

Robustness of optimal random searches in fragmented environmentsM. E. Wosniack,^{1,*} M. C. Santos,^{1,†} E. P. Raposo,^{2,‡} G. M. Viswanathan,^{3,4,§} and M. G. E. da Luz^{1,||}¹*Departamento de Física, Universidade Federal do Paraná, C.P. 19044, 81531-980 Curitiba-PR, Brazil*²*Laboratório de Física Teórica e Computacional, Departamento de Física, Universidade Federal de Pernambuco, 50670-901 Recife-PE, Brazil*³*Departamento de Física Teórica e Experimental, Universidade Federal do Rio Grande do Norte, 59078-970 Natal-RN, Brazil*⁴*National Institute of Science and Technology of Complex Systems, Universidade Federal do Rio Grande do Norte, 59078-970 Natal-RN, Brazil*

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The random search problem is a challenging and interdisciplinary topic of research in statistical physics. Realistic searches usually take place in nonuniform heterogeneous distributions of targets, e.g., patchy environments and fragmented habitats in ecological systems. Here we present a comprehensive numerical study of search efficiency in arbitrarily fragmented landscapes with unlimited visits to targets that can only be found within patches. We assume a random walker selecting uniformly distributed turning angles and step lengths from an inverse power-law tailed distribution with exponent μ . Our main finding is that for a large class of fragmented environments the optimal strategy corresponds approximately to the same value $\mu_{\text{opt}} \approx 2$. Moreover, this exponent is indistinguishable from the well-known exact optimal value $\mu_{\text{opt}} = 2$ for the low-density limit of homogeneously distributed revisitable targets. Surprisingly, the best search strategies do not depend (or depend only weakly) on the specific details of the fragmentation. Finally, we discuss the mechanisms behind this observed robustness and comment on the relevance of our results to both the random search theory in general, as well as specifically to the foraging problem in the biological context.

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I. INTRODUCTION

Statistical physics (SP) is well suited to study complex systems [1,2]. So, given the tight interrelation of the latter with diverse biological phenomena—especially concerning movement and dispersal [3–5]—SP methods have become important tools in analyzing various aspects of ecological systems [6–8]. In particular, in the 1990s there was a surge of interest in quantifying the role of diffusion as bottlenecks in the reaction rates of biological processes [2,6,8]. A predator, for instance, must somehow find (and consume) the prey, and the type of diffusion (e.g., normal versus anomalous) can either enhance or reduce the corresponding encounter probabilities and rates. Considerable progress was made in pinpointing how diffusion influences the search efficiency in homogeneous landscapes [2,6,8]. However, relatively less is understood about how the degree and type of heterogeneity determine efficiency of search in more realistic disordered environments [8].

Though homogeneous search landscapes are not uncommon, the existence of some degree of heterogeneity or fragmentation in the spatial distribution of targets (the “objects” to be found) is reportedly much more frequent [9–23], either in the form of patchy aggregates with characteristic scales or hierarchical structures consistent with scale-free fractal patterns. For this very reason, comprehending the interplay between the disordered patchy nature of environments and the relative chances of locating these patches is relevant in a

variety of scenarios [8]. For instance, in ecological phenomena the survival of individuals (or even species) searching for targets, such as food or mates, strongly depends on their abilities to choose a suitable search strategy among a large set of possibilities (many of them leading to rather inefficient returns). As a specific example, the biodiversity on islands might depend on the patches’ colonization skills of the originally emigrated species [24]. Also, rates of migrations among patchy habitats determines geographic [25] and genetic [26,27] similarities and dissimilarities of populations, e.g., whether or not an original group can go through speciation while dispersing [28]. Finally, ensuring that reserves are accessible to as large as possible a number of species is a major goal in conservation efforts [29,30].

In this work we present a comprehensive numerical analysis of searches taking place in different fragmented landscapes. We consider a superdiffusive Lévy random walk model, embodying the Brownian case in a proper limit. The rules of movement and detection are very simple and independent on the local density of targets. We address the statistical efficiency of the search and its relation to the dynamics of the encounter rates in a large set of spatially heterogeneous distributions. A surprising robustness of the optimal strategy—which moreover is similar to that for a homogeneous environment—is observed to pervade distinct classes of multifragmented landscapes with several degrees of heterogeneity. The implications of our results are discussed in the context of the animal foraging problem [2–4,6,8].

A few comments regarding the adopted framework here are in order. First, our model based on a single (truncated Lévy) strategy differs from the composite Brownian [31], adaptive [32], and intermittent [33] approaches previously assumed for patchy environments. In the former two [31,32], the forager employs distinct “modes” of searching depending

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if the space region is or is not plentiful of targets. In the latter, the walker pursues a Lévy-modulated dynamics [33], which incorporates a time-discrete reorientation mechanism (with Lévy statistics) into a continuous scanning process given by a correlated random walk. All these models are more complex and eventually more biologically adjusted than the present one (but see Sec. IV). In fact, they address a “sophisticated” searcher, in the sense it possesses inner (although basic) degrees of freedom to properly control the switches of behavior [34,35]. In this way, ours can be faced as a generic procedure, using dynamical rules which are straightforward, single moded, and plastic (in opposition to standing on habitats with specific features). So, the main purpose is to check if a minimal strategy, entirely stochastic (with no extra information), can capture the essence of the process, furthermore allowing efficient searching in distinct fragmented landscapes.

Second, the above goal moreover bears a second relevant aspect in the general theory of random search. Our fragmented media with well-defined characteristic scales contrast with the scale-free fractal environments considered in [36], as well as with the heterogeneous search generated by a distribution of initial distances to the last target found [37]. The question is then if the specific scales and the discontinuities of patchy landscapes will change the typical outcomes of the Lévy strategy in other backgrounds. Our findings here point to a universal optimization, leading to a fair unique optimal exponent irrespective of the target’s distribution, provided their densities are not too high [38] and they always can be revisited (the so-called nondestructive search [39]).

This work is organized as follows. In Sec. II we introduce the dynamical rules of the random walk search model and the general features of the fragmented search space. In Sec. III we present the detailed numerical studies of the different properties of random search in these landscapes. Furthermore, we make comparisons between the results for the distinct analyzed landscapes. Finally, in Sec. IV we present final remarks and the conclusion.

II. MODEL

To study the random search problem in fragmented environments we first specify the landscape features and the dynamical rules of movement as described below.

The search takes place in a landscape with total area $A = M \times M$ and periodic boundary conditions. Pointlike targets are available only within the N_p patches randomly distributed in A , as shown in Fig. 1. Each patch n ($= 1, 2, \dots, N_p$) is a circular region of radius $R^{(n)}$ containing a homogeneous distribution of $N^{(n)}$ nondestructive (unrestrictedly revisitable) targets. Thus, in each patch, neighbor targets are separated on average by the distance (with $\rho^{(n)}$ the targets density)

$$l_t^{(n)} = \frac{1}{\sqrt{\rho^{(n)}}}, \quad \rho^{(n)} = \frac{N^{(n)}}{\pi R^{(n)2}}. \quad (1)$$

A random walker with no memory or other information about the landscape performs the search for targets in this environment. The rules of movement are illustrated in Fig. 2, defined as follows [39].

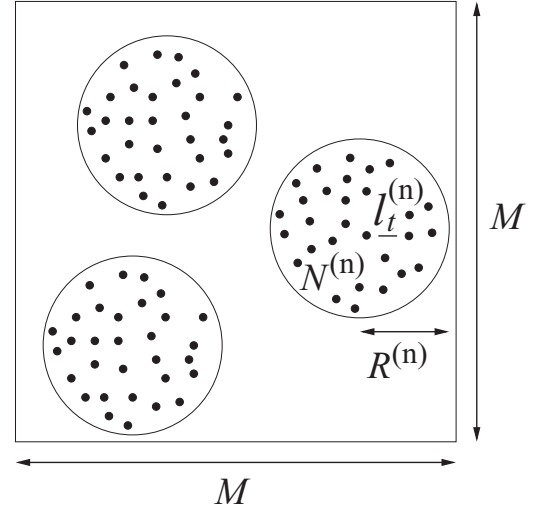


FIG. 1. Fragmented search space of area $A = M \times M$ with N_p circular patches ($N_p = 3$ in this example). The patch n ($n = 1, 2, \dots, N_p$) contains $N^{(n)}$ targets homogeneously distributed in an area $\pi R^{(n)2}$. The average separation between neighbor targets in patch n is denoted by $l_t^{(n)}$.

(i) If there are targets located within a “radius of vision” distance r_v , the searcher moves on a straight line to the closest one.

(ii) If there are no targets within r_v , the searcher chooses a direction at random and a distance ℓ from a probability density function (pdf) $P(\ell)$. Then, it moves in a straight line, always looking for targets within the radius of vision r_v along the way. If it does not detect a target, it stops after traversing ℓ and chooses a new direction and distance to move. Otherwise, it proceeds to the target as in rule (i).

We are most interested in the regimes of low and intermediate target density within the patches. So, the search rule (ii) becomes comparatively much more frequent than the detection rule (i), resulting in a richer structure for the trajectories pattern.

For $P(\ell)$, we assume a truncated Lévy distribution of step lengths [40]

$$P(\ell) = \frac{\mu - 1}{r_v^{1-\mu} - M^{1-\mu}} \times \begin{cases} \ell^{-\mu}, & \text{if } r_v < \ell \leq M, \\ 0, & \text{otherwise.} \end{cases} \quad (2)$$

Above, the range $r_v < \ell \leq M$ is justified by the following. First, by direct inspection a target located within the distance

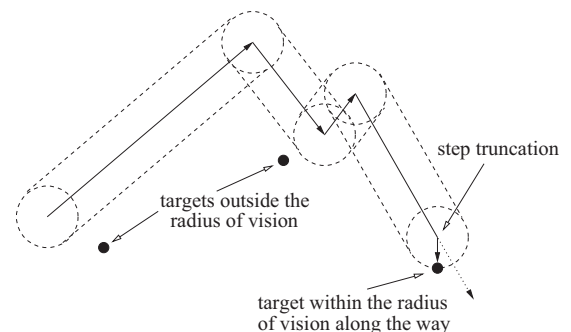


FIG. 2. Illustration of a sequence of random steps evolving according to the search dynamical rules (i) and (ii), Sec. II.

r_v is always detected by the searcher [rule (i)]. Hence the searching process should involve only step lengths larger than r_v . Second, the power-law Lévy distributed step lengths are effectively truncated at the distance M , corresponding to the limit scale of the environment. Of course, unbounded (infinite) displacements are naturally forbidden in realistic searches.

To understand how the power-law exponent μ in Eq. (2) influences the search strategies, we recall that for large times t the mean-square displacement of the Lévy random walker goes as t^{2H} , with H the Hurst exponent [8]. Thus, in the limit $M \rightarrow \infty$: (a) Eq. (2) represents the long-range asymptotic behavior of the family of Lévy stable distributions [2]; (b) the self-affine property $P(\gamma\ell) = \gamma^{-\mu}P(\ell)$ holds true, yielding a path with spatial scale invariance; and (c) the exponent $\mu > 1$ fixes the diffusivity properties of the walker (notice in this limit a value $\mu \leq 1$ implies a non-normalizable pdf). For $1 < \mu \leq 3$ the step length distribution variance diverges and the search consists of rare but statistically relevant long steps alternating between many small displacements. Moreover, for a Lévy walk one has that $H = 1$ for $1 < \mu \leq 2$, $H = (4 - \mu)/2$ for $2 \leq \mu \leq 3$, and $H = 1/2$ for $\mu \geq 3$ [8]. Then, the values $\mu \rightarrow 1^+$, $1 < \mu < 3$, and $\mu \geq 3$ correspond, respectively, to the extreme ballistic, superdiffusive, and normal (Brownian) dynamics.

In the low-density regime, with $l_t \gg r_v$, we observe that the above properties (a)–(c) typical of nontruncated Lévy walks are retained to a considerable extent during the search process [40–42]. Thus, by changing μ for a large enough value of M , we are actually “tuning” the rate in which the searcher visits new (faraway) regions. So, the particular distribution and availability of targets strongly influences the balance between spending more time in a local “scanning” for targets or moving to previously unvisited faraway spots in order to enhance the search efficiency. As a consequence, we should expect an optimal strategy characterized by a particular value of the exponent $\mu = \mu_{\text{opt}}$, established from the best compromise between these two mechanisms [8,42].

As for the target’s revisitability, we consider the nondestructive case [39], in which the targets are always available and can be visited any time by the searcher. Though this is a simplifying assumption [43], it is rather appropriate in usual fragmented landscapes [44], supported by empirical data (see, e.g., Ref. [45]). Indeed, the very idea of a patchy distribution is that the density is vanishingly low everywhere, except in particular regions. But, within such areas, the relatively high amount of resources makes local depletion at short-time scales irrelevant [46].

For each set of parameters that define a fragmented search space we perform \mathcal{N} simulation runs over which averages are performed. In each run the searcher starts at a random point in the empty region outside the patches, stopping when a total of T targets are found. The statistical efficiency of the search, η , is defined [41] as the ratio between T and the total distance L traversed along the search, i.e.,

$$\eta = \frac{T}{L}. \quad (3)$$

Since L is a function of the search strategy parametrized by the exponent μ , the optimal strategy is found for the value $\mu = \mu_{\text{opt}}$ which maximizes η , i.e., minimizes L for T fixed.

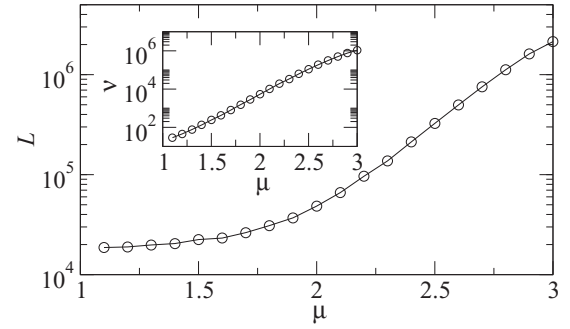


FIG. 3. Average distance traversed L and the number of steps v necessary to detect for the first time the single patch ($R = 0.2M$) as a function of μ in log-linear plots. The ballistic dynamics $\mu \rightarrow 1^+$ emerges as the search strategy that minimizes both quantities, representing the most efficient way to find the patch (but not the targets). Here $L(\mu = 2)/L(\mu = 1.1) = 2.87$ and $v(\mu = 2)/v(\mu = 1.1) = 187$.

Lastly, we mention two technical points. Once a target is found, it is set undetectable during the first step after the encounter. This is to avoid the searcher becoming trapped by the last target found. From the second step on, however, this last target again becomes visitable. In some statistically irrelevant situations in the high-density regime, it may happen that the distance between two targets in a patch is smaller than r_v . In this case, to prevent a dynamical trap of the walker between these two targets, we apply a small translation to the searcher (taking these targets out of its radius of vision) each time the walker finds one of them.

In the next sections we discuss the random searches in heterogeneous environments with single and many patches. Unless otherwise explicitly mentioned, we set $r_v = 1$, $M = 10^4$, $\mathcal{N} = 2.5 \times 10^3$, and $T = 10^4$.

III. RESULTS AND DISCUSSION

A. Single-patch case

Here we study the searches performed in a landscape with just a single patch, $N_p = 1$. Though this may actually represent a less realistic (or less common) limit situation, it is certainly useful for comparisons with the much more frequent multifragmented case of many distinct patches heterogeneously distributed in the search space (studied in the next section). Nevertheless, we can mention some concrete examples of single-patch random search (foraging) activity by solitary bees [47] and birds living in small islands [48].

Essentially, the search dynamics in a single-patch landscape can be subdivided into two processes, namely, the detection of the sole patch and the task of finding T targets in its interior. For the former, Fig. 3 shows for $R = 0.2M$ (other R 's give the same results) that the distance traversed L and the number of steps v necessary to find the patch for the first time are both minimized for the ballistic strategy, $\mu \rightarrow 1^+$. Indeed, the ballistic walker is the one that heads most efficiently to new (previously unvisited) regions, being in this sense just the opposite of the Brownian searcher. Hence it would yield the most efficient way to find the single patch (if this was the only task).

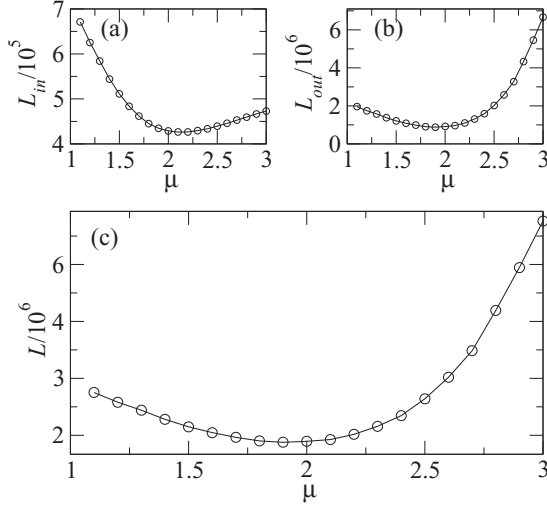


FIG. 4. Average distances traversed (a) inside L_{in} and (b) outside L_{out} a single patch (with $R = 0.2M$ and $l_t = 10r_v$) as function of μ . The search task is to find $T = 10^4$ targets. (c) Average total distance traversed, $L = L_{in} + L_{out}$.

To characterize the full process, i.e., of finding $T = 10^4$ targets in a search run, we write $L = L_{in} + L_{out}$, with L_{in} (L_{out}) denoting the distance traversed by the searcher inside (outside) the single patch. Notice that L_{in} is associated with the scanning of targets within the patch, whereas L_{out} corresponds to the first time detection of the patch *and* subsequent events where the searcher leaves the patch and then returns to it.

A typical example is shown in Fig. 4, with $R = 0.2M$ and $l_t = 10r_v$. For L_{in} versus μ , Fig. 4(a), there is a minimum when $\mu \approx 2$. From this point on, as the dynamics goes either ballistic ($\mu \rightarrow 1^+$) or Brownian ($\mu \rightarrow 3$), L_{in} increases monotonically, moreover with $L_{in}(\mu \rightarrow 1^+) > L_{in}(\mu \rightarrow 3)$. This faster increasing rate of L_{in} for $\mu \rightarrow 1^+$ is due to the small but non-negligible number of long individual steps taken within the patch (especially in the patch target density, ρ , low limit), starting to occur as the search strategy tends to a ballistic behavior. Indeed, the summed individual steps in the case of μ small make L_{in} larger than L_{in} from the sum of a large number of small displacements when $\mu \rightarrow 3$ (Brownian). Hence the minimum L_{in} is reached for an intermediate value, $\mu \approx 2$, which represents the best compromise between not taking excessively large individual steps, nor performing a large number of small displacements. Actually, the location of of such a minimum should be expected. Within the patch (of a not too high ρ) the scenario is similar to a nondestructive random search in a homogeneous distribution of targets, for which $\mu \approx 2$ [39] leads to the highest efficiency.

Interestingly, the distance L_{out} traversed in the empty region, i.e., outside the single patch, *also* displays a global minimum at $\mu \approx 2$, Fig. 4(b). This should be confronted with the result in Fig. 3, in which the distance traversed to find the patch for the first time is minimized for the ballistic strategy. So, we can conclude that the subsequent events of revisiting (i.e., finding again) the patch after having departed from it alters the optimization trend. Indeed, in the case of Fig. 4, if the searcher has just left the patch, a large step (more likely for $\mu \rightarrow 1^+$) taken in the wrong direction leads to

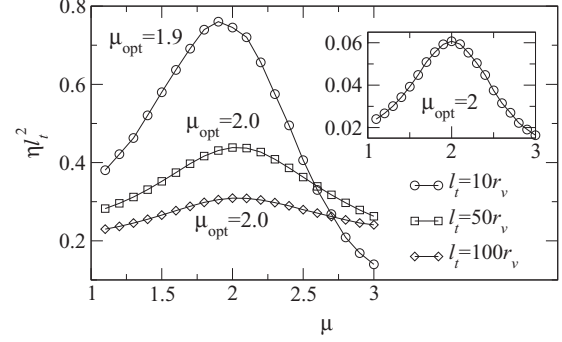


FIG. 5. Average efficiency η (multiplied by l_t^2 to put all curves in a same scale) to find $T = 10^4$ targets vs μ , with $R = 0.2M$ and different l_t . Inset: the same plot for $R = 0.05M$ and $l_t = 10r_v$. In each case, the μ_{opt} value is indicated.

empty faraway regions, so that the return to the patch becomes more difficult. This reasoning is confirmed by computing the average number of revisits to the single patch, which shows a dependence on μ qualitatively very similar to that of Fig. 4(b) (so not shown here). Also, $L_{out}(\mu \rightarrow 1^+)/L_{out}(\mu \rightarrow 3) < 1$ for the parameters used in Fig. 4. However, we observe that these quantities become comparable in scarcer regimes, say, $l_t = 100r_v$. Therefore, again the minimum $L_{out}(\mu \approx 2)$ originates from the compromise between taking long steps, which can drive the searcher too faraway in the empty space ($\mu \rightarrow 1^+$), and performing a large number of small steps ($\mu \rightarrow 3$), which maintains the searcher close to the patch, but with considerable inefficient oversampling of the search space.

As the exponent $\mu \approx 2$ minimizes both L_{in} and L_{out} , it also minimizes the total distance L traversed in the search, Fig. 4(c), and thus maximizes η of Eq. (3), Fig. 5. The effects on the optimal value μ_{opt} of both the density of targets inside the single patch and the patch relative size can be appreciated in Fig. 5. First, for a fixed R , a scarcer patch, i.e., a patch with larger l_t , leads to μ_{opt} closer to 2, which is the value for nondestructive searches in homogeneous landscapes [39]. For instance, for $R = 0.2M$ in the main plot of Fig. 5, we obtain $\mu_{opt} \approx 1.9$ for $l_t = 10r_v$, whereas μ becomes practically 2 for $l_t = 100r_v$. Note that within the patch, the steps j sweep the search space in the form of strips of width $2r_v$, but in higher densities often they are shorter than ℓ_j due to the truncations, Fig. 6(a). On the other hand, for lower ρ 's and in the ballistic limit, some of these strips are long corridors which may even cross (or almost cross) the whole patch without detecting a target, Fig. 6(b). Second, by fixing $l_t = 10r_v$ and comparing the search efficiency for radii $R = 0.2M$ and $R = 0.05M$ (inset of Fig. 5), we observe that a smaller patch generally leads to a smaller η for each μ , also giving rise to a lower relative gain of the ballistic strategy respect to the Brownian one. As the searcher hits the border of a smaller patch more often [confront the two cases in Fig. 6(a)], a larger distance is traversed in the empty region outside the patch, implying a lower efficiency.

The direct inspection of the search trajectories is also very helpful to understand the mechanisms of efficient searches, since it reveals interesting aspects manifested in the averaged statistical quantities discussed above. Figure 7 shows search

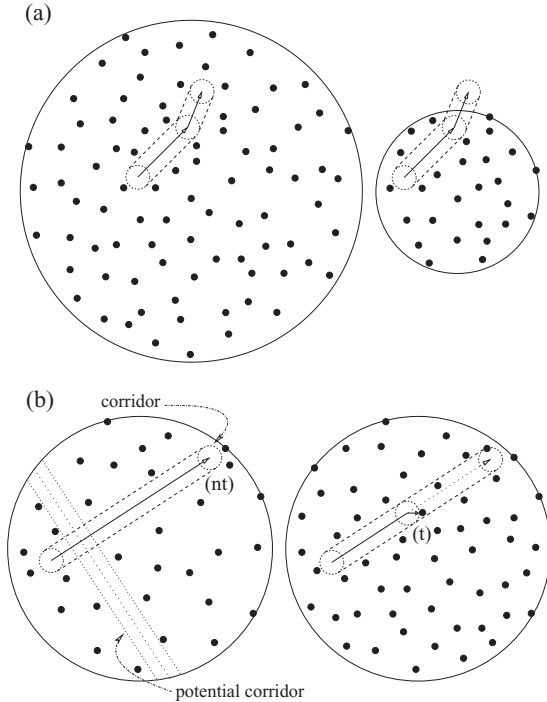


FIG. 6. (a) Comparison between patches of same targets ρ but with different radii R . Clearly, for smaller values of R the searcher leaves the patch more often. (b) Patches of same R but with different ρ . For higher densities, the truncation of a step j due to an encounter [rule (ii) of Sec. II] is more frequent, leading to a swept area in the form of a truncated (shorter than ℓ_j) strip [step (t)]. In lower densities, long “corridors” crossing the whole (or almost the whole) patch without a detection event [step (nt)] can take place, especially in the ballistic limit.

paths to find $T = 100$ targets, with $R = 0.2M$, $l_t = 10r_v$, in the following cases: the $\mu = 1.1$ ballistic limit (a),(b); the exponent $\mu = 2$ around the optimal value (c),(d); and the $\mu = 3$ Brownian behavior (e),(f).

For Figs. 7(a) and 7(b), the existence of long steps allows an efficient first detection of the patch, in agreement with Fig. 3. Once inside the patch, the searcher leaves it frequently, and, if a wrong direction is taken, the existence of long steps can eventually drive the searcher far away from the targets region, as previously discussed. Inside the patch some steps are truncated due to the encounter of targets. We notice in Fig. 7(b) that for a density of targets not so low there are no long corridors (see also discussion about Fig. 6), and the searcher does not go too deep inside the patch. Actually, long corridors (depicted in Fig. 6) are common in scarcer landscapes such as for $l_t = 100r_v$.

When compared to Fig. 7(a), the first encounter of the patch occurs after a longer trajectory if $\mu = 2$, Fig. 7(c), again a result consistent with Fig. 3. The relevant fact is that once entering the patch, the searcher is already able to encounter the $T = 100$ targets in a single visit. This contrasts with the ballistic strategy, in which the same task is achieved only after many (re)visits to the single patch [e.g., three in Fig. 7(a)]. As a consequence, although the first finding of the patch demands a longer path for $\mu = 2$, the whole distance traversed in the

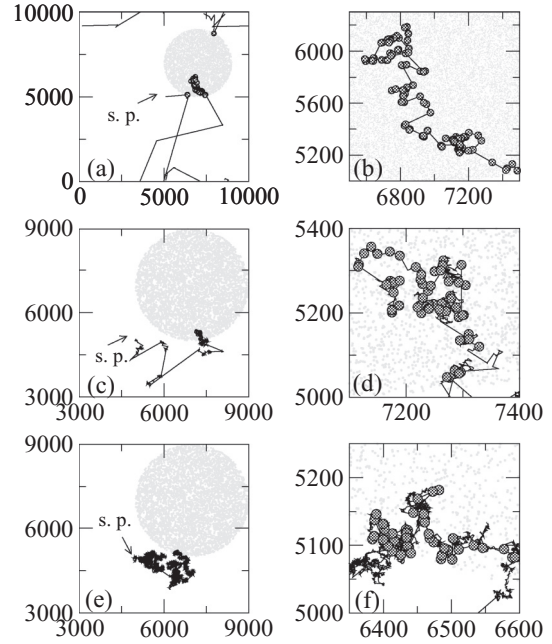


FIG. 7. Search paths to find $T = 100$ targets in a single patch, $R = 0.2M$ and $l_t = 10r_v$. (a),(b) In the ballistic limit, $\mu = 1.1$, from the starting position (s.p.) in the empty region the searcher readily finds the patch (gray region). Subsequently, the searcher leaves the patch and returns to it frequently. The encounters of targets within the patch are indicated in (b) by small circles. (c),(d) For the optimal strategy, $\mu = 2$, the search is completed with only one visit to the patch. Detail of the patch in (d) shows that the targets found are grouped in a small area. (e),(f) In the Brownian case, $\mu = 3$, typical short steps make the first finding of the patch more difficult. The search process inside the patch, shown in (f), takes place in a rather small area, if compared to the scales in (b) and (d).

empty region outside the patch, L_{out} , ends up being smaller than for the ballistic strategy, in agreement with Fig. 4.

From the trajectory in Fig. 7(e) we see that the small step lengths typical of Brownian motion render the first detection of the patch more difficult. When the patch is found, the searcher tends to remain looking for targets close to the border, doing local scanning with considerable overlap over an area comparatively smaller than that in both $\mu = 1.1$ and $\mu = 2$ cases [observe the scales in Figs. 7(b), 7(d), and 7(f)]. This implies a large number of small displacements to find $T = 100$ targets, which makes the distance L_{in} traversed inside the patch larger than in the optimal strategy $\mu = 2$.

Lastly, we display in Fig. 8 the exact location of $T = 10^4$ found targets after one search run, considering $\mu = 1.1, 2, 3$ and $l_t = 10r_v$ and $100r_v$. For all values of μ , a deeper exploration into the patch region is naturally facilitated in more scarce regimes, $l_t = 100r_v$. In this case, the large number of revisits to the patch leads to a nearly homogeneous pattern. In the denser regime, $l_t = 10r_v$, these revisits are less frequent, and the patch is well explored only for low μ . Indeed, the finding of unpreviously visited targets is favored in the ballistic limit as $\mu \rightarrow 1^+$, whereas revisits of targets increase in the Brownian regime $\mu = 3$. The optimal strategy thus balances between finding a relatively high number of new targets, while

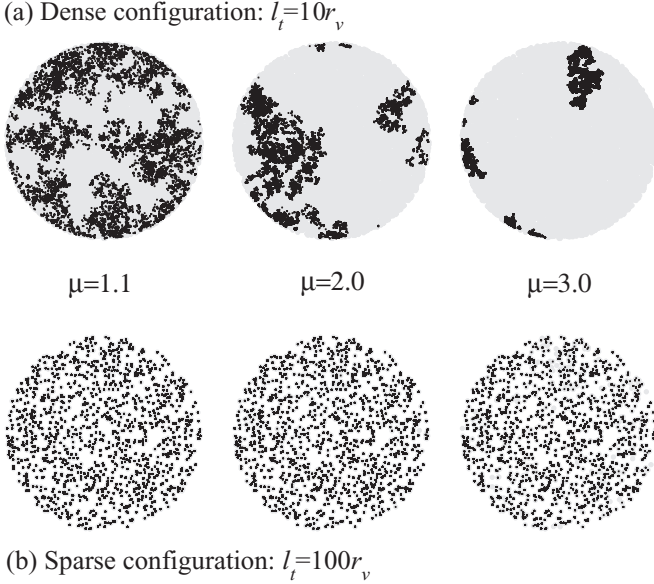


FIG. 8. Locations of the $T = 10^4$ targets found (black dots) along a search with $R = 0.2M$ for $\mu = 1.1, 2, 3$, and average separations between targets (a) $l_t = 10r_v$ and (b) $l_t = 100r_v$.

still scanning locally for already visited close targets in an efficient way.

B. Multiple patches case

We now turn to the much richer and more relevant case of fragmented environments with multiple patches. Of course, various aspects can be explored, such as the number, size, form, and density of the patches. But given that (e.g., in the ecological context) patchy landscapes are ubiquitous [49,50] and that the degree of homogeneity among the patches [51] is a fundamental, yet not a completely understood, factor determining population dynamics, in the following we essentially contrast the results for the cases of identical (i.e., for all n , $R^{(n)} = R$ and $l_t^{(n)} = l_t$) and heterogeneous N_p patches randomly placed in the search environment. Typical configurations are depicted in Figs. 9 and 10. Comparison with the single patch case (Sec. III) is also performed. The simulation details and search rules are the same described in Sec. II.

In Fig. 11 we show the average distances traversed inside (L_{in}), outside (L_{out}), and in total $L = L_{in} + L_{out}$, for a search in a landscape with $N_p = 10$ identical patches of $R = 0.1M$ and $l_t = 10r_v$. Inside the patches, the search dynamics is essentially that within a single patch (Sec. III, Fig. 4). Hence, in Fig. 11, also $L_{in}(\mu \approx 2)$ emerges as a minimum due to the same compromise mechanisms. But differently from the single-patch case, once the border of a patch is reached, there exist randomly distributed patches to be encountered in the otherwise outer empty region. Interestingly, then a similar competition of mechanisms is established, however, in a larger scale: the searcher can either return to the patch just explored or take longer steps to visit other patches (see below). Thus the same reasoning applies to L_{out} and again the strategy with $\mu \approx 2$ is the one that minimizes L_{out} and, consequently, the

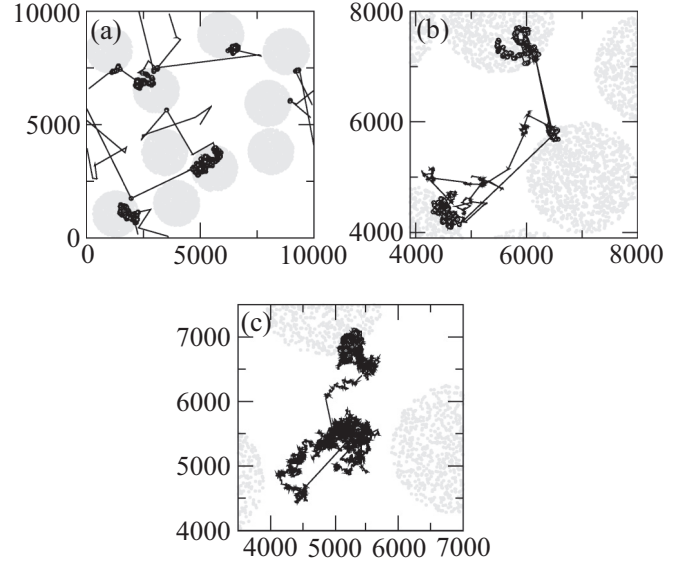


FIG. 9. Typical trajectories (along which the searcher finds $T = 10^3$ targets) for a fragmented landscape with $N_p = 10$ identical patches (gray regions). Here, $R = 0.1M$ and $l_t = 10r_v$. (a) In the ballistic regime $\mu = 1.1$, the searcher visits seven patches. This number gradually decreases as the Brownian limit approaches: (b) three visited patches in the optimal strategy with $\mu = 2$ and (c) only one patch visited for $\mu = 3$.

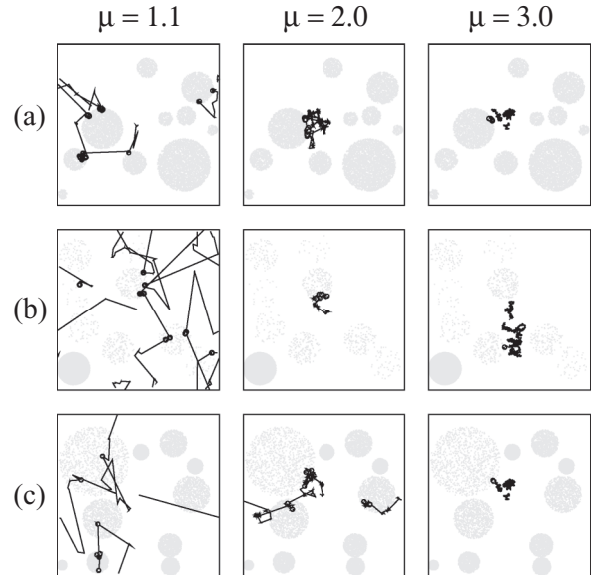


FIG. 10. Trajectories in a fragmented landscape with $N_p = 10$ heterogeneous patches (gray regions). The searcher finds $T = 10$ targets using ballistic ($\mu = 1.1$), optimal ($\mu = 2$), and Brownian ($\mu = 3$) strategies. The darker the patch, the higher its target density. (a) Patches with same density, $l_t = 10r_v$, and radii uniformly distributed in the range $0.03M \leq R^{(n)} \leq 0.3M$. (b) Patches with same radius, $R^{(n)} = 0.1M$, and densities uniformly distributed in the interval $5r_v \leq l_t \leq 350r_v$. (c) Patches with distinct sizes, but fixed number of targets inside (10^3), so that the smallest (largest) patches are also the densest (scarcest) ones. In this case, neighbor targets distances vary uniformly in the range $17r_v \leq l_t \leq 170r_v$.

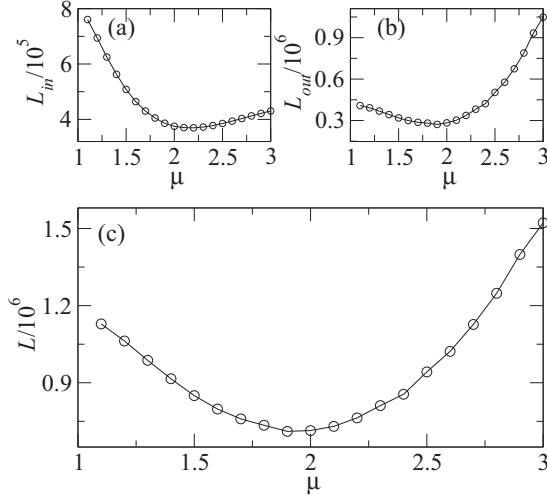


FIG. 11. Average distances (along a search for $T = 10^4$ targets) traversed (a) inside [L_{in}] and (b) outside [L_{out}] $N_p = 10$ identical patches ($R = 0.1M$, $l_t = 10r_v$) as function of μ . (c) $L = L_{in} + L_{out}$.

total distance L . Through many simulations we have verified this to be equally true in scarcer environments.

Along the search, the fraction N_v/N_p (%) versus μ for N_v the number of distinct visited patches in the cases of identical patches, $N_p = 5$ and 10 , and $l_t = 10r_v$, $25r_v$, and $100r_v$, is shown in Fig. 12. In the scarce scenario, $l_t = 100r_v$, for any μ we can expect the necessity of many distinct visits to the patches to finally complete the task of finding $T = 10^4$ targets. Hence all the patches should be accessed ($N_v = N_p$), exactly as seen in Fig. 12. Moreover, as we have numerically verified, there are many revisits to all the N_p patches, especially in the ballistic search, when events of leaving the patch without a target detection are not so rare at low target concentrations. On the other hand, in denser regimes ($l_t = 25$ and more notably $l_t = 10$) the searcher remains longer inside a patch, thus tending to decrease N_v . For a Brownian strategy ($\mu = 3$), the small step lengths make it rather improbable for the searcher, once leaving a patch, to reach distant targets. So, to return to the previously visited patch is the common (although not the exclusive) dynamics. For instance, for $\mu = 3$, in average only about 6 (2) out of $N_p = 10$ available patches are visited when $l_t = 25r_v$ ($l_t = 10r_v$), Fig. 12. The difficulty to visit

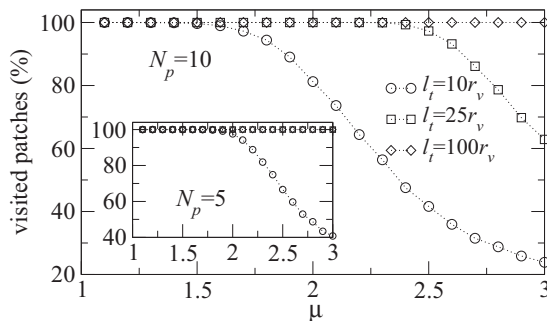


FIG. 12. Percentage of distinct visited patches vs μ along a search for $T = 10^4$ targets in a landscape with $N_p = 10$ and $N_p = 5$ (inside) identical patches. Here $R = 0.1M$.

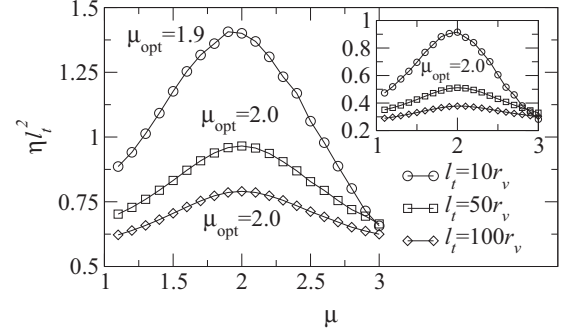


FIG. 13. Scaled average search efficiency ηl_t^2 along a search for $T = 10^4$ targets as a function of μ in a fragmented landscape with $N_p = 10$ and $N_p = 5$ (inset) identical patches of $R = 0.1M$. The μ_{opt} values are also indicated.

new patches is gradually surpassed as superdiffusive strategies with lower values of μ are considered. Indeed, as observed for $N_p = 10$ in Fig. 12, for $l_t = 25r_v$ most of the strategies ($1 < \mu \lesssim 2.5$) still can visit all patches. This is also true for $l_t = 10r_v$, but then in the smaller interval of $1 < \mu < 0.7$. Finally, smaller values of N_p usually favor the increasing of N_v/N_p , inset of Fig. 12. All these results are corroborated by the patterns illustrated in Fig. 9.

The average search efficiencies for $N_p = 10$ and $N_p = 5$ (inset) identical patches of radius $R = 0.1M$ and $l_t = 10r_v$, $50r_v$, $100r_v$ are shown in Fig. 13. The efficiency enhances with N_p since then naturally more targets are available. This increase, however, is not linear: changing the number of patches N_p —say, doubling it—does not keep the visitation rate constant (cf. Fig. 12). Furthermore, tantamount to the single-patch landscape in Fig. 5, we observe a same optimal strategy $\mu_{opt} \approx 2$ in basically all cases (but see below). It is important to mention that similar η profiles, reflecting analogous mechanisms of balance in efficient searches, emerge from adaptive [32] and intermittent [33] models in landscapes with identical patches or in fractal environments [36]. Finally, some comment on why we have a slightly smaller $\mu_{opt} = 1.9 < 2$ for $N_p = 10$, $R = 0.1M$, and $l_t = 10r_v$ in Fig. 13 is in order. For these parameters, both the target density inside each patch and the global density of patches in the environment are relatively high. Thus truncations [rule (ii) in Sec. II] either to find a target (within a fragment) or to locate a patch (in the whole environment) are also relatively more frequent. Because of these truncations, the original steps taken inside (with $\mu = 1.9$) effectively become akin to the advantageous power-law distribution with $\mu = 2$, whereas a modest diffusivity increase (a bit smaller μ) outside can be useful in looking for patches.

Lastly, we consider the more general case of fragmented landscapes with a random distribution of multiple heterogeneous patches (which, as it concerns conservation measures and biodiversity maintenance, seems to be more adequate than habitats with homogeneous patches [29]). Three configurations illustrated in Fig. 10 are addressed: (a) patches with the same target density but different sizes, (b) patches with the same size but different target densities, and (c) the most complex case of patches with distinct sizes and densities,

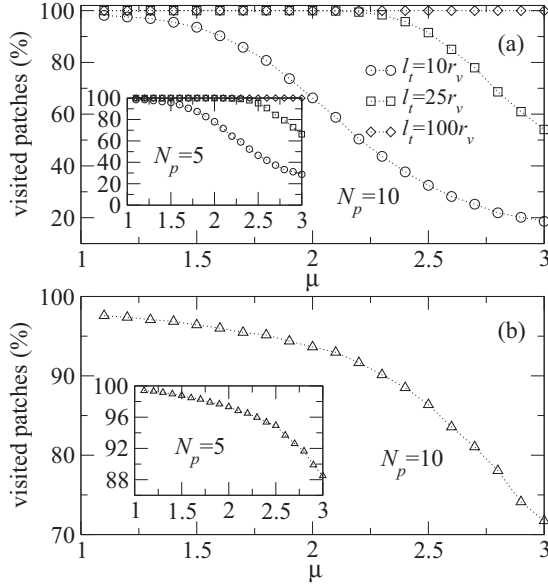


FIG. 14. Percentage of distinct visited patches vs μ along a search for $T = 10^4$ targets in a landscape with $N_p = 10$ and $N_p = 5$ (inside) heterogeneous patches. (a) Patches of a same l_t , but radii uniformly drawn from $0.03M \leq R \leq 0.3M$. (b) Patches of radius $R = 0.1M$, but neighbor targets distances uniformly drawn from $5r_v \leq l_t \leq 350r_v$. Due to the discussed mechanisms (main text), the % variation of visited patches in the entire range $1 < \mu \leq 3$ in (b) is much smaller than in (a).

but fixed number of targets inside. The distributions of heterogeneities in the patches' radius and density are generated by uniformly selecting random values from a specified range (see Fig. 10).

In landscapes where the patches have different $R^{(n)'}s$ but a same density (or equivalently a same l_t), Fig. 10(a), generally the searcher finds larger patches more easily, also spending more time in their interior. In spite of this, N_v/N_p as a function of μ in a long search for $T = 10^4$ targets, Fig. 14(a), follows a pattern similar to that of identical patches, Fig. 12. When the sizes are all the same but the l_t 's vary, Fig. 10(b), the patches contributing the most to the search efficiency are just the denser ones. So, a wide distribution of target densities ($5r_v \leq l_t \leq 350r_v$) for patches of a fixed radius ($R = 0.1M$) can significantly affect the number of distinct visited patches, Fig. 14(b). For instance, the existence of a considerable number of rather dense patches makes a 100% of visitation very hard to achieve, even for a ballistic regime. On the other hand, as the very scarce patches found add almost no targets to the search counting, then even a Brownian searcher can visit around 70% ($N_p = 10$) and 85% ($N_p = 5$) of the total landscape patches [compare Figs. 12 and 14(b)]. This can be realized by inspecting the trajectories for the $\mu = 1.1$ ballistic case in Fig. 10(b). Indeed, the searcher sometimes entirely crosses low-density patches through a long corridor (Fig. 6) without a detection.

We also have analyzed the case in which the number of targets inside each patch is fixed, but R can vary, Fig. 10(c). It yields a heterogeneous distribution in which the smallest (largest) patches are also the densest (scarcest) ones. The

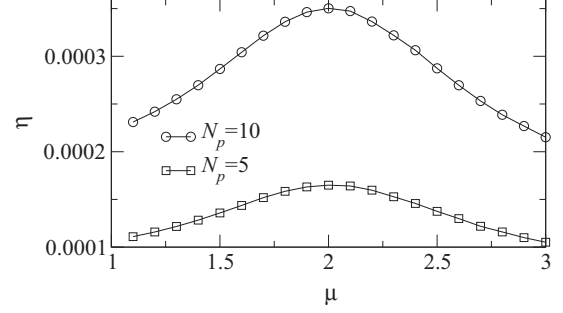


FIG. 15. Search efficiency η vs μ along a search for $T = 10^4$ targets in a fragmented landscape with $N_p = 10$ and $N_p = 5$ heterogeneous patches [parameters as in Fig. 10(c)]. For both N_p 's, $\mu_{\text{opt}} \approx 2$.

small dense regions, which contribute the most to the search efficiency, are now the hardest to find. Conversely, the more easily detected larger patches are scarce, so the searcher leaves them quickly, sometimes with no target detection. As a consequence, a subtle balance between opposite trends is established, resulting in a much longer search total traversed distance L for a given task (finding $T = 10^4$ targets), along which essentially all patches gets visited at least once [e.g., for the parameters in Fig. 10(c), even the Brownian searcher visits around 97% of the patches if $N_p = 10$ and 100% if $N_p = 5$].

Finally, we consider the search efficiency behavior for landscapes with heterogeneous patches. Remarkably, for the three types of situations depicted in Fig. 10, the profile of the average η is found to be similar to that for the distribution of fully identical patches, Fig. 13 [for instance, in Fig. 15 we show η as a function of μ using the parameters of Fig. 10(c)]. Furthermore, in the many examples tested, essentially $\mu_{\text{opt}} \approx 2$. We thus conclude that the robustness of the optimal strategy with unlimited revisits of targets actually holds across homogeneous landscapes as well as fragmented environments with several degrees of heterogeneity.

IV. FINAL REMARKS AND CONCLUSION

In this work we have extensively studied random search walks in fragmented environments, considering truncated (at the landscape maximum size M) Lévy searches. These encompass extreme ballistic ($\mu \rightarrow 1^+$), superdiffusive ($1 < \mu < 3$), and Brownian ($\mu = 3$) long-term search dynamics. We have assumed both environments with only a single patch and multifragmented landscapes with randomly distributed identical and heterogeneous patches. We have investigated the features of the search paths with distinct dynamics (controlled by μ) and affected by the environment characteristics. Furthermore, average quantities such as the distances traversed within and outside the patches, the number of distinct visited patches, and search efficiency have been analyzed. Especially, for the heterogeneous patches case we have studied the effect on the search efficiency of the heterogeneity in the patches sizes and/or in the target densities within the patches.

In patchy landscapes the search consists essentially in finding the individual patches and looking for targets in their interior. When target revisits are unlimited, an efficient

search must suitably balance these two processes occurring in distinct scales. (1) On one side, in a “local scale” within the patches, the finding of a relative high number of new targets (typically spanning distances of the order of R and favored by strategies with a higher degree of superdiffusivity and long steps: smaller μ 's) must counterbalance diffusive strategies which render more extensive and detailed local scanning for targets (covering few r_v units and demanding much shorter displacements: $\mu \rightarrow 3$). (2) On the other side, in an interpatch “global scale,” the frequent departures from a patch in the low-density regime also demand an efficient compromise between looking in the empty region for distant patches possibly containing unvisited targets, carried out by a ballistic searcher, and returning to the patch just explored, favored in a Brownian strategy.

Interestingly, the advantage that ballistic searchers have to encounter the first patch does not prevail in the long run, as visits to many patches also offer benefits. Therefore, at the extent self-affine invariance holds true [up to M ; see the discussion after Eq. (2)], to deal with the above (1),(2) trends, a same $\mu_{\text{opt}} \approx 2$ (intermediate) superdiffusive solution for the optimal search strategy emerges, properly handling the landscape multiple (but finite) scales. We thus can conclude that the robustness of $\mu_{\text{opt}} \approx 2$, when target revisits are unlimited, actually takes place not only in homogeneous landscapes, as previously reported [39] (see also [52]), but too in fragmented environments with diverse degrees of heterogeneity.

As already mentioned, there are very interesting theoretical descriptions [31–33] for foraging in patchy habitats based on mode behavior (interchangeable depending on the local availability of targets). In a concrete ecological system, the forager then should be able to detect the presence of regions

richer or scarcer in targets to switch to a proper mode. There is a vast literature discussing when an animal is or is not able to detect patches and which mechanisms are used for such, for instance, either by “sensing” a short-term change in the encounter rates [53,54] or using other cues, e.g., smelling a different local environment [55]. The fact is that this awareness process is rather complex [56], with many individuals being (or not) capable of directly identifying a patch from an otherwise empty matrix [56,57]. Our framework assumes the second type of forager. Certainly, the possibility of information gathering during the search might lead to higher efficiencies by using mode-drive strategies instead of the present one. In fact, along this line a nice approach, based on Lévy processes, has been developed in [33]. We shall mention that presently we are working on a model based on mode behavior, but in which each mode is entirely based on a Lévy process (results to appear in the near future).

Finally, we observe that our findings are relevant to a better understanding of the stochastic mechanisms [58] of efficient searches in multifragmented heterogeneous environments in several practical contexts. In particular, the searches performed by animals for food resources and even mates (animal foraging) is a highly significant problem with potentially drastic ecological implications [8,42]. Indeed, the choice of a suitable foraging strategy may render the difference between a successful adaptation to a specific environment and the death of an individual or the extinction of a species due to, e.g., starvation [59].

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