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# Deterministic response threshold models of reproductive division of labor are more robust than probabilistic models in artificial ants

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## Abstract

We implement an agent-based simulation of the response threshold model of reproductive division of labor. Ants in our simulation must perform two tasks in their environment: forage and reproduce. The colony is capable of allocating ant resources to these roles using different division of labor strategies via genetic architectures and plasticity mechanisms. We find that the deterministic allocation strategy of the response threshold model is more robust than the probabilistic allocation strategy. The deterministic allocation strategy is also capable of evolving complex solutions to colony problems like niche construction and recover from the loss of the breeding caste. In addition, plasticity mechanisms had both positive and negative influence on the emergence of reproductive division of labor. The combination of plasticity mechanisms have an additive and sometimes emergent impact.

**Keywords:** reproductive division of labor, response threshold, polyethism, plasticity, artificial ant colony

# 1 Introduction

The emergence of reproductive division of labor has been identified as a critical step in each of the major evolutionary transitions in biology (Szathmáry & Smith, 1995; Smith & Szathmary, 1997; Szathmáry, 2015). Despite being critical in these transitions, reproductive division of labor is rare among animals, being observed primarily among eusocial animals like ants, bees, termites, and mole rats (Crespi & Yanega, 1995; Burda et al., 2000; Wilson & Hölldobler, 2005; Nowak et al., 2010; Gadau et al., 2012; Brahma et al., 2018; Pagano, 2020). Humans, though not commonly grouped in with these other animals, also engage in division of labor in general as well as reproductive division of labor specifically. For this reason, studying reproductive division of labor in eusocial animals is a tool for better understanding the emergence and prevalence of division of labor in human cultures (Jaffé, 2017) and may help in engineering better social and artificial systems (Campos et al., 2000; Bonabeau, 2002; Mohan & Baskaran, 2012; Zhang et al., 2017; Wu et al., 2018; Lu et al., 2020).

Cognitive ethologists explain animal behavior by positing cognitive states that govern that behavior (Dennett, 1991, 2003, 2007; Marriott et al., 2010). This is necessarily a methodology of abduction. Ethologists imagine that cognitive states must be present to explain the behaviors of animal minds, even though those cognitive states can never be observed directly. Instead, observations are made of the subject's behavior and compared to hypotheses generated from the cognitive theory. Theories are validated if they can make accurate explanations and predictions of animal behavior.

A challenge faced by this methodology is that commonly competing theories can offer equally valid explanations of behavior, while positing different cognitive states in their explanations. To some extent these differences can be discarded as semantic, if indeed both theories make identical predictions. However, other times, when theories appear to make different hypotheses experiments to untangle the differences have mixed results (Tripet & Nonacs, 2004) leaving the questions unanswered.

This challenge arises from the fact that complex animal behaviors emerge from a wide variety of factors. Division of labor in insects has been found to emerge from factors among genetics, nutrition, hormones, neurobiology, environmental stimuli, experience, age, and social contact between individuals (Beshers & Fewell, 2001; Korb et al., 2009; Tarapore et al., 2010; Duarte et al., 2011; Gadau et al., 2012; Gordon et al., 2019). While theories of ant behavior recognize this, they do not incorporate all of these factors in a predictive framework. This is in part because it is difficult to observe or control for these factors in experimentation, especially genetic and neurobiological factors, and it is time consuming to reproduce results with different individuals, species, or over

evolutionary time.

To combat these challenges biologists and social scientists have turned to agent-based modelling and agent-based simulations. Agent-based models and simulations emerged as a new tool in the 1980s-2000s (Lopez, 1987; Franks & Tofts, 1994; Bonabeau, 2002), gained popularity and validation in the 2000s-2010s (Heath et al., 2009; Allan, 2010) and has now been accepted as a powerful research tool in a variety of fields (Abar et al., 2017; Gerst et al., 2013; Fagiolo et al., 2019) including biology (Bryson et al., 2007; Bauer et al., 2009; Abar et al., 2017; Metzcar et al., 2019). In agent-based simulations researchers have direct access to, and control over, agent genetic, neural and cognitive states. Other aspects of agent behavior, like environment topology and network dynamics of socialization, can be included in models, and then controlled in experimentation. This allows for a richer and more detailed formulation of models, that can then be tested in controlled experiments, and validated through comparison to real world data (Bryson et al., 2007; Heath et al., 2009; Prabhakar et al., 2012; Fagiolo et al., 2019). In addition, simulation allows for rapid reproducibility of experiments in different controlled environments.

Our experiment is embedded in a research program spanning a few decades that studies ant division of labor through simulation (Franks & Tofts, 1994; Theraulaz et al., 1998; Campos et al., 2000; Gautrais et al., 2002; Merkle & Middendorf, 2004; Waibel et al., 2006; Jeanson et al., 2007; Gove et al., 2009; Marriott & Gershenson, 2011; Prabhakar et al., 2012; Duarte et al., 2012; Bae & Marriott, 2019; de Oliveira & Campos, 2019). A common cognitive theory of division of labor is the *response threshold* theory (Bonabeau et al., 1996, 1998; Duarte et al., 2011). The cornerstone of this theory is the assertion that ants perceive quantitative stimuli that trigger particular behaviors when the stimuli is sufficiently strong. The level of stimuli at which a behavior is triggered is called the behavior's *response threshold*. Variations in the details of this theory lead to a family of related models.

The majority of these simulations are Monte Carlo simulations relying on a simple mathematical model of response thresholds. This model was presented in Theraulaz et al. (1998) and this research program was focused on exploring how this model of the response threshold theory of division of labor is impacted by plasticity (Theraulaz et al., 1998; Jeanson et al., 2007), population size (Gautrais et al., 2002; Jeanson et al., 2007), demand for work, age-based role switching, finite life-spans (Merkle & Middendorf, 2004), and genetic evolution (Duarte et al., 2012; de Oliveira & Campos, 2019).

Table 1 outlines some important features of these variant models. We note that much of the prior work occurs in simulations with fixed population sizes, abstract tasks and environments, no plasticity, and without evolution or even agent mortality. The stark simplicity of these models make them easier to study analytically and computationally, though it also makes them susceptible to criticism that too much has been abstracted away to

| <b>Work</b>                  | <b>Pop. Size</b>             | <b>Tasks</b>                      | <b>Environ.</b> | <b>Plasticity</b> | <b>Fitness</b> | <b>Mortality</b> |
|------------------------------|------------------------------|-----------------------------------|-----------------|-------------------|----------------|------------------|
| Theraulaz et al. (1998)      | Fixed (5)                    | Abstract (2)                      | Abstract        | Associative       | None           | None             |
| Gautrais et al. (2002)       | Fixed (5-1000)               | Abstract (1 or 2)                 | Abstract        | Associative       | None           | None             |
| Merkle & Middendorf (2004)   | Fixed (100)                  | Abstract (2)                      | Abstract        | Associative       | None           | Max age          |
| Waibel et al. (2006)         | Fixed (100)                  | Abstract (5)                      | Abstract        | None              | Colony         | Generation       |
| Jeanson et al. (2007)        | Fixed (2-1000)               | Abstract (2 to 20)                | Abstract        | None              | None           | None             |
| Gove et al. (2009)           | Fixed (14,000)               | Abstract (1 to 50)                | Abstract        | None              | Colony         | None             |
| Marriott & Gershenson (2011) | Emergent (0-100)             | Explicit (2)                      | Cont.           | Age based         | Emergent       | Max age          |
| Duarte et al. (2012)         | Structure (1000/100)         | Abstract (2)                      | Abstract        | None              | Colony         | Generation       |
| de Oliveira & Campos (2019)  | Emergent Structure (5000/50) | Abstract <sup>1</sup> (3, 4 or 7) | Abstract        | None              | Colony         | Random           |
| Bae & Marriott (2019)        | Emergent (0-1700)            | Explicit (3)                      | Discrete        | None              | Emergent       | Max age          |

Table 1.1: A non-exhaustive list of previous studies that model ant division of labor through simulation. <sup>1</sup>One model in this study uses reproduction as an explicit task. Cont. = Continuous.

capture real world phenomena accurately.

In contrast, our agent-based model (Marriott & Gershenson, 2011; Bae & Marriott, 2019) can test the same theory in a variety of structured environments in order to incorporate critical features of situated and embodied cognition (Clark, 1997; Ziemke, 2003; e Costa & Rocha, 2005). Within the environment we can define explicit tasks, like foraging and reproduction, that require complex patterns of behaviors to complete. Performing these tasks may fail, or result in variable rewards or costs. Ants can die of starvation, violence or old age. Ants can reproduce and spread their genetic information to their offspring. Ants can have different behavioral, morphological and physiological traits based on genetics. Ants can learn from their environment and their behavior. Ants can communicate with and learn from one another.

Prior simulations aim to answer questions of the type “Does factor X impact the evolution or self-organization of division of labor?” Through situated and embodied agent-based models we can begin to answer questions of the type “How does factor X impact the evolution and self-organization of division of labor?” and we can answer these questions in the context of multiple factors at once. The factors we consider in our experiment are the task allocation strategy (how response thresholds determine behavior), genetic architecture (how genes influence response thresholds), plasticity (how individual and social plasticity influence response thresholds), and morphology and physiology (how variation between ants impact division of labor).

We find that artificial colonies with a deterministic allocation strategy display a robust set of behaviors enabling them to thrive in a variety of environmental, genetic and intellectual conditions (in contrast to a probabilistic allocation strategy). In the deterministic strategy when our workers benefit morphologically and physiologically from specialization we observe colony demographics typical of natural colonies. In rare cases the breeding caste will die off but the deterministic strategy can recover from this catastrophe as is also observed in natural colonies (Majoe et al., 2021). When the deterministic strategy is combined with synergistic plasticity mechanisms, the colonies are capable of niche construction, even in very volatile conditions. Finally, an associative plasticity mechanism results in emergent age polyethism in our colonies with a deterministic strategy. In addition, we find that plasticity mechanisms operate best within the deterministic allocation strategy, resulting in both adaptive and maladaptive impacts on the emergence of division of labor.

The study of ant behavior through simulation has led to applications in robotics (Wu et al., 2018; Lu et al., 2020) and networking (Zhang et al., 2017) and other areas of engineering (Mohan & Baskaran, 2012). We add a discussion as to the ways our simulation can inform other artificial life research, in particular, to the use of several interacting features in our model of investigation instead of a single or few features. We find that our more detailed

model of behavior enables us to observe more complex and nuanced behavior among our simulated agents.

## 2 Model

Below we describe our agent-based model in detail, outlining the environment, genetic architecture, and learning mechanisms. We have extended the agent-based model of Bae & Marriott (2019) to include the deterministic allocation strategy and four plasticity mechanisms. In addition, we have made specific changes to some simulation parameters. Specifically, we reduced the mutation range to  $[-0.05, 0.05]$ , we increased breeder mortality to 0.001 per tick, and we added a death risk to all ants outside the mound of 0.01 per tick. These parameters are discussed more in context below.

### 2.1 Environment

An ant mound is placed in a  $60 \times 80$  toroid of patches. So long as the maximum food level (100000 units) is not reached each patch is selected with a small probability and so long as it is empty of food and is at least  $d = 3$  patches from any other patch with food then  $k = 200$  units of food is added to that patch ( $k = 200$  represents 20 meals or 4 loads for the default ant). Food is added to the environment every 50 ticks. The food distribution and optimal foraging strategy are held constant throughout our experiment (as experimentation in Bae & Marriott (2019) indicated no major impact on division of labor from different foraging strategies).

Ants leave outgoing and incoming pheromones used in foraging. Outgoing trails of pheromones lead to (possibly depleted) food locations and incoming trails lead to the mound. Since most of our ants follow the solitary exploration strategy the outgoing trails are commonly ignored. However, all ants follow incoming trails home to the mound. The details of this mechanism are functional in foraging, but do not impact patterns of division of labor. Interested readers can find the details in Bae & Marriott (2019).

### 2.2 Ant Behavior

Ant metabolism is regulated by hunger and energy. Hunger increases 1 per tick regardless of task, and energy depletes by 1 per tick when an ant is outside the mound. Eating a meal removes 10 units of food from the stores of the mound and replenishes the hunger variable. The energy variable is fully replenished whenever an ant is in the mound.

Ants in our simulation have two tasks: foraging and breeding. When an ant is idle it must select a new task.

Our ants have a *breed* meme with real values in the range [0, 1]. The *breed* meme serves as the response threshold and is used to determine what task is performed by an ant. These allocation strategies are explained in detail below.

An ant selecting the foraging task leaves the nest and searches for food until it: reaches its carrying capacity, depletes a food site, runs out of energy, or becomes hungry. In all cases, it returns to the mound, drops off any food it is carrying, replenishes energy, has a meal (if hungry) and selects a new task.

An ant selecting the breeding task first checks if the stored food is more than twice the current population of ants and larvae. This value allows every ant and larvae two meals (because larvae need two meals to mature), and breeding is only possible in this state, which prevents the colony from over breeding into starvation. If breeding is possible, the ant will breed immediately. If not, the ant idles and is added to a “stand-by” list where it waits until randomly selected to breed or 100 ticks passes.

When breeding occurs, the breeding ant does not become the genetic parent of the offspring. This is because under this model dedicated breeders would birth more dedicated breeders (and no workers). Instead we select a member of the population based on fitness to be the genetic parent. While this may appear artificial it has biological correlates in ants like *Pogonomyrmex barbatus* where worker and queen castes are genetically different and arise from mating with different lineages (Gadau et al., 2012; Cahan et al., 2004).

Our model uses a simple additive fitness function to measure an ant’s success at foraging and breeding. Let  $n_f$  be the number of meals returned (per tick) by the ant and let  $n_b$  be the number of offspring created (per tick). The weighted fitness function is  $w_f \cdot n_f + w_b \cdot n_b$ . As should be expected, the evolutionary dynamics of these experiments are quite dependent on the weights selected, potentially biasing the fitness function towards either foragers or breeders. We have conducted our experiment in a space of parameter values that does not favor either task. We include more details on this at the end of this section.

For computational efficiency we avoid sorting our ants by fitness. Instead we discard all ants below the mean fitness - twice - to get our potential parents. This produces a group of the top (roughly) quartile of ants. A genetic parent is selected randomly from this group whenever a new larvae is produced. The new larvae is an asexual clone of its genetic parent with its genes mutated.

Larvae eat a meal when created and again after 100 ticks at which point they mature as an adult ant and select their first task. If there is no meal they die. (This is rare.)

When an ant successfully breeds it gets fitness credit for reproducing (unlike the genetic parent). The ant must then enter a cool-down period determined by its genetics before it selects a new task, which represents the time it

invests in laying an egg and recovering.

## 2.3 Ant Genetics

Ants have a *breed* gene that has a real value in the range  $[0, 1]$ . Reproduction is asexual and mutation occurs 5% of the time, resulting in a real-valued additive change to the gene selected uniformly from the range  $[-0.05, 0.05]$ . Under experimental settings this gene may be pleiotropic, meaning that it impacts more than a single trait. We call this the *pleiotropic architecture*. Potentially the *breed* gene impacts behavioral, morphological and physiological traits.

Upon birth the *breed* gene is copied into the *breed* meme. The *breed* meme determines the response thresholds of the ant. The gene and the meme are kept separate following the dual inheritance model (Marriott & Chebib, 2016b,a) so that the gene will be passed down in reproduction, while the meme will be subject to plasticity and be used to determine behavior. As our first experiment, we implement two allocation strategies (inspired by Waibel et al. (2006)) and one control allocation strategy.

The *probabilistic* allocation strategy was deployed in Bae & Marriott (2019). This mechanism selects a task at random using the *breed* meme to determine the probability distribution. Specifically, the breed task is selected with probability *breed* and the forage task with probability  $1 - \textit{breed}$ .

The *deterministic* allocation strategy compares the *breed* meme to environmental stimuli to select a task. We interpret the *breed* meme as representing a desired food-to-population ratio between 2 and 4 times the current combined ant and larvae population. We normalize this ratio in the range  $[0, 1]$  in order to compare it to the *breed* meme (it's response threshold). If  $1 - \textit{breed}$  is less than the normalized ratio the ant attempts to forage, otherwise it breeds.

Depending on the pleiotropic architecture the *breed* gene also impacts morphological and physiological differences between ants. Our ants can die violent deaths when outside the mound (0.1% chance of death per tick), starvation deaths when a hungry ant attempts to eat and there is no food (these are rare) or they can die by old age after 100 ticks. The chance of dying by old age is  $0.1\% + \textit{breed} \cdot 0.9\%$  when the *breed* gene impacts lifespan, but is 0.5% when the *breed* gene does not impact this trait. In control runs our ants must recover for 50 ticks after laying an egg before they can perform another task. If the *breed* gene impacts recovery time it is  $1 + (1 - \textit{breed}) \cdot 99$  ticks. In control runs the ants have 250 energy when foraging, otherwise, an ant will have  $5 + (1 - \textit{breed}) \cdot 495$  energy. Finally, our ants can carry 50 units of food in control runs. Otherwise they can carry  $1 + (1 - \textit{breed}) \cdot 99$  units of food.

Four different architectures were implemented to explore trade-offs caused by pleiotropy. First, we test when

the *breed* gene has only behavioral impacts (no pleiotropy) determining only the *breed* meme upon birth. The other three experimental runs consider when the *breed* gene impacts all traits, just the breeder traits (lifespan and recovery time) or just the worker traits (carrying capacity and energy). Many pleiotropic architectures were possible but were not explored in this experiment to keep our scope manageable (though four others were explored in Bae & Marriott (2019)).

## 2.4 Ant Plasticity

We consider four possible plasticity mechanisms that apply nudges to the meme whenever a new task is selected. The *random* plasticity mechanism applies a real-valued change to the *breed* meme selected uniformly from the range  $[-0.05, 0.05]$ . The *environmental* plasticity mechanism will compare the *breed* meme to the normalized food-to-population ratio (as described above) and nudge the meme towards the normalized food-to-population ratio. The *experiential* plasticity mechanism will nudge the meme towards the task that was just selected (this is an identical plasticity mechanism to that used in Theraulaz et al. (1998); Gautrais et al. (2002); Merkle & Middendorf (2004)). We call these three nudges the *individual* plasticity mechanisms as they embody non-social mechanisms of individual learning. Our final mechanism, the social plasticity mechanism, embodies social learning. The social plasticity mechanism selects another ant from the pool of potential parents (described above) and nudges the *breed* meme towards the *breed* meme of the mentor ant. All nudges have magnitude capped at 0.05 or the distance to the target.

## 2.5 Experimental Setup

Our experiment was first designed to test the differences between the *deterministic* and *probabilistic* response threshold allocation strategies. In contrast to these mechanisms we also deploy a *control* allocation strategy in which ant behavior is always determined by a fair coin flip regardless of genetics or memetics.

In the experiment we vary the plasticity mechanisms employed. The *random*, *environmental*, *experiential* and *social* settings test when only a single plasticity mechanism is employed. The *none* setting is the control setting with no plasticity, and the *all* setting tests all plasticity mechanisms. Finally, the *individual* setting tests all plasticity mechanisms other than the social mechanism.

Both experiments are conducted using the four pleiotropic settings: *none benefit*, *queens benefit*, *workers benefit* and *both benefit*. This is a reproduction and extension of the primary experiment in Bae & Marriott (2019).

The experiments were conducted simultaneously yielding 63 experimental and control settings. Specifically,

we have 7 settings using the control allocation strategy (varying the 7 plasticity settings) and 28 settings each for the deterministic and probabilistic allocation strategies. Both strategies are tested with all combinations of the 4 pleiotropic architectures and the 7 plasticity settings for a total of 28 configurations each.

Each run was initialized with a small population (100) of generalist ants with *breed* gene initialized to 0.5. The experiment was carried out for 100000 ticks with data samples every 50 ticks. Every data sample includes the number of ants and larvae, and the amount of food stored in the mound. The ants are also partitioned into three roles: breeding, foraging, and idling. We also track population genetics and memetics.

## 2.6 Balancing the Fitness Function

In both the probabilistic and deterministic selection mechanisms we searched for a dynamic sweet spot using a binary search by hand (the control runs are unaffected by fitness weights). Workers have a natural bias as food can be returned at a faster rate than breeders can produce larvae. So we set the worker weight to 1 and vary the breeder weight. Both the plasticity mechanisms and pleiotropic schemes impact the sweet spot in a number of ways. In particular, these variables impact where the sweet spot is, how large it is, and how the ants respond within the sweet spot. Table 2.1 shows the fitness weights used for our experimental runs and we discuss the impact of these mechanism below.

The only fitness values we have not shared are those for the deterministic allocation strategy when queens benefit from the pleiotropic architecture. This is because there is no clear sweet spot in these runs as discussed below. However, for our simulations we used values between 1 and 2 for the breeding rate for all runs.

## 3 Data and Discussion

Figures 3.1-3.10 display the genetic and memetic dynamics of our 63 simulation runs. The dynamics are displayed in a time series from left to right over 100000 ticks. Each vertical slice represents the genetic (or memetic) distribution of the *breed* gene (left plots) or meme (right plots) for that tick. The distribution divides the population into 20 buckets of size 0.05 to cover the range of genetic values [0, 1] (with 0 representing all workers at the bottom and 1 representing all breeders at the top of each plot). Taken as a percentage of the whole population we then represent the population of a bucket with a color. Each figure contains seven runs, one for each plasticity setting, for one allocation strategy combined with one pleiotropic architecture.

| Selection     | Plasticity                    | Pleiotropy | Breeding Weight        |
|---------------|-------------------------------|------------|------------------------|
| Control       | None/Rand/Env/Exp/Ind/Soc/All | None       | 1                      |
| Deterministic | None/Rand/Env/Exp/Ind/Soc/All | None       | 1.38                   |
| Deterministic | None/Rand/Env/Exp/Ind/Soc     | All        | 2                      |
| Deterministic | All                           | All        | 2.5                    |
| Deterministic | None/Rand/Env/Exp/Ind/Soc/All | Queens     | Varies between 1 and 2 |
| Deterministic | None/Soc/All                  | Workers    | 2                      |
| Deterministic | Rand/Env/Exp/Ind              | Workers    | 2.5                    |
| Probabilistic | None/Rand/Env/Exp/Ind/Soc/All | None       | 2.5                    |
| Probabilistic | Rand/Exp                      | All        | 2.5                    |
| Probabilistic | None/Ind/Soc                  | All        | 3                      |
| Probabilistic | Env                           | All        | 3.5                    |
| Probabilistic | All                           | All        | 4.5                    |
| Probabilistic | Soc                           | Queens     | 1.5                    |
| Probabilistic | None/Rand/Env/Exp/Ind/All     | Queens     | 2.5                    |
| Probabilistic | None/Rand/Env/Exp/Ind/All     | Workers    | 3.5                    |
| Probabilistic | Soc                           | Workers    | 5                      |

Table 2.1: Fitness weights for different simulation types

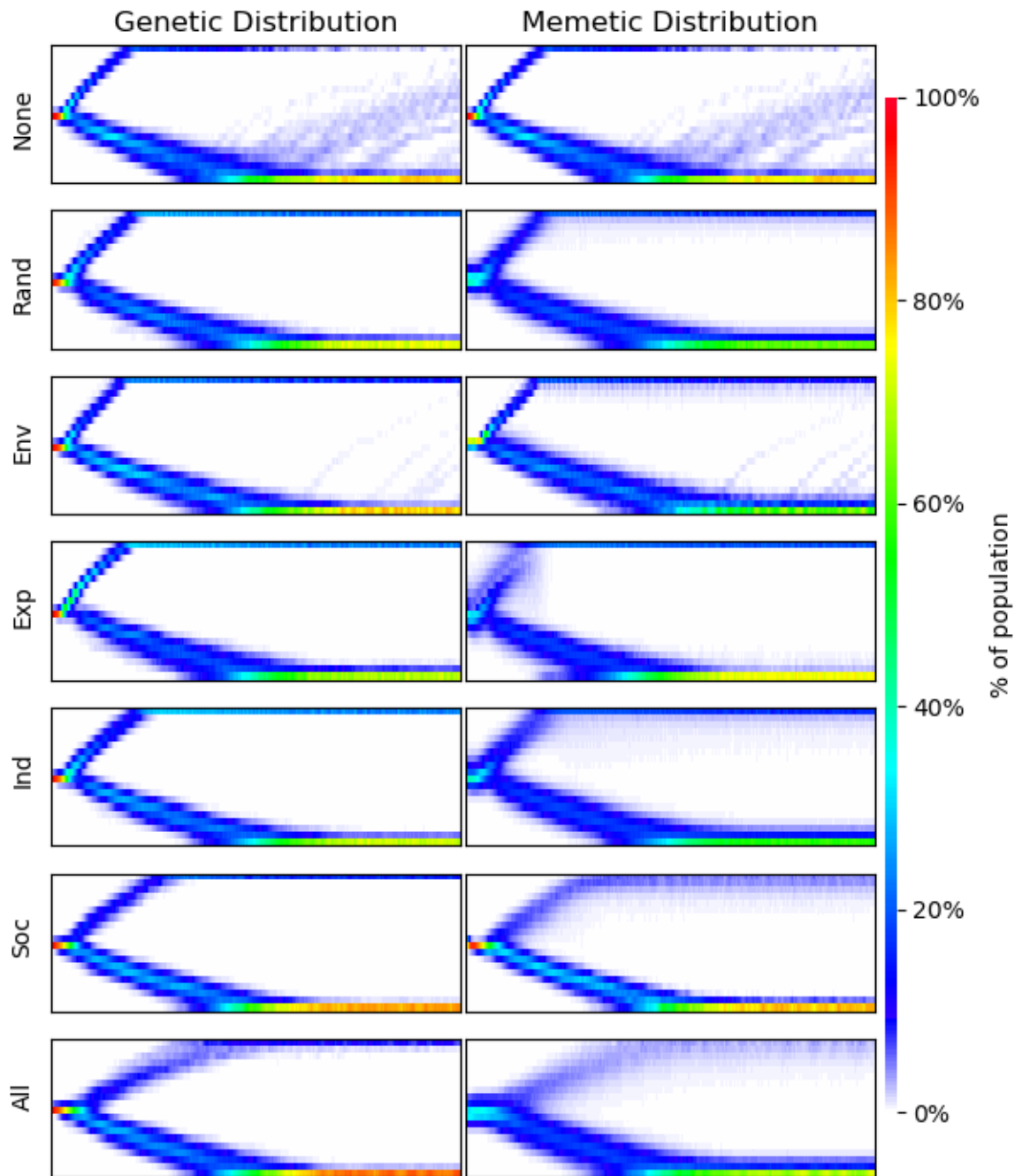


Figure 3.1: Deterministic Allocation Strategy when Workers Benefit from the Pleiotropic Architecture

### 3.1 Deterministic allocation strategy can recover from loss of breeding caste

Figure 3.1 presents the genetic and memetic dynamics for the deterministic selection mechanism when workers benefit from pleiotropy. All plasticity mechanisms in these runs result in division of labor. The breeder population specializes first and rapidly into a discrete caste. The workers follow, more slowly, likewise specializing into a discrete caste (if a bit more varied than the breeders). Under these settings the population maintains a large worker population ( $> 70\%$ ) and a small queen population ( $< 25\%$ ). This is similar to the real world ant populations, and contrary to some of the results we found under other experimental settings, in particular when both workers and queens benefit from the pleiotropic architecture.

When both workers and queens benefit from the pleiotropic architecture there is a tendency for the population to clog up with long-lived breeders (often idling in the probabilistic allocation strategy). This is obviously sub-optimal from a colony perspective, but also not likely to correlate with any real world observed colony dynamics. This makes us conclude that these combinations of pleiotropic architecture and allocation strategies are rare or do not occur in natural systems. On the contrary the more realistic demographics occur when the deterministic allocation strategy is combined with a pleiotropic architecture that benefits worker morphology and physiology.

In addition to these real world demographics, some runs fall victim to a potential catastrophe befalling any population with reproductive division of labor - the loss of the breeder caste (Majoe et al., 2021). This occurs reliably to colonies with no plasticity and also to some colonies with environmental plasticity or with all plasticity mechanisms. The other runs are shielded from collapse by the plasticity mechanism(s) they employ.

Collapse of the breeder caste occurs due to a population dynamic that is unique to the combination of the deterministic allocation strategy and when workers benefit from the pleiotropic architecture. In these settings the population oscillates as the colony likewise oscillates between phases of breeding and foraging. Both of these oscillations track on the oscillation of the food-to-population ratio between the two extremes and resemble the dynamics of Lotka-Volterra equations of predator-prey relationships (Berryman, 1992).

Under most settings colonies find an equilibrium where the food-to-population ratio is just high enough for breeding to occur. When our oscillating populations are at this level, because of the low number of breeders, breeders breeding alone are not sufficient to keep up with the food being added to the mound nor maintain the current population. So food stores rise and the population drops. This results in the food-to-population ratio increasing to the other extreme. As it does, the colony behavior does not change. This is because all ants are specialized as breeders or workers, and thus will remain in the current task. That is, until the food-to-population ratio reaches (or exceeds) the other extreme when all workers are recruited to breed.

When this occurs no ants are foraging and many new larvae are being produced so the food-to-population

levels begin to drop. This typically is sufficient to replace any lost population from the last phase and return the food-to-population ratio to the lower extreme. If, during the phase of population loss, all of the breeding class die off we enter a collapsed state.

With no plasticity (or with environmental plasticity) a new breeder caste emerges out of the worker caste and evolves towards being genetic breeders again. This occurs thanks to the feedback provided by the deterministic allocation strategy and is amplified when there is no plasticity.

Consider the no plasticity case for a moment. In this case, with no plasticity, ant genetics are directly responsible for behavior and so selection can finely differentiate between genetically very similar ants. If the breeder caste collapses as the food-to-population levels rise the first workers recruited to breed are those least specialized in foraging. In addition, they will be the last to return to working as the food-to-population levels begin to drop as the breeding phase begins. This means during this phase they will breed the most and gain the most fitness benefit from breeding. Selection is able to fixate on this population under these settings and drive it back towards a pure breeding caste. One aspect important to this analysis is that all ants are equally effective at reproduction in these settings and that we do not see the same collapse or population structure when this is not the case (Figure 3.2).

The environmental plasticity mechanism is the only plasticity mechanism that shows an ability to also recover from collapses. However, it is also the only one susceptible to collapses other than when all plasticity mechanisms are employed. One explanation of these results is that plasticity helps to shield the breeder caste from collapsing in the first place. Even if the environmental plasticity mechanism is still susceptible to collapse, its considerably less susceptible than with no plasticity. Finally, when all plasticity mechanisms are employed the breeder caste can still collapse, but the worker caste is unable to recover, and we explain this due to the noise added to selection from plasticity so selection cannot fixate on the slight genetic specialists and reward them. As a result this combination of plasticity mechanisms is maladaptive in this context.

The environmental plasticity mechanism has a positive feedback relationship with the deterministic allocation strategy (below). After a collapse, as the food-to-population level rises, workers will have their memetics nudged towards breeding due to the environmental signal. This will ensure that there are some on the leading edge, and those on the leading edge are most likely to also be on the leading edge of the genetic distribution (due to the Baldwin effect) and thus selection can still take hold. That is, plasticity from this mechanisms is not noise relative to selection as it is in the other mechanisms.

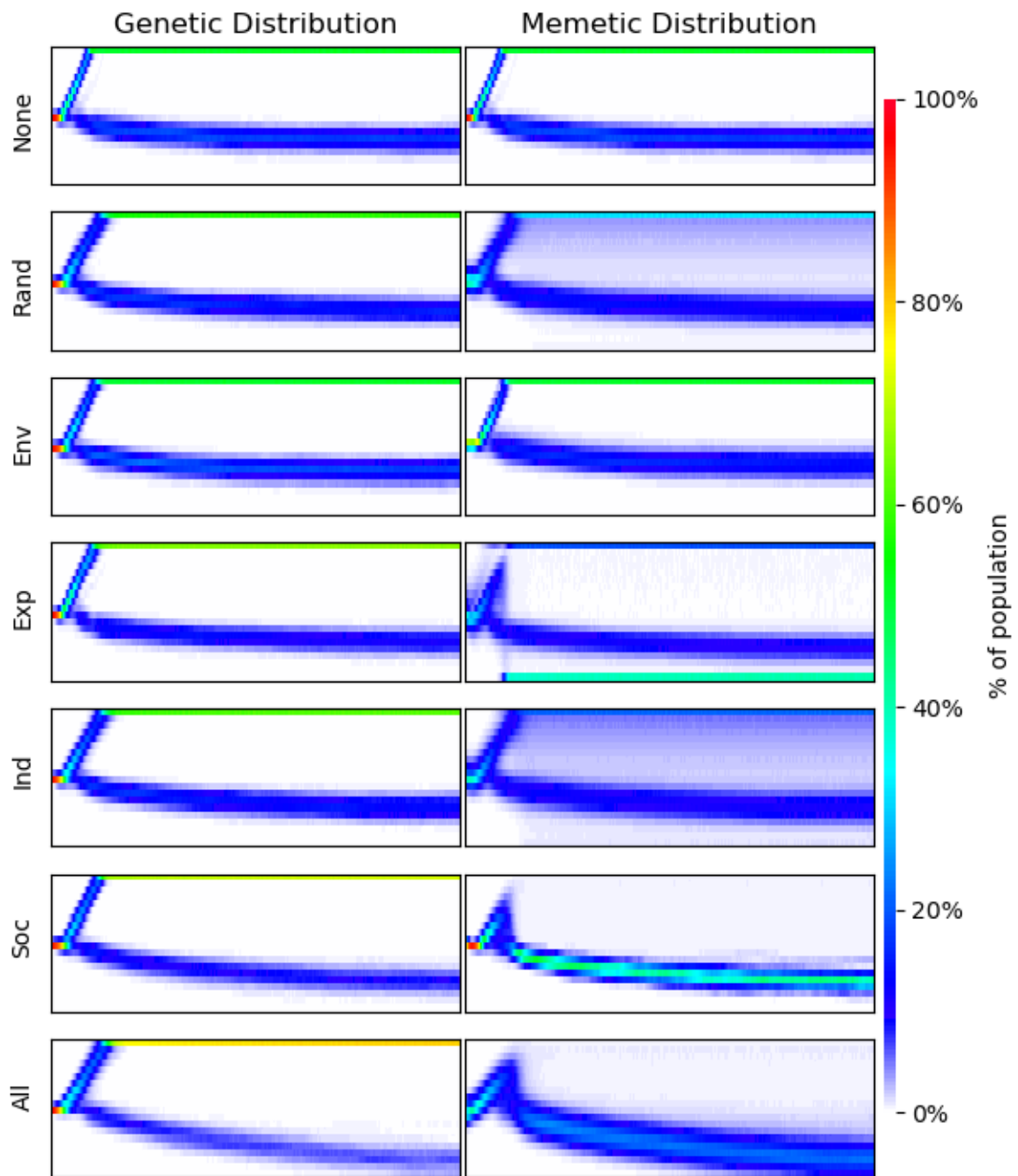


Figure 3.2: Deterministic Allocation Strategy when Both Queens and Workers Benefit from the Pleiotropic Architecture

### **3.2 Deterministic allocation strategy is more robust to genetic and environmental parameters**

Our fitness function is used in biological reproduction to select genetic parents and in the social plasticity mechanism to select a model to imitate. This means that it represents the influence of genetic and environmental parameters that influence ant behavior during reproduction (and social learning). Our fitness function defines an infinite parameter space with the foraging weight  $w_f$  and the breeding weight  $w_b$ . While the probabilistic allocation strategy is only viable within a narrow range (that we call the “sweet spot” above) the deterministic allocation strategy is viable throughout the entire space.

A biased fitness function has different impacts on the simulation based on the allocation strategy employed. Under the probabilistic allocation strategy ants can become behaviorally pure - exclusively breeding or exclusively foraging. Not only does this not match observations of individual ants (except in the largest colonies) (Jeanson, 2019) but also if a population consists only of pure breeders (or pure foragers) then one role is being neglected and the colony collapses. Thus, at the extremes of the fitness function the probabilistic allocation strategy is infeasible.

The deterministic allocation strategy is still affected by the fitness function, but the colony is more robust. Behaviorally pure ants do not exist under this allocation strategy. Instead ants at the extremes are the last to switch roles, but will do so if environmental conditions demand it. As a result, if the fitness function is in one of the extremes the colony is still viable (though the genetic dynamics are uninteresting as all ants specialize in the role dictated by the fitness function as expected).

We interpret these results to suggest that the deterministic allocation strategy should be more common in nature. Populations using the probabilistic allocation strategy are more likely to experience genetic and environmental conditions that would lead to a colony collapse, and those that do exist in nature must occupy niches within which fitness conditions are cooperative. On the contrary the colonies employing the deterministic allocation strategy are likely to evolve through changing genetic and environmental conditions by adapting their reproductive division of labor to new conditions.

### **3.3 Deterministic allocation strategy and environmental plasticity mechanism have synergy resulting in niche construction**

Both the deterministic allocation strategy and the environmental plasticity mechanisms attempt to bring the food-to-population level in line with individual ants’ memetic value. When the population has a narrow genetic profile and the food-to-population ratio is in equilibrium with this profile the colony and their environment

(fitness function) exist in a constructed niche. The food-to-population levels are kept within acceptable ranges for the population and the population memetics are kept near the same mean.

This can be seen the most in the deterministic allocation strategy when queens benefit from the pleiotropic architecture (Figure 3.3 and 3.4). These settings were characterized by a fragile equilibrium that would collapse to either all breeders or all workers (Figure 3.4). The cause of the collapse was minor differences in the initial evolution of the complex system. However, the environmental plasticity mechanism displays an ability to maintain the equilibrium longer (though still eventually collapses). We argue this is due to the constructed niche that the population is able to exist in for longer than their peer populations.

We can see this effect to a lesser extent when there is no pleiotropic architecture (Figure 3.5). While other plasticity mechanisms tend to increase memetic variability (see also Figure 3.6) the environmental plasticity mechanism decreases variability enforcing conformity around the population center. Note this narrowing effect only occurs when there is a single population in equilibrium with the environment. When both workers and queens benefit from the pleiotropic architecture two populations emerge, one in equilibrium (the breeders) and one not (the workers) and the one not in equilibrium is skewed towards the one in equilibrium.

### **3.4 Deterministic allocation strategy results in age polyethism with experience based plasticity**

A curious observation of ant behavior for response threshold theories of division of labor is what's called *age polyethism* (Franks & Tofts, 1994; Tripet & Nonacs, 2004; Marriott & Gershenson, 2011). Among many ant colonies it is observed that roles selected correlate with the age of the ant. This is commonly addressed in response threshold theories by positing that one mechanism of plasticity is based on age or experience. We have not included a mechanism based on age in our model, though we do have one based on experience and we do observe age polyethism in some of these colonies.

Since we do not directly gather data on roles selected at different ages we must infer age polyethism from the genetic and memetic data we have gathered. We see the clearest evidence using the deterministic allocation strategy when both queens and workers benefit from the pleiotropic architecture (Figure 3.2) using the experiential plasticity mechanism.

In these setting we see the genetic distribution includes a discrete breeder caste (around 65% of the population) and a continuous worker caste. The memetics display three distinct populations with some members in between. The first two populations map directly onto the genetic populations. The population of discrete queens however is much smaller (less than 20% of the population) representing the actual demand for breeding in the colony. The

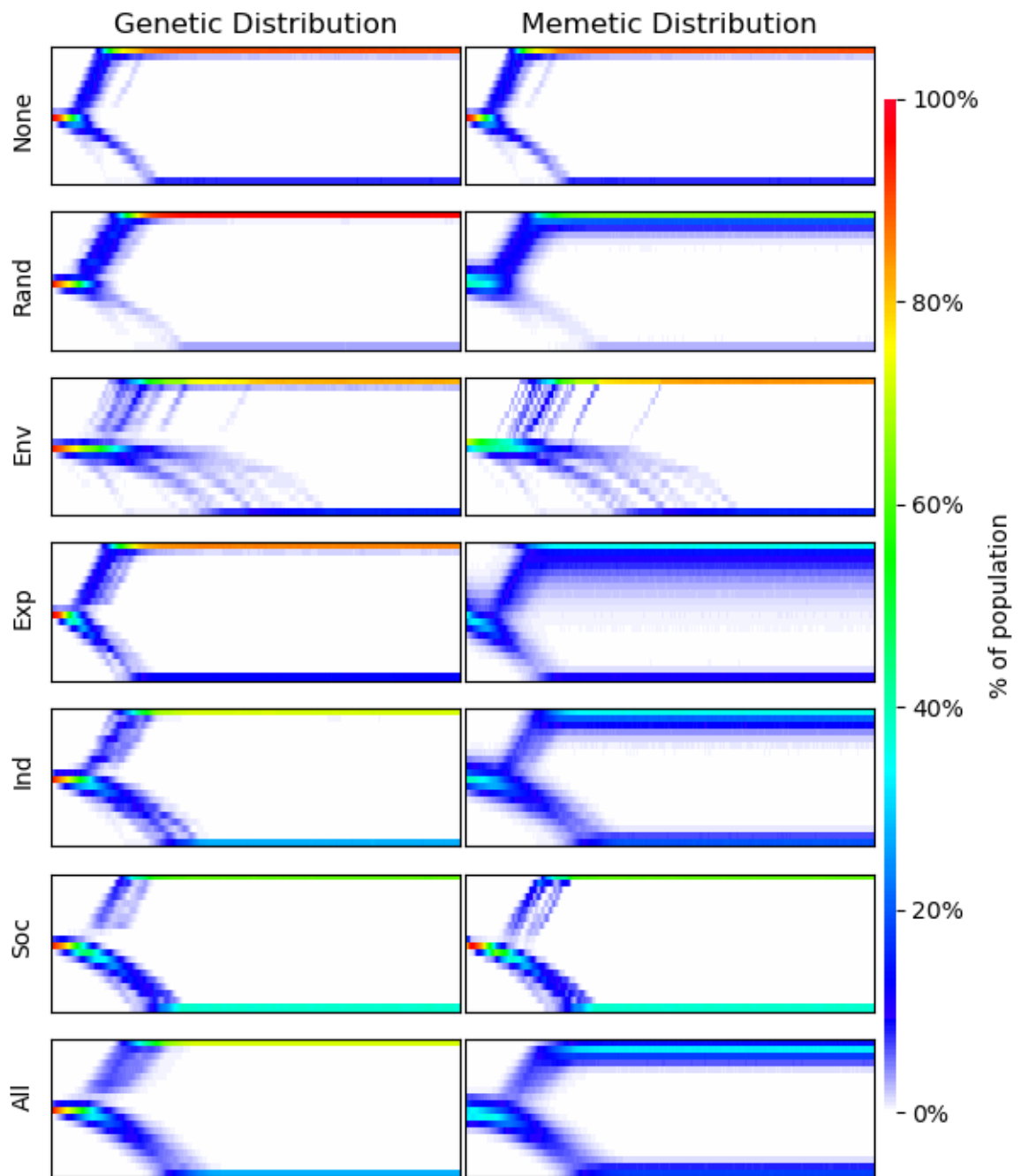


Figure 3.3: Deterministic Allocation Strategy when Queens Benefit from the Pleiotropic Architecture

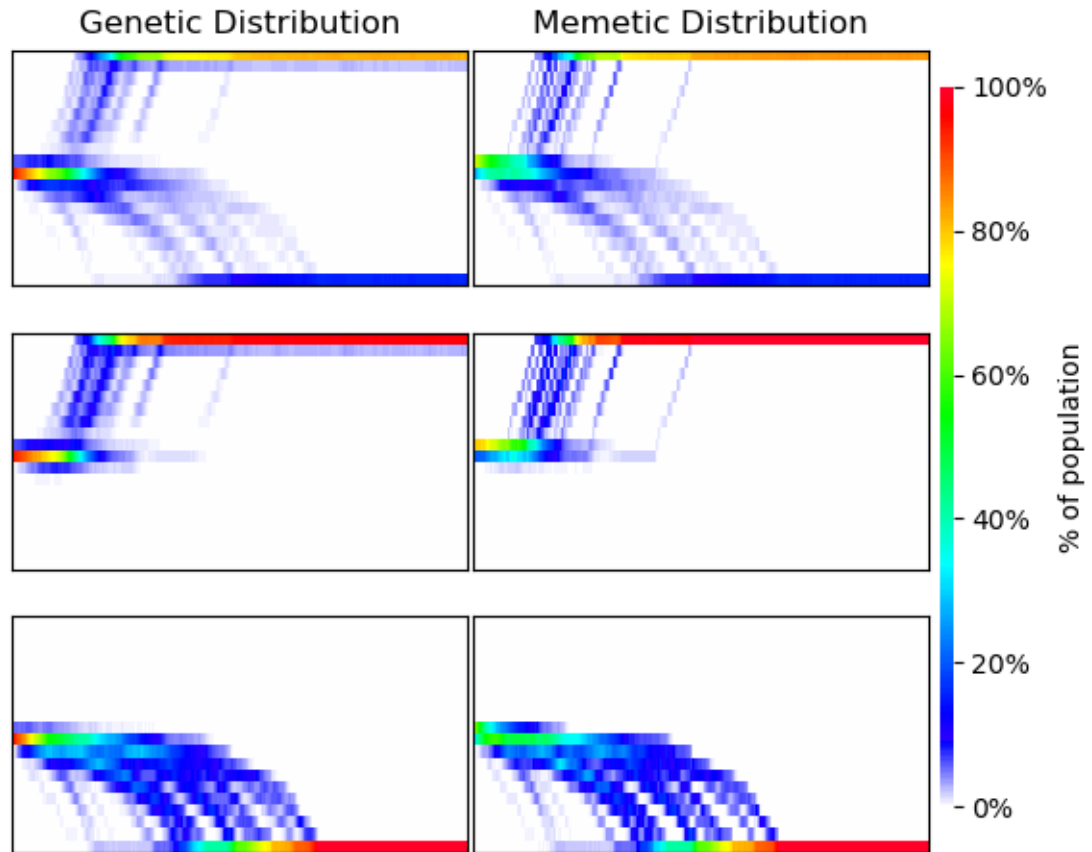


Figure 3.4: Deterministic Allocation Strategy when Queens Benefit from the Pleiotropic Architecture and with Environmental Plasticity - The first row is the aggregated data. In the second and third rows we have filtered the runs that collapse to either breeders or workers to show this is specialization without division of labor.

remaining breeders are recruited to forage on occasion, and when they are, the plasticity mechanism nudges them towards foraging. This begins a feedback loop as they are now less likely to return to breeding, especially under normal equilibrium conditions. As a result they stumble all the way to the foraging edge. The only ants that can be relied on to produce new offspring are the newborn queens that have not had time to adjust due to plasticity from when they were born.

While age polyethism among the breeders is clearest in this case, it occurs also with all non-social plasticity mechanisms, with the social plasticity mechanism for a similar reason, and then again with all plasticity mechanisms. It appears some age polyethism also emerges with random plasticity pulling dedicated breeders away from the extreme. The emergence of age polyethism as a solution to the colony overproducing queens is another

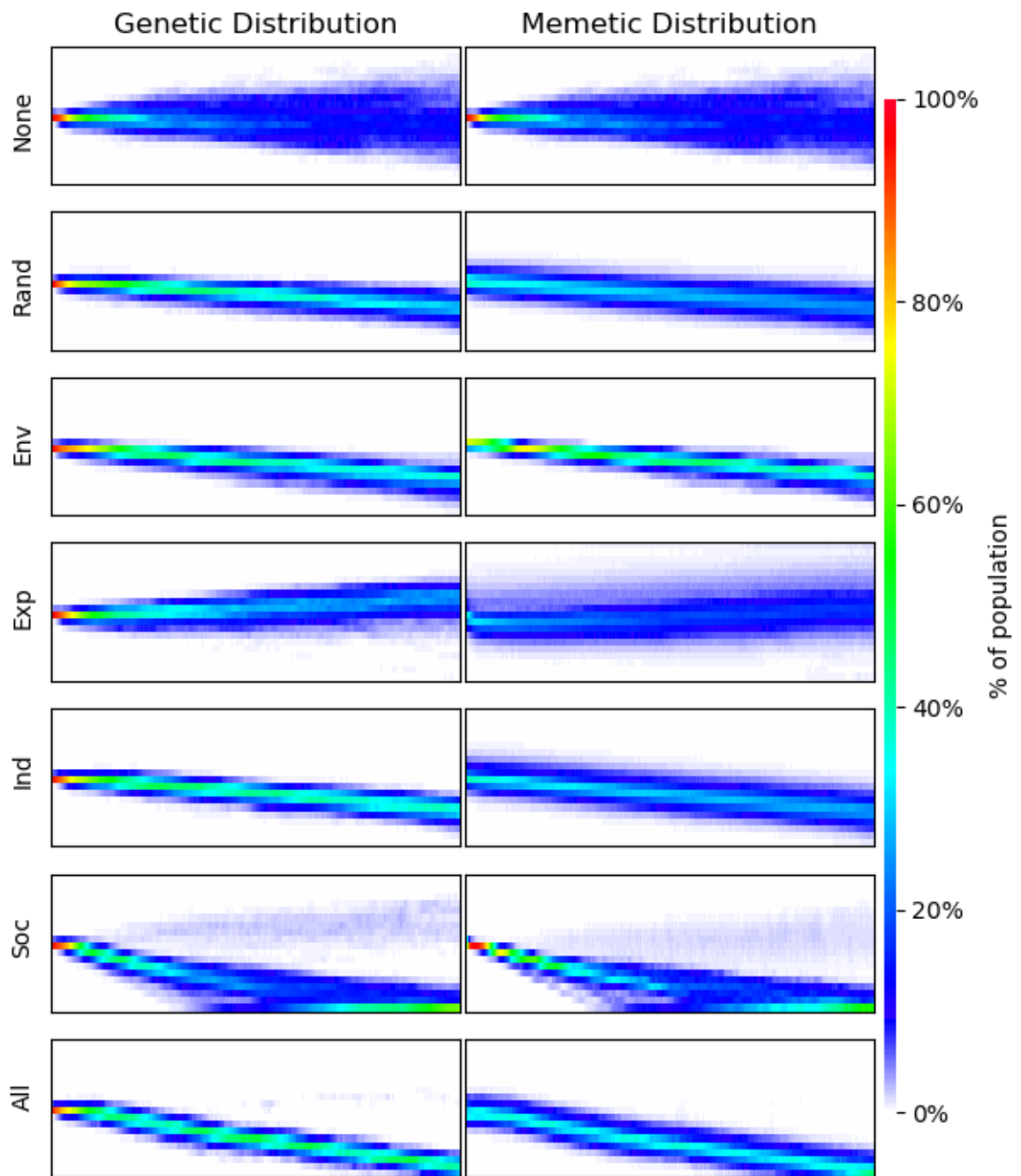


Figure 3.5: Deterministic Allocation Strategy with No Pleiotropy

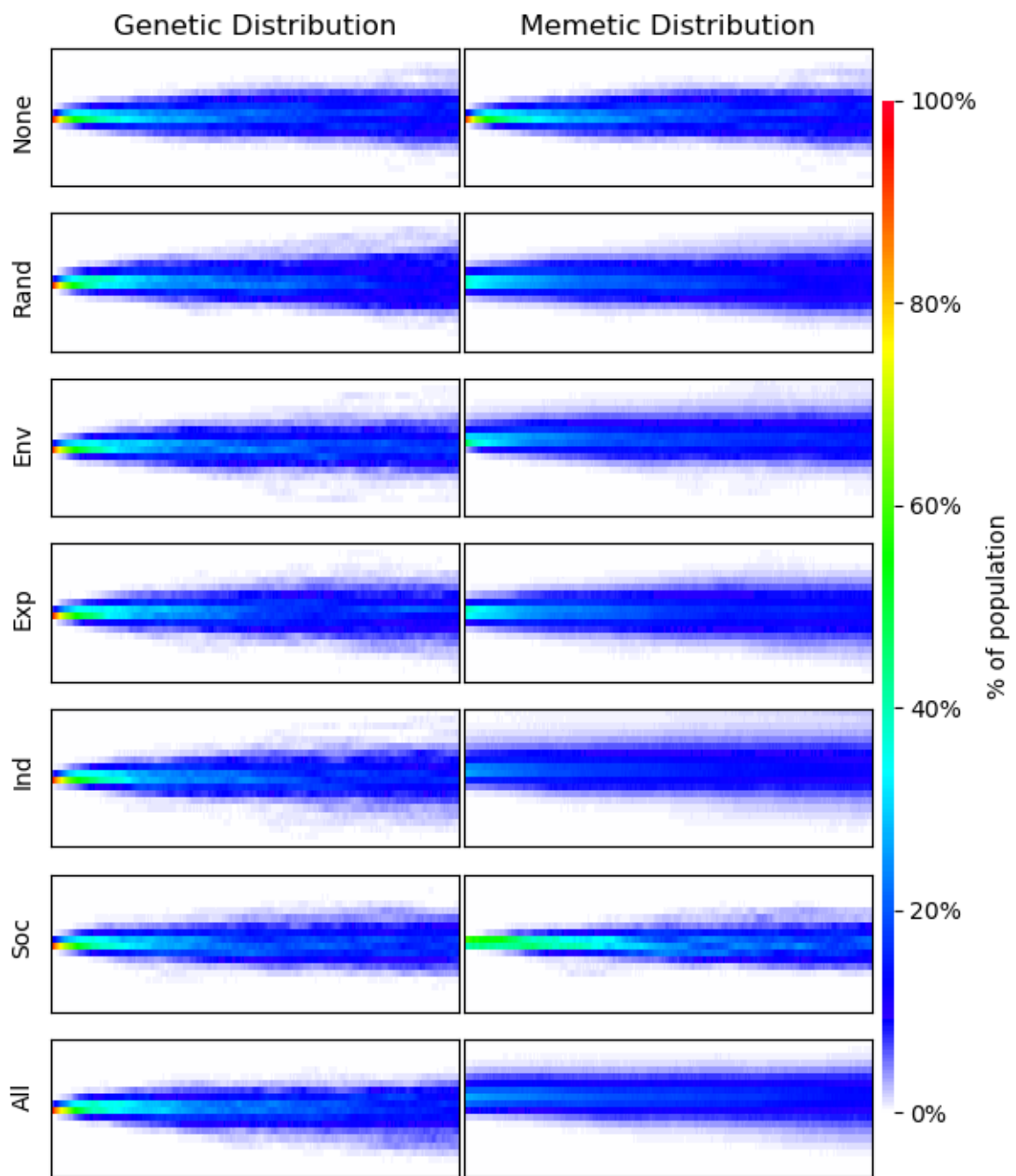


Figure 3.6: Control Allocation Strategy with No Pleiotropy

robustness characteristic of this allocation model.

### **3.5 Plasticity can be adaptive or maladaptive for reproductive division of labor**

While reproductive division of labor is not adaptive for all colonies we wished to consider in cases where it is, is plasticity adaptive for supporting evolution to reproductive division of labor? We found that the answer was both positive and negative depending on conditions.

One effect of plasticity upon evolutionary dynamics is called the hiding effect (Paenke et al., 2006; Marriott & Chebib, 2014). Through the hiding effect a mechanism of plasticity can slow the evolution of an adaptive trait. There are multiple ways this may occur but one that plays a role in our simulation is the addition of noise in the mapping of genotype to phenotype. This means that the connection between genetics and selection is weaker.

We can see a clear example of the hiding effect in the deterministic allocation strategy with no pleiotropy (Figure 3.5). With no plasticity a generalist population emerges that can be tipped towards division of labor after some time. However, most runs with plasticity result in generalist populations that do not tip towards division of labor. The social plasticity mechanism is able to maintain two populations in some runs, but not when combined with the non-social plasticity mechanism.

A similar genetic dynamic occurs in the probabilistic allocation strategy with queens benefiting from the pleiotropic architecture (Figure 3.7). That is, a generalist population eventually faces pressure to divide into two specialized populations. However, in most of these settings plasticity does not have a hiding effect. The social mechanism does to some extent, but the others either do not effect the genetic dynamics, or increase selection towards division of labor. This is often called the Baldwin effect, when selection towards a trait is increased by plasticity (Hinton & Nowlan, 1987; Paenke et al., 2006; Marriott & Chebib, 2014). The Baldwin effect is clearest when all plasticity mechanisms are deployed. This shows how the plasticity mechanisms can have an additive and sometimes emergent impact in combination.

This also shows an interesting side of the social plasticity mechanism, which in these settings operated as a hiding effect when alone, and aided in the Baldwin effect when combined with the non-social mechanisms. This pattern is repeated when both workers and queens benefit from the pleiotropic architecture (Figure 3.9) and the relationship is reversed when workers benefit from the pleiotropic architecture (Figure 3.8). That is, in the last case the social plasticity mechanism has a Baldwin effect when alone and a hiding effect when combined with the non-social mechanisms.

One conclusion we draw from these results is that plasticity mechanisms are more likely to occur in com-

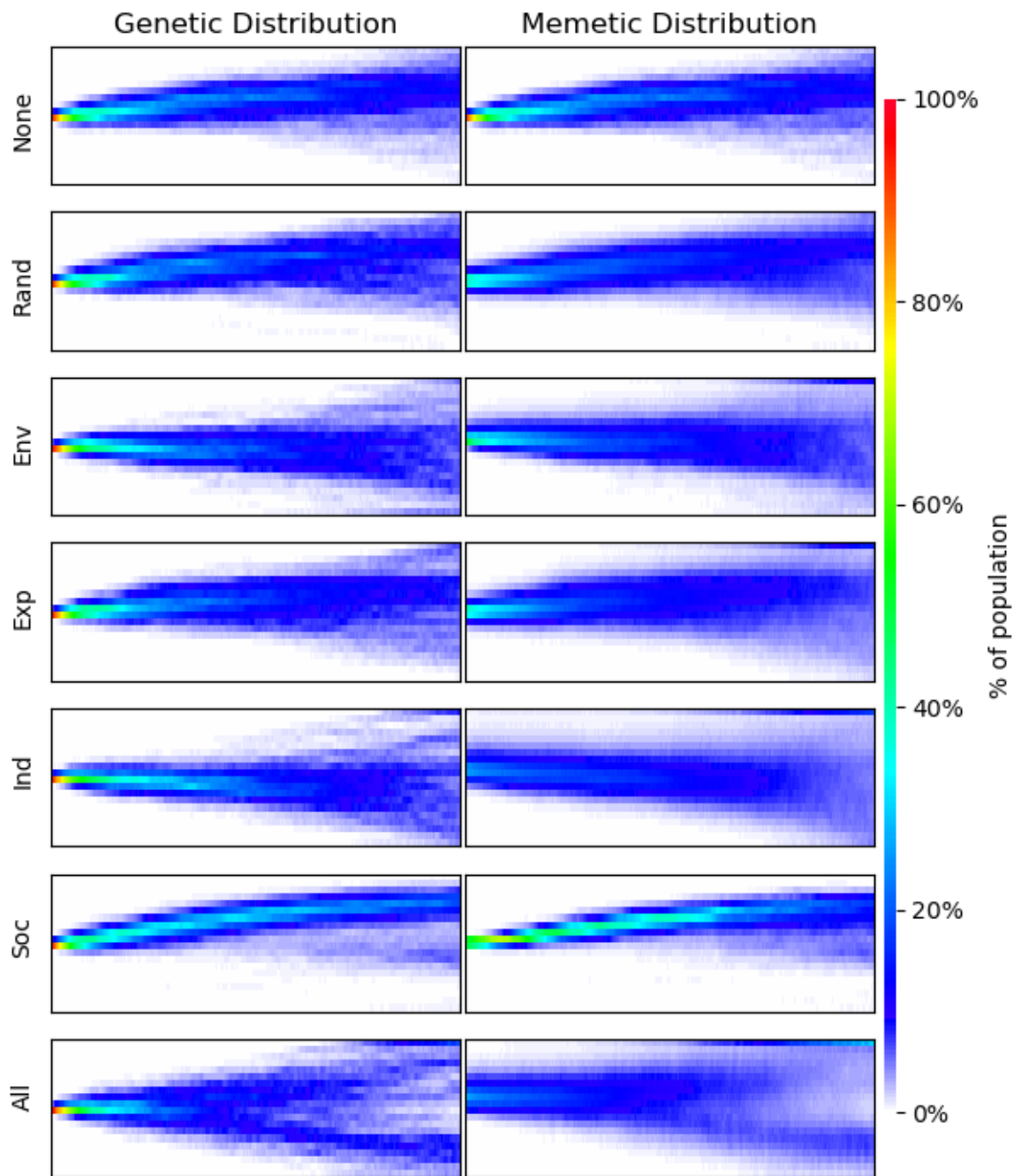


Figure 3.7: Probabilistic Allocation Strategy when Queens Benefit from the Pleiotropic Architecture

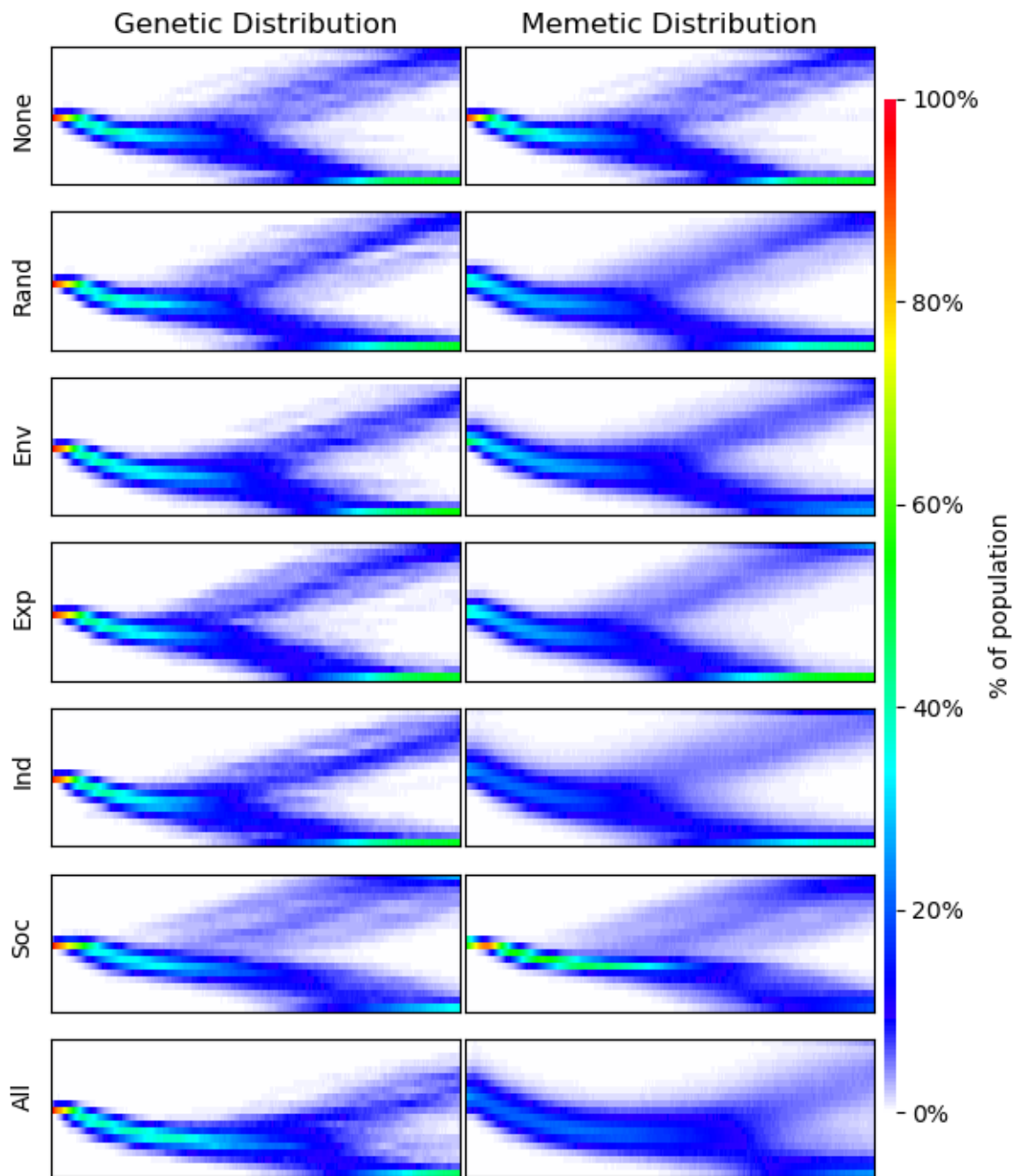


Figure 3.8: Probabilistic Allocation Strategy when Workers Benefit from the Pleiotropic Architecture

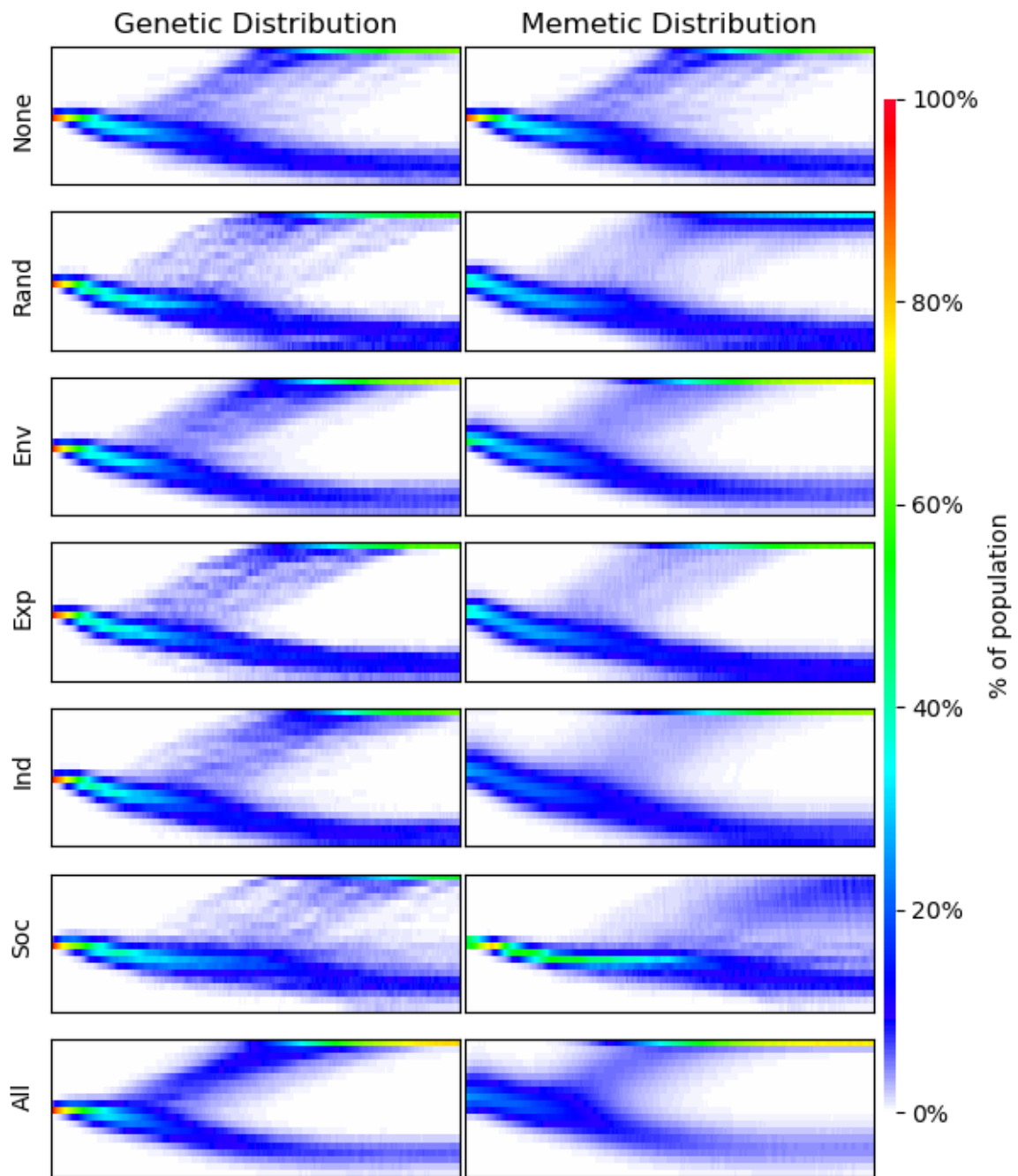


Figure 3.9: Probabilistic Allocation Strategy when Both Queens and Workers Benefit from the Pleiotropic Architecture

ination with others, due to the robustness benefits, as opposed to occurring in isolation. This is probably the most true of the social plasticity mechanism, which in practice is usually more complex than the non-social mechanisms, so likely emerges in combination with other mechanisms already deployed.

## 4 Conclusion

We have presented an agent-based model of the response threshold theory of division of labor that incorporates factors of pleiotropic genetics, plasticity and embodied cognition situated in a dynamic environment. No prior model has incorporated this many relevant features into a detailed model realized in simulation. Through simulation we studied how each of these factors impacts the evolution and emergence of division of labor. The population dynamics and demographics displayed by our simulation better correspond to those of natural colonies than prior work.

We have identified conditions under which colonies might naturally fall victim to the collapse of the breeding caste, as well as the conditions under which such a collapse can be overcome. In our simulation when workers benefit morphologically and physiologically from specialization, but breeders do not, conditions are set for colonies to efficiently out-forage their breeding capabilities due to an overproduction of workers. In extreme cases of overproduction, the breeding caste is neglected and dies out. If ants in such a colony have no plasticity, or if they have an associative reinforcement plasticity, they can replace the missing caste. Other plasticity mechanisms insulate the colony from the collapse in the first place.

When plasticity mechanisms of individual ants and the self-organization mechanisms of the colony both focus on the same metric (in our case the food-to-population ratio), the result is a form of niche construction. The ants respond to a mismatch between environmental conditions and the desired conditions by both changing the conditions, and their desired state. This resulted in ants with homogeneous behavior profiles that were better able to occupy their constructed niche even in volatile environmental conditions.

Age polyethism is an emergent property of our agent-based model as opposed to an active mechanism. That is, we have not built age-based switching or awareness of age into ant cognition, though we still observe age polyethism among our colonies in certain circumstance. In particular, when our ants benefit morphologically and physiologically from specialization, and when they employ the deterministic allocation strategy, colonies tend to overproduce genetic queens, whom change behaviorally into workers as they age.

We deployed the deterministic allocation strategy against an alternative probabilistic one, and we found the

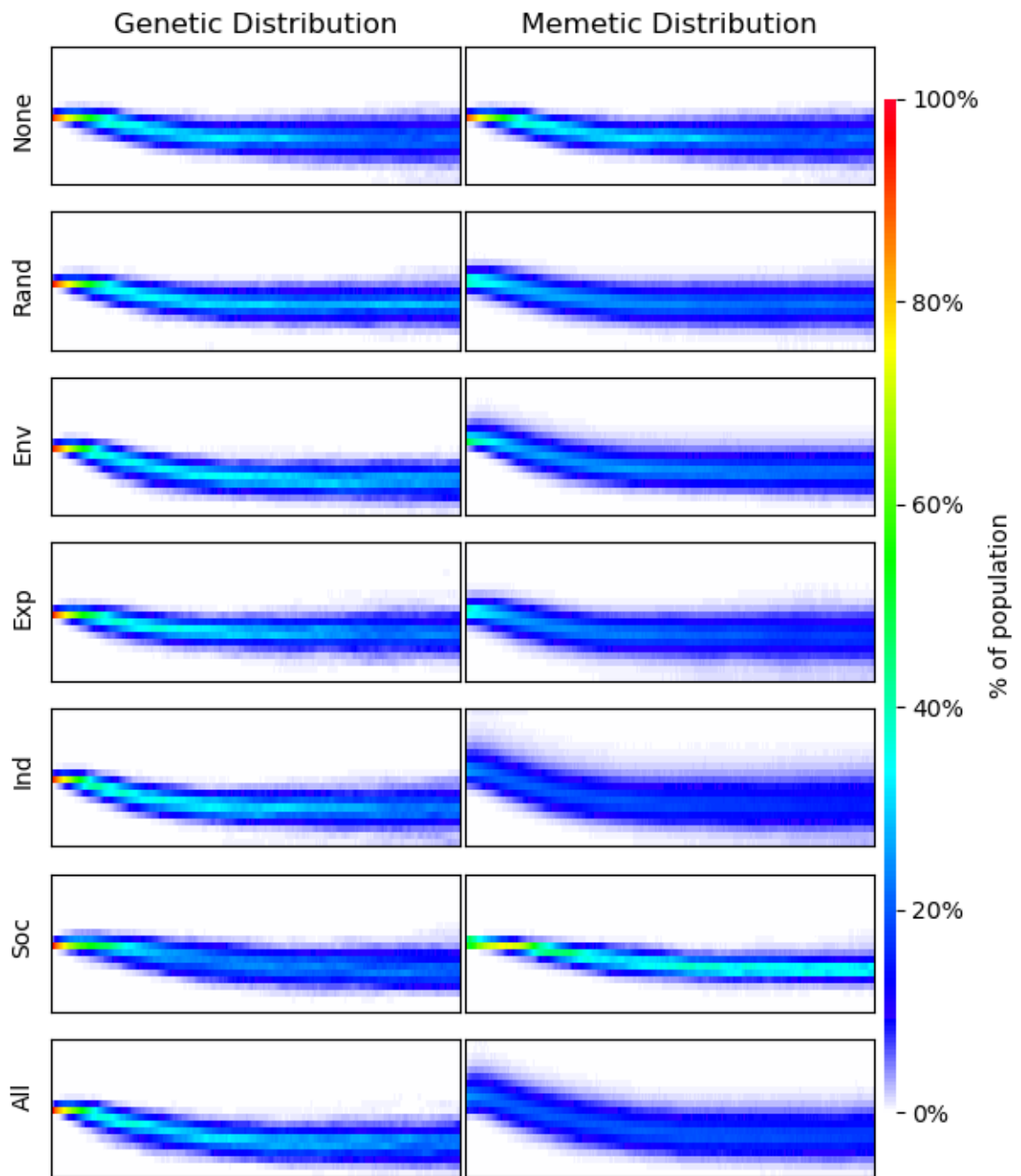


Figure 3.10: Probabilistic Allocation Strategy with No Pleiotropy

probabilistic strategy more fragile to external conditions and less able to benefit from plasticity. When fitness conditions exited a “sweet spot” the probabilistic colonies collapsed, whereas the deterministic ones were robust. The plasticity mechanisms we tested in our ants had varied impact on the behavior of ants using the deterministic allocation strategy, but in most cases failed to have the same impact on the behavior of probabilistic ants.

Within the context of the division of labor the plasticity mechanisms we tested were both adaptive and maladaptive when combined with the deterministic allocation strategy. In some cases they sped up specialization, while in others they slowed its progress or shielded its emergence altogether. In particular the social plasticity mechanism showed volatility depending on the other mechanisms and factors it was combined with.

The major conclusions drawn thus far are intended to inform discussions of division of labor behavior in ants and other social animals. However, the last couple conclusions begin to inform discussion of artificial life experimentation or engineering of systems incorporating a variable number of artificial agents. The probabilistic model was selected for convenience, as these models often are. Probabilistic models appear in scientific theories as a place holder for uncertainty, and so can be found somewhat regularly. Probabilistic models appear in artificial life simulations for the same reason, but also because they are typically easy to code. We find in this experiment that despite this ease, the probabilistic model was less realistic in its behavior and more fragile to varying conditions. As a recommendation to other researchers and engineers we suggest finding deterministic models of animal behavior whenever possible.

Another benefit of our model is that it incorporates multiple factors into a single model. Artificial life simulations are focused on studying complex phenomena that result from the interactions of a variety of factors, though we often focus our models on only a single factor while abstracting away the others. While this can be a useful tool to study factors in a controlled setting we regularly neglect to conduct these same experiments in combination with the other factors in order to study their synergies. Artificial life simulations are such that you can build a model with many complex interacting parts, and then control each part so you can study them in isolation as we have done here.

While we believe this work provides important insights into ant behavior and artificial life research, we also believe there are a few drawbacks and directions for continued study. We believe the pleiotropic architectures considered in this work are but the first step in considering different ways genes could interact to contribute to the behavioral, morphological and physiological differences among ants. The single gene model should be expanded to a multiple gene model to see how this may have constrained the results. Beyond this our current model focuses heavily on genetic contributions and we could also expand the model to strengthen the impact of

other factors. One direction that might necessitate this is expanding the task structure to include brood care and nest maintenance (the later would require adding nest structure to the model as well).

We believe the parameters of our current model could be rebalanced to result in demographics that better match ant populations. Our colonies had a tendency to produce more breeders than is naturally observed, and while several colonies overcame this with plasticity or other solutions, we would like to conduct these experiments again in an attempt to find a parameter space where breeders are not as prevalent.

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