Nonstationary dynamics of encounters: Mean valuable territory covered by a random searcher

Daniel Campos,[1,*] Frederic Bartumeus,[2,3,4] and Vicenç Méndez[1]

[1]*Grup de Física Estadística, Departament de Física, Universitat Autònoma de Barcelona, 08193 Barcelona, Spain*
[2]*Centre d'Estudis Avanats de Blanes (CEAB-CSIC), 17300 Girona, Spain*
[3]*CREAF, 08193 Barcelona, Spain*
[4]*ICREA, 08010 Barcelona, Spain*

Inspired by recent experiments on the organism *Caenorhabditis elegans* we present a stochastic problem to capture the adaptive dynamics of search in living beings, which involves the exploration-exploitation dilemma between remaining in a previously preferred area and relocating to new places. We assess the question of search efficiency by introducing a new magnitude, the mean *valuable* territory covered by a Browinan searcher, for the case where each site in the domain becomes valuable only after a random time controlled by a nonhomogeneous rate which expands from the origin outwards. We explore analytically this magnitude for domains of dimensions 1, 2, and 3 and discuss the theoretical and applied (biological) interest of our approach. As the main results here, we (i) report the existence of some universal scaling properties for the mean valuable territory covered as a function of time and (ii) reveal the emergence of an optimal diffusivity which appears only for domains in two and higher dimensions.

I. INTRODUCTION

The last years have witnessed increasing interest of physicists and applied mathematicians in the principles driving optimization of random searches and problems related to efficient exploration or area coverage by random walkers [1–5]. This interest has often (though not exclusively) been motivated by ecological problems in cell biology [6] or animal foraging [7–9]. The fact that many ecologists have found it convenient to interpret organisms' trajectories in terms of random walks of different types (e.g., Brownian, Lévy, multimodal) as a way to compare and classify their patterns of motion has facilitated this and has led to a fruitful interaction between the two communities [1,6].

Within this context, concepts from statistical physics such as the mean first-passage time and the territory covered by the walker have been used as measures of search or area-coverage performance in living beings. This, however, implicitly assumes that throughout the search process the organism has a well-defined and static purpose (e.g., reaching food at a given position). This is in clear contradiction to experimental observations. Foraging trajectories and motor decisions of real organisms show that search in living beings is highly adaptive [10–12], even for extremely simple forms of life [13], due both to the exchange of information with the environment and to the internal dynamics of the organism. Quoting [14], many aspects of search "...depend on the animal's internal state: how recently it has eaten, the presence of food in the digestive tract, the quantity and nature of stored reserves such as fat or glycogen." So, more sophisticated measures are required to capture the adaptive dynamics of these systems; this represents one of the main goals of the present article.

As a paradigmatic case study, consider the organism *Caenorhabditis elegans*, which has been recurrently used to elucidate the basis of the biochemical circuits responsible for hunger and satiety, as well as the corresponding motor outputs these generate [9,14–17]. For this, *C. elegans* movements are tracked once individuals, after being cultured under controlled conditions, are moved to a different environment. If the new environment shows a high nutrient concentration, quiescent (i.e., low or null) movement is observed [18]. For low nutrient concentrations, instead, a motor response ("search for food") becomes activated. Figure 1(a) shows a typical trajectory of an individual displaced from nutrient-rich to nutrient-poor media. After movement reactions due to manipulation, a motor response starts. The individual spirals around its initial position and executes strong turns, expecting to find resources where they were available previously. The curvature of these spirals becomes gradually smaller; hence, a larger exploration area is apparently assumed by the individual through time. After approximately 1 h, widening of the territory coverage, and the addition of complex movement features, the individual drastically changes its motion pattern and decides to depart from the original area by following a more or less straight line.

A lesson from these observations is that, at least over a range of relevant time scales, search is clearly a *nonstationary* process. Actually, the computational problem the organism is trying to solve is itself nonstationary [9]. Organisms use motion mechanisms that presumably adapt better to their prior expectations. In resource-plentiful environments, the prior is that *food is near*. As evidence departs from that expectation, expectations must change (e.g., *a larger area should be explored*), and movement towards regions which were not given any importance or value previously is initiated. Thus the exploration-exploitation trade-off in such situations is tuned dynamically by the organism, and the initial state in which exploitation of the nearby region is promoted (driven by the initial prior expectation) evolves in time to enhance exploration gradually.

The most natural framework to describe this process would be that of inference (either Bayesian or other) methods [19,20]. Alternatively, random walks with different self-avoidance [21]
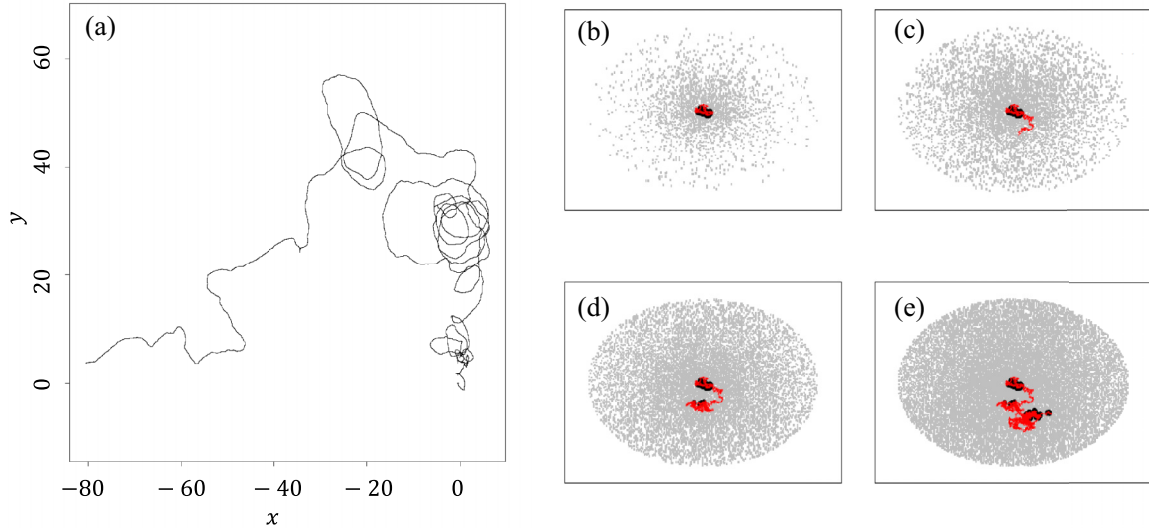
———
*daniel.campos@uab.es

FIG. 1. (a) Individual *C. elegans* trajectory obtained after passing it from a nutrient-rich to a nutrient-poor environment, with the starting point defined at (0,0). (Experimental data generated at William S. Ryu Lab, University of Toronto, Canada.) (b–e) Snapshots at increasing times [from (b) to (e)] of a single realization of the stochastic process described in the text. Red lines represent the walker trajectory. Sites on the lattice become valuable with time (shown in gray). Sites in black are those visited after they become valuable, so the objective of the walker should be to maximize the black region.

or memory [22,23] effects have been used as convenient approximations. However, first-passage, area-coverage, and similar measures hardly ever permit an analytical treatment in these cases. As an alternative approach, we here introduce a novel stochastic (search) problem in which we consider that the internal (search) plan of the organism changes with time while the motion pattern it follows is still stationary, for simplicity (e.g., Brownian motion or any classical model of biological transport). We do this by introducing the idea that not all the territory covered by the organism is equally beneficial or valuable for it; instead, we define a *valuable* region, which is the one of interest to the organism and which grows with time (this makes the dynamics of the problem nonstationary). We intend to provide a toy approximation to the experimental situation described above for the *C. elegans* case, where the region that the organism considers worth exploring seems to change gradually with time. As we show, this approach allows us to derive meaningful measures of search performance (in terms of the mean valuable region visited by the organism) that take explicitly into account the nonstationarity of the process and are analytically treatable for a wide range of situations.

II. GENERAL MODEL

Consider a random walker of size b initially set at the origin of an infinite domain in d dimensions. Each infinitesimal volume in the domain can be either in a *valuable* or a *nonvaluable* state, where we assume that value represents a variable which measures the potential benefit that visiting this region has for the walker. For simplicity, we assume that at $t = 0$ the whole domain is nonvaluable. Subsequently, each infinitesimal volume $d\mathbf{r}$ can become valuable after a random waiting time exponentially distributed at rate $\beta(\mathbf{r})$. Afterwards, when a valuable region is visited by the walker it again becomes nonvaluable, forever (see Fig. 1, right, for a particular

realization of the process). The magnitude of interest in this problem is then the valuable territory visited by the walker after a given time. Note that in the limit $\beta(\mathbf{r}) \to \infty$, for all $\mathbf{r}$, this will reduce to the classical problem of computing the territory covered by a random walker [24–29].

We note at this point that the experimental evaluation of $\beta(\mathbf{r})$ from real trajectories is problematic, since it would require disentangling movement from the internal state of the organism. So, in practice this function should be seen as a phenomenological proxy to understand and/or predict (to a first approximation) the drivers of the movement. Using the *C. elegans* experiment above as a reference, for example, it seems reasonable to consider that the rate $\beta(\mathbf{r})$ is a monotonically decreasing function of the distance to the origin; for simplicity, we explore here the case $\beta(\mathbf{r}) = \beta_\alpha r^{-\alpha}$, with $r = |\mathbf{r}|$ and $\alpha \geqslant 0$, so the whole valuable region will expand on average from the origin outwards (as in Fig. 1, right; see gray region) at a rate determined by β_α and α. The random walker must then reach a nontrivial balance between gradually exploring farther areas of the domain and not departing from the valuable region.

III. MEAN VALUABLE TERRITORY COVERED UP TO A GIVEN TIME

We compute $V(t)$, the mean *valuable* territory covered by the individual up to time t, averaged over all possible realizations (we do not explicitly include any symbol to denote "average," to simplify notation). While we focus here on the space-continuous version of the problem, we note that the case of discrete walks could be studied equivalently.

In analogy with classical approaches used to compute the territory covered by a random walker [24,25] we can write in our case

$$V(t) = \int_{\mathbb{R}^d} d\mathbf{r} \int_0^t dt \, f_V(\mathbf{r}^{(b)}, t; \mathbf{0}), \tag{1}$$

where $f_V(\mathbf{r}^{(b)},t;\mathbf{0})$ is the probability distribution function to reach the vicinity of point $\mathbf{r}$ for the first time *after it becomes a valuable site*, provided the walk starts from the origin $\mathbf{0}$. We use the notation $\mathbf{r}^{(b)}$ to represent the boundary of a sphere of radius b around point $\mathbf{r}$, where b denotes the size of the walker or its effective detection radius.

Due to the Markovian nature of the transition from *nonvaluable* to valuable (as waiting times before switching are exponential), and assuming that the motion of the walker is Markovian too, $f_V(\mathbf{r}^{(b)},t;\mathbf{0})$ can be computed in terms of the classical first-passage distribution $f(\mathbf{r}^{(b)},t;\mathbf{0})$. The corresponding relation will satisfy

$$f_V(\mathbf{r}^{(b)},t;\mathbf{0}) = f(\mathbf{r}^{(b)},t;\mathbf{0})(1 - e^{-\beta(\mathbf{r})t}) + [f(\mathbf{r}^{(b)},t;\mathbf{0})e^{-\beta(\mathbf{r})t}]$$
$$\times * [f(\mathbf{r}^{(b)},t;\mathbf{r}^{(b)})(1 - e^{-\beta(\mathbf{r})t})] + \dots. \quad (2)$$

Here, the asterisk ($*$) denotes time convolution and $e^{-\beta(\mathbf{r})t}$ represents the probability that the site $\mathbf{r}$ has not switched to valuable yet at time t. The first term on the right-hand side (r.h.s.) then corresponds to the case where the first passage through $\mathbf{r}$ occurs after the site has become valuable, the second term corresponds to the case where the first passage occurs before the site becomes valuable but the second passage occurs after it, and so on. Using the time convolution theorem the previous expression, (1), can be simplified in the Laplace space as

$$\hat{V}(s) = \frac{1}{s} \int_{\mathbb{R}^d} d\mathbf{r} \left[\hat{f}(\mathbf{r}^{(b)},s;\mathbf{0}) - \hat{f}(\mathbf{r}^{(b)},s+\beta(\mathbf{r});\mathbf{0}) \right.$$
$$\left. \times \frac{1 - \hat{f}(\mathbf{r}^{(b)},s;\mathbf{r}^{(b)})}{1 - \hat{f}(\mathbf{r}^{(b)},s+\beta(\mathbf{r});\mathbf{r}^{(b)})} \right], \quad (3)$$

where the hat denotes the Laplace transform and s is the Laplace variable. This expression, which represents one of our main results, can also be derived in an alternative way that may help to clarify its specific meaning; details are provided in the Appendix.

We now illustrate the utility of this approach by exploring the idealized case of a Brownian particle of characteristic size b moving within a space of dimension d with diffusion coefficient D. For this case, the solution of the first-passage distribution in the Laplace space is known to obey, for $r > b$ [25,30],

$$\hat{f}(\mathbf{r}^{(b)},s;\mathbf{0}) = \left(\frac{b}{r}\right)^{\frac{d}{2}-1} \frac{K_{\frac{d}{2}-1}(\sqrt{s/D}\,r)}{K_{\frac{d}{2}-1}(\sqrt{s/D}\,b)}, \quad (4)$$

where $K_n()$ is the n-order modified Bessel function of the second kind. Inserting (4) into (3) and using Laplace inversion one could then numerically compute the mean valuable territory covered by the walker.

We focus our attention on the asymptotic (large-t) properties of $V(t)$. For this, it is convenient to introduce the characteristic size of the valuable region, R_V, and the characteristic size of the area explored by the random walker, R_E. For Brownian particles we have $R_E \approx \sqrt{2dDt}$. Also, for a nonvaluable-to-valuable rate of the type $\beta(r) = \beta_\alpha r^{-\alpha}$, as we consider here, $R_V \approx (\beta_\alpha t)^{1/\alpha}$ follows. It is clear then that when R_V is asymptotically smaller than R_E (this happens for $\alpha > 2$) then the number of valuable sites encountered by the walker per unit time will decrease gradually, so the overall number

of sites will saturate. No characteristic scaling properties can be obtained for this case [note that the same will happen if $\beta(r)$ includes a cutoff such that it equals 0 for sufficiently large times, a situation that could also be biologically plausible under some conditions]. On the contrary, if R_V increases more rapidly with time than R_E (it is, for the case $0 \leqslant \alpha < 2$), then in the asymptotic limit all sites visited by the walker will be valuable. The asymptotic scaling of $V(t)$ will then be the same as that for the classical problem of the territory covered by a walker [25], which reads $V(t) \sim \sqrt{t}$ for $d = 1$, $V(t) \sim t/\ln t$ for $d = 2$, and $V(t) \sim t$ for $d \geqslant 3$.

Interestingly, if $0 < \alpha < 2$ but the growth of the valuable region is initially slow (for example, because β_α is small), a new intermediate regime, also characterized by universal scaling properties, emerges for the region where $\beta_\alpha^{-1} < t$ (so the valuable region is already large) but still $R_V < R_E$. This regime is revealed by carrying out random-walk simulations of the process and can be analytically described by first expanding for $\beta_\alpha \to 0$ in Eqs. (3) and (4) and subsequently exploring the large-time regime. This procedure reveals that the transient regime behaves as

$$V(t) \sim \begin{cases} t^{(3-\alpha)/2}, & d = 1, \\ t^{(4-\alpha)/2}/\ln t, & d = 2, \\ t^{(4-\alpha)/2}, & d = 3, \end{cases} \quad (5)$$

which agrees very well with the results found from simulations in one and two dimensions (Fig. 2). The emergence of this universal transient regime may have potential implications on the evolution of exploration strategies through time. Assuming that our dynamics could roughly reproduce the search dynamics of a real organism (as in the *C. elegans* case), we have that the characteristic exponent in the transient regime is always larger than the asymptotic one (at least for $\alpha < 2$), which means that the exploration rate is higher during the transient regime. So one could speculate, for example, on the possibility that the drastic change in the exploration rate that occurs in the transition to the asymptotic regime could be detected by the organism somehow and trigger an internal response in order to switch its motion strategy.

IV. SEARCH EFFICIENCY

We aim now at providing a measure of search efficiency. For this, we consider that the search process will end up after a random time τ, as is reasonable in most experimental situations. This random time represents the time before the organism gets exhausted or before it gives up searching for any other reason. Assuming, for simplicity, that this random time also follows an exponential distribution with mean τ, we find that τ^{-1} can be formally interpreted as a "mortality" rate, in analogy with the terminology used for mortal random walks [31,32]. We can then define, following the guidelines of those works, the mean valuable territory covered by the walker before giving up searching:

$$V_\tau = \int_{\mathbb{R}^d} d\mathbf{r} \int_0^\infty dt\, e^{-t/\tau} f_V(\mathbf{r}^{(b)},t;\mathbf{0}). \quad (6)$$

As a result of this definition, it is not difficult to check that V_τ easily connects to the solution, (3), above through $V_\tau = \tau^{-1}\hat{V}(s = \tau^{-1})$. Figure 3 (solid lines) shows the results
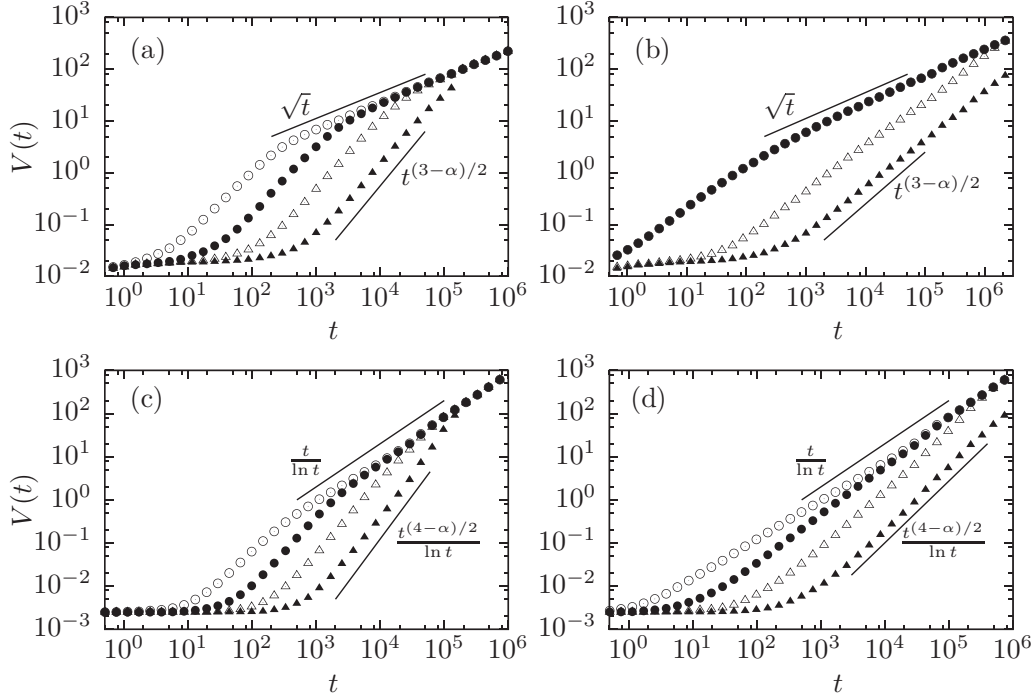
FIG. 2. Mean valuable territory covered by a Brownian walker up to time t for different values of d and α, with (a) $d = 1$, $\alpha = 0$, (b) $d = 1$, $\alpha = 1$, (c) $d = 2$, $\alpha = 0$, and (d) $d = 2$, $\alpha = 1$. Symbols correspond to the numerical results obtained for β_α: 10^{-2} (open circles), 10^{-3} (filled circles), 10^{-4} (open triangles), and 10^{-5} (filled triangles). Solid lines showing the asymptotic scaling and the new (α-dependent) intermediate scaling reported here are provided as a visual guide.

found by introducing (4) into this definition and evaluating the corresponding integrals numerically. We additionally show that an excellent agreement is found by comparing these results to those obtained through simulations reproducing the random-walk process described before (Fig. 3; symbols).

Exact analytical expressions for V_τ are not attainable except in some particular cases as, for instance, $\alpha = 0$. Here, however, we provide accurate approximations by studying

separately the two main regions of interest, $(D\tau)^{\alpha/2} \ll \beta_\alpha \tau$ and $(D\tau)^{\alpha/2} \gg \beta_\alpha \tau$, which correspond to $R_E \ll R_V$ and $R_E \gg R_V$, respectively, during a search of duration τ.

In the regime $(D\tau)^{\alpha/2} \ll \beta_\alpha \tau$ analytical approximations are hard to obtain since there are no parameters for which a perturbative analysis can be satisfactorily used. We provide instead a heuristic approximation by assuming that all sites visited by the particle (within the maximum radius R_V) are likely to be valuable; this leads to

$$V_\tau \approx \int_b^{R_V} \frac{2\pi^{d/2}}{(d/2)!} r^{d-1} dr f(\mathbf{r}^{(b)}, t; \mathbf{0}), \tag{7}$$

where we have used that the infinitesimal volume element in d dimensions is $\int_{\mathbb{R}^d} d\mathbf{r} = \frac{2\pi^{d/2}}{(d/2)!} \int r^{d-1} dr$ under isotropic conditions. By introducing (4) into this expression we obtain

$$V_\tau \approx \frac{2b}{\eta}(1 - e^{-\eta(1-\nu)}) \qquad (d = 1), \tag{8}$$

$$V_\tau \approx \frac{2\pi b^2}{\eta} \frac{K_1(\eta) + \nu K_1(\eta\nu)}{K_1(\eta)} \qquad (d = 2), \tag{9}$$

$$V_\tau \approx \frac{4\pi b^3}{\eta^2}(1 + \eta - (1 + \eta\nu)e^{-\eta(1-\nu)}) \qquad (d = 3). \tag{10}$$

We have introduced here the nondimensional parameters $\nu \equiv \beta_\alpha \tau / b^\alpha$ and $\eta \equiv b/\sqrt{D\tau}$. The former provides the relation between the characteristic time scale of the valuable to nonvaluable transition and the time scale τ, while the latter gives a relation between τ and the movement time scale.

We focus next our interest in thé regime $(D\tau)^{\alpha/2} \gg \beta_\alpha \tau$, where the nontrivial balance between staying close to the origin and gradually exploring farther areas will be especially determining. In this case we can expand the expression for V_τ in the limit

$\beta_\alpha \to 0$ and solve analytically the integrals obtained. This procedure leads to

$$V_\tau = b\nu\eta^{\alpha-1}e^\eta[(1+\eta)\Gamma_{1-\alpha}(\eta) - \Gamma_{2-\alpha}(\eta)] \qquad (d=1), \qquad (11)$$

$$V_\tau = \frac{\pi b^2}{2}\nu\left(\frac{\eta}{2}\right)^{\alpha-2}\left[\frac{\mathrm{G}_{1,3}^{3,0}\left(\begin{array}{c}1\\0,2-\frac{\alpha}{2},1-\frac{\alpha}{2}\end{array}\Big|\frac{\eta^2}{4}\right)}{\mathrm{K}_0(\eta)} - \frac{\eta}{2}\frac{\mathrm{G}_{1,3}^{3,0}\left(\begin{array}{c}1\\0,1-\frac{\alpha}{2},1-\frac{\alpha}{2}\end{array}\Big|\frac{\eta^2}{4}\right)}{\mathrm{K}_1(\eta)}\right] \quad (d=2), \qquad (12)$$

$$V_\tau = 2\pi b^3\nu\eta^{\alpha-2}e^\eta\left[\Gamma_{3-\alpha}(\eta) - \frac{\eta^2}{1+\eta}\Gamma_{2-\alpha}(\eta)\right] \qquad (d=3). \qquad (13)$$

Here, $\Gamma_m(z)$ denotes the incomplete gamma function with argument m, and $\mathrm{G}_{p,q}^{m,n}(\begin{array}{c}a_1,\ldots,a_p\\b_1,\ldots,b_q\end{array}|z)$ is the Meijer G function.
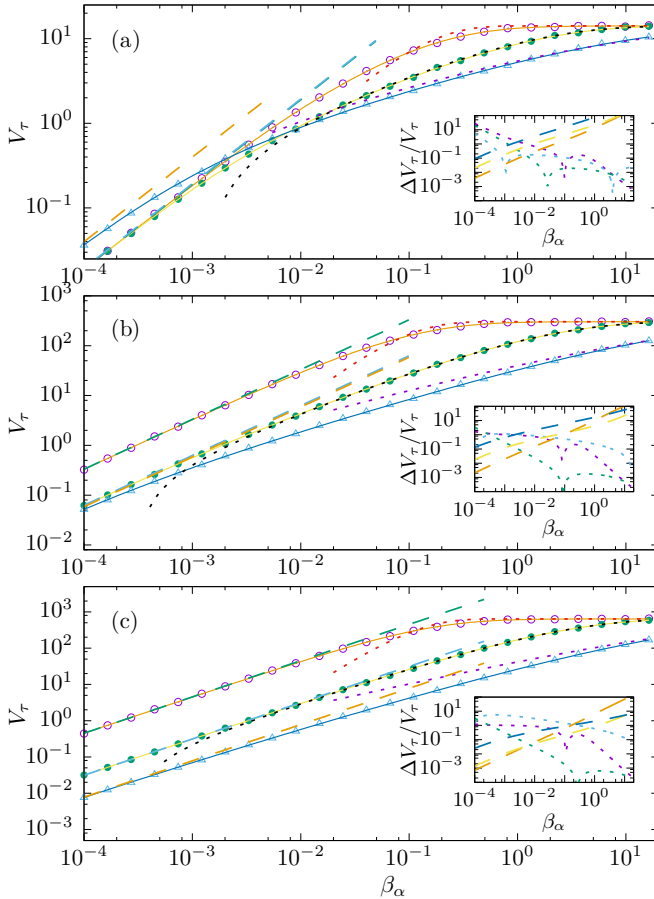

FIG. 3. Mean valuable territory covered by a Brownian walker up to a characteristic leaving time τ for different α values in (a) one, (b) two, and (c) three dimensions. Symbols correspond to random-walk simulations, with $\alpha = 1$ (open circles), $\alpha = 2$ (filled circles), and $\alpha = 3$ (triangles). Solid lines correspond to the numerical computation of V_τ from (6), while dotted and dashed lines correspond to approximations in Eqs. (8)–(10) and (11)–(13), respectively. Insets: Relative error found by the approximations (with ΔV_τ the absolute value of the difference between the approximation and the exact solution); again, dotted and dashed lines correspond to the approximations in Eqs. (8)–(10) and (11)–(13). Values used in all cases are $b = 0.25$, $D = 1$, and $\tau = 50$ (one dimension) or $\tau = 200$ (two and three dimensions).

The validity of the approximations presented in the limits $(D\tau)^{\alpha/2} \ll \beta_\alpha\tau$ and $(D\tau)^{\alpha/2} \gg \beta_\alpha\tau$ is verified in Fig. 3 (dotted and dashed lines, respectively), where it clearly shows that each approximation fits the numerical solutions as long as the corresponding regimes are approached. The insets in that figure also show the relative error done by the approximations used [dotted lines correspond to the approximation, (8)–(10); dashed lines, to (11)–(13)], where it is clear that the error tends to decrease gradually in the corresponding limits, as expected; note also that some strange effects, giving rise to one or several peaks in the relative error, appear in the regime of intermediate β_α for the approximation, (8)–(10), which should be attributed to the inaccuracy of the approximation in that regime.

Finally, we address the problem of optimizing V_τ. When we plot V_τ as a function of η [or, equivalently, as a function of $D = \tau^{-1}(b/\eta)^2$], we find some situations where a maximum of V_τ appears (Fig. 4). This optimum does not exist in the classical problem of computing the territory covered by the Brownian walker, since that magnitude increases monotonically with D [25]. In our case, instead, if the valuable region does not expand rapidly enough, in the limit $\eta \to 0$ (or, equivalently, $D \to \infty$, so movement is very fast), the walker will depart from the valuable region and search will be inefficient (i.e., V_τ will be small). Since slow diffusion or $\eta \to \infty$ leads to a large trajectory overlap and is also inefficient, an intermediate η_{opt} is expected.
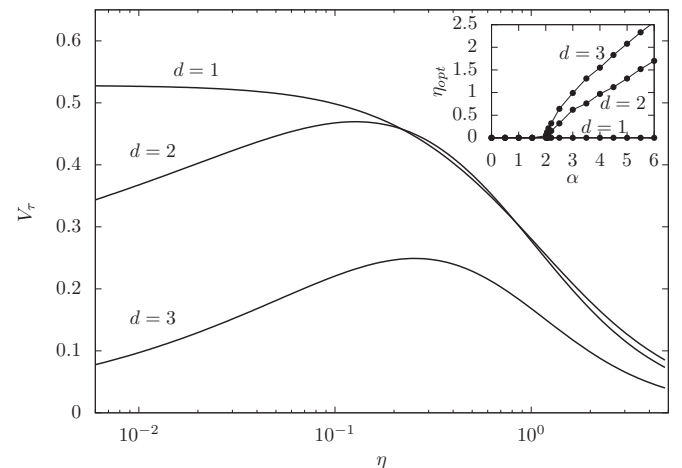

FIG. 4. V_τ as a function of the nondimensional parameter η [computed from (6)]. Inset: Optimal values of η maximizing V_τ. In all cases shown we have used parameter values $b = 0.25$, $D = 1$, $\beta_\alpha = 0.001$, and $\tau = 200$.

An intermediate optimum η_{opt} (or, equivalently, D_{opt}) indeed arises for $\alpha > 2$ in two and three dimensions (see inset, Fig. 4). This holds in higher dimensions too, as we could verify from our expressions above (results not shown). Note that for $\alpha > 2$ the size of the valuable region, R_V, grows in time more slowly than the size of the area explored, R_E, as discussed above; in the limit $\eta \to 0$ movement is thus too fast and the valuable region is consequently missed, so reducing V_τ. Instead, the intermediate optimum η_{opt} does not exist for one-dimensional systems; in that case, we observe that increasing D (it is, in the limit $\eta \to 0$) leads to the saturation of V_τ. We attribute this result to the recurrence properties of one-dimensional Brownian motion: since walkers always have a unit probability of coming back to the origin (and to the valuable region) the disadvantages of departing too rapidly from the origin are compensated by the higher capacity of return they have in that case.

Finally, we also note that small values of α also preclude the possibility that the maximum in V_τ appears. In that case, the valuable region (R_V) grows more rapidly than the region explored by the searcher (R_E); this, in the end, reduces the problem again to that of maximizing the territory covered by the walker, and so the classical result (where the territory covered increases monotonically with D) is recovered.

V. DISCUSSION

In this paper we have introduced a new magnitude, the mean *valuable* territory covered by a random walker $V(t)$, which is of specific interest for addressing the idea of search efficiency in nonstationary contexts such as the one described above for the experiments with *C. elegans* [9]. Two novel results have been provided, which are absent in the classical problem of computing the *territory covered by a Brownian particle*. First, we have shown that when the growth of the valuable region is initially slow (but asymptotically faster, in the long-time regime) compared to that of the region explored by the individual, then a transient regime appears characterized by a universal scaling of $V(t)$ with time. Second, the optimum diffusivity (which corresponds to a correct balance between covering the valuable region exhaustively and avoiding unnecessary overlaps) emerges in two and higher dimensions. This idea connects easily to the exploration-exploitation trade-off typically employed by biologists to characterize many foraging situations [9], where trajectory overlap would represent here a measure of exploitation and the area coverage would be related to exploration.

Following the initial idea of the article (optimization of random searches in living organisms) we can intuitively conclude from our results and discussion above that finding a global optimum for V_τ would probably involve an adaptive pattern of motion, e.g., by using a tunable diffusion coefficient D to increase the efficiency by gradually adapting the capacity of area coverage. Note that random-walk models combining different movement scales have already been explored in similar contexts [8]. In more sophisticated models of motion we expect that this dynamics will become even richer, since there we have different parameters controlling movement (e.g., speed, persistence length). For example, generalization of our results to the case of persistent random walks (which are often used to fit animal trajectories) is easily attainable. We have already started exploring that idea and have checked that some properties of the Brownian case, such as the transient scaling, (5), still hold, which confirms the robustness of our findings.

We also note that to keep our approach simple we needed to consider nonstationarity only at the level of the value dynamics, while the searcher movement is kept stationary. This does not undermine, however, the potential interest of our framework for theoretical biologists and ecologists. Generally speaking, the spreading dynamics of valuable sites from an initial position we have considered represents the spatial dilution through time of an initial "attraction" point, which may represent home, a temporary hide, or an exploitable area. Exploring new territory means departing from well-known areas, which are usually the most valued (e.g., already proved subsistence, less risk, exploitable resources), towards unknown territory. This kind of dynamics is typical of central-place foraging [33] and, more generally, exists in patch-leaving behavior [9]. A gradual shift in the relative value of the core vs the outer territory would then represent an effective or phenomenological driver for this type of exploratory dynamics. Additionally, real environments involve the continuous extinction and emergence of food sources or items, which may be implemented in our model by introducing a more complex dynamics for $\beta(r)$ instead of simply radial growth. While the experimental determination of this function remains an open issue, we note that our approach could possibly be used in an inverse way too, so one could try to infer from real trajectories the valuable region the individual is trying to optimize or, alternatively, an expression for $\beta(\mathbf{r})$. Altogether, we expect that these ideas will open a new line of research on the formidable problem of using statistical physics to infer biologically relevant information from trajectories of living organisms.

APPENDIX: ALTERNATIVE DERIVATION OF $\hat{V}(t)$

Since we consider that the derivation of $\hat{V}(t)$ provided in Eqs. (2) and (3) is mathematically more clear and elegant, we want to stress here that there is an alternative formula that probably provides a more intuitive understanding of the exact meaning of that function.

The following derivation can be seen as a generalization of those provided in some of our previous works [8,33]. To proceed, we first define $q(\mathbf{r}^{(b)}, t; \mathbf{0})$ as the rate at which walker trajectories departing from $\mathbf{0}$ pass at time t through the boundary $\mathbf{r}^{(b)}$. Accordingly, the rate at which walker trajectories departing from $\mathbf{0}$ pass through the boundary $\mathbf{r}^{(b)}$ *before that site has become valuable* will be

$$e^{-\beta(r)t} q(\mathbf{r}^{(b)}, t; \mathbf{0}). \tag{A1}$$

Taking these considerations into account, the trajectories contributing to $q(\mathbf{r}^{(b)}, t; \mathbf{0})$ can then be divided into three terms

as

$$q(\mathbf{r}^{(b)},t;\mathbf{0}) = f_V(\mathbf{r}^{(b)},t;\mathbf{0}) + f_V(\mathbf{r}^{(b)},t;\mathbf{0}) * q(\mathbf{0}^{(b)},t;\mathbf{0}^{(b)})$$
$$+ e^{-\beta(r)t} q(\mathbf{r}^{(b)},t;\mathbf{0}), \quad \text{(A2)}$$

where, again, the asterisk denotes convolution in time. Note that the first and second terms on the r.h.s. account for all trajectories that pass through $\mathbf{r}^{(b)}$ *after that site has become valuable*. In this case it might be that the present is the first time the walker has reached $\mathbf{r}^{(b)}$ since the site became valuable; this is the contribution of the first term on the r.h.s. If there was a previous visit to $\mathbf{r}^{(b)}$ since the site become valuable, this contributes to the second term on the r.h.s.

If we carry out the Laplace transform of Eq. (A2) with respect to time, we can obtain an explicit expression for $f_V(\mathbf{r}^{(b)},t;\mathbf{0})$:

$$\hat{f}_V(\mathbf{r}^{(b)},s;\mathbf{0}) = \frac{\hat{q}(\mathbf{r}^{(b)},s;\mathbf{0}) - \hat{q}(\mathbf{r}^{(b)},s+\beta(r);\mathbf{0})}{1 + \hat{q}(\mathbf{0}^{(b)},s;\mathbf{0}^{(b)})}. \quad \text{(A3)}$$

Next, we introduce this expression into the definition of $\hat{V}(t)$ [Eq. (1)] to get, after Laplace transforming,

$$\hat{V}(s) = \frac{1}{s} \int_{\mathbb{R}^d} d\mathbf{r} \left[\frac{\hat{q}(\mathbf{r}^{(b)},s;\mathbf{0}) - \hat{q}(\mathbf{r}^{(b)},s+\beta(r);\mathbf{0})}{1 + \hat{q}(\mathbf{0}^{(b)},s;\mathbf{0}^{(b)})} \right]. \quad \text{(A4)}$$

The last step of the derivation consists of writing this expression in terms of the first-passage distribution $f(\mathbf{r}^{(b)},t;\mathbf{0})$. This can be obtained by recovering the well-known relation for Markovian processes between this distribution and $\hat{q}(\mathbf{r}^{(b)},s;\mathbf{0})$ (see, e.g., [8], [33]):

$$\hat{f}(\mathbf{r}^{(b)},s;\mathbf{0}) = \frac{\hat{q}(\mathbf{r}^{(b)},s;\mathbf{0})}{1 + \hat{q}(\mathbf{0}^{(b)},s;\mathbf{0}^{(b)})}. \quad \text{(A5)}$$

This leads almost immediately to

$$\hat{q}(\mathbf{r}^{(b)},s;\mathbf{0}) = \frac{\hat{f}(\mathbf{r}^{(b)},s;\mathbf{0})}{1 - \hat{f}(\mathbf{0}^{(b)},s;\mathbf{0}^{(b)})}. \quad \text{(A6)}$$

So, inserting Eq. (A6) into Eq. (A4) and assuming that first-passage distributions under initial conditions $\mathbf{0}$ or $\mathbf{0}^{(b)}$ are equivalent for b small enough, then we finally obtain the result, (3):

$$\hat{V}(s) = \frac{1}{s} \int_{\mathbb{R}^d} d\mathbf{r} \left[\hat{f}(\mathbf{r}^{(b)},s;\mathbf{0}) - \hat{f}(\mathbf{r}^{(b)},s+\beta_{\mathbf{r}};\mathbf{0}) \right.$$
$$\left. \times \frac{1 - \hat{f}(\mathbf{r}^{(b)},s;\mathbf{r}^{(b)})}{1 - \hat{f}(\mathbf{r}^{(b)},s+\beta_{\mathbf{r}};\mathbf{r}^{(b)})} \right]. \quad \text{(A7)}$$

[1] G. M. Viswanathan, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley, *The Physics of Foraging* (Cambridge University Press, Cambridge, UK, 2011).

[2] O. Bénichou, C. Loverdo, M. Moreau, and R. Voituriez, Rev. Mod. Phys. **83**, 81 (2011).

[3] O. Bénichou and S. Redner, Phys. Rev. Lett. **113**, 238101 (2014).

[4] M. Chupeau, O. Bénichou, and R. Voituriez, Nat. Phys. **11**, 844 (2015).

[5] M. Chupeau, O. Bénichou, and S. Redner, Phys. Rev. E **93**, 032403 (2016).

[6] V. Méndez, D. Campos, and F. Bartumeus, *Stochastic Foundations in Movement Ecology: Anomalous Diffusion, Front Propagation and Random Searches* (Springer-Verlag, Berlin, 2013).

[7] G. M. Viswanathan, S. V. Buldyrev, S. Havlin, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley, Nature **401**, 911 (1999).

[8] D. Campos, F. Bartumeus, E. P. Raposo, and V. Méndez, Phys. Rev. E **92**, 052702 (2015).

[9] F. Bartumeus, D. Campos, W. Ryu, R. Lloret-Calbot, V. Méndez, and J. Catalán, Ecol. Lett. **19**, 1299 (2016).

[10] M. A. Baars, Oecologia **44**, 125 (1979).

[11] J. M. Fryxell *et al.*, Proc. Natl. Acad. Sci. USA **105**, 19114 (2008).

[12] N. E. Humphries *et al.*, Nature **465**, 1066 (2010).

[13] I. Tagkopoulos, Y.-C. Liu, and S. Tavazoie, Science **320**, 1313 (2008).

[14] T. Gallagher, T. Bjorness, R. Greene, Y.-J. You, and L. Avery, PLoS ONE **8**, e59865 (2013).

[15] S. W. Flavell *et al.*, Cell **154**, 1023 (2013).

[16] T. Gallagher, J. Kim, M. Oldenbroek, R. Kerr, and Y.-J. You, J. Neurosci. **33**, 9716 (2013).

[17] J. Ben Arous, S. Laffont, and D. Chatenay, PLoS ONE **4**, e7584 (2009).

[18] L. C. M Salvador *et al.*, J. Roy. Soc. Interf. **11**, 20131092 (2014).

[19] J.-B. Masson, Proc. Natl. Acad. Sci. USA **110**, 11261 (2013).

[20] A. J. Calhoun, S. H. Chalasani, and T. O. Sharpee, eLIFE **3**, e04220 (2014).

[21] H. Freund and P. Grassberger, Physica A **190**, 218 (1992).

[22] D. Boyer and P. D. Walsh, Philos. Trans. R. Soc. A **368**, 5645 (2010).

[23] D. Boyer and C. Solis-Salas, Phys. Rev. Lett. **112**, 240601 (2014).

[24] J. W. Haus and K. W. Kehr, Phys. Rep. **150**, 263 (1987).

[25] A. M. Berezhkovskii, Yu. A. Makhnovskii, and R. A. Suris, J. Stat. Phys. **57**, 333 (1989).

[26] H. Larralde, P. Trunfio, S. Havlin, H. E. Stanley, and G. H. Weiss, Phys. Rev. A **45**, 7128 (1992).

[27] S. Havlin, H. Larralde, P. Trunfio, J. E. Kiefer, H. E. Stanley, and G. H. Weiss, Phys. Rev. A **46**, R1717(R) (1992).

[28] S. B. Yuste and L. Acedo, Phys. Rev. E **60**, R3459(R)) (1999).

[29] S. Condamin, O. Bénichou, V. Tejedor, R. Voituriez, and J. Klafter, Nature **450**, 77 (2007).

[30] R. H. Ritchie and A. Y. Sakakura, J. Appl. Phys. **27**, 1453 (1956).

[31] S. B. Yuste, E. Abad, and K. Lindenberg, Phys. Rev. Lett. **110**, 220603 (2013).

[32] D. Campos, E. Abad, V. Méndez, S. B. Yuste, and K. Lindenberg, Phys. Rev. E **91**, 052115 (2015).

[33] D. Campos, F. Bartumeus, V. Méndez, and X. Espadaler, J. Roy. Soc. Interf. **11**, 20130859 (2013).