Lévy movements and a slowly decaying memory allow efficient collective learning in groups of interacting foragers

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Many animal species benefit from spatial learning to adapt their foraging movements to the distribution of resources. Learning involves the collection, storage and retrieval of information, and depends on both the random search strategies employed and the memory capacities of the individual. For animals living in social groups, spatial learning can be further enhanced by information transfer among group members. However, how individual behavior affects the emergence of collective states of learning is still poorly understood. Here, with the help of a spatially explicit agent-based model where individuals transfer information to their peers, we analyze the effects on the use of resources of varying memory capacities in combination with different exploration strategies, such as ordinary random walks and Lévy flights. We find that individual Lévy displacements associated with a slow memory decay lead to a very rapid collective response, a high group cohesion and to an optimal exploitation of the best resource patches in static but complex environments, even when the interaction rate among individuals is low.

INTRODUCTION

Learning is evidenced through changes in animal behaviour as a result of experience and is well documented in many species. Learning brings numerous ecological advantages by improving the foraging efficiency [1], increasing the ability to escape from predators [2] or through the choice of major low-cost migrations corridors between seasonal ranges [3, 4], for instance. Learning processes are comprised of several steps that are necessary for a proper information acquisition based on experience, such as the collection, storage and retrieval of information. These steps are directly conditioned by the intrinsic cognitive capacities of the individual, and, in the case of foraging, the strategies used to explore the environment [5]. A learning process is deemed successful when the organism has the ability to choose among various options with a bias toward the most rewarding ones, based on previous experience. During the process, past events can be recent or remembered over long periods of time [6, 7]. In this sense, we can define learning as in the context of machine learning: *improved performance on a specific task due to prior experience* [5].

The learning of spatial features in an environment is closely related to exploratory behavior. Some strategies may be more beneficial than others to collect information across different spatial and temporal scales. A body of studies have reported Lévy patterns in the foraging movements of diverse animal species [8–13]. Lévy flights (LF) are random sequences of independent displacements whose lengths are drawn from a probability distribution function having a power-law tail [14, 15]. An important statistical feature of LF is scale invariance in space and time [16], which makes them a convenient modelling tool to analyze animal paths that involve multiple spatial or temporal scales. Such trajectories quickly diffuse in space and can be depicted as composed of many random walks with small, local displacements connected to each other by displacements of widely varying lengths [11]. Patterns resembling Lévy flights (or the related Lévy walks) have been observed in the movements of seabirds [8, 17], marine predators [18], foraging bumble bees [9], African jackals [19], spider monkeys [12], or Drosophila flying in a small circular arena [20], among others.

As mentioned above, important steps during a learning process are the storage and retrieval of information, two cognitive processes that depend on the memory capacity of the organism. Spatial memory is documented in many animal species, from large herbivores to birds [1, 21–23]. The use of memory, as well as its decay over time, can be inferred by fitting models to real trajectories obtained from tracking devices in foraging landscapes where the resource patches are well identified [24, 25]. Recent theoretical approaches incorporating memory-based movements into ordinary random walks models have shown how spatial learning can emerge in principle. This phenomenon is noticeable by frequent revisits to certain places where resources are located [26] or through the emergence of home ranges and preferred travel routes [27, 28].

Theoretical studies often assume that individuals have an infinite memory capacity, *i.e.*, the ability to remember all the sites they visit. Despite the fact that such simplification has brought important insights on the

effects of memory on space use and the emergence of site fidelity, it is well known that memory actually decays in time: it is easier to remember recent events than those that happened far in the past. Memory decay has been incorporated into optimal foraging theory [29], whereas it has been well documented empirically in many animal species such as coal tits [30], desert ants [31], golden lion tamarins and Wied's marmosets [32]. In the case of bison [1], a memory kernel slowly decaying with time as a power-law better described the revisitation patterns than the more standard exponential kernel. Memory decay is thought to be advantageous when the environment is changing over time [29]. Memory decay can enhance the foraging success of primates because it allows the animals to constantly update the relevant features of their environment [32].

The above studies have mainly focused on individual learning. However, many animal species live in groups and sociability brings many benefits, ranging from a reduced predation risk [33–36] to an increased foraging efficiency in uncertain environments [37–40]. The concept of collective learning describes any learning process that is mediated by the transfer of information, skills or strategies that were obtained in social contexts. Such interactions can modify individual behavior and lead to coordinated collective dynamics [5]. There are several types of collective learning, but all of them include the exchange of useful information in a direct or indirect way. Individuals can increase their probability of adopting a certain behavior in the presence of a peer, like in the case of bison, which are more likely to travel to a given new location when another animal in the group knows about this location. [41]. The interest of an individual about a particular location can arouse the interest of others, as in elephants, where matriarchs lead herds to waterholes unknown by the rest of the group [42], or in killer whales, where old females tend to lead the displacements of the group when prey abundance is low [43]. Novel individuals can copy a model behavior through observation that results in a reliable and similar outcome, as in fish where naive individuals learn migration routes through associations with experienced individuals [44]. Given that individual and collective learning could benefit from each other [45–48], we extend the definition of learning exposed above to define collective learning as: the improved performance of a group to solve a specific task due to the accumulation of individual experience and the transfer of social knowledge.

Several spatially explicit models have shown that spatial learning in groups can be affected by the rates at which individuals interact or use previous information [46–48]. For instance, collectives of interacting random walkers with infinite memory capacities were studied in [46]. In heterogeneous environments, these models naturally exhibit collective learning over a wide range of parameters, a phenomenon noticeable by the capacity of the foraging group as a whole to strongly aggregate and localize around the richest resource sites available in the environment.

Despite these advances, there is still a lack of understanding on how different combinations of individual exploration types and memory capacities affect the emergence of collective learning. Here, we computationally analyze a model swarm without a leader, whose task is to find and exploit the resource sites of highest reward in an environment containing many resource sites. In particular, we study the effects of forager individual dispersion, modelled by LF movements of varying exponent, combined with a power-law memory decay, on the emergence of collective learning through information transfer, and contrast the results with those obtained from movements of constant step length or perfect memory [46]. We find that LF dynamics and a moderate memory decay allow for a fast and effective collective learning in complex environments, even if those are static.

MODEL

The collective foraging model presented here extends the one studied in [46]. Briefly, the motion of individuals is assumed to be driven by the combination of two basic movement modes: standard random walk displacements (with probability $1-q$) and preferential returns to places visited in the past (with probability q). In the latter mode, an individual chooses a particular site from its own experience (with probability $1-\rho$) or from the experience of another group member (with probability ρ). The probability to choose a particular site for revisit is proportional to the accumulated amount of time that the individual (or its peer) has spent at that site. Therefore, the sites that are often occupied have a higher probability of being revisited in the future: they are linearly reinforced [26, 46]. Since this preferential dynamics depends on the whole history, it implies that each individual in the swarm can remember which sites were previously visited as well as the duration of these visits, either by its own experience (memory) or by *communication* with peers (social interaction). Such communication takes place on an information transfer network in which the agents are represented by nodes, and the links between agents allow information exchange.

Environment. We consider a discrete lattice of $L \times L$ sites in two dimensions ($2d$), with unit spacing and reflective boundaries. The coordinates of a site n are a pair of integers (x, y). On the lattice, resources (or targets) are randomly distributed with density $\delta < 1$, hence, on

average, there are $M = \delta L^2$ targets in the system. To each target i we assign a fixed weight or attractiveness γ_i (related to the site "reward" in the context of learning), which is a random number uniformly distributed in the interval $(0, \gamma_{max})$, where $\gamma_{max} < 1$ is a given parameter. Let $\mathbb{T} = \{(T_i, \gamma_i)\}_{i=1}^{M}$ denote the set that contains the positions T_i and weights γ_i of the targets. The target of highest weight $\gamma_{\rm best} = \max_{i=1,...,M}\{\gamma_i\}$ is the best target and is denoted as $\mathrm{T}_{\rm best}$.

Foragers. We consider N walkers with random initial positions on the lattice, connected by a complete communication network. Namely, every walker can communicate with any other group member [49]. The time variable t is discrete and during a time step $t \to t+1$, each walker $l = 1, ..., N$ updates its position $\mathbf{X}_t^{(l)}$ as follows.

(*i*) *Self-memory mode*: If not on a target, with probability $q(1-\rho)$ the walker resets to a site that it visited in the past, that is: $\mathbf{X}_{t+1}^{(l)} = \mathbf{X}_{t'}^{(l)}$ where t' is an integer in the interval $[0, t]$ chosen according to a probability distribution $p_t(t')$ given *a priori* and denoted as:

$$p_t(t') = \frac{F_t(t')}{C(t)} \tag{1}$$

with $C(t) = \sum_{t'=0}^{t} F_t(t')$ a normalization factor and $F_t(t')$ a memory kernel function. Here we consider a power-law memory decay given by

$$F_t(t') = (t - t' + 1)^{-\beta} \tag{2}$$

where $\beta \geq 0$. If $\beta = 0$, one recovers the linear preferential visit model with non-decaying memory [46], where the probability to visit a site is simply proportional to the total amount of time spent on that site up to t. With $\beta > 0$, it is more likely that the individual chooses a recently visited place for relocation, rather than a site visited long ago. The rule in Eq. (2) is then equivalent to assuming that each site (target or not) has an accumulated weight for the forager, such that each visit to a given site (at time t') produces an increment of 1 of this weight. At later times ($t > t'$), this increment decreases from its initial value 1 and tends to zero as a power-law. Hence, frequently visited sites have a larger accumulated weight and are more likely to be revisited again (preferential visit mechanism) but sites that have not been visited for a long time have vanishing weights and tend to be forgotten by the forager.

(*ii*) *Information transfer mode*: If not on a target, with probability $q\rho$ the walker l randomly chooses another walker (m) and relocates to a place already visited by m, according to the same preferential rule with memory decay: $\mathbf{X}_{t+1}^{(l)} = \mathbf{X}_{t'}^{(m)}$ where t' is again a random integer in the interval $[0, t]$ chosen with the probability distribution $p_t(t')$.

(*iii*) *Random motion mode*: If not on a target, with probability $1-q$ the walker l performs a random displacement, or $\mathbf{X}_{t+1}^{(l)} = \mathbf{X}_t^{(l)} + \boldsymbol{\ell}_t$. Here, $\boldsymbol{\ell}_t = (\ell_x, \ell_y)$, where ℓ_x and ℓ_y are two integers independently drawn from the distribution:

$$p(\ell) = \frac{C}{|\ell|^{1+\mu}}, \qquad \ell = \pm 1, \pm 2, \pm 3... \tag{3}$$

with C a normalization constant and $0 \leq \mu \leq 2$. When $\mu \geq 2$, the random walk process becomes asymptotically Gaussian, similarly to an ordinary random walk with small jumps, *e.g.*, to nearest neighbours (n.n.) lattice sites. Conversely, when $\mu \to 0$, the dynamics approximately correspond to random relocation in space, where very large displacements across the landscape are frequent. For intermediate values of μ, self-similar Lévy flights are generated.

(*iv*) Feeding: If on a target (*i.e.* if there exists an i such that $\mathbf{X}_t^{(l)} = T_i$), the walker l stays on that site with probability γ_i, and with the complementary probability $1 - \gamma_i$ leaves the site using one of the movement rules (*i*) – (*iii*) above with their respective probabilities.

In summary, the parameter q represents the probability of memory use (while $1 - q$ is the probability to perform a random step), whereas ρ is the interaction parameter, or the probability that the walker uses, in the memory mode, the experience of another individual. The mean time spent feeding on a target T_i during a visit is $1/(1 - \gamma_i)$, which can be considered as the mean reward associated to T_i. By setting $\beta = 0$ (perfect memory) and if the jumps in the random motion mode are limited to nearest neighbours (n.n.) lattice sites, one recovers the model of ref. [46]. See also refs. [47, 48] for other variants of this model.

With these simple rules, collective learning may emerge via the localization of a large fraction of the individuals around a good resource site, chosen among the many resource sites available in the foraging domain (phenomenon of *selective localization*). Figure 1 displays an example of spatial configuration obtained at large time in a simulation by iterating the rules (i)–(iv), for a swarm of interacting foragers with non-decaying memory and performing Lévy flights with index $\mu = 0.5$. One notices a highly non-uniform distribution of foragers around a few resource sites of high attractiveness.

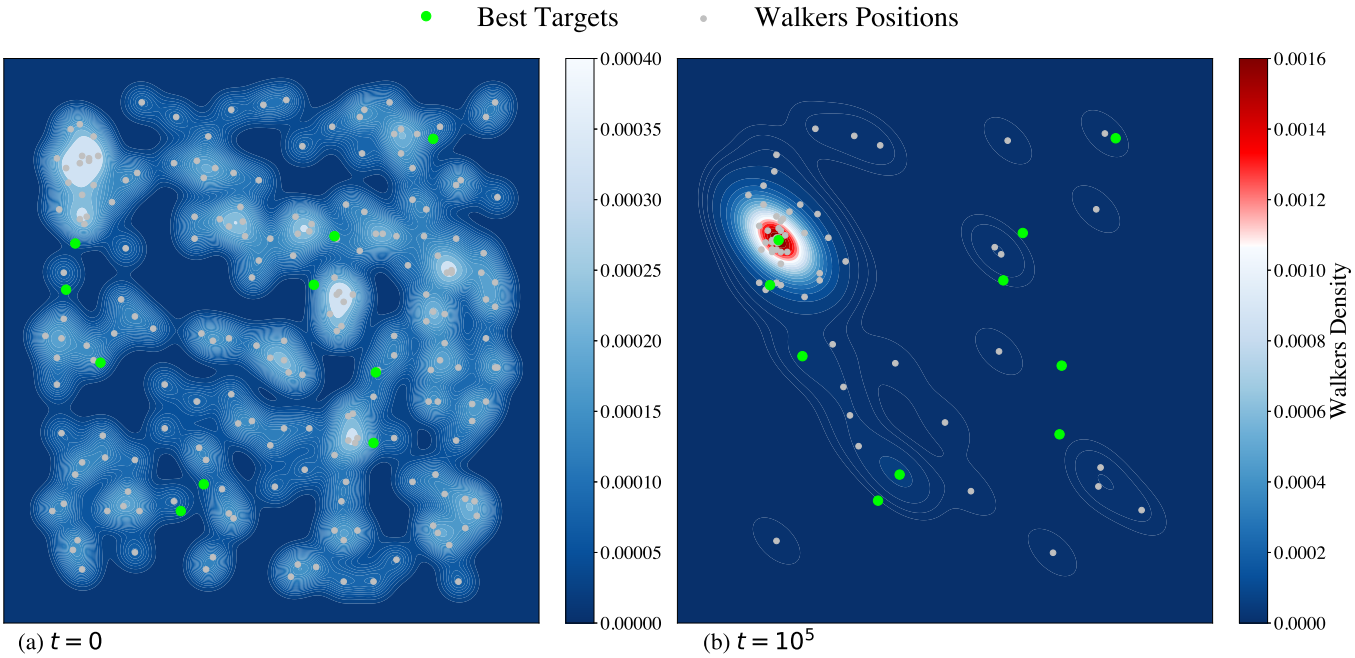

FIG. 1. Initial (a) and final (b) positions of 200 walkers (white dots) after $t = 10^5$ iterations of the dynamical rules (i)–(iv) in a two-dimensional environment of size $L = 200$. The most attractive resource sites (with $\gamma \geq 0.85$) are represented by green circles (among a total of 100 which are not shown). The values of the other parameters are $q = 0.25$, $\beta = 0$, $\rho = 0.5$, $\gamma_{max} = 0.9$, and $\mu = 0.5$. Initially all the walkers are randomly distributed across the square environment. Note that at the end of the simulation, most of the walkers aggregate around a very attractive resource site, as indicated by the color gradients showing the density of walkers.

RESULTS

Infinite Memory ($\beta = 0$)

Figure 2 shows the occupation probability P_{T_i} of each target T_i as a function of its weight γ_i, for nearest neighbour (n.n) and LF random jumps. At large times, a steady state is reached and P_{T_i} is defined as the probability that a walker chosen at random occupies the target T_i. This quantity gives us a measure of how selectively foragers choose their resources. The figure also shows the fraction of individuals that have visited the best target at least once at time t, denoted as $N_{T_{best}}(t)$. This quantity grows in time for different combinations of memory use and communication probabilities, q and ρ, respectively.

In Figures 2(a)-(b), when interactions and memory are at play, P_{T_i} is the largest for $\gamma_i = \gamma_{\max}$ and decays very quickly as γ_i decreases. In the n.n. case, the occupation probability of the resource site $\mathrm{T_{best}}$, denoted as $P_{\mathrm{T_{best}}}$, rises to about 0.25 in certain environments. Therefore, there is a probability of order 1 to find any forager (at a given time) on the site giving the maximum reward, out of the $L^2 = 40,000$ visitable sites. For the LF dynamics, $P_{\mathrm{T_{best}}}$ grows to about 0.35 in some environments. It is important to notice that when the swarm individuals do not communicate with each other (pink squares), one still observes some localization around the best resource site with LF jumps, whereas this phenomenon almost vanishes with n.n. jumps.

When the foragers do not use memory (blue circles, n.n. and LF), the selectivity disappears altogether. In this case, the foragers are memory-less random walkers. Their occupation probability of a site i in the steady state can be calculated exactly and is given by $P_i^{(RW)} = C(L)/(1-\gamma_i)$, where $\gamma_i = 0$ for a non-target site and $C(L) = 1/[\sum_{j=1}^{L^2}(1-\gamma_j)^{-1}]$ is a normalization factor. This result is independent of the step distribution $p(\ell)$. As $C(L) \propto 1/L^2$, the occupation probability of any site is very small, even for $\gamma_i = \gamma_{max}$. One can also show that if these walkers interact (*e.g.*, every individual can jump with probability ρ to the site currently occupied by another forager chosen at random), the asymptotic occupation probability is given by the same $P_i^{(RW)}$ as above.

The emergence of selective localization in our model with n.n. dynamics is thus only possible with both memory use and communication, while for the LF dynamics, individual memory use is sufficient in principle.

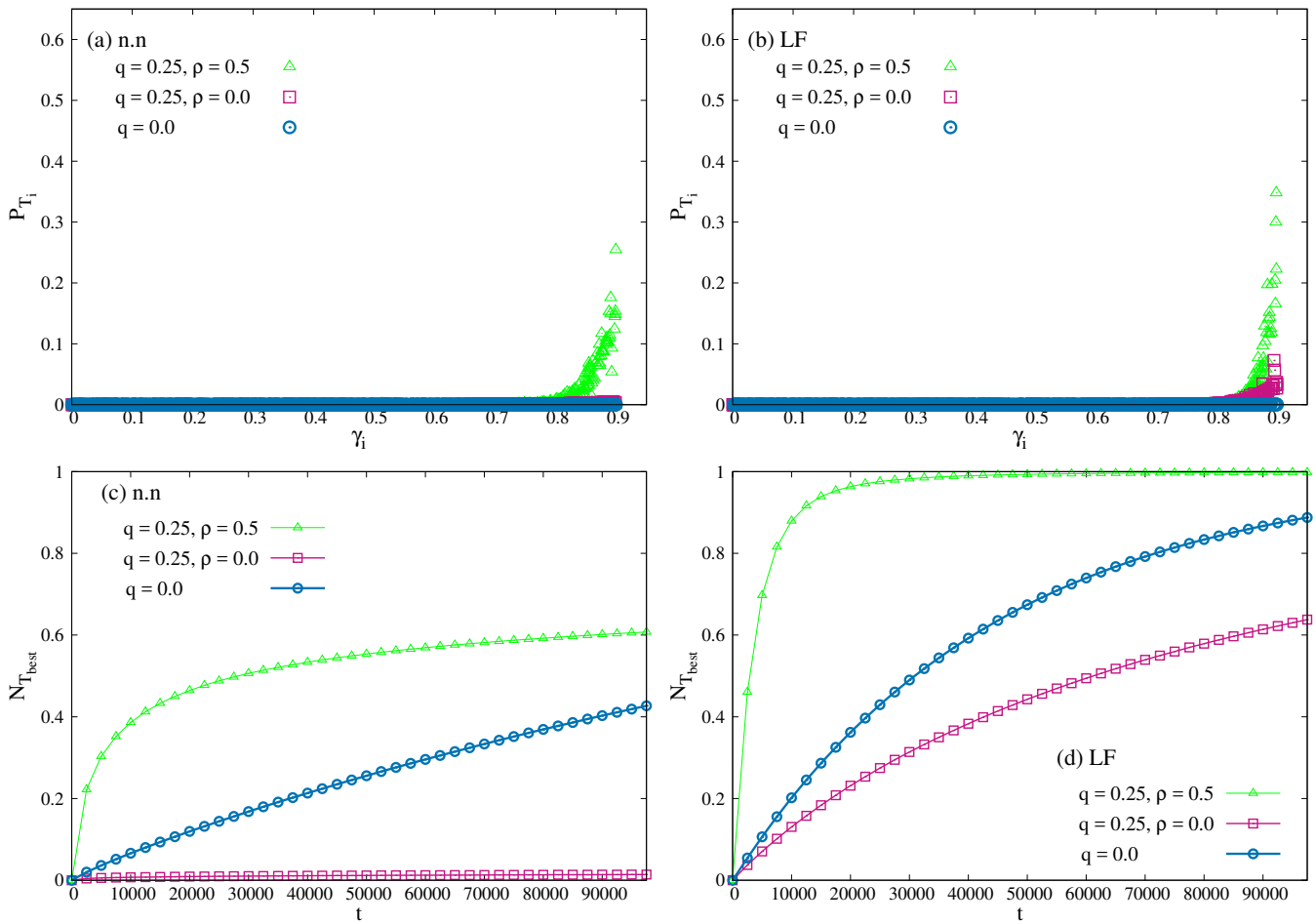

FIG. 2. *Infinite memory case.* Simulations with $N = 200$ walkers in an environment with 200×200 lattice sites, $\delta = 0.0025$ ($M = 100$ resource sites), $\gamma_{max} = 0.9$ and $t = 10^5$. (a) Final target occupation probability P_{T_i} for n.n. dynamics vs. the target weight γ_i. Each point represents a target. (b) Same quantity as in (a) for LF dynamics with index $\mu = 0.5$. (c) Fraction of swarm individuals that have visited the best target site at least once at time t, for different memory and communication rates. (d) Same quantity as in (c) for Lévy flight dynamics with index $\mu = 0.5$. P_{T_i} and $N_{T_{best}}(t)$ are obtained from averaging over 1000 independent dynamics in a same environment. The data from 10 different environments are aggregated in (a) and (b), and averaged in (c) and (d).

Figure 2(c) shows that for a n.n. swarm with memory but without communication ($q = 0.25$ and $\rho = 0$, pink squares), very few individuals can find the best target site. This is because memory causes each individual to explore intensively a limited region of space around its starting point, which is unlikely to contain the best site. In the absence of memory and communication, the agents perform pure random walks ($q = 0$, blue circles) and can visit the best target by chance: $N_{\mathrm{T_{best}}}(t)$ grows linearly with t at short times. However, in the same swarm with memory and information transfer ($q = 0.25$ and $\rho = 0.5$, green triangles), a much larger number of individuals rapidly find the best target, although this fraction remains well below 100% afterwards. In Figure 2 (d), LF dynamics exhibit similar trends. In this case, though, even in the absence of communication many individuals that use memory can find the best target. Thanks to LFs, individuals actually explore distant parts of the environment and can encounter the best target by themselves more easily. Importantly, in LF swarms with memory and communication, after a short time practically 100% of the individuals have encountered the best target.

Figure 3(a) displays the variations with ρ of the occupation probability $P_{\mathrm{T_{best}}}$ for both n.n. (pink) and LF dynamics (blue). This probability grows rapidly with ρ and reaches a plateau, whose value is higher for LFs. To achieve their plateau value, LF swarms need a larger communication rate ($\rho \geq 0.2$ vs. $\rho \geq 0.1$ for n.n. dynamics).

Figure 3(b) shows the asymptotic cohesion reached by

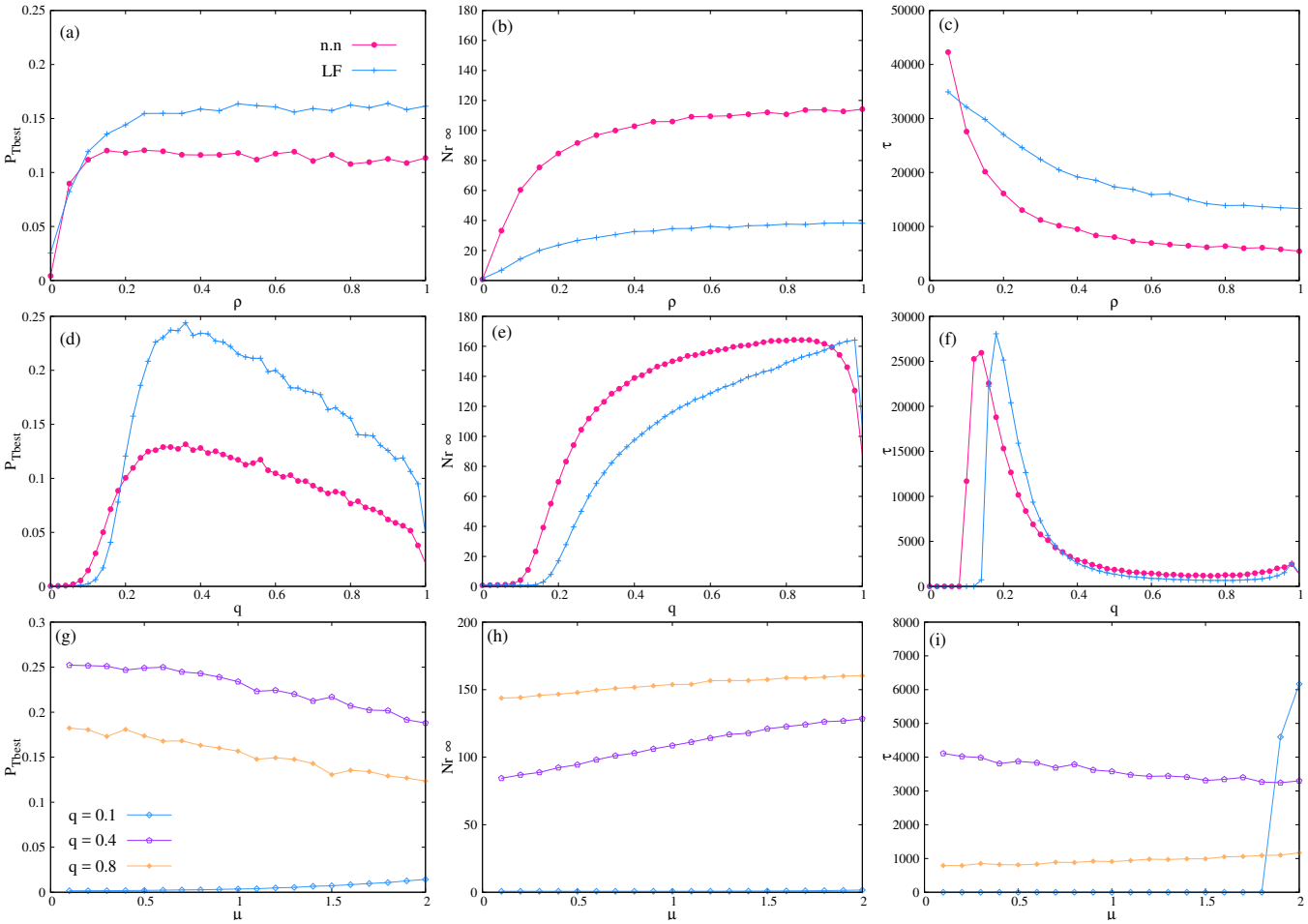

FIG. 3. *Infinite memory case.* Occupation probability of the best target, $P_{\mathrm{T_{best}}}$ (left column), asymptotic cohesion N_{r_∞} (center column) and learning time τ (right column), as function of: (a)-(c) the information transfer rate ρ, with $q = 0.25$ and $\mu = 0.5$; (d)-(f) the rate of memory use q, with $\rho = 0.5$ and $\mu = 0.5$; and (g)-(i) the Lévy index μ, for different values of memory use. The other parameters are those of Fig. 2. All the curves are averages over ten different landscape configurations.

the swarm at large times, denoted as N_{r_∞}, as function of the interaction parameter ρ. To compute N_{r_∞}, we define the neighbourhood of a forager by a disk of radius $r = L/(2\sqrt{N})$ centred at the forager position. The length r represents half the mean distance between two neighbouring foragers if these would be distributed at random in space. For each forager, at time t, we determine the number of other group members located in its neighbourhood and take the average over all foragers, denoted as $N_r(t)$ [46]. We define N_{r_∞} as the limit of $N_r(t)$ when $t \to \infty$, in the steady state. This quantity also reaches a plateau as ρ increases. The swarms with n.n dynamics are very cohesive. This is expected because n.n. dynamics, with a frequent use of memory ($q = 0.25$), does not give the time to the individuals to diffuse away from the best resource sites. On the other hand, the large jumps of the Lévy processes are likely to spread the group further around these sites, producing less cohesion. Nevertheless, LF swarms remain much more cohesive than foragers randomly distributed in space, as examplified by Fig. 1.

Figure 3(c) displays the typical time the swarm takes to reach half of its asymptotic cohesion. We denote this quantity as τ, which is a measure of the time taken by the collective learning process, *i.e.*, the adaption time of the group to the environment. The variations of τ as a function of ρ exhibit a slow decay until a finite asymptotic value is reached. Hence, more frequent interactions accelerate the convergence toward collective learning, which is faster for n.n. groups than for LF groups.

In the following panels, we fix $\rho = 0.5$ and study the influence of the other parameters on the quantities $P_{\mathrm{T_{best}}}$, N_{r_∞} and τ.

Figure 3(d) displays the variations of the occupation probability $P_{\mathrm{T_{best}}}$ with the rate of memory use q. There exists a threshold value above which the swarm presents

collective learning, and this value is lower in n.n. than in LF dynamics. After the learning threshold, $P_{\mathrm{T_{best}}}$ reaches an optimum at a certain $q = q^*$. For $q \gtrsim 0.2$, LF swarms exhibit a better performance than n.n. swarms. In both cases, an excessive use of memory leads to a degraded localization around the best target site. When $q \to 1$ in our model, each individual tends to get "trapped" in the first visited site, reducing its exploration capacity to zero. Figure 3(e) shows that, as in Fig. 3(b), the cohesion of the n.n. swarms is larger than for LF swarms. In both cases the asymptotic cohesion of the swarm decays abruptly when q approaches unity. In Figure 3(f), the learning time τ exhibits a maximum right after the learning threshold, whereas it further decays until reaching an much lower asymptotic value, that is roughly the same in both dynamics.

These results are further complemented by studying the effects of the Lévy index μ, as shown in Figs. 3(g)-(i). At large rates of memory use (*e.g.*, purple line of Fig. 3(g)), localization improves as the flights becomes more super-diffusive (smaller μ), despite of being less cohesive (Fig. 3(h)) and slightly slower in learning (Fig. 3(i)). Thus, the exploratory flights with shorter step lengths (larger μ), and hence closer to n.n. dynamics, are slightly more cohesive and learn slightly faster. At small rates of memory use, localization and group cohesion are very weak, while τ is not well-defined because no aggregation occurs.

Memory decay ($\beta > 0$)

The occupation probability of each target as a function of its attractiveness γ_i is now shown in Figure 4 for a non-zero value of the memory decay parameter ($\beta = 1$). In Fig. 4(a)-(b) we show P_{T_i} for n.n. and LF swarm, respectively. As in the perfect memory case, P_{T_i} is very small fo almost all γ_i's but becomes very large (of order 1) when γ_i is close to γ_{max}, provided that memory use and communication are at play in the group (grey triangles). Again, our model foragers are attracted to the best target sites and localize very selectively. When communication is suppressed ($\rho = 0$, blue circles) P_{T_i} drops abruptly for all γ_i in n.n swarms. For LF swarms, though, the lack of communication does not destroy selectivity but decreases it by a factor of about 3 [see further Fig. 5(a), green curve]. When the individuals are memory-less ($q = 0$, green crosses) selectivity completely disappears in both dynamics, as expected. By comparing with Fig. 2, one notices that memory decay in the LF swarm markedly improves the selective localization on good targets compared to the case of infinite memory (see a value of $P_{T_{\mathrm{best}}}$ above 0.60 in Fig.4(b)). Although memory is crucial, allowing the individuals to forget about those sites visited in the far past, gives to the group opportunities to find and exploit better resource sites, even in a static environment.

To discuss the properties of n.n. and LF swarms with memory decay, we computed $P_{\mathrm{T_{best}}}$, N_{r_∞}, and τ as a function of the communication rate ρ, the memory decay index β, and the Lévy index μ, respectively.

For both n.n. and LF swarms, when β is fixed to 1, the probability $P_{\mathrm{T_{best}}}$ is approximately doubled compared to the case $\beta = 0$ (Fig. 5(a) vs. Fig. 3(a)). It also depends remarkably little on ρ (as far as $\rho > 0$) and even slightly *decreases* with increasing the frequency of interactions. The curves of the cohesion N_{r_∞} in Fig. 5(b) reach plateau values at large ρ that are nearly twice the ones of Fig. 3(b). One of the most spectacular effect of memory decay, though, is the decrease of the learning time τ by a factor ranging between 5 (at $\rho = 0.1$) and 12 (at $\rho = 0.4$), compared to the perfect memory case (see the scale of the y-axis of Fig. 5(c) vs. 3(c)).

The above quantities are thus impacted by the memory decay exponent. The other parameters being fixed ($\rho = 0.5$, $q = 0.25$), the occupation probability of the best target $P_{\mathrm{T_{best}}}$ as a function of β for n.n. (yellow curve) and LF swarms with $\mu = 0.5$ (green curve) is shown in Figure 5(d). In both dynamics, intermediate values of memory decay improve localization and, notably, $P_{\mathrm{T_{best}}}$ reaches a maximum for a particular value of β ($\beta^* \approx 0.8$ for n.n and $\beta^* \approx 1.5$ for LF). The improvement in localization properties brought by memory decay is more significant for LF swarms. In this case, the occupation probability of the best site at optimality, $\beta = \beta^*$, is on average 0.42, which is larger than the value with $\beta = 0$ by a factor of 2.5. In both dynamics (n.n and LF), a high memory capacity ($\beta \sim 0$) actually causes the group to reinforce those sites visited at the beginning of the search, which are not necessarily the most attractive sites. On the other hand, at low memory capacity ($\beta >> 3$) the motion of individuals become similar to memory-less random walkers.

Similarly to $P_{\mathrm{T_{best}}}$, the cohesion reaches a maximum close to $\beta = 1$ (Fig 5(e)), the n.n. swarms being again more cohesive that LF ones. Note that the maximal cohesion is not reached at the exact same value β^* above. Nevertheless, high levels of aggregation are associated with an intensive exploitation of the best resource site.

As mentioned before, the learning time τ drastically decreases with β, until a plateau is reached at about $\beta \simeq 1$, see Figure 5(f). When individuals have an infinite memory capacity ($\beta = 0$), the group takes comparatively a considerable time to cluster around the best resource sites.

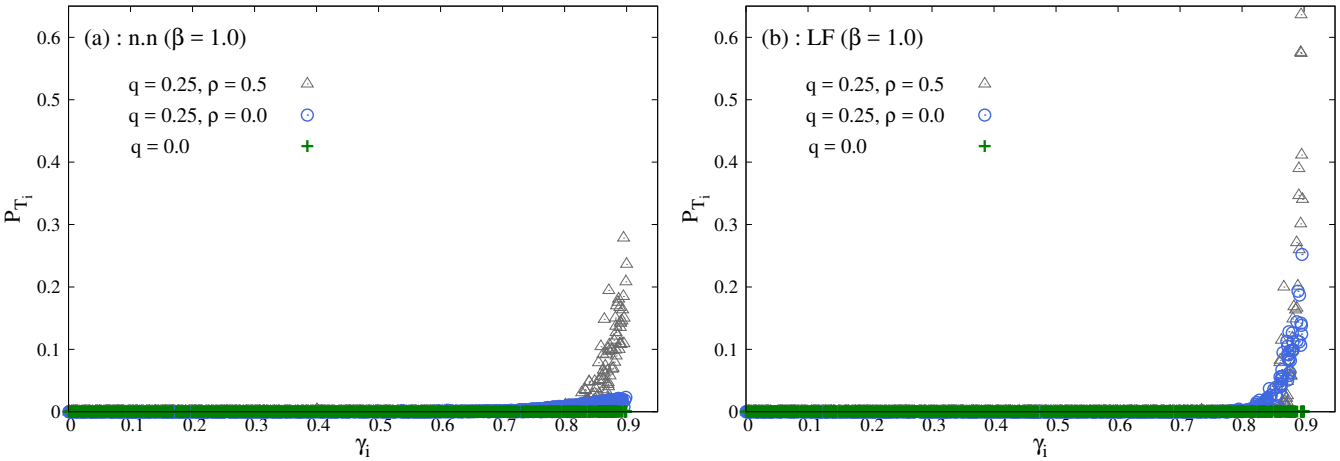

FIG. 4. *Memory decay case.* Simulations with $N = 200$, $\gamma_{max} = 0.9$, and $\beta = 1$. (a) Final target occupation probability P_{T_i} for n.n. dynamics vs. the value γ_i of the target, with $\beta = 1$. (b) Same as (a) but for Lévy flight dynamic with $\mu = 0.5$. In all cases each point represents a target and P_{T_i} is obtained from averaging over 1000 independent walks dynamics in a same environment. Ten different landscapes are shown.

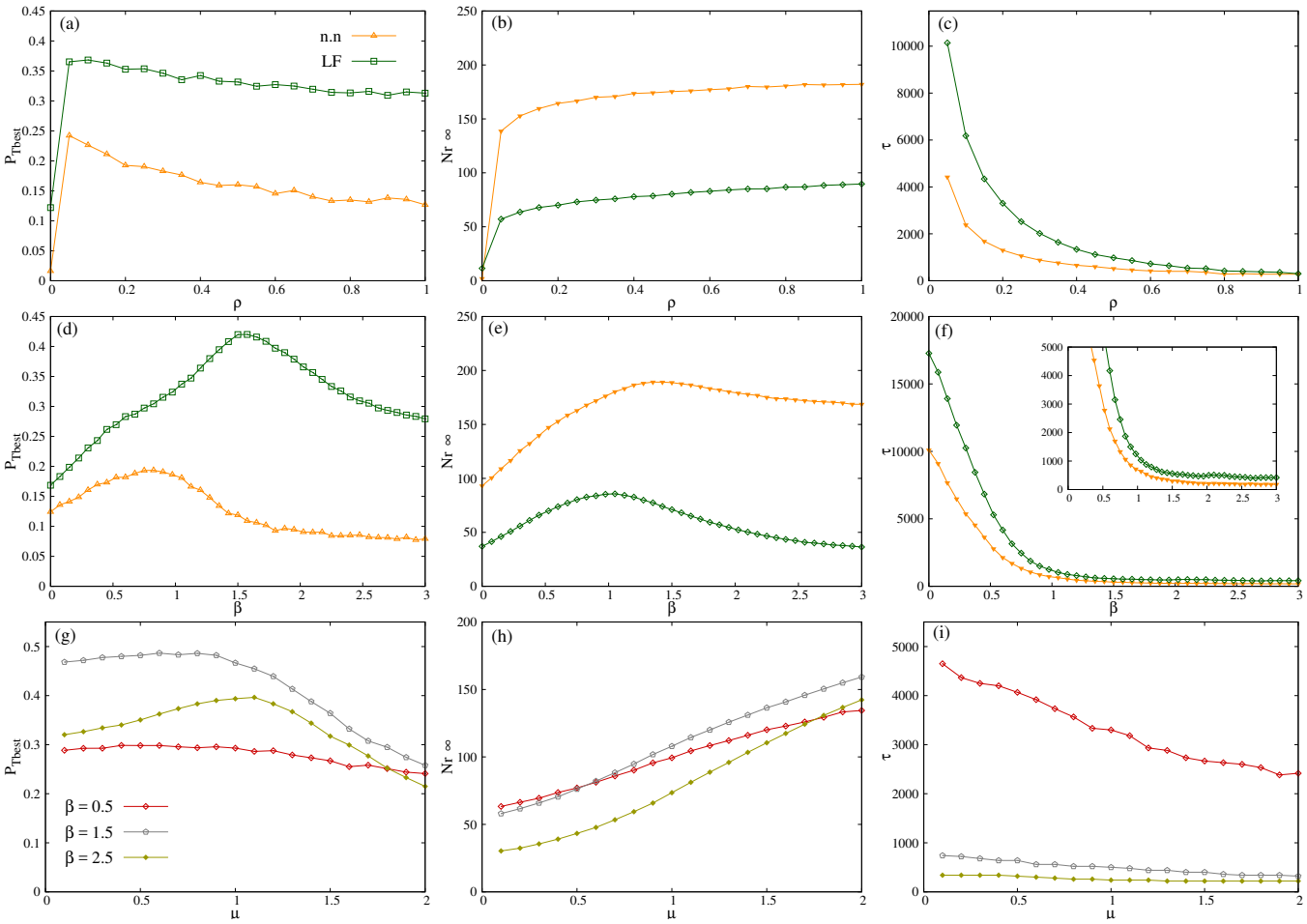

FIG. 5. *Memory decay case.* Occupation probability of the best target $P_{\mathrm{T_{best}}}$ (left column), asymptotic cohesion N_{r_∞} (center column), and typical learning time τ (right column), as function of: (a)-(c) the rate of information transfer ρ (with $\mu = 0.5$ and $\beta = 1$); (d)-(f) the memory decay exponent β (with $\rho = 0.5$ and $\mu = 0.5$); and (g)-(i) the Lévy index μ, for $\beta = 0.5$ (red line), $\beta = 1.5$ (grey line) and $\beta = 2.5$ (green line), with $\rho = 0.5$. In all cases $q = 0.25$. The other parameters are those of Fig. 2. All the curves are averages over ten different landscape configurations.

In summary, by choosing $\beta \simeq 1$ for n.n. swarms and $\beta \simeq 1.5$ for LF swarms, a good compromise is achieved for a quick convergence, a selective exploitation and a high group cohesion.

To address the effects of the long exploratory random jumps on the group properties, we computed the three quantities above as a function of the Lévy index μ for different values of β. In Fig. 5(g), with a slow memory decay ($\beta = 0.5$), the occupation probability $P_{\mathrm{T_{best}}}$ stays almost constant (around 0.3) as μ varies. With a more pronounced forgetting ($\beta = 1.5$ and 2.5), $P_{\mathrm{T_{best}}}$ becomes non-monotonic with μ and reaches a maximum value close to $\mu = 1$. On the other hand, one can observe that swarm aggregation increases as the individuals perform shorter steps (have a larger μ) for all the values of β considered (Fig. 5(h)). The cohesion of a swarm with slowly diffusing individuals is indeed not disrupted by large steps, which are more frequent in the highly super-diffusive regime (small μ). Finally, Figure 5(i) shows that the learning time τ slightly decreases with μ. In this example the swarm with the slower forgetting ($\beta = 0.5$, red line) has a learning time much larger than the other two.

DISCUSSION

Groups of social agents are often more effective in solving complex tasks than isolated individuals, not only in ecology [46] but also in the area of artificial intelligence [50] or in the context of the discovery of innovations, where social connections play an important role [51]. Individual experience and the transfer of valuable information that can be exploited by others are essential in the emergence of collective learning and novelties in human societies [51]. In the present study, the discovery by an individual of a foraging site not visited previously is a consequence of its random exploration of the environment. On the other hand, how much information can an agent store depends on its memory capacity, and how much information it retrieves relates to how often the individual takes memory-based decisions.

With these elements, we have developed a model of interacting agents with memory and observed the emergence of collective states of learning. We have analyzed different individual exploratory behaviors and memory features, which are used by the foragers to visit resource patches according to their attractiveness. As a consequence of pairwise interactions, in all cases the whole group gathered very selectively around the best resource site among the many sites available in the environment, except when individuals use their memory very little. The reward obtained by the individuals of the group is much higher than what they would achieve on their own, without information sharing. We have compared the effects on learning of the use random walks or Lévy flights in the exploratory mode, as well as the effects of a perfect memory capacity or a memory that decays over time as a power law.

In the prefect memory case, the cohesion of n.n swarms converges faster and to higher values than in LF swarms (larger N_{r_∞} and smaller τ). However, LF groups localize more strongly on the most attractive target (larger $P_{\mathrm{T_{best}}}$), meaning that the group takes advantage of the valuable information collected by individuals, which is facilitated by their long exploratory steps.

When memory decays with time, we found qualitatively similar results. Nevertheless, some progressive forgetting considerably reduces the time needed by the group to find and gather around the best resource sites. Concomitantly, individuals exploit these sites more intensively and are more cohesive. Therefore, a decay of memory allows the group to learn faster and better. In particular, an intermediate value of the decay exponent maximizes resource exploitation. If memory decays too fast, collective learning degrades and the group becomes similar to a swarm of interacting but memory-less random walks. Although n.n. swarms converge even faster than LF swarms to the steady state, they localize less effectively. Thus, LF movements with a proper amount of memory decay seem to represent an advantageous individual strategy for maximising the foraging success of the group (indicated by a combination of high $P_{\mathrm{T_{best}}}$ and small τ), as a result of efficient collective learning.

The ability to transfer information is essential to the emergence of collective learning. Surprisingly, the aforementioned efficient strategies requires a fairly small amount of interactions among foragers. In comparison, stronger interactions (higher ρ) are needed to reach high levels of collective learning in the perfect memory case, see Figs. 3(a)-(c) vs. Figs. 5(a)-(c).

The outcome of collective actions is not always rewarding and can be costly instead. Inspired by the homing behavior of pigeons, a model of two coupled neural networks aiming to learn a correct navigation angle showed that the performance of solo learners was actually better than the collective performance of democratic pairs of learners [52]. In this study, learning was faster and final performance higher when pair members contributed less equally to decision making. The high collective performance exhibited in the present model, in contrast, might be a consequence of the complexity of the foraging environment and of the large

number of individuals, who can explore different regions of space in parallel. However, the (slight) decrease of performance with the strength of interactions, observed in Fig. 5(a), while the cohesion increases in Fig. 5(b), is worth being noticed. This sub-optimal patch exploitation due to an excess of interactions could be caused by the presence of conflicting information in the social network about the location of the best resource sites.

A wealth of theoretical studies have discussed the optimality of random Lévy walks for encountering resources in unknown environments [9, 53–56]. Here we have shown that multiple scale movements can also be useful for learning purposes, when dispersed information about resources needs to be collected during a memory-based process. In a model similar to ours, where individuals performed random exploratory Lévy walks at constant speed (instead of jumping from one site to another in one time-step like here), a large fraction of the group could also aggregate around a salient resource site of the environment [47]. Aggregation even reached a maximum for a particular value of μ, which decreased as the use of memory was more frequent. Here we find that increasing μ favours cohesion, at the expanse of less exploitation of the best site.

In social species such as spider monkeys, the individuals have mental maps to navigate their environment and also exhibit movements characterized by a Lévy index of $\mu \sim 1$ [12, 57]. Spider monkeys travel in small subgroups of varying composition and size across their home range and can communicate over large distances through vocalizations [58]. Information transfer processes and their effects on collective dynamics have also been measured in this species [59]. By monitoring visits to certain food patches, knowledgeable and naive individuals can be identified, and it has been demonstrated that the arrival of naive individuals to novel food patches is accelerated by social information [59]. Our model exhibits a similar phenomenon, as illustrated by Fig. 2(c)-(d) regarding the number of individuals that have visited a particular site at a given time, in the presence or absence of interactions.

It is well accepted that forgetting improves reinforced learning since unimportant information disappears, making room for more valuable one [30–32, 60]. Here, we have allowed memory to decay slowly in time as a power-law instead of exponentially. The classical Ebbinghaus' "forgetting curve" obtained from experiments conducted on human subjects is well fitted by a double power-law or a simple power-law function with a small exponent (in the interval $0.1 - 0.2$), rather than by an exponential or a double exponential [61]. The collective decay of public memories in human societies can be described as an exponential at short time and a power-law with $\beta = 0.3$ at large time [62]. In the context of movement ecology, the ranging patterns of bisons are well fitted by power-law memory kernel with $\beta = 1$ [1]. Similar data of Elk movements were successfully fitted by a slower-than-exponential decay [24]. With the model proposed here, we have shown that memory decay is an important driver of a fast and efficient collective learning in static but complex environments. It would be interesting to probe other types of memory kernels on the group performance.

In its present form, our computational model considers resource patches that are always available and ignores competition among foragers. However, even the best food patch may not be sufficiently large for being occupied by a large number of individuals at the same time. In addition, patch depletion by some foragers may affect the attractiveness perceived by others during future visits, unless the patches refresh very rapidly. These effects should favour the occupation of other good but sub-optimal patches with a larger probability and cause a decrease in cohesion by splitting the group into several subgroups, akin to fission-fusion societies [63]. We nevertheless expect that patch choice should remain very selective for medium-sized groups, even in the presence of competition.

Even though our work represents a step toward the understanding of some mechanisms responsible for efficient collective learning in ecology, other aspects remain elusive. The effects of the number of foragers on the learning time and performance remain unknown, but the fact that too many interactions seem to affect learning would suggest that very large groups could also find conflicting information to make optimal decisions. In addition, we have considered stationary environments. It would be interesting to study in future work how the foragers of our model adapt to changing environments with ephemeral resources, a case where the decay of memory might also be beneficial.

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