporation rate is initially set to $evap = 1.6 \times 10^{-5}$ per time step and then modified to explore its impact on the emerging 3D architectures.

Model parameter	Description	Value
$spontDrop$	Spontaneous dropping probability	10^{-4}
$drop1$	Dropping probability in the case of exactly one marked neighbour	10^{-3}
$amplifDrop$	Factor modulating the dropping probability	0.036
$evap$	Evaporation rate of the building pheromone	3.2×10^{-4} to 8.0×10^{-7}
$spontPick$	Spontaneous picking-up probability	10^{-2}
$amplifPick$	Factor modulating the picking-up probability	1.0

Table 1: Parameters values used in simulations. Rates and probabilities apply to one time step. See Fig 2 for the use of these parameters.

Pillars and roofs

When running this model one can observe the formation of pillars. When the height of the pillars becomes high enough, pellets are added on the pillars' sides; this rapidly increases
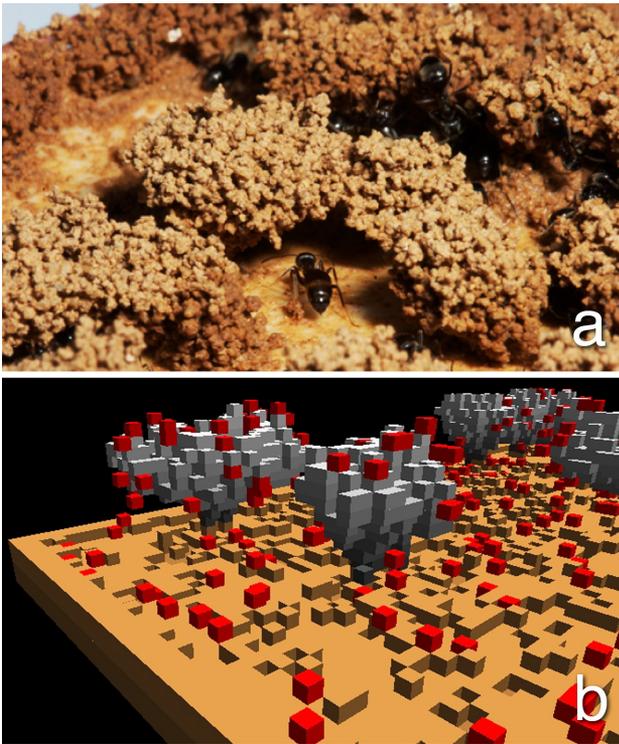
Figure 3: A comparison of the structures built in experiments and in a simulation of the model. (a) An arch that covers a passage between two pillars built by ants in experimental conditions. (b) A close view of a simulation result with the same initial conditions as the ones used in experiments. The model is able to reproduce the characteristic shapes observed in these experiments. The parameter values used in this simulation are listed in table 1.

the surface of the pillar top, leading to the formation of some kind of hat or roof. These roofs look quite similar to the ones we got in the experiments (see figure 3). Moreover, when two roofs are close enough to each other, they can merge. The result is an arch that covers a passage between the two pillars.

Physical stress due to gravity and decreasing cohesion due to evaporating water should finally lead to collapsing roofs and pillars, an event that was sometimes observed in the experiments. The current version of the model does not include these processes, but when inter-pillar distance is not too large this should not be much of a problem.

Effect of the decay of the building pheromone on 3D architectures

To explore the diversity of nest architectures the model is able to produce, we investigate the role of the decay rate associated with the building pheromone. This is already known to be a key ingredient of the self-organization in social insects, it has a major impact on the collective dy-

namics such as: trail formation and path choice in ants (Goss et al., 1989; Beckers et al., 1992; Jeanson et al., 2003; Sumpter and Beekman, 2003), construction of pillars in termites (Deneubourg, 1977; Franks and Deneubourg, 1997; Bonabeau et al., 1998), construction of wall in ants (Franks et al., 1992), digging networks of galleries in ants (Buhl et al., 2005).

Figure 4 shows that the evaporation rate of the building pheromone is indeed a highly influential parameter on the resulting structures.

When there is a strong evaporation rate ($evap = 3.2 \times 10^{-4}$), the final structure is laminar (figure 4 (a)). In the early steps, agents begin building several tiny pillars on the unmarked initial surface. They cover them with thin roofs or capitals. The surface of these roofs increases, several roofs merge, forming a thin first layer that becomes the first floor. In the next steps, the construction dynamics undergo the same cycle of events, leading to a new floor. Moreover agents can enlarge the pillars by adding new pellets on their sides.

When the evaporation rate is smaller ($evap = 1.6 \times 10^{-5}$), the structure is still laminar, but the layers are less plane than in the previous case (figure 4 (b)). The initial phase is similar to the previous condition, but there is a larger number of pillars and the capitals are thicker. After the completion of the first floor, the construction of new pillars occurs at a faster rate than with the higher evaporation rate. A closer look at the growth and the evolution of the nest structure reveals that while the whole structure remains quite similar in time, it is constantly destroyed and rebuilt. The consequence of this remodelling process, in which the ants destroy what they have built previously, is a progressive drift of all the layers from the top to the bottom. It seems that a kind of wave runs though the whole structure. These traveling waves are indeed the simple consequence of the fact that the only place where the ants can pick up some building material is the bottom layer. So it quite naturally induces a kind of symmetry breaking in the remodelling process.

Finally when the evaporation rate is very low ($evap = 8 \times 10^{-7}$, figure 4 (c)), the model leads to a sponge-like structure that looks similar to the nest built by *Lasius niger*. In a first step, pillars also emerge and are covered with capitals that are more spherical than in the two previous cases. Thus, when the capitals merge, the layer is thicker. In a second step, pellets can be dropped anywhere on the new floor. No pillar emerges in this case, the layer is just thickened. Sometimes, a little heap appears by chance, a new pillar is built and starts to grow. This new pillar merges quickly with the structure in its vicinity, leading to the formation of a chamber. The next floor is built when many chambers have been created and closed. In the next steps, the construction dynamics undergoes the same cycle of events: (1) thicken the floor ; (2) emergence of few little pillars ; (3) fusion of the roofs, which leads to the formation of chambers.
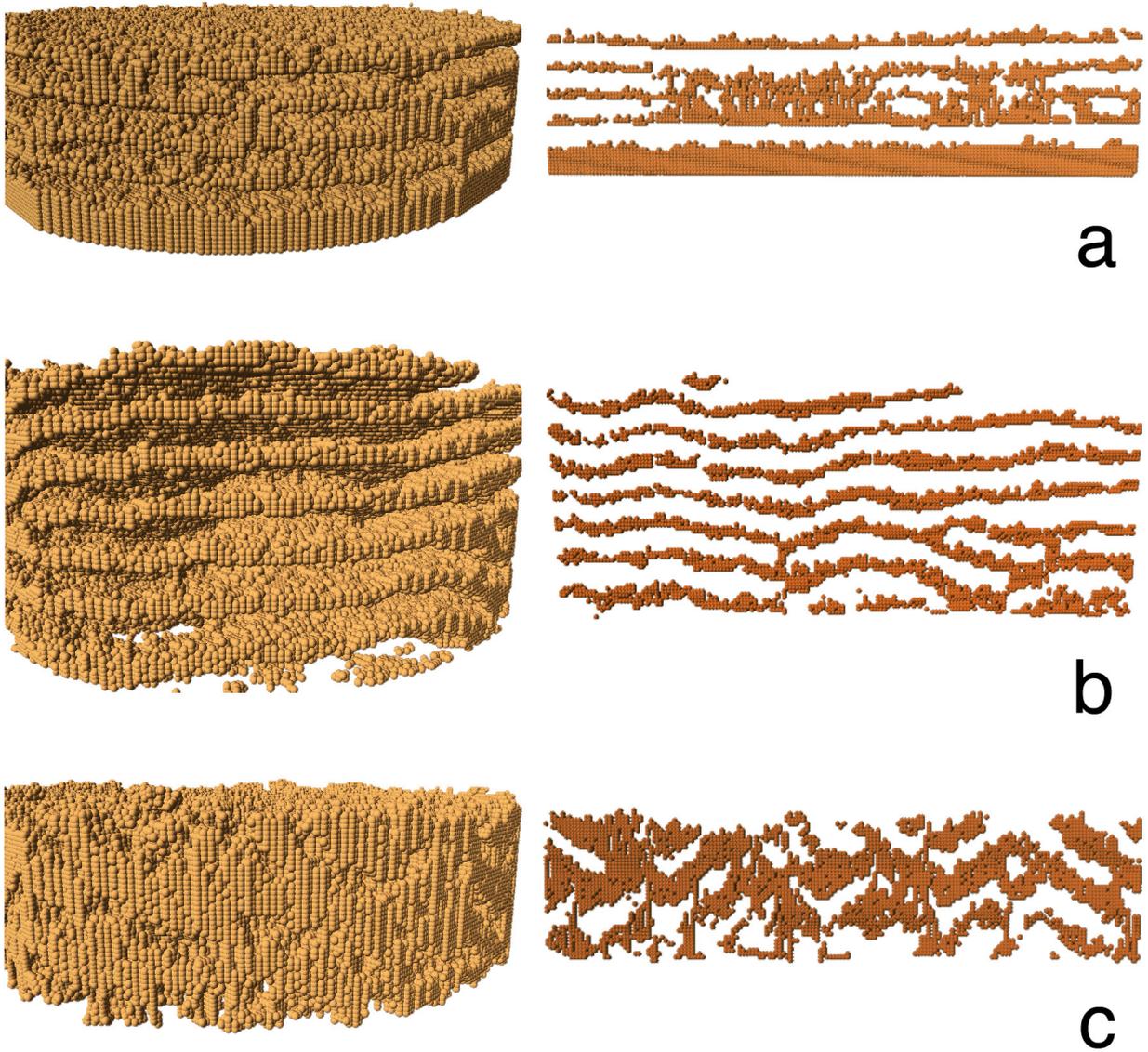
Figure 4: The influence of the evaporation rate of the building pheromone on the nests structure. Left : 3D structure. Right : Vertical cut ($x \in [98; 101]$. (a) With a strong evaporation rate ($evap = 3.2 \times 10^{-4}$), the construction process leads to the formation of a laminar structure. The horizontal layers are connected with thick pillars. (b) With an intermediate evaporation rate ($evap = 1.6 \times 10^{-5}$), the structure is still laminar, but sometimes two successive layers can intersect and form a ramp that connects successive floors (c) When the evaporation rate is very low ($evap = 8 \times 10^{-7}$) we get a sponge-like structure.
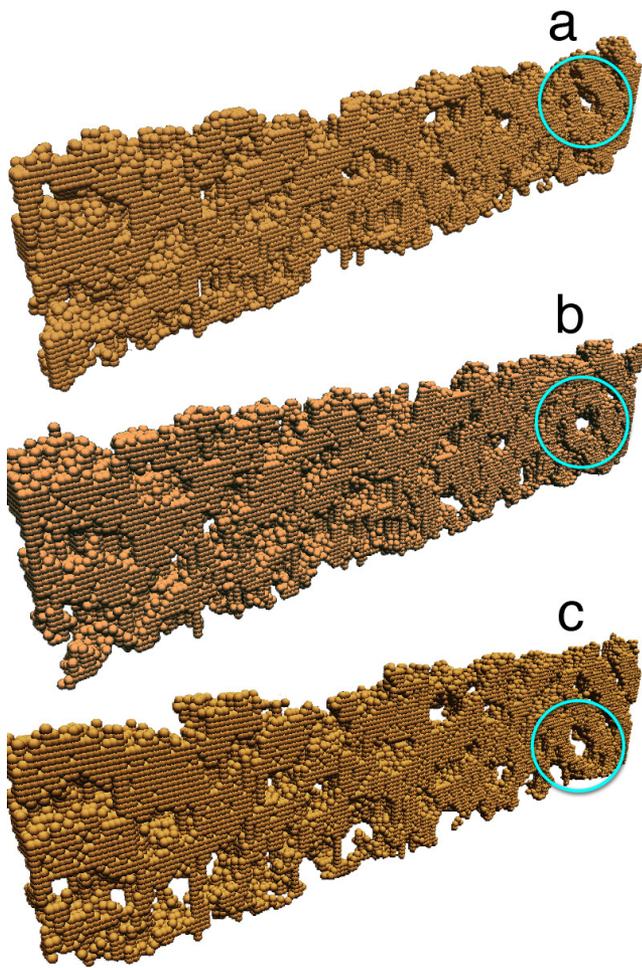
Figure 5: A closer look on the building dynamics in the case of a very weak evaporation rate (8×10^{-7}). (a) to (c) show three successive steps of a simulation. The circle marks a chamber "moving" downwards.

Discussion and conclusion

In this paper we introduced a 3D model of collective ant nest construction. This model is based on stochastic individual rules derived from the experimental analysis of building behaviour in the ant *Lasius niger*. The model also integrates logistic constraints, that is physical limitations on the movement of ants imposed by the nest architecture. Such constraints have been previously implemented by Ladley and Bullock (2005) to simulate the formation of the royal chamber and covered lanes in termites.

There are two main differences with this previous work. First, in our model there is no chemical template created by the diffusion of pheromones. This contrasts with termites, because the queen releases a pheromone that controls the distance at which workers start to build. At the very beginning, this chemical template strongly interacts with the self-organizing building processes. And this combination gives rise to pillar-like structures formed at roughly regular spatial intervals, but at a specific distance from the queens body. In ants, the effect of the body-template begins to work later in the construction process, when the pillar-like structures have reached a critical size. The consequence is the formation of a double regular spatial pattern: the first one characterizes the spatial distribution of the pillars and the second one characterizes the layered structure of the nest. The second difference is a constant remodelling process that results from the ants activity. In our model, ants continuously destroy what they have built previously. Once a layer is in place, all its surface is eroded as a consequence of the ants digging activity and rapidly the material accumulates on the underneath surface. As a main consequence all the layers drift progressively downwards. And the speed of the travelling and remodelling wave results from a balance between the net deposition rates of building material at the upper and lower surfaces of a layer.

Sometimes, ants may accumulate by chance a little bit more material on the underneath surface of an existing layer. This gives rise to a new pillar growing from top to bottom. Once this pillar is built, it remains in place because the virtual ants can only dig on the bottom layer and not on the sides. This creates a kind of defect that propagates within the structure as the remodelling process goes on. The same process also produces connection areas between different layers close to these pillars. The motion of ants is in turn channeled by the spatial distribution of these connection areas. Then, depending on the evaporation rate, this channeling process may also promote the deposition of building material on the edges of the pillars, thus changing their size and shape.

Our model showed that the resulting nest structure strongly depends on the evaporation rate of the building pheromone. When the evaporation rate is very high ($evap = 3.2 \times 10^{-4}$), only the very latest depositions of material can enhance the accumulation of more material. In these conditions, only a small number of pillars can be built, there is a strong competition among pillars to attract builders and the distance between pillars increases. The second consequence is a much more important enlargement of the capitals on top of the remaining pillars. As soon as a capital is built, the material is deposited at a faster rate on its border and the resulting shape of the roof becomes flat and thin. When the evaporation rate is less important ($evap = 1.6 \times 10^{-5}$), the number of pillars increases and the enlargement of the capitals on top of the pillars is also much more important. Each pillar becomes a seed from which a new layer is growing. Since at each level there exist several seeds from which different layers are growing, it may happen that one of these layers collides with another one that is a part of the next level below. This results in the formation of inter-crossings of ceilings and floors belonging to two successive layers, leading

to the formation of ramps. Finally, when there is a very weak evaporation of the building pheromone ($evap = 8 \times 10^{-7}$), the enlargement of the capitals becomes even more important. After having merged the capitals still increase their size and the floor of the new layer is so attractive that the depositions of building material occur more or less uniformly over the whole surface. Instead of well-defined pillars and floors, ants build globular structures enclosing empty and irregular chambers. The whole structure adopts a sponge-like structure.

The same kind of architectural diversity is observed in *Lasius* species. The ant *Lasius fuliginosus* builds a sponge-like nest (Figure 1 (a)), whereas *Lasius pallitarsis* and *Lasius niger* nests show layered structures (Figures 1 (b) and (c)). Our model shows that the same mechanisms can account for significant changes in the nests shape.

These variations may have several origins: it might be a consequence of the variation of environmental conditions (e.g. temperature and humidity levels). If these conditions change, the same species will be able to build nest structures that look very different, for example in *Acromyrmex* ants (Bollazzi et al., 2008) or in *Macrotermes* termites (Korb, 2003). But this variation may also result from the physical properties of the building pheromone itself. In particular one may imagine that different species of ants or termites can use similar building rules but different chemical cues. Physical and chemical properties of the building pheromone could thus play a key role in the diversity of nest architectures built by ants and termites. This is an important issue that needs to be addressed in future experimental work.

Acknowledgements

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