

Population Dynamics and Evolution of Phenotypic Attributes During Multi-Agent Foraging

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ABSTRACT

We use a stochastic birth-death process to model a multiple-agent competitive foraging task with the goal of understanding the population's dynamics and the evolution of phenotypes across generations. Agents forage for a limited amount of resources (food) in a finite domain. Speed of movement and the acuity of their senses allow them to locate and reach resources. However, sharpened senses and higher mobility are also metabolically costly. There is thus a trade-off between the benefit imparted by a phenotype and the required metabolic cost to sustain it. We allow these attributes to evolve by assuming that the phenotype of an agent and its descendants vary by a small, random amount. We show that different phenotypes are selected dependent on the resource generation rate. Semi-analytic and differential equation models can capture population dynamics over time. We also discuss different conditions which lead to the *co-existence* of subgroups with different attributes and *incipient speciation*.

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List of Notations

Ω	foraging domain
b	length of side of foraging domain
$ \Omega $	area of foraging domain
n	number of agents
m	number of resources
P_i	location of i^{th} agent
R_j	location of j^{th} resource
l_0	initial metabolic score(IMS)
$\bar{l}(t)$ or $\bar{l}$	average metabolic score (MS) of an agent at time t
λ	resource replenishment rate
ρ	resource density
η	average run (flight) distance
$\delta(m, b)$	distance from a point to the nearest of the m resources
$\bar{\delta}(m, b)$	expected minimum distance from a point to the nearest resource
s	speed
a	acuity
F	energy (caloric value) associated with a resource
θ	a direction chosen by an agent while foraging: $\theta \in (0, 2\pi)$

$C(s, a)$	metabolic cost per unit time given the pair of attributes, s and a
D	matrix of <i>Euclidean distances</i> between agents and resources
f	frequency of direction change
$\bar{B}_r$	closed disk with radius r
K_b	birth propensity
K_d	death propensity
x_0	initial agent density
$x(t)$ or x	average agent density in the domain at time t
Θ_B	minimum metabolic energy threshold for birth
Θ_D	maximum metabolic energy threshold for death
$g(n, \lambda)$	resource collection rate
ϵ_s, ϵ_a	sources for phenotypic variance (mutation parameter)
$\mathcal{N}(0, \sigma^2)$	normal distribution with mean 0 and variance σ^2

1 Introduction

Living organisms must compete for the available resources to survive and thrive in their natural environment. This contest, both between members of the same species and members of different species, often leads to adaptation and evolution. The evolutionary process drives the development and refinement of different phenotypes over time. These phenotypes are characterized by different attributes that include the type, range and acuity of the senses (hearing, vision, olfaction) that enable the organism to perceive their environment, as well as the physical characteristics that enable the organism to navigate the environment (agility, speed). Even though there has been a significant amount of work done in studying the evolutionary process as a whole [21, 53, 81, 94], comparatively little research has been dedicated to exploring the connections between the evolution of different attributes within a single species.

Few quantitative methods are available to investigate whether and how evolution leads to trade-offs between different phenotypic attributes of a species [34, 76]. Recent quantitative studies about the relation between vision, hearing and olfaction based on anatomical sizes of sensory organs of mammals suggest a correlation between vision and hearing [76]. Ontogenetic development of sensory organs and their use are both metabolically expensive as sensory receptors and neuronal ganglia require high adenosine triphosphate (ATP) consumption. This creates two contrasting evolutionary pressures to either save energy by decreasing size and performances of sensory organs or demands for higher energy cost in order to develop and maintain sensory organs with higher sensitivity [76]. Likewise high speed locomotion is metabolically costly [3, 40, 86] leading to similar evolutionary pressures. Keeping in mind competition among organisms, limited resources and pressure to gain and conserve metabolic energy, one must consider how changes in one phenotypic attribute will affect others [7, 55, 56, 96].

Since the overall fitness of a species is in part determined by metabolic limitations, optimizing all of its traits at once is highly unlikely [34, 55, 56, 92]. This is evident in nature since there is no single creature that is superior to all others in every aspect. For instance humans, despite

being arguably the most intellectually-advanced species on earth, are nowhere close to having the best eyesight or the highest speed of movement in the animal kingdom. Here, we investigate, both theoretically and numerically, the correlation between the evolution of two separate attributes: speed and sensory acuity. In addition, we explore the relationship between the variations in these attributes and the resulting changes in dynamics these variations usher over time in a controlled environment with limited resources and extreme competition.

We develop a simple, abstract model that describes the ability of an organism to sense, and its ability to physically explore and traverse the environment. Most organisms interact with the world using their senses and organs that allow them to move, and interact with objects in their surroundings. They can sense different aspects of the environment including heat, chemical composition, as well as light and vibration. All organisms also interact with the environment physically, and have specialized parts to do so: From the flagella in bacteria, and the arms of hydra, to the appendages of mammals. To capture these characteristics of living beings using an abstract model we define *acuity* as a measure of an organism’s ability to detect an item of interest, such as prey or any other (exhaustible) source of nourishment, in its vicinity. We do not specify the exact sense, or combination of senses the organism might use to detect such items. We also introduce *speed* to quantify the rate at which an organism moves through and explores its environment. We again do not specify how the animal performs such movements: It could be swimming, flying, walking or somersaulting.

Central to our model is the idea that both high acuity and high speed are costly. Better senses require a larger number of receptors, and, even more importantly, a more extensive and metabolically expensive processing system (e.g. nervous system) to process and interpret the information communicated by the senses [76]. Similarly, higher speed not only requires more energy to achieve, and maintain (due to, for example, friction or the need to dissipate heat generated during locomotion), but can also be the result of larger bodies and stronger limbs which again come with a higher metabolic cost [38, 39]. There is also a trade-off between speed, maneuverability and motor control which reduces the benefit of higher speed [21, 111, 114]. We develop a simple model to

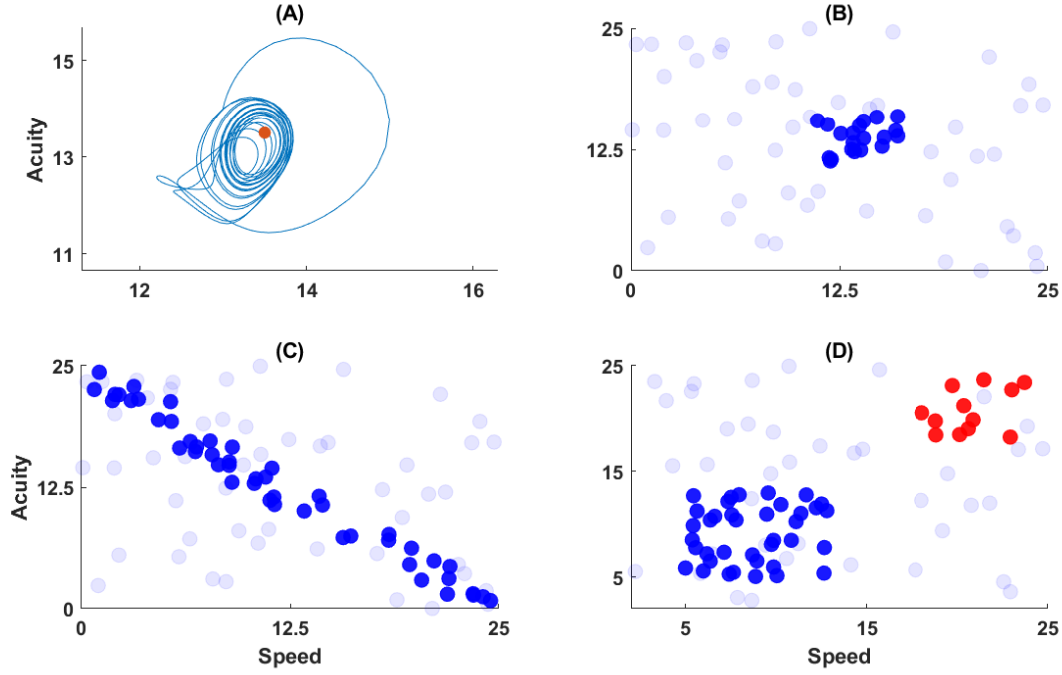


Figure 1: **(A)** An example of a potential trajectory of average attributes in phenotype space. In this case the average speed and acuity do not converge to an equilibrium, but keep oscillating. **(B)** Under some conditions a population starting with some random distribution of phenotypic attributes converges under evolutionary pressure, and the final population can consist of individuals with closely related phenotype. **(C)** Under different conditions, a population can consist of individuals that exhibit a trade-off between the attributes, or **(D)** the population can split into two groups with different phenotypes. Light blue dots represent random initial phenotypic attributes.

examine some fundamental questions (see Fig. 1): Under what environmental conditions can we expect the evolution of specialized organisms that have acute senses, and/or travel at higher speed? Do some environments lead to the evolution of one attribute at the expense of another? Under our assumptions can some environments lead to speciation and support, for example, a few members of a fast species with acute senses and high metabolism, and many slow, obtuse organisms with a low metabolisms? We also explore the dynamics of populations and their attributes to see whether they exhibit oscillations over generations, or whether they approach a stationary distribution.

1.1 Notations and Definitions

Our model describes how a group of agents (organisms) interact with the environment and each other. The agents and the environment are described using several features that are abstractions of different characteristics shared by most living beings, and parts of the environment they interact with. In the model agents are confined to a two-dimensional domain, and expend metabolic energy to locate resources and move towards them in order to consume them. Our model consists of the following components and characteristics which we define precisely in the following chapters:

- **Resources:** We assume that resources that can be consumed by the agents are distributed throughout the environment. These resources are renewable, and generally appear at random points in the domain at a fixed rate per unit area. We assume that each resource, when consumed, provides a fixed amount of metabolic energy (F) to an agent, energy that can be used for movement or sensing. We assume that the value F represents the metabolic energy that can be used for sensing and movement, which will be lower than the total caloric value of the resource.
- **Speed:** We define the *Euclidean Distance* that an agent travels in a unit of time as the agent’s speed. We assume that movement requires a speed-dependent amount of metabolic energy.
- **Acuity:** We measure an agent’s ability to locate a resource using acuity, defined as the radius of the disc around an agent throughout which the agent can sense (locate) a resource. In other words, this is the maximal distance at which an agent can “see” a resource ¹. Higher acuity requires a higher rate of metabolic energy expenditure.
- **Foraging:** Foraging is the process of searching for resources which includes random motion in the domain to find the resource and motion towards a detected resource in order to consume it.

¹although we will sometimes say that the agent “sees” a resource, the model is agnostic about the particular sense or combination of senses that an agent uses to locate resources.

- **Run (flight) length:** The distance covered by an agent in a straight line with constant velocity before changing direction while exploring the environment. Agents move in straight lines, but turn occasionally. The turns occur according to a Poisson process with a fixed average distance, so that faster agents turn more frequently.
- **Cost of Motion:** Agents use metabolic energy as they move and sense the environment. Since we assume that agents always move in an effort to collect resources, the cost of motion is the rate at which energy is expended both for sensing and movement.
- **Metabolic score of an agent (MS):** The metabolic energy available to the foraging agent. The score increases every time an agent collects a resource, and decreases during other times at a rate determined by the agent's speed and acuity.
- **Birth:** In the full version of the model we will assume that each agent with a sufficiently high metabolic score can reproduce asexually resulting in the birth of a new agent.
- **Phenotypic vector:** A pair of attributes that determine the phenotype of each agent. Phenotypes are assigned at the beginning of the simulation, and at each birth. At the beginning of the simulation phenotypic vectors may be identical for all agents or they can be sampled from some distribution.
- **Dispersal distance:** This is the displacement of individual agent from its natal location (co-ordinate). When an agent is born, it takes the same location as the parent or disperses to a new location in the vicinity of the parent.
- **Phenotypic variance:** Phenotypic variance is the variance among phenotypic vectors which measures the diversity across the population. Such variability is needed for evolution [16].
- **Mutation:** A mutation results in a difference (usually very small) between an agents' phenotypic attributes at birth and those of its parent. Mutations generate phenotypic variance and can increase such variance in the population.

- **Death:** We also assume that agents die at a rate that is dependent on an agent’s metabolic score. Agents with a low metabolic score die at a higher rate.

These features are not meant to capture the full diversity of foraging modes, and environmental interactions that characterize even simple organisms. However, they allow us to define a somewhat tractable model of foraging that captures essential features of the process, the basic attributes necessary for foraging, and how these attributes can evolve over generations.

1.2 What Is Foraging?

Foraging or searching is one of the most ubiquitous behaviors in nature. Organisms must forage for food and shelter as these are essential for survival and reproduction [98, 99]. Foraging consists of learning, communication, statistical inference and decision making which provide opportunities to optimize rewards under environmental and physiological constraints. Thus the ability to forage is one of the determinants of fitness, and foraging is fundamental to natural selection [68].

Births, deaths, immigration, and emigration are the elementary processes that determine population dynamics. When viewed from the perspective of the consumer, the resources it gathers through foraging partly determine its *fitness* since they determine the probability that the organism will survive and proliferate. In turn, the survival and proliferation probabilities of individual organisms determine changes in population size. Decisions to disperse or shift habitats also affect population dynamics, and these factors may differ from one environment to the next (we will not consider immigration and emigration here). The relationships between foraging decisions and demographic rates thus link foraging theory and population dynamic theory [98]. It is possible that several different species’ dynamics are closely related to the foraging choices made by one species. For instance, predator foraging choices can have a significant impact on the mortality rates of prey species. Such dynamics are often described and determined by *Lotka-Volterra* equations (Eq. (1)) for two interacting species as predator and prey [108].

$$\frac{dm}{dt} = \alpha m - \beta mn, \quad \frac{dn}{dt} = \gamma n + \delta nm, \quad (1)$$

where, n is the number of predators, m is the number of prey, and $\alpha, \beta, \gamma, \delta$ are parameters which describe the growth rates and interactions between the two species.

The choices of competitors in foraging can also change the resource availability for competing species that share a common resource. All of these indicate that foraging choices can influence and drive population dynamics. Thus, foraging behavior impacts population dynamics and also has complementary impacts on foraging behavior itself.

While population dynamics is strongly determined by foraging behavior, the evolution of such behaviors themselves are directed by external factors like resource availability. The uncertainties and variations of resource availability shape foraging strategies. Any fluctuations in resource accessibility or unstable prey population dynamics, which are spatial or temporal in nature, can produce an unstable resource environment for the species which rely on these resources for food. For instance, the effect of temporal variation in the abundance of preferred prey type on a forager's decision is to be selective or opportunistic [98]. Phenotypes with attributes that are able to support effective foraging in an unpredictable environment can be better at surviving and reproducing, and thus have higher fitness.

Effective foraging always comes with a question: What is the best strategy organisms should follow to locate and exploit resources in an environment? This question becomes more relevant when the organisms have limited sensory capacities and when resources are rare. Random search models are typically used to describe animals foraging for food or other resources [24, 112]. In these models, one or more agents (organisms) search a landscape to identify targets whose positions are unknown at the outset. The agents' movements are subject to other external or internal limitations, such as the environmental context of the terrain or the individual's physical condition, and are characterized by a particular search strategy. The success of the strategy is also determined by the distribution of resources in the environment: Rare and patchy resources will typically require different search strategies than resources that are abundant and evenly distributed [9, 73, 106, 107].

In response to such limits on the movements, and variations in resource distribution, evolution can lead to the emergence of a strategy or strategies that optimize search efficiency [20]. In

foraging theory, it has often been asserted or assumed that the flight lengths of a forager have a characteristic scale with a well defined variance taken from Gaussian, Rayleigh and other classical distributions [106, 107]. These distributions of flight lengths influence the efficiency of exploration, impact the resource encounter rates, and can dominate the overall foraging efficiency. Therefore foragers may adopt a strategy suited to their environment or may enhance their efficiency by employing flexible strategies to explore unpredictable environments. The following are some common search strategies used in models and based on random walks with variations in the distribution of flight lengths:

(a) Brownian motion and random walks.

Brownian motion is the movement of suspended particles in a fluid medium, which is caused by collisions with the molecules of the medium and occurs in a random and continuous fashion. The movement represented by an abstract mathematical model describing this phenomenon is also known as Brownian motion [30]. A stochastic process that describe the path where each step and directions are taken from some particular distributions, is known as a random walk. Random walk processes can be used to model diffusion process as the expression of Brownian motion [24]. It is common to model movement of biological systems using random walks. This is a vast and expanding area of applied mathematics, particularly in ecology (animal movements) and cell movements [67]. Animal movements in search of food, resources, shelter, and population redistribution and dispersal are often modeled and simulated using random walks.

When a forager selects a random direction and moves in a straight line in that direction until it finds a resource, this type of movement is termed *ballistic motion*. In ballistic motion, a forager changes the direction only when it finds a resource. The path between two successive foraging successes is a straight line and the velocity is constant during that motion. Instead of moving in a straight line until finding a resource, if a forager selects a distance from a fixed probability distribution, moves up to that distance or until finds a resource, and selects a new

direction and new step length, the resulting search strategy constitutes a random walk. When the direction of the current step is independent of the previous steps' length and directions, the random walks are called uncorrelated and unbiased random walk (UCRW). UCRWs are the first simple model of movement where each location depends only on the location at the end of the previous step. The location of an agent at the end of each step thus satisfies the Markov property. The motion is unbiased due to the absence of a favored direction; each step's movement is independent from previous directions. A UCRW on an infinite domain can be rescaled appropriately, and by "zooming out" such a random walk converges to Brownian motion [24]. On the other hand in correlated random walks (CRWs) successive steps have correlated directions and/or lengths. This may create a bias towards a particular direction for some time. However, unless correlation is perfect, this bias weakens over time to eventually have a uniform distribution of directions. When there is a consistent bias in direction, the probability of net displacement in that direction will be greater resulting in a *drift-diffusion model* (See Appendix A).

(b) Lévy walk.

Studies of foraging movement have shown that animals can exhibit unique patterns of foraging when they have no or little prior knowledge of food location [9, 89, 106, 107]. The patterns do not resemble Brownian motion or a random walk. Sometimes, foragers travel large distances in a single direction followed by a sequence of much shorter excursions (see Fig. 2B) This tactic can allow foragers to quickly obtain food in an unfamiliar area, particularly when the food distribution is patchy. It has been analytically demonstrated that the best approach for random searches is a model in which distance between two successive directions changes follows inverse-square power law distribution [9, 106].

Studies have shown that the distances that animals travel can follow a power-law distribution. The flight lengths, η_j , associated with target searching are said to follow a power law

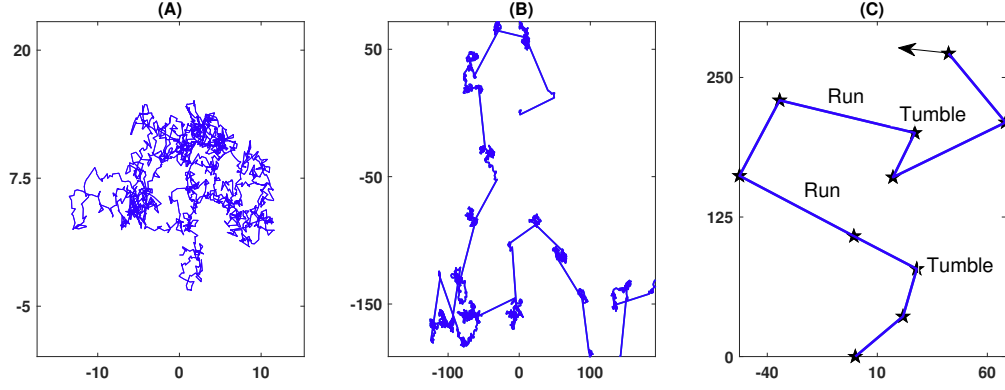


Figure 2: Foraging strategies in an unknown resource distribution environment; **(A)** Brownian motion, **(B)** Lévy walk, and **(C)** run-and-tumble motion.

distribution if

$$P(\eta_j) \sim \eta_j^{-\mu},$$

where η_j is the step length and $1 < \mu \leq 3$ is a parameter [106]. Choosing $\mu < 1$ does not give a probability distribution which can be normalized, unless it is truncated at some finite value [23]. For $\mu = 1$, the resulting random walk becomes ballistic motion. Similarly, when $\mu > 3$, asymptotically the resulting random walk approaches Brownian motion.

Lévy walk paths are self-similar, fractal and scale free. A forager following a Lévy walk strategy does not have to adjust its range of motion to the environment under consideration. Therefore, a Lévy walk describes animal movements in a flexible and concise manner. Regardless of the value of μ chosen, a Lévy walk leads to more efficient searches when target sites are sparsely and randomly distributed because the probability of returning to a previously visited location is lower than for a Gaussian distribution. The foragers might follow Lévy walks because N Levy walkers cover a larger areas, and overlap less in their searches compared to N Brownian walkers [9, 106].

Although the theoretical research on Lévy walk search optimality has had a significant impact, there are still a number of significant areas of ambiguity. Some authors believe that non-Lévy

processes could be misidentified as Lévy process, and vice-versa, due to the limitations on sampling of paths that do not reflect actual movements [6, 85]. Others claim that Lévy walks with the parameter $\mu \approx 2$ can offer a foraging efficiency that is higher than other exponents [84].

(c) Run-and-tumble motion

The motion of animals varies according to the shape and behavior of the organism, and is shaped by their habitats. For instance, *E. coli* is one of several bacterial species that propel themselves by alternating between ‘runs,’ or periods of practically straight-line travel at nearly constant speed, and ‘tumbles,’ which are sudden and rapid changes in direction that happen stochastically at an approximately constant rate [12, 102]. *E. coli* cells are shaped like rods with hemispherical end caps and long, helical filaments called flagella. The direction in which these flagella rotate is controlled by intra-cellular signals, and thus determines the direction in which the cell can move, and the speed of movement [12]. Computational and analytical models for such run-and-tumble motions have been derived on the basis of following observations [12, 52, 109, 102]:

1. The runner moves in a straight line during a ‘run.’
2. Run velocity is approximately constant, and ‘tumble’ duration is negligible compared to run times.
3. The position of the bacterium does not change during a ‘tumble.’

Such models often also assume that the duration of runs follow an *exponential distribution* [12]. Let s be the average linear speed of a cell during a run, f_η , the tumbling frequency or reciprocal of the average run length time, $\hat{t}$, then the average cell run distance, η , (displacement between two consecutive tumbles) is given by,

$$\eta = s \cdot \hat{t},$$

and the measure of motion, also called the motility coefficient², is given by

$$\mu_0 = \frac{s^2}{n_D f_\eta (1 - \cos \theta)} \quad (2)$$

where n_D is the dimensionality of the system and θ is the average turn angle between successive runs [79, 82, 90, 109]. Eq. (2) relates population and single-cell parameters. Even though there are other parameters involved, the run and tumble motions can be well described by two stochastic variables $s(t)$ and $\psi(t)$ where $s(t)$ is speed and $\psi(t) = \cos \theta(t)$ is the direction change during tumble. In such cases, the statistical properties of run and tumble motions can be described by a *Langevin equation* for the variables (s, ψ) with particular control parameters as [31, 32];

$$\frac{ds}{dt} = \lambda_0 [s - s_s(\beta)] + \zeta_s(t) \quad \text{and} \quad \frac{d\psi}{dt} = \rho [1 - \gamma \sin \delta \theta] + \zeta_\psi(t)$$

where $\lambda_0, \beta, \gamma, \delta$ and ρ are control parameters, s_s is steady state speed, and ζ_s and ζ_ψ model Gaussian noise.

There are many experimental findings that have been used to support theoretical investigations of run and tumble motion in self-propelled microorganisms [12, 32, 79]. Though we do not restrict ourselves to the movement of any unicellular or self-propelled organisms, we consider movements in our model as ‘run-and-tumble’ motion.

1.3 Energy Cost of Physiology and Locomotion

All organisms require energy to live. Metabolic processes in living organisms include the transformation of energy from one form to another. Different parts of the body go through these metabolic processes at varying rates, and an animal’s activity also affects its metabolic rate. Metabolic activity is also essential for the assimilation of food required for products like amino acid and other

²the ability of living systems to move and carry out mechanical work at the expense of their metabolic energy is known as motility [5].

nutrients necessary for life. The synthesis of significant amounts of biomass and energy is necessary for cell division and reproduction, which are both metabolically costly processes. Thus, it is not surprising that a cell’s decision to begin dividing is influenced by both its metabolic state and the presence of nutrients [46]. Moreover, organisms which require less metabolic energy for maintenance and have efficient metabolic process are likely to survive and proliferate [15, 100].

In mammals the metabolic energy used by sense organs, the transport of information and neural processing of that information is high. The visual system, for instance, demands a high amount of energy [51, 64, 75, 110]. A significant amount of energy is required to maintain the basic function of the brain. The energy required by tissues other than brain, are highly variable. However, the metabolic energy used by the brain varies much less and resting energy required in the brain is a considerable part of total energy consumed [64]. Thus, use or nonuse of sensory systems does not make a significant difference in metabolic energy cost. Hence, the metabolic energy cost related to the acuity of the different senses can be a large proportion of an organism’s energy expenditure, whether the organisms is actively engaged in sensing or not.

The minimal energy required per unit time when an animal is at rest is known as basal metabolic rate (BMR). This means that it includes the energy required for proper cellular functions, neuronal activity in animals with brains, and other processes that consume energy while the animal is at rest. BMR is considered as a baseline to make comparison of energy expenditure during physical activities, however one needs to consider conditions like thermoneutrality. The animal must be in a complete rest state while measuring BMR. In one of the earliest attempts, Kleiber concluded that BMR is proportional to the animal’s mass raised to the power $3/4$ [49]. There have been many refinements of Kleibler’s conclusion, but in all cases BMR was found to scale sublinearly with mass.

Regarding the energetics and mechanics of animals’ terrestrial locomotion, Heglund et al. (1981) concluded that the mechanical power P expended by a bird or mammal per unit mass is given by [29, 39, 103],

$$\frac{P}{M} = 0.478 \cdot s^{1.53} + 0.685 \cdot s + 0.072 \quad (3)$$

where s is average ground speed and M is the mass of the animal.

This equation is independent of mass on the right hand side and hence, can be applied equally to a small or a large animal [39]. This equation also shows that total mechanical work performed per gram of muscle increases with increase in speed. Experiments based on the oxygen consumption by different animals show that metabolic cost of transport is also proportional to a power of animal's mass so that the metabolic power required for walking, running or swimming is proportional to $(\text{body mass})^\alpha \times (\text{speed})^\beta$ depending on the environment. Alexander, et al. concluded that the powers in this expression satisfy $\alpha < 1$ and $\beta \in (2, 2.8)$ [2, 3, 4]. However, for animals moving in a similar environment in similar ways, mechanical cost of transport, that is $\{\text{power}/(\text{mass} \times \text{speed})\}$, is independent of body mass for specific modes of walking and running [2, 3, 4].

Since, animals don't often spend a lot of time at their BMR, the field metabolic rate (FMR), which measures how much energy an animal uses while roaming around in its natural habitat, is a more useful metric of energy consumption during exploration and foraging [71]. The FMR measures an animal's overall energy expenditure, sheds light on its energetic strategies and hence includes the implicit energy costs of other sensory activities. For example, animals not only expend energy while in motion but also expend energy on the sensory mechanisms that allow them to extract relevant information from their environment. From the sensors of unicellular organisms' used to sense nutrient substrates, heat, light etc. to the sensory systems of mammals composed of million of neurons, all use a significant portion of an organism's energy budget [110, 51, 75]. Hence a general model of energy cost for foraging must account for all such implicit energy expenditures.

In motile unicellular organisms, metabolic cost for motion is also a significant part of their total metabolic cost. For instance, in the absence of flagella, soil bacteria *P. putida* adapt faster and are more resistant to oxidative stress, presumably because of the negative metabolic impact of the flagella [61]. As a result, flagellar motility serves as an example for the classic trade-off that occurs when gaining environmental benefits comes at a high metabolic cost. The average metabolic cost for run-and-tumble motion of flagellated bacteria is proportional to the square of speed [66]. Flagellar size and number can impact drag, and determine the resources required to

maintain them. However, they also determine speed and stability of the direction of motion. Thus both the metabolic cost and the benefit to a bacterium is a function of flagellar length and number, as well as the properties of the environment [66]. With these available methods and applications to scale the metabolic cost of locomotion, we, in our model, devise cost of motion as the function of square of speed.

1.4 Optimal Foraging Theory

Organisms forage for food in order to gain sufficient energy and resources to survive and reproduce. The study of how organisms can best use food resources to optimize their chances of survival and reproduction is known as optimal foraging theory. Spatially implicit patch-use models that highlight the impact of various patch-leaving criteria on foraging effectiveness have historically dominated this research. Optimal foraging theory was introduced to the field of ecology in order to determine which types of food should make up a species' diet and which patches it should feed on to function in the most economical way [28, 57]. The assumption is that animals have to strike a balance between two opposing strategies: investing a lot of time and energy into finding highly rewarding food sources, or investing little time and energy and rely on more common but potentially less rewarding food sources. Animals whose behavioral strategies increase their net energy intake per unit time spent on foraging are favored by natural selection [28, 57]. Optimal foraging theory also uses the marginal value theorem, that explains the process of exploitation of discrete resource patches [19, 87], however the process of finding such patches is often ignored.

Some classical models of optimal foraging theory [19, 28, 57] consider foragers in environments of resource patches. These patches can differ in resource density and quality. The average time required to travel between patches is often fixed and the probability of revisiting the same patch is zero in a short period of time. The proportion of a particular patch type present in the environment determines the probability of visiting that patch. Since resource availability and consumption decrease as resources are exhausted continuously from the patch, a forager acts in accordance with the marginal value theorem to maximize its rate of overall resource intake. The 'marginal value

theorem’ states that “the forager should leave the current patch when its rate of resource intake in that patch is equal to the expected rate of resource intake, calculated as the average rate throughout the foraging area” [19]. The second rate depends on the probability that the organism will find another patch upon leaving, and the resources available in the new patch.

Most optimal foraging theory based studies demonstrate their effectiveness through quantitative evidence. However there have been some criticisms of these models’ validity and limitations. Since the optimal model represents foraging as a deterministic process and some theoretical approaches ignore the inherent stochasticity of the foraging environment, information on patch quality and expected resource uptake rates as deterministic parameters is circular and even incomplete [77, 87]. Optimal foraging theory assumes that the organisms’ foraging strategies is improved via natural selection [28, 57], however natural selection is a passive process that selects for genetically based features that improve an organisms’ reproductive success rather than an all-powerful force that creates ideal designs [83, 87]. Similarly, the assumption that foraging behaviors are independent from other traits may not hold as organisms are integrated systems as opposed to associations of non-interaction pieces [83]. Simple stochastic models can be used to solve complex foraging problems. Optimal foraging theories based on stochasticity and random walk approaches in general should enhance biologically precise modeling by highlighting congruity in search strategy design [10, 77, 107].

In patchy resource environments, a hybrid foraging model which uses both random search and informed motion based on the memory can appropriately predict the process of searching for food. In such a mixture model, a forager can estimate patch locations incrementally and store positional target information with few parameters. In some cases, a hybrid model can result in motion that resembles Lévy walks. Depending on the strength of the memory effects, foragers optimize search efficiencies by continuous re-visitation of non-destructive³ targets [73]. To understand the mechanisms behind the general rules for patch leaving decisions given by optimal foraging theory, a Bayesian approach has been used which treats patch leaving behavior as a statistical inference and

³forager may visit and collect the resource from the same target site many times.

decision problem. This recent approach uses probabilistic sequential updating and derives stochastic differential equations about expected resource replenishment rate in the current patch and thus generates analytically tractable models associated with optimal patch leaving strategies [47].

As we examine the changes in population and attributes over time, we also consider a resource environment on which resources are distributed in patches within the foraging space. However, we're not trying to determine the best strategy for staying on any particular patch. Instead, since the patches in our model change over time, we're focusing on the agents' capacity to locate and exploit these patches, how this affects their fitness, and how it ultimately impacts the evolution of their attributes.

1.5 Stochastic Birth-Death Processes and Evolution

Evolutionary dynamics is determined by the probabilities of births and deaths in a population. Only populations of reproducing individuals can undergo evolution. Since changes in population due to birth and deaths describe who survives and who does not, such changes affect which traits evolve over time. However, some ecologists who study population dynamics ignore the prospect of evolutionary change affecting the creatures they are investigating due to the challenges to grasp the effects of continuously changing interactions between populations [104]. Population dynamics models often assume that evolutionary processes move too slowly compared to ecological scales. However recent studies have challenged these assumption and claim that population and evolutionary dynamics may progress on similar time scales [65, 104]. These studies assert that the relationship and interactions between population and evolutionary dynamics are important and hence any population or evolutionary dynamics model must include the interplay between them.

Simplified population growth models are often described using non-linear population models. The best known is captured by the *logistic growth equation*:

$$\frac{dx}{dt} = \alpha x \left(1 - \frac{x}{K}\right) \quad (4)$$

where α is the intrinsic growth rate, x is the population density, and K is the carrying capacity of the environment. This equation which accounts for competition among the member of similar species, has been extensively employed to describe and predict a wide range of growth process. The parameter K in Eq. (4) is due to environmental factors and can be experimentally determined. The logistic equation describes how a stable population is reached after exponential growth in an environment with limited resources and other constraints.

Two (or more) competing species can be modeled by extensions of the logistic growth equation, of which the *Lotka–Volterra equation* (Eq. (1)) is a special case. In addition to describing intraspecies competition, Lotka–Volterra equations also describe how the presence of competitive species affects the growth of both species. A more general form of Eq. (1) can be written as;

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 (\alpha_{10} - \alpha_{11}x_1 - \alpha_{12}x_2) \\ \frac{dx_2}{dt} &= x_2 (-\alpha_{20} + \alpha_{21}x_1 - \alpha_{22}x_2).\end{aligned}\tag{5}$$

where x_1 and x_2 are prey and predator densities respectively. The parameter $\alpha_{10} > 0$ is the prey growth rate, α_{11} and α_{22} are intraspecies competition rates, and α_{20} is the death rate of predators.

Using the Lotka–Volterra system to model the population dynamics driving evolutionary processes requires addressing several challenges. First, the dynamics of Lotka–Volterra systems are not stable and often display divergent extinction of one species or cyclic oscillation. This divergent extinction of one species is also seen in the stochastic version of the Lotka–Volterra equations [63]. Contrary to most natural predator-prey interactions, which occasionally display stable and sustained coexistence, we do not have a solution for asymptotic stability in Lotka–Volterra systems [63, 101]. Secondly, to solve these models (Eqs. (4) and (5)) the parameters and interaction rates due to ambient features must be known. The utility of both models depend on the reliability of experimentally determined parameters and rates. In a population, individual characteristics like phenotypes, genotypes and other physical states determine birth-death and interaction rates, however such rates also depend on a variety of other factors, including their own characteristics, those of competing individuals from similar or different species, and the environment. Therefore,

as populations and the environment change through time, birth–death and interaction rates often fluctuate as well. Hence, knowing how these rate changes as the environment changes is essential to understand the evolutionary dynamics that is driven by the underlying birth and death process in the populations.

The evolutionary dynamics driven by a birth–death process depends on birth and death rates which are in turn determined by a combination of phenotype, environment and interactions with other organisms. These rates are not experimentally derived, constant parameters but rather dynamically changing functions of current states and hence they need to be updated after every event. Sequences of births and deaths describe a stochastic process in which the configuration of population changes with every birth or death. A mechanistic approach based on the fundamental events of births and deaths occurring in individual organisms has been proposed in order to build a generic model of evolution [27]. This approach consists of a population of types⁴ of individuals $x_1, x_2, \dots, x_{n(t)}$, where x_i is the type of i -th individual, $n(t)$ is population size at current time t . If $b_i(t)$ and $d_i(t)$ are the birth and death rates of individual i at time t , then these become complicated functions of ‘internal’ and ‘external’ states at time t , given by:

$$\begin{aligned} b_i(t) &= b_i(x_i, E(t)) \\ d_i(t) &= d_i(x_i, E(t)). \end{aligned} \tag{6}$$

where $E(t)$ consists of external(environmental) factors like competing species, resource environment and other abiotic factors.

After each birth or death event, the configuration of the population changes. When an individual is added to the population through a birth, the offspring type is determined by several factors like the parents’ type, mutation/recombination, environmental factors⁵, etc. In a simple birth process, the newborns have the same phenotype as their parents. The effect of mutations can be modeled by selecting the phenotype of the descendants from a distribution that is centered around at the

⁴here ‘type’ characterizes individuals by phenotypic or genotypic differences.

⁵for example, the sex of some reptiles at birth is influenced by the ambient temperature.

parents’ phenotype. In this way variability is introduced into the population. Phenotypes that provide a reproductive advantage will be more likely to take over the population, and dominate, unless variability is too high. Thus births, deaths and phenotypic variability in the population drive evolution. The resulting dynamics can be shown as a cloud of points that moves around in ‘phenotype’ space [27]. Individuals are represented by the points in this cloud, which moves as some of the points vanish and new ones appear in other places (see Fig. 1). Hence, the evolutionary dynamics are represented by the cloud’s collective movement.

1.6 Evolutionary Constraints and Trade-offs

An evolutionary trade-off occurs when evolutionary processes advance one characteristic of an organism at the detriment of another. Trade-offs are the process by which one feature is improved at the expense of another trait [34, 92, 93]. There is broad agreement that resource constraints (such as those related to energy, habitat/space, or time) prevent the simultaneous optimization of multiple features. Rather the process can be viewed as optimization under constraints. As a result improvement of one attribute which increases fitness may impact another attribute whose impact on the animal’s fitness may be smaller than that of the first attribute [34].

In evolutionary biology, predicting traits always requires discussions of trade-offs. Fitness trade-offs limit and influence the evolution of traits to maximize survival and fertility. Statistical correlations and functional relationships are often included in the trade-off, and have been observed in many examples of life history⁶ traits [92, 113]. The impacts of trade-offs on organisms can be proximate or ultimate. These have been examined at various levels, including the population level to understand how trade-offs affect ultimate evolutionary trajectories, and the mechanistic level to understand proximate causes. Some important categories of trade-offs that are frequently discussed in the literature to classify and study it are allocation constraints, functional conflicts as well as physiological and ecological circumstances [34].

There are allocation constraints when the overall amount of a resource is limited, making it

⁶the general characteristics of the life cycle, such as the rate of growth, the age of maturity, the length of life, and the frequency of reproduction, are included in the life history.

necessary to reduce allocation to one attribute or trait in order to increase allocation to another. In biological system, the case is more complicated and multiple hierarchical constraints exist. Constraints relating to resources, however, may not result in trade-offs unless the organism is fully utilizing these resources. Trade-offs can result from functional conflicts when features improve the performance of one task while degrading the performance of another [42]. For example, higher speeds are beneficial to flee from predator yet detrimental to manoeuvrability and motor control [111]. Similarly integrator molecules, which simultaneously influence several attributes through numerous biochemical and physiological pathways, can have both positive and negative effects on fitness-related traits [34].

The trade-off between costs and benefits is created also by selective pressures⁷, and this trade-off eventually affects the fitness of the organism. Like other systems, the nervous system too is under selective pressure to produce adaptive behavior, but it also has costs associated with how much energy it uses. For instance, the total energy budget of an animal as well as the way energy costs are distributed throughout the nervous system both serve as constraints on the amount of energy that can be used for sensory processing. This affects the evolution of sensory systems, causing trade-offs between sensory systems encoding different modalities [75]. However in some cases, the sensory systems are interconnected in such a way that there is a correlation, and possible cooperation between different senses [76]. Indeed, when a model is defined by only two traits, then the ecological and evolutionary dynamics are influenced by possible co-operation or trade-off between these two traits. In the absence of other infringing factors, a simple bivariate correlation between two traits can be used to measure the trade-off between them. Although such an analysis can be easily expanded to trade-offs involving three or more traits, we only address a trade-off involving two traits for the sake of simplicity.

Based on the phenotypic variances and covariances, we can characterize the trade-off function

⁷selective pressure is any external or internal factor for certain phenotypes that result in survival benefit or disadvantages.

as follows [92, 93]:

$$a = \left(\mu_a - \frac{\sigma_{P_{sa}}}{\sigma_{P_s}^2} \mu_s \right) + \frac{\sigma_{P_{sa}}}{\sigma_{P_s}^2} s \quad (7)$$

where μ_s and μ_a are mean values of traits speed (s) and acuity (a) respectively; $\sigma_{P_{sa}}$ is the phenotypic covariance between s and a , and $\sigma_{P_s}^2$ is the phenotypic variance of trait s .

This dissertation deals with constraints and trade-offs between attributes. For example, modeling foraging with ‘run and tumble’ search requires the agents to be equipped with attributes like speed and acuity. Due to competition, limitation of resources and expense of energy for traits, there is a constraint on the total energy available to carry out the functions of these attributes. We will examine the extent of these trade-offs, their impacts on fitness of agents and the direction of the evolutionary trajectory. Moreover, we argue that constraints and trade-offs between traits are important to the study of evolutionary dynamics and this dissertation will attempt to further these studies by providing an another approach to mechanistic model of population dynamics and evolution.

1.7 Agent-based Modeling

The applications of ‘conventional’ differential equation (ordinary differential equation and partial differential equation) and statistical (regression and extrapolation) modeling to establish and test evolutionary dynamics have limitations. Firstly, we need to have sufficient evidence, data over long period of time, to generate and validate these models. Secondly, differential equations and statistical modeling are thought to have restrictive assumptions that hinder their application in certain examples [8, 13]. In many such cases, the control parameters and interaction rates are pre-determined, and used in the equations and statistical models as constants. However such parameters are changing due to ever changing interactions between agents. In theory, everything can be accomplished by the use of equations, but the complexity of differential equations rises exponentially with the complexity of behavior and the number of interacting species. To overcome such limitations and to provide a design and implementation of system composed of many individuals whose local

interaction produce an aggregate behavior, *agent-based models* have been used [8, 13, 112].

The purpose of agent-based modeling (ABM) is to identify the emergent behavior of ‘agents’ that can not be readily predicted by analytical treatment of rules themselves. In ABMs, an agent describes an autonomous decision making entity which interacts with the environment and make decision on the basic of sets rules. Such agents have the capacity to evolve, allowing unexpected behaviors to appear. The following characteristics show why ABM is superior to other modeling techniques: ABMs are flexible, captures emergent phenomena, and offer a natural description of many complex system composed of interacting units. These benefits are largely driven by ABM’s capacity to describe emergent phenomena [13].

In this dissertation, we apply ABMs to understand several perspectives of agents’ foraging behaviors and their evolution. Since foraging is one of the most important tasks organisms perform and different behaviors evolve as the consequences of advantages and fitness of adapted organisms over changing environment, it is important to understand the effect of interactions between individuals and emergent behaviors. Foraging consists of many steps like searching, collecting and communication. It has become an active research area due to the ready application of foraging models to real world problems [112]. ABMs are convenient when agent’s individual behavior is non-linear; is characterized by threshold, or exhibits memory, and path-dependency. Often differential equation models smooth any variations however ABMs do not, so that the deviation from predicted aggregate behaviors can also be captured [13]. We propose and simulate some ABM models to understand foraging, probabilistic transition by birth-death and evolution of behaviors. We also discuss the effects of foraging on agents’ ‘fitness’ to the evolution of attributes by the means of ABM with plausible challenges to fit it to observational data.

1.8 Motivation and Outline of this Dissertation

Living organisms have the ability to sense their environment and respond to numerous chemical and physical stimuli. Such senses and responses are carried out as the function of what we call different attributes of the organism. An attribute characterizes, for example, an organism’s sense of smell,

hearing, its ability to move, or its ability to resist infection, or heal from an injury ⁸. Each attribute has its own role in survival and impacts the ‘fitness’ of the organism. These attributes sometime function independently and sometime work together to help the organism perform certain task. As we discussed in Subsection 1.6, the increase in ‘fitness’ due to changes in one attribute can cause corresponding changes in other attributes leading to trade-offs between the two attributes. These trade-offs partly determine the phenotypes of organisms and can direct evolutionary trajectories.

The question that motivate this dissertation is: Up to what extent are these attributes responsible for the survival and ‘fitness’ of an organism, and how do the trade-offs and constraints impact the evolution of the attributes? If agent ‘A’ and ‘B’ are foraging in a certain environment where they have to collect resources. ‘A’ can sense resources up to distance a_A in all directions and moves s_A units every unit of time. However, ‘B’ can sense resources up to a_B units (say smaller than a_A) in all directions, but can move s_b units with $s_B > s_A$ in unit of time. There are two main questions: On average, does one agent collect more resources over time than the other? Which agent will have more progeny, and whose progeny will constitute the population in the future?

This study aims to discover the evolutionary dynamics inspired from the organisms’ foraging behaviors. We simulate multi-agent foraging to understand different structures of foraging, to discover the relative importance of attributes for the foraging success and ultimately to understand evolution of these attributes. Our goal here is to capture some well known foraging strategies, present a simple but tractable model of foraging in a typical environment, and show how foraging success drives the evolution of a population towards an improved ‘fitness’ regime. We discuss the challenges and issues understanding the evolution of foraging behaviors.

This dissertation is organized as follows:

- In **Chapter 2**, we present the ABM of foraging and derive an expression to estimate resource collection rate for foraging agents. We also discuss the metabolic cost function, changing metabolic scores, and evolutionary and non-evolutionary birth–death processes.

⁸here, we will focus on the senses, and ability to move, and will not model an organisms response to pathogens or injury. However, a similar approach could be used to examine trade-offs between a wider range of attributes.

- In **Chapter 3**, we develop a system of non-linear differential equations whose solution determines the population size and average metabolic energy equilibria and their local stability. We numerically solve this system and discuss the stability of different fixed points under various initial conditions.
- In **Chapter 4**, we summarize the results about how different phenotypes are able to collect resources in competitive environment. We show that there is a fixed carrying capacity in a given environment and certain behavioral rules which is independent of the initial number of agents and their attributes. We also show that the transition to stable co-existence of multiple phenotypes can be observed in patchy resource environment. We also compare the population dynamics obtained from ABM simulation to that from a mean-field model.
- In **Chapter 5**, we summarize the findings of this study, present limitations, and discuss open issues for future research direction.

2 Experimental Setting and Methods

To address the question of how different traits evolve under competition and under metabolic constraints we use agent-based modeling (ABM). We model a population of foraging agents that search for and collect resources in order to survive. The model includes resources that represent nutrients necessary for survival. The consumption of these resources increases an agent’s “metabolic score” which represents the metabolic energy the agent has available at any time, and thus determines an agent’s propensity to reproduce and die. Each agent has two attributes, *speed* and *acuity*, which determine its behavior, but do not change over the agent’s lifetime. Finally, we also define the mutation rate which quantify how much the attributes of an offspring can differ from those of the parent.

We start by 1) a description of the domain on which the agents forage, 2) the agents’ movement rules, and 3) the rules for reproduction and death. We assume that evolution is driven by mutations, and capture this by differences in a descendant’s attributes from those of their parents. Limitations on the resources and competition provide evolutionary pressure. The distribution of attributes in the population changes dynamically as individuals that are less well adapted to the environment are replaced by fitter individuals.

2.1 Domain and Resource Generation

We assume that the domain, Ω , on which the agents move is rectangular with size $b \times b$, where length is measured in arbitrary units. We assume that the domain has periodic boundaries and is thus effectively a torus. We assume periodic boundary conditions for computational convenience and to minimize edge effects. To simplify computations, we later compute the distance between resources and the agents as the *Euclidean distance* between the two on the $b \times b$ square Ω . Our results do not depend fundamentally on this assumption. We will also examine the impact of domain size on the foraging dynamics of agents, and the evolutionary dynamics of the population.

To survive, agents forage for resources on this domain. Resources appear according to a spatial

point process, with each point representing one resource unit. This unit could represent a fruit, an insect, or a molecular resources, *i.e.* anything that an agent can translate into energy. For simplicity we assume that resources do not move. Each resource unit has the same caloric value, and thus has the same effect on an agent's stored metabolic energy when consumed. We model only the caloric intake of an agent, and assume that all of their other needs for survival are met if their metabolic score is sufficiently high. We define the resource density, ρ , as the average number of resources per unit area, so that the probability that a small area, A , of size, $|A|$ contains a resource is $\rho|A| + o(|A|)$. As resources appear and are consumed, the density, ρ , can change.

We mainly consider the following two methods of resource generation:

- (a) Resources appear at a constant rate, λ , per unit time and unit area, and thus follow a spatial Poisson process. We will first assume that resources appear with equal probability at any point in the domain: The probability that a single resource appears in an small area, A , of size $|A|$ in an interval of length Δt is equal to $\lambda|A|\Delta t$ (ignoring higher order terms in Δt and $|A|$). Equivalently, the number of resources that appear in an area of arbitrary size, $|A|$ and time interval of arbitrary length, T is a random variable following a Poisson distribution with parameter $\lambda|A|T$. If the rate at which agents collect resources is lower than the rate at which they appear in the environment, $\lambda|\Omega|$, the number of available resources diverges. Similarly, a high rate of foraging and low replenishment rate, λ , can lead to few or no resources available in the environment during most of the time.
- (b) Resources appear in the domain so that resource density is fixed. In this case a resource is reintroduced whenever one is consumed by an agent, so that the rate of consumption and replenishment are equal. As the resource density is fixed, there is no possibility of resource explosion as in the previous case.

The second case is less realistic: It is hard to think of a natural process that would generate exactly one resource, whenever another is consumed (although some plants will generate more nectar when nectar is consumed by insects, such nectar production is highly variable [74]). However, this

assumptions simplifies the analysis in some cases, and thus we include it.

In both cases, the expected minimum distance between an agent and resources is a key factor in determining whether the environment is high or low in resources (We discuss about the expected minimum distance between an agent an resources in detail in Subsection ??). If this distance is smaller than the average acuity of foraging agents, then the environment is high in resources, while if it is larger, then the environment is low in resources. Ultimately, by simulating and analyzing both high and low resource environments, we establish a more complete understanding of the complex dynamics of evolution in response to resource availability.

Later, we consider other types of spatial processes including those that result in the clustering of resources. In such cases, resources appear in different sized stationary or non-stationary patches. If the resource replenishment process has a fixed rate we have used non-stationary patches whereas with fixed resource densities we used stationary patches. We also examined the effect of changing the caloric value of each resource when holding the total calories generated per unit area and time constant. This affects the variability of the energy available per unit area, as fewer resources with a higher caloric value will result in higher fluctuations than many resources with low caloric value.

2.2 Agent Movement Rules and their Foraging Strategy

We next describe how we model the movement of agents, their foraging strategies, the energetic cost of locomotion, and resource and energy collection rates. To find and collect resources, agents need to traverse the domain. Resources and agents can be located anywhere in the domain, Ω , and are not constrained to lie on a grid. The agents follow a prescribed strategy, described below, to collect resources, and each agent’s resource collection rate (r_i) is defined as the amount of resources collected per unit time by that agent. To compute this rate, we simulate a population of agents that forage, collect resource, reproduce and die according to the rules which we describe below.

Each agent, i , is characterized by a pair of attributes, speed and acuity which do not change over an agent’s lifetime. Agents are thus characterized by a *phenotype vector*, $\xi_i = \{s_i, a_i\}$. Speed is the rate at which an agent covers distance, while acuity is defined as the maximal distance at

which an agent can sense a resource. An agent’s metabolic score changes continuously as the agent expends energy on movement, sensing, and collecting resources. The mutation rate is nonzero when we simulate evolving populations. Mutations are determined by the same distribution for all agents in the population.

2.2.1 Initialization

We initialize each simulation by placing a “foraging” agent or agents randomly with uniform probability into the domain, Ω . Each agent is characterized by an initial phenotype vector which is generated uniformly at random from a range $\{[s_{min}, s_{max}], [a_{min}, a_{max}]\}$. These attributes will be constrained by metabolic limitations – *e.g.* an agent moving too fast may be expending too much energy and may not collect sufficient resources to support this rate of movement. An agent moving too slowly may not be able to gather sufficient resources to survive. Moreover, we will initially assume that these attributes are fixed, but later allow descendants of an agent to have phenotypes that differ from those of the parent. When the simulation starts, we seed the domain with an initial set of resources, or allow them to appear at a fixed rate.

We denote the position of agent i at time t by $P_i(t)$ where $1 \leq i \leq n$, and the location of j^{th} resource by R_j where $1 \leq j \leq m$. Resources do not move, and thus their location is independent of time⁹. Here n and m are the total number of agents and resources at some time. These numbers can vary if agents reproduce or die, and if the resource number is not fixed. We define the resource density as $\rho = m/|\Omega|$. Thus ρ, n and m generally depend on time, but we suppress this dependence.

Agents moving in a straight line may not be able to explore the domain effectively. Thus, to forage successfully, agents need to change their direction of movement occasionally. Similarly, agents who change their direction of motion too frequently tend to repeatedly revisit regions they have just left, and thus explore the domain inefficiently. Therefore we selected the frequency of direction change, f_i , in such a way that agents move an average distances, *i.e.* perform an average straight run of length η independent of speed and agent number, before changing direction. This

⁹strictly speaking, resources need to be renumbered as they are consumed and generated. We take an arbitrary enumeration at a point in time.

ensures that the difference in the area being explored by an agent depends only on the speed of the agent. Finally, we let D_i be the m -vector of Euclidean distances between each agent, i , at position P_i in the domain, and each resource, j at position R_j ,

$$D_i = \begin{bmatrix} d(P_i, R_1) & d(P_i, R_2) & \dots & d(P_i, R_m) \end{bmatrix}$$

We can also define the $n \times m$ matrix D where the i -th row is the vector D_i .

2.2.2 Exploration and Foraging Strategies

Each agent uses the following foraging strategies to explore the domain Ω , and to collect resources that become visible. Agents move according to two different rules, depending on whether a resource is visible or not:

1. If there is a resource within the radius given by the agent's acuity, that is if $\min_m D_i \leq a_i$, the agent will move towards the nearest resource at its prescribed speed (See Fig. 3B). An agent that reaches a resource consumes it, the resource disappears, and the metabolic score of the agent increases by the amount equal to the caloric value of the resource.
2. If no resource is visible, that is, $\min_{i \in 1, \dots, m} D_i > a_i$, an agent moves in a fixed direction, θ_i . The agent moves in the same direction for random interval of time (See Fig. 3A). These intervals follow an exponential distribution with mean η . Thus, when resources are not visible agents exhibit a run-and-tumble type motion characteristic of some bacteria [12, 52, 102, 109].

By assumption, the average length of the runs, η , is equal for all agents, irrespective of their speeds.

Hence, an agent moves in a direction θ_i which changes to a new direction $\theta'_i \sim \mathcal{U}(0, 2\pi)$, with probability $f_i \Delta t + o(\Delta t)$ in a small interval of length Δt . The new direction is chosen independently from the previous one. An agent covers on average a distance $\eta = s_i / f_i$ before changing directions. For a fixed η , agents with slower speed should have smaller frequency of direction change whereas agents with faster speeds change direction more frequently.

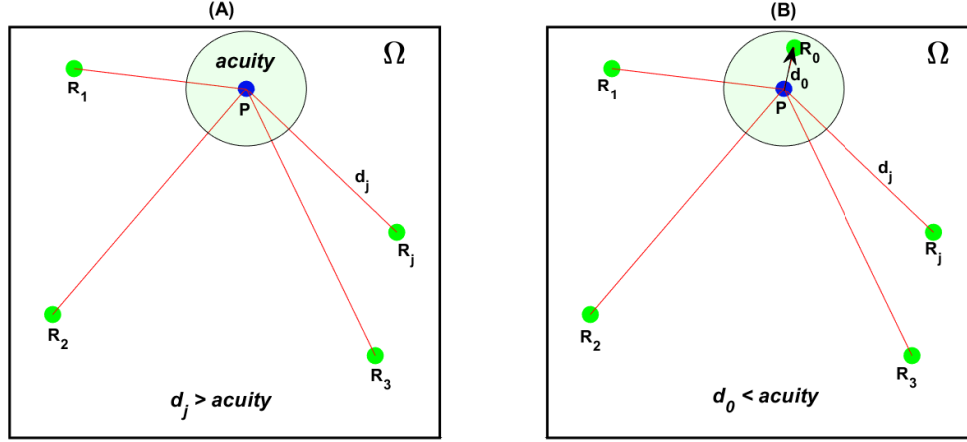


Figure 3: Movement of agents in the domain Ω where P is a foraging agent with acuity ' a ', and $R_1, \dots, R_j$ are resources. The light green circle represents the region in which an agent can 'see' a resource; the length of the red line gives the distance, d_j , between the agent and j^{th} resource. **(A)** Since $d_j > a$, agent P cannot 'see' any resource and hence moves in a direction that has been assigned uniformly and at random, and panel **(B)** since $d_0 < a$, the agent can see resource R_0 , and moves towards it.

Although this model approximately describes the movement of some bacteria [44], we do not aim to model the movement of any particular type of organism. The assumption about how agents move can be easily adjusted to produce foraging strategies more similar to those of other species. Since typical mechanisms of agents' foraging strategies are greatly influenced by the local environmental conditions like density and distribution of resources [78], we can adjust η and f_i or the rules according which an agent moves to mimic other foraging behaviors.

To simulate this type of motion, we discretize time into increments of size Δt , and define the position of agent i recursively as

$$P_i(t + \Delta t) = P_i(t) + s_i \cdot (\cos \theta_i(t), \sin \theta_i(t)) \Delta t \quad (8)$$

If no resources are visible to the agent i , then $\theta_i(t + 1) = \theta_i(t)$ with probability $1 - f_i \Delta t$. With probability $f_i \Delta t$ a new direction is drawn from the uniform distribution, $\theta_i(t + 1) \sim \mathcal{U}(0, 2\pi)$ independently from the previous direction.

If a resource is visible, the agent moves towards the resource along the straight line that connects the position of the two. Thus, the position of the agent is still updated using Eq. (8), but with $\theta(t)$ being the angle pointing from the agent to the resource. This movement is *ballistic*. We assume that the agent stops at the resource location, and thus use an update $P_i(t + \Delta t) = R_j$ when the resource is reached. When an agent finds a resource at location R_j , it consumes the resource which therefore disappears from the domain, Ω . We chose the increments Δt to be sufficiently small so that the simulation outcomes do not depend on increment size (See Subsection 4.1).

Algorithm 1 Single agent foraging

Input: speed(s_1), width (b) of Ω , acuity (a_1), resource density, time (t), Δt , run distance (η).

Output: Resource collected F_t

Initialize:

Agent's location $P_1(x, y) \in (0, b) \times (0, b)$, resources location $R_1(x, y), R_2(x, y), \dots, R_m(x, y) \in (0, b) \times (0, b)$, choose a random angle $\theta \sim \mathcal{U}(0, 2\pi)$, iteration(i) = 1.

while $k < iteration$ **do**

$D_1 = (d(P_1, R_1), d(P_1, R_2), \dots, d(P_1, R_m))$

if $\min_j \{d_j\} \leq a_1$ **then**

move towards j^{th} resource so that new position is $P_1(t + \Delta t) = P_1(t) + s_1 \left(\frac{P_1(t) - R_j}{|P_1(t) - R_j|} \right) \Delta t$

If agent's location resource location; move up to the resource location only, and **Update:**

$F_{t+\Delta t} = F_t + 1$; sample a new direction $\theta^* \sim \mathcal{U}(0, 2\pi)$ and let $\theta = \theta^*$

else

new position: $P_1(t + \Delta t) = P_1(t) + s_1 \cdot (\cos \theta(t), \sin \theta(t)) \Delta t$

generate a random number $r \sim \mathcal{U}(0, 1)$

If $r < f_1 \cdot \Delta t$; sample a new direction $\theta^* \sim \mathcal{U}(0, 2\pi)$ and let $\theta = \theta^*$

2.3 Single Agent Foraging

We first examine the impact of the different attributes on the foraging success of a single agent. In this section we also discuss some details of the numerical implementation of the model.

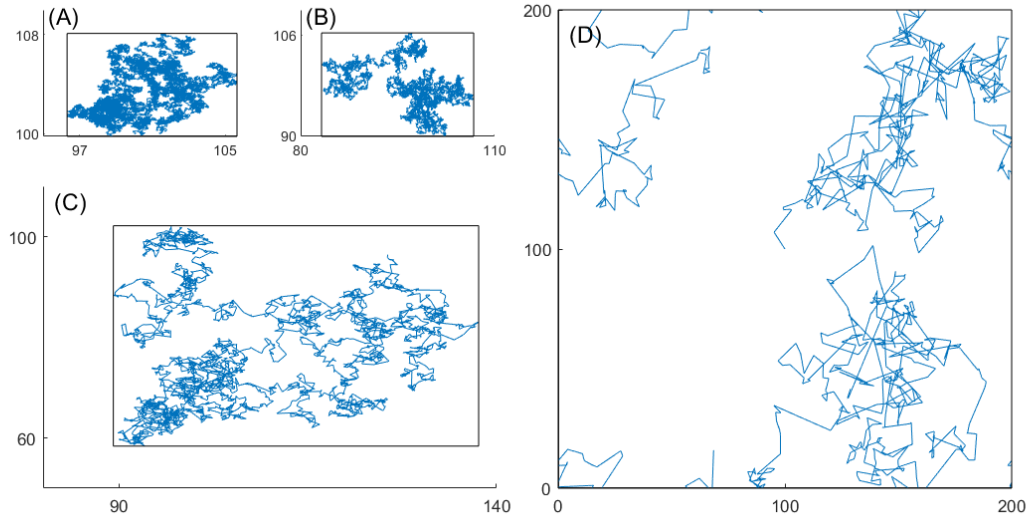


Figure 4: Rectangular parts of the foraging space defined by the maximum displacement from an initial position are shown along with the path of a single agent foraging on a 200×200 domain, with speed $s = 1$, total simulation time of 500 units, and $\Delta t = 0.1$. Here the average distance between changes in motion direction, η , was **(A)** $\eta = 0.5$, **(B)** $\eta = 1$, **(c)** $\eta = 5$ and **(D)** $\eta = 20$. For a fixed time realization when the average run distance η is small agents explore a smaller area of the domain.

When the average distance between turns, η is small an agent changes direction frequently, and thus explores a limited area. Figure 4 suggests that the area an agent can explore increases with η so that an agent can forage more effectively [48]. We generally keep the run distance η larger than the expected distance between an agent and its nearest resource to ensure effective exploration.

In the case of a single agent, or, more generally, when agents do not interact strongly, we will approximate the resource collection rate as a function of the agent's speed and acuity. The resource collection rate translates directly into the rate at which the metabolic energy of the agent increases. On the other hand, we will also assume that metabolic energy is expended on movement and sensing. A higher speed and acuity will allow for a higher rate of resource collection, but will also require a greater rate of energy expenditure. Thus even in the absence of interactions with other agents, we expect that there is an optimal set of attributes that allows an agent to optimize the rate of increase in metabolic energy.

Let $\delta(m, b)$ be the distance from a point to the nearest among m other points placed uniformly, and independently at random in the domain Ω . Also, let $\bar{\delta}(m, b)$ be the *average* minimum distance from a location chosen uniformly and at random in the domain to the closest of m other points placed uniformly and independently at random inside a square of side length¹⁰ b . In the single agent, single resource case, $\bar{\delta}(1, b)$ is the average distance between an agent and a resource placed uniformly at random in the domain, Ω . Moreover, the minimum distance $\delta(m, b)$ between an agent and the closest of m resources in the single agent-multiple resources environment is a non-negative random variable with range $[0, \sqrt{2}b]$. In other words, we can think of $\delta(m, b)$ as the random variable $\delta(m, b): \Omega \rightarrow [0, \sqrt{2}b]$, that maps the location $u \in \Omega$ to the distance of the nearest resource. If a_1 is the acuity of the agent, *Markov's Inequality* yields;

$$Pr(\delta(m, b) \geq a_1) \leq \frac{\mathbb{E}(\delta(m, b))}{a_1} = \frac{\bar{\delta}(m, b)}{a_1}. \quad (9)$$

The probability that the distance to the nearest resource is larger than the agent's acuity is thus bounded above by a term proportional to the inverse of the acuity of an agent. This is a very conservative estimate in our case, as we will see below.

When $\bar{\delta}(m, b) \ll a_1$ (larger acuity), an agent is likely to see at least one resource at any time. According to the movement rules we described, we expect the agents to be moving towards a resource most of the time, rather than forage randomly. The expected time to reach the nearest resource equals $\bar{\delta}(m, b)/s_1$ and so the expected rate of encounters with resources equals $s_1/\bar{\delta}(m, b)$. On the other hand when $\bar{\delta}(m, b) \gg a_1$ (smaller acuity or fewer resources), an agent may not see a resource for a considerable time, and will thus have to forage, *i.e.* head in a random direction and explore. In this case the expected rate of finding a resource is $\mathcal{P} \cdot s_1/\bar{\delta}(m, b)$ where $\mathcal{P}$ is the probability of selecting the correct direction towards the resource which is given by the likelihood of choosing a correct direction which we explain and compute in Eq. (13) below. In this argument we assumed that the average run distance is larger than the average minimum distance between

¹⁰note that this is also the average distance between one of $m + 1$ points chosen in the same way and its nearest neighbor.

agent to the resources.

2.3.1 Single Agent in a Fixed Resource Density Environment

As we explained in Subsection 2.1 resources can be generated either with a *fixed resource replenishment rate* or with a *fixed resource density*. We start by considering the process of resource replenishment with a *fixed resource density*. To approximate the resource collection rate we need to estimate the following two properties of points that follow a spatial Poisson process. These will allow us to estimate the average distance between an agent and the closest resource and hence the rate at which the resources are collected average distances between an agent and resources.

(a) *Average distance between two points chosen uniformly and at random in a square, $\bar{\delta}(1, b)$*

Let Ω be a square from $\mathbb{R}^2$ and assume that we chose two points (x_1, y_1) and (x_2, y_2) independently and uniformly from Ω . The *Euclidean distance* between these two points is $\|x - y\| = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$.

Let b be the length of a side of the square Ω , then the average distance between two points is the expected distance which is the quadruple integral of the *Euclidean distance*, given by;

$$\bar{\delta}(1, b) := \mathbb{E}[\|x - y\|] = \frac{1}{b^4} \int_0^b \int_0^b \int_0^b \int_0^b \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2} dx_1 dx_2 dy_1 dy_2 \quad (10)$$

Now, we consider two random variables u and v drawn from the standard uniform distribution on $[0, b]^2$. To find the distribution of the difference between the variables, *i.e.* $|u - v|$, we need to find the probability density for $|u - v| = w$. For two independent random variables, each having the continuous uniform distribution on the unit interval, their sum follows a *triangular distribution*, and w has a probability density function of $2(1 - w)$ with support $0 \leq w \leq 1$ [60]. The integral in Eq. (10) can be expressed in terms of the distribution of $|x_2 - x_1|$ by x and for $|y_2 - y_1|$ by y .

For a unit square, it follows that $\bar{\delta}(1, 1) = 4 \int_0^1 \int_0^1 \sqrt{(x^2 + y^2)}(1 - x)(1 - y) dx dy = \frac{(2 + \sqrt{2} + 5 \ln(\sqrt{2} + 1))}{15}$.

We can generalise this average distance for a unit square to the square of any side length b ;

$$\bar{\delta}(1, b) = \frac{(2+\sqrt{2}+5\ln(\sqrt{2}+1))}{15} \cdot b.$$

Once we find the distance between two uniformly and independently distributed points inside a square, we can use this as the expected distance between a foraging agent and a resource inside a square shaped foraging domain. This computation ignores the periodic boundary conditions, however if the domain is large the error thus introduced will be small.

- (b) *Average minimal distance between an agent and the closest of m resources chosen uniformly and at random in a square, $\bar{\delta}(m, b)$.*

We estimate the expected minimum distance from a point to one of m independently and uniformly chosen points inside a square. We start with a unit square, and let $R_1, R_2, \dots, R_m$ be the positions of m points placed uniformly and independently on the unit square. This gives the resource density, $\rho_R = m/|\Omega|$. Since the points are chosen uniformly and independently, the distribution of points in small bounded regions inside the square is approximately a *spatial Poisson point process* [69]. Let $\bar{B}_r$ be an arbitrary closed disc of radius r with area πr^2 . For a small disk contained completely inside the domain Ω , the number of points inside the disc follows a *Poisson distribution*.

Now for an additional point, P , representing the foraging agent independently placed inside the unit square, we define $V = \{\min_j |P - R_j| : P \text{ is a foraging agent}\}$ be the distance to the nearest resource. The distance from P to its nearest point inside a square follows an exponential distribution and for large m , this distribution asymptotically approaches the *Rayleigh distribution* [50]. Hence, the probability density function of the distance from P to its nearest point can be approximated in the form of $f_V(r) = 2\pi r m \exp(-\pi r^2 m)$. The expected value of V , $\bar{\delta}(m, 1) = \mathbb{E}[V]$ is given by;

$$\bar{\delta}(m, 1) \approx \int_0^\infty r f_V(r) dr = \int_0^\infty 2\pi m r^2 e^{-\pi r^2 m} dr = \int_0^\infty e^{-\pi r^2 m} dr = \frac{1}{2\sqrt{m}} \quad (11)$$

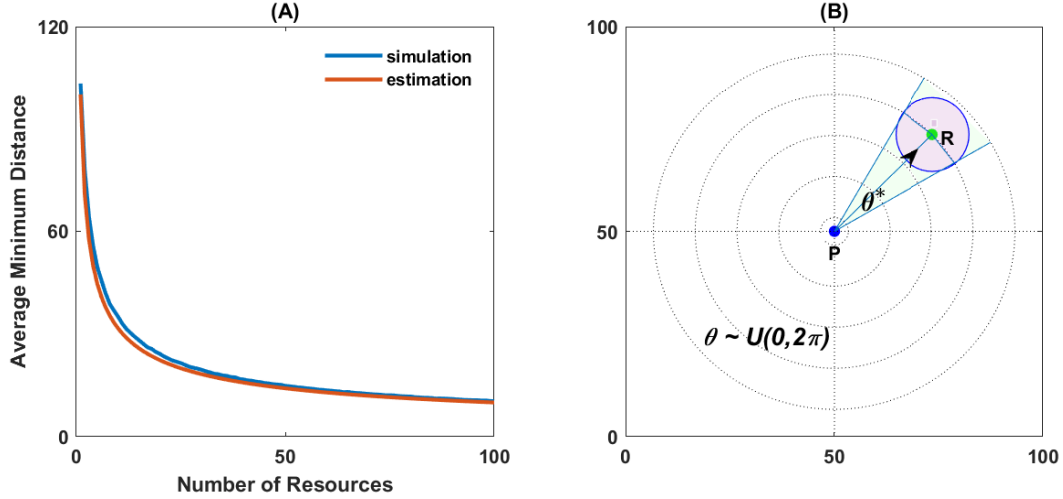


Figure 5: **(A)** The average minimum distance between m -resources and a foraging agent, and **(B)** when an agent's acuity is smaller than the average distance between the agent and the closest resource, the agent moves towards the nearest resource R with probability $\frac{\arcsin\{\frac{a_1}{\bar{\delta}(m,b)}\}}{\pi}$.

This generalizes to an estimate on a square of any side length b ,

$$\bar{\delta}(m, b) \approx \int_0^\infty e^{-\pi r^2 \frac{m}{|A|}} dr = \frac{1}{2\sqrt{\frac{m}{|A|}}} = \frac{b}{2\sqrt{m}} \quad (12)$$

The estimate of the minimum distances between an agent and one of m resources in Eq. (12) agrees well with numerically obtained values (See Fig. 5A).

Eq. (9) suggests that if the acuity of an agent exceeds the average distance to the closest resource, then most of the time there is at least one resource that is visible to the agent. If no resources are visible to the agent, the probability of the agent obtaining the nearest resource depends on the agent's direction of movement. Suppose that an agent is about to choose a new movement direction. We can approximate the probability that the agent selects a direction that will bring it within the acuity radius, a_1 of the nearest resource, R (See Fig. 5B).

A single foraging agent chooses a random angle and moves in the same direction until it either observes a resource, or changes direction again. We can estimate the resource collection rate by

considering two cases:

1. If the minimum distance to the closest resource is smaller than the agent's acuity, $a_1 > \bar{\delta}(m, b)$, then the agent is likely to see at least one resource most of the time. Hence, the rate at which the agent will gather resources can be approximated by the average time it takes the agent to move between a resource, and its nearest neighbor, $\frac{s_1}{\bar{\delta}(m, b)}$.
2. If the agent's acuity is smaller than the expected distance to the nearest resource, $\bar{\delta}(m, b) > a_1$, an agent placed at random in the domain is likely not to have a resource within its sight, and will hence be forced to forage. To find the expected rate of encounter with the nearest resource at location R_j , we need to find the range of directions an agent has to take so that it will have the resource at R_j within its sight before it chooses a new random direction. Let θ^* be the angle between two tangents drawn from the agent's position on the circular disc around R_j of radius a_1 . Then θ^* is the range of directions an agent can take upon turning so that it will detect the resource while moving along this direction. The agent will encounter the resource, unless it happens to turn beforehand (this is again unlikely if we assume that run distances are sufficiently large). Fig. 5B, shows that $\sin \frac{\theta^*}{2} = \frac{a_1}{\bar{\delta}(m, b)}$ which gives us $\theta^* = 2 \arcsin \frac{a_1}{\bar{\delta}(m, b)}$.

The estimate of the probability that an agent turns in the right direction to spot the nearest resource when turning, is

$$\begin{aligned} \mathcal{P}_{est} = \frac{\mathbb{E}[\theta^*]}{2\pi} &= \frac{\mathbb{E}\left[2 \arcsin \frac{a_1}{\bar{\delta}(m, b)}\right]}{2\pi} \\ &= \frac{1}{\pi} \mathbb{E}\left[\arcsin \frac{a_1}{\bar{\delta}(m, b)}\right] \end{aligned}$$

where $\bar{\delta}(m, b)$ is the minimum distance between an agent to m resources in its neighborhood.

The second estimate relies on a couple assumptions: The distance between turns needs to be large enough so that the probability that the agent turns before having the resource within sight is small. We could improve the estimate slightly by taking accounting for the probability that the

agent does not turn during the trip to the resource, but we found that such a correction does not have a large impact. Also, we neglect the probability that the agent will see the second farthest, third farthest, or any of the farther resources before turning again. This is justified if the turning rate is not too small, and the resources are not too dense. Indeed, if resource density is high, the first estimate is likely to hold, since agents will have a resource in view most of the time.

When m is large and when we repeat the same process for many independent trials, the average value of minimum distance between an agent will converge to the expected value, and since $f(x) = \arcsin x$ is a non-negative, strictly increasing, convex function in $(0, 1)$, using *Jensen's inequality* twice, we have

$$\begin{aligned}
\mathcal{P}_{est} &\geq \frac{1}{\pi} \arcsin \left\{ \mathbb{E} \left[\frac{a_1}{\delta(m, b)} \right] \right\} \\
&= \frac{1}{\pi} \arcsin \left\{ a_1 \mathbb{E} \left[\frac{1}{\delta(m, b)} \right] \right\} \\
&\geq \frac{1}{\pi} \arcsin \left\{ a_1 \frac{1}{\mathbb{E}[\delta(m, b)]} \right\} \\
&= \frac{1}{\pi} \arcsin \left\{ \frac{a_1}{\bar{\delta}(m, b)} \right\}
\end{aligned}$$

The right hand side in this inequality is the lower bound for the probability to select the correct direction, which gives us an estimate of the lower bound for the resource collection rate when the acuity of an agent is small, or when resources are few (Fig. 6). It follows from Subsection 2.3 that the rate of encounter with the nearest resource is therefore $\mathcal{P} \frac{s_1}{\delta(m, b)}$, where the lower bound for the probability is estimated by $\mathcal{P}_{est} \geq \frac{1}{\pi} \arcsin \left\{ \frac{a_1}{\bar{\delta}(m, b)} \right\}$.

Summarizing, the rate of encounters of a single agent, r_1 , with resources can be bounded by the two estimates,

$$r_1 \geq \frac{1}{\pi} \arcsin \left\{ \frac{a_1}{\bar{\delta}(m, b)} \right\} \cdot \frac{s_1}{\bar{\delta}(m, b)} \quad \text{for } a_1 < \bar{\delta}(m, b) \quad (13a)$$

$$r_1 \leq \frac{s_1}{\bar{\delta}(m, b)} \quad \text{for } a_1 > \bar{\delta}(m, b). \quad (13b)$$

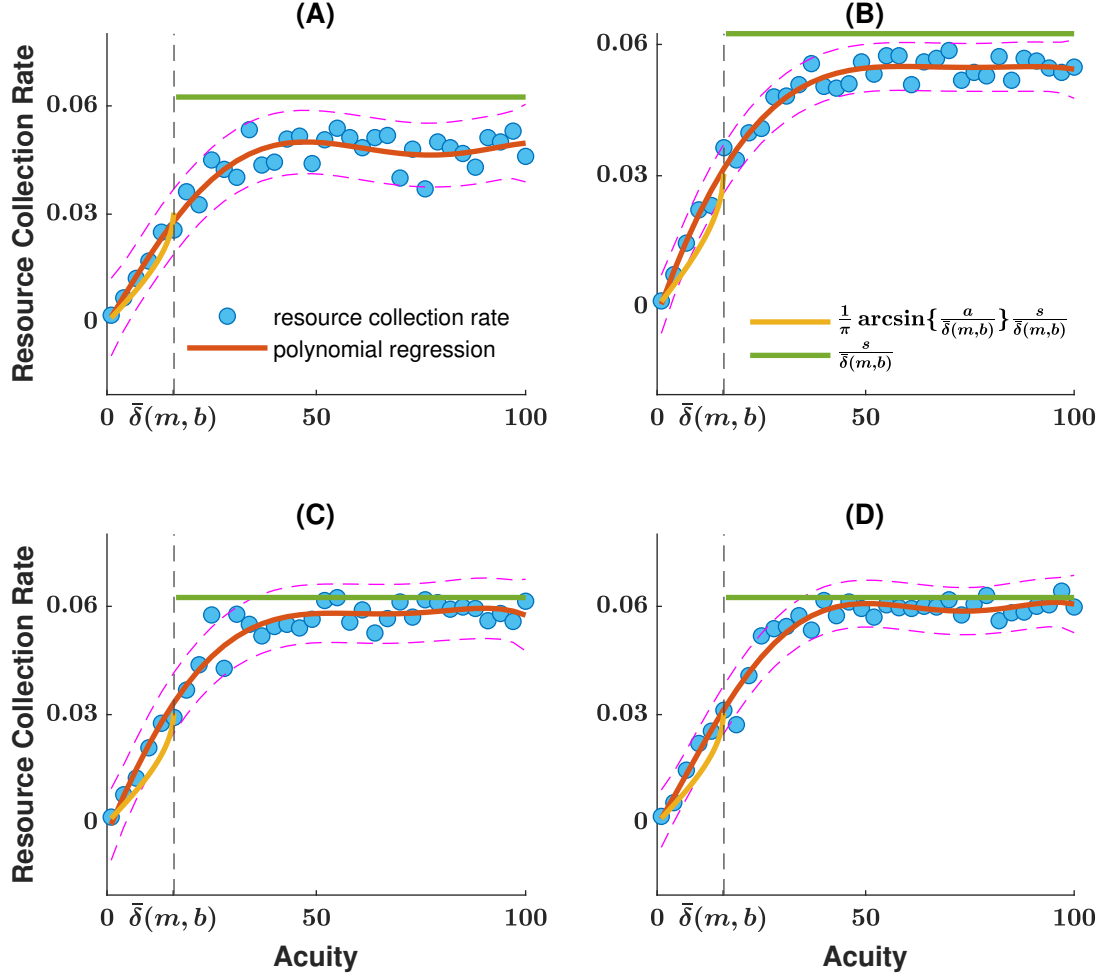


Figure 6: The resource collection rate for a single agent can be approximated both when i) the acuity, a_1 satisfies, $a_1 < \bar{\delta}(m, b)$ and ii) when $a_1 > \bar{\delta}(m, b)$. When $a_1 < \bar{\delta}(m, b)$, this approximation gives a lower bound, and when $a_1 > \bar{\delta}(m, b)$ the approximation provides an upper bounds for the resource collection rate. Foraging simulations were performed on domains of different sizes: **(A)** $|\Omega| = 200 \times 200$, **(B)** $|\Omega| = 400 \times 400$, **(C)** $|\Omega| = 600 \times 600$, and **(D)** $|\Omega| = 800 \times 800$ space, speed = 1; resource density (ρ) = 1/1000 per unit area.

When we estimate the resource collection rate by assuming that $a_1 < \bar{\delta}(m, b)$, this neglects the possibility that even if this condition holds sometimes a resources may be inside the acuity range of the agent. Moreover, the foraging space we consider is a finite square with periodic boundary conditions. When approximating the average minimum distance between an agent and a resources, we assumed that the number of resources is high and the distances between agent to resources follows a generalized exponential distribution. These assumptions limit our approximation to regimes where *boundary effects* are not significant.

The lower bound, Eq. (13a), we obtained when $a_1 < \bar{\delta}(m, b)$ agrees well with the resource collection rate computed from simulations (See Fig. 6 and 7). When $a_1 > \bar{\delta}(m, b)$ the upper bound in the same equation again agrees well with the numerically obtained resource collection rate (See Fig. 6). Note that the values of the two functions defining the bounds in Eq. (13) do not agree at $a_1 = \bar{\delta}(m, b)$. This is also where the assumptions we made in the derivation of these bounds fail, and neither expression provides a good estimate of the resource collection rate when compared to empirical results.

Resource availability near a single foraging agent changes only due to its own activity. Similarly, when agent density is low, we can assume that interactions between agents are rare and can be neglected. In such cases, we can describe the resource collection rate as a function of *speed*, *acuity* and $\bar{\delta}(m, b)$, as we have done here.

Below we show how to obtain an estimate that bounds the resource collection rate, and use this estimate to understand the dynamics of the population of foraging agents in Section 3.

2.3.2 Single Agent in a Fixed Resource Replenishment Rate Environment

In another model of resource generation, we assume that resources appear at a *fixed rate*, but that the number of resources in the domain can fluctuate as they are consumed and regenerated. We let λ be the number of resources that appear per unit area per unit time, and assume that this rate is independent of the action of the agent or agents. If the agent does not consume any resources, the expected resource number grows with time t as $\lambda \cdot |\Omega| \cdot t$. The expected distance from an agent to the

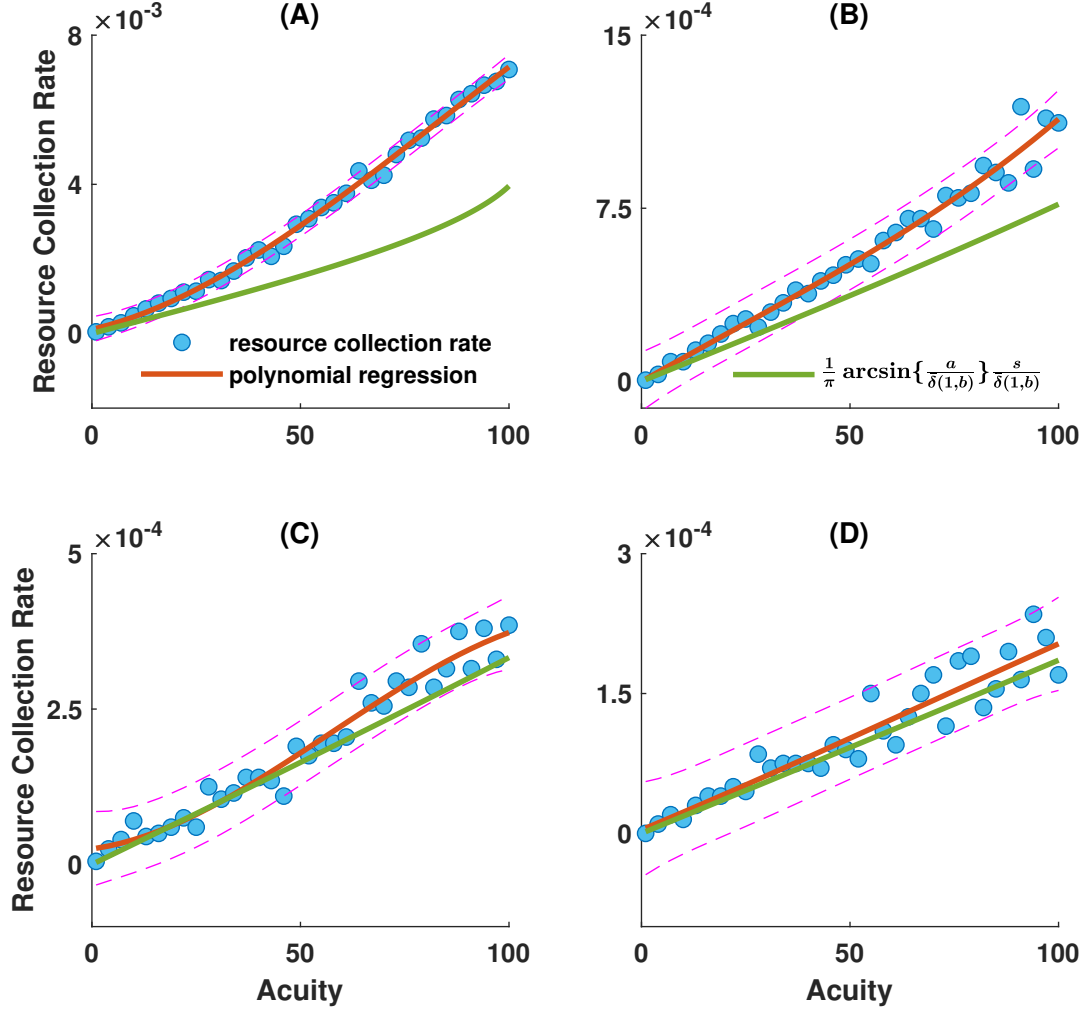


Figure 7: The empirically estimated resource collection rate and its estimate given by Eq. (13a) on domains of different sizes: (A) 200×200 , (B) 400×400 , (C) 600×600 , and (D) 800×800 spaces with single agent and single resource, resource density (ρ) = $1/|\Omega|$. This estimate gives the lower bound for the rates. When acuity is smaller than the expected distance between an agent and a resource, speed = 1, time = 200000.

nearest resource decreases as more resources are accumulated, and equals $\bar{\delta}(m, b) \approx \frac{b}{2\sqrt{\lambda|\Omega|t}} = \frac{1}{2\sqrt{\lambda t}}$ (See Eq. (12)) in the absence of resource consumption.

When this expected distance to the nearest resource becomes smaller than agent's acuity, agents see a resource most of the time. Assuming that we start with an empty domain with a single agent, the time for this condition to be satisfied is approximately $t > \frac{b^2}{4a_1^2\lambda|\Omega|} = \frac{1}{4a_1^2\lambda}$. Indeed, the acuity of an agent, a_1 , will exceed the expected distance to the nearest resource, $a_1 > \bar{\delta}(m, b)$ when $a_1 > \frac{b}{2\sqrt{\lambda|\Omega|t}} = \frac{1}{2\sqrt{\lambda t}}$, giving the previously mentioned estimate.

If agents are foraging and consuming resources and a resource is always visible, then the expected time to reach the nearest resource when it is visible now becomes $\frac{\bar{\delta}(m, b)}{s_1}$. Hence, the rate at which agents consume resources when the expected distance to the nearest resource is $\bar{\delta}(m, b)$ is then $s_1/\bar{\delta}(m, b)$. In equilibrium, the resource collection rate equals the resource replenishment rate and hence,

$$r_1 = \frac{s_1}{\bar{\delta}(m, b)} = \lambda|\Omega|. \quad (14)$$

To verify this prediction, we simulated a single foraging agent in a fixed resource replenishment rate environment. We assumed the agent has speed 10 and acuity 10 and simulated environments with different resource replenishment rates. We computed the average distance between an agent and its nearest resource, the resource collection rate and the number of resource available in the domain at each instant of time. At equilibrium, the estimated resource collection rate, $s_1/\bar{\delta}(m, b)$, equals the exact resource collection rate which is also equal to resource replenishment rate (See Fig. 8A and 8B). The variability in the resource collection rate obtained using Eq. (14) and shown in Fig. 8B is due to the fact that the number of available resource in the estimate was obtained from simulations to compute the average minimum distances.

At equilibrium, when the resource collection rate equals the resource replenishment rate, we can also estimate the resource density in the domain (See Fig. 8C and 8D). If $\bar{\delta}(m, b)$ is the expected minimum distance between agent to resources at equilibrium, then $\frac{s_1}{\bar{\delta}(m, b)} \approx \lambda|\Omega|$, which implies $\bar{\delta}(m, b) \approx \frac{s_1}{\lambda|\Omega|}$, *i.e.* $\frac{b}{2\sqrt{m}} \approx \frac{s_1}{\lambda|\Omega|}$. We therefore see that $m \approx \left(\frac{\lambda|\Omega|b}{2s_1}\right)^2$, where m is the current

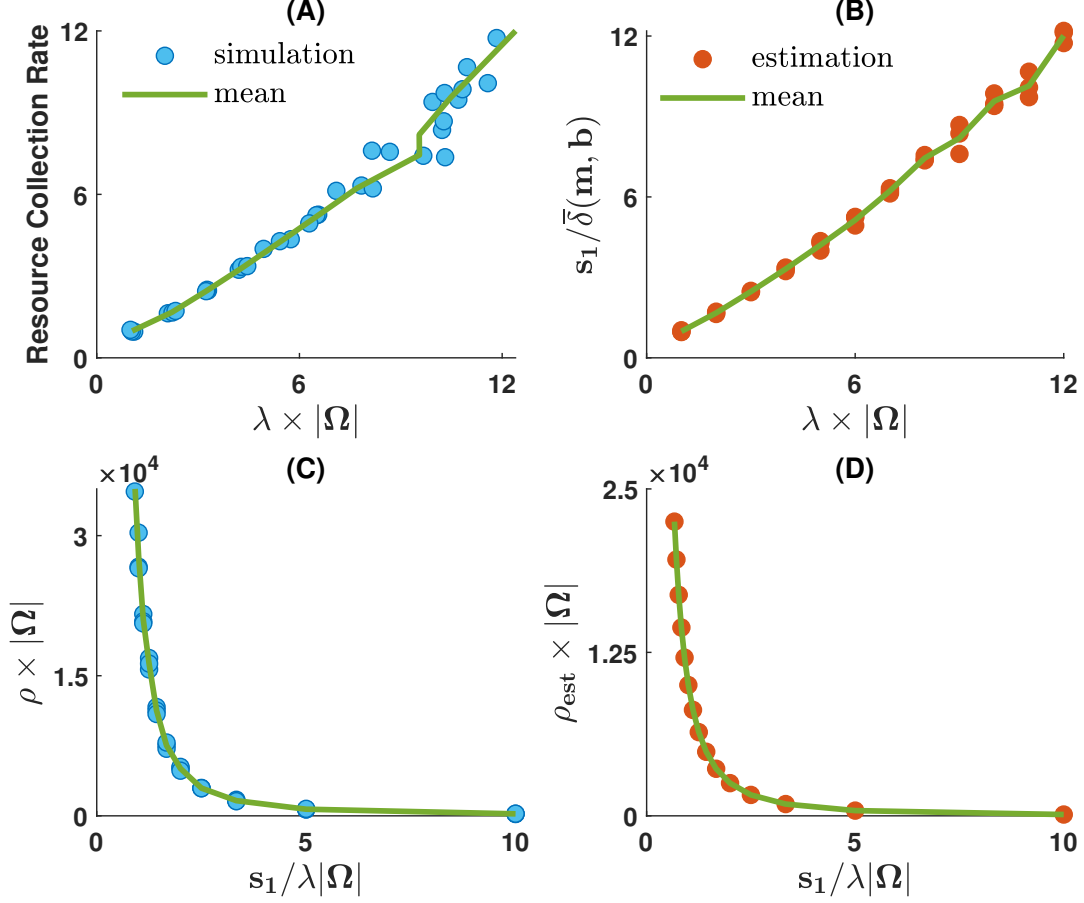


Figure 8: The resource replenishment rate, resource collection rate and resource density in fixed resource replenishment environment with single agent simulations after equilibrium is reached: **(A)** resource collection rate in a single foraging agent simulation, **(B)** resource collection rate estimated as $s_1/\bar{\delta}(m, b)$, **(C)** resources available for foraging after equilibrium, and **(D)** estimation of available resources ($\rho \times |\Omega|$) as $\left(\frac{\lambda|\Omega|b}{2s_1}\right)^2$. Simulations were performed on a domain of size 200×200 , with a single agent with speed, $s_1 = 10$, and acuity $a_1 = 10$. The resource replenishment rate in the entire domain was set to $\lambda|\Omega| = 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12$ per unit time. The simulation time was set to 50000 units.

number of resources in the domain.

The estimate of $\bar{\delta}(m, b)$ given by Eq. (12) has limitations which restrict the applicability of the estimate of the resource collection rate given in terms of the upper and lower bounds in Eq. (13). First, the domain, Ω , has periodic boundary conditions. For simplicity we assumed a square domain to estimate the expected distance between the nearest resource and an agent. Second, the estimate of the expected minimum distances from an agent to the closest of m resource, $\bar{\delta}(m, b)$, is an approximation that improves with resource number, m . We thus obtain a good agreement between the estimated resource collection rate and simulation results with longer simulation times and larger domains. When an agent detects a resource and moves towards it, the position of an agent becomes dependent on previous positions resulting in a directed motion towards the resource (not *i.i.d.* anymore). Hence, the average minimum distance from the agent to the nearest among m resources available in the simulation cannot be used to estimate the resource collection rate. In this case, we can numerically estimate the average minimum distance from a randomly placed agent and a resource by the expected minimum distance Eq. (12).

2.4 Multi-Agent Foraging

We next turn to the case of multiple agents foraging in the domain Ω defined in Subsection 2.1. We again assume that the resource number is fixed, or replenished at a fixed rate. These resources are generated in the domain with homogeneous or clustered patterns. Multiple foraging agents are characterized with phenotype vectors $\xi_k = \{s_k, a_k\}$, where s_k is the speed and a_k is the acuity of agent k , with $1 \leq k \leq n$ and n is the number of agents. A phenotype vector can be assigned by independently sampling attribute values from some distribution for each agent. In addition, a linear combination of the attributes could be constrained by some metabolic limitation¹¹. We denote the initial position of the k^{th} agent by $P_k(0)$ and the location of j^{th} resource by R_j where $1 \leq j \leq m$ (m resources). However, as resources are replenished and consumed, so R_j and m change with time in the simulation. To keep the notation simple, we suppress this dependence on time.

¹¹later we will assume that the phenotypes can be changed through an evolutionary process, and show that such constraints arise through selection.

When the simulation starts, multiple foraging agents characterized by phenotype vectors $\xi_k = \{s_k, a_k\}$ are introduced independently and uniformly in the domain at positions $P_1(0), P_2(0), \dots, P_n(0)$. We assign at the same time the first set of resources which are also distributed uniformly and independently on locations whose positions are given by R_j where $1 \leq j \leq m$ (m resources). The number of resources that will appear later in the simulation is determined by resource density ρ , in case we keep the resource density fixed, or by the resource replenishment rate λ in which case an average of $m = \lambda|\Omega| \cdot t$ resources appear in the domain over an interval of length t .

Let $D(t)$ be the initial distance matrix ($m \times n$) between each agent to each resource at time t ,

$$D(t) = \begin{bmatrix} d_{11}(t) & d_{12}(t) & \dots & d_{1n}(t) \\ d_{21}(t) & d_{22}(t) & \dots & d_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ d_{m1}(t) & d_{m2}(t) & \dots & d_{mn}(t) \end{bmatrix}.$$

If the resource number is not fixed then the dimension of the matrix D changes as simulation progresses since resources are being consumed and new resources appear in the domain.

In simulations of the ABM model we update the state of the population at discrete time increments, Δt . To simulate multi-agent foraging, we choose Δt in such a way that any further finer subdivision of time does not result in appreciable differences in the dynamics. If $d_{kj}(t) = 0$ (the k^{th} agent is exactly on the top of j^{th} resource), we update the location of agent to the resource location and assume that the resource is consumed. If $d_{kj}(t) \leq a_k$ (resource R_j is visible to agent A_k), the agent A_k moves towards the resource along the line joining the agent location and resource location covering a distance $s_k \cdot \Delta t$ distance during a time increment Δt . If the movement causes the agent to overshoot the resource location, we assumed that the agent stops exactly at the resource location. The average overshoot depends on Δt , but we chose a sufficiently small increment so that resource encounters occur on only few time-steps, and this assumption does not affect the outcome of the simulations. The agent A_k moves according to the same rules as described in the single agent case

and the position of agent i is updated recursively as;

$$P_k(t + \Delta t) = P_k(t) + s_k \cdot (\cos \theta_k(t), \sin \theta_k(t)) \Delta t. \quad (15)$$

where $\theta_k \in \mathcal{U}(0, 2\pi)$. As described earlier, if no resource is visible to the agent, on average this movement direction changes after covering a run-distance η . Hence a foraging agent who does not observe a resource changes direction at rate $f_k = s_k/\eta$, and this rate can differ between agents.

With multiple foraging agents, when agent density is low, we can assume that interactions between agents are rare and can be neglected. In such cases, we can describe the resource collection rate as a function of speed, acuity and the average distance to the nearest resource, $\bar{\delta}(m, b)$ as in the previous subsection. However when the number of agents is larger, and their density increases, interactions between agents also increase. They often ‘compete’ for the same resource which may become visible to multiple agents at the same time¹². Thus, the presence of other agents can affect the foraging ability of other agents by changing the resource availability near it. Therefore, unlike in the case of a single agent, interactions between agents can affect their ability to forage.

2.4.1 Synchronized Movement of Multiple Agents and Under-Harvesting

In simulations with agents that share similar attributes, we observed the emergence of synchronous movement of a group of agents foraging in a domain, Ω . Agents with similar speeds and large acuities will often follow the same path after reaching a resource in the same time increment, or getting close to the same resource. The emergence of synchronisation is due in part to time discretization in simulations: When two agents with similar speed reach the same resource within a time Δt , they split the resource and end up at the same location at the end of the time-step. If resources are densely distributed, both agents will then continue to the *same* closest visible resource. Since their speeds are similar, they can again reach the resource within the same time increment. They can thus move identically for a long time. In these cases, synchrony is a numerical

¹²When two or more agents arrive at a resource at the same time-step, they share it equally. In general, sharing of resources happens rarely since the time increments are small. However, it does happen with a high resource replenishment rate in non-evolving birth death simulations. We discuss these cases in Subsections 2.4.1 and 2.5

artefact due to the discretization of time.

However, the tendency to synchronize movements is not only due to discretization errors. In simulations, as Δt approaches zero, the chance of two agents reaching the same resource at the same time increment also goes to 0, unless they start at the same distance from a resource, and move at equal speeds. However, we observed that decreasing Δt does not prevent agents from synchronizing. This synchronous behavior is more prevalent when resource density is high. The reason is that two or more nearby agents with the same or similar speeds, and large acuities will tend to converge onto the same nearest resource. This will cause the distance between them to decrease as they approach the resource, until one of them reaches it and consumes it. The agents now form a pack around the consumed resource, and if the next closest resource is within the acuity radius of this pack, then the pack will move on to this next resource. If the speeds of the agents in the pack are close the distance between them contracts. When more than one agent reaches a single resource, they occupy same location and now they move to the another resource together¹³. If resource density is very high, then it becomes less likely that two nearby agents are going to have the same closest resource to start with. Similarly, if agent speeds differ, then the slower agents eventually lag behind the faster, breaking the synchrony of movement. However, when speeds are similar, the slower agents can follow the slightly faster agents for a considerable time.

Due to the contraction in distances between the agents the synchronous pattern of movements becomes difficult to break. The group of synchronously moving agents can sometimes grow until it contains most of the population. This pattern leads the average resource collection to approach one resource per synchronous group per the average time to go from one resource to the next closest resource. Synchronisation thus decreases the agent's ability to collect resources, which in simulations causes resources to start accumulating due to under-harvesting.

To break such synchronous behavior we can assume that agents do not always move towards the closest resource. Rather, we assume that an agent chooses to move towards a resource within an agents' acuity range with probabilities inversely proportional to the square of the distance between

¹³We observed synchronous movements in high resource density, non-evolving birth death simulations when offspring with the same phenotypes share the same location as their parents upon birth.

the agent and the resource. This breaks synchrony, and the resource collection rate of the group of foraging agents becomes approximately the sum of the resource collection rates of individual agents,

$$\sum_n r_i = n \times \bar{r} = \lambda \cdot |\Omega|,$$

where $\bar{r}$ is average resource collection rate of an individual agent and n is the number of foraging agents.

In birth–death simulations, another main source of the synchrony is due to sharing of the location by parents and new-borns. In non–evolving population, when an offspring is produced with the same attributes as parent, it starts foraging from the same location as the parent and both of them move together towards any resources within their acuities. In high resource density environment, this creates a synchronous motion between the similar phenotypes. To break such synchronous behaviors, we assume that the new–born is not reproduced exactly at the parent’s location but around the parent location within some distance. We define the distance between the parent and the new–born at the time of birth as *dispersal distance*. We generate the dispersal distance by sampling from a bivariate normal distribution with zero mean, and fixed variance. The position of the offspring is obtained by adding the result to the parent’s location. The effect of dispersal distance is discussed in the result section.

When acuity is small or when there are few foraging agents, the group of agents can only sense resources in a small area. Similarly, when the resource density is low, the average distance between agents and the resources becomes large. In such cases, agents have to explore a larger area to gather resources, and it takes longer for the sum of resource collection rate and the resource replenishment rate to equalize.

On the other hand, when acuity is large, or when the resource density is high, the average minimum distance between resources and agents becomes small, and agents see resources most of the time. The resource collection rate again approaches $\frac{s_k}{\delta(m,b)}$ for each agent. Equilibrium is attained when the acuity satisfies $a > \bar{\delta}(n \cdot m, b) \approx \frac{b}{2\sqrt{n \cdot m}}$ where n and m are the number of agents

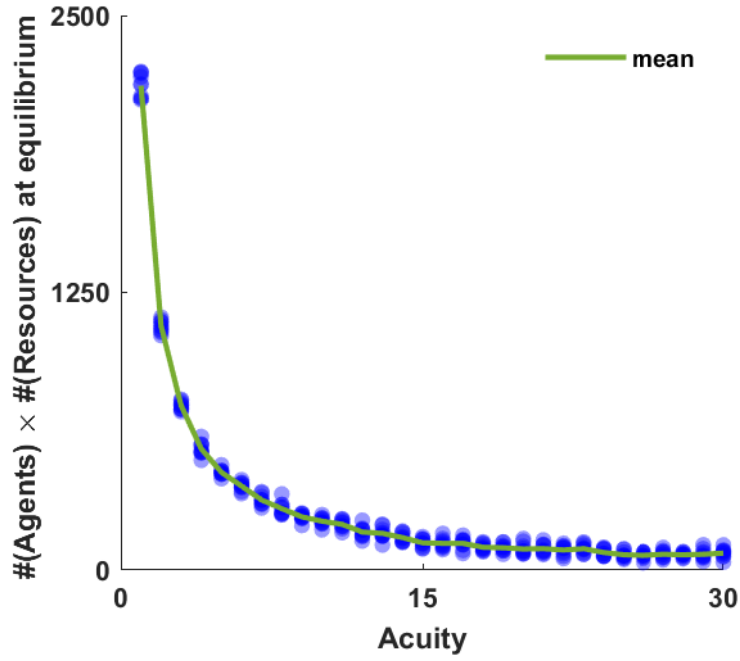


Figure 9: The product of the number of resources and number of agents at equilibrium, is inversely proportional to the acuity of agents. For each simulation, we chose acuities independently with uniform probability in $[1, 30]$, and also number of agents from $[5, 50]$ in a 200×200 domain, with replenishment rate $\lambda = 1/|\Omega|$ per unit time. Speed = 10, time = 10000.

and number of resources available in the domain respectively, which also show that the sum of resource collection rates of all agents, is equal to the resource replenishment rate. However, the time to reach this equilibrium differs for various acuities. In such cases, the product of the number of resources and number of agents at equilibrium is inversely proportional to the acuity of agents (See Fig. 9).

2.4.2 Resource Collection and Metabolic Cost of Motion

In Subsection 1.1.2, we discussed the energy expended on sensing and locomotion. The energy expended on locomotion mostly depends on the speed, body temperature and the mass of the organism. Besides speed and mass, organisms expend energy on sensing and processing sensory information. The processing of sensory information can also take a considerable amount of metabolic energy: For instance, in humans the brain is responsible for 20% of the energy used, and much

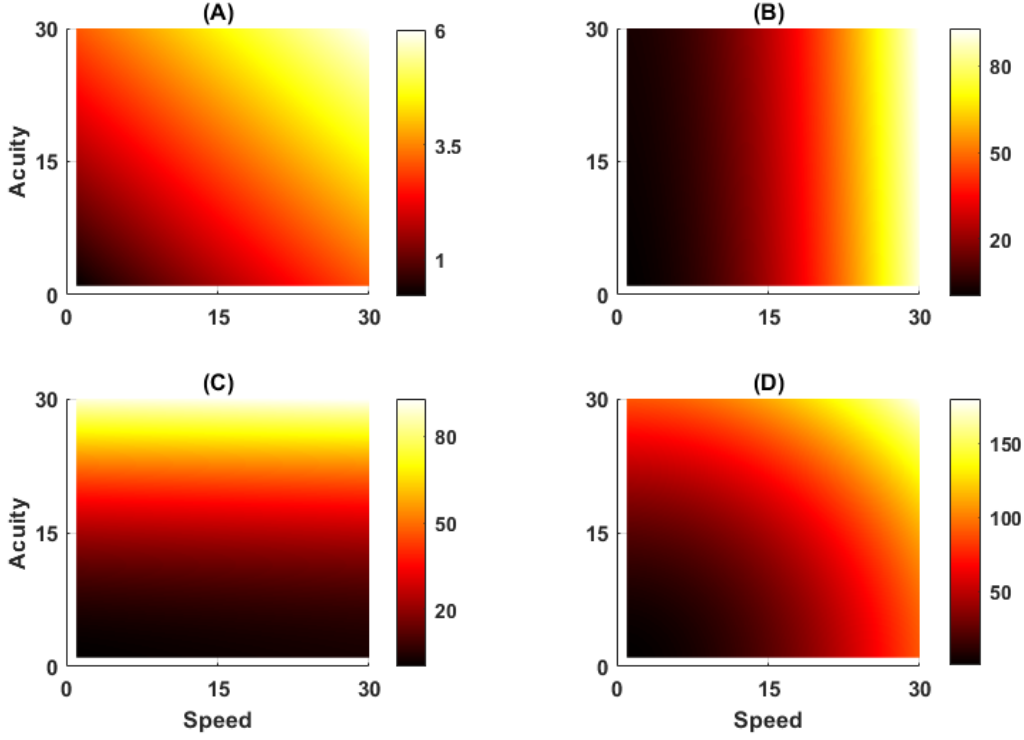


Figure 10: Metabolic cost with different cost functions: **(A)** $C = \alpha s + \beta a$, **(B)** $C = \alpha s^2 + \beta a$, **(C)** $C = \alpha s + \beta a^2$, and **(D)** $C = \alpha s^2 + \beta a^2$.

of this energy is expended on processing information arriving from the senses. Thus part of the metabolic energy is expended even in the absence of movement.

In general, the *basal metabolic rate* is affected by body temperature, and body mass [22]. In our model, we do not explicitly consider mass and resting body temperature and assume that energy expenses related to mass and resting body temperature are part of the static cost which are implicitly included in the basal metabolic cost. Here, we assume that *metabolic cost* of motion as the energy expenses to forage per unit time.

$$C(s, a) = \alpha s^\gamma + \beta a^\delta \quad (16)$$

where s , a are speed, acuity of a foraging agent, and α, β, γ and δ are non-negative constants.

Higher speeds require more energy to achieve and maintain, but also typically require larger bodies and stronger limbs which are again energetically costly [38, 39]. In aquatic and terrestrial locomotion, the total energy cost of motion per unit mass is a function of speed [3, 4, 39] and can be approximately modeled as cost proportional to s^γ where $\gamma \in [1.5, 2.8]$.

Although the energy cost necessary to maintain a given speed is relatively simple to model, the energy cost of sensory processing is difficult to measure. For instance, the visual system contains different components ranging from the eye’s retina and muscles needed for its movement, to different areas of the brain dedicated to processing visual information. Each of these components consumes energy, but in an amount that depends on the component and on the task [110]. Similarly, the metabolic cost of the neural mechanism starting from retinal neurons to the cost of transmitting, processing and decoding information is much larger than the thermodynamic¹⁴ minimum [51]. In our model, we assume that metabolic costs of sensory processing scale equally for all agents, and this cost is directly related to the ‘sharpness’ of their sense [64]. We assume that the acuity cost (sensory metabolic cost) depends linearly on the acuity, and is added to the cost of movement to determine the total metabolic expenditure of the agent so that $\gamma = 2$ and $\delta = 1$. Hence, Eq. (16) becomes:

$$C(s, a) = \alpha s^2 + \beta a \tag{17}$$

Since each resource collected provides a fixed amount of metabolic energy, agents with higher resource collection rates have more metabolic energy (a higher metabolic score) at their disposal and thus can use this energy to explore the foraging area better. Moreover, resource availability and collection rates are among the main factors which determine the ecological dynamics of populations and species [80]. Among specific phenotypes, the resource collection rate of an agent in *fixed resource replenishment rate* environments is predominantly determined by competition and the resource replenishment rate itself. Because of interactions between agents, the resource collection rate of an agent in simulations with multiple agents becomes a function of the number of agents and the resource replenishment rate. Hence, the resource collection rate of an agent is a function

¹⁴The minimum value of internal energy of a closed system at equilibrium

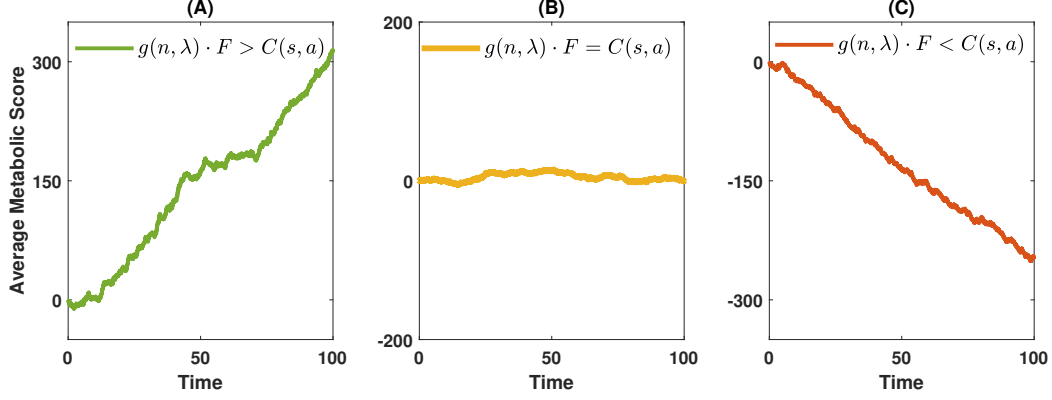


Figure 11: Average metabolic energy trajectories in simulations with different *resource replenishment* rates: when, **(A)** $g(n, \lambda) \cdot F > C(s, a)$, **(B)** $g(n, \lambda) \cdot F = C(s, a)$, and **(C)** $g(n, \lambda) \cdot F < C(s, a)$.

$\bar{r} = g(n, \lambda)$ that depends on the replenishment, and the total number of interacting agents, n .

Since, we assumed that each resource provides a fixed amount of metabolic energy, F , if $g(n, \lambda) \cdot F > C(s, a)$, agents gain metabolic energy (Fig. 11A) and, if $g(n, \lambda) \cdot F < C(s, a)$, agents lose energy (Fig. 11C), on average. At the ‘break even’ point when $g(n, \lambda) \cdot F = C(s, a)$, agents collect exactly enough resources to offset the energy expended for foraging (Fig. 11B). The agents with higher resource collection rates can regenerate metabolic energy faster and will be ‘fitter’ in the *birth-death* simulations we consider subsequently.

We next considered multi-agent foraging simulations and estimated the average resource collection rates of multiple foraging agent with different foraging strategies. Clearly, when the resource replenishment rate, λ , is fixed and many agents are competing for resource, the resource collection rate is lower than in the single agent case, and decreases with the increase in number of agents. In the next subsection, we discuss the *birth and death* of agents and the dynamics of the population.

2.5 Birth-Death and Dynamics of Population

We next assume that agents whose metabolic energy drops too low are likely to die, while those whose metabolic energy exceed that needed to sustain motion and sensing are likely to reproduce.

Often a ‘fitness function’ that depends on the attributes of an agent, and defines how many descendants an agent has on average is introduced in order to study the evolution of a population. The optimization of this ‘fitness function’ is thus typically considered to be the outcome of evolutionary models [27]. However, it is not always the case that a fitness function can be defined, and therefore that evolution can be viewed as a process that optimizes fitness. For instance, even in simple models phenotypes can exhibit oscillations and chaotic behavior and thus do not have to converge to the maximum of a fitness function [88].

Therefore, rather than focusing on optimization, we consider a *stochastic birth-death process* [27]. Birth and death events across the entire population typically lead to the emergence of successful phenotypes. However, these phenotypes are not necessarily optimal, and may be able to coexist with other phenotypes, and might even be labeled as “sub-optimal” if using optimization approaches [54].

With multiple foraging agents, we assume that agents reproduce or die at rates that depend on the metabolic score. While the metabolic score determines the birth and death rates, several other factors determine the metabolic score of an agent. Such factors are not limited to the attributes, but also include factors like the number and attributes of competing foraging agents, and the density and distribution of resources.

We start simulations with a population of n agents with the same assumptions and rules defined in Subsection 2.4. Agents in the population start foraging with an initial metabolic score, l_0 , which provides them with a head start to make sure that the metabolic scores remain positive in the early exploring stages. Upon initiation resources can be sparse, and agent may not be able to find them as quickly as in equilibrium. We assume that agent i reproduces according to a non-homogeneous Poisson process with rate $b_i(t)$. Hence the probability of reproduction is $b_i(t)\Delta t + o(\Delta t)$ in a small time interval Δt . An agent dies with probability $d_i(t)\Delta t + o(\Delta t)$. Both $b_i(t)$ and $d_i(t)$ are functions of the metabolic scores of the agent i at time t . At birth a single agent generates a single descendant. The offsprings’ phenotype is a copy of the parents’ phenotypes (see below for mutations which we will include later), and the metabolic score of the parent is equally divided among the two descendants after deducting a ‘birth energy cost’. We assume that this cost is

the energy required to produce a descendant. A death removes the agent from the population. Since, birth and death rates depend on the current metabolic scores, they change continuously as successful foraging increases the metabolic scores, and foraging consumes energy.

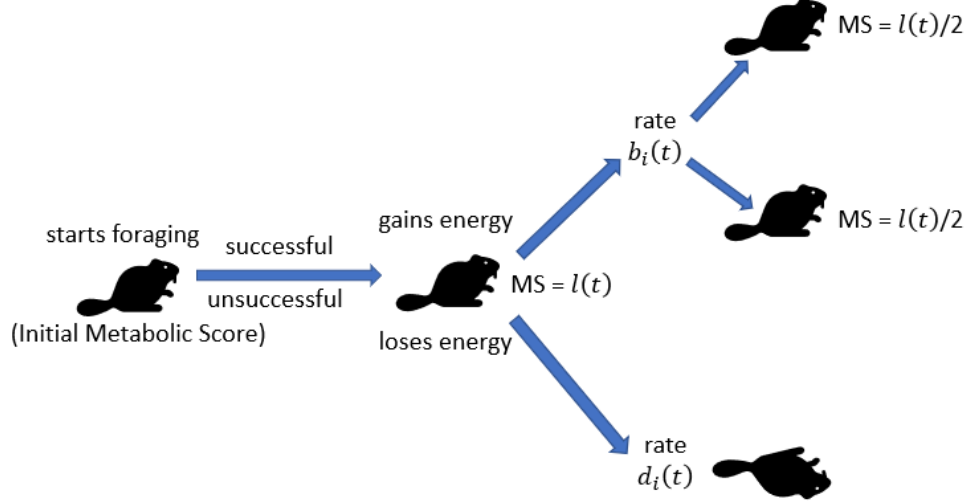


Figure 12: The probabilities of reproduction (birth) and death are determined by birth and death rates, which are functions of the metabolic score of an agent. These rates thus define a birth death process which depends on the ability of an agent to gather resources. Here $MS = l(t)$ is the metabolic score.

This birth-process generates selective pressure on the phenotypes. Those that can forage effectively will have a higher metabolic score, and hence produce more descendants. Those that do not forage effectively will have lower metabolic scores, and will be more likely to die.

We use the following birth-death rates,

- a. **Birth-death with metabolic score threshold:** In this type of birth-death process, we use maximum and minimum metabolic score thresholds to define birth and death. A minimum metabolic score, Θ_b , is required for a birth. If this threshold is met or exceeded an agent reproduces immediately. If the metabolic score falls below a threshold, Θ_d , the agent dies immediately. We assume that $0 \leq \Theta_d < l_0 < \Theta_b$. We also choose Θ_d and Θ_b so that $\Theta_d < \Theta_b/2$, which ensures that newborn agents do not have a metabolic score that falls below the death threshold immediately after birth. The probability of a birth, $b_i(t)\Delta t$, and

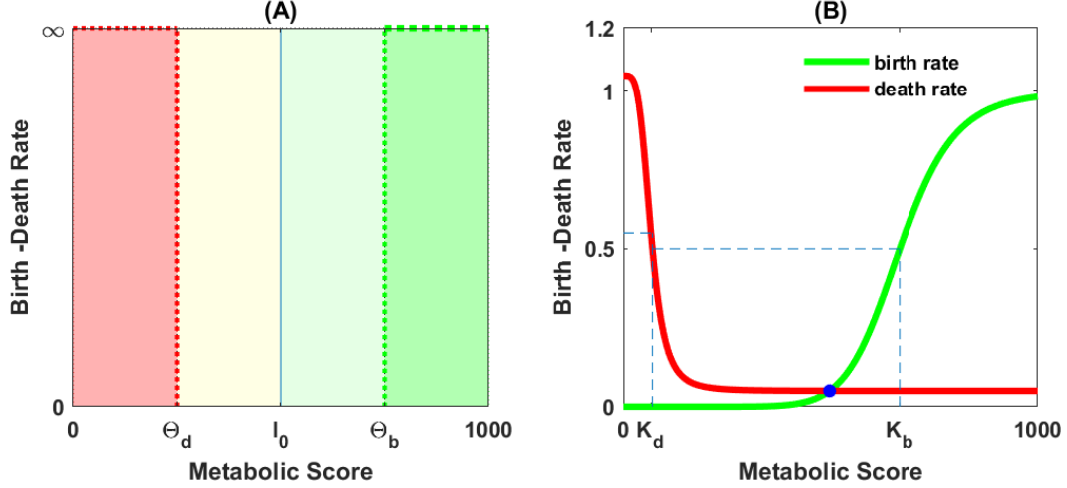


Figure 13: Two kinds of proposed birth-death functions: **(A)** birth-death defined in terms of thresholds on the metabolic score, $l_i(t)$ of agent i , and **(B)** birth and death rates defined using *Hill functions* of the metabolic score with *Hill coefficients* $\{\alpha, \beta\} \geq 2$. Here, the initial metabolic score is l_0 .

probability of death, $d_i(t)\Delta t$, in a small time increment Δt , (omitting terms that vanish as $\Delta t \rightarrow 0$) are give by the following step functions:

$$b_i(t)\Delta t = \begin{cases} 1 & \text{if } l_i(t) \geq \Theta_b, \\ 0 & \text{if } l_i(t) < \Theta_b, \end{cases} \quad \text{and} \quad d_i(t)\Delta t = \begin{cases} 1 & \text{if } l_i(t) \leq \Theta_d, \\ 0 & \text{if } l_i(t) > \Theta_d. \end{cases} \quad (18)$$

While implementing the model numerically, we assume that the following three events are mutually exclusive; 1) birth of an offspring, 2) death, or 3) foraging only, within a short time interval Δt . The range of metabolic scores $l(t) \in [\Theta_d, \Theta_b]$ is an exclusively foraging zone (See Fig. 13A).

b. Probabilistic birth-death

In a second model we define birth and death probabilities using *Hill functions* of an agent's *metabolic score*. We use a *Hill coefficient* $\alpha, \beta \in [0.5, 4]$. The birth rate is defined in terms of the constant (K_b) that defines the point at which the rate reaches half its maximum.

Similarly, the death rate is defined in terms of the half-max constant (K_d). The constants K_b and K_d are fixed for all simulations and are independent of initial metabolic scores. Hence, the rates are given by,

$$b_i(t) = \frac{(l_i(t))^\alpha}{(l_i(t))^\alpha + (K_b)^\alpha} \quad (19)$$

$$d_i(t) = \frac{(K_d)^\beta}{(l_i(t))^\beta + (K_d)^\beta} + c, \quad (20)$$

where c is a small *uniform death rate* for higher *metabolic score* such that $0 < c \ll 1$. The rates in Eqs. (19) and (20) are continuous, and defined for all values of the metabolic score, $l_i(t)$. There is always some chance that an agent will die or reproduce, regardless of the metabolic score (See Fig. 13B).

The birth-death processes defined in a (a) and (b) above are both *stochastic*. For instance, while simulating using thresholds, a population can initially increase exponentially leading to competition among agents for resources. This causes resource collection rates to decrease. As a result, agents cannot get sufficient resources to sustain the metabolic costs of foraging and maintain metabolic scores above threshold, Θ_d . Indeed, as continuously cycling environment from *higher population-high competition* to *lower population-lower competition* leads to the cycle of low average metabolic scores to higher average metabolic scores and ever changing birth-death rates. Later in Section 3, we will demonstrate by numerical simulations that this type of dynamics leads to dampened oscillations and eventually to a stationary distribution in population size and phenotype.

2.6 Evolution of Attributes

For the stochastic birth death processes described in Subsection 2.5, the structure of the population changes when an individual gives birth or dies. When an individual dies and is removed from the population, their phenotype is removed and as a result, the composition of the population changes. Similarly when an individual reproduces, and their offspring is added to the population, in nature the attributes of this offspring are determined by various factors [27]. We consider two ways of determining the phenotype of the offspring in our model: In a non-evolutionary process a newborn

has the same attributes as their parent. However, populations in nature are diverse. There are numerous potential sources of such phenotypic diversity within any given population, each with distinct underlying causes. A species' capacity to respond to the forces of selection depends on the source and extent of such phenotypic variability [16]. Thus, to capture evolutionary processes using our model which includes asexual reproduction only, we assume that mutations drive phenotypic variability across generations: The offspring has different attributes from those of the parent, but its phenotype remains constant throughout an organism's lifetime. More precisely, consider an agent A , whose phenotype is represented by an order pair (s, a) . In the *non-evolutionary* birth process its offspring A' has the same phenotype as the parent. However, in the *evolutionary* birth process the phenotype of the offspring is a random perturbation of that of the parent, but the two are equal on average.

Thus, we assume that at reproduction the attributes of the offspring are chosen randomly and independently from some distribution whose mean equals that of the parent's attributes. These mutation distributions can be *Gaussian* or *uniform*, depending on the model we select. We also assume that the variability in speed and acuity are independent. Therefore, the new-born agent's phenotype is $(s \pm \epsilon, a \pm \epsilon')$, where $\epsilon, \epsilon' \in \mathcal{N}(0, \sigma^2)$ or $\mathcal{U}(0, \phi)$, and independent. We tune and choose the *Gaussian* and *uniform* distribution parameters σ and ϕ in such a way that we can achieve 'slower' or 'faster' evolution, and simulate the evolutionary process until the population reaches a stationary distribution of attributes. When there is no variance at birth, we can observe selection without evolution when starting with a range of phenotypes. In this case we typically observe a group of identical winning phenotypes. In contrast, larger variances in phenotypes at reproduction lead to a wider distribution of phenotypes at equilibrium (See Fig. 14) with sudden declines and spikes in population.

Fig. 14 shows the population dynamics and phenotypic clouds for some typical cases, where we seek to identify the conditions and sources for phenotypic variances. We will discuss these dynamics in more detail in the results section.

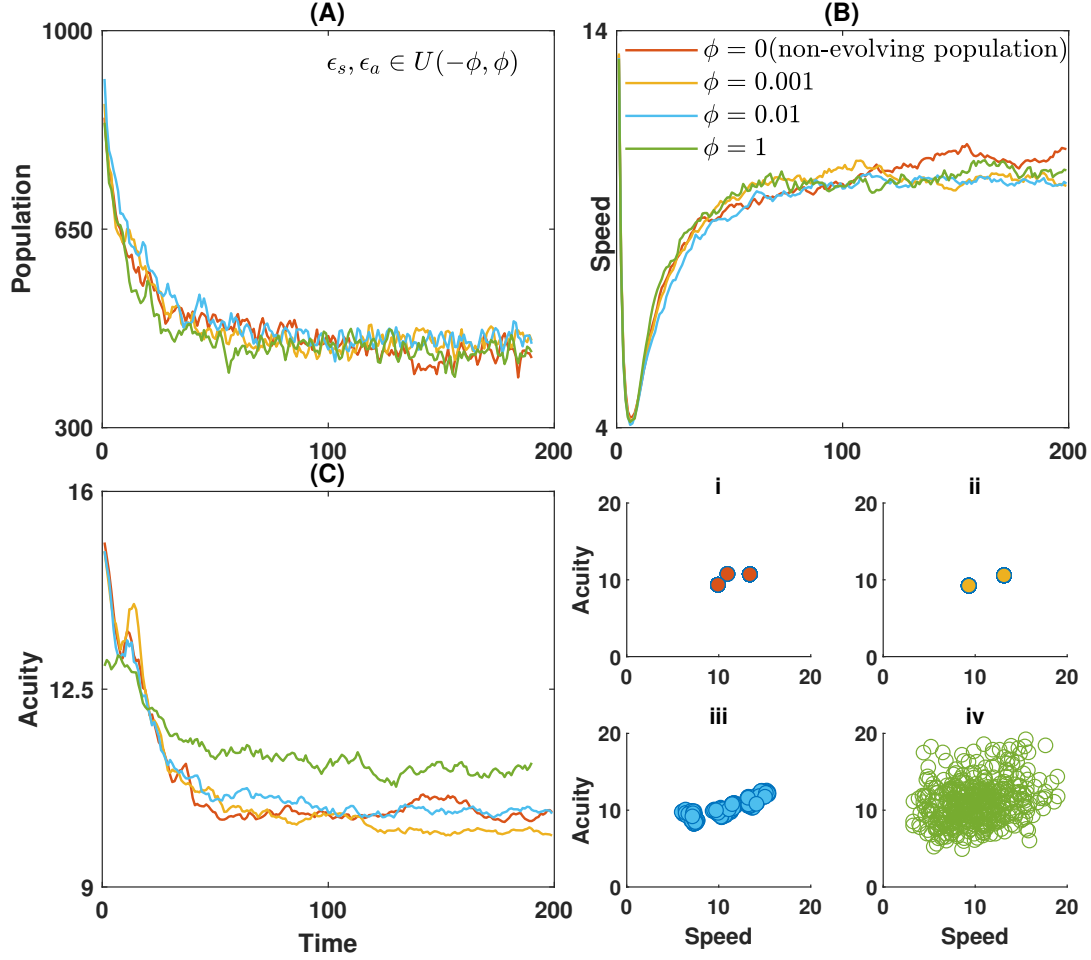


Figure 14: Dynamics with non-evolving and evolving population. Increase in mutation leads to larger variation in population size, and changes attribute distribution in equilibrium. **(A)** Population, **(B)** speed, **(C)** acuity as functions of time. Bottom right **(i – iv)** : scatter-plots of attributes with mutation $\epsilon_s, \epsilon_a \in \mathcal{U}(-\phi, \phi)$. **i)** $\phi = 0$ (non-evolving population), **ii)** $\phi = 0.001$, **iii)** $\phi = 0.01$, and **iv)** $\phi = 1$. $|\Omega| = 400 \times 400$, $\lambda = 1/500$ per unit area.

3 Mean Field Model and Semi-Analytic Approach

Agent-based models are often relatively easy to describe and implement, but their dynamics can be difficult to analyze [13, 59]. While the mechanisms and immediate effects of individual interactions are easy to understand, the behaviors that emerge on the level of the population are often difficult to predict [59]. Reduced, tractable mathematical models of the population dynamics can be difficult to derive rigorously because agents interact between themselves and their environment, which can make it hard to describe their joint behavior. In our case, it is challenging to derive a mathematical model of the average population dynamics rigorously due, in part, to the unique individual attributes of each agent in the population and the stochasticity of the birth-death processes. In evolving population, these processes become even more complicated due to continuously changing phenotypes of the offsprings.

In our agent-based model we assumed that each foraging agent has their own phenotype, so that phenotypes can differ across the population. As we will see, under evolutionary pressure phenotypes can converge, so that the population becomes more homogeneous. However, if we assume that descendants differ from their parents due to mutations, some variability can and will be maintained. Even with similar or identical phenotypes it can be difficult to find a reduced model of population dynamics. Here we derive a mean field model of the aggregate population behavior that is valid when the individuals in the population do not interact strongly [13].

3.1 Reduced Model Characteristics

We next describe a formal model of the dynamics of a non-evolving population. This model takes the form of a system of differential equations that describe the averaged dynamics of the agents. The reduced model describes the evolution of the population size, and the average metabolic score of the agents.

We base the reduced model on the following set of assumptions:

1. The overall dynamics of the population is captured well by the average population density

and average metabolic score. Hence, we do not keep track of each agent's metabolic score, but consider the average metabolic score and total metabolic score of the population.

2. We assume the agents in the population have the same fixed phenotype, and assume there is no phenotypic variation at birth. Hence, all descendants share the same phenotypic attributes, and metabolic costs of their parents.
3. We assume that the resources added to the system and their metabolic energy content are available to all of the agents. Hence the average metabolic score increases at a rate equal to the resource replenishment rate times metabolic energy of resource. The metabolic costs of movement and sensing represent a metabolic energy sink.

When the agents in a system interact according to a given set of rules, in ABM simulations we recursively update the state of the system according to the outcome of these interactions. It is challenging to obtain the probability of all possible states of the system, as we would have to account for all possible agent positions and directions, along with resource locations. Hence, we approximate only the average properties of the system of interacting agents.

In the absence of strong interactions, we can often approximate the evolution of averaged quantities, such as population size, and mean metabolic score using a *mean-field model*. In this case the evolution of the N -body system is approximated by the dynamics of a single body by averaging the interactions between the individual agents and the environment, and assuming that interactions between agents are negligible. We develop a mean field model by describing the population of agents using a continuous, time dependent variable which is determined by agent density at an instant of time, t . To formalize the model, we recall some parameters/variables defined earlier from the *list of notations* and from Subsection 1.1. We will develop the mean field model in term of the following quantities:

- resource replenishment rate per unit area, λ ,
- resource density, ρ ,

- initial agent density, x_0 , and agent density at a given time, $x(t)$,
- the metabolic score (energy) gained by consuming a single resource, F ,
- the initial metabolic score of an agent, l_0 , and the average metabolic score of an agent at time t , $\bar{l}$.

We derive the mean field model for a unit foraging area and can extend it to any other arbitrary area Ω . The total number of agents in an area Ω of size $|\Omega|$ at time t is $x(t)|\Omega|$. In the same area, resources are replenished at a rate of $\lambda|\Omega|$ resources per unit time. The average total metabolic score of all agents in that area is $x(t)|\Omega|\bar{l}(t)$. We will use the reduced equations to compute the limiting average of the population. Thus we look for the equilibrium solutions of the population density and average metabolic scores. At equilibrium the resource collection rate of the population equals the resource replenishment rate.

In order to survive and reproduce in a competitive environment, agents have to collect resources at a rate such that the metabolic score gained must exceed, or equal, the metabolic cost per unit time $C(s, a)$ (See Subsection 2.4.2). In the mean-field model, we assume that the average resource collection rate of an agent per unit area is a function of the agent density and the resource replenishment rate, and hence has the form $g(x, \lambda)$. More resources can be collected when the replenishment rate is higher. Moreover, at higher agent densities resources are shared due to competition. In Subsection 2.4, we have verified that the resource collection rate is a function of resource replenishment rate and the number of foraging agents. Hence, the resource collection rate is directly proportional to the resource replenishment rate and is inversely proportional to the agent density. If ρ is the resource density (in a unit area) at any instant of time t , the rate of change of resource density is

$$\frac{d\rho}{dt} = \lambda - g(x, \lambda) x. \quad (21)$$

While the solution of Eq. (21) gives the resource density at any instant of time t , the expression is complicated due to the birth-death process, as the resource collection rate is continuously changing with the number of agents in the domain. When the system approaches an equilibrium, the

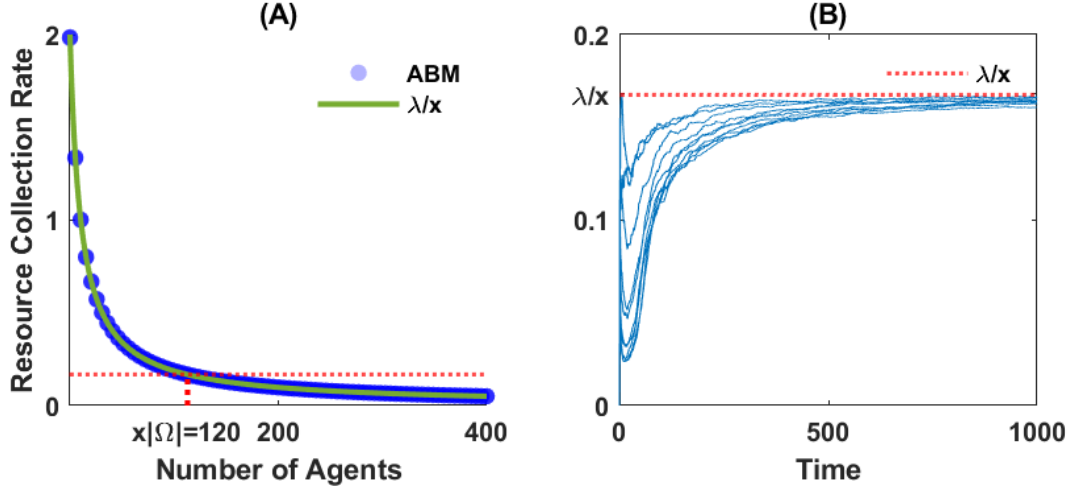


Figure 15: Resource collection rates are shown in two panels: **(A)** non birth-death simulations with similar phenotypes $\xi_k = (10, 10)$, where the resource collection rate is a function of resource replenishment rate and agent density, and **(B)** non-evolving birth-death simulations in which the trajectory of resource collection rate attains an equilibrium of λ/x . In each non birth-death simulation, identical agents are placed on a 200×200 space with a resource rate of $\lambda = 0.0005$ and a simulation time of 10000. In each birth-death simulation, a random number of identical agents with $\xi_k = (10, 10)$ are placed on a 200×200 space with a resource rate of $\lambda = 0.0005$, $F = 100$, and a simulation time of 10000. In birth-death simulations, the initial increase in population causes a decrease in the resource collection rate, but ultimately it attains an equilibrium of λ/x .

resource collection rate in a unit area approaches the resource density, which in turn depends on the replenishment rate. At equilibrium the resource collection rate equals the resource replenishment rate, and so

$$g(x, \lambda) = \frac{\lambda}{x}.$$

We have thus obtained a resource collection rate, under the assumption that the system is in equilibrium, and hence the resource density, ρ , is constant.

We ran simulations using evolutionary and non-evolutionary birth-death processes and found that the average resource collection rate is approximated well by the ratio of resource replenishment rate and agent density at equilibrium. Fig. 15B shows how the resource collection rate attains an equilibrium λ/x in a typical non-evolving population simulation and resource collection rate attains a value of λ/x in different non birth-death simulations (Fig. 15A).

3.2 Mean Field Model of Agent Density and Metabolic Scores

Non-linear models, such as the *logistic growth model* in Eq. (4), are often used to describe population dynamics. Such models are defined in terms intrinsic growth rate and other terms characterizing population size changes. However, in the foraging model we described, such rates are difficult to obtain since they change as the population grows and evolves. We therefore model a non-evolving birth-death process in a foraging population by considering a system of differential equations, namely, the rate of change of metabolic score, and the rate of change of agent density. We next provide a nonlinear second order differential equation that describes the evolution of these quantities. Although the full equation cannot be solved explicitly, we can find the equilibria analytically.

3.2.1 Rate of Change of Average Metabolic Score

Each resource has a metabolic score (caloric value) F , which equals the increase in an agent's metabolic score when consumed. The metabolic score of an agent thus increases at a rate equal to the product of F and the resource collection rate. Similarly, the agent's movement and sensing reduce its energy budget at a rate $C(s, a)$.

If $\bar{l}$ is the average metabolic score, and x is the agent density at any instance of time, the rate of change of the average metabolic score per unit area due to foraging gains and losses is then given by,

$$\frac{d\bar{l}}{dt} = \frac{\lambda}{x} F - C(s, a),$$

where we have used the resource collection rate at equilibrium, $g(x, \lambda) = \frac{\lambda}{x}$. However, this equation is incomplete, as it does not account for the change in the average metabolic score due to births. After each birth, the agent's metabolic score is equally divided between the parent and offspring, and the rate of these events is given by the birth rate r_b . Hence,

$$\frac{d\bar{l}}{dt} = \frac{\lambda}{x} F - C(s, a) - r_b \bar{l} \ln 2. \quad (22)$$

We can use this equation to define equilibria of the system: When the rate of gain of metabolic score exactly meets the current metabolic energy dissipation rate, we have

$$\frac{\lambda F}{x} = C(s, a) + r_b \bar{l} \ln 2.$$

In this case there is no net gain in the metabolic score, and $\bar{l}$ approaches a fixed point $\tilde{l}$. When $\bar{l}$ becomes constant, x approaches a fixed point $\tilde{x}$. Indeed, $\tilde{l}$ and $\tilde{x}$ are the equilibrium solutions of the system defined by Eq. (27) discussed next.

3.2.2 Rate of Change of Agent Density

To model the evolution of the agent density, we use the birth–death dynamics described in Subsection 2.5. In particular, we assume that the dependence of the birth rate on the metabolic score of an agent is given by the *Hill equation* defined by Eq. (19) in Subsection 2.5.

Similarly, to define the death rate of an agent, we use the same *Hill equation* (Eq. (20)) in Subsection 2.5. We assume that an agent can die even with a large metabolic score, and that there is a small uniform constant death rate, c , in the population,

$$r_d = \begin{cases} \frac{(K_d)^\beta}{\bar{l}^\beta + (K_d)^\beta} + c & \bar{l} \geq 0 \\ \infty & \bar{l} < 0 \end{cases} \quad (23)$$

We recall from Section 2.5 that birth-death rates can also be defined using *Heaviside step functions* in terms of thresholds on the metabolic scores (Eq. (18)). Using Heaviside functions in the resulting mean field ODEs would lead to a discontinuous right hand side, and potential numerical problems. We therefore approximate these step functions using logistic functions. The logistic functions give the probabilities of birth and death in a small time interval as follows;

$$\begin{aligned} p_b &= \frac{1}{1 + \exp\{-2k(\bar{l} - \Theta_b)\}} \\ p_d &= \frac{1}{1 + \exp\{2k(\bar{l} - \Theta_d)\}} \end{aligned} \quad (24)$$

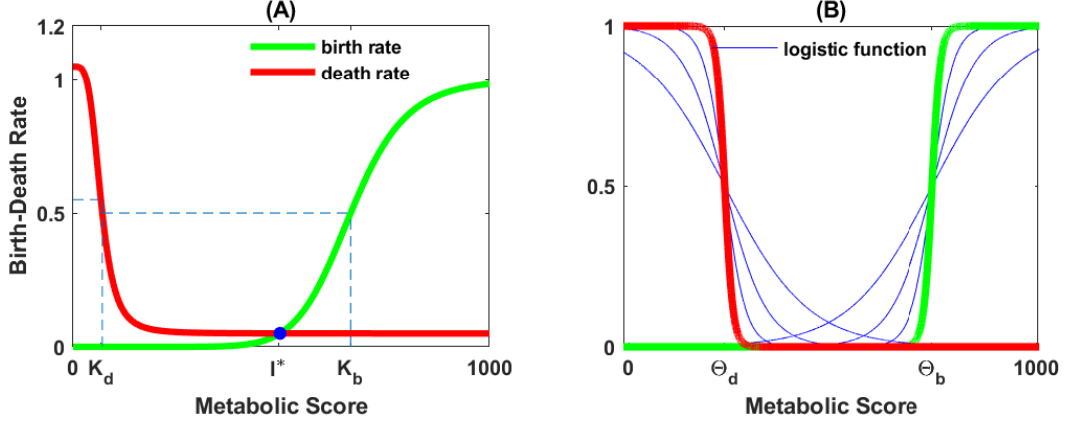


Figure 16: Birth–death rates by *Hill functions* and the thresholds on metabolic scores: **(A)** birth and death rates defined using *Hill functions* of the metabolic score with *Hill coefficients* $\{\alpha, \beta\} = 2$, and **(B)** birth and death rates translated from Heaviside step function (Eq. (24)).

where for larger k the transition of probability is sharp, and approaches the step function in Eq. (18) in the limit, *i.e.*

$$p_b = \lim_{k \rightarrow \infty} \frac{1}{1 + \exp\{-2k(\bar{l} - \Theta_b)\}} = \begin{cases} 1 & \text{if } \bar{l} \geq \Theta_b \\ 0 & \text{if } \bar{l} < \Theta_b \end{cases} \quad (25)$$

and similarly for the probability of death.

As in the ABM model, we choose the thresholds so that $\Theta_d < l_0 < \Theta_b$ and $\Theta_d < \Theta_b/2$. Any metabolic scores $\bar{l} \in (\Theta_d, \Theta_b)$ fall in the zone where there is no birth or death. Indeed, the equality holds in the limit of the smooth approximation of step function defined by logistic functions (Eq. (24)), these logistic functions are well approximated by *Hill equations* and vice-versa [1, 35].

We thus obtain the following systems of non-linear differential equations with initial conditions;

$$l(0) = l_0, \quad x(0) = x_0$$

- When birth-death occurs with *threshold* on metabolic score,

$$\begin{cases} \frac{d\bar{l}}{dt} = \frac{\lambda}{x}F - C(s, a) - \ln 2 \left(\frac{\bar{l}}{1 + \exp\{-2k(\bar{l} - \Theta_b)\}} \right) \\ \frac{dx}{dt} = \left(\frac{1}{1 + \exp\{-2k(\bar{l} - \Theta_b)\}} - \frac{1}{1 + \exp\{2k(\bar{l} - \Theta_d)\}} \right) x \end{cases} \quad (26)$$

- When birth rate and death rates are determined by *Hill equations*, then the system becomes;

$$\begin{cases} \frac{d\bar{l}}{dt} = \frac{\lambda}{x}F - C(s, a) - \ln 2 \left(\frac{\bar{l}^\alpha}{\bar{l}^\alpha + (K_b)^\alpha} \right) l \\ \frac{dx}{dt} = \left(\frac{\bar{l}^\alpha}{\bar{l}^\alpha + (K_b)^\alpha} - \frac{(K_d)^\beta}{\bar{l}^\beta + (K_d)^\beta} - c \right) x \end{cases} \quad (27)$$

To find the stationary points and their stabilities of the Systems (26) and (27), we set left hand sides to zero. When $\frac{dx}{dt} = 0$ from System (26), we get metabolic score $(\tilde{l}) = (\Theta_b + \Theta_d)/2$ which is one of the stationary point.

Now from $\frac{d\bar{l}}{dt} = 0$;

$$\begin{aligned} 0 &= \frac{\lambda}{x}F - C(s, a) - \ln 2 \left(\frac{\tilde{l}}{1 + \exp\{-2k(\tilde{l} - \Theta_b)\}} \right) \\ &= \frac{\lambda}{x}F - C(s, a) - \frac{\ln 2}{2} \left(\frac{\Theta_b + \Theta_d}{1 + \exp\{-2k((\Theta_b + \Theta_d)/2 - \Theta_b)\}} \right) \\ &= \frac{\lambda}{x}F - C(s, a) - \frac{\ln 2}{2} \left(\frac{\Theta_b + \Theta_d}{1 + \exp\{k(\Theta_b - \Theta_d)\}} \right) \end{aligned}$$

For $k \geq 1$ and for larger difference between birth threshold and death threshold $(\Theta_b - \Theta_d)$, the denominator of the second term is very large compared to the first term. Hence we can neglect the second term so that we get the equilibrium point for the agent density as,

$$\tilde{x} = \frac{\lambda}{C(s, a)}F.$$

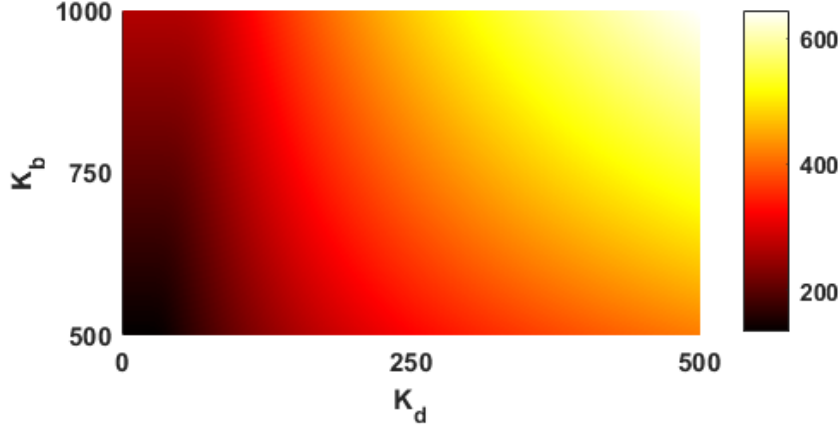


Figure 17: Stationary points (metabolic scores ($\tilde{l}$)) to the System (27) obtained from Eq. (30) with different birth propensities (K_b) and death propensities (K_d), $\alpha = \beta = 4$.

Similarly, for the System (27), by equating the LHS to zero, we have

$$\tilde{x} = \frac{\lambda}{C(s, a) + \ln 2 \left(\frac{\tilde{l}^{\alpha+1}}{\tilde{l}^\alpha + (K_b)^\alpha} \right)} F, \quad (28)$$

and

$$\left(\frac{\tilde{l}^\alpha}{\tilde{l}^\alpha + (K_b)^\alpha} - \frac{(K_d)^\beta}{\tilde{l}^\beta + (K_d)^\beta} - c \right) \tilde{x} = 0.$$

Since, if agent density is 0, either this is a ‘trivial’ solution or the death rate exceeds the birth rate. So, for $\tilde{x} \neq 0$, $\tilde{l}$ is obtained by the solution of

$$\tilde{l}^{\alpha+\beta}(1-c) - c(\tilde{l}^\alpha K_d^\beta + \tilde{l}^\beta K_b^\alpha) - (1+c)K_d^\beta K_b^\alpha = 0. \quad (29)$$

For $\alpha = \beta$

$$\tilde{l}^\alpha = \frac{1}{2} \left(\frac{c}{1-c} (K_d^\alpha + K_b^\alpha) + \sqrt{\left(\frac{c}{1-c} \right)^2 (K_d^\alpha + K_b^\alpha)^2 + 4K_d^\alpha K_b^\alpha \left(\frac{1+c}{1-c} \right)} \right) \quad (30)$$

For any admissible parameter values, Eqs. (28) and (29) give a single fixed point $(\tilde{l}, \tilde{x})$. We analyze the stability of the fixed point as follows:

Let,

$$\begin{cases} \phi(\bar{l}, x) = \frac{\lambda}{x} F - C(s, a) - \ln 2 \left(\frac{\bar{l}^\alpha}{\bar{l}^\alpha + (K_b)^\alpha} \right) \bar{l} \\ \psi(\bar{l}, x) = \left(\frac{\bar{l}^\alpha}{\bar{l}^\alpha + (K_b)^\alpha} - \frac{(K_d)^\beta}{\bar{l}^\beta + (K_d)^\beta} - c \right) x \end{cases} \quad (31)$$

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \phi}{\partial \bar{l}} & \frac{\partial \phi}{\partial x} \\ \frac{\partial \psi}{\partial \bar{l}} & \frac{\partial \psi}{\partial x} \end{bmatrix} = \begin{bmatrix} -\ln 2 \frac{1+(\alpha+1)\left(\frac{K_b}{\bar{l}}\right)^\alpha}{\left(1+\left(\frac{K_b}{\bar{l}}\right)^\alpha\right)^2} & -\frac{\lambda}{x^2} F \\ \frac{x}{\bar{l}} \left(\frac{\alpha \left(\frac{K_b}{\bar{l}}\right)^\alpha}{\left(1+\left(\frac{K_b}{\bar{l}}\right)^\alpha\right)^2} + \frac{\beta \left(\frac{K_d}{\bar{l}}\right)^\beta}{\left(1+\left(\frac{K_d}{\bar{l}}\right)^\beta\right)^2} \right) & \left(\frac{\bar{l}^\alpha}{\bar{l}^\alpha + (K_b)^\alpha} - \frac{(K_d)^\beta}{\bar{l}^\beta + (K_d)^\beta} - c \right) \end{bmatrix} \quad (32)$$

For fixed point $(\tilde{x}, \tilde{l})$, the *Jacobian* has the form; $\mathbf{J} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ where $a < 0$, $b < 0$, $c > 0$ and $d = 0$.

The eigenvalues of $\mathbf{J}$ are $\frac{a \pm \sqrt{a^2 + 4bc}}{2}$. For $a < 0$, $b < 0$ and $c > 0$, the discriminant $(a^2 + 4bc)$ determines the nature of eigenvalues. Since a is negative, and $4bc$ is large (negative) as compared to a^2 , $a^2 + 4bc < 0$. So the eigenvalues are imaginary with negative real part $(a/2)$. This shows that the only equilibrium solution $(\tilde{l}, \tilde{x})$ for the System (27) is indeed a stable focus.

For example, we take *Hill coefficients* $(\alpha, \beta) = 4$ and solve the equations¹⁵. For $K_b = 1000$, $K_d = 100$, $\lambda = 1/500$ and $F = 25$ on 200×200 space, the equilibrium point is $(\tilde{l}, \tilde{x}) = (336.8, 143.5)$ and the *Jacobian* evaluated at equilibrium point is

$$\mathbf{J}|_{(\tilde{l}, \tilde{x})} = \begin{bmatrix} -0.043 & -0.097 \\ 0.034 & 0 \end{bmatrix}$$

with eigenvalues $\lambda_1 = -0.02 - 0.05i$ and $\lambda_2 = -0.02 + 0.05i$. This shows that the equilibrium point $(\tilde{l}, \tilde{x}) = (336.8, 143.5)$ is stable. The solution path¹⁶ forms a spiral sink near the equilibrium point.

We have established a limited mean field model to find the dynamics of agent density and their metabolic scores which are carried with two types of stochastic birth death processes. The dynamics of these two Systems (26) and (27) will be used to analyze and compare with the ABM results.

¹⁵to solve the equations numerically we used *MathWorks-vpasolve*[41]

¹⁶we obtained the phase portrait in Fig. 18 using PhasePlane App in MATLAB [43]

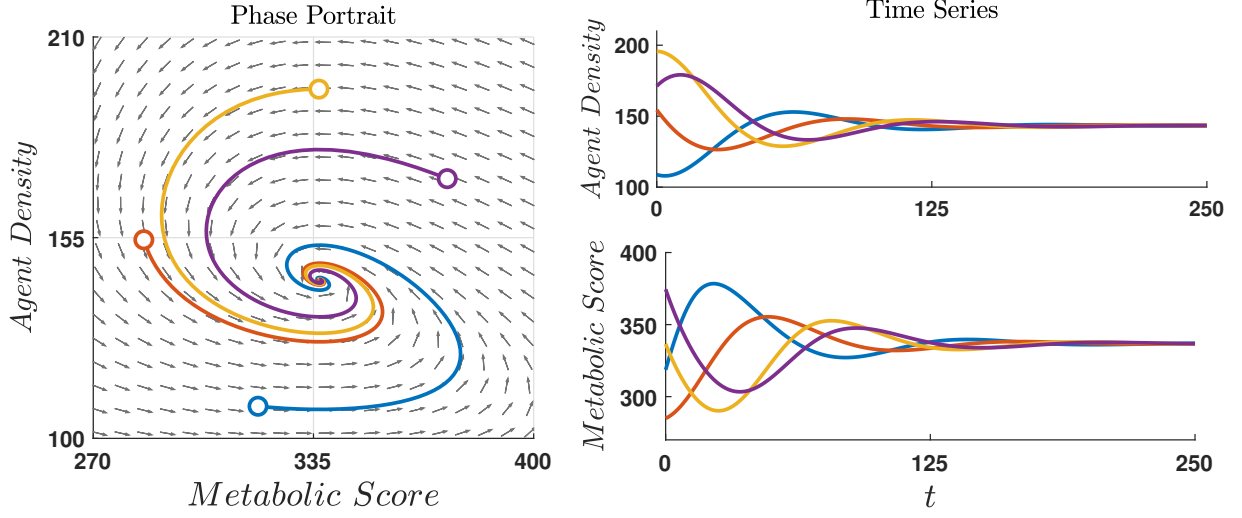


Figure 18: Stability of the equilibrium point to the System (27) for $K_b = 1000$, $K_d = 100$, $\lambda = 1/500$ and $F = 25$ on 200×200 space: $(\tilde{l}, \tilde{x}) = (336.8, 143.5)$.

When births and deaths are modeled using thresholds on the metabolic scores, it takes longer to achieve a stationary distributions due to ‘foraging only’ zones, and the method in which birth and death rates are determined by *Hill equation* of metabolic score, often achieves stationarity quickly. We will present these and other comparisons in the result section next.

4 Results

In previous sections we defined a stochastic evolutionary birth-death process that was the basis of an agent-based modeling (ABM) approach. We also defined a limited corresponding analytic description of the model in terms of a non-linear system of ordinary differential equations. In this section, we analyze the data obtained from ABM simulations, and compare and contrast this data with analytical results. We show that the resource environment and the dynamics of the birth-death process used to define our ABM lead to selection of particular phenotypes. While the birth-death rates are determined only by the agents' metabolic scores, the phenotypes go through selective pressures since they determine these metabolic scores. We find that in some resource environments (for instance, homogeneous resource distribution with high replenishment rates in the domain), the phenotype may experience weaker selective pressure, whereas in other resource environments (low resource replenishment rates or patchy resource distribution), phenotypes go through strong selective pressures. We show that populations that experience strong selective pressures converge to phenotypes in a narrow range of values that are adapted to such hostile environments. Thus we find that the birth-death process creates a variation among the phenotypes, forces the model to select the competitive ones and hence directs the overall evolutionary process.

To establish and verify the assertions in the previous paragraph we simulated the ABM using the algorithm and methods explained in Section 2. We ran simulation on two-dimensional domains of varying sizes, including 100×100 , 200×200 , 400×400 and 800×800 with different initial phenotypes. The attributes (speed and acuity) of the agents determine how they explore their environment in search for resources. The phenotypes which allow for effective exploration of the environment and maximization of the net metabolic energy gain per unit time, are more likely to replicate. In what we call the 'evolutionary model' offspring can acquire mutations resulting in *phenotypic variance* at birth. This can occasionally produce 'fitter' phenotypes, *i.e.* phenotypes that forage more successfully than their ancestors and thus have a higher probability of reproducing. Agents which cannot sustain the required metabolic costs of foraging are more likely to die, and the

death process also alters the phenotypic composition of the population. In the ‘non-evolutionary’ model offspring do not acquire mutations (no variance at birth), so that newborns are copies of their parents. In this model the ‘fittest’ phenotypes are selected among the initial phenotypes in the population. Changes in the phenotypic composition of the population in non-evolutionary birth-death processes are caused solely by selection on the phenotypes that are available initially. When we include mutations changes in the phenotypic composition are due to both selection and mutation.

Further technical details about the the ABM simulations are described in Appendix B.

4.1 Dependence of Dynamics on Simulation Parameters

Before presenting the analyses and results, we briefly discuss the accuracy of the numerical implementation of the ABM. In particular, we checked that our simulation results are independent of the size of the discrete time increment, Δt , we used in our simulations. Since our ABM is defined in continuous time, and it is simulated using a discrete approximation of the model it is important to show that the time increment is small enough to give accurate results, yet not too small to be computationally inefficient. Smaller increments lead to longer and slower simulations, while larger increments may not provide a valid results.

We ran simulations with different time increments, Δt , and here show some of the resulting population sizes in equilibrium along with the average attributes (Fig. 19). Note that when the time increment is smaller than about 0.1, any further reduction in the increment does not alter the results. To verify this, we performed corresponding simulations on 200×200 and 400×400 spaces with the parameter in the ranges that are discussed below, and found that a time increment of 0.1 is sufficient in all cases we examined. We therefore chose an increment of size 0.1 in our simulations.

Similarly, in ABM simulations, the values of some variables must be fixed at the beginning of the simulations. We will see that these initial values often do not impact the long term dynamics of the population. In Subsection 2.5, we assumed that the agents in population start foraging with the initial metabolic scores (l_0) to assure that they have sufficient metabolic energy in the early

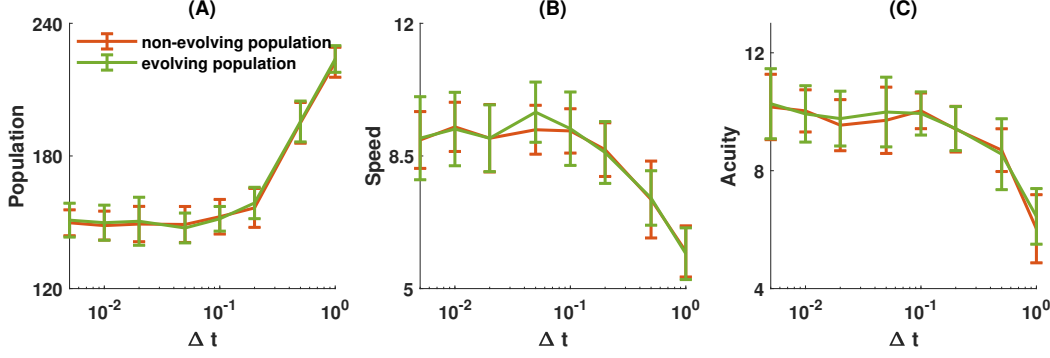


Figure 19: Semi-log plots of showing population, speed, and acuity versus the time increment used in simulations, Δt . Error bars represent the standard deviation of the final population and attributes, based on 10 independent simulations for each time increment, Δt , and for each evolving and non-evolving populations. Simulations start with an initial population 10000 and a domain of size 200×200 , $\lambda = 1/500$, $F = 25$ and $T = 10000$. For evolving population; ϵ_s and ϵ_a are taken uniformly random from $U(-\phi, \phi)$ where $\phi = 0.05$.

exploratory stages. We fix this initial value, l_0 , to a constant between K_d and K_b , depending on the resource availability and competition at the beginning of simulation, as we explain next. For smaller l_0 , the probability of survival of agents with high speed and high acuity (metabolically costly attributes) is low at the early exploring stage, so phenotypes with less costly attributes are selected for. Moreover, the phenotype once eliminated cannot re-emerge in the non-evolving population model. Considering these facts, we chose initial metabolic score¹⁷ sufficient for an organism to survive over a relatively long initial time. However, the long term behavior of the population is not sensitive to this initial value, as long as the initial metabolic score is sufficiently high for the initial population to survive, and individuals do not starve before they are able to find and reach any resources (Fig. 20B, 20D and 20F).

As we discussed earlier, to forage effectively agents need to change their direction appropriately. Recall that we define the frequency of direction change, f_i , for each agent so that all agents move an average distance, defined by the run-length η , before changing direction (see Subsection 2.2). This fixed average run distance ensures that, on average, each agent eventually explores an area

¹⁷with $(l_0) = 0$, the current metabolic score becomes negative at the first instant of time Δt for all unsuccessful agents and hence death rate become infinity.

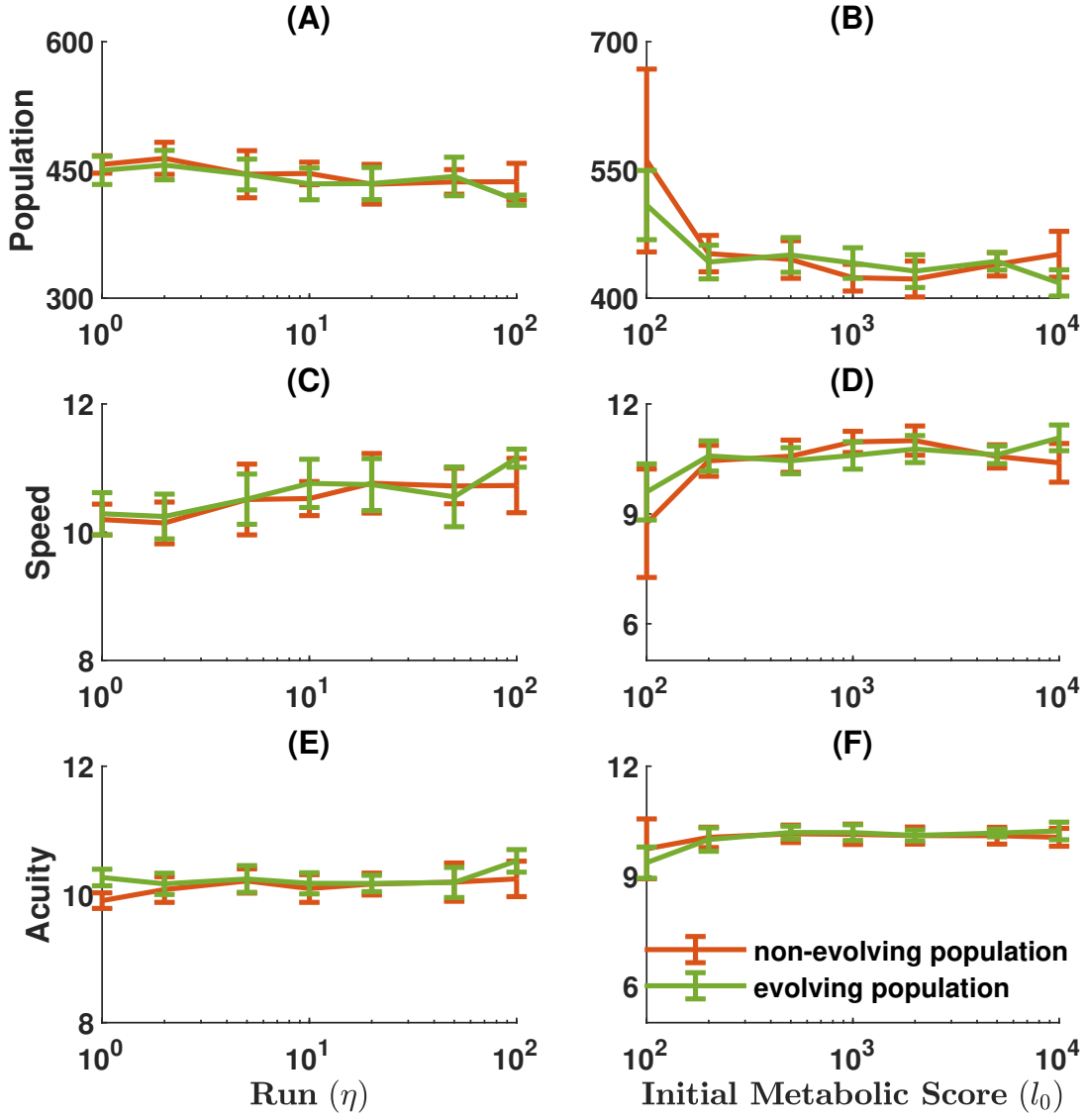


Figure 20: Semi-log plots of (A), (B), (C), (D), (E), and (F) showing population, speed, and acuity as a function of average run distance (η) on the first column and versus initial metabolic score (l_0) on the second column. Error bars represent the standard deviation of the final population and attributes, based on 10 independent simulations for each run and initial metabolic score, and for each evolving and non-evolving population. The results show that the equilibrium is independent of the choice of run distance and initial metabolic score, with consistent patterns observed across multiple independent simulations. Simulation on a domain of size 400×400 , with $\lambda = 1/500$, $F = 25$ and $T = 10000$. For evolving population; ϵ_s and ϵ_a are sampled uniformly at random from $U(-\phi, \phi)$ where $\phi = 0.05$.

in a given amount of time whose size depends solely on the speed of the agent. Thus all agents have the same average run distance, but faster agents will explore an area more quickly. While modeling single agent foraging earlier (see Subsection 2.3), we fixed η to ensure effective foraging. However, since resources are being accumulated at a fixed resource replenishment rate, agents start to exploit (when resource density in the domain becomes high enough so that resource is being available inside ones acuity range) their acuities instead of exploring the domain, even for smaller η . Hence, at high resource replenishment rates agents will go from one visible resource to the next, and will not spend much time seeking resources they cannot see. In that case the choice of η does not impact the long term dynamics of the population and the evolution of attributes (Fig. 20A, 20C and 20E). When resource rate is very low (highly competitive foraging simulation), the choice of η does impact the dynamics. Since smaller values of η result in less effective exploration and foraging, such values also favor agents with larger acuities. To overcome such dependency, we typically chose the η larger than expected distance between an agent to its nearest resources (see Eq. (12)) *i.e.*, $\eta \geq \frac{1}{2\sqrt{\lambda}}$.

4.2 Non-evolutionary Birth-Death Process

In order to understand the population dynamics and selection of phenotypes in non-evolutionary birth-death process, we generally start simulations by considering a large number of agents (usually ≥ 10000) with distinct phenotypes chosen randomly and uniformly from $\{[s_{min}, s_{max}], [a_{min}, a_{max}]\}$. Because non-evolutionary birth-death processes don't naturally introduce variation, we need a large number of agents to ensure that there is enough variability in the population. We initially place each agent to a location P_i chosen uniformly and at random in the domain. This ensures that a diversity of phenotypes at the start of the simulation. These phenotypes have different attributes and different metabolic costs, and hence the 'fittest' among the phenotypes is expected to survive.

However, when our goal is to compare the competitive foraging and resource collection rates of different phenotypes, we conduct simulations using only a few "representative" phenotypes. Likewise, if we want to investigate the population dynamics, specifically the carrying capacity, of

identical phenotypes in non-evolving birth-death simulations, we start the simulation with a smaller number of initial agents. In short, the initial number of agents in a simulation can be tailored to fit the specific objective of the model.

In our model, the dynamics of the stochastic birth-death processes are determined by agents' foraging abilities and their metabolic energy accumulation rates. In such cases, the pivotal part of the process is to model the resource collection rates. In Subsection 2.3, we have estimated the upper bound and lower bound for the resource collection rates (Eq. (13)) for a single foraging agent. We can extend the same estimates to multi-agent foraging. However, the estimate works only for populations composed of agents with similar phenotype. In heterogeneous populations individual resource collection rates are determined by the different phenotypes, which makes the analysis more difficult. Moreover, our reduced models do not capture evolution.

We therefore simulated the model numerically to estimate the resource collection rates of such heterogeneous populations. We started with 900 agents on domains of different areas ranging from 50×50 to 800×800 . Each agent was assigned a phenotypic vector ξ_i , and these vectors took all possible integer-valued ordered-pairs of speed and acuity from a range $[1, 30]$. We set the resource replenishment rate to be constant at λ resources per unit time per entire domain¹⁸. This means that the resource replenishment rate per unit area was smaller in the larger domains, but the total amount of resource generated per unit time was constant. In larger domains the resources are therefore more sparsely distributed.

The resource collection rates in the smaller domain are mainly determined by competing agents' speeds. Acuity is not a strong determinant, unless it becomes too small to observe even closeby resources, and agents engage in futile exploration (Fig. 21A). This makes sense as in smaller domains resources are more densely distributed. However, in larger domains with more sparsely distributed resources both speed and acuity are important for effective foraging (Fig. 21E and 21F).

Fig. 21 shows that speed is crucial for effective resource collection in a competitive environment. We next show how the resource collection rate affects the rates of births and deaths. When agents

¹⁸we note a slight abuse of notation here: Previously λ denoted the resource generation per unit time per unit area.

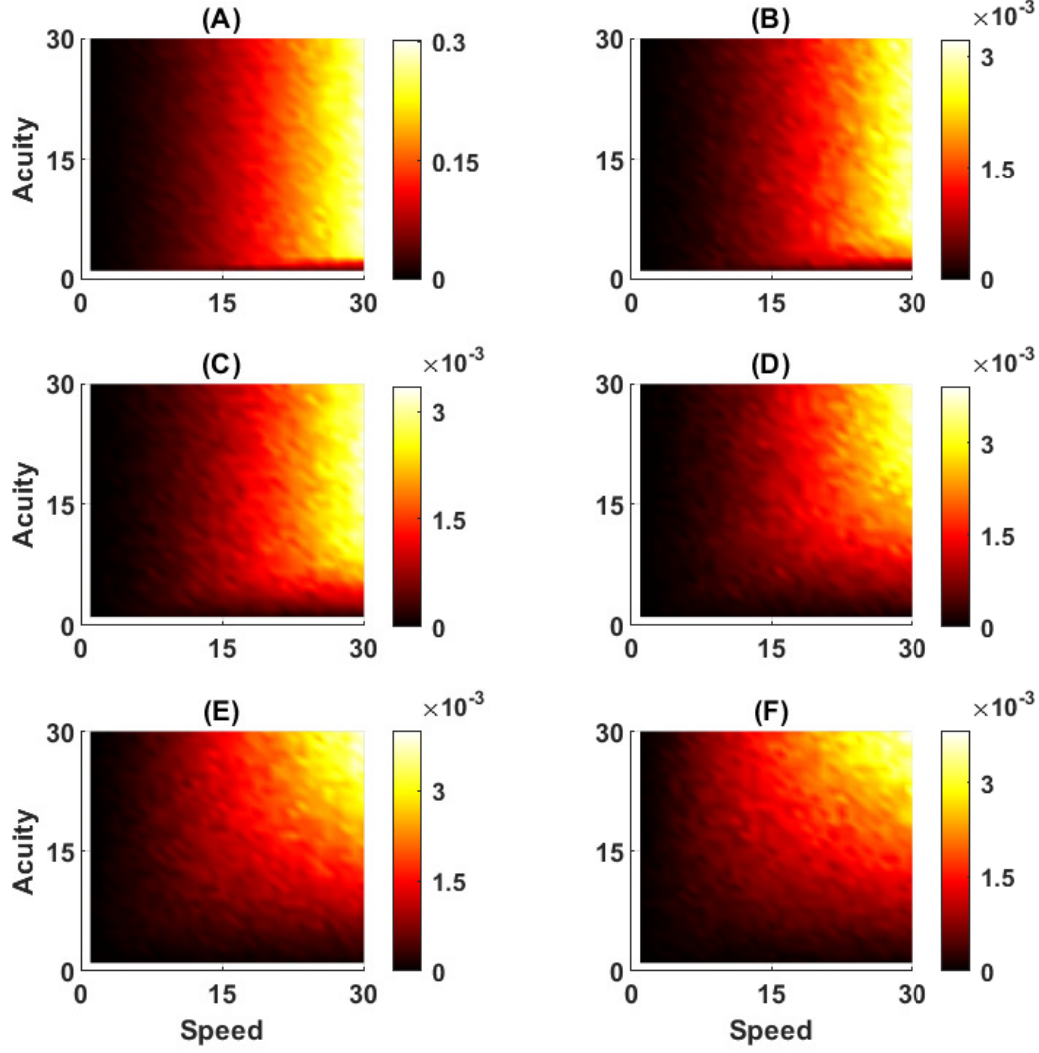


Figure 21: Resource collection rate for each of 900 agent attributes in different domains: (A) 50×50 , (B) 100×100 , (C) 200×200 , (D) 400×400 , (E) 600×600 , and (F) 800×800 spaces. Agents' attributes are chosen from $[1, 30]$ and a resource collection rate was obtained for every integer-valued ordered pair. Ten independent simulations were used for each estimate. Resource replenishment rate was set to $\lambda = 1$ resource per unit time on the entire domain and $T = 10000$.

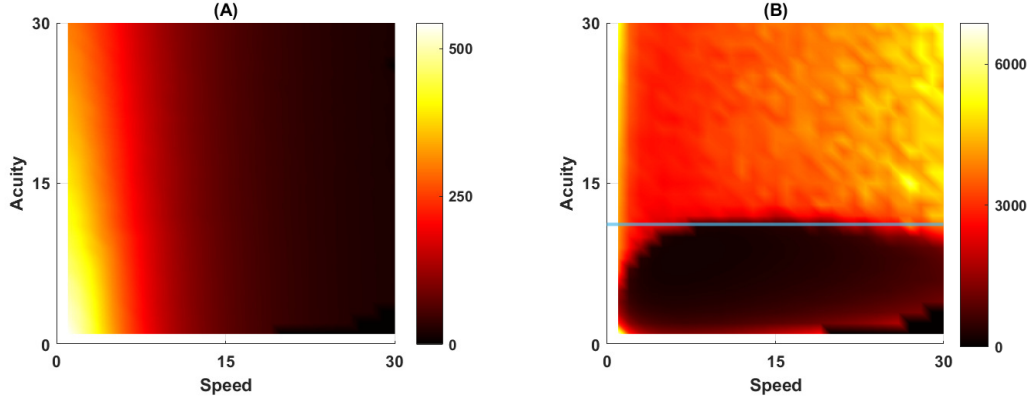


Figure 22: Non-evolving population with similar phenotypes: **(A)** population size, **(B)** available resources as a function of speed and acuity in a 200×200 domain at the equilibrium. Horizontal blue line separates the simulations which end with high resource density and low resource density. Each non-evolving birth-death simulation starts with the same phenotype and 100 agents. Resource replenishment rate was set to $\lambda = 1/500$ resources per unit time, $F = 25$ per resource and $T = 10000$.

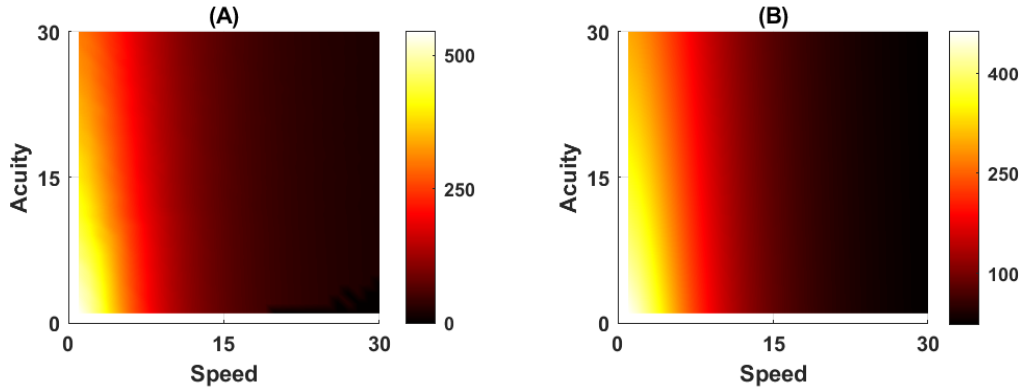


Figure 23: **(A)** Simulation result where the population as the function of speed and acuity in a 200×200 domain at the equilibrium. Each non-evolving, birth-death simulation starts with the same phenotype and 100 agents. Resource replenishment rate was set to $\lambda = 1/500$ resources per unit time, $F = 25$ per resource and $T = 10000$. **(B)** Number of agents ($\tilde{x} \times |\Omega|$) given by the equilibrium solution of Eq. (27) with the following parameters; $K_d = 100$, $K_b = 1000$, $\lambda = 1/500$, $|\Omega| = 200 \times 200$, $F = 25$, $T = 100$, and random initial agent density and initial metabolic scores.

with similar attributes compete with each other, the metabolic cost of these attributes dictates the population dynamics. Phenotypes with very costly attributes may forage to just maintain their energy requirement. Agents able to collect excess energy reproduce. However reproduction is costly, as energy is divided between parent and offspring. Hence, higher speeds and acuity typically lead to a smaller population, given equal resource rates (see Fig. 22A). To compare these result with the minimal mean field model described in Subsection 3.2, we recall at equilibrium the agent density for the system described by Eq. (27) is given by;

$$\tilde{x} = \frac{\lambda}{C(s, a) + \ln 2 \left(\frac{\tilde{l}^{\alpha+1}}{\tilde{l}^\alpha + (K_b)^\alpha} \right)} F,$$

where $\alpha = \beta$, K_b and K_d are birth and death propensities respectively, λ is resource replenishment rate, F is the caloric value of the resource, and $\tilde{l}$ is the equilibrium point for the average metabolic score.

Population (carrying capacity) of certain environment with non-evolving birth-death process are well approximated by above equilibrium points and the simulation results given in Fig. 22A agree with solution of the System (27) as shown in Fig. 23. In such similar phenotypes simulations, the number of available resource in the domain (resource density) at the equilibrium are determined by the agents' acuities. Some simulations attain equilibrium with low resource density and some with high resource density. The separation between simulations which result to high resource or low resource are due to synchronous movements of agents and under-harvesting (see Fig. 22B), which we discuss in the following Subsection 4.3.

4.3 Synchronized Motion and Spikes in Population Size

Although the non-evolving population dynamics is mainly dictated by the metabolic cost of motion, and speed is more costly than acuity, the resource density at equilibrium is determined by the agents' acuity in simulations with similar phenotypes, with non-evolving birth death processes (see Fig. 22B). When agents have larger acuity, they may not use it as speed is needed to reach the resource

before the other agent that ‘claim’ that resource. In such cases, many agents ‘see’ the same resource but only few can exploit it. In this case we observed collective motion of agents towards a single resource. As a consequence agents can lose energy rapidly by futilely following resources that are visible but that they fail to reach before others do. For the few successful agents who are either faster or happen to be closer to the next resource, the energy can be shared (if they reach the resource in the same time step) and used to sustain them. Hence the probability of these agents to go through birth process is small. Due to a lack of phenotypic variance, every agent moves in similar patterns within groups, resulting in under-harvesting. As a consequence, more resources are accumulated in the space, resulting in higher resource density.

We have identified following conditions to have such synchrony in birth–death simulations:

- The population is non-evolving with uniform phenotypes, so that the new-borns are the same phenotypes as the parents.
- The acuity is larger than the average minimum distance between a foraging agent and resources. For example, in a typical case on 200×200 space with $\lambda = 1/500$, the average minimum distance between an agent and resources (at the time of resource replenishment) is;

$$\bar{\delta}(m, b) = \frac{1}{2\sqrt{\lambda}} = \frac{1}{2\sqrt{1/500}} \approx 5\sqrt{5}.$$

So if any acuity $a > 5\sqrt{5}$ (in Fig. 22B), we see the high resource density at the equilibrium above the *acuity line* $a = 5\sqrt{5}$.

- The *dispersal distance* must be zero or small compared to an agent’s acuity. In such cases, offspring is placed at the same location or very near to heir parent at birth.

Hence, the periodic spikes in the non-evolving population are mainly due to the high resource rate, high acuity and small dispersion distance. We verify these facts by simulating a population on a domain of size 200×200 with resource rate $1/500$, speed $s = 25$ and acuity $a = 25$ for all agents in the population. We start the simulation with random number of identical agents with

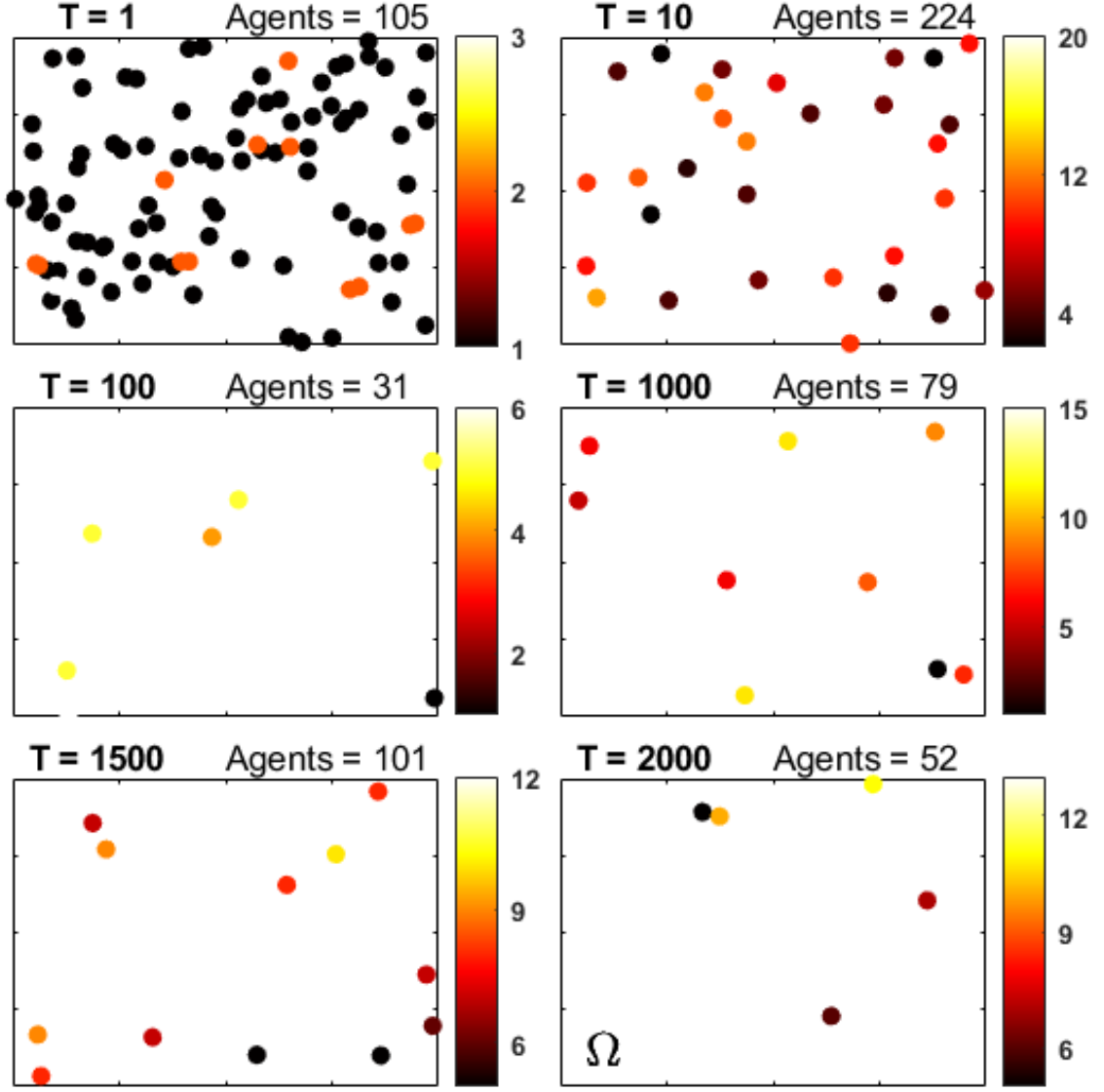


Figure 24: Snapshots of synchronized motion of agents in domain. The simulation starts with identical agents on random location in the domain. Since the birth-death process is non-evolving, the phenotypes have same attributes and the dispersal distance is small (0.1), the agents form groups and start to move together. Even though the number of agents is high, due to synchronous movement and the fact that many agents share the same coordinates, we see only a few dots (in the scatter plot) towards the end of the simulation. Simulation on 200×200 space, resource replenishment rate (λ) = $1/500$, $F = 25$, $s = 15$, $a = 30$, initial number of agents = 100, and $T = 2000$.

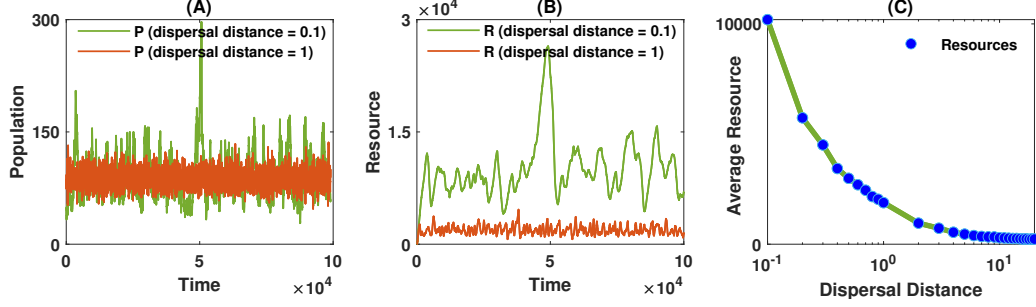


Figure 25: An example of the result of synchronous movement of similar phenotypic agents leads to the spikes in population and resource density at equilibrium when dispersal distance is small. Trajectory of: (A) population, and (B) resources available on the space with two different dispersal distances. (C) Semi-log plot of dispersal distance with resources (density) at the equilibrium. Though the average population remains almost the same with different dispersal distances, the resource density remains high with small dispersal distance. Simulation on 200×200 , resource replenishment rate (λ) = $1/500$, $F = 25$, $s = 25$, $a = 30$ and $T = 10000$.

these attributes and perform the simulation with various dispersal distances. Figs. 25A and 25B show the spikes in population and resource density. Although the average population remains same on these simulations, the resource density at equilibrium increases with a decrease in dispersal distance¹⁹ (Fig. 25C).

4.4 Population and Attributes as Functions of Resource Environment

The foraging patterns in simulations with heterogeneous populations are distinct and complex, in contrast to those of homogeneous phenotypes. When agents with different attributes compete for resources in an environment it becomes challenging to analytically describe the extent of interactions between them. In an evolving population, due to the differences in traits and phenotypic variances emerging from mutation during birth, the mean field model described in Section 3 may not be able to capture the evolution of attributes. To find the population dynamics of an evolving population and the trajectory of the attributes as the population evolves, we simulated the evolution of populations in different environments with different initial parameters.

¹⁹the notion of dispersal distance is mainly applied to explain synchrony and spikes in non-evolving population. In evolving population, the model itself creates a phenotypic variance and hence the synchrony vanishes within short period of time, however we take standard normally distributed dispersal distance in all birth-death simulations.

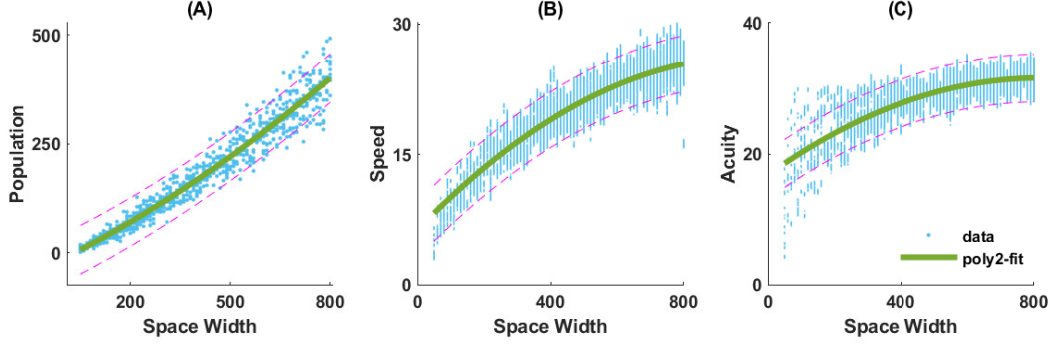


Figure 26: Population and attributes in different domains with low resource rate $\lambda = 1.25 \times 10^{-4}$, high caloric value $F = 400$: **(A)** population, **(B)** speed, and **(C)** acuity vs the width of $|\Omega|$, $T = 10000$. For evolving population: $\epsilon_s, \epsilon_a = 0.05$.

As we saw in previous sections the resource collection rates for certain homogeneous phenotypes mainly depend on the resource environment itself. We extend this idea to evolving populations, and validate our assertion that the population size and attributes at equilibrium are determined by the resource environment.

To understand the results of our simulations, we will assume that the resource environment characteristics are features, *i.e.* independent variables, and use them to predict the population size, speed and acuity in equilibrium. In particular the resource environment is defined by the following features,

$$\text{Features (input)} = \left\{ \begin{array}{c} \text{Resource Rate} \\ \text{Resource value (energy)} \\ \text{Size of space} \end{array} \right\} \Rightarrow \left\{ \begin{array}{c} \text{Population} \\ \text{Speed} \\ \text{Acuity} \end{array} \right\}.$$

Here we also indicate that the features of the environment are used to predict the features of the population at equilibrium.

Although agents need to accumulate metabolic energy to forage and reproduce, the quality of resources (metabolic energy per resource) is also critical for a successful foraging. For instance if the resource density is high but the resources have less energy (low ‘quality’) then the agents have to

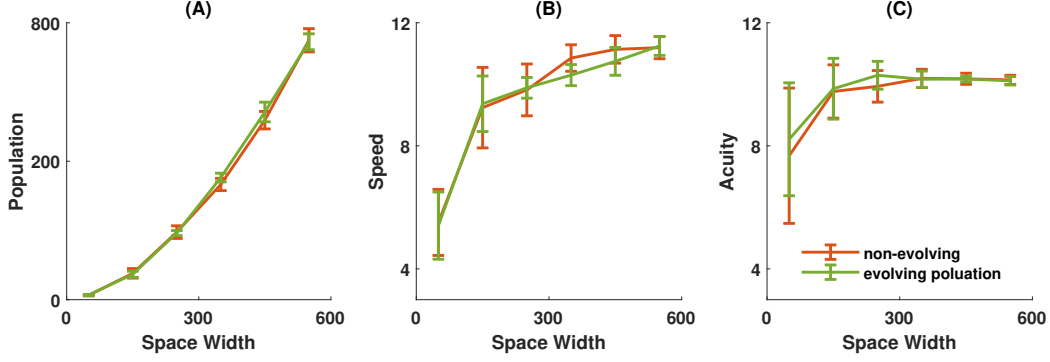


Figure 27: Population size and attributes at equilibrium in different domains with high resource rate $\lambda = 2 \times 10^{-3}$, low caloric value $F = 25$: **(A)** population, **(B)** speed, and **(C)** acuity vs the width of Ω , $T = 10000$. For evolving population: $\epsilon_s, \epsilon_a = 0.05$. For non-evolving population, simulations start with 10000 agents randomly assigned to various attributes chosen from $s_k \in [1, 30]$ and $a_k \in [1, 30]$.

forage for a considerable time to increase their metabolic score by an appreciable amount. However, if the resource density is low with high caloric value (high ‘quality’) then agents need to find fewer resources, but may need to put more effort into finding such high energy resources. Hence, fixing the average total energy (caloric value) input rate per unit area, we performed simulations on two kinds of resource environments: **(a)** high resource rate (low quality), and **(b)** low resource rate (high quality). In both low resource rate (Fig. 26) and high resource rate (Fig. 27) environments, the population size grows as a quadratic function of space width. However, speed and accuracy at equilibrium grow initially as a function of space-size and eventually settle to high values for larger spaces.

Since these simulation were performed with fixed resource values (high quality and low quality resources) and fixed resource rates, the results thus obtained could not elucidate the effects of interaction between different input features. When the resource rate and resource values (caloric value) change simultaneously along with change in domain size, then the problem becomes multi-dimensional. We use multivariate polynomial regression on row staked multidimensional data to fit a second degree polynomial [18], and estimate the values of output with the fitted polynomial as follows.

We simulate agents foraging on domains of sizes ranging between 50×50 and 800×800 , in increments of 50 units per side. For every simulation we chose a resource rate which was either low $\lambda = 1.25 \times 10^{-4}$ or high $\lambda = 2 \times 10^{-3}$, and a corresponding resource value (caloric value of each resource) ranging between 10 to 1600, with intervals of 40. The initial number of agents was set to 10000, and each agent was equipped with initial attributes s_k and a_k chosen randomly from a fixed range. We ran 10 independent trials for each domain and each resource value to find the final population, speed and acuity.

Once this data was generated we fit the resulting speed, acuity and population size to the parameters characterizing the environment using polynomial regression. We assumed a linear dependence on the parameters, except for the domain side, b . We also included possible interactions between domain size and resource caloric value, F . We hence obtained the following model for the data,

$$\begin{cases} X = \beta_0^X + \beta_1^X b + \beta_2^X F + \beta_3^X b^2 + \beta_4^X b \cdot F \\ s = \beta_0^s + \beta_1^s b + \beta_2^s F + \beta_3^s b^2 + \beta_4^s b \cdot F \\ a = \beta_0^a + \beta_1^a b + \beta_2^a F + \beta_3^a b^2 + \beta_4^a b \cdot F. \end{cases} \quad (33)$$

Here X is the population size at equilibrium, s the average speed, and a the average acuity at equilibrium. Since from single-variable relation (see Figs. 26 and 27), the population has a non-linear relation with $|\Omega|$, for a fixed resource environment.

The second-degree polynomial fit to the data given by Eq. (33) is shown in Fig. 28. The *goodness of fit* for the fitted value with respect to actual values are presented in the Fig. 29, and the coefficients of fitted second degree polynomials with R-squared values, mean absolute error (MAE), mean-squared error (MSE) and 95% confidence interval are listed on the Tables 1 and 2. Since the size of second degree terms ($\beta_3^s b^2$ and $\beta_3^a b^2$) are very small as compared to the size of first degree terms ($\beta_1^s b$ and $\beta_1^a b$) for attributes, a linear model would be sufficient to capture the dependence of the attributes on the domain size. Similarly, the terms which represent the interaction between domain width and resource value ($\beta_4^s b \cdot F$ and $\beta_4^a b \cdot F$) for attributes are negligible as compared to the first degree terms for resource value ($\beta_2^s F$ and $\beta_2^a F$), showing that

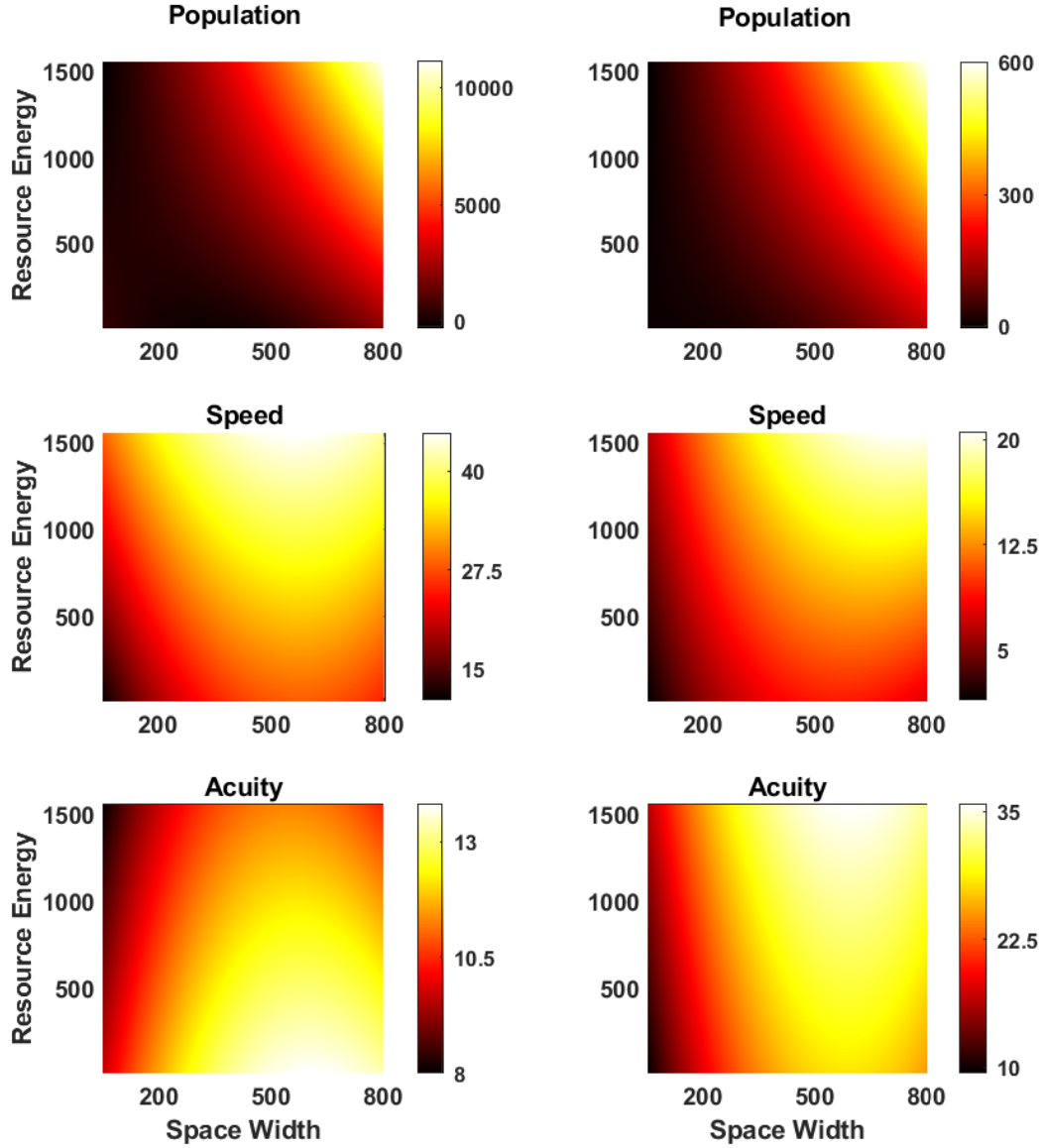


Figure 28: Second degree polynomial fit for population, speed and acuity for two resource environments; first column: high resource rate ($\lambda = 2 \times 10^{-3}$) environment, and second column: low resource rate ($\lambda = 1.25 \times 10^{-4}$) environment. The domain Ω and resource value (caloric value) are randomly chosen from discrete uniform distributions. $T = 10000$, ϵ_s and $\epsilon_a = 0.05$.

there is roughly a linear relation between resource values and attributes.

$\lambda = 0.002$	Population	Speed	Acuity
β_0 (95% C.I.)	808.454 (728.6, 888.3)	7.575 (6.925, 8.856)	8.8995 (8.496, 9.303)
β_1 (95% C.I.)	-6.103 (-6.547, -5.659)	0.0707 (0.0636, 0.0778)	0.0161 (0.0138, 0.0183)
β_2 (95% C.I.)	-0.982 (-1.056, -0.9086)	0.0111 (0.0099, 0.0122)	-0.001 (-0.0013, -0.0006)
β_3 (95% C.I.)	0.0094 (0.0089, 0.0098)	-6.125e-05 (-6.933e-05, -5.318e-05)	-1.316e-05 (-1.571e-05, -1.063e-05)
β_4 (95% C.I.)	0.0086 (0.0084, 0.0088)	-5.867e-07 (-4.011e-06, 2.838e-06)	-1.043e-06 (-2.122e-06, -3.469e-08)
R-Square -	0.9852	0.7671	0.4925
MSE -	6.866e+04	17.68	1.752
MAE -	179.606	3.260	0.9048

Table 1: Coefficients of multi-polynomial regression fit for high-resource rate environment

4.5 Birth-Death Process Selects Competitive Phenotypes.

Since resources are readily available in a high resource rate environment, agents evolve with lower attribute values (Figs. 27B and 27C). However, if the resource energy (caloric value) is also high, then agents will evolve with higher speeds to outcompete other foraging agents. The fitness of phenotypes with these attributes is mainly determined by the resource environment, and initial attribute values do not impact the emergence of these traits. Moreover, other initial values like number of agents and initial metabolic scores do not influence the ultimate evolution process.

One of the key features of our model is that the birth-death rates do not depend on the agent’s phenotype directly. The fitness of an agent is impacted by the phenotype only because the phenotype determines an agent’s ability to forage and accumulate metabolic energy. Similarly, the

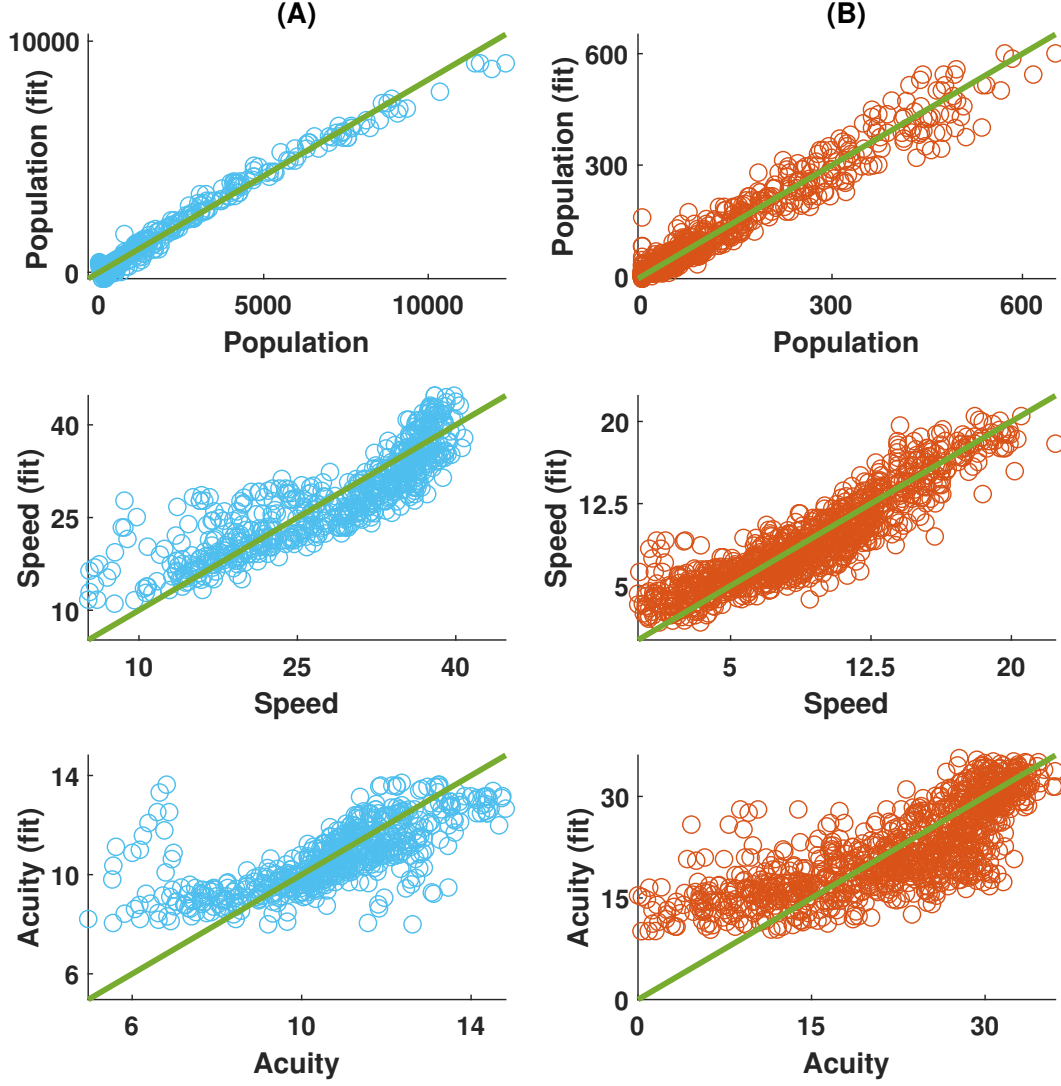


Figure 29: Goodness of fit of 2nd-degree polynomial for model predicted values versus the true values. First column: high resource rate ($\lambda = 2 \times 10^{-3}$) environment and second column: low resource rate ($\lambda = 1.25 \times 10^{-4}$) environment. The domain Ω and resource value (caloric value) are randomly choose from a given range. $T = 10000$, ϵ_s and $\epsilon_a = 0.05$.

$\lambda = 1.25\text{e-}04$	Population	Speed	Acuity
β_0 (95% C.I.)	9.093 (2.574, 15.61)	-0.2721 (-0.7444, 0.2001)	5.748 (4.441, 7.055)
β_1 (95% C.I.)	-0.0806 (-0.1155, -0.04575)	0.0333 (0.03086, 0.03591)	0.0760 (0.06903, 0.08301)
β_2 (95% C.I.)	-0.0271 (-0.03287, -0.02133)	0.00286 (0.002444, 0.00328)	0.0044 (0.003251, 0.005565)
β_3 (95% C.I.)	0.00033 (0.0002917, 0.0003699)	-2.971e-05 (-3.255e-05, -2.688e-05)	-6.48e-05 (-7.265e-05, -5.696e-05)
β_4 (95% C.I.)	0.00038 (0.000373, 0.0004068)	6.898e-06 (5.674e-06, 8.122e-06)	8.006e-07 (-2.585e-06, 4.187e-06)
R-Square -	0.9564	0.8324	0.6004
MSE -	677.98	3.5585	27.2402
MAE -	16.3996	1.4506	4.0356

Table 2: Coefficients of multi-polynomial regression fit for low-resource rate environment

population of a certain environment depends on the birth–death rates and hence on the resource rates and phenotypes. Since the model is based on the assumption that offspring has the same phenotype as the parent up to a small difference due to mutation, we look into the direction of change in phenotype and overall dynamics of population.

To understand how competitive phenotypes are selected we simulated the population in different resource environments. We started the simulations with a large number of agents, each characterized by a phenotypic vector, $\xi_k = (s_k, a_k)$, where $s_k \in [s_{min}, s_{max}]$ and $a_k \in [a_{min}, a_{max}]$ were selected uniformly and at random from the corresponding interval. Fig. 30 shows that if, for fixed average energy per unit area, the resource rate is low, then agents with higher attribute values are selected for. In the case of non evolving population, once any phenotype dies and a trait is removed from the space, there is no mechanism for the emergence of such traits again. Hence phenotypes with lower attributes become fit and population remains higher in non-evolving simulations.

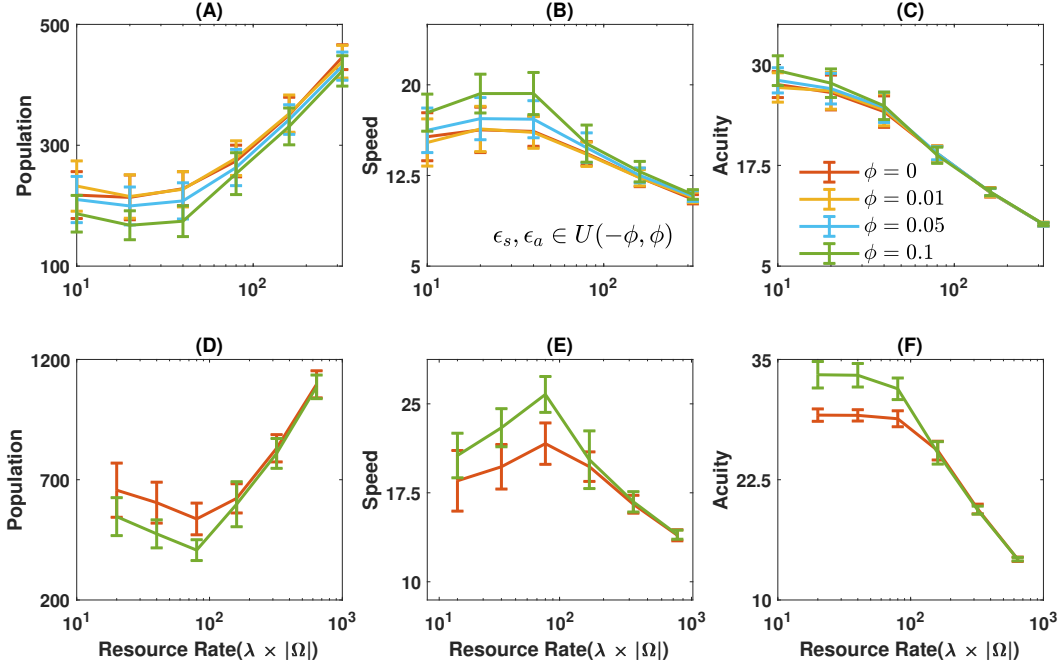


Figure 30: Population and attributes at equilibrium for evolving ($\phi > 0$) and non-evolving ($\phi = 0$) population simulations; first row: 400×400 and second row: 800×800 spaces. Each semi-log plot consists of data from six different resource rate–energy pairs ($\lambda \times |\Omega|, F$) so that average energy per unit area is constant $\lambda|\Omega|F = 32000$ and $T = 10000$.

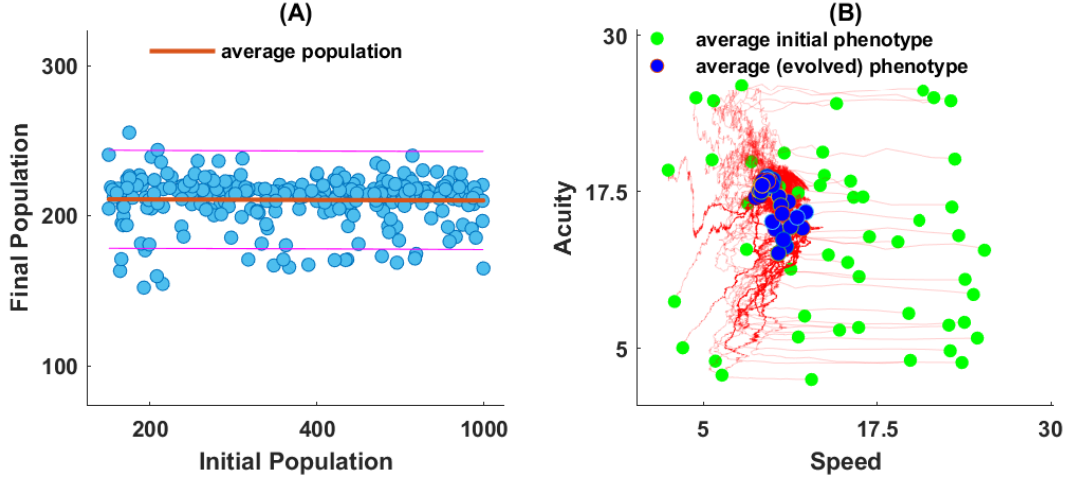


Figure 31: Population and attributes are independent of initial population and phenotypes from which the simulations start. With random initial population and phenotypes, the model selects the ‘fit’ phenotypes and attains an equilibrium with an average stationary population. Panel **(A)** population and its average over 500 simulations. In panel **(B)** a green dot represents the average initial phenotype, blue dot represents the average (evolved) phenotype, and red line shows the trajectory of the average phenotype on the phenotype space for a single simulation. Simulations on 200×200 space, resource rate $\lambda = 1/500$, $F = 100$, $T = 10000$, and $\epsilon_s, \epsilon_a = 0.05$.

The stochastic birth–death process in agent-based simulations is indeed independent of choice of initial values, and the ‘fit’ phenotypes survive as the result of the birth–death process. Although the time to reach equilibrium (when average population and available resources become stationary in the space) may differ for different initial conditions, ultimately the process reaches a particular distribution of phenotypes (see Fig. 31). Interestingly, as shown in Fig. 31, speed seems to be under stronger selective pressure, and reaches equilibrium before acuity. This could be due to the higher metabolic cost of this attribute.

4.6 Multimodality and Co-existence

When we explore the process of selection of ‘fit’ phenotypes in a certain environment, we generally track the average phenotypes and their trajectories in phenotype space (see Fig. 31). However, the evolved population may consist of heterogeneous phenotypes and there may be intrinsic distributions of different traits. To characterize the resulting distributions we performed further simulations

starting with 10000 agents on domains of size 400×400 and 800×800 . Each agent was again initially assigned a phenotype vector $\xi = (s_k, a_k)$ where s_k and a_k were sampled from $[s_{min}, s_{max}]$ and $[a_{min}, a_{max}]$ uniformly and at random, respectively. The energy produced per unit area was fixed, and we varied both the resource rate and the resource energy simultaneously.

When resource rate and resource energy were changed in different simulations, the population dynamics also changed. Although the average energy supplied to the system per unit area was fixed, different distributions of attributes emerged in the system at equilibrium. In some cases, two or more distinct phenotypes appeared to co-exist in the simulations. To verify this observation, we performed an additional 100 simulations on each environment described above, and tested whether the resulting equilibrium were multimodal. We found that some of the resource environments produced bi-modal distributions of attributes. Histograms and the distribution plots of speed and acuity show that the distributions of these attributes are indeed bi-modal in some cases (see Figures 32B, 32C, 33 and 34). This indicates that in some cases two groups of agents with distinct phenotypes could co-exist for extended amounts of time in our simulations.

The multi-modal distributions of attributes shown in Figures 33 and 34 are based on the final attributes collapsed over 100 simulations. This leaves open the possibility that such multimodality is due to different distributions being reached in different simulations, rather than coexistence. To verify that this is not the case, we re-ran several of these simulations in environments in which multimodality was apparent (see Fig. 35). We found that, with suitable resource environments, the multimodal distribution of speed emerges from a single simulation also, as the birth-death simulation progresses. We also applied *Hartigan's dip statistics test* [36, 37, 58] to confirm multimodality in these distributions. The dip statistic test result are consistent with multiple peaks seen in the distribution plots (see Appendix D).

When resources are abundant, most agents can obtain resources and competition is weaker. As a result, most phenotypes with higher attributes or lower attributes can collect resources, survive and multiply. On the other hand, if resources are rare, only the faster and more efficient exploring phenotypes can obtain resources. Hence there will be stronger competition, which creates a strong

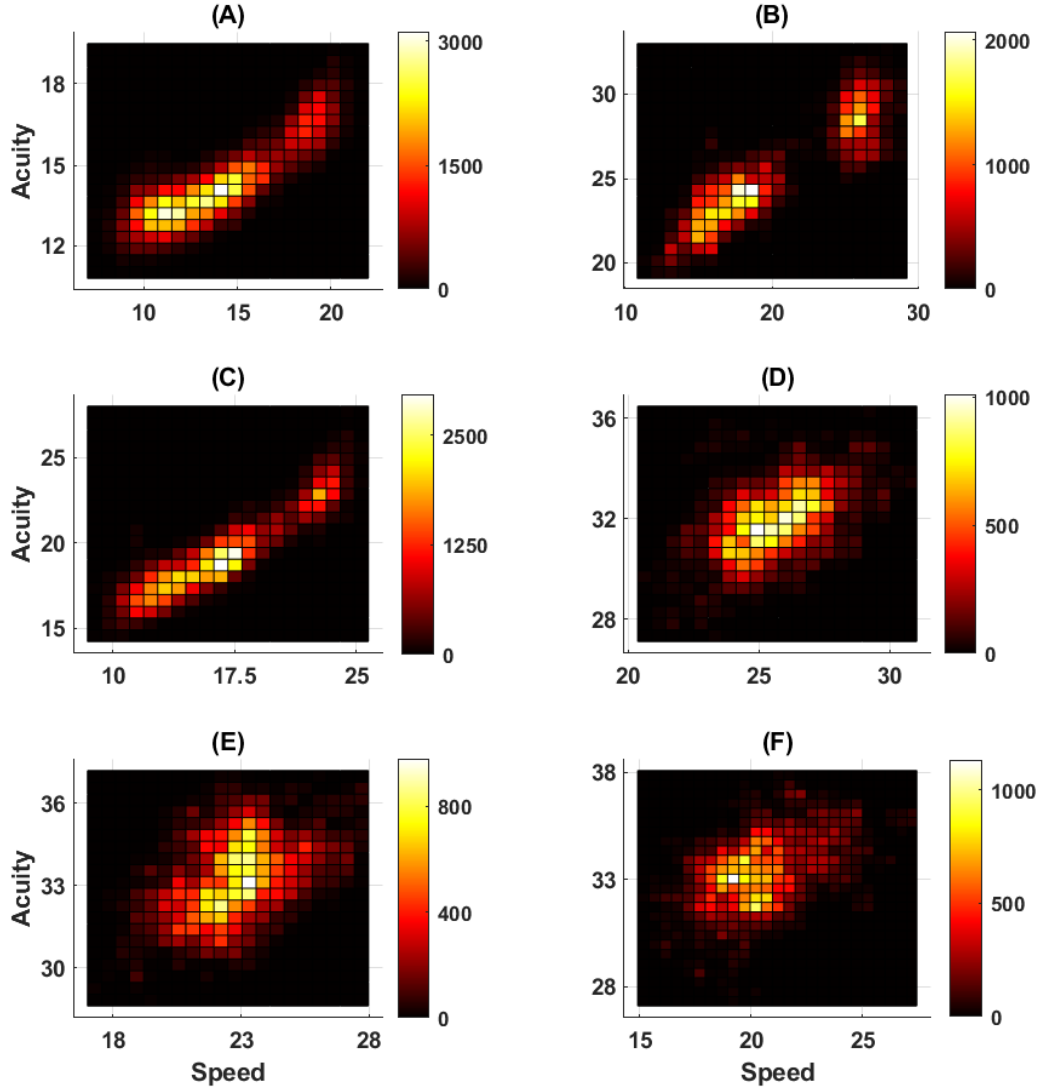


Figure 32: Estimated densities of speed and acuity: for evolving ($\phi = 0.05$) population simulations on 800×800 spaces. Each plot consists of data from six different resource rate–energy pairs $(\lambda \times |\Omega|, F)$: **(A)** (640, 50), **(B)** (320, 100), **(C)** (160, 200), **(D)** (80, 400), **(E)** (40, 800), and **(F)** (20, 1600), so that average energy per unit area is constant $\lambda|\Omega|F = 32000$. $T = 10000$, on 800×800 space. Data is pooled across 100 independent simulations for each case.

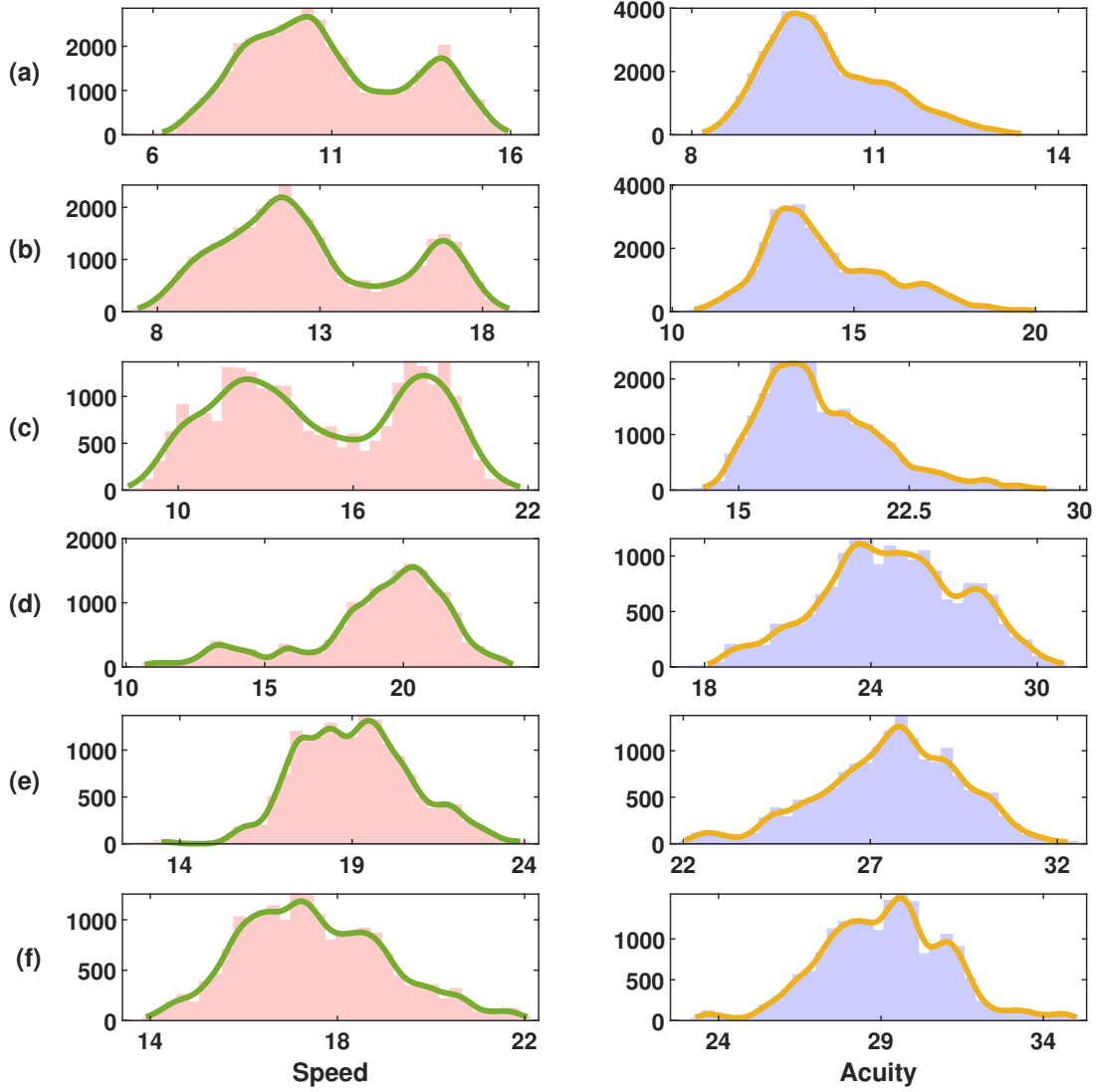


Figure 33: Distributions of speed (first column) and acuity (second column): for evolving ($\phi = 0.05$) population simulations on 400×400 spaces. Each plot consists of data from six different resource rate–energy pairs $(\lambda \times |\Omega|, F)$: **(a)** (640, 12.5), **(b)** (320, 25), **(c)** (160, 50), **(d)** (80, 100), **(e)** (40, 200), and **(f)** (20, 400), so that the average energy generated per unit area was constant. $\lambda \times |\Omega| \times F = 8000$, $T = 10000$. Data is pooled across 100 independent simulations for each case.

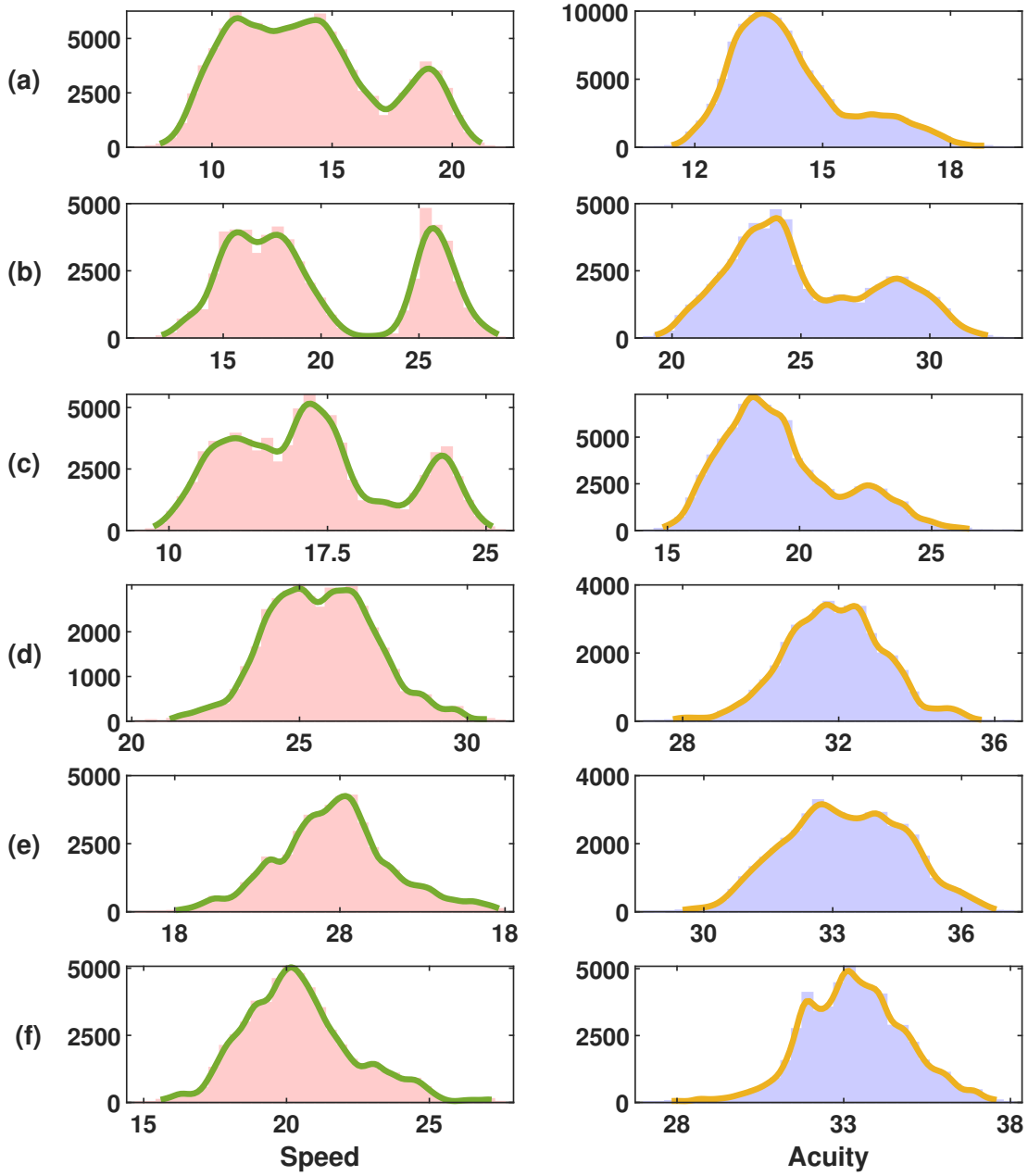


Figure 34: Distributions of speed (first column) and acuity (second column): for evolving ($\phi = 0.05$) population simulations on 800×800 spaces. Each plot consists of data from six different resource rate–energy pairs ($\lambda \times |\Omega|$, F): **(a)** (640, 50), **(b)** (320, 100), **(c)** (160, 200), **(d)** (80, 400), **(e)** (40, 800), and **(f)** (20, 1600), so that the average energy generated per unit area was constant. $\lambda \times |\Omega| \times F = 32000$, $T = 10000$. Data is pooled across 100 independent simulations for each case.

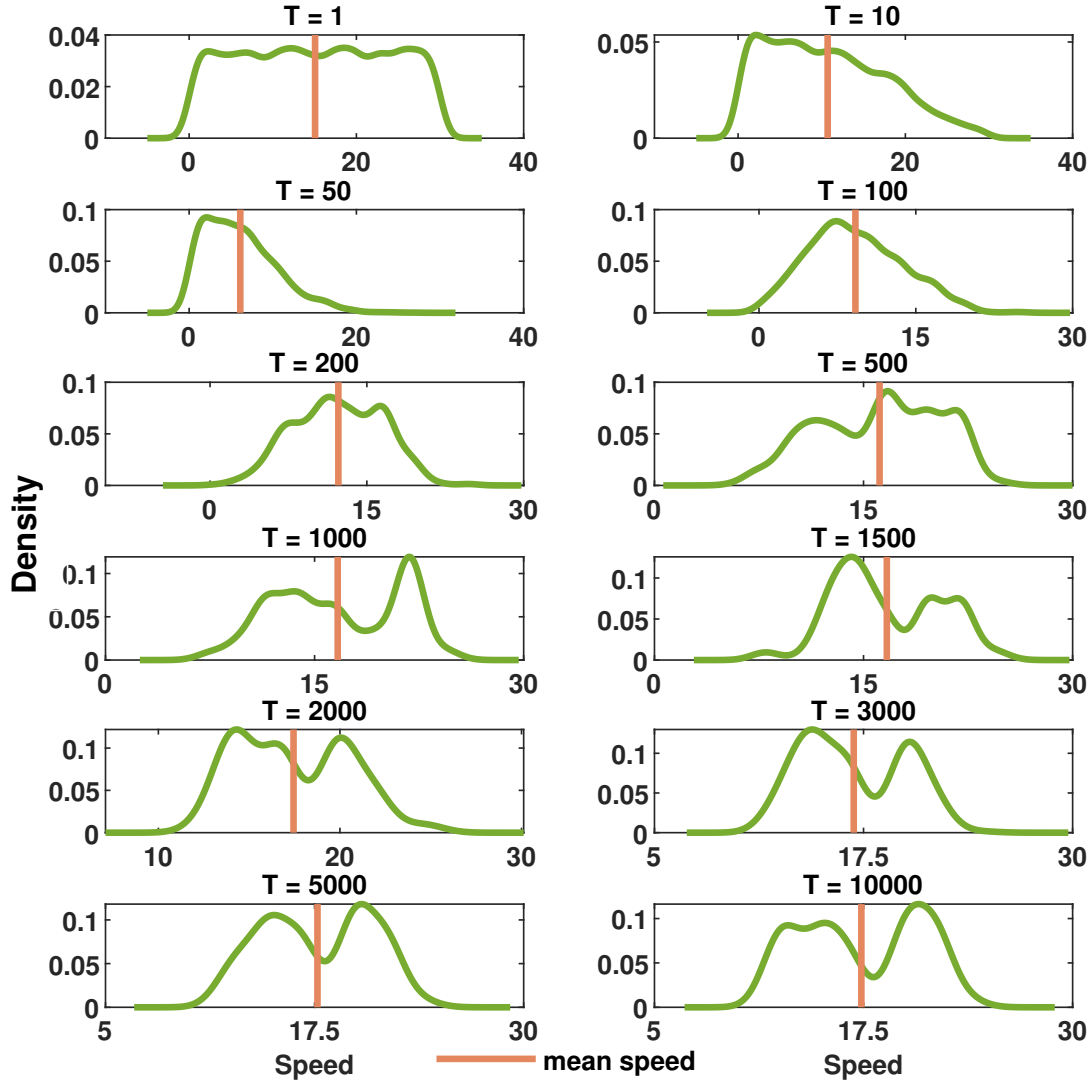


Figure 35: Kernel density estimates of the distribution of speed in a typical simulation where bi-modality of phenotypes emerges. The evolving ($\phi = 0.05$) population simulation starts with a uniform distribution of speed and ultimately shows the bi-modal distribution. Here $\lambda = 1/500$, $F = 25$ and $T = 10000$ on 400×400 space.

selective pressure favorable to the agents with higher speed and acuity. So the phenotypes with higher attributes may have higher chances of finding resources and reproducing, passing these competitive attributes to the offsprings. Between these two extreme conditions, the birth-death processes lead to bimodal and multimodal distribution of attributes. In these cases, a few agents with high metabolism can coexist with a mass of agents with low metabolism. Moreover energy expended depends quadratically on speed (Eq. (17)) and higher speed agents can search for the resource swiftly. Hence, small changes in speed can have a significant impact on foraging success and energy expenditure process. Accordingly, the histograms and probability distribution functions for speed show distinctive bimodality when some unique resource conditions are met in the foraging spaces.

4.7 Distribution of Resources and Dynamics of the Population

We have seen in the previous subsection that distinct phenotypes can co-exist in some environments. These resource environments were homogeneous, and resources appeared randomly and uniformly in the domain. We observed a similar kind of bi-modal distribution of attributes with ‘patchy’ resource environments. In such environments resources appear in patches of various size (radius or width w), and are replenished by resources for a certain time. Let λ be the resource rate on a domain $|\Omega|$. We started simulations with $\lambda \times |\Omega|$ resources at locations distributed in the domain uniformly and at random. For every interval of Δt , on average $\lambda \times |\Omega| \times \Delta t$ resources were added to the system within a distance w around any of the previous resource location. In that way we can have $\lambda \times |\Omega|$ patches of resources in the domain at any instant of time t . This process repeats up to a fixed time, the *patch duration*, K , and further resource appear at a new location which is chosen uniformly and at random in the domain. Regardless of w , if $K = 0$, then every new resource belongs to a new patch, and we have a homogeneous resource environment. For larger values of K , the patches can become more dense, and patches are permanent when $K = T$.

In some cases, when the rate of resource generation is high in a patchy resource environment, the dynamics of the population and the distribution of attributes are similar to those in homogeneous

Distribution of Speed

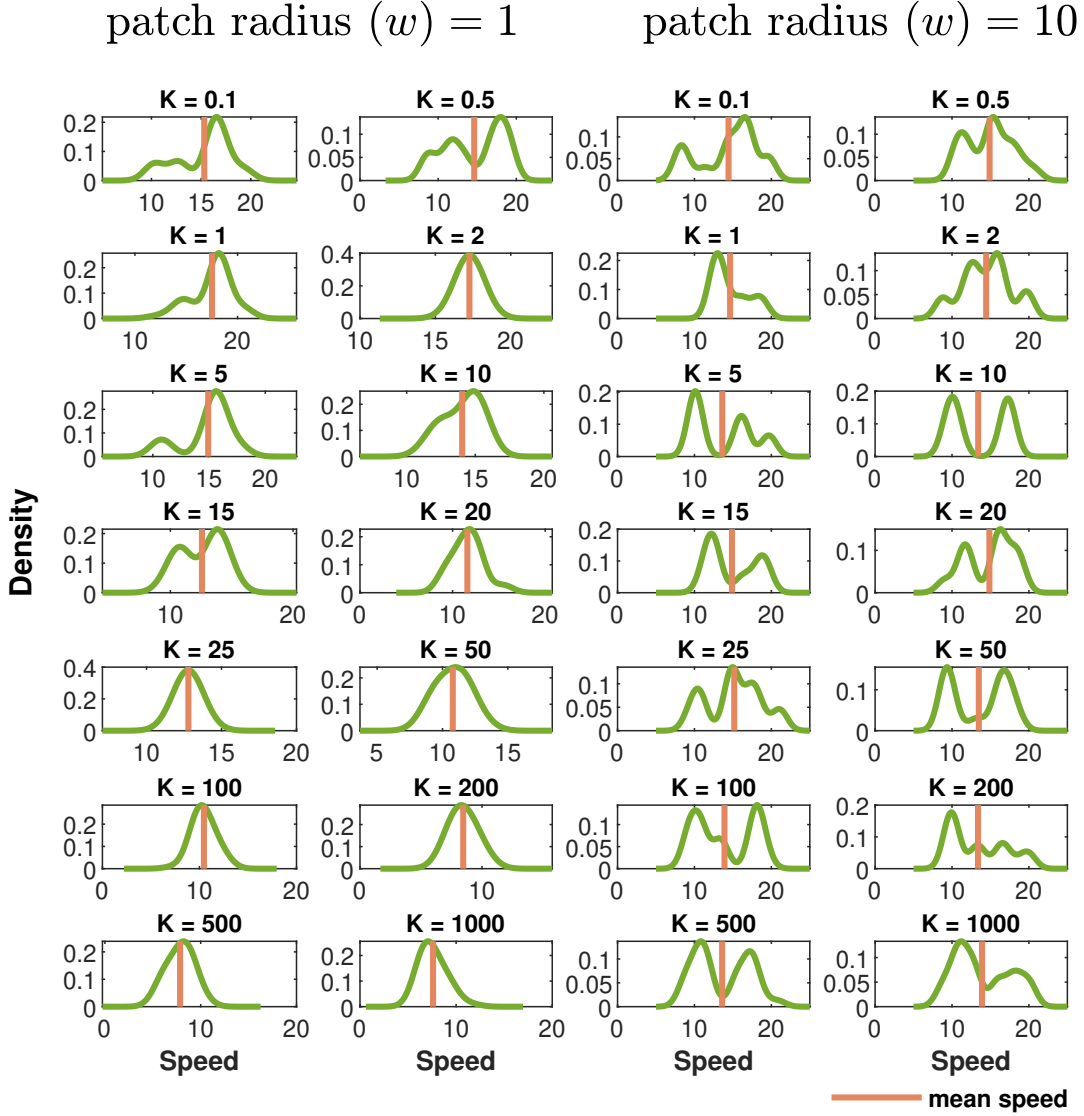


Figure 36: Kernel density plots for evolved speed on patchy resource environment with fixed K ; left two columns: patch radius, $w = 1$, and right two columns: patch radius, $w = 10$. High resource rate (λ) = $1/500$, $F = 25$, $\phi = 0.05$, and $T = 10000$ on 400×400 space.

resource environments. When $K = 0$, the resource environment becomes homogeneous. Similarly, when w is large ($w > 1/2\sqrt{\lambda}$) and resource rate is high, then most of the patches overlap with each other and the resource environment is again approximately homogeneous. For $w < 1/2\sqrt{\lambda}$, some patches do not overlap with each other. In such an environment some agents tend to explore new patches, while others stay and forage inside patches. While faster agents can explore and forage quickly, the slower ones tend to stay in a patch to collect resources, expending less metabolic energy, and reproducing quickly. We hence observe the bimodality in the distribution of speed in patchy resource environment (see Fig. 36). However, these bimodalities can often shift their peaks and cause changes in the the average speed of agents.

When resource rate is low, then the average distance between two patches becomes large. For smaller w and larger K , agents with lower speed emerge. These agents forage inside small dense patches, and proliferate and evolve with smaller attribute values (see Fig. 37). When a patch is exhausted, some of these phenotypes are able to find another patch. The low metabolic cost and high population size allows the population to disperse and some of them to find a new patch, although many die in the voyage. Hence for smaller w , larger K in low resource rate environment, agents with smaller attributes can be fit. Indeed, due to stronger selective pressures and uncertain resource environment, we see multimodality in few instances only (see Fig. 37).

4.8 Correlations and Trade-offs Between Attributes

In Subsection 1.6, we discussed how constraints on available resources can lead to phenotypic trade-offs. While the parameter values may vary quantitatively, these trade-offs are often present. Additionally, some phenotypic traits have correlated roles in determining an organism’s fitness, meaning that changes in one trait can impact others. While phenotypic models²⁰ typically assume that trade-offs are fixed functions, this is not always accurate [93]. Nonetheless, phenotypic models based on a fixed trade-off function still offer a broad qualitative prediction of the equilibrium state that a population would reach in response to changes in selection pressure [93].

²⁰model based on observable traits and characteristics of an organism.

Distribution of Speed

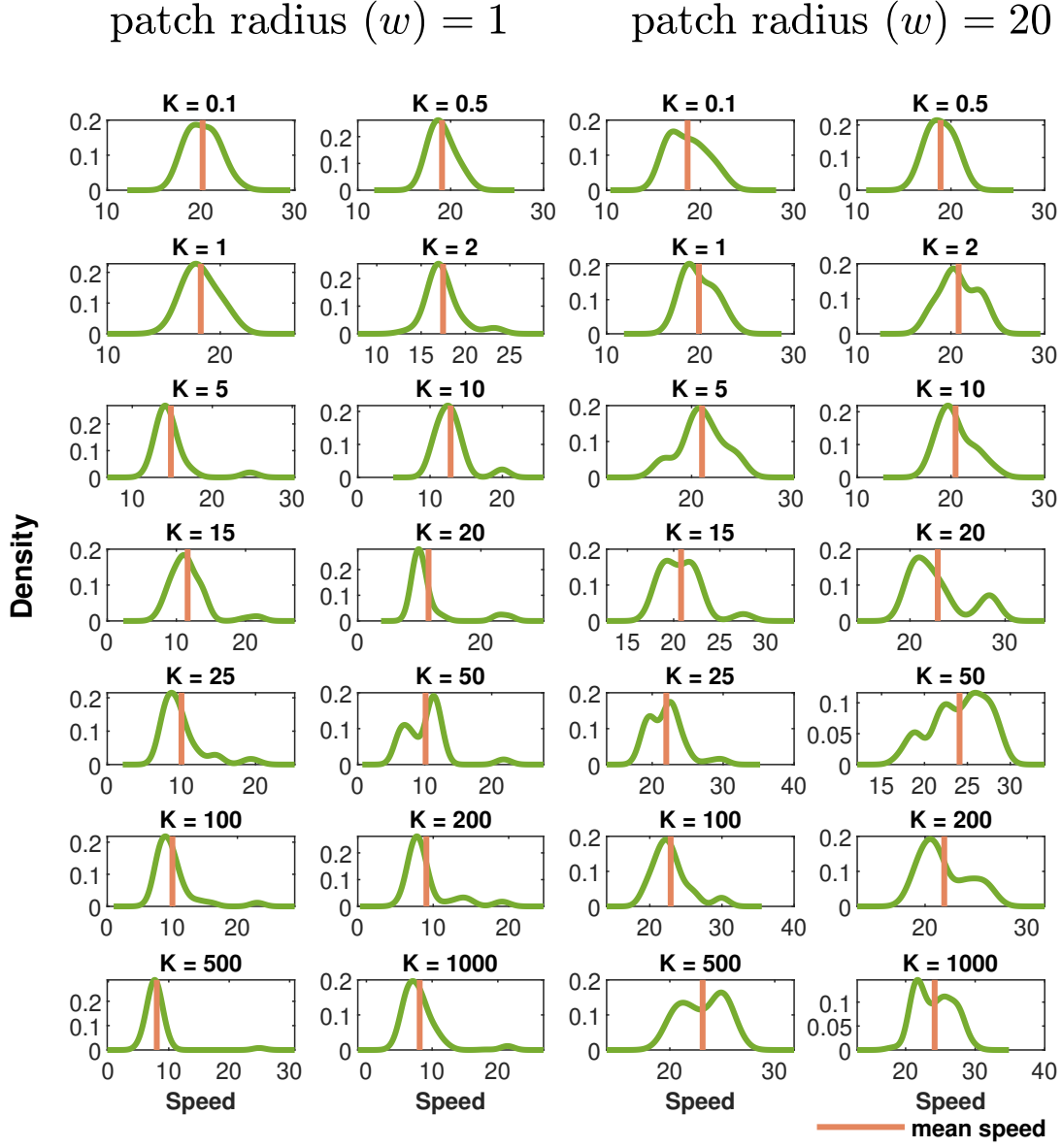


Figure 37: Kernel density plots for evolved speed on patchy resource environments with fixed K ; left two columns: patch radius $w = 1$, and right two columns: patch radius, $w = 20$. Low resource rate (λ) = 1.25×10^{-4} , $F = 400$, $\phi = 0.05$, and $T = 10000$ on 400×400 space.

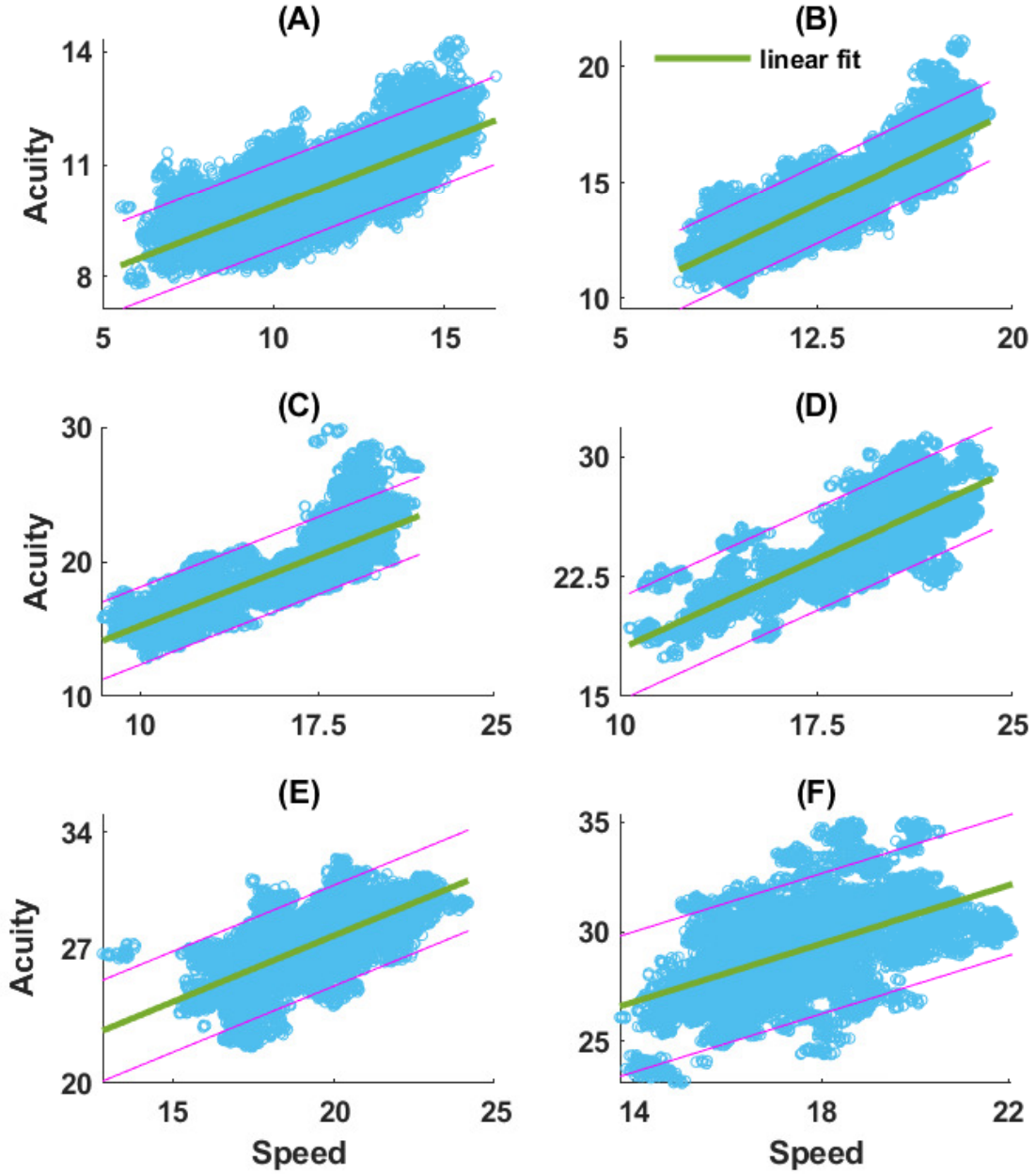


Figure 38: Scatter-plots of speed and acuity where each dot represents a phenotype at the equilibrium, for evolving ($\phi = 0.05$) population simulations on 400×400 spaces. Each plot consists of data from six different resource rate–energy pairs $(\lambda \times |\Omega|, F)$: **(A)** (640, 12.5), **(B)** (320, 25), **(C)** (160, 50), **(D)** (80, 100), **(E)** (40, 200), and **(F)** (20, 400), so that average energy per unit area is constant $\lambda|\Omega|F = 8000$. $T = 10000$. Green lines show the linear fits, which represent the linear approximation to the relationship between the speed and acuity.

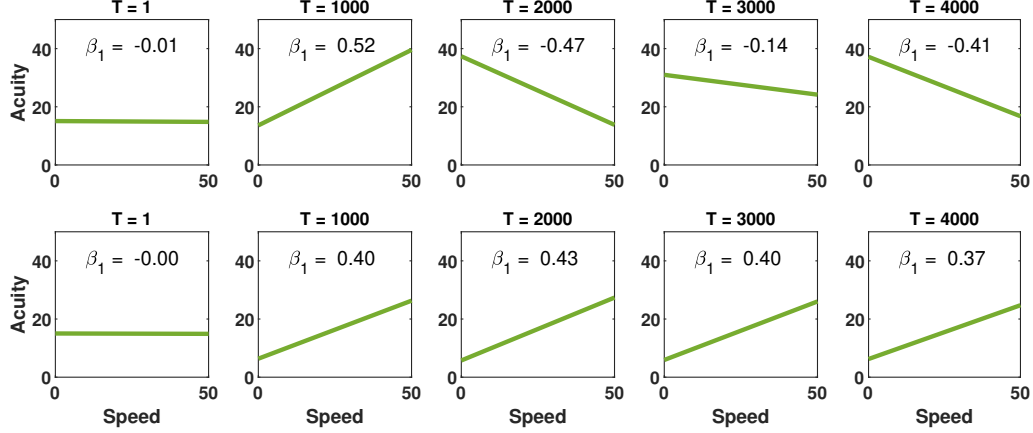


Figure 39: Linear regression analysis of the relationship between two traits (speed and acuity) over time, depicted as a series of subplots. The subplots show snapshots of the linear regression line at different time stamps, starting with the initial horizontal line (left column) and ending with the final linear relationship (rightmost column). The simulations were conducted in two different resource environments, with the first row representing a low resource rate-high energy environment, and the second row representing a high resource rate-low energy environment. The initial attributes were chosen randomly, resulting in a zero slope. As the selective pressure weakens, only the changes in the intercept become visible, and with strong selective pressure, both the intercept and slope (β_1) change. Evolving ($\phi = 0.05$) population simulation on 200×200 domain, $(\lambda|\Omega|, F) = (10, 1600)$ for low resource rate-high energy environment and $(\lambda|\Omega|, F) = (320, 50)$ for high resource rate-low energy environment, $T = 4000$.

Even though the two traits (speed and acuity) usually show convergences, exhibiting bimodal distribution in some environments, their transient relation shows a linear model. Fig. 38 also illustrates the linear relation and positive correlation between speed and acuity that we observed in our simulations. To infer the strength of the correlation between them in different resource environments, we find the coefficients (slope and intercept) for the linear regression fit, as described in the next paragraph.

When the resource rate is low but the energy of the resources is high, the agents in the simulation must search for the scarce, high-calorie resources in the environment. To do this effectively, they require a high speed, but also some level of acuity. However, an agent's success is largely determined by its speed, as those that can collect resources more quickly are more fit and have more offsprings. As a result, the agents evolve to have higher speed and lower acuity, leading to a negative correlation

between these traits (see Fig. 39). However, there are some lines (for some time instants) in the plot with higher intercepts, which correspond to agents with high speed and low acuity. On the other hand, when the resource environment has high resource rate but low energy per resource, most agents are able to easily obtain resources. In this scenario, a wide range of phenotypes emerge in the space, which maintains the variances of the attributes. As a result, only the intercept of the regression line changes (see Fig. 39 second row). Based on this evidence and observing the distributions of attributes over time, it appears that, with the weaker selective pressure, the slope of the regression line remains constant but the intercept changes due to changes in average attributes. However, if the selective pressure is strong enough, then both slope and intercept of the regression line change, resulting the substantial change in the correlation between two attributes.

4.9 Mean Field Model and Numerical Solution of *Non-linear ODEs*

Here, we assume that the birth-death process in foraging game as a non linear phenomenon, whose solution may not be explicitly established. So instead of solving such non-linear systems explicitly, we only look for equilibrium solutions if the system is stable and approximate the solutions numerically. Our main goal of use of mean-field model is to gain further insight of population dynamics with agreement with simulation result.

In Section 2, we have explained in detail about the agent based foraging and stochastic birth death simulation models. Using these agent based simulation, we have explained population dynamics and distribution of attributes in different resource environments. These simulation models are flexible and can accommodate any number of parameters however are difficult to calibrate and sometime lack analytic insights [13]. So, an analytical perspective at aggregate level driven by mean-field model and differential equations can complement simulations, and provide a tool for comparison to choose the right approach for our population and attribute dynamics problem.

We have seen in Subsection 4.2, that the population dynamics for non-evolving population with similar phenotypes can be well approximated by solutions of a non-linear system of differential equations (see Fig. 23). Here, we compare the dynamics of evolving populations and the solution

of this system of non-linear differential equation.

We have derived a ‘limited’ system of non linear differential equation to model the population dynamics in Section 3. These systems given by Eqs. (26) and (27) track changing population densities and metabolic scores, and their equilibria. We have discussed the stability of such equilibrium points in Subsection 3.2.2. Here we compare the equilibrium solutions of system to the population dynamics obtained from agent based simulation.

Recall from Section 3 the following equilibrium points for the system of non-linear differential equation as;

$$\tilde{l}^\alpha = \frac{1}{2} \left(\frac{c}{1-c} (K_d^\alpha + K_b^\alpha) + \sqrt{\left(\frac{c}{1-c} \right)^2 (K_d^\alpha + K_b^\alpha)^2 + 4K_d^\alpha K_b^\alpha \left(\frac{1+c}{1-c} \right)} \right)$$

and

$$\tilde{x} = \frac{\lambda}{C(s, a) + \ln 2 \left(\frac{\tilde{l}^{\alpha+1}}{\tilde{l}^\alpha + (K_b)^\alpha} \right)} F,$$

Where $\alpha = \beta$, K_b and K_d are birth and death propensities respectively, λ is resource replenishment rate, and F is the caloric value of the resource.

First, we run ABM simulations of stochastic birth-death processes, where the population can evolve with the mutation factors ϵ_s , where we set $\epsilon_s = 0.05$. We fix the average energy rate per unit area, and vary the resource rate and resource energy (caloric value) alternatively. For instance, in 400×400 space, we fix the total metabolic score per unit time $\lambda \times |\Omega| \times F = 4000$. For every combinations $(\lambda \times |\Omega|, F)$, we performed separate simulations, and recorded the average metabolic score, population, average speed and average acuity over time. Since the resource environment are different in each case, these simulations result to the different population and attribute dynamics. We recorded the final attributes, and used them in the system of differential equation, solved it, and keep the track of population and metabolic score trajectories (see Fig. 40).

For low resource rate environments (Figs. 40A and 40B), both ABM and DE models predicted similar trajectories of population and average metabolic scores over time. Some of the population

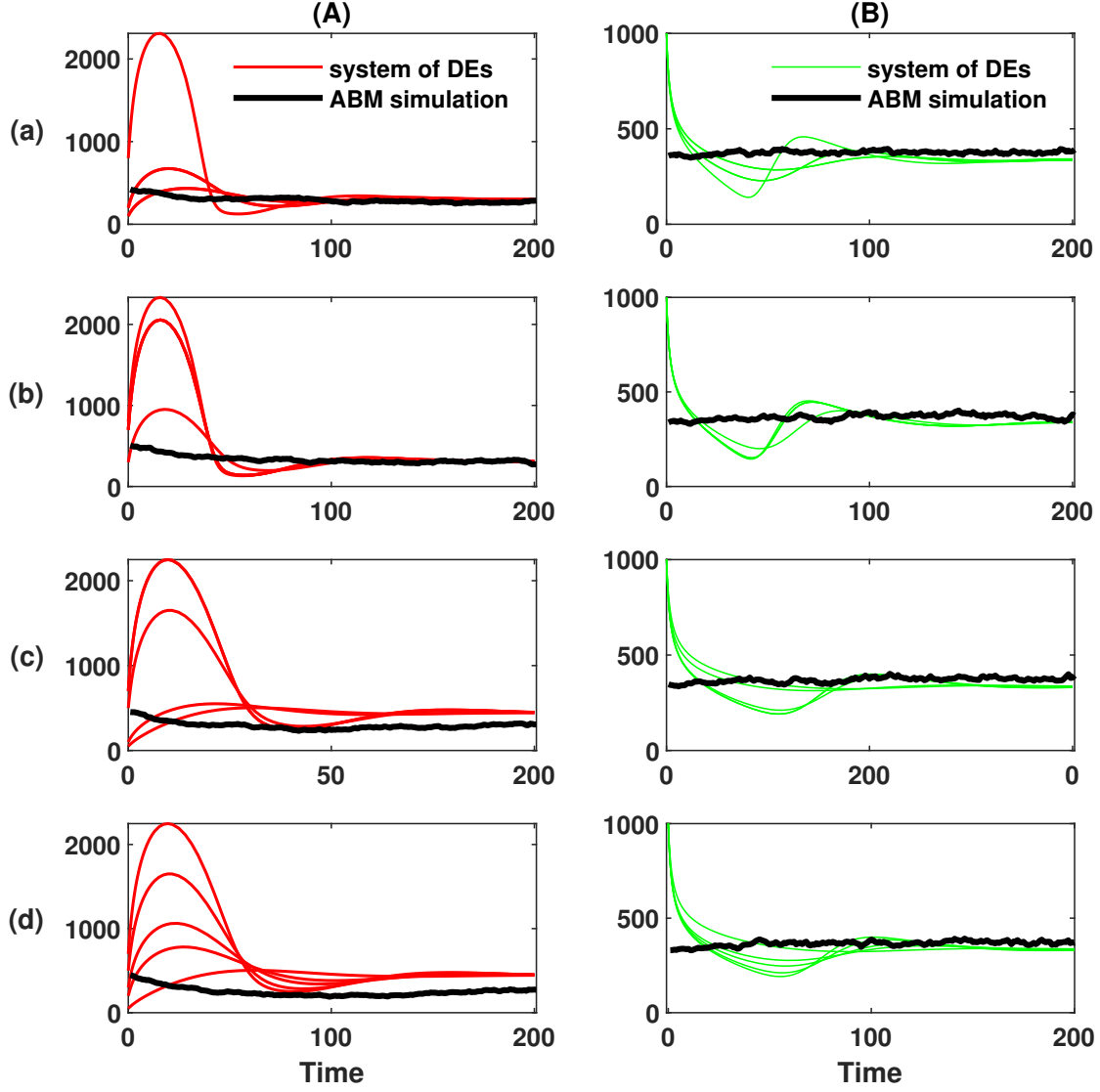


Figure 40: Comparison of trajectories of population and metabolic scores, obtained from ABM and numerical solution of differential equations for different resource environments. Along the columns, are: **(A)** population, **(B)** average metabolic score. The differential equations were solved for 5 different initial conditions (initial agent's density and initial metabolic scores). Along the rows, are plots for 4 different resource environments: **(a)** $(\lambda \times |\Omega|, F) = (40, 100)$, **(b)** $(\lambda \times |\Omega|, F) = (80, 50)$, **(c)** $(\lambda \times |\Omega|, F) = (160, 25)$, **(d)** $(\lambda \times |\Omega|, F) = (320, 12.5)$. $|\Omega| = 400 \times 400$, $T = 5000$ for ABM and time $(t) = 200$ for system of differential equations.

trajectories from the differential equation model show steady growth of at the initial stage due to large random initial metabolic scores. The differential equation model shows that the population ultimately reached its equilibrium point regardless of initial values. Despite yielding the same equilibrium population and average metabolic energy, the ABM simulation and mean-field model exhibit different trajectories. This can be attributed to the fact that the mean-field model's time to reach equilibrium varies greatly with different initial conditions, leading to distinct trajectories.

However, there are few cases where the two models produce different results (see Figs. 40c and 40d). The main source of discrepancy between two models, is due to uncertainties and fluctuations of the resource environment. Since two models have different time scales, and are capable of treating stochastic events and interactions in different ways, such discrepancy arise. When resource rates are high enough that an agents can 'see' a resource on every instant of time, then there is a noticeable impact of interactions between agents, which leads to short-term synchrony of agents' movement and under-harvesting of resources. Many agents emerge with lower speed and acuity, however due to synchrony they can not proliferate. As a result, agent-based simulations yield equilibrium populations that are lower than those predicted by the mean field model.

5 Conclusion

In this dissertation, we have examined the impact of two abstract phenotypic attributes on the survival, fitness, and evolution of foraging agents. We have also scaled the trade-offs between two attributes namely ‘speed’ and ‘acuity’, and the effect of metabolic energy constraints on such attributes. We have also used a modified population dynamics model to explore the evolution of attributes of agents foraging in an environment with randomly distributed resources. We were able to identify the phenotypes which are able to collect resources efficiently in competitive environments. In that way, we were able to identify the ‘fit’ phenotypes and direction of selection pressure which lead towards the evolution of phenotypic attributes.

We have shown that a fixed carrying capacity characterizes a given environment and fixed behavioral rules. This carrying capacity is independent of the initial number of agents and their attributes. We have demonstrated how delayed environmental feedback leads to population collapse, and a smaller space with high resource replenishment rates leads to spikes. We have shown that there is a linear relation of population with resource replenishment rates and metabolic score (caloric value) of resources. We have also shown that multiple types phenotypes can coexist at equilibrium in homogeneous and patchy resource environments.

We have used both stochastic agent-based simulation and a mean field model to understand the process of population and evolutionary dynamics. For a non-evolving population, we have derived a system of differential equation whose solution predicts the population for a certain environment. At equilibrium the ABM results agree well with the solutions of the minimal mean field model whose solutions we obtained by using MATLAB[®] (see Appendix C) [41, 95].

Our main results are based on agent-based simulations of a stochastic birth-death process to understand evolutionary dynamics. In high resource rate environments, we observed co-existence of phenotypes with higher speed and lower speed. We were thus able to identify the resource environment characteristics that support multiple phenotypes at equilibrium. Similarly, we were able to compare the population dynamics to the system of non linear differential equation, with some

discrepancies. These discrepancies were due to the time-scale differences, fluctuation in average metabolic scores and hence fluctuation in birth-death rates in agent-based simulations. Since our mean-field model is limited and allows for the exploration of the population dynamics only, to fully comprehend and analyze the stochastic birth-death process using the mean-field model, more robust and hierarchical attribute comparison methods are necessary.

5.1 Limitations of Research

Natural phenomena are often described by models, and such models are used to explain and to make predictions. A model which is simple enough to understand and visualize, yet sufficiently accurate to predict some aspects of the natural world, is a decent model. However, there are always explicit as well as implicit limitations associated with any model. Our assumptions may not capture all facets of phenomena we want to investigate. The assumptions we made to simplify the model potentially exclude details of the process and may have implications for the results we presented. Here, we discuss some of important generalized assumptions, their role and impact on the proposed model, and their effects on our results. We also discuss some of the important overlooked assumptions which are otherwise relaxed in our case to make the model more tractable.

(a) Metabolic cost and definition of acuity

We defined acuity as the radius of a closed disc around an agent throughout which it can sense a resource. Acuity could be a combined effect of vision, olfaction and hearing by which an agent locates the resource. Much work has been done to scale the metabolic cost related to the overall visual system [75, 76, 110]. However, a general model or data on relative energy costs of the combined sensory systems and the total energetic cost of the associated nervous system is not available, making it difficult to scale the energy cost of acuity. The metabolic cost of acuity varies greatly among different species as they have different levels of sharpness of the senses. Since we consider the metabolic cost for acuity as the static cost which is the basic metabolic cost at rest related to all senses, we assume that this cost does not vary

abruptly with variation in acuity, and hence a linear cost function is a suitable approximation (Eq. 17).

There would be a significant impact on the result if we changed this to a non-linear cost function. In such cases changes in the cost function would result in changes in birth-death rates, and hence the overall dynamics of the population.

We also assumed that agents will always detect objects within a given distance. More realistically agents are less likely to detect objects that are further away. Moreover, some agents could have a poor chance of detecting resources, but have a chance to sense them even when they are far away. Others could be very good at spotting closeby resources, but may not detect resources that are far. Such tradeoffs are different from the ones we considered here, but our model could be easily extended to capture such descriptions of acuity.

(b) Asexual reproduction vs sexual reproduction

A common method of reproduction in both prokaryotes and eukaryotes, is asexual reproduction, which does not involve the formation of gametes [14, 26]. Many unicellular and multicellular plants and some common phyla of animals reproduce asexually. Most of the examples of asexual reproduction are often considered primitive genetic and evolutionary processes due to their relative simplicity compared to sexual reproduction across different organisms. [14]. Asexual reproduction can provide many crucial advantages over sexual reproduction, such as rapid population growth, not requiring mobility or mates, and convenience in the case of hardship. Even with such advantages, organisms which generally reproduce asexually, can exhibit sexuality, and a balance between asexual and sexual reproduction to maintain genetic diversity [11, 72].

In our ABM model, we only considered asexual reproduction due to its simplicity and its prevalence among many organisms. Our model can be modified to include sexual reproduction in which agents are assigned a gender, and can switch between the strategies of foraging and finding mates determined by some function of their metabolic scores. The newborn agent's

phenotype would then be determined by a combination of parents' phenotypes.

(c) Resource shelf-life and depleting resource environment

We considered resources with a fixed replenishment rate and fixed density which do not have shelf-lives. With this assumption, a resource does not change in its quality, energy content and accessibility once it appears in the domain. With a fixed resource rate, consumption of resource does not alter the replenishment of new resources. In such cases, agents are prompted to resource exploration and consumption which in turn changes the fitness. The phenotypes which successfully explore such resources environment are more fit, and drive the evolutionary dynamics. However, these phenotypes may not be able to explore in any other type of resource environment. When resource environment changes, one needs to redefine the model and hence overall evolutionary dynamics would be different for the new environment. Exploring these possibilities will be an interesting direction to further the understanding the evolution of attributes.

(d) Metabolic cost of the birth process

In our model, we do not consider any costs or penalties for the birth process itself. However, organisms must spend a large proportion of available resource to give birth, and hence there is a trade-off between their allocations of resources and energy needed for reproduction and other aspects of life-history [45, 97]. One could also extend our model to account for the cost of reproduction and birth. However, the fact that energy is split between the parent and the offspring at birth can be viewed as a penalty of this type.

(e) Agent's lifespan and evolution timescale

The time-scale of an individual's lifespan is much shorter than the evolutionary process itself. The effects of environmental changes, physiological manipulations like dietary changes can be seen in the behaviors of organisms within their lifespan, however it is hard to scale effects of those individual level manipulations to the evolutionary process [34]. Also organisms'

behaviors are not simply limited to foraging and reproduction, many microorganisms show complex social behaviors like cooperation in foraging and communicating too [25]. A recent study has shown that the short term behavioral changes in some phenotypes of population are not persistent, and for a visible change to phenotypes which accumulates to the change in population level, it takes at least a million year [105]. It is challenging to find a common model that captures the complex behaviors and adaptations within the lifespan and yet is applicable to million year long evolutionary processes. A more comprehensive model with a larger, hierarchical phenotype space that can accommodate both short term changes and long term evolution would address these challenges. However, the implementation of such a model requires computationally efficient tools due to explosion of the interactions and complexity of phenotypes.

- (f) Application of mean-field model to similar phenotypes, non-evolving population only

The mean-field model proposed here by the system of non-linear differential equation (Sec. 3) is limited to model the equilibria of population dynamics only. In the system, there is no mechanism to integrate evolving attributes, so it cannot capture, in the present form, changing attributes over time. Similarly, the attributes (speed and acuity) only contribute to the cost functions $C(s, a)$ and do not determine agents foraging capacities. Due to these limitations, the system of non-linear differential equation can be used to estimate non-evolving populations and metabolic scores for similar phenotypes only.

5.2 Discussion and Future Directions

Agent-based modeling has been used widely in literature. In this dissertation, we have implemented a ‘multi-agent foraging’ approach to explore the evolution of phenotype attributes. The agents in our model have limited ‘acuity’ to sense resources and are characterized by ‘speed’ that determines how quickly they explore their environment. We also compared agent-based simulations and a limited mean field model to predict the population dynamics.

There are some important areas for further investigation into the model, which we have not explored here. Firstly, the design of the model could include more realistic features of environment and attributes of agents inspired by real organisms. For instance, a model which considers more comprehensive attributes, physiological, biotic as well as abiotic factors (age, sex, availability of mates and resources etc.) that shape the birth-death process could better describe actual evolutionary dynamics. In this way we can compare our model to the behaviors of real organisms and better understand evolutionary processes. Secondly, we could develop a more comprehensive mean field model, which could include a description of the evolution of multiple attributes. ABM results could then be compared and tested using this mean field model. Finally, when we consider agents in a model with many complex attributes, then the behavior of these agents behaviors is also complex. One can imagine the agents with sensory capacities who can process information and respond accordingly. The evolutionary process would focus largely on evolution of sensory attributes. Direct implementations of such models would be challenging. However, our model could become the basis for more realistic models of complex foraging organisms and the evolution of their physiological attributes.

APPENDIX

A. Random Walks, Brownian Motion, and Drift-Diffusion Model

Consider a walker start walking on a one dimensional space which has been divided into discrete points. The distance between two points is Δl and that's the length walker moves in a short period of time Δt . The walker movement is random so that it has equal probability of moving either to the left or to the right at the time Δt . For example, when the walker starts moving from the origin, its position at even numbered time is at even numbered distance either to the left or to the right only. We use *combination* to find the probability [24] that the walker is even numbered distance (say $m\Delta l$) after n (even) time steps ($n\Delta t$) as;

$$\begin{aligned} p(m, n) &= \binom{n}{\frac{n-m}{2}} \left(\frac{1}{2}\right)^n \\ &= \frac{n!}{2^n ((n+m)/2)! ((n-m)/2)!} \end{aligned}$$

This can be generalized by considering a *probability distribution function* $\phi(x)$, that represent the probability of x successes in n *Bernoulli* trials. Such *Bernoulli* trial has two possible outcome: probability 'success' p and probability of 'failure' $q = 1 - p$. We have the binomial distribution as follows;

$$\phi(x) = \binom{n}{x} p^x q^{n-x}$$

,

When n is very large this binomial distribution is well approximated by the normal distribution. So, for $t = n\Delta t$, taking the limit $\Delta l, \Delta t \rightarrow 0$ and $n \rightarrow \infty$ the binomial probability distribution function can be written as

$$\begin{aligned}
\phi(x) &= \frac{1}{\sqrt{2\pi npq}} \exp\left(\frac{-(x - np)^2}{2npq}\right) \\
&= \frac{1}{\sqrt{4\pi Dt}} \exp\left(\frac{-(x - \frac{2D}{q}t)^2}{4Dt}\right)
\end{aligned}$$

where D is a constant called *diffusion coefficient* given by $2D = (\Delta l)^2/\Delta t$. Now if we add a waiting time to above process, i.e., at each time step Δt , the walker moves: (a) either to the left with probability p , (b) or to the right with the probability q , and (c) or stays at the same location with the probability $1 - p - q$, we have

$$\phi(x, t + \Delta t) = \phi(x, t)(1 - p - q) + \phi(x - \Delta l, t)q + \phi(x + \Delta l, t)p.$$

Using *Taylor Series* expansion about (x, t) and taking limits $\Delta l, \Delta t \rightarrow 0$

$$\frac{\partial \phi}{\partial t} = -u \frac{\partial \phi}{\partial x} + D \frac{\partial^2 \phi}{\partial x^2} \tag{A1}$$

where

$$u = \lim_{\Delta l, \Delta t \rightarrow \infty} \frac{\Delta l(q - p)}{\Delta t}, \quad D = (p + q) \lim_{\Delta l, \Delta t \rightarrow \infty} \frac{(\Delta l)^2}{2\Delta t}.$$

The Eq. (A1) is *drift-diffusion* equation, whose first term is drift(bias) term and second term is diffusion. It can be extended to N -dimensional space and is widely used in to model the movement of organism and cells.

B. Details About *Agent-Based* Simulations

In the Agent-based modeling, we simulated multi-agent foraging and stochastic birth-death process in a continuous domain Ω with $|\Omega| = b \times b$. The resources in the domain appeared at the location chosen uniformly random(for homogeneous resource environment) in the domain either by constant rate λ or by making constant density ρ per unit time. When the resources replenished at constant

rate, they appeared according to a *spatial Poisson point process* distributed with rate (and mean) λ . The domain $|\Omega|$ generally had size 200×200 or 400×400 , however we also used domains of other sizes to explore the effect of size of domain on the population and attributes.

In each simulation, 10000 agents each equipped with attributes $(\xi_i = (s_i, a_i))$ were introduced in the domain. We took large number of initial agents to make sure that the phenotypic vector ξ_i may take all possible order-pairs of speed and acuity from an initial range $[1, 30]$. We ran most of the simulation sufficiently long (typically $T > 10000$), so that the system has converged to a stationary distribution. In fact, for evolving populations we initiated the simulations with any initial number of agents with randomly chosen attributes however the time to achieve the stationary distribution depends upon initial parameters.

To reduce noise and variability associated with stochastic birth–death process, we took at least 10 independent simulations with similar initial parameters for all agents. We took averages of population and attributes, and the standard errors.

The agent-based models for foraging and stochastic birth–death process were simulated in the MATLAB[®] [62] computing environment. Similarly, other multiple MATLAB[®] in-build functions and applications like *ode45* [41, 95], *PhasePlane* App [43] were used to simulate, analyze and visualize the data. All foraging simulations to find resource collection rates and stochastic birth–death simulations were run in computing server with Intel[®] Xenon[®] CPU E5-2690 v4. Generally, 100 stochastic simulations with same initial parameters were run independently by MATLAB[®] *parfor* loop. Run-time was depended upon initial conditions, domain size and how fast the resource density grew up.

C. System of Non-linear ODEs and Equilibrium Points

Consider, a system of differential equation;

$$\left. \begin{aligned} \dot{u}_1 &= f_1(t, u_1, u_2, \dots, u_n) \\ \dot{u}_2 &= f_2(t, u_1, u_2, \dots, u_n) \\ &\vdots \\ \dot{u}_n &= f_n(t, u_1, u_2, \dots, u_n) \end{aligned} \right\} \quad (\text{A2})$$

It is written as;

$$\dot{\mathbf{u}} = \mathbf{f}(t, \mathbf{u}) \quad (\text{A3})$$

$$\text{where } \mathbf{u} = \begin{pmatrix} u_1 \\ \vdots \\ u_n \end{pmatrix} \in \mathbb{R}^n, \quad \text{and} \quad \mathbf{f} : \mathbb{R}^{n+1} \longrightarrow \mathbb{R}^n.$$

This System (A3) is *autonomous* if it can be expressed as: $\dot{\mathbf{u}} = \mathbf{f}(\mathbf{u})$. Such *autonomous* system is called *linear* if there exists a $A \in \mathbb{R}^{n \times n}$ such that ;

$$\dot{\mathbf{u}} = A\mathbf{u} \quad (\text{A4})$$

If a system can not be written as the form $\dot{\mathbf{u}} = A\mathbf{u}$ for some matrix A , such system is called *nonlinear system* of differential equations.

Consider an autonomous *non-linear system* $\mathbf{f} : \mathbb{R}^n \longrightarrow \mathbb{R}^n$ as;

$$\dot{\mathbf{u}} = \mathbf{f}(\mathbf{u}) \quad (\text{A5})$$

We define the equilibrium points or fixed points of this System (A5) as the points $\tilde{\mathbf{u}}$ such that $\mathbf{f}(\tilde{\mathbf{u}}) = 0$.

We determine the stability of these equilibrium points by linearizing the system about the equilibrium points. Let $\mathbf{u} = \tilde{\mathbf{u}} + \boldsymbol{\epsilon}$ be any point near to $\tilde{\mathbf{u}}$. We can expand $\mathbf{f}(\tilde{\mathbf{u}} + \boldsymbol{\epsilon})$ applying

Taylor's theorem as;

$$\mathbf{f}(\tilde{\mathbf{u}} + \boldsymbol{\epsilon}) = \mathbf{f}(\tilde{\mathbf{u}}) + D\mathbf{f}(\tilde{\mathbf{u}})\boldsymbol{\epsilon} + O(|\boldsymbol{\epsilon}|^2) \quad (\text{A6})$$

where $D\mathbf{f}(\tilde{\mathbf{u}})$ is the *Jacobian matrix* given by,

$$\mathbf{J}|_{\mathbf{u}=\tilde{\mathbf{u}}} = \begin{bmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} & \cdots & \frac{\partial f_1}{\partial u_n} \\ \frac{\partial f_2}{\partial u_1} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \vdots \\ \frac{\partial f_n}{\partial u_1} & \frac{\partial f_n}{\partial u_2} & \cdots & \frac{\partial f_n}{\partial u_n} \end{bmatrix} \quad (\text{A7})$$

Since $\tilde{\mathbf{u}}$ is a fixed point of the system, $\dot{\mathbf{u}} = \dot{\boldsymbol{\epsilon}}$ and $\mathbf{f}(\tilde{\mathbf{u}}) = 0$. The behavior of the stationary points of the non-linear System (A5) can be predicted by;

$$\dot{\boldsymbol{\epsilon}} = \mathbf{J} \boldsymbol{\epsilon} \quad (\text{A8})$$

This is a linear system in $\boldsymbol{\epsilon}$ where $\mathbf{J}$ is an $n \times n$ *Jacobian* matrix evaluated at the equilibrium point. The solution of the System (A8) can be written as a superposition of $e^{\lambda_i t}$ where $\{\lambda_i\}$ is the set of eigenvalues of the Jacobian $\mathbf{J}$ evaluated at $\tilde{\mathbf{u}}$ [17, 91]. These eigenvalues can be expressed in the form of $Re(\lambda_i) + iIm(\lambda_i)$. Now the exponential terms in the solution become,

$$e^{\lambda_i t} = e^{Re(\lambda_i)t} e^{i Im(\lambda_i)t} = e^{Re(\lambda_i)t} (\cos Im(\lambda_i)t + i \sin Im(\lambda_i)t).$$

This shows that the imaginary part only adds-up oscillation to the solution however if the real part of any eigenvalue is positive then the solution grows-up exponentially with time, and the trajectories of solution move away from equilibrium point. Hence, if all the eigenvalues of Jacobian $\mathbf{J}$ evaluated the equilibrium point $\tilde{\mathbf{u}}$ have negative real parts then the equilibrium point $\tilde{\mathbf{u}}$ is stable. If any of the eigenvalues has positive real part then the equilibrium point is unstable [91].

Here, we prove the stability of equilibrium points of the System (27) by numerically calculating the eigenvalues of matrix $\mathbf{J}$ (Eq. (32)) for different values of K_b and K_d .

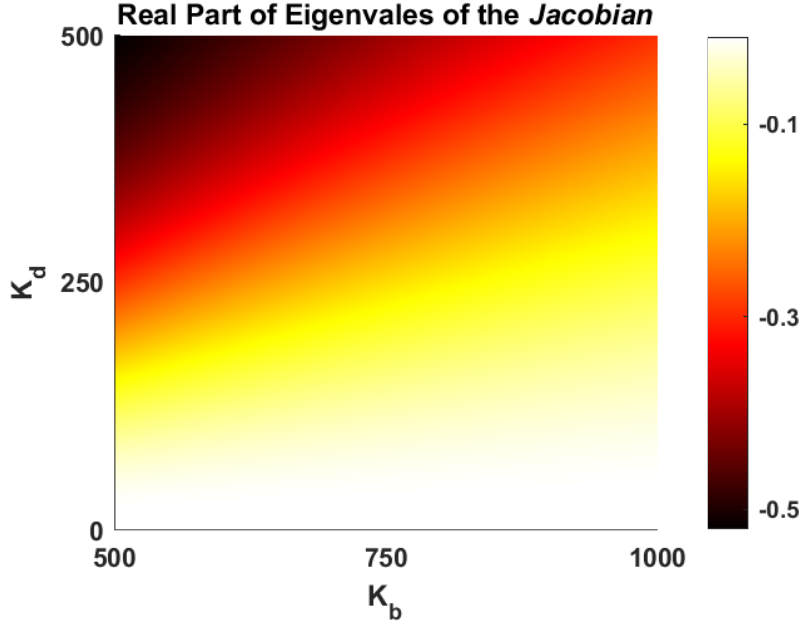


Figure 41: Experimental evidence showing that the eigenvalues of the Jacobian matrix $\mathbf{J}$ (Eq. (32)) has negative real parts. The System (27) is defined for different values of K_b , K_d , and the $\mathbf{J}$ is evaluated at the equilibrium points. The eigenvalues are calculated and their real parts are plotted. System defined for $\lambda = 0.005$, $F = 25$, speed = 10, acuity = 10, and $\alpha, \beta = 4$.

D. Hartigan's Dip Test of Unimodality

Multimodality occurs in the data if more than one local maxima occur in its probability density function. Generally, it is possible to identify the bimodality and multimodality in the univariate data by observing the shape of histogram and density plots, however identifying and scaling the multimodality in multivariate data is often challenging. There are few tests available to discover the multimodality in a distribution. *Hartigan's dip test for unimodality* is one of the such tests which compare the empirical distribution function of the data set with a unimodal distribution that has the smallest value deviations from the empirical distribution function [36, 37]. In *Hartigan's test*, data is sorted and empirical distribution function is computed. A dip statistics is defined by taking the maximum difference between empirical distribution function and a fitted unimodal distribution. Then, the Monte Carlo simulation method is used to compute the p -values of dip statistics. Any p -values less than 0.05 implies significant bimodality, and values greater than 0.05 but less than 0.1

suggest the bimodality with marginal significance [33]. A package '*dip test*' is available in R-program to apply *Hartigan's dip test* [58, 70].

E. Numerical Solution of Non-linear Ordinary Differential Equations (ODEs) by Using *ode45*

One of the prominent solver for the numerical solution of ordinary differential equations is the function *ode45* in MATLAB®[95, 41]. This function is based on *Runge-Kutta* method with changing time-steps to have efficient computation. This function is able to solve a general system like (A3). This method is also known as single-step ODE solver where it approximates the behavior of the model at time $t + \Delta t$ by considering the behavior only at the time between t and $t + \Delta t$. Indeed, each successive steps are independent of previous steps. The *ode45* also utilizes continuous extension and interpolation in between time-steps in the case when the solution changes considerably between a single time-step and values computed only at the end points of time-steps may not be adequate to plot the phase portraits.

An ODE with single solution component can be directly solved by defining span of time “tspan”. The output contains two corresponding column vectors “time points” and “solution at the time points.” However, for a system of ODEs with more than one solution components or for higher-order ODE, following are the steps to use *ode45* [95]:

- Write the given system as a sequence of first order ODEs for each solution component. If the system is higher-order, rewrite it as a system of first-order ODEs by using suitable substitution.
- Next, we need to define the “tspan” and any initial conditions. Once we solve using *ode45*, the output contains a column vector “time points” followed by solution matrix with size “total time steps” by “number of first order equations.”

These solution components can be plotted against ‘time’ on suitable scales as required.

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