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RESEARCH ARTICLE

Simulating capture efficiency of pitfall traps based on sampling strategy and the movement of ground-dwelling arthropods

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Abstract

1. Pitfall traps are frequently used to capture ground-dwelling arthropods, particularly beetles, ants and spiders. The capture efficiency of a pitfall trapping system strongly depends on the number and opening size of traps, how traps are distributed over the sampling area (spatial arrangement) and the movement characteristics of arthropods.
2. We use numerical simulations for a single species to analyse the trap count patterns that emerge from these variables. Arthropod movement of individuals is modelled as correlated random walks, with multiple traps placed over an area, and catches are simulated as individual interaction with traps. We consider four different types of spatial arrangements of traps across a homogeneous landscape: grid (i.e. rectangular array), transect, nested-cross and randomised. We contextualise our results by considering the locomotion of *Pterostichus melanarius*, a highly active carabid beetle often serving as a biocontrol agent for the suppression of pest insects and weeds.
3. By simulating the trapping of randomly moving ground-dwelling arthropods, we show that there is an optimal inter-trap separation distance (trap spacing) that maximises captures, that can be expressed using exact formulae in terms of trap opening sizes, sampling area and trap number. Moreover, for the grid and

nested-cross arrangements, larger trap spacing to maximise spatial coverage over the whole sampling area is suboptimal. Also, we find that over a large sampling area, there is a hierarchical order for spatial arrangements in relation to capture efficiency: grid, randomised, transect, followed by the nested-cross. However, over smaller sampling areas, this order is changed as the rate at which trap counts accumulate with trap number varies across arrangements—eventually saturating at different levels. In terms of movement effects, capture efficiency is maximised over a narrow diffusive range and does not depend strongly on the type of spatial arrangement—indicating an approximate optimal mode of arthropod activity, i.e. rate of spread.

4. Our approach simultaneously considers several important experimental design aspects of pitfall trapping providing a basis to optimise and adapt sampling protocols to other types of traps to better reflect their various purposes, such as monitoring, conservation or pest management.

KEYWORDS

arthropod movement, capture efficiency, diffusion, inter-trap spacing, pitfall trapping, random walk, sampling strategy, spatial arrangement

1 | INTRODUCTION

Pitfall trapping is a widespread technique in ecology for sampling ground-dwelling and randomly moving arthropods (hereafter 'arthropods' for brevity), with various applications (Bestelmeyer et al., 2000; Greenslade, 1964; Martín-López et al., 2011; O'Hara et al., 2008; Pimentel, 2009). During a typical pitfall trapping protocol, several traps are installed in the sampling area, and the identity and abundance of species caught are routinely monitored and recorded after a few consecutive days, several weeks or even months depending on the study focus (Henderson & Southwood, 2016; Price & Feer, 2012). These trap counts are then used in various estimations and indices, from relative population abundance of specific species, activity-density, microhabitat use or movement patterns of individuals to species richness and diversity of ground-dwelling assemblages (Hohbein & Conway, 2018; Montgomery et al., 2021). Trap counts depend on various biological, physical or environmental factors that can influence locomotor activity of arthropods (Baars, 1979; Engel et al., 2017; Koivula et al., 2003; Melbourne, 1999; Petrovskii et al., 2012; Raworth & Choi, 2001). Moreover, experimental design such as trap type (shape, size, depth, inclusion of bait/attractant, killing agent) and sampling strategies (spatial arrangement, number of traps, number of trap-nights, digging-in effect) are additional parameters that can potentially affect trap counts and the taxa caught (Brown & Matthews, 2016; Digweed et al., 1995; Engel et al., 2017; Greenslade & Greenslade, 1971; Hohbein & Conway, 2018; Jiménez-Carmona et al., 2019, 2020; Koivula et al., 2003; Work et al., 2002). Understanding the impact of these methodological factors on trap counts is thus crucial to draw inferences and conclusions in ecology (Cheli & Corley, 2010).

An efficient sampling strategy requires careful planning and must particularly consider the number of traps and their spatial arrangement (Woodcock, 2005). There are two types of pitfall trap spatial arrangements that are the most common in ecological studies. In the first type, traps are placed in a grid formation (i.e. rectangular array) spanning the area sampled, where the distance between adjacent traps are the same and predetermined (Corti et al., 2013; Crist & Wiens, 1995; Niemelä et al., 1992; Pérez-Bote & Romero, 2012; Raworth & Choi, 2001). This provides an even coverage of the sampling area, and traps are also easily located. In the second type, traps are aligned and form a transect (i.e. a straight line), with a fixed inter-trap distance (Crist & Wiens, 1995; Kharboutli & Mack, 1993; Larsen & Forsyth, 2005; Leasure et al., 2012). The transect trap arrangement is particularly useful for identifying the effects of environmental gradients (e.g. land use intensity) on arthropod communities (Larsen & Forsyth, 2005) and calculating distance-based biodiversity metrics (e.g. beta diversity, Koleff et al., 2003). In a few studies, traps are placed at random locations, enabling design-based inference (Williams & Brown, 2019). Other more specialised spatial arrangements have been proposed for improved estimates of population densities, e.g. the nested-cross array, a cross-shaped arrangement with variable distances between traps increasing by a constant factor along each wing (Perner & Schueler, 2004). Also, less conventional arrangements have been used, e.g. traps placed in pairs (two-circle method, Zhao et al., 2013), in triangular or circular formations (Hood et al., 2022) or in clusters (Hohbein & Conway, 2018). Finally, pitfall traps can be placed in a targeted (and ultimately opportunistic) manner to sample specific habitats or taxa rather than areas and populations (e.g. by placing traps near piles of dead wood to sample saproxylic beetles, Ulyshen & Hanula, 2009).

In addition to the sampling strategy deployed, the movement of the arthropods on or close to the ground also has important consequences for pitfall trapping success. At the individual level, this movement can be idealised as a random process which is described by random walks (RWs; Codling et al., 2008; Kareiva & Shigesada, 1983). For a discrete-time continuous space equivalent, the modelling procedure maps an actual arthropod's curvilinear movement path into a series of discrete steps linking successive individual locations (Berg, 1993; Turchin, 1998). The simple random walk (SRW) is one of the earliest models and considers movement paths to be uncorrelated and unbiased (Lin & Segel, 1988; Okubo, 1980). In this case, movement in any direction is equiprobable, and thus completely random. Although simplistic, in some instances, the SRW has served as a useful null model (e.g. the movement of infected ants, see Hughes et al., 2011). More realistically, in a homogeneous environment, a ground-dwelling arthropod is likely to continue moving in a similar direction, at least in the short term, with gradual rather than abrupt turns (Kareiva & Shigesada, 1983; Codling et al., 2008). To reflect this in movement models, the orientations of successive steps are correlated, and thus referred to as the correlated random walk (CRW; Bovet & Benhamou, 1988; Hall, 1977; Patlak, 1953). CRWs have been used to model the movement of several ground-dwelling arthropods, e.g. ants, beetles (Bailey et al., 2021; Byers, 2001; Reynolds et al., 2013). By simulating the random movement of ground-dwelling arthropods, and computing trap counts as frequency of encounters with virtually placed traps, it is possible to analyse the direct effect of movement such as diffusion and tortuosity (i.e. the amount of turning in the individual paths) on pitfall trap efficiencies (Miller et al., 2015).

The virtual ecologist approach where simulated data and observer models are used to mimic real species provides a framework for the assessment of sampling protocols and analysis in spatial ecology (Zurell et al., 2010). Individual-based models can be used to simulate the movement of individuals in a population, their encounters with multiple virtual traps placed over a simulation area (analogous to a sampling area) and by extension of the entire trapping process (Bearup et al., 2016; Byers, 1993; Grimm & Railsback, 2005; Miller et al., 2015; Petrovskii et al., 2012, 2014). Such theoretical attempts have been crucial for investigating the effectiveness of sampling designs and strategies, and provide a strong basis for empirical validation (Engel et al., 2017). Individual-based models pose some advantages over field experiments as they are relatively cost-effective, less time-consuming and labour-intensive, and easy to replicate whilst ensuring homogeneity. For instance, simplifying assumptions such as constant environmental conditions and identical movement capacities across individuals can allow for increased focus on the process of interest—whilst minimising or removing potential sample biases (Petrovskii et al., 2012). A coherent analysis of some aspects of optimal trap design or strategies may be extremely challenging if relying solely on empirical observations (Ahmed & Petrovskii, 2019). While a simulation study alone is not able to replace the complexity of empirical field tests, the two research approaches are complementary and progress is enhanced when they are used in combination.

In this study, we used numerical simulations to examine pitfall trap capture efficiency based on spatially explicit arthropod movement in relation to (1) the optimal trap separation distance that maximises captures, and how this spacing depends on trap size, trap number and the size of the sampling area. We investigate (2) which of the four spatial arrangements capture more individuals, and how this order can be altered under different geometrical scenarios. We further analyse (3) the effects of arthropod movement on captures, such as diffusion and tortuosity, and to add realism, we contextualise our results by considering the movement of a model species, the ground-dwelling carabid *Pterostichus melanarius* (Coleoptera: Carabidae). Information such as this is useful for improving trap count interpretations and contributes towards developing more effective sampling strategies for monitoring or management of populations of arthropod species.

2 | MODELLING MOVEMENT AND TRAPPING OF GROUND-DWELLING ARTHROPODS

2.1 | Random walk framework

We model the independent movement of individuals in a population of M ground-dwelling arthropods over space using a discrete time RW. The curvilinear movement path of an individual $\mathbf{x}=(x(t), y(t))$ over a given time interval $0 \le t \le T$ can be mapped as a RW of n steps with location $\mathbf{x}_i=(x_i, y_i)$ at time t_i, where $i=0, 1, 2, \ldots, n$ is the number of steps. The step length, which is the distance between any two successive steps is $l_i=|\mathbf{x}_i-\mathbf{x}_{i-1}|$ with mean step length $E[l]$. Individual locations are recorded at discrete times t_i, and it is assumed that the duration between subsequent movement bouts is the same, as individual telemetry data often work with regular time steps (Cagnacci et al., 2010; Růžičková & Elek, 2021). Therefore, $t_i=i\Delta t$, where Δt is a constant time increment independent of the step number i. The total duration of the n-step RW is then $T=n\Delta t$, with total path length $L=nE[l]$ and mean speed $E[v]=E[l]/\Delta t=L/T$.

If we consider an arthropod at location $\mathbf{x}_{i-1}=(x_{i-1}, y_{i-1})$ at time t_{i-1}, then the location $\mathbf{x}_i$ at the next time step t_i can be expressed as

$$\mathbf{x}_i = \mathbf{x}_{i-1} + (\Delta \mathbf{x})_i, \qquad (1)$$

where $(\Delta \mathbf{x})_i=(\Delta x_i, \Delta y_i)$ is a step vector for the ith step along the walk, its components being random variables. This step vector can be expressed in terms of step lengths l_i and step orientations (or headings) θ_i written in polar coordinates as $(\Delta \mathbf{x})_i=(l_i \cos \theta_i, l_i \sin \theta_i)$. The turning angle α_i can then be measured as the difference between the orientations of two successive steps $\alpha_i=\theta_i-\theta_{i-1}$, and the individual movement trajectory can be simulated given that the probability distributions of l and α are prescribed. The RW framework for modelling arthropod movement is an idealisation (Figure 1), which is commonly used in the literature (Bailey et al., 2021; Kareiva & Shigesada, 1983; Miller et al., 2015; Turchin, 1998).

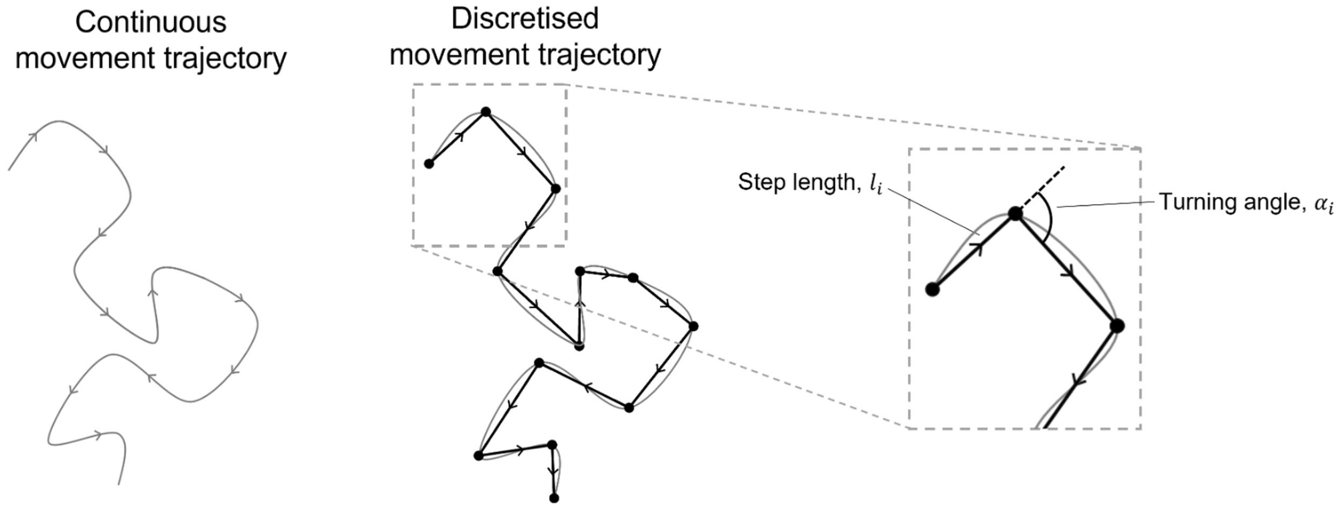

FIGURE 1 Mapping the continuous movement trajectory of a ground-dwelling arthropod as a series of discrete steps with step lengths l_i and turning angles α_i resulting in the random walk.

2.2 | Simple random walk

For a SRW, the probability distributions of step increments $\phi(\Delta x)$ and $\phi(\Delta y)$ are both centrally symmetric with zero means and the same finite variance. This ensures that the movement is completely random such that the direction of movement is completely independent of the previous directions moved, and there is no long-term directional bias in the walk (Weiss, 1994). We choose to consider normally distributed increments

$$\phi(\Delta x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\Delta x)^2}{2\sigma^2}}, \quad \phi(\Delta y) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\Delta y)^2}{2\sigma^2}}, \tag{2}$$

with $E[\Delta x] = E[\Delta y] = 0$ and $\mathrm{var}[\Delta x] = \mathrm{var}[\Delta y] = \sigma^2$, where σ quantifies the mobility of the arthropod (Ahmed & Petrovskii, 2019; Petrovskii et al., 2012). The choice of normal increments leads to standard diffusive movement which is often observed and used in various movement phenomena and the corresponding SRW can be considered as a discrete-time equivalent of Brownian motion (Codling et al., 2008; Petrovskii et al., 2012). From Equation (2), the probability distribution functions for step lengths l and turning angles α can be derived (see Petrovskii et al., 2014), and are given by

$$\lambda(l) = \frac{l}{\sigma^2} e^{-\frac{l^2}{2\sigma^2}}, \quad \psi(\alpha) = \frac{1}{2\pi}, \tag{3}$$

where $\lambda(l)$ is the Rayleigh distribution and $\phi(\alpha)$ is the uniform distribution bounded between $-\pi$ and π. The mean and mean-squared step lengths are

$$E[l] = \frac{\sigma\sqrt{2\pi}}{2}, \quad E[l^2] = 2\sigma^2, \tag{4}$$

which serve as useful characteristic length scales for each step in the RW. The mean speed is given by $E[v] = \frac{\sigma\sqrt{2\pi}}{2\Delta t}$, and therefore an increase in the mobility parameter σ corresponds to a larger mean speed for a fixed time step Δt.

2.3 | Correlated random walk

A CRW allows for correlation between the orientations of successive steps, resulting in a short-term localised directional bias known as 'forward persistence' (Benhamou, 2004; Bovet & Benhamou, 1988; Hall, 1977; Kareiva & Shigesada, 1983). This provides a more realistic description in contrast to the SRW, as ground-dwelling arthropods in the short term are more likely to keep moving in the same direction than to perform abrupt turns. In this case, the distribution of turning angles is zero-centred, centrally symmetric and peaks around the mean value. An example of such is the von-Mises distribution $\psi(\alpha)$ with mean value $E[\alpha] = 0$,

$$\psi(\alpha) = \frac{e^{\kappa \cos\alpha}}{2\pi I_0(\kappa)}, \quad I_0(\kappa) = \frac{1}{2\pi}\int_{-\pi}^{\pi} e^{\kappa \cos\alpha} d\alpha, \tag{5}$$

where $\psi(\alpha)$ is bounded between $-\pi$ and π, and $I_0(\kappa)$ denotes the zeroth-order modified Bessel function of the first kind with concentration parameter $\kappa > 0$ (Abramowitz & Stegun, 1972). Whilst the choice of the underlying distribution can have an effect on certain qualities of the RW model, such as expected location and mean square displacement (MSD; Bailey & Codling, 2021; Bartumeus et al., 2008; Codling et al., 2010), the von-Mises distribution has been identified to well describe the observed data (Goodwin & Fahrig, 2002; Schtickzelle et al., 2007) and has often been used in similar simulation studies (Ahmed & Petrovskii, 2019) and in the analysis of movement data (Nicosia et al., 2017).

The turning angle distribution is characterised by the mean cosine c and the mean sine s, defined as

$$c = E[\cos\alpha] = \frac{1}{2\pi}\int_{-\pi}^{\pi} (\cos\alpha)\psi(\alpha) d\alpha, \quad s = E[\sin\alpha] = \frac{1}{2\pi}\int_{-\pi}^{\pi} (\sin\alpha)\psi(\alpha) d\alpha, \tag{6}$$

both lying between 0 and 1. Since we consider $\psi(\alpha)$ to be zero-centred and symmetric, the mean sine is null, i.e. $s = 0$. The mean cosine c written as a function of κ measures the strength of the forward persistence, and for the von Mises distribution is computed as

$$c = \frac{I_1(\kappa)}{I_0(\kappa)}. \tag{7}$$

If $c=0$, the turning angle distribution reduces to the uniform distribution (see Equation 3), in which case the SRW is a special case of the CRW. With increasing c, there is a greater tendency to move in a similar direction as that at the previous step, and at the other extreme end, $c=1$ corresponds to straight line (or ballistic) movement (Benhamou, 2004).

The MSD and the sinuosity index (S) are key metrics that characterise individual movement paths, and the diffusion coefficient (D) measures the rate of spread of an individual in space. The MSD is the expected value of the squared Euclidean distance between an individuals' initial and final positions, and can be computed for a balanced CRW (i.e. left and right turns are equiprobable) as

$$\mathrm{MSD} = nE\left[l^2\right] + 2E\left[l\right]^2 \cdot \frac{c}{1-c} \cdot \left(n - \frac{1-c^n}{1-c}\right), \tag{8}$$

which is expressed in terms of moments of step length l, mean cosine of the turning angle c and the number of steps in the walk n (Codling et al., 2008; Hall, 1977; Kareiva & Shigesada, 1983). For a large number of steps n, the MSD approaches

$$\mathrm{MSD}^* = n\left(E\left[l^2\right] + 2E\left[l\right]^2 \cdot \frac{c}{1-c}\right), \tag{9}$$

where '*' is included here to distinguish this asymptotic MSD from that presented in Equation (8).

The diffusion coefficient D in the long term can be related to the asymptotic MSD as follows

$$D = \frac{\mathrm{MSD}^*}{4n\Delta t} = \frac{1}{4\Delta t}\left(E\left[l^2\right] + 2E\left[l\right]^2 \cdot \frac{c}{1-c}\right). \tag{10}$$

The sinuosity index S measures the tortuosity in an individual's movement path, and can be related to the diffusion coefficient as

$$S = \sqrt{\frac{E[v]}{D}} = 2\sqrt{\frac{L}{\mathrm{MSD}^*}}, \tag{11}$$

where $E[v]$ is the mean speed and $L=nE[l]$ is the total path length (Benhamou, 2004, 2006; Codling et al., 2008, see also Ahmed et al., 2021).

2.4 | Simulating trapping for ground-dwelling arthropods

To simulate trap counts for a population of ground-dwelling arthropods, the initial location $\mathbf{x}_0$ of M^* individuals is drawn independently and at random in a circular region of radius R. Any individuals initially occurring within the traps are then removed, resulting in a remaining population of M individuals. In polar coordinates, the initial location is given as

$$\mathbf{x}_0 = \left(R\sqrt{U}, 2\pi U\right), \tag{12}$$

where U is a random variable drawn from the uniform distribution between 0 and 1. A number of J circular traps are placed with centres at $\mathbf{x}_j^* = \left(x_j^*, y_j^*\right)$, $j=1, 2, \ldots, J$, according to a specified spatial arrangement. All traps are circular and have the same opening size measured by the trap radius r (see Figure 2a). This trap shape is most often used

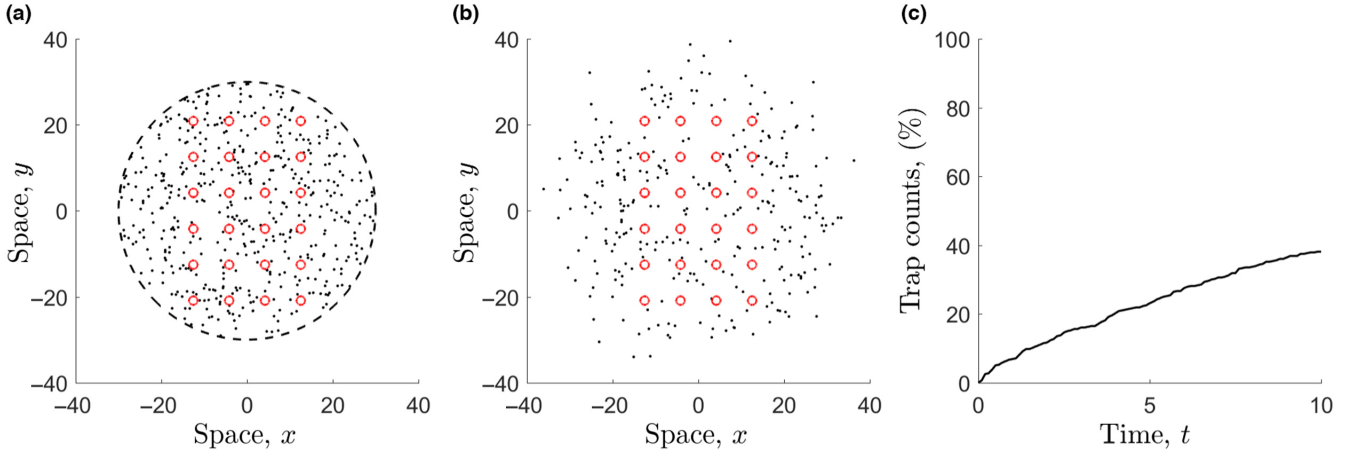

FIGURE 2 Simulation of trap counts. (a) A population of $M^*=500$ individuals are initially uniformly distributed over a circular simulation area of radius $R=30$. In all, 24 circular traps of radius $r=1$ are placed according to a 4 by 6 grid spatial arrangement (red circles) with an inter-trap spacing of 8.36 (which is 80% of the maximum possible spacing). From the initial population, 20 individuals that occur within these traps are removed, resulting in a true population of $M=480$. The population is not confined and can move beyond the sampling area at subsequent steps. (b) Snapshot of the population distribution at time $t=10$ (time increment $\Delta t=0.1$, $n=100$ steps) where each individual performs a simple random walk with normally distributed increments (Equation 2). The mobility parameter is set to $\sigma=0.5$ and the mean step length is less than the trap diameter ($E[l]=0.63<2$, Equation 4); therefore, undetected trap passes are negligible. A total of 183 individuals have been trapped, but this count can vary with each run due to the randomness of the individual movement. (c) Trap counts are recorded at each time step, and represented as a stochastic trajectory with 183/480 = 38.1% of the true population trapped at $t=10$. This is an example of the simulation process where using different trap arrangements and movement parameters based on taxon characteristics can be tested.

in pitfall trapping studies and has been shown to be the most efficient in retaining captures (Ahmed & Petrovskii, 2019; Luff, 1975). In practice, different types of non-pitfall traps are also used to catch various arthropods, flying as well as ground-dwelling (O'Hara et al., 2008). Although our primary focus is on pitfall trapping, the results that follow are also applicable to other types of traps and various taxa. In this case, the trap radius r can be considered as an interception distance, i.e. an individual has to be in close proximity to the trap location for successful trapping (Miller et al., 2015). We consider the sampling area to be non-confined so that individuals can move beyond this region or even return during the course of their movement. This is to avoid any unnecessary geometry-specific biases, or any complexities that can arise due to individual interactions in the case a boundary was present (Bearup & Petrovskii, 2015; Christensen et al., 2021; Cocconi et al., 2021).

Once the initial distribution is defined, the movement of each individual is modelled by a CRW of n steps (of which the SRW is a special case) with normally distributed increments (Equation 2) and uniformly distributed initial step directions. The model assumes that each individual moves independently so that there are no changes in direction due to interactions. At each time step t_i along the movement paths, those individuals that are located within any of the j traps, with condition

$$|\mathbf{x}_i - \mathbf{x}_j^*| < r,\ i = 0, 1, \ldots, n,\ j = 1, 2, \ldots, J, \tag{13}$$

are deemed to be trapped and removed, Figure 2b. Trap counts are computed as the total number of individuals caught in all traps at each time step, and expressed as a proportion of the initial population size M. These counts are summed cumulatively across time steps, and represented as a monotonically increasing stochastic trajectory over discrete time, Figure 2c. The magnitude of stochastic fluctuations in trap counts is reduced by averaging over multiple simulation runs, resembling averaging counts from a collection of multiple samples in the field.

The RW model is a position jump process where only individual locations are recorded at each time step. This simulation artefact can potentially result in an underestimation of trap counts because for an actual movement path, trap encounters in between subsequent locations can be undetected. However, in the case of circular traps, if the mean step length is less than the trap diameter (i.e. $E[l] < 2r$), then the probability of undetected trap passes is very low, and thus the impact on trap counts is negligible (see figure 6.4 in Ahmed et al., 2021).

2.5 | Spatial arrangements and inter-trap spacings

To analyse the impact of trap placement on trap counts, we consider four different spatial arrangements (1) randomised, (2) grid, (3) transect and (4) nested-cross (Figure 3). For any type of arrangement, the minimum separation distance (i.e. distance between trap centres of any two adjacent traps) is equal to the trap diameter $d_{\min} = 2r$ to ensure that traps do not overlap. For the randomised arrangement, the locations of trap centres $\mathbf{x}_j^*$, are uniformly distributed over a circle of radius $R - r$ so that all traps lie within the sampling area, given in polar coordinates as

$$\mathbf{x}_j^* = \left((R-r)\sqrt{U}, 2\pi U\right),\ j = 1, 2, \ \ldots, J, \tag{14}$$

where U is a random variable drawn from the uniform distribution between 0 and 1, and therefore traps are separated by a randomised distance d, Figure 3a. For the grid arrangement, traps are placed in a rectangular array (p by q traps), with a fixed value for d. Here, p and q are chosen so that arrangement elongation is minimised, e.g. in the case of 24 traps, we have 4 by 6 traps (instead of 3 by 8 or 2 by 12), Figure 3b. This is to maximise coverage in both horizontal and vertical directions. In the case of a linear transect arrangement, traps are placed in a straight line (or equivalently along a diagonally oriented line) with a fixed value for d, Figure 3c.

In general, for any arrangement with a fixed separation between traps, the distance depends on the radius of the sampling area R, the number of traps J and the trap radius r (Woodcock, 2005). In the case of maximal spatial coverage, whilst ensuring that all traps lie within the bounds of the sampling area, the maximum separation distance $d_{\max}$ can be expressed in terms of these variables.

For the grid arrangement where traps are placed in a p by q rectangular array with total number of traps $J = pq$, we have that

$$d_{\max} = \frac{2(R-r)}{\sqrt{(p-1)^2 + (q-1)^2}}, \tag{15}$$

which, in the case of a square arrangement ($p = q$), simplifies to

$$d_{\max} = \frac{2(R-r)}{\sqrt{2}\left(\sqrt{J}-1\right)}. \tag{16}$$

For the transect arrangement, we have

$$d_{\max} = \frac{2(R-r)}{J-1}. \tag{17}$$

Using these upper bounds, a normalised separation distance δ (i.e. a proportion of the maximum possible inter-trap spacing) can be defined as

$$\delta = \frac{d - d_{\min}}{d_{\max} - d_{\min}},\quad 0 \le \delta \le 1, \tag{18}$$

where $d = d_{\min}$ at $\delta = 0$ and $d = d_{\max}$ at $\delta = 1$. For the nested-cross arrangement (Figure 3d), the number of traps placed is a multiple of 4, i.e. one trap along each wing in each configuration (Perner & Schueler, 2004). In this case, inter-trap separation distances are variable and increase by a constant factor w along each wing, with minimum and maximum possible values

$$w_{\min} = \frac{2r}{x_1^*} + 1,\quad w_{\max} = \left(\frac{R-r}{x_1^*}\right)^{\frac{4}{J-4}}, \tag{19}$$

where the first trap along the horizontal right-wing is placed with coordinates $(x_1^*, 0)$. Similarly, a normalised separation factor ω can be defined as

$$\omega = \frac{w - w_{\min}}{w_{\max} - w_{\min}},\quad 0 \le \omega \le 1, \tag{20}$$

where $w = w_{\min}$ at $\omega = 0$ and $w = w_{\max}$ at $\omega = 1$.

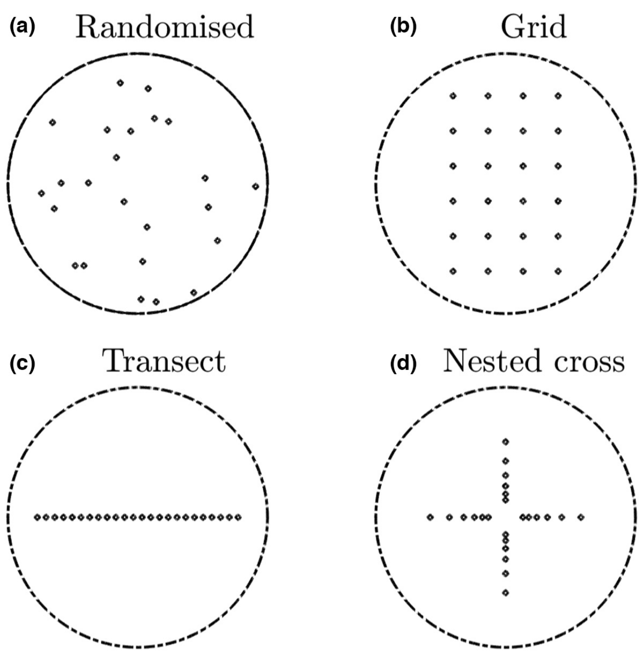

FIGURE 3 Spatial arrangements of traps. (a) randomised, (b) grid (specific 4 by 6 case), (c) transect and (d) nested-cross. The illustration is shown here with $J=24$ circular pitfall traps of radius r placed within a circular unconfined sampling area of radius R. For plots (b, c), inter-trap spacing is 80% of the maximum possible value d_{max}, and for plot (d) 90% of the maximum separation factor w_{max}. However, we later consider a varied trap number starting with a minimum of 4 traps and increasing by 4 traps in each configuration, with varied trap spacing. Trap placement is always ensured to be symmetrical with respect to the horizontal and vertical axes, except for the randomised arrangement.

2.6 | *Pterostichus melanarius* as a model species

For purposes of interpretation and to provide ecological context, we consider the ground beetle *P. melanarius* (Illiger, 1798) as a model species, which is a close representative of other carabid species from the same genus (Raupach et al., 2020) and some other beetles with similar biological and physical traits, e.g. *Poecilus cupreus* (Linnaeus, 1758) (Bailey et al., 2021). *P. melanarius* is distributed across Europe and Asia, often occurring in high abundances and being a dominant ground beetle species especially in agricultural landscapes (e.g. Bažok et al., 2007). In North America, it is one of the most successful introduced and established arthropod invaders (Niemela et al., 1997). This species is a generalist predator and thus considered to be a beneficial insect in many different agricultural systems (Busch et al., 2021), as it is an important natural enemy of several pests and thus often serves as a biocontrol (Sunderland, 2002), e.g. for the field slug *Deroceras reticulatum* (O.F. Müller, 1774) (McKemey et al., 2003), the blueberry maggot *Rhagoletis mendax* (Curran, 1932) (Renkema et al., 2012) and consumption of weed seeds (Frei et al., 2019). Therefore, trapping of *P. melanarius* is predominately for monitoring and conservation purposes (Chiverton, 1984; Dixon & McKinlay, 1992). The typical size of this species is around 1.27–1.87 cm with a mean body length of 1.57 cm (Hůrka, 1996), and a trap size of $r=5$ cm considered later in this study is sufficiently large for the effective trapping of this species. Moreover, movement data are readily available for *P. melanarius* (e.g. see Allema et al., 2014), and several modelling studies based on trapping have used this species as a viable candidate to present examples (Allema et al., 2019; Petrovskaya et al., 2018; Petrovskii et al., 2014).

2.7 | Modelling a realistic trapping scenario

To interpret the effects of changes in trap counts in relation to movement diffusion, spatial and temporal units must reflect those corresponding to the locomotion and dispersal traits of *P. melanarius*, including the length scales of the experimental setup. Pitfall trap radius can range between 0.01 and 0.1 m with a median of 0.03 m (Brown & Matthews, 2016); we consider $r=0.1$ m with a sampling area of radius $R=10$ m (with area 314 m^2) to reflect a typical trapping scenario in the field. Usually, the movement of ground-dwelling arthropods is tracked in the field for a few days or weeks (Růžičková & Elek, 2021), and emptying frequency of pitfall traps varies significantly, with trap count data recorded daily, weekly, monthly (Holland & Reynolds, 2005) or on a shorter timescale, e.g. every 3 hours (Tuf et al., 2012). We chose to compare trap counts after a duration of 2.5 days because considerable count differences using different trap arrangements begin to appear up to this time and is sufficient to discern trapping efficiency (see later Figure 6 for trapping simulations for *P. melanarius*). However, for other study aims, the simulation experiment could be run for a longer duration to reflect trap monitoring for several weeks. In an $n=1000$ step RW (as used in our simulations), the total duration of 2.5 days corresponds to a time increment of $\Delta t=0.06$ h (3.6 min) between successive steps. In relation to the locomotion of the ground beetle *P. melanarius*, it has been empirically observed that the mean speed ranges between 2 and 2.8 m/h in cereal fields, and 1.5 and 2.5 m/h in a wood (Wallin & Ekbom, 1988). To reflect this, we chose the length scale for steps in the RW as $\sigma=0.1$ m, which translates to a mean step length of $E[l]=0.125$ m (Equation 4), with a mean speed of $E[v]=2.09$ m/h.

3 | ANALYSIS OF SIMULATED TRAP COUNTS

3.1 | Optimal trap spacing

In the case of the grid arrangement with $J=24$ traps, the capture efficiency peaks at $\delta \simeq 0.8$, Figure 4a. From Equation (18), this implies that the optimal separation distance is $d_{\text{opt}} \simeq 0.8 d_{\text{max}}$, i.e. 80% of the distance that maximises spatial coverage over the sampling area. We also found that this also applies for different trap numbers. Also, using Equation (15) we obtain

$$d_{\text{opt}} \simeq 0.8\left(\frac{2(R-r)}{\sqrt{(p-1)^2+(q-1)^2}}\right), \tag{21}$$

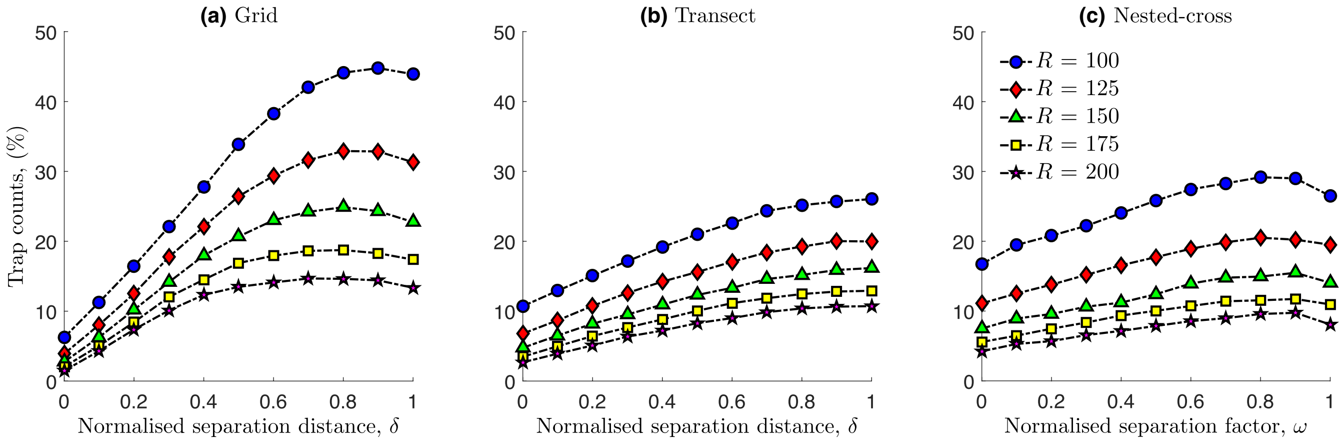

FIGURE 4 Trap counts computed for the (a) grid and (b) transect arrangements as a function of normalised separation distances δ, or in the case of the (c) nested-cross arrangement, in terms of normalised separation factors ω. A total number of $J=24$ traps of equal radius $r=1$ are placed over a circular sampling area of varying sizes $R=100$, 125, 150, 175, 200. For the grid arrangement, traps are placed in a $p=4$ by $q=6$ rectangular array, and for the nested-cross arrangement, the first trap along the horizontal right-wing is placed at $(x_1^*, 0)=(4, 0)$. $M^*=10{,}000$ individuals are placed over the site, and those individuals occurring within the traps are removed. Each individual in the remaining population independently performs a SRW with normally distributed increments with mobility parameter $\sigma=1$ (Equation 2). Trap counts are computed using the simulation methodology described in section 2.4 and recorded after each walker executes at most $n=1000$ steps. This total step number is sufficiently large so that trap counts are approaching saturation. Each simulated count is averaged over 10 simulations so that differences in trap counts are <1% and thus negligible.

which determines the optimal grid separation distance in terms of the size of the sampling area R, trap size r and the number of traps J placed in a p by q rectangular array.

For the transect arrangement, the largest trap counts are obtained when $\delta \simeq 1$, i.e. when spatial coverage is maximised with separation distance

$$d_{\text{opt}} \simeq \frac{2(R-r)}{J-1}, \tag{22}$$

given by Equation (17), Figure 4b. For the nested-cross arrangement, the peak trap count occurs when $\omega \simeq 0.9$ (Figure 4c), i.e. the optimal separation factor is 90% of w_{max}, and therefore

$$w_{\text{opt}} \simeq 0.9\left(\frac{R-r}{x_1^*}\right)^{\frac{4}{J-4}}, \tag{23}$$

from Equations (19 and 20). Conversely, for a chosen separation distance, these formulae can also be used by field ecologists to explicitly define the area of the sampling space ($A=\pi R^2$), as this information is often omitted when reporting sampling methodology. For example, on rearranging Equation (21), one gets

$$A \simeq \pi\left[r+\frac{5}{8}d_{opt}\sqrt{(p-1)^2+(q-1)^2}\right]^2. \tag{24}$$

Usually in empirical field studies, the trap size is much less than the size of the sampling area, i.e. $r/R \ll 1$, in which case Equations (21–23) simplify to

$$d_{\text{opt}} \simeq \frac{1.6R}{\sqrt{(p-1)^2+(q-1)^2}},\quad d_{\text{opt}} \simeq \frac{2R}{J-1},\quad w_{\text{opt}} \simeq 0.9\left(\frac{R}{x_1^*}\right)^{\frac{4}{J-4}}, \tag{25}$$

for the grid, transect and nested-cross arrangements, respectively. For example, in the case of 24 traps in a $p=4$ by $q=6$ grid configuration, we obtain $d_{\text{opt}} \simeq 0.27R$ from Equation (25). Thus, the capture efficiency, relative to the given number of traps, is maximised if the trap separation distance d is approximately 27% of the radius of the sampling area R.

The optimal arrangements for the grid and nested-cross ensure that no traps are on the boundary of the sampling area. For the transect arrangement only, the outer two traps are on the boundary, and for the randomised arrangement, it can be expected that only relatively few traps are on/close to the boundary. Therefore, the boundary effects in our model are assumed to be negligible, but could be accounted for by considering a sampling area which lies within a larger landscape, introducing a buffer region so that individuals can enter the sampling area from outside (Royle & Converse, 2014). In this case, captures can be computed as a percentage of the 'effective sample area'.

3.2 | Effect of the trap arrangement, trap number and trap size

There is a clear hierarchy among the four spatial arrangements of traps in terms of capture efficiency. If the size of the sampling area is relatively large in relation to individual movement diffusion, the ranked order is grid, randomised, transect followed by the nested-cross, Figure 5c,d. However, if arthropods disperse over a smaller area with the same diffusivity, this order can change, in which case the randomised and nested-cross are more efficient than grid and transect designs, respectively, Figure 5a,b. The critical trap number where this transition occurs is lower for increasing trap size. For instance, the randomised arrangement is more capture efficient than the grid arrangement if at least 28 traps are placed with size $r=1$ over a sampling area of size $R=100$, but this occurs at a lower trap number of 24 traps in case of $r=2$ c.f. Figure 5a,b. One explanation for this result is that trap counts accumulate at a slower rate with increase in trap number—approaching saturation, but the underlying rates of decline vary between spatial arrangements. Also, for a large trap number over small areas of dispersal, the placement of any additional traps does not necessarily result in a substantial increase in captures, Figure 5a,b. To determine how these trap arrangements are ranked in terms of efficiency based on a site to trap size ratio requires further investigation, i.e. simulating trap counts whilst considering incremental increases in both *r* and *R* with varying rates of individual movement diffusion.

3.3 | Effect of movement diffusion

Based on the choice of movement parameters that reflect the locomotion of *P. melanarius*, a general observation is that trap counts rapidly increase with small increases in diffusivity at low diffusion values, followed by a peak, and a subsequent decline. In the cases of the grid and randomised arrangements, the decline is also relatively rapid and thus similar trap counts are obtained at both low or high levels of diffusion—which corresponds to whether movement paths are highly tortuous or not. In contrast, for the transect and nested-cross arrangements, the decline is gradual, and the differences in trap counts at both extreme ends are substantial. The peak occurs over a narrow diffusive range, between $D=0.28\,\text{m}^2/\text{h}$ ($c=0.6$, $S=2.74$) and $0.61\,\text{m}^2/\text{h}$ ($c=0.8$, $S=1.86$), and thus can be independent of the type of arrangement. Therefore, for *P. melanarius*, there is an approximate unique mode of activity (i.e. rate of spread) that translates to maximal trap counts (Figure 6).

4 | DISCUSSION

The theory behind the trapping of ground-dwelling arthropods moving randomly has been well developed (see e.g. Miller et al., 2015) and has often been tested and validated against empirical field studies (Adams et al., 2020; Bearup et al., 2016; Manoukis et al., 2014). Although numerical simulations provide a useful modelling framework, a key assumption in our study is that individuals are treated as homogeneous i.e. identical in terms of biological and physical characteristics in a constant environment, whereas real-world trapping contexts are more complex. In practice, capture rates can be influenced by various factors, e.g. heterogeneity in the population distribution, individual interactions, environmental or habitat differences, taxonomic groups, species, sexes and life stages (Hillen & Painter, 2013; Luff, 1975; Schmidt et al., 2006; Yamashita et al., 2010), albeit attempts have been made to standardise the trapping process to limit some of this variability (Brown & Matthews, 2016; Saska et al., 2021). The simulations could be developed further to account for these context-specific scenarios. Also, we expect that our results on optimal trap spacings and optimal spatial arrangements are applicable towards a population consisting of multiple ground-dwelling arthropod species from the same genus that exhibit random walking behaviour with similar movement

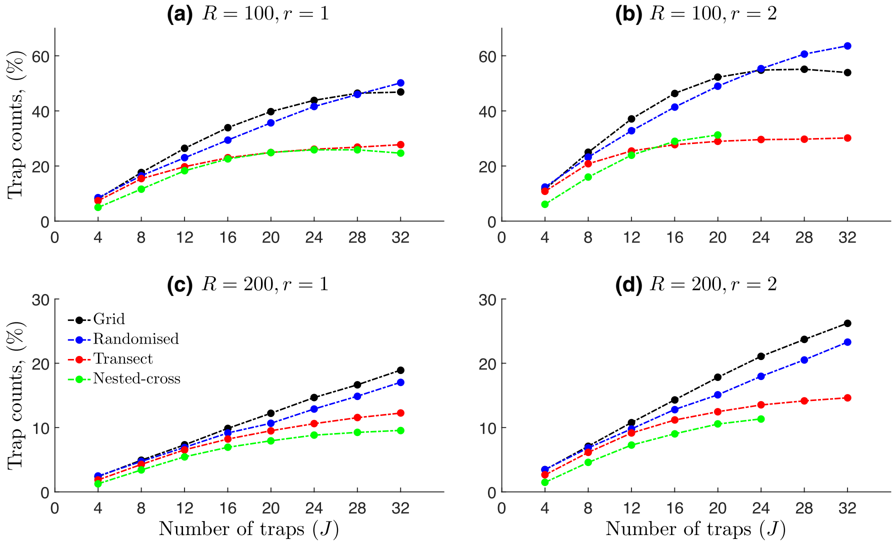

FIGURE 5 Trap counts computed for the different spatial arrangements with total number of traps $J=4, 8, 12, \ldots, 32$ with trap radius $r=1$ or 2, over a sampling area of sizes $R=100$ or 200. For the grid and transect arrangements, traps are separated at optimal distances d_{opt} computed from Equations (21 and 22), respectively. For the nested-cross arrangement, we use the optimal separation factor w_{opt} (computed with $x_1^*=4$), Equation (23). Note that these optimal values depend on the trap number *J*, trap size *r* and the size of the sampling area *R*, and thus varied across these different scenarios. In cases with a larger trap size (b–d), nested-cross arrangements were only possible with a lower trap number to ensure traps were placed within the confines of the sampling area. The initial population size prior to removal is $M^*=10{,}000$ individuals, and the movement type is a SRW with mobility parameter $\sigma=1$, and each individual executes at most $n=1000$ steps. These parameters are the same as that in Figure 4.

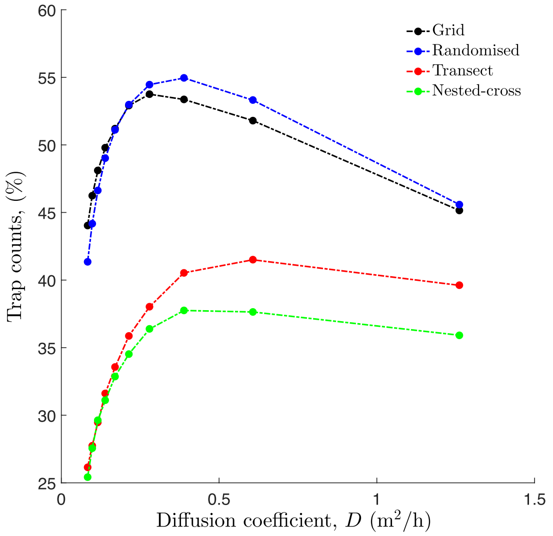

FIGURE 6 Trap counts as a function of movement diffusion for *Pterostichus melanarius* which ranges between $D=0.08\,\text{m}^2/\text{h}$ ($c=0$, $S=5.01$) and $D=1.26\,\text{m}^2/\text{h}$ ($c=0.9$, $S=1.29$), with step length scale $\sigma=0.1$ m, time increment $\Delta t=0.06$ h and step number $n=1000$. Trap counts are recorded after a maximum path length of $L=125.33$ m has been reached (Equations 9–11). We considered $J=24$ traps of radius $r=0.1$ m placed according to different spatial arrangements on a sampling area of size $R=10$ m, with optimal trap spacings: d_{opt} for grid (Equation 21), d_{opt} for transect (Equation 22) and w_{opt} for nested-cross (Equation 23).

traits and movement paths in a particular habitat. Nevertheless, this requires empirical validation under controlled field trials, or at least smaller-scale laboratory experiments.

4.1 | Trap spacing

Trap separation distances vary significantly in empirical field studies, ranging between 0.15 and 100 m, but the most common spacings used are 1–2 m, 5 m or 10 m (Hohbein & Conway, 2018; Ward et al., 2001). A standardised trap spacing of 10 m has been proposed based on reviews of pitfall trapping methods for arthropods (Hohbein & Conway, 2018), whereas others have suggested 50 m to minimise trap interference (Larsen & Forsyth, 2005). Our view is that these recommendations would benefit further from accounting for key variables such as trap size, sampling area size and the number of traps used.

Pitfall traps that are spaced widely apart have been observed to capture more individuals than traps placed closely together, e.g. 5 or 10 m inter-trap spacings resulted in more captures than 1 m (Digweed et al., 1995; Ward et al., 2001). Our simulation results in Figure 4 confirm this for all trap arrangements considered. It has also been stated that it may be desirable to increase trap separation by ensuring that there is an even coverage of traps over the entire sampling area (Woodcock, 2005). Although we found this to be the case for the transect arrangement (Equation 22), for the grid arrangement slightly more captures can be obtained if the inter-trap spacing is approximately 80% of that which maximises spatial coverage, and for the nested-cross arrangement, 90% of the maximum possible separation factor. Moreover, Equations (21–23 and 25) are generic and provide functional relationships for optimal trap spacings in terms of trap size, sampling area size and trap number. This is a novel and important development, as the effect of trap spacing on captures had thus far been poorly understood.

As an example, the activity and population density of *P. melanarius* was studied in a mark–recapture experiment with the use of 156 pitfall traps of diameter 60 mm ($r=0.03$ m) placed in a 12 by 13 grid arrangement over farmland with an effective sampling area of 8268 m^2 (Thomas et al., 1998). The inter-trap spacing used was 10 m along the north–south axis, and 5.3 m along the east–west axis, and was scaled due to the confines of the hedgerow. Assuming a homogeneous landscape with no barriers, we estimate from Equation (21) that a constant optimal trap separation distance is 5.04 m, in both the vertical and horizontal directions. Similar estimates can be obtained for other types of spatial arrangements, from Equations (22 and 23). Alternatively, if the size of the sampling area A is undefined, it can be estimated for a chosen separation distance d_{opt}, from Equation (24). For example, consider a grid with 16 traps placed in a $p=4$ by $q=4$ arrangement, with trap size $r=0.05$ m, and inter-trap spacing $d_{\text{opt}} = 5$ m, the effective sampling area is $A \simeq 556.4$ m^2 (corresponding to a radius $R=13.3$ m for a circular field, or side lengths 23.6 m for a square field).

This demonstrates the usage and applicability of these formulae, at least for species that exhibit random walk behaviour. Future studies should aim to develop formulae that accounts for variation in movement across individuals within the same species, or even among populations (Shaw, 2020) so that their trapping arrangements can be optimised. Also, these formulae can be utilised to investigate other important aspects of sampling design, such as, e.g. the minimum inter-trap spacing required to ensure that traps are spatially independent—which can, in turn, limit the number of traps placed over a predetermined sampling area.

4.2 | Trap number and spatial arrangements

Considerable research effort has focused on aspects of trap design, e.g. trap colour, material, shape, size, type of killing preservative (Boetzl et al., 2018; Cheli & Corley, 2010; Lange et al., 2011), leading to recommendations of a standard design (Brown & Matthews, 2016; Saska et al., 2021). In contrast, some studies have shown that sampling strategies can influence trap count interpretations (Baker & Barmuta, 2006; Perner & Schueler, 2004; Ward et al., 2001), but the impacts of spatial arrangements on capture efficiency remain unclear, even though some attempts have been made to address this knowledge gap (e.g. Crist & Wiens, 1995; Ellis & Bedward, 2014; Perner & Schueler, 2004).

An extensive review of pitfall trapping methods for estimating arthropod abundance reported that the most used arrangement is transect, followed by grid (Hohbein & Conway, 2018). Instead, we found that the grid and random arrangements are considerably better at maximising capture rates than both the transect and nested-cross arrangements when sampling within a homogeneous area, see, e.g. Figure 5a or d. If, however, hypotheses require sampling across narrow environmental gradients (e.g. along a river running down a mountain; Larsen & Forsyth, 2005), then a transect approach may still be preferred, but consideration as to whether this can consist of, for example, multiple grids, may optimise both aspects of the experimental design.

In the case of non-pitfall traps, it has been shown that the capture efficiency is similar regardless of whether traps are placed in a grid or at random (Byers, 1993). This is consistent with our simulation results, as the trap count differences amount to a few percent (see Figure 5e or f). We note, however, that even slight improvements in capture efficiency can help in high-risk contexts such as pests, invasive species or species of conservation concern that are damaging at low densities. In the case of frequent trap encounters with arthropods moving with the same diffusivity over smaller sampling areas, these differences can be substantial as saturation in captures occurs much faster for the grid, rendering the random arrangement more efficient (see Figure 5a or d).

Our focus has been on optimising capture efficiency, which has obvious applications for pest monitoring and removal; however, field ecologists may have other goals when undertaking trapping, e.g. how the placement of traps and their inter-trap spacings can affect the sampling duration to reach a minimum sample size, plateauing of capture rates (i.e. accumulation), trade-off between number of traps versus time deployed, distribution of captures across traps. The simulation methodology described in this study can be utilised to investigate these different lines of enquiries and could be a focal point in future studies.

4.3 | Arthropod movement

The trapping theory posed in this study is generic and could be applied towards various ground-dwelling arthropods given information about the species' locomotion. Arthropod movement data are usually recorded as a sequence of geo-coordinates of individual positions at regular time intervals (Cagnacci et al., 2010; White & Garrott, 1990). The movement path of a specific species can be modelled using RWs once probability distributions are fitted against distributions of observed step lengths and turning angles (Byers, 2001, 2009; Engel et al., 2017; Morales et al., 2004). Key parameters relating to the movement characteristics of the species such as the mean speed $E[v]$, the diffusion coefficient D and the sinuosity index S (Equations 10 and 11) can be directly computed from the statistical measures of these probability distributions. A simulation experiment can then be conducted for various trapping scenarios, resembling the trapping of this target species under different sampling strategies.

To connect our simulations to an ecological context, in Figure 6 we used parameters resulting in a mean speed representative of the ground beetle *P. melanarius*, and varied the strength of the forward persistence c in the movement paths. In our simulations, the diffusion coefficient and sinuosity index varied between $D=0.08\,\mathrm{m}^2/\mathrm{h}$, $S=5.01$ (corresponding to completely random motion, $c=0$) and $D=1.26\,\mathrm{m}^2/\mathrm{h}$, $S=1.29$ (in the case of high forward persistence, $c=0.9$; see Figure 6). This is consistent with empirical studies on the activity density of *P. melanarius*, where D is estimated to be around 1 and $1.16\,\mathrm{m}^2/\mathrm{h}$ (for females and males, respectively; Thomas et al., 1998). However, the movement of *P. melanarius* can be influenced by various aspects, internal and external, as has been previously documented in other carabid species. For instance, activity levels can vary if beetles are starved or satiated (Fournier & Loreau, 2001; Grüm, 1971), intermittency, e.g. periods of rest (Bailey et al., 2021), habitat characteristics (Allema et al., 2014; Goodwin & Fahrig, 2002; Růžičková & Veselý, 2018), possible competition with other species (Růžičková et al., 2021). We estimated that for *P. melanarius*, trap counts are maximised over a narrow diffusive range between $D=0.28\,\mathrm{m}^2/\mathrm{h}$, $S=2.74$ ($c=0.6$) and $0.61\,\mathrm{m}^2/\mathrm{h}$, $S=1.86$ ($c=0.8$). The reported D values indicate a faster rate of spread corresponding to a low level of path tortuosity, which, based on our calculations, can lead to a lower capture efficiency (Figure 6). Moreover, this also reinforces the fact that separating the effects of activity and population density for carabid beetles based on trap counts can be a challenging task (Thomas et al., 1998); for instance, in the case of the grid or randomised arrangements, similar trap counts can be obtained for *P. melanarius* that exhibits both low and high movement diffusion. Although we present the methodology to determine the impact of movement diffusion on trap counts, generalisations to other arthropod taxa require either testing for select species, or by considering a range of mean speeds (i.e. varied mobility) in the simulations.

The traps considered in this study are passive so that arthropods move completely independently and are not aware of trap locations. However, in practice, capture rates can be increased with the use of non-pitfall traps baited with a lure, e.g. odours, semiochemicals, sex pheromones or light (e.g. panel or multiple funnel traps, Lindgren, 1983; Miller et al., 2013; also see Byers, 1999; Byers et al., 1989; O'Hara et al., 2008). This is useful, for instance, in monitoring or for the direct control of arthropod pest populations at low densities (McCullough et al., 2011), or to detect foreign or 'exotic' pests as they invade a novel environment (Rassati et al., 2015). Once a trap is baited, and the arthropod population is receptive to the lure, the movement is locally biased towards the trap location and can be modelled as a biased and correlated random walk (BCRW; Benhamou, 2006; Codling et al., 2008, 2010). This provides a more flexible approach to modelling arthropod movement, as it allows individuals to move with both some knowledge of their previous direction, as well as with a preference towards a specific direction or target (Bailey et al., 2018). In this case, one can expect the strength of the global bias component to be dependent on individual location in reference to where traps are placed, with an increase in attraction closer to the traps. Analysis of baited trapping systems in the presence of multiple traps is under-studied from a modelling perspective and yet to be developed, albeit with some recent progress (see e.g.

Alqubori & Petrovskii, 2022), and is an important line of direction for future research work.

4.4 | Real-world examples for field applications

In community monitoring programs that is for the assessment of arthropod abundance and diversity, for practical reasons often a lower number of traps (around 8–12) are placed at small spatial scales, with smaller opening size $r = 0.05$ m (Brown & Matthews, 2016; Work et al., 2002). If 8 traps (4 by 2) are used covering an area of 50 m^2, the grid arrangement is the most capture efficient with optimal inter-trap spacing of 2 m from Equation (21), also see Figure 5. Similarly, this applies for 12 traps (4 by 3) over the same area with a trap spacing of 1.7 m from Equation (21). If, however, a transect arrangement is used, which is often the case to identify the effects of environmental gradients (Baker & Barmuta, 2006), the recommended trap spacing is 1.1 m for 8 traps, and 0.7 m for 12 traps, from Equation (22). Such information is translatable, and thus more broadly useful for developing effective sampling strategies, e.g. eLTER which aims to set up a pan-European pitfall trap monitoring scheme (Haase et al., 2018; Mirtl et al., 2018), and NEON (National Ecological Observatory Network) which is involved in large-scale pitfall trapping of ground beetles (Hoekman et al., 2017). For reference, c.f. the study on the community structure of darkling beetles *Eleodes* spp., where 80 traps were placed over an area of 638 m^2, equivalent to around 8 traps per 64 m^2 or 12 traps per 96 m^2 (McIntyre, 2000).

Besides focusing on entire arthropod communities with the use of pitfall traps, other types of non-pitfall traps are used to capture target species. For example, these species could be of conservation concern (rare and endangered species, Hoekman et al., 2017; Knapp et al., 2020; Martín-López et al., 2011) or important for pest monitoring and management (El-Sayed et al., 2006; Schlyter et al., 2001). Such target species are often either rare (i.e. endangered species or newly arrived invasive species currently occurring in low abundances) or highly abundant (i.e. invasive species requiring pest management). In either context, species can be targeted for several reasons, e.g. monitoring red list species for conservation purposes (The IUCN Red List of Threatened Species, 2022) or the direct control of pests can be achieved by mass trapping or lure-to-kill approaches (El-Sayed et al., 2006). In both cases, a higher number of traps are used. For instance, if we consider a trap location with an interaction distance of $r = 0.1$ m, and if 20 traps are placed covering an area of 50 m^2, the randomised arrangement is the most efficient, Figure 5b. If used, however, there would be a trade-off between increased capture efficiency and the additional effort required to locate traps for sampling.

4.5 | Broad applicability to other ecological problems

The results of this study are also relevant in other ecological contexts. For instance, trap cropping is a pest control strategy where non-host plant stands are installed to attract pests to reduce the pest density in the main protected crop (Banks & Ekbom, 1999; Hannunen, 2005; Holden et al., 2012). The capture efficiency of the trap crop system depends on the interplay between the physical design and the movement characteristics of the pests. The methods and simulation design presented in this study could be applied to determine optimal inter-trap crop distances, their placement and the effects of pest movement (diffusion, tortuosity), and thus contribute towards an optimal physical design for pest control. Analogously, 'sentinel plantings' of trees from a potential invaded range have been grown in the native range of some invasive insect pests to understand the likelihood of invasive species establishment and spread. This study's theory could help determine the distance between stands of sentinel trees (Britton et al., 2010).

Another example is for examining encounter rates between randomly moving animals and multiple immobile non-revisitable targets (Bartumeus et al., 2005; Gurarie & Ovaskainen, 2013; James et al., 2008). The study of encounters is fundamental to many ecological processes, e.g. searching for food items, suitable habitat patches or avoiding predators. Our study could provide insights on how the distribution of targets/resources impacts encounter or capture probabilities. In addition, the simulation methodology can be easily modified to incorporate revisibility so that individuals that encounter the traps are not removed from the population. With this, individuals continue to perform the RW, and can thus encounter traps multiple times during their movement—which directly relates to wildlife monitoring with the use of camera traps (Burton et al., 2015). This also has applications towards foraging efficiency (Viswanathan et al., 2011), that is the capacity for a predator to catch a prey within a detection radius *r*, which is equivalent to trapping by a circular trap with radius *r*, but after prey detection the predator reorientates and continues to move (Benhamou & Collet, 2015). This range of scenarios demonstrates the potential applicability of our numerical simulations (given some modifications) across several ecological contexts, and further contributes towards addressing problems arising in contemporary spatial ecology.

AUTHOR CONTRIBUTIONS

Danish A. Ahmed conceived the ideas and designed methodology; Danish A. Ahmed and Ayah Beidas conducted the numerical simulations; Danish A. Ahmed led the writing of the manuscript. All authors contributed critically to the drafts, providing important ecological context to interpret the results and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All illustrations and MATLAB simulation codes are publicly and freely available on GitHub at https://github.com/daa119/pitfall_trapping and Zenodo at https://doi.org/10.5281/ZENODO.8033956 (Ahmed, 2023).

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