Resource ephemerality influences effectiveness of altruistic behavior in collective foraging

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Abstract In collective foraging, interactions between conspecifics can be exploited to increase foraging efficiencies. Many collective systems exhibit short interaction ranges, making information about patches rich in resources only locally available. In environments wherein these patches are difficult to locate, collective systems might exhibit altruistic traits that increase average resource intake compared to non-interacting systems. In this work, we show that resource ephemerality and availability highly influence the benefits of altruistic behavior. We study an agent-based model wherein foragers can recruit others to feed on patches, instead of exploiting these individually. We show that the net gain by recruiting conspecifics can be estimated, effectively reducing the decision on patch detection to one based on a threshold. Patches with qualities above this threshold are expected to increase foraging efficiencies and should therefore induce recruiting of others. By letting foragers assume Lévy searches, we show that recruitment strategies with contrasting diffusion characteristics optimize conspecific encounter rates. Our results further indicate that active recruitment is only beneficial when patches are scarce and persistent. Most interestingly, the effect of choosing suboptimal threshold values is small over a wide range of resource ephemeralities. This suggests that the decision of whether to recruit others is more impactful than fine-tuning the recruitment decision. Finally, we show that the advantages of active recruitment depend greatly on both forager density and their interaction radius, as we observe passive strategies to be more efficient, but only when forager densities or interaction ranges are large.

Keywords collective foraging, altruistic behavior, ephemeral landscapes

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1 Introduction

Collectively foraging for resources is critical to the survival of many animal species. In principle, foraging entails the entire process of searching for resources whose locations within the environment are often unknown. To detect these resources, foragers must resort to random searches. Whereas individual random searches can be optimized over a wide range of environmental constraints (Viswanathan et al., 1999; Bartumeus et al., 2005; Wosniack et al., 2015b; Zhao et al., 2015; Bartumeus et al., 2016), a collective system can potentially exploit interactions to further increase the foraging efficiency (Pitcher et al., 1982; Torney et al., 2009; Bhattacharya and Vicsek, 2014; Falcón-Cortés et al., 2019; Nauta et al., 2020b). While the impact of foraging efficiency with respect to survival is evident, collective foraging additionally provides an important source of inspiration for designing artificial systems (Winfield, 2009; Rausch et al., 2020c). In general, collective systems rely on possibly intricate communication patterns that are essential to spread information within the system. This is a crucial aspect for the emergence of many types of collective dynamics, with applications ranging from understanding and controlling epidemiology (Avin and Ercal, 2005; Pastor-Satorras et al., 2015) to sensor networks (Akyildiz et al., 2002; Dall and Christensen, 2002; Díaz et al., 2009; Barthélemy, 2011). Identifying and understanding essential parts of the decision processes that underlie collective foraging, therefore, proves largely beneficial for designing efficient artificial systems.

Many foraging environments contain ample resources distributed according to fragmented, or patchy, distributions (Levin, 1976; Fauchald, 1999; Levin, 2000; Kéfi et al., 2007; Weimerskirch, 2007; With and Pavuk, 2011; Khaluf et al., 2017). In such systems, locating the patches rich in resources is difficult for individuals. Rather obviously, groups and collective systems can benefit from interactions between conspecifics (Berdahl et al., 2013), effectively parallelizing the search (Cvikel et al., 2015). Then, for example, by joining successful conspecifics, aggregations on salient patches can occur (Haney et al., 1992; Jeanson et al., 2005; Eftimie et al., 2007; Olson et al., 2009; Ding et al., 2019). However, when the number of foragers feeding on the patches increases, foraging efficiencies might fall due to competition for resources on the patches (Ranta et al., 1993). This on-patch competition introduces an important distinction between groups and collective systems. However, the terms used to describe these distinct systems are often used interchangeably (see e.g., Berdahl et al., 2013; Bhattacharya and Vicsek, 2014, among others).

In particular, we argue that group (or social) foraging should describe groups of foragers wherein individuals do not necessarily display behavior that maximizes group foraging efficiencies. Instead, they often favor individually optimal behavior, as hypothesized by the selfish herd hypothesis (Hamilton, 1971). Group foraging has been extensively studied using numerous decision processes, interaction models, and resource landscapes (Barnard and Sibly, 1981; Ruxton et al., 1995; Beauchamp and Giraldeau, 1996; Giraldeau and Beauchamp, 1999; Bhattacharya and Vicsek, 2014). While it has been observed

that grouping provides individual advantages such as reduced predation risk (Krause et al., 2002; Beauchamp, 2004; Ioannou et al., 2008) and reduced risk of starvation (Clark and Mangel, 1984; Beauchamp, 2005), these advantages do not necessarily translate to higher group foraging efficiencies (Monaghan and Metcalfe, 1985; Rita and Ranta, 1998; Beauchamp, 2005, 2007; Svanbäck and Bolnick, 2007). This indicates that it is important to distinguish between individuals living in groups and individuals who are part of a collective, especially in the context of foraging. In contrast with groups, we argue that collective systems should exhibit traits that aim to maximize collective benefits. This effectively eliminates the on-patch resource competition encountered in group foraging, as it is not a disadvantage that resources need to be shared. As an effect, it allows individuals to instead favor behavior that is advantageous for the collective, but importantly not necessarily advantageous for the individual itself. Such behavior includes altruistic behavior that has been observed in collective systems, such as active inhibition of visitation to exhausted patches (Wendt et al., 2020), optimal task allocations (Von Frisch, 1967; Cerdá et al., 2009; Landgraf et al., 2011), and (active) recruitment towards salient patches (Detrain et al., 1999; Riley et al., 2005; Detrain and Deneubourg, 2008; Dechaume-Moncharmont et al., 2005; Cerdá et al., 2009; Shaffer et al., 2013; I'Anson Price and Grüter, 2015), the latter of which is studied in this work.

Obviously, the benefits of collective (altruistic) behavior depend strongly on resource distribution. Static resource distributions wherein patch locations and their respective qualities are known result in ideal free distributions that optimize foraging efficiencies (Fretwell and Lucas, 1969; Rosenzweig, 1981). However, patch locations and qualities are most often not known. In addition, resource distributions are not static but possess potentially complex dynamics, expressed by resource locations changing over time. Precise resource locations are often tied to seasonality (Jonzén et al., 2004), other periodic changes (Calle et al., 2016), or more complex resource dynamics, possibly leading to random patch durations (Pulliam and Millikan, 1982). Additionally, resource consumption, akin to destructive foraging (Raposo et al., 2003), in combination with spatial characteristics of the resource distribution, can lead to ephemeral resource aggregations (Sims et al., 2008; Ferreira et al., 2012; Bhattacharya and Vicsek, 2014).

Patchy and ephemeral resource landscapes imply that full global information, e.g.,global knowledge about salient patch locations, is not necessarily beneficial for a collective system (Martínez-García et al., 2013). For example, if the information on patches rich in resources is disseminated across vast distances, it is highly likely that these patches have already disappeared once the information reaches eligible conspecifics. Moreover, when rapid decision making is concerned, lower levels of connectivity are preferred (Franks et al., 2003; Pirrone et al., 2014; Valentini et al., 2015). These types of collective systems have also been observed in swarming animals, where social interactions were purposely limited to enhance collective responses (Gordon et al., 1993; Ballerini et al., 2008; Attanasi et al., 2014; Mateo et al., 2017). Despite the obvious disadvantages, highly connected systems that facilitate global infor-

mation dissemination have been extensively studied in the context of group and collective foraging (Bhattacharya and Vicsek, 2014; Lihoreau et al., 2017; Falcón-Cortés et al., 2019). Additionally, previous work has studied the effect of (static) topological networks, such as scale-free networks (Ramos-Fernández, 2005; Ramos-Fernández et al., 2009; Falcón-Cortés et al., 2019; Rausch et al., 2019, 2020b). However, foraging systems with reduced information dissemination caused by short communication ranges have not been thoroughly discussed, although these limitations are encountered in many artificial collective systems (Shklarsh et al., 2011; Brambilla et al., 2013; Hamann, 2018; Khaluf et al., 2018; Rausch et al., 2020a).

In this work, we study collective foraging in patchy and ephemeral resource landscapes, wherein foragers can only interact with conspecifics over relatively short distances. We study altruistic systems with active recruitment, as foragers that have detected a patch can choose to recruit others over individually exploiting the resources on the patch. Such recruiting schemes have been mostly observed in ants (Detrain et al., 1999; Detrain and Deneubourg, 2008; Dechaume-Moncharmont et al., 2005; Cerdá et al., 2009; Shaffer et al., 2013) and bees (Riley et al., 2005; I'Anson Price and Grüter, 2015) and embody the underlying premise of a collective system: altruism. Note that since the individual that detected the patch does not consume resources itself, recruitment represents pure altruistic behavior. It carries similarities with resource sharing (Rausch et al., 2020b), which, besides in swarming insects, has been observed in social mammals such as primates (Winterhalder, 1996) and wolves (Mech and Boitani, 2010). Obviously, and as we shall show, recruitment should only be viable if the expected net gain of the collective is positive (Ruxton et al., 2005). In other words, when patches are ephemeral, and the recruiter does not encounter conspecifics before the patch disappears, it would have been better – both at the individual and collective level – if it had individually exploited the patch. Therefore, at patch detection, each forager needs to assess whether the patch is of sufficient quality to deem recruiting others as efficient behavior.

To make this decision, we argue that each forager needs to be able to estimate conspecific encounter rates. In this work, we show that under some reasonable assumptions, encounter rates can be estimated by which individuals can decide whether to recruit or not. When designing artificial systems, these estimates can be given as prior information. More specifically, we shall show that our model effectively describes a threshold foraging model (Piatt and Methven, 1992; Giraldeau and Beauchamp, 1999; Ruxton et al., 2005), where only patches above a certain threshold provide a positive gain by recruiting others. Following observations from natural systems (Boyer et al., 2006), we consider ephemeral resource landscapes wherein the patches containing resources have durations sampled from an inverse power law (see section 2.1). By studying different levels of resource ephemerality and resource availability, we show that recruiting others increased collective foraging efficiencies, but only if patches are both difficult to locate and persistent. Thus, our results show that altruistic behavior can decrease foraging efficiencies when patches are readily available or when patches persist over time scales shorter than those

over which others can be recruited. Additionally, while we present a rudimentary scaling analysis that reveals optimal choices of thresholds, we show that precise computation of these thresholds is not necessary for altruistic behavior to be beneficial. Interestingly, the choice of whether to recruit at all is a far more important decision. Finally, we show that the benefits of recruitment depend strongly on forager density and communication ranges. More specifically, simple group strategies, which are not necessarily altruistic, can outperform collective strategies when random conspecific encounter rates are high, which occurs when forager density is high. This illustrates the complexity of the decision process that individuals within a collective might undergo, as the most efficient strategy can critically depend on the many variables present in the system.

2 Model

2.1 Environment description

In this work, we model our environment as a two-dimensional area of dimension $L \times L$ with periodic boundaries. This design reflects environments that are much larger than the individual and allows us to study the macroscopic properties of the collective in isolation of more invasive boundary effects. Within the environment, we spatially distribute M patches uniformly. We couple patch quality and patch duration by assuming that higher quality patches are available for longer times. This assumption is largely based on the fact that foragers spend more time in high quality patches than in low quality ones (Charnov, 1976; McNair, 1982; Bonser et al., 1998; Wajnberg et al., 2000; Nonacs, 2001; Watanabe et al., 2014), as foraging in patchy environments is often understood as an evidence accumulation process (McNamara, 1982; Haccou et al., 1991; Davidson and El Hady, 2019). We let the duration of a patch τ follow an inverse power law with stable parameter γ as

$$p(\tau) = \begin{cases} A\tau^{-\gamma} & t_{min} \leq \tau \leq t_{max}, \\ 0 & \text{otherwise}, \end{cases} \tag{1}$$

where $A = (\gamma - 1)/(t_{min}^{1-\gamma} - t_{max}^{1-\gamma})$ a normalization constant. Note the lower truncation at t_{min} that indicates patches exist at least for some period of time. Since we are interested in realistic ephemeral landscapes, patches should not be of extremely long (potentially infinite) duration, as ensured by the upper truncation at t_{max}. These scale-free, inverse power law distributions have been widely observed in natural systems (Johnson et al., 2004; Enquist and Niklas, 2001; Niklas et al., 2003; Boyer et al., 2006; Sims et al., 2008). In the asymptotic limit of $t_{max} \to \infty$, we have for $\gamma \to 1$, that the patch distribution is rather broad, implying that patches of almost all possible durations will appear within the environment. In contrast, when γ increases the inverse power law loses its heavy tail and converges to a normal distribution for $\gamma \geq 3$. Most

notably, for $\gamma \gg 1$, the environment consists of patches of duration t_{min}, since the probability of patches of longer duration appearing becomes negligible in practice. In order to preserve overall statistical properties of environments patch density is kept constant throughout the experiments by respawning a new patch at a random location each time a patch disappears (see below).

In this work, we assume patches to be of infinite capacity (but of finite duration) as to model an ephemeral landscape wherein short-term (over) consumption does not deplete patches. While this assumption might appear counter-intuitive, systems wherein (small) groups of individuals cannot fully exhaust ephemeral patches are widespread (Pulliam and Millikan, 1982). Examples are bats preying on insect swarms (Levin et al., 2013) or fish (Otálora-Ardila et al., 2013; Egert-Berg et al., 2018), whales foraging on seasonally available krill (Heide-Jørgensen et al., 2007; Laidre et al., 2010), birds feeding on vast swarms of insects (Brown, 1988), and fish feeding on mobile prey (Baird et al., 1991). Moreover, having (potentially) infinite patch density, but limited patch availability, effectively captures effects similar to patch exhaustion due to resource consumption. It allows us to model ephemeral resource landscapes without having to take into account short-term resource competition on the patches.

We should mention that the spatial distribution of resources (and subsequently the patches wherein they reside) often follow fractal distributions (Weimerskirch, 2007; Sims et al., 2008; Ferreira et al., 2012; Bhattacharya and Vicsek, 2014), where intra-resource distances are distributed according to an inverse power law as Eq. (1). However, fragmented environments wherein resources are contained in uniformly distributed fixed size patches are observed in natural systems (Beaver, 1977; Atkinson and Shorrocks, 1981) and subsequently extensively studied in the context of foraging (Boyer et al., 2006; Wosniack et al., 2015a,b; Falcón-Cortés et al., 2019; Nauta et al., 2020a). Since we focus on large-scale systems, we can omit more complex, within-patch resource distributions and dynamics by assuming that subsequent resource encounters on patches take place on time scales smaller than considered time step sizes. This assumption allows us to study the (dis)advantages of collective (altruistic) behavior in isolation of other, possibly intrusive, effects. We consider more detailed spatial resource distributions and dynamics to be out of the scope of this work.

2.2 Individual behavior

We consider a homogeneous collective system of N foragers. Each individual forager is able to detect patches within a detection radius $R \ll L$. Foragers are able to observe patch duration (i.e. patch quality) instantaneously. They can interact with conspecifics within an interaction radius $r > R$ (but $r \ll L$, see Appendix A). More specifically, we focus on interaction ranges below a critical value $r < r_c$ as values above this critical value result in fully connected communication networks. Fully connected networks enable formation of global information whereas information is most often locally bound in col-

lective systems (see Appendix A for a more detailed discussion). Additionally, we consider foragers with constant velocities (see below).

We discretize time into steps of fixed size and start by uniformly distributing foragers and having them explore the environment using a Lévy walk. Lévy walks have been extensively studied in foraging literature as recent advances in data logging techniques highlight them as efficient random searches when patches (or resources) are sparsely distributed (Viswanathan et al., 1996, 1999, 2011; Sims et al., 2008; Zaburdaev et al., 2015). Whereas robustness of Lévy walks in a foraging context has been widely established (Raposo et al., 2003; Ferreira et al., 2012; Wosniack et al., 2015a,b; Zhao et al., 2015), it is currently debated whether animals truly execute Lévy walks (Benhamou, 2007; Edwards, 2011; James et al., 2011; Pyke, 2015). Despite the ongoing debate, many empirical foraging studies have established the existence of Lévy walks in natural systems (see e.g., Reynolds et al., 2007; Humphries et al., 2010; Ariel et al., 2015).

Lévy walks are characterized by having flight lengths sampled from an inverse power law with parameter α, i.e.

$$p(\ell) = \begin{cases} Z\ell^{-\alpha} & \ell_0 \leq \ell \leq L, \\ 0 & \text{otherwise,} \end{cases} \qquad (2)$$

where ℓ_0 is the minimum step size, L the environment size, and $Z = (\alpha - 1)/(\ell_0^{1-\alpha} - L^{1-\alpha})$ the normalization constant. Lower and upper truncation ensure that displacements occur on spatial scales that are relevant to the problem (Pyke, 2015). After sampling a flight length, foragers move in a straight line, with fixed step size (velocity) ℓ_0, until its full length has been traversed. The travel angle is randomly sampled between 0 and 2π. Note that convergence of the above inverse power law towards a Gaussian process is ultraslow, and hence the general characteristics of Lévy distributions are conserved throughout the collective foraging process (Mantegna and Stanley, 1994).

In the limit $L \to \infty$, Lévy walks encompass several distinct modes depending on the Lévy parameter α. These modes characterize spatial displacement and range from ballistic (straight line) motion for $\alpha \to 1$ to anomalous diffusion for $1 < \alpha < 3$ and normal diffusion (Brownian motion) for $\alpha \geq 3$. As Lévy walks encompass several distinct modes of diffusion, they serve as a useful tool from a more practical perspective. Due to their simplicity and robustness for maximizing foraging efficiencies in sparse resource landscapes they have been applied extensively in artificial systems (see e.g., Sutantyo et al., 2013; Beal, 2015; Dimidov et al., 2016; Nauta et al., 2020b). For a more detailed description of Lévy walks and their characteristics we refer the interested reader to more detailed descriptions (e.g., Viswanathan et al., 2011; Zaburdaev et al., 2015).

While searching the environment, foragers can encounter both patches and conspecifics. A rudimentary scaling analysis (Appendix B) shows that, in order to maximize group search efficiencies, the decision at patch detection is

equal to a threshold decision model (Piatt and Methven, 1992; Giraldeau and Beauchamp, 1999; Ruxton et al., 2005). Thus, on encountering a patch, individual foragers commence to recruit conspecifics when the (remaining) duration τ exceeds a threshold τ_c. Interestingly, heavy tailed patch distributions drastically reduce the necessity for choosing optimal thresholds (see section 3.3). In other words, while individual decisions can follow a threshold model, the binary decision whether to recruit or not is more impactful than following a strategy with a precise threshold value.

Inspired by Bartumeus et al. (2008), we consider active recruitment to be a random search as well, but for conspecifics instead of patches. We let recruiting foragers additionally follow a Lévy walk, but with a different parameter α'. Diffusion of individuals within our system of foragers will therefore be described by a vector $\boldsymbol{\alpha} = (\alpha, \alpha')$, where α is the parameter for the random search and α' for the recruiting search. The goal of recruiting is to encounter conspecifics and subsequently communicate the location of the previously detected patch. Then, encountered conspecifics travel to the advocated patch and proceed to feed on the resources residing on the patch. To facilitate this, the recruiting forager has access to a simple, finite-length memory component wherein the location and the duration (quality) of the patch are stored. Note that memory formation occurs only at patch detection. The recruiting forager effectively acts as an advocate for the patch and induces ephemeral aggregations of multiple foragers onto the patch. More specifically, since we consider interaction radii larger than the patch detection range ($r > R$), recruiters effectively enlarge patch detection ranges such that others, that would otherwise not be aware of the patch, can benefit.

In summary, individual foragers apply the following set of rules, given a prior threshold τ_c:

(i) When detecting a patch, if $\tau > \tau_c$, try to recruit others by executing a Lévy search with parameter α'. Recruiting stops when the time needed to travel towards the advocated patch exceeds the remaining duration of the patch.

(ii) When detecting a patch, but $\tau \leq \tau_c$, stay and feed on the patch by continuously consuming resources with rate ϵ. Feeding stops when the patch disappears.

(iii) When detecting a recruiting conspecific, travel towards the advocated patch and, once on the patch, feed with rate ϵ until the patch disappears.

(iv) When neither a patch nor a recruiting conspecific is detected, continue the Lévy search with parameter α.

(v) This rule pertains to the regeneration of patches once depleted. After the duration τ of the patch has been expired, the patch is replaced by a new patch at a random location and a new duration sampled from the inverse power law with parameter γ (see Eq. (1)). Thus, the total number of available patches M remains fixed.

Note that once a patch has been detected, only the forager that first detected it will try to recruit others. As a result, recruited foragers in (iii) proceed to
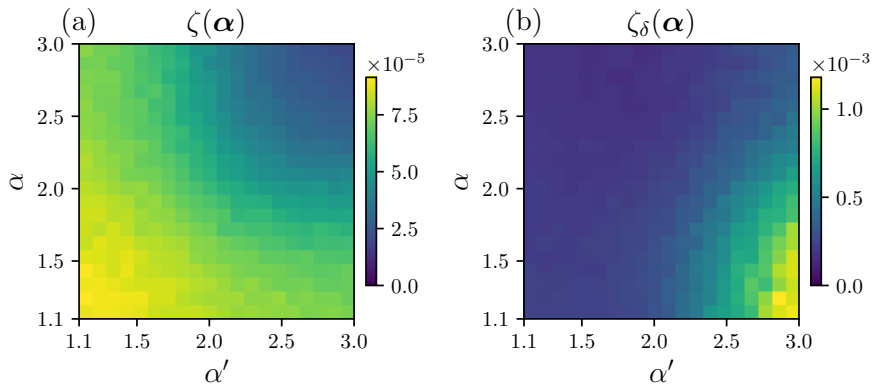
Fig. 1 Conspecific encounter rates ζ for systems with a single recruiter and $\boldsymbol{\alpha} = (\alpha, \alpha')$. Encounter rates are obtained for $t = 500$, i.e. in the short timescale $1 \ll t \ll L/\ell_0$ (see text and Appendix B). Recall that α is the stable parameter for searchers and α' of the recruiter(s). (a) The encounter rate normalized by the total distance traversed $\mathcal{L}$ (see Eq. (3)). (b) The encounter rate normalized by the displacement from the patch δ, i.e. $\zeta_\delta = n_e/\delta$ (see Eq. (B.12)).

feed on the patch and not subsequently start recruiting as well. While more complex systems most likely do not display such binary modes of behavior, we assume a more simplified model as to keep our numerical approach and the accompanying scaling analysis tractable. Furthermore, information on patch duration and location is forgotten after the patch has disappeared, thus memory duration, and subsequent recruiting behavior, has finite lengths. Finally, while flights can be truncated upon both patch and conspecific detection, we do not study (group) diffusion characteristics in this work. A more thorough investigation in potential crowding effects, by additionally taking finite-size effects into account, is warranted when one aims to implement our model in more realistic artificial systems, or when studying different scales over which foraging takes place.

3 Results

We study a system of $N = 256$ foragers in the $L \times L$ environment with $L = 1000$. We consider equal step size and patch detection radius $\ell_0 = R = 1$ and normalize consumption rate $\epsilon = 1$. Interactions with conspecifics can occur when the distance is smaller than $r = 0.0375L \approx \frac{1}{2}r_c$ (Appendix A). While the interaction radius and forager density influence the metrics that will be presented, we found that general characteristics did not change when properly accounting for the number of foragers (but see the discussion on density-related effects in section 3.4). Patch durations are distributed according to the inverse power law with minimum duration $t_{min} = 10$ and maximum duration $t_{max} = L/\ell_0 = 1000$. While the minimum patch duration ensures patches ex-

ist at least for some time that they can be detected, the maximum duration is fixed at L/ℓ_0 as we assume patches for which recruiting distances can be longer than the environment size unrealistic. Unless mentioned otherwise, we compute statistical averages over 250 different foraging instances of duration $T = 10^5$ steps.

3.1 Conspecific encounter rates

Let us first briefly discuss a non-interacting group of N foragers foraging in an ephemeral landscape. This is achieved by considering both $\tau_c = \infty$ and $r = 0$. Such systems define group foraging in a selfish system where foragers do not take others into account. Patch distribution and patch ephemerality define a destructive foraging instance for uniformly distributed targets for which it is known that the optimal Lévy parameter $\alpha_{opt} \to 1$ (Viswanathan et al., 1999; Bartumeus et al., 2005; Ferreira et al., 2012). In other words, ballistic motion provides the highest patch encounter rates and therefore the highest search efficiencies.

When foragers are able to interact with conspecifics ($\tau_c \leq t_{max}$, $r > 0$) we also expect the patch detection rate to be maximum for $\alpha_{opt} \to 1$. Hence, recruiters should aim to choose α' to accommodate the highest possible encounter rates *with conspecifics* who execute Lévy walks with $\alpha \to 1$. Previous work on Lévy searches for dynamic targets who were executing Lévy walks with a different parameter concluded that the most contrasting diffusion optimized search efficiencies (Bartumeus et al., 2008), i.e. $\alpha'_{opt} \geq 3$ as $\alpha \to 1$, or vice versa. However, forager densities at which Bartumeus et al. (2008) studied the destructive foraging differs from our perspective. Here, we additionally consider a different timescale as patches are of (relatively) short and finite duration ($T \gg t_{max}$). Therefore, recruiters need to encounter conspecifics within a relatively short time scale, which contrasts with the long time scale discussed in Bartumeus et al. (2008). Finally, we study perception ranges for conspecifics to be larger than detection ranges for patches (i.e., $r > R$), while these ranges are equal in Bartumeus et al. (2008), as they focus on predator-prey type relations between foragers and resources.

To study what parameters maximize the number of encounters we introduce the conspecific encounter rate ζ as an analogue to the target search efficiency (Viswanathan et al., 1999)

$$\zeta = \frac{n_e}{\mathcal{L}}, \tag{3}$$

where n_e is the number of unique conspecifics encountered within travel distance $\mathcal{L}$. To study encounter rates in more detail, let us temporarily consider a system of N foragers where only a single forager, the recruiter, is recruiting conspecifics. Note that although forager density N heavily influences the rate of conspecific encounters, we found overall characteristics to be similar for different values of N (Appendix C). Results for systems with $N = 256$ are

presented in Fig. 1a. We see that when $\alpha, \alpha' \to 1$, conspecific encounter rates are maximized. However, one should be careful not to normalize by the travel distance, as it is actually the displacement from the advocated patch δ that is of importance. If recruiters can recruit others while remaining close to the advocated patch, the efficiency of recruiting should be higher. The reason is that encountered conspecifics need not travel long distances to arrive on the patch and are therefore able to feed for longer. As seen in Fig. 1b, contrasting strategies with $\alpha' = 3$ as $\alpha \to 1$ are maximizing encounter rates when normalizing by the displacement (Appendix B). Importantly, encounter rates are maximal when $\alpha \to 1$. This is desired as ballistic motion provided maximum patch detection rates as well. Therefore, in following experiments, we study systems with fixed $\boldsymbol{\alpha} = (1.1, 3.0)$.

We would briefly like to mention the fact that, while we have studied Lévy walks with stable parameters $1 \leq \alpha, \alpha' \leq 3$, the above results indicate that the best strategies are those at the extremes of the studied parameter range. Recall that in the asymptotic limit of $L \to \infty$, these values represent ballistic motion for $\alpha \to 1$ and Brownian motion for $\alpha' = 3$. Hence, one might argue why we do not study ballistic searchers and Brownian recruiters in favor of more complex Lévy searches with parameters α and α'. We argue that Lévy walks serve as an extremely useful tool to study the influence of movement characteristics, as a single parameter encompasses multiple distinct scales of movement (see section 2.2). Therefore, even though we encounter measures to be maximized at the extremes of the studied parameter range, we deem it worthwhile to use Lévy walks as the movement model. Finally, when spatial resource distributions are non-uniform, intermediate values of α have been found to optimize Lévy searches (Ferreira et al., 2012; Wosniack et al., 2015a,b). Hence using Lévy walks as a prior movement strategy appears appropriate over a wide range of systems, as it is both efficient and flexible.

3.2 Collective search efficiency

Next, we study collective foraging for homogeneous systems with $\tau_c \geq 0$ and $r > 0$. Note that all foragers can start recruiting others when patch durations exceed the threshold ensuring decentralized behavior typical of swarm systems (Brambilla et al., 2013; Hamann, 2018). To study the foraging efficiency of the collective system, we define the group search efficiency as the average foraging efficiency of its members (Bhattacharya and Vicsek, 2014; Nauta et al., 2020b)

$$\eta = \frac{1}{N} \sum_i \frac{k_i}{\mathcal{L}_i},$$

(4)

with k_i and $\mathcal{L}_i$ the number of resources consumed respectively the total distance traversed by forager i.

Let us first discuss two contrasting systems, where one is comprised of purely altruistic foragers with $\tau_c = 0$ and the other a selfish system with
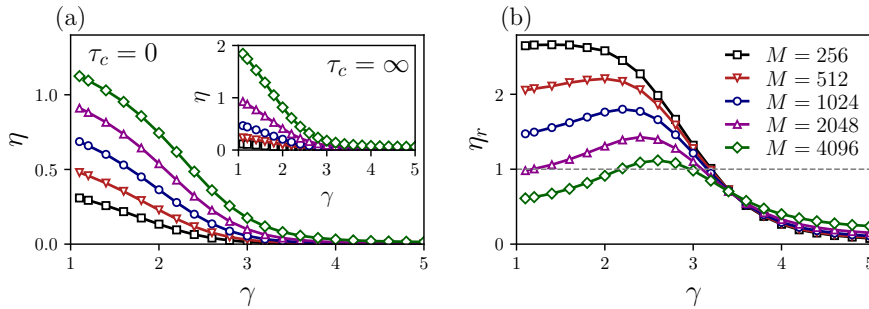
(a)

(b)

Fig. 2 Group search efficiency η versus the stable parameter γ for different patch availability M. (a) Group search efficiencies for fully altruistic collective systems ($\tau_c = 0$). Inset displays group search efficiency for individual groups of (selfish) foragers ($\tau_c = \infty$). (b) Relative group search efficiency $\eta_r = \eta(\tau_c = 0)/\eta(\tau_c = \infty)$. Points above the dashed line at $\eta_r = 1$ depict environmental constraints wherein recruitment (altruistic behavior) results in a positive gain in the group search efficiency. Points below the dashed line indicate environments wherein individual searches (selfish behavior) is preferred.

$\tau_c = \infty$. Note that when $\tau_c = 0$, all patch detections lead to recruiting behavior, whereas recruiting behavior is never induced for $\tau_c = \infty$. We see in Fig. 2 that both the number of patches M and the stable parameter of the resource distribution γ heavily influence both the group search efficiency η and the benefits of recruitment. Further inspection of the distributions over individual search efficiencies η_i displays more details on the effects of γ on the group search efficiency (Fig. 3).

As γ increases, group search efficiencies for both systems decrease regardless of the value of M. The reason is that resources become increasingly ephemeral and as such the search for patches becomes increasingly difficult. This is highlighted by noting that selfish systems with $\tau_c = \infty$ have low search efficiencies as well. Thus, when patch encounters are already rare, a system of collective foragers does not benefit from recruiting as patches are too short-lived to effectively recruit others (Fig. 2a). As a result, the relative group search efficiency decreases as γ increases from $\gamma \approx 3$ onward (Fig. 2b). This effect is additionally observed in the individual distributions (Fig. 3). For low γ, individual efficiencies for altruistic groups are distributed around means higher than for selfish groups. High γ, in contrast, indicates systems wherein most individuals consume little to no resources. This effect is exacerbated when M is small (inset Fig. 3c).

Search efficiencies increase as γ decreases since patches of longer duration become more readily available. Unsurprisingly, larger number of patches result in higher search efficiencies for both selfish and altruistic systems. However, when patches are less numerous, the benefits of recruiting others increase for $\gamma \lesssim 3$. In this range of γ, lifetimes of some patches are relatively long due

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[2] Note that R^2 here pertains to the statistical measure, not the square of the patch detection radius R.

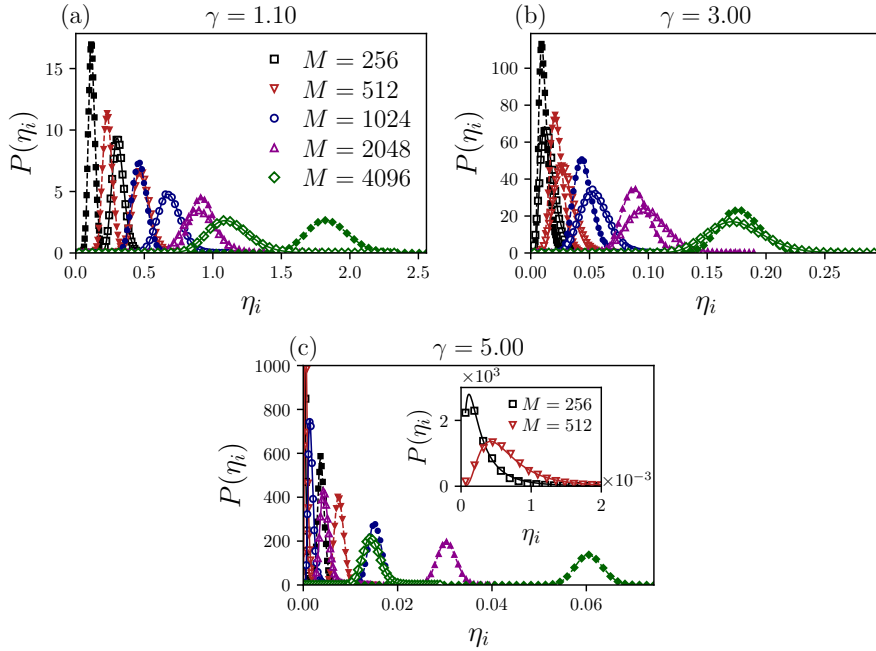**Fig. 3** Probability density function $P(\eta_i)$ of individual search efficiencies $\eta_i = k_i/\mathcal{L}_i$ for different stable parameters γ and resource availabilities M. Empty markers and solid lines indicate altruistic systems with $\tau_c = 0$. Filled markers and dashed lines indicate selfish systems with $\tau_c = \infty$. Lines (both solid and dashed) are fitted log-normal distributions. We found $R^2 > 0.98$ for all fitted curves[2](see Appendix D and Table D.1). (a) Density for high resource persistence. (b) Density for intermediate resource persistence. Note that distributions for $\tau_c = 0$ and τ_c are do not differ significantly for all M, indicating $\eta_r \approx 1$, as expected from Fig. 2. (c) Density for low resource persistence. Inset displays details on the (skewed) fitted log-normal distribution for $\gamma = 5$ and $M = 256, 512$.

to the dominance of heavy tails in the distribution. If patches are relatively sparse, recruiting others to these rich patches becomes much more beneficial as conspecifics are less likely to encounter patches by themselves. In contrast, when M increases, we note that the relative search efficiency decreases as $\gamma \to 1$. The reason for this is twofold. First, due to a high number of available resources, individuals are more likely to encounter patches by themselves, reducing the number of 'free' foragers (Fig. 4a). Here, 'free' foragers are those who are eligible to be recruited as they are not feeding, recruiting, or already being attracted, i.e. those who are actively searching for patches. Hence, recruiting instances are less likely to result in patch encounters by conspecifics thereby decreasing the group search efficiency. This is additionally reflected in Fig. 4b, as the number of conspecifics per recruit instance decreases as M and γ increase. Second, for large M, the distance needed to travel towards the advocated patch when a forager is being recruited approaches the mean free path λ of the environment. Note that λ indicates the average distance be-
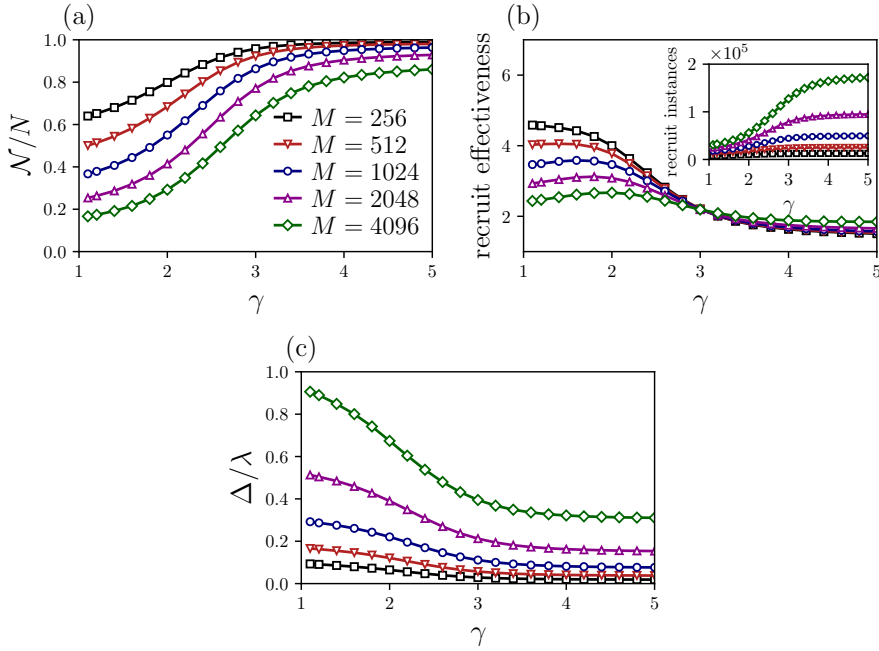
Fig. 4 Effectiveness of recruiting behavior for an altruistic system ($\tau_c = 0$). (a) Fraction of the number of 'free' foragers $\mathcal{N}$ of the total population N at each recruit instance (see text). (b) The effectiveness of recruiting as the total number of conspecifics recruited divided by the total number of recruit instances. Inset displays the absolute number of recruit instances. (c) Average distance needed to travel towards the patch upon being recruited Δ, normalized by the mean free path $\lambda = L^2/2RM$. Environments wherein $\Delta < \lambda$ indicate (potential) benefits of recruiting instances, whereas environments where $\Delta \gtrsim \lambda$ have individual searches equal to more efficient than being recruited (see text).

tween subsequent patch encounters and decreases as M increases. If the travel distance towards the advocated patch approaches (or exceeds) λ, it becomes just as (or more) beneficial to search for patches individually, as is the case for large M (Fig. 4c). As a result, altruistic group search efficiencies fall below values of selfish groups.

3.3 Threshold decision making

Having established that recruitment is only beneficial when patches are sparse and persistent, we would like to discuss effects of the threshold τ_c. Recall that foragers only start recruiting others when the patch duration is higher than a specific threshold τ_c (see section 2.2 and Appendix B). As visible in Fig. 5, the effect of the threshold on the group search efficiency is not significant when resource distributions are either fully dominated by the heavy tail ($\gamma \approx 1$), or when the heavy tail is suppressed ($\gamma \gg 1$).
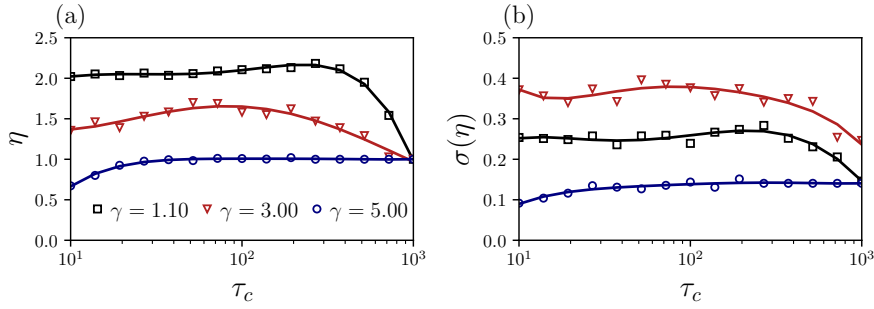
Fig. 5 The influence of the threshold τ_c on the group search efficiency η. Note that $\tau_c = t_{min} = 10$ corresponds to a fully altruistic system and $\tau_c = t_{max} = 1000$ to a selfish one. Results are obtained for $M = 512$, but similar results are obtained for other values of M. Lines are a guide to the eye. (a) Normalized group search efficiency η versus the threshold τ_c. Note the optimal value for $\gamma = 3$ at $\tau_c \approx 100$ (see text). (b) The standard deviation of η. Standard deviation is largest when $\gamma = 3$ due to high variation in the resource ephemerality.

In the former, decreases in search efficiencies become significant as τ_c approaches the maximum patch duration. The reason for this observation is that, when $\gamma \approx 1$, foragers will try to recruit others for (often occurring) patches with long duration regardless. Hence, it does not matter if τ_c is much smaller, and relatively large ephemeral aggregations still occur on these long duration patches. Since these aggregations account for a large portion of the total group search efficiency, the effect of τ_c on η is small as $\tau_c < t_{max}$. Only when τ_c approaches t_{max}, foragers stop recruiting others to patches with long durations, hence reducing the group search efficiency.

In contrast, for $\gamma \gg 1$, τ_c influences the search efficiency only when it approaches the minimum patch duration. In this regime, the heavy tails of the inverse power law distribution are suppressed and extremely few patches with durations $\tau \gg t_{min}$ are present in the environment. Hence, for $\gamma = 5$, we see that when τ_c is sufficiently large to ensure recruiting behavior for (almost) all encountered patches, the search efficiency becomes independent of τ_c. Interestingly, recruiting does not provide a beneficial strategy in this regime anyways, regardless of the choice of τ_c (Fig. 2).

More interesting dependence on τ_c is visible for distributions where the heavy tail is suppressed, but only to some extent, i.e. for $\gamma \approx 3$. Here, we observe an optimal threshold at $\tau_c \approx 100$. Patch durations below this threshold are of relatively small duration such that the expected number of conspecifics encountered in that time is small (Fig. B.2). Hence, the collective is better off by individually exploiting these patches, as trying to recruit others will most likely lead to a negative gain. Patches above this threshold do provide a net gain, which is why search efficiencies are maximized for this precise choice of threshold. However, note that the variation of the search efficiency is additionally maximized for these intermediate values of γ, because variation in resource ephemerality is high when heavy tails are only partially suppressed.
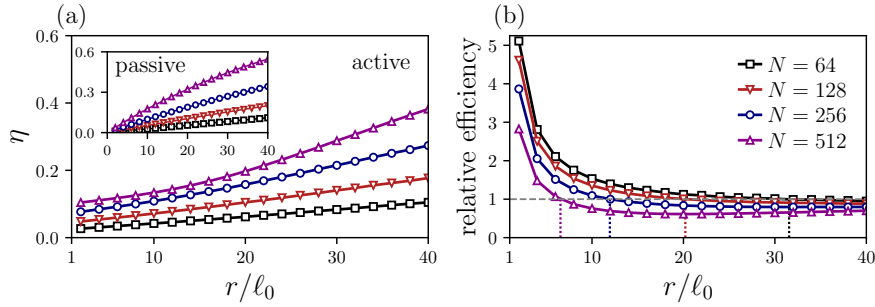
(a)

(b)

Fig. 6 Group search efficiencies for active and passive recruiters versus the normalized interaction radius r/ℓ_0 for different forager numbers N. Results are obtained for $M = 256$ and $\gamma = 1.1$ in order to simulate environmental conditions under which recruitment is known to be beneficial (see Fig. 2). (a) The group search efficiency η for active recruitment (with $\alpha' = 3$). Inset shows the group search efficiency for passive recruitment (static recruiter). (b) The relative efficiency as $\eta_{\text{active}}/\eta_{\text{passive}}$. Dashed line at 1 indicates the threshold and individual dotted vertical lines indicate interaction radii r' above which passive recruitment becomes more efficient.

Finally, we would like to emphasize that precise (optimal) computation for τ_c is not a necessity for the collective system to benefit from the described altruistic behavior. As long as patches are difficult to locate (small M) and persistent ($\gamma \lesssim 3$) does recruiting others results in an increase in group search efficiencies. This has possible far-reaching implications for designing artificial systems, as these results appear to indicate that prior beliefs do not determine whether altruistic behavior is advantageous or not. Additionally, as priors for more complex collective systems often difficult to estimate, our results seem to imply that these are not necessary. While it might occur that more intricate patch or forager dynamics necessitate more precise threshold approximations, or even updating current beliefs as estimates deviate from their initial values (Clark and Mangel, 1986; J. Valone, 2006; Marshall et al., 2013), we argue that simply always trying to recruit others is an advantageous strategy given that patches are persistent and interaction radii are small.

3.4 Effect of forager density on recruitment behavior

Finally, we would like to address the effect of forager density on the effectiveness of active recruitment. While the above results consider systems that actively recruit for conspecifics, searching conspecifics can be informed more passively by having the recruiter remain on the patch while continuously announcing its location to passersby, here called *passive recruitment*. Increased foraging efficiency of such a strategy is implied by noting that, when searching for conspecifics, a recruiter should not stray far from the patch (see section 3.1 and Fig. 1). Note that these strategies effectively reduce the system to a group foraging system (see our discussion in section 1), where foragers join

successful nearby foragers that have detected a patch (as in, e.g., Beauchamp and Giraldeau, 1996; Ruxton et al., 2005; Bhattacharya and Vicsek, 2014).

To appropriately compare active and passive recruitment strategies, let us consider an environment with conditions such that altruistic systems ($\tau = 0$) outperform selfish systems ($\tau = \infty$). Under these conditions, passive recruitment outperforms active recruitment only when interaction radii are sufficiently large, i.e. $r > r'$ (Fig. 6). Here, r' is the interaction radius above which passive recruitment results in higher foraging efficiencies than active recruitment. As N increases and $r > r'$, (random) encounter rates increase, reducing potential advantages of active recruitment. Furthermore, passively announcing becomes more efficient due to weakly decreased encounter rate (Fig. B.3a) and a decrease in total travel distance (Fig. C.4a). Indeed, our results indicate that r' is smaller for higher forager densities (Fig. 6b).

For $r < r'$, we find that active recruitment outperforms passive recruitment due to increased recruit efficiencies (Fig. C.4c,d). Here, recruit efficiencies are computed by measuring the number of resources consumed by *recruited* foragers, i.e. it acts as an indication of the remaining time upon patch arrival. Hence, higher recruit efficiencies indicate that active recruitment results in conspecifics arriving earlier on the ephemeral patches, thus consuming more resources per distance traveled when compared with passive recruitment strategies. Moreover, for r small and approaching the patch detection radius ($r \approx R$), we find active recruitment to outperform passive recruitment substantially. The reason for this can be understood when considering that recruitment effectively transforms the search for difficult to detect patches to a search for more easily detectable conspecifics. Then, when interaction radii decrease, it becomes more difficult to detect searching foragers. In the limit where $r \leq R$, passive recruitment cannot be considered beneficial as it becomes more likely (or just as likely for $r = R$) to encounter patches than conspecifics. In contrast, active recruitment, while displaying decreased foraging efficiencies as r decreases (Fig. 6a), displays higher relative foraging efficiencies when compared to passive recruitment. The reason is that the patch itself remains exploitable, while the recruiter effectively simulates an additional patch detection opportunity with some radius $r > R$. In this regime, patch detection can result from detecting the patch itself or by detecting the active recruiter, thus increasing the patch detection probability significantly and leading to higher relative foraging efficiencies.

We would like to emphasize that, while passive recruitment strategies appear enticing due to increased foraging efficiencies for sufficient $r > r'$, many collective systems exhibit small interaction radii. For example, honeybees recruit others by touch (Dornhaus and Chittka, 2004; von Frisch, 2013; I'Anson Price and Grüter, 2015), i.e. $r \approx \ell_0$. Additionally, scalable collective robot systems exhibit interaction radii that extend only several body lengths (Rubenstein et al., 2012; Sutantyo et al., 2013; Hamann, 2018). Thus, despite the simplicity of passive recruitment strategies, which one might desire over more complex active recruitment strategies, the above results indicate that

active recruitment is more likely to be advantageous for realistic collective foraging systems with small interaction ranges.

These density related effects display that, while (active) recruitment can be considered beneficial for the collective, the recruitment strategy itself should critically depend on individual and collective variables, such as the interaction radius and the forager density. Further investigation into optimal recruitment strategies is considered to be a topic for future research.

4 Conclusion

In this work, we have studied a collective system capable of altruistic behavior. Foragers that detected patches could, instead of feeding individually, decide to recruit others to increase the overall resource intake of the collective. We showed that by coupling patch quality and patch duration, recruiting times of individuals could be estimated by performing a scaling analysis of the underlying Lévy random search. Our analysis showed that this effectively reduces the decision on patch detection to a threshold decision. Patch qualities above this threshold are expected to have a positive net gain when actively recruiting others. Indeed, our agent-based model displayed increased collective search efficiencies, but only when patch ephemerality was not too high and patches were difficult to locate. Moreover, we showed that the influence of the threshold is small compared to the decision of whether to recruit or not. Only when patch ephemerality was intermediate, i.e. when high quality patches appeared sporadically, did a more fine-tuned threshold resulted in higher collective foraging efficiencies. However, increases in search efficiencies were relatively small. Therefore, always recruiting remained a valid strategy that resulted in increased group search efficiencies, potentially alleviating the necessity for individuals to determine optimal thresholds.

We considered patch quality (duration) to be instantaneously available and an objective measure identical for all individuals. Realistically, this assumption does not necessarily hold since patch quality can be subjective or change over time depending on the needs of the individual or the collective (Torney et al., 2011; De Fine Licht and Boomsma, 2010; Lihoreau et al., 2017). Additionally, satiation might influence individual decisions, as individuals tend to change behavior based on their internal state (Schadegg and Herberholz, 2017; Landayan et al., 2018). Thus, while including yet more crucial pieces of natural foraging behavior into a model might prove difficult, it is critical to understand the decision process that members of a collective undergo.

Furthermore, in this work, we assumed that individuals were only able to communicate over short distances. While we argued that information being only locally available is not necessarily detrimental, studies on natural systems have found that animals can transfer information across potentially large distances (Ramos-Fernández, 2005; McComb et al., 2003; Frey and Gebler, 2003; Martínez-García et al., 2013; Carlson et al., 2020) or form ephemeral groups that can lead to vastly different communication networks (Pinter-Wollman

et al., 2014), such as topological distances (Ballerini et al., 2008; Mateo et al., 2019) or scale-free networks (Falcón-Cortés et al., 2019; Ramos-Fernández et al., 2009; Rausch et al., 2019). Further investigation into the ranges over which collective systems can communicate, and the effect on decision processes, should therefore be considered.

Additionally, as mentioned previously, nest formation can circumvent the lack of long communication ranges as widely observed in swarming insects such as ants (Pinter-Wollman et al., 2013) and bees (Visscher, 2007). Such systems, studied as *central place* foraging, consider individuals that return to a single nesting site after successful foraging in order to communicate with others. This type of foraging has been observed across a wide range of animal species (Andersson, 1981; Rosenberg and McKelvey, 1999; Campos et al., 2014; Rozen-Rechels et al., 2015). This work studies a system where the spatial forager distribution is essentially uniform and only results in higher forager densities when ephemeral aggregations form on the patches. Although known that spatiality affects decision making (Reina et al., 2018), how exactly different behavior can induce more efficient spatial distributions is not yet fully understood. Nonetheless, we believe that the model presented here may help the design of more efficient artificial systems, as well as potentially help to explain empirical data on collective foraging.

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A   The interaction graph

Here, we aim to get an understanding of the effect of the interaction radius r on the macroscopic behavior of the collective system. Possible interactions between individuals, and thereby their collective behavior, are fully characterized by the resulting proximity graph given this interaction radius. In this interaction graph interpretation, each individual represents a vertex where edges between vertices denote interaction and only exist when the distance between two vertices is smaller than r. The foragers' positions define a random geometric graph albeit that the distribution over time is not necessarily uniform due to the ephemeral aggregations on patches. Below, we illustrate that an initial uniform distribution makes certain values of the interaction radius uninteresting to (artificial) collective system studies.

Let us consider a uniform distribution of vertices (forager positions). Formally, one can define the connectivity (or degree) of a random geometric graph as the average number of connections per vertex:

$$\kappa = 2E/N, \tag{A.1}$$

where E is the number of edges within the graph. Let us furthermore define the size of the giant component to be $NG(\kappa)$, where G indicates the fraction of vertices present in the giant component. It is known that there exists a critical connectivity κ_c for which, in the limit of $N \to \infty$, we have that $G \to 1$ for any $\kappa > \kappa_c$ (Dall and Christensen, 2002). In two-dimensional systems, the value of κ_c can be numerically computed to be $\kappa_c \approx 4.5$. Even though this behavior formally only holds in the limit of $N \to \infty$, the phase transition is apparent even at relatively small N (Fig. A.1).

In this work, individual foragers can be thought of as circles within the environment, each occupying an area of $V = \pi r^2$, which is related to the connectivity through

$$\kappa = NV. \tag{A.2}$$

From these equations, we can express the interaction radius in terms of the connectivity

$$\frac{r}{L} = \sqrt{\frac{\kappa}{\pi N}}, \tag{A.3}$$

where we have substituted $r \leftarrow r/L$ to express the interaction radius in terms of the environment size L. From this equation, we can immediately compute the critical radius by simply substituting $\kappa = \kappa_c$, and can therefore extract a critical interaction radius r_c above which the network has a giant component containing all individuals.

When the communication network is fully connected, information (e.g. on patch locations) is not locally bound. Therefore, a fully connected network can be assumed to posses global information properties. This regime is out of our current interest, since both natural systems and artificial systems do not
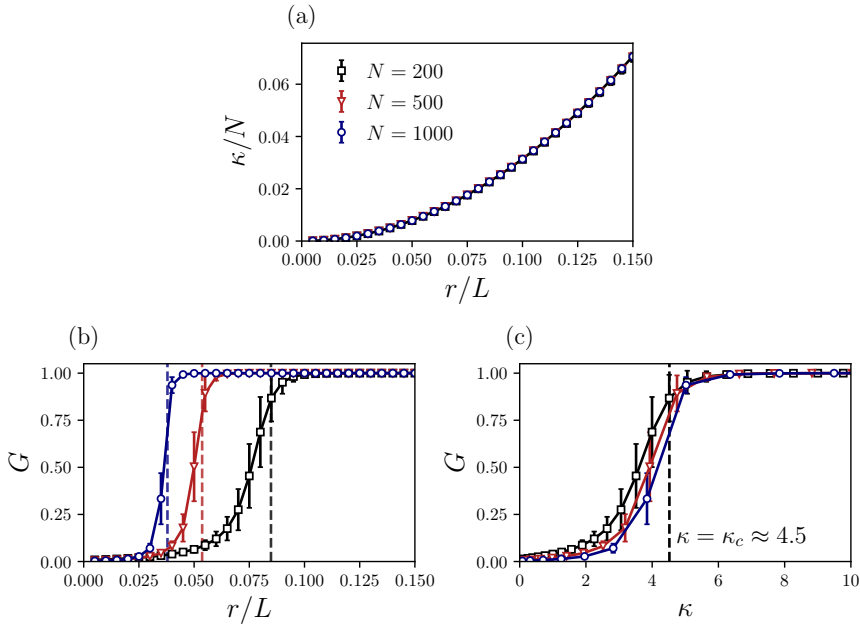
(a)

(b)   (c)

Fig. A.1 Numerically computed connectivity κ and giant component parameter G for different vertex numbers N. (a) The normalized connectivity of the resulting random geometric graphs. Note that all vertex numbers collapse onto the same value where $\kappa/N = \pi(r/L)^2$ as per Eq. (A.2). (b) The resulting giant component parameter G as a function of the normalized interaction radius. Dotted vertical lines correspond to the critical radius defined by Eq. (A.1). (c) The same giant component parameter expressed in terms of the connectivity. Note the collapse of the distinct vertex numbers onto the same curve for which any $\kappa > \kappa_c \approx 4.5$ the resulting giant component contains all vertices. In all plots error bars represent 1 s.d. computed over 1000 separate random geometric graphs.

possess global information, but instead rely on locally available information to base their decisions on (see e.g., Brambilla et al., 2013; Hamann, 2018). Therefore, we focus solely on systems with interaction radii $r < r_c$. In particular, we choose $r = \frac{1}{2}r_c \approx 0.0375L$ (see section 3).

Appendix B   Optimal recruitment for Lévy searchers

Below, we perform a scaling analysis and show that the decision to recruit upon patch detection is a threshold decision where patches with qualities above the threshold result in an expected positive gain and should therefore encourage recruiting. We shall show that the threshold depends on both the forager density, the movement of others, and the range at which foragers can perceive one another.

Let us consider a system of N foragers where one of the foragers detects a patch at time t_0. Without loss of generality, we set $t_0 = 0$, and the forager has to decide whether to recruit others or exploit the patch individually. Since we

consider collective foraging in this study, we assume that successful foragers only start recruiting if the expected net gain by recruiting is positive. Recall (see section 2.1) that the quality of the patch is defined by its (remaining) duration τ. Then, assuming a fixed consumption rate ϵ, we define the net gain g as the difference between individual exploitation and the expected intake rate by recruiting conspecifics:

$$g = -g_{exploit} + g_{recruit}$$
$$= -\epsilon\tau + \epsilon \int_0^\tau n(t, \boldsymbol{\alpha})dt, \tag{B.4}$$

where $n(t, \boldsymbol{\alpha})$ is the expected (average) number of conspecifics feeding on the detected patch at time $t > 0$. Note the dependence on the vector $\boldsymbol{\alpha} = (\alpha, \alpha')$, where α and α' the Lévy parameters of the searchers respectively the recruiter(s) (see section 3.1). The first term in Eq. (B.4) is simply the resource intake for a single forager feeding on the patch. The second term describes the expected number of resources consumed (by others) over the remaining time before the patch disappears. We can rewrite this term by considering the fact that only conspecific encounters up to some time $s(\tau)$ are 'successful' encounters, wherein the recruited forager has enough time to still feed on the patch. Thus we find that

$$g_{recruit} = \epsilon \int_0^{s(\tau, \alpha')} n(t, \boldsymbol{\alpha})dt, \tag{B.5}$$

where $s(\tau, \alpha')$ depends on the distance the focal forager displaces itself from the detected patch. We would like to emphasize that, for estimating $n(t, \boldsymbol{\alpha})$, one not only needs to consider the expected encounter rate with conspecifics, but also the expected displacement from the patch for the recruiter (section 3.1).

B.1   Scaling analysis

The expected time over which the message on the patch location should be disseminated depends on both the remaining time τ and the Lévy parameter of the recruitment search α'. If we consider the focal forager having a displacement $\delta(t, \alpha')$ after some time $t < \tau$, we find that

$$s(\tau) = \tau - \delta(t, \alpha')/\ell_0, \tag{B.6}$$

where ℓ_0 (the step size) the constant velocity of the forager. When assuming time scales are relatively short, i.e. $1 \ll t \ll L/\ell_0$, we know that the spatial moments of the Lévy walk scale as[3] (Nakao, 2000; Vahabi et al., 2013)

$$\left\langle |x|^k(t) \right\rangle \simeq \begin{cases} t^{k/(\alpha-1)}, & 1 < \alpha < 3 \text{ and } 0 < k < \alpha - 1, \\ t, & 1 < \alpha < 2 \text{ and } k \geq \alpha - 1, \\ t^{k/2}, & \alpha = 3 \text{ and } k > 0 \end{cases} \tag{B.7}$$

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[3] note that here α depicts the stable parameter for any Lévy search
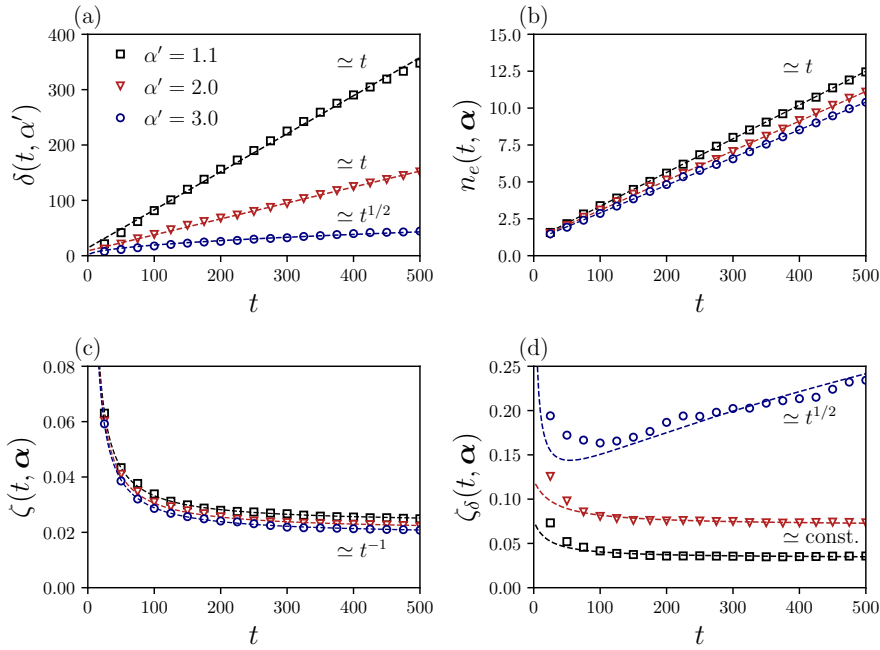
Fig. B.2 Scaling analysis of the conspecific encounter efficiency. The appropriate scaling is valid in the asymptotic limit $1 \ll t \ll L/\ell_0$ (see text). (a) The displacement $\delta(t, \alpha)$ from a patch detected at $t = 0$ for different stable recruitment parameters α. (b) The number of conspecifics encountered n_e within a time t for $\boldsymbol{\alpha} = (\alpha, \alpha')$. Here, searchers execute ballistic motion with $\alpha = 1.1$ and recruiters walk with Lévy parameter $\alpha' = 3$ (see text and section 2.2). We find $n_e \simeq t$ for all values of α, α' that we studied. (c) The conspecific search efficiency $\zeta = n_e/\ell_0 t \simeq t^{-1}$ (see text). (d) The normalized conspecific search efficiency $\zeta_\delta = n_e/\delta$. In all figures, dashed lines are fits obtained with non-linear least squares analysis. Scaling of the quantities with time is indicated. Results are obtained by averaging over 250 realizations of an appropriately sized system with $L = 1000$, $N = 256$, $\ell_0 = 1$ and $r = 0.0375L$ (see section 3).

Note that the appropriate timescale wherein the above results hold are applicable to ephemeral landscapes, assuming patch duration is finite and truncated (see section 2.1). One recovers the expected displacement with α' for $k = 1$,

$$\delta(t, \alpha') = \langle |x|(t) \rangle \simeq \begin{cases} t^{1/(\alpha'-1)}, & 2 < \alpha' < 3, \\ t, & 1 < \alpha' \leq 2, \\ t^{1/2}, & \alpha' \geq 3 \end{cases} \quad \text{(B.8)}$$

We find our results to match this type of scaling (Fig. B.2a).

The expected number of conspecifics feeding at the patch due to having been recruited can be estimated as

$$n(t, \boldsymbol{\alpha}) \simeq n_e(t - \delta(t, \alpha')/\ell_0, \boldsymbol{\alpha}), \quad 0 < t < s(\tau, \alpha') \quad \text{(B.9)}$$
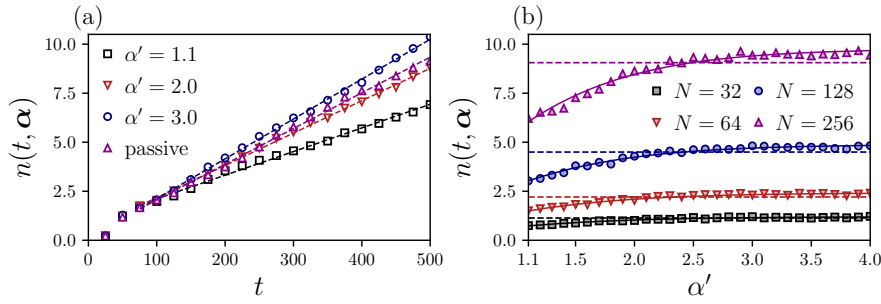
Fig. B.3 (a) The number of recruited conspecifics feeding on the patch at time t for different Lévy parameters α' and passive recruitment (static recruiter, see section 3.4). Dashed lines are linear fits obtained with non-linear least squares analysis. Averages are obtained over 250 realizations. (b) The expected number of conspecifics feeding on the patch due to having been recruited, $n(t, \boldsymbol{\alpha})$, as a function of $\boldsymbol{\alpha} = (\alpha, \alpha')$ with fixed $\alpha = 1.1$. Different colors indicate different forager densities, as the number of available foragers depends greatly on the patch distribution (Fig. 4). Dotted lines indicate passive recruiters, effectively approximating group-like foraging (see section 3.4). Note that for $\alpha' \gtrsim 3$ the number of foragers feeding on the patch displays a plateau due to the Lévy walk asymptotically converging to Brownian motion as per the central limit theorem. Averages are obtained over 1000 realizations for $t = 500$. Lines are a guide to the eye.

where $n_e(t, \boldsymbol{\alpha})$ is the expected number of conspecifics encountered within some time t. In other words, the number of foragers feeding on the patch at time t, is approximately equal to the number of encountered foragers at time $t - t'$, with $t' = \delta(t, \alpha')/\ell_0$ the time needed to travel to the patch from distance $\delta(t, \alpha')$. Estimating the number of conspecific encounters requires one to estimate search efficiencies for other Lévy searchers, which to the best of our knowledge has not been done analytically. Numerical simulations reveal linear scaling $n_e \simeq t$ for all values of $\boldsymbol{\alpha}$ that we have studied (Fig. B.2b), and subsequently $n \simeq t$ (Fig. B.3a). A more thorough analytical scaling analysis is considered to be out of scope of this work.

Having established how conspecific encounter rates scale, let us consider the conspecific search efficiency (see section 3.2)

$$\zeta(t, \boldsymbol{\alpha}) = \frac{n_e(t, \boldsymbol{\alpha})}{\ell_0 t} \qquad \text{(B.10)}$$

as the number of conspecifics found per distance traveled. It acts as a primer for the choice of α', i.e. what kind of diffusion should a forager that aims to maximize the number of conspecifics encountered within the remaining patch duration τ. As is known (see e.g.,Viswanathan et al., 1999; Bartumeus et al., 2005), ballistic motion for $\alpha^* \to 1$ maximizes the search efficiency in ephemeral landscapes where patch locations are uniform. When assuming the remainder of the collective is executing a Lévy search with α^*, we find that a parameter leading to contrasting diffusion, i.e. $\alpha' \geq 3$, optimizes search efficiencies for conspecifics in the short timescale (Fig. 1). Using this and the above scaling

analysis for the displacement and expected number of encountered conspecifics, we find $\zeta(t, \boldsymbol{\alpha}) \simeq t^{-1}$ (Fig. B.2c).

However, recall that we are not interested in the number of conspecifics encountered per distance traveled, rather as a function of the displacement from the patch, i.e.

$$\zeta_\delta = \frac{n_e(t, \boldsymbol{\alpha})}{\delta(\alpha')}. \tag{B.11}$$

The reason being that recruiting conspecifics while close to the advocated patch results in faster exploitation rates, because recruited foragers arrive at the patch earlier. Since we know the displacement scales as $\delta \simeq t^{1/(\alpha'-1)}$ for $\alpha' > 2$ (Eq. (B.8)), and encounters as $n_e \simeq t$, we find the properly normalized conspecific search efficiency scales as

$$\zeta_\delta(t, \boldsymbol{\alpha}^*) \simeq t^{1/2}, \tag{B.12}$$

where $\boldsymbol{\alpha}^* = (1.1, 3.0)$. In contrast, values of $\alpha' < 2$ result in linear scaling of the displacement, $\delta \simeq t$, hence $\zeta_\delta(t, \boldsymbol{\alpha}) \simeq$ const., i.e. the normalized conspecific search efficiency approaches a constant value as t increases. Our numerical results indeed verify this behavior, as can be seen in Fig. B.2c,d.

The difference in scaling for $\alpha' \leq 2$ and $\alpha' > 2$ explains why the conspecific search efficiency is maximized with contrasting diffusion characteristics ($\alpha' \geq 3$ as $\alpha \to 1$). While for $\alpha' \leq 2$ the rate of new conspecific encounters approaches a constant value, it grows with $t^{1/(\alpha'-1)}$ when $\alpha' > 2$, hence resulting in increased ζ (Fig. 1b and Fig. B.2d). It additionally raises the question if different strategies, such as simply announcing while remaining on the patch (i.e., $\delta = 0$), might be more efficient. We compare active recruitment via Lévy walks with a passive strategy in section 3.4 and below in Appendix C.

B.2   Threshold decision making

Here, we wish to illustrate that the foragers can be equipped with an effective threshold for which patches with qualities above this threshold should have an expected positive net gain and thus should trigger (active) recruitment. As a result, our model effectively resembles a threshold model, where recruiting others occurs only when the forager expects the collective to benefit (see section 2.2). Recall that we assume that foragers can estimate the optimal recruiting time $s(\tau, \alpha')$ for a given patch duration τ by estimating its displacement following the above scaling analysis. As the coefficients of both the displacement and the number of conspecifics encountered can be numerically computed, we can pre-compute $s(\tau, \alpha')$ from Eq. (B.6) and Eq. (B.8), and subsequently the expected net gain from Eq. (B.4), $s(\tau, \alpha')$ and Eq. (B.9). Since $n(t, \boldsymbol{\alpha}) \simeq t$, we

can write $n(t, \boldsymbol{\alpha}) = d_1 t + d_2$. Then net gain g becomes

$$g = -\epsilon\tau + \epsilon \int_0^{s(\tau,\alpha)} n(t, \boldsymbol{\alpha}) dt$$
$$= \epsilon \left(\frac{1}{2} d_1 s^2(\tau, \alpha) + d_2 s(\tau, \alpha) - \tau \right), \qquad (B.13)$$

where we have simply integrated the linear approximation of $n(t, \boldsymbol{\alpha})$. By determining the coefficients, which in artificial systems can be computed beforehand (i.e. be assumed prior knowledge to the forager), one can find critical durations for which $g(\tau_c) = 0$, $\tau_c > 0$. Existing numerical schemes, such as the Newton-Raphson method, can be applied to find these roots.

Then, at patch detection, foragers should recruit when $\tau > \tau_c$ and exploit individually when $\tau \leq \tau_c$. Therefore, advantages of collective behavior depend heavily on the distribution over patch durations (see section 3.2). The threshold τ_c ensures that foragers are not recruiting others towards patches that are not worth the effort and therefore serve as a filter on the individual level. In turn, thresholds greatly simplify decisions of recruited foragers, since instead of a (potentially complex) decision they should simply always travel towards the advocated patch.

We would like to emphasize that our results (see section 3.3 and Fig. 5) appear to indicate that the specific choice of threshold does not significantly influence the resulting group search efficiency. This is possibly an artifact of the ephemeral patch distribution that we study here. Hence, different patch distributions might result in more precise estimations of τ_c to be far more beneficial for recruiting foragers than the one studied in this work.

Appendix C Density effects

Forager density affects patch encounter rates and subsequently the number of recruit instances. As a result, passive strategies can become more beneficial (increase foraging efficiency) as interaction radii increase (section 3.4). Note that, despite the apparent increase in foraging efficiency, active recruitment result in more conspecific encounters than passive recruitment (Fig. B.3). Therefore, we compare active and passive recruitment in more detail to investigate when passive recruitment might be more efficient.

To this end, we study a system of N foragers in environmental conditions wherein altruistic recruitment ($\tau = 0$) outperforms selfish systems ($\tau = \infty$). This is realized for persistent patches ($\gamma = 1.1$) and low patch densities ($M = 256$), as indicated in Fig. 2. In such environments, we observe that total travel distances are lower for passive recruitment, as the passive recruiter is always on the patch ($\delta = 0$). In contrast, active recruiters increase the distance towards the patch (as $\delta \propto t^{1/2}$, see section B and Fig. B.2) and thereby increasing distances towards the patch upon recruitment. Note that total travel distances increase with the interaction radius as expected. The (small) decrease for high forager densities as r increases results from the approximately
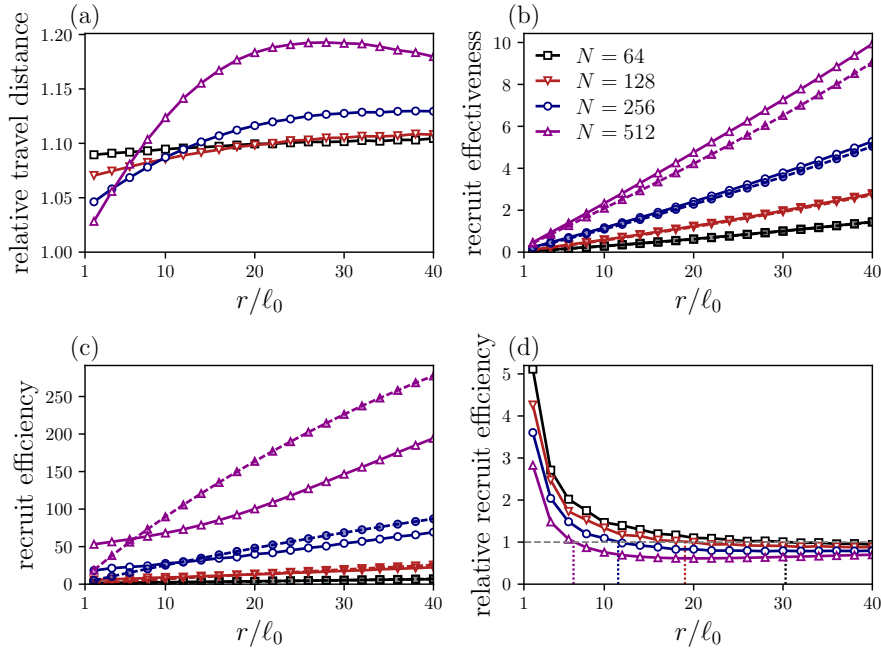
Fig. C.4 Comparison of the effect of forager density on the effectiveness and efficiency of recruitment between active and passive recruitment strategies. Results are obtained for $M = 256$ and $\gamma = 1.1$ in order to simulate environmental conditions under which recruitment is known to be beneficial (see text and Fig. 2). Solid lines indicate active recruitment with Lévy walks with $\alpha' = 3$ for searching foragers with $\alpha = 1.1$. Dashed lines in (b) and (c) indicate passive recruitment. (a) Total relative travel distance, computed by dividing total travel distance $\mathcal{L} = \sum_i \mathcal{L}_i$ for active recruitment by total travel distance for passive recruitment. Note that relative travel distance is always greater than 1, indicating that passive recruitment carries lower total travel distances (see text). (b) The recruit effectiveness as the total number of conspecifics recruited divided by the total number of recruit instances. (c) The recruit efficiency as the total number of resources consumed divided by the travel distance (see text and section 3.4). (d) The relative recruit efficiency as the recruit efficiency of active recruitment divided by the recruit efficiency of passive recruitment. Dotted vertical lines indicate interaction radii above which passive recruitment has higher recruit efficiencies than active recruitment. Note that interaction radii for which this occurs are (approximately) equal to those where the forager efficiency indicates similar effects (Fig. 6).

uniform forager distribution on patch detection, leading to instantaneous attraction at distances shorter than r. This induces an overall reduction in the total travel distance.

While larger distances towards the patch seem counter-productive, as the search efficiency is inversely related to the travel distance (Eq. (4)), simulations reveal that foraging efficiencies are higher when actively recruiting, but only when interaction radii are sufficiently small (Fig. 6). The reason is twofold. First, the recruit effectiveness is larger for active recruitment (Fig. C.4b) as the encounter probability is higher for active recruiters than passive recruiters (Fig. B.3a). Second, for sufficiently small interaction radii, the *recruit effi-*

ciency is larger when actively recruiting conspecifics. The recruit efficiency is computed by the number of resources consumed after being recruited, divided by the total distance traveled, and is shown in Fig. C.4c,d. When actively recruiting, conspecifics arrive on ephemeral patches earlier than when passively recruiting, thus increasing the total number of resources consumed on the patch before it disappears (see also section 3.4).

The benefits of active recruitment depend strongly on the forager density and their interaction radius, because, when interaction radii are sufficiently large, advantages of active recruitment disappear. Travel distances in systems with passive recruitment decrease, due to the recruiter not moving and decreased distances towards the patch upon being recruited (Fig. C.4a), hence increasing the foraging efficiency. This effect is amplified when forager densities are high, resulting in active recruitment being only beneficial when interaction radii are smaller than several body lengths (see Fig. 6b, Fig. C.4d and our discussion in section 3.4).

Appendix D   Distribution over individual search efficiencies

To measure distributions over individual search efficiencies presented in Fig. 3, we numerically compute histograms by computing search efficiencies for each individual forager and attributing them to 50 logarithmically spaced bins between $\eta_i = 0$ and $\eta_i = \eta_{max}$. Here, η_{max} is the greatest measured individual foraging efficiency encountered during our simulations for a specific parameter setting and can be empirically determined.

For generating the fits of the individual search efficiencies in Fig. 3, we use non-linear least squares to fit a log-normal distribution to the empirically obtained histograms using the SciPy Python package (Virtanen et al., 2020). To measure the statistical accuracy of the fitted curves, we compute the coefficient of determination R^2, and found $R^2 > 0.98$ for all curves shown in Fig. 3 (Table D.1).

	$\gamma = 1.1$			$\gamma = 3$			$\gamma = 5$	
M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$	M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$	M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$
256	0.996	0.999	256	0.999	0.986	256	0.998	0.998
512	0.998	0.999	512	0.999	0.993	512	0.999	0.992
1024	0.999	0.999	1024	0.999	0.996	1024	0.999	0.998
2048	0.999	0.999	2048	0.999	0.998	2048	0.999	0.999
4096	0.999	0.999	4096	0.999	0.999	4096	0.999	0.999

Table D.1 R^2 values for fitted log-normal distribution shown in Fig. 3 for all shown values of γ and M. $R^2_{\tau=0}$ corresponds to altruistic (collective) systems that always recruit and $R^2_{\tau=\infty}$ are for selfish (group) systems without interaction (see section 3.2).