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Towards transient space-use dynamics: re-envisioning models of utilization distribution and their applications

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Abstract

Background Models of utilization distribution in the form of partial differential equations have long contributed to our understanding of organismal space use patterns. In studies of infectious diseases, they are also being increasingly adopted in support of epidemic forecasting and scenario planning. However, as movement research shifts its focus towards large data collection and statistical modeling of movement trajectories, the development of such models has notably slowed.

Methods Here, we demonstrate the continued importance of modeling utilization distribution to predict variation in space-use patterns over time. We highlight the considerable, yet largely untapped, potential of such models, which have historically been limited by the steady-state assumption due to longstanding technical constraints. Now, by adapting existing computational tools primarily developed for material science and engineering, we can probe beyond the steady states and unlock from them a broad spectrum of complex, transient space-use dynamics. Our approach requires little experience in numerical analysis and is readily accessible to model practitioners in ecology and epidemiology across diverse systems where movement is a critical feature.

Results We illustrated our approach using a mix of canonical and novel case studies, covering topics from wildlife translocation to vaccine deployment. First, we revisited a classical model of canid territorial formation driven by scent-mediated conspecific avoidance. Transient space-use analysis uncovered previously hidden spatial dynamics that are ecologically informative. Next, we applied our approach to long-distance movement on realistic landscapes. Habitat and land-use heterogeneities markedly affected the transient space-use dynamics and short-term forecasts, even when the steady state remained unchanged, with direct implications for conservation management. Finally, we modeled transient space-use dynamics as both a response to and a driver of transient population dynamics. The importance of this interdependence was shown in the context of epidemiology, in a scenario where the movement of healthcare personnel is influenced by local outbreak conditions that are stochastically evolving.

Conclusions By facilitating transient space-use analysis, our approach could lead to reevaluations of foundational ecological concepts such as home range and territory, replacing static with dynamic definitions that more accurately reflect biological realities. Furthermore, we contend that a growing interest in transient space-use dynamics, spurred by this work, could have transformative effects, stimulating new research avenues in ecology and epidemiology.

Keywords Utilization distribution, Transient dynamics, Space-use pattern, Home range, Territory, Disease ecology, Epidemiology

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Background

Historically, quantitative studies of animal movement in the context of ecology have frequently focused on capturing animal space-use patterns, i.e., the geographic region where individuals or groups are likely found. Among the common measures of space-use pattern (e.g., minimum convex polygon, local convex hull), utilization distribution (UD) holds particular importance in the development of animal movement theory. A UD explicitly describes an individual's probability of being at a location at any given time [1]. It is conventionally used to quantify area-restricted space-use patterns, i.e., a home range or a territory, that one or multiple animals presumably form and maintain during the study period.

Models of UD have been extensively developed to understand the relationship between specific movement mechanisms and the spatial structure of UD [1–3]. Most early models follow basic principles of statistical mechanics and are formulated as Fokker–Planck equations, a class of partial differential equation that describes how a probability density function, e.g., a UD, evolves over time. In the past three decades, they have deepened our insights into the causes, processes, and ecological consequences of animal movement and gave mechanistic explanations to widely observed phenomena such as territorial separation [4, 5], predator–prey distribution [6], and home range expansion/contraction [7]. In an era when acquiring accurate movement data was both prohibitively expensive and technically challenging, these mechanistic (“classical”) space-use models played a critical role in laying the theoretical groundwork that gave rise to the modern field of movement ecology.

At the start of the millennium, major advances in biologging and tracking technology facilitated a surge in high-resolution movement data [8, 9]. As the collection of these data became more accurate and cost-effective, the emphasis in movement modeling shifted from predicting space-use patterns to estimating actual movement trajectories (or paths). Concurrently, the development of statistical movement models accelerated, filling missing details in movement trajectories often by integrating additional data streams, including biometrics, meteorological data, and habitat indices [10–12]. New frameworks for statistical modeling emerged, including state-space models [13, 14], resource-selection analysis [15], and integrated step-selection analysis [16], all of which are adept at inferring key determinants of movement decisions and predicting changes in movement trajectories (see [17] and references therein). The application of Fokker–Planck equations shifted as well, simple expressions, for instance, ones that exclude non-diffusive movement, are now routinely used as process models in a hierarchical Bayesian setting, fitted to observational data to predict population

and disease spread [18–20]. In contrast, classical space-use models and, by extension, the interest in forecasting UD, appear to have receded from the mainstream of movement research (but see [21, 22]).

Nevertheless, UD as a concept remains essential for gaining a holistic view of an animal's spatial behavior [3, 23, 24]. Rather than pinpointing the exact locations of a given individual over time, UD provides a comprehensive measure that can encompass the entire space an individual might occupy over a timescale much longer than the observation period. UD may also describe a space occupied by multiple individuals, both observed and unobserved, sharing similar movement behaviors. In essence, it represents the aggregate outcome of many realized and potential movement trajectories. Because a UD inherently accounts for a large number of possibilities, the resulting inferences are less susceptible to the confounding effects of process randomness and measurement errors that commonly affect trajectory estimation. UD are therefore well-suited for drawing ecological generalities, which may inform conservation strategies for managing hypothetical, future scenarios not yet empirically studied.

Beyond ecological applications, UD has become a useful tool in predicting and managing the spread of infectious diseases [25–29], functioning similarly to the concept of activity space [30]. Unlike in wildlife ecology in which the interest primarily lies in estimating where an animal is most likely present, disease ecology and epidemiology are generally motivated by risk assessment, an objective that requires knowing not only areas where hosts tend to visit, but also less frequented areas where transmission potential is elevated due to spatial and demographic factors (e.g., contact structure, geographic variations in pathogen viability, local seroprevalence, localized behaviors). By encompassing areas that hosts rarely visit, UD predictions enable us to identify high-risk areas that are difficult to detect from population monitoring alone. Moreover, policy decisions in response to a novel outbreak often need to be made amidst information uncertainty, including a lack of movement data that could have implications for management decisions and success. Indeed, current studies suggest that modeling UD based on simple, general movement assumptions could help optimize surveillance systems in spillover prevention [31] and inform deployment strategies in vaccine rollout [32]. As more movement and mobility data are incorporated into disease forecasts, the use of UD in disease modeling will likely grow in the coming years.

In recent years, much of the progress in our understanding of UD has been driven by statistical ecology. While traditional UD estimation methods, notably kernel density estimator (KDE) and convex hull-based

approaches (e.g., minimum convex polygon), do not explicitly account for temporal information in movement data, vastly improved versions are now widely available. For example, autocorrelated KDE (AKDE) addresses an individual's positional autocorrelation and involves methods that could characterize non-stationary space use [33, 34], temporal adaptive KDE (TAKDE), on the other hand, applies a sliding window mechanism to achieve real-time UD estimation [35]. Comparatively, PDE-based models, a “principal workhorse” that can predict variations in both space and time in a unified manner [22], have been under-exploited. Yet, they offer several distinct benefits: the equations provide clearly defined movement mechanisms in relation to biotic and abiotic factors; the models facilitate the detection of emergent properties of complex ecological systems; and perhaps more importantly, the framework is fundamentally predictive, hence, it can support the forecasts of species responses to global change. In this study, we adopt a PDE-based approach and highlight the need for a renewed focus on this classical modeling framework.

In classical space-use models, UDs are generally characterized solely by the steady-state (equilibrium) solutions, depicting the stabilized space-use pattern as time approaches infinity. Transient (nonstationary) UD dynamics, i.e., how the pattern evolves over time *before* stabilization, were seldom explored. This gap stems partly from the significant technical challenges involved in obtaining the transient solutions of Fokker–Planck equations, a nontrivial task that required substantial expertise in numerical analysis ([refer to Box for prior efforts to circumvent these challenges](#)). Nonetheless, increasing evidence suggests that space-use patterns exist mostly in a state of transition [7, 36, 37]. By predominantly focusing on the steady states, previous models may have overlooked significant amounts of transitional details. The problem becomes more pressing in light of recent studies suggesting that forecasts of transient, sometimes short-lived, space-use patterns can better inform conservation and outbreak management actions than static, long-term forecasts [38, 39]. For example, when controlling newly invading pest animals, predicting their transient space-use dynamics, e.g., slow diffusion immediately after introduction followed by rapid dispersal [40], can reveal a brief grace period in which spatially targeted interventions are highly effective.

As is evident from numerous publications (e.g., [39, 41–43]), the importance of modeling transient dynamics is widely acknowledged in population, community, and disease ecology. Here, we extend the discussion to movement ecology with the goal of cultivating new perspectives and promoting real-time forecasts of movement-driven systems [39, 44]. In particular, we

demonstrate that, without transient analysis, the full potential of UD remains largely untapped.

In this paper, we modeled transient UDs mechanistically in the classical framework, free from the conventional constraints of steady state. The models can capture an individual's probable locations at any time-scale, including its long-term area coverage. By giving a consistent interpretation of UD independent of time, we effectively bridged two opposing concepts in statistical ecology: occupancy distribution and range distribution [33]. Our approach is computational, mathematically tractable, and broadly accessible. Spatially explicit, complex interactions, e.g., stigmergy [45], can be readily represented in the model equations, which are solvable over arbitrary duration and spatial domain. Using only basic movement information, we may generate temporally detailed space-use forecasts. This low input requirement enables powerful inferences even when empirical movement data is sparse or of inconsistent quality, situations where statistical movement models are greatly disadvantaged.

Re-envisioning models of UDs from the perspective of transient dynamics motivate new lines of research. For instance, by charting the system's behavior over time, transient solutions permit investigation into the relative timing of movement-related phenomena. To demonstrate, we revisit a classical space-use model built on the assumption of scent-mediated conspecific avoidance [5, 46, 47], questioning whether scent marks will continue to accumulate after territories have been established. Additionally, hidden dynamics in classical space-use models can now be unlocked in search of general patterns. We illustrate this by uncovering new dynamical features from the previous example, modeled at a higher spatial dimension and with more individuals.

Transient space-use analysis can also support environmental impact assessment, particularly in conservation. Environmental disturbances such as extreme weather events or local resource depression often exert negligible long-term impacts on an animal's space-use pattern or bear little relevance to immediate management decisions. Instead, impacts over shorter, more ecologically relevant timescales may be far more pronounced and even meaningful [48, 49]. We demonstrate this scenario by modeling an individual as it travels, while foraging, across a heterogeneous landscape, and then assessing the differences in transient space-use patterns with and without land use changes.

Transient space-use dynamics can simultaneously be a response to and a driver of transient population dynamics in space [50, 51]. Modeling this cross-scale interaction between the movement of individual units and population densities has diverse applications. As an example, to

control an epidemic, decision-makers may need to adapt the deployment strategies for healthcare workers to take into account local outbreak intensities (densities of new infections). What movement rules to follow once the workers are in the field, e.g., prioritizing the protection of regions most at risk, might critically influence overall response effectiveness [52]. We explore this sample question by modeling the deployment of a vaccination team into a human population experiencing an outbreak, using a classical space-use model in conjunction with stochastic, agent-based simulations.

Our approach to finding transient solutions employs FiPy, an actively maintained, open-source PDE solver that can be applied to a wide range of Fokker–Planck equations. Alternative PDE solvers and their attributes are listed in Supplementary Information for further reference. Our case studies offer detailed examples of transient space-use analysis at a level of abstraction appropriate for most ecologists and epidemiologists with respect to numerical expertise. To demonstrate the degree of spatial complexity and insights achievable even with simple movement mechanisms, we limit our case studies to systems where all individuals display a centralizing tendency and directional preferences toward single fixed-point attractors.

Box: Competing approaches to modeling transient space-use dynamics

Agent-based models are another common approach for modeling individual-level movement processes (e.g., [71]). They simulate the movements of one or more individuals on a finite landscape, the step length and direction of each movement decision can be determined by ecological interactions as well as by spatial memory (see [72, 73]). Because a UD represents the full probability distribution generated by an infinite number of simulation replicates, each yielding a unique movement trajectory, a sufficiently large number of replicates must be run to gain a clear, representative picture of how individual space-use patterns emerge over time, a process that is computationally prohibitive. In practice, transient dynamics data are frequently discarded from the main analysis when exploring UDs (but see [38]).

Some recent agent-based models have directly addressed transient space-use patterns. For example, by characterizing movement as random choices amongst nearest-neighbor lattice sites, excluding those that contain repellent environmental cues, i.e., conspecific scent marks, Potts et al. [50] demonstrated long-term instability along UD boundaries (territorial borders). This model can be subsequently reduced to a set of mean-field PDEs that analytically relate specific

behavioral parameters (i.e., scent-marking rate) to summary spatial statistics (i.e., the diffusion constant of a territory border). Yet, the mathematics are incompletely understood and the analysis is technically demanding, making these models unwieldy for data fitting and hypothesis testing (but see [22] for recent advances).

In contrast to agent-based models, classical space-use models explicitly describe how a UD will evolve according to specific movement mechanisms, including group attraction and repulsion, topographical resistance, and habitat selection [3]. There, its time derivative is expressed as a Fokker–Planck equation, a modeling approach that has appeared in both discrete and continuous forms in the seminal works by Okubo [74] and Moorcroft and Lewis [1]. However, solving the Fokker–Planck equation over time (i.e., obtaining the transient UDs) is often nontrivial, whether approached analytically or numerically. As a result, modelers have conventionally adopted the simplifying steady-state assumption by setting the time derivative to zero before solving the equation.

Analyzing the existence and stability of steady states can provide insights into transient dynamics [75, 76]. Common techniques include linear analysis, amplitude equation formalism [77], and the use of energy functional minimizers [78]. Their findings are typically validated through numerical simulations starting with a small perturbation of a steady state. Although such perturbations will eventually decay, they may initially grow rapidly and persist for extended periods, resulting in long transients. The maximum instantaneous rate at which perturbations are amplified is measured by reactivity [79]. In contrast, resilience measures how quickly a stable system returns to its original state after being perturbed [80], that is, the duration of transients. Together, reactivity and resilience describe solution behavior at the temporal extremes, i.e., as time approaches zero (present) and infinity (distant future), respectively. Neither metric captures the entire range of transient behavior between these extremes. This limitation is particularly evident in movement research, such as studies examining changes in an animal's space-use pattern following translocation, where the dynamics of interest might not be reflected in the system's asymptotic behavior.

Several models have addressed these shortcomings of steady-state analysis by approximating transient UDs through a concatenation of sequential steady states, each computed numerically under a unique set of parameters that represents the environmental condition at a specific time [4, 7, 47]. More recently,

these analyses have been enhanced through the use of numerical continuation methods [81]. However, these models implicitly assume that UD's stabilize more quickly than any fundamental changes in their underlying movement behaviors, implying a rate inequality that is possibly unrealistic [82]. The solutions likewise represent only the present ($t = 0$) and long-term ($t = \infty$) states of the system, omitting what occurred in the interim.

Methods

Classical space-use models require descriptions of the underlying movement behavior (e.g., step length, turning angle) and local responses to environmental conditions (e.g., preference for resource-rich habitats, avoidance of foreign scent marks). In animal home range and territory models, these mechanisms are typically described as a combination of random and directed movements in a Fokker–Planck equation:

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = \nabla^2 [d(\mathbf{x}, t)u(\mathbf{x}, t)] - \nabla \cdot [c(\mathbf{x}, t)u(\mathbf{x}, t) \vec{\mathbf{x}}] \quad \text{Transient term} \quad \text{Random movement} \quad \text{Directed movement} \quad (1)$$

where $u(\mathbf{x}, t)$ denotes the individual's UD at time t , and $\vec{\mathbf{x}}$ is a unit vector indicating the direction of the mean center of attraction relative to the individual's current position. In the simplest case where a central point attractor is the only source of movement bias, the local strengths of random and directed movements at time t , as represented by the diffusion term $d(\mathbf{x}, t)$ and the advection term $c(\mathbf{x}, t)$, may be reduced to constant coefficients d and c . Here, a steady-state UD can be derived analytically [1, 7], assuming that the individual moves in a radially symmetric manner within a finite two-dimensional landscape Ω with zero-flux boundary condition.

Transient solutions of a Fokker–Planck equation typically need to be found using numerical techniques. FiPy (www.ctcms.nist.gov/fipy), developed for material science research by the National Institute of Standards and Technology (NIST), is a powerful PDE solver based on standard finite volume method that we can leverage to uncover transient UD's [53]. Written in Python, FiPy inherits the language's growing usage, easily legible syntax, and extensibility across its large libraries of algorithms for scientific computing (e.g., NumPy, SciPy) and visualization (Matplotlib). It solves PDEs by reformulating the values of the dependent variable into discrete points on a meshed domain. The original PDE, thus reduced to a linear set of algebraic equations, can then be efficiently solved as a sparse matrix using an iterative

scheme. The temporal solutions of the equation are contained within the cells that constitute the mesh.

Background on numerical PDE solver

Several methods and tools for solving PDEs are available today (see Table in Supplementary Information). Many are impractical for use by movement modelers who wish to work at a high level of mathematical abstraction without being overwhelmed by details of numerical analysis. Some proprietary solvers (e.g., built-in toolboxes in MATLAB and Mathematica) are widely adopted, but they can be costly and lack versatility. There are also several R-based options, which may be more syntactically familiar to many quantitative ecologists. A popular solver is deSolve [54], which uses the method-of-lines (MOL) approach instead of finite volume or finite element methods. It works by first discretizing only the spatial components of a PDE, then approximating the equation with a system of ordinary differential equations that are solved forward in time. MOL produces fairly accurate solu-

tions for 2-dimensional advection-diffusion problems [55], however, it is incapable of handling elliptic PDEs, i.e., when the time derivative is removed. Thus, it cannot be used to compare transient dynamics with respect to steady-state solutions unless the latter were already known in their analytical forms (but see R packages ReacTran and RoosSolver [54]).

In the Python environment, FiPy is a well-established solver that comes with easy customization, relatively short set-up time to program, open-source nature, and the capability to handle arbitrary combinations of elliptic, hyperbolic, and parabolic PDEs. Solution precision in FiPy can be further enhanced through a “sweeping” procedure. The overall runtime can also be shortened through parallel computing by exploiting third-party packages (e.g., PETSc, Trilinos). Models of three-dimensional space use in studies of avian and marine ecology, or those that require more topographically realistic spatial domain, can employ polygonal meshes constructed by Gmsh. Compared to several R-based methods, FiPy accommodates greater model complexity while requiring fewer lines of code to implement (Supplementary Information).

Transient space use can be modeled on a landscape that is either homogeneous or heterogeneous, incorporating physical barriers (e.g., [56]) and resource fragmentation (e.g., [57]). In our models of transient space-use dynamics, we assumed movement is limited inside a bounded landscape Ω with reflective edges, thus ensuring that the

area integrations of all UD solutions are maintained at unity. We defined Ω by constructing a mesh of either one- or two-dimensional space that consists of equidistant grid cells. At each time step, local UD solutions are determined at the cell centers, and the values between adjacent cells are estimated as flux across their boundaries (i.e., faces). When configuring the landscape, it is important to decide on the tradeoff between spatial and temporal resolutions. According to the Courant–Friedrichs–Lewy (CFL) criterion (see [58]), increasing the spatial resolution (i.e., number of grid cells) shortens the maximal allowed time-step size, thereby increasing the computational time. Placing the point attractor at a cell center helps to keep the solutions robust to approximation error even under relatively low spatial resolution.

We optimized the precision of our UD solutions by testing different approximation schemes that are available for discretizing the advective term in the Fokker–Planck equation. In all our analyses, we adopted the explicit Van Leer flux splitting method, which we found to outperform many alternatives. Hybrid, powerlaw, and related exponential-difference schemes, are arguably more versatile but have been criticized for giving qualitatively erroneous solutions under misalignment between the main advective direction and the mesh coordinates [59].

We demonstrated our modeling approach using both classical and new case studies.

Results

Case study 1: extending mechanistic home range (territory) analysis

We may obtain transient solutions of classical space-use models with well-known steady-state solutions. As an example, we revisited the scent-mediated territory formation model [1, 5], in which two individuals, U and V, deposit scent marks in mutual defense against foreign encroachment near their respective den sites at opposite ends of the landscape. Encounter with foreign scent marks causes one to a) “over-mark” at a rate proportional to the local density of foreign scent marks, and b) gravitate more toward its den site. On a one-dimensional landscape, this system can be modeled as follows:

$$\begin{aligned}\frac{\partial u(x, t)}{\partial t} &= d\nabla^2 u(x, t) - c\nabla \cdot [u(x, t)\tanh(\alpha|x - x_u|)\vec{x}_u q(x, t)], \\ \frac{\partial v(x, t)}{\partial t} &= d\nabla^2 v(x, t) - c\nabla \cdot [v(x, t)\tanh(\alpha|x - x_v|)\vec{x}_v p(x, t)], \\ \frac{dp(x, t)}{dt} &= u(x, t)[1 + mq(x, t)] - p(x, t),\end{aligned}$$

$$\frac{dq(x, t)}{dt} = v(x, t)[1 + mp(x, t)] - q(x, t). \quad (2)$$

Here, $u(x, t)$ and $v(x, t)$ represent the two individuals' UD. ∇ and ∇^2 express their drift and diffusion processes. \vec{x}_u and \vec{x}_v are unit vectors pointing towards their exclusive den sites, x_u and x_v . The inclusion of the hyperbolic tangent function removes the mathematical discontinuities at the point attractors, thereby reducing numerical noise; α controls the smoothness of step transition between opposite-signed unit vectors. $p(x, t)$ and $q(x, t)$ are nondimensionalized scent-mark densities associated with U and V, respectively; deposited marks decay at a unit rate over time. m denotes the strength of the over-marking in response to foreign scent marks. Temporal variations in scent-mark densities are governed by ordinary differential equations.

We initialized both individuals using the same UD centered at the origin (mimicking wildlife translocation) and ran the model forward in time. Note that although our model parameters are dimensionless, in practice, they can be specified in compatible units. For example, c can be measured in km per day, d in km² per day, and the domain size in km². The sequential UD solutions then represent space-use variation across fractional days. If we assumed these units in our model, under the constraint of the CFL criterion, each time step would last around 0.0014 day (2 min) and the terminal time (time step 10,000) would correspond to roughly 14 days. Finally, we examined the system's convergence toward previously published steady-state solutions.

Our numerical solutions showed that the two scent-avoidant individuals released from the same site will eventually reach the steady-state UD solutions (Fig. 1). The space-use patterns recreated the classic findings in White et al. [5] and Moorcroft and Lewis [1]: there exists a mutually avoided area separating the territories (a “buffer zone”), which is maintained by collective scent marks.

The transient UD solutions revealed additional details (Fig. 1). They showed that the buffer zone appeared relatively early during the process of territorial separation (Fig. 1e). Surprisingly, each animal briefly increased its presence in areas close to its rival's den site, before rapidly retreating once the owner's markings began to accumulate (Fig. 1e–h). We further observed that, over time, the interior of each territory is used more uniformly, and the activity level inside the buffer zone may also increase (Fig. 1g–i). Finally, the build-up of scent marks inside the buffer zone continues long after both UD solutions have stabilized (Fig. 1j–l). This suggests that, by measuring the markings directly, e.g., using chemical assays or biomarkers, one may estimate territory persistence, which could be indicative of population viability.

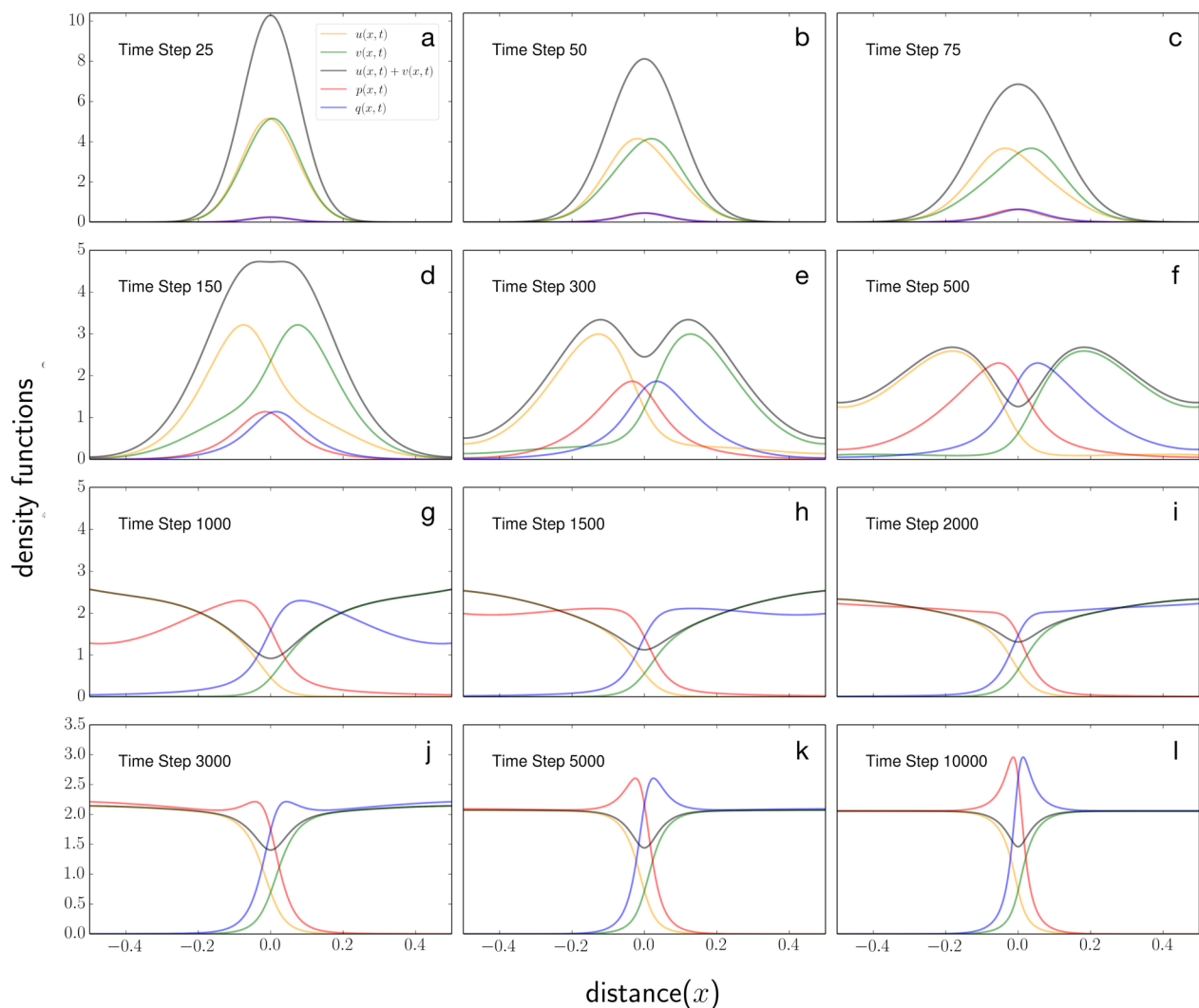


Fig. 1 Territorial separation of two individuals (or individual packs) on a one-dimensional landscape in avoidance of scent marks deposited by one another in the environment. Den sites are located at the two ends of the landscape. The yellow and green lines represent the individual UD's; their sum is shown in black. The respective individual scent-mark densities are displayed by the red and blue lines. The process of spatial segregation during the initial 10,000 time steps post-release is captured by the transient UD dynamics; mutually deterrent boundary markings continue to accumulate long after space-use convergence

We can also expand the model to four territorial individuals interacting on a two-dimensional landscape, all initialized at the origin with a bivariate normal UD and moving toward separate den sites under the same set of behavioral parameters (Fig. 2). At this higher spatial dimension, with a larger population size, we observed the emergence of a ring-like scent-mark distribution, which quickly disappeared as the system approached its steady state (Fig. 2d–f). In scenarios where scent marking is accompanied by pathogen shedding (see [60]), this result suggests that transient disease hotspots may form, potentially sparking cryptic outbreaks.

Case study 2: incorporating heterogeneous landscape structures

The role of landscape heterogeneity (e.g., terrain steepness, resource gradient) in determining space-use patterns has been repeatedly explored in mechanistic home range models [4, 47, 61]. However, these studies placed little emphasis on space-use patterns beyond the vicinity of the steady-state UD. How landscape changes might accelerate, delay, or even prevent the realization of the expected UD has typically been left unanswered.

In these examples, we tracked transient UD's on heterogeneous landscapes. As in Case Study 1, transient analyses are useful for exploring space-use dynamics of

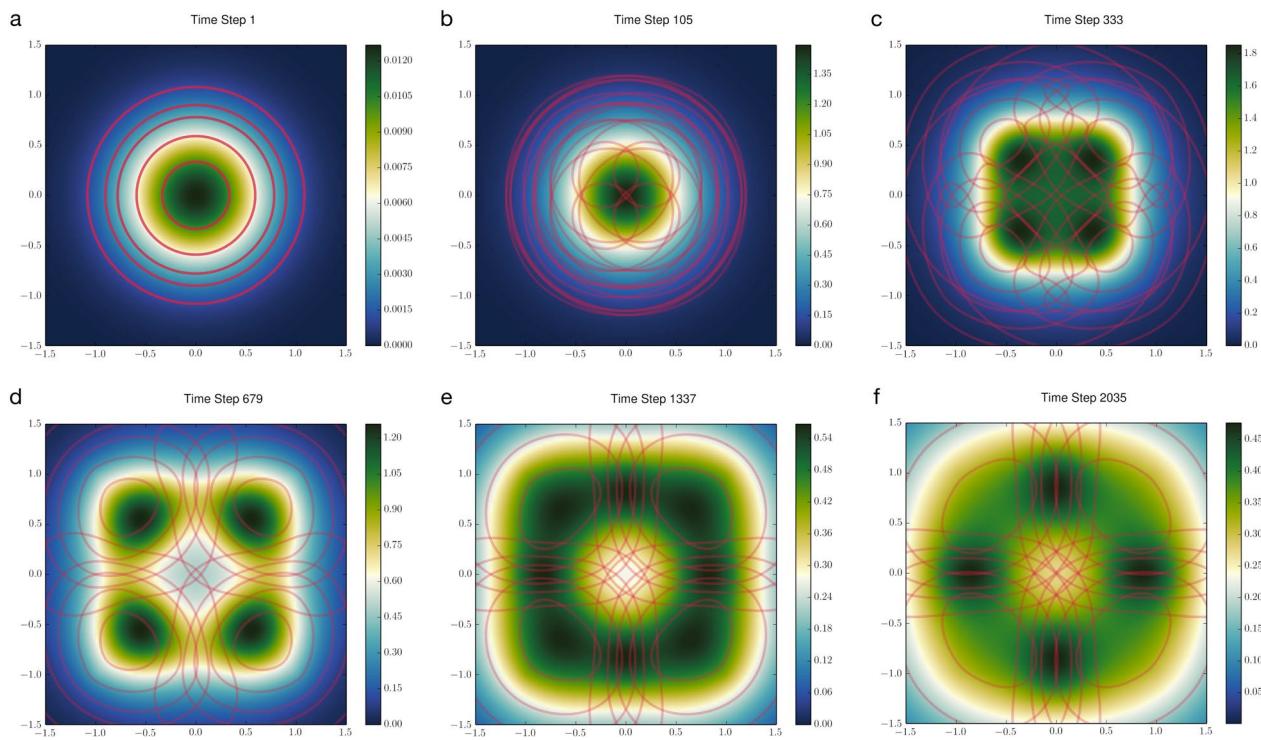


Fig. 2 Territorial separation of four individual (or individual packs) on a two-dimensional landscape in avoidance of scent marks deposited by all others in the environment. Den sites are located at $(\pm 1, \pm 1)$. Red lines are contour maps illustrating each individual's UD at the 20%, 50%, 70%, 80%, and 90% probability levels. The color gradient shows the accumulative scent-mark densities

translocated wildlife. We defined our model domain Ω as a physical landscape with spatially fragmented resource distribution. At the start of each model, a group of individuals, with initial locations characterized by a bivariate normal UD, began relocating to an arbitrarily located home range center \mathbf{x}_u , which acts as a point attractor. The individuals move at a speed $\lambda(\mathbf{x})$ that decreases with local resource density, reflecting increased residence time in resource-rich areas. This common behavior can be described by a simple equation derived from a continuous-time, correlated random walk that combines diffusive foraging and site-fidelity, i.e., an Ornstein–Uhlenbeck process [62]:

$$\begin{aligned} \frac{\partial u(\mathbf{x}, t)}{\partial t} &= d_0 \lambda^2(\mathbf{x}) \nabla^2 [u(\mathbf{x}, t)] \\ &- c_0 \lambda(\mathbf{x}) \nabla \cdot [u(\mathbf{x}, t) \tanh(\alpha |\mathbf{x} - \mathbf{x}_u|) \vec{\mathbf{x}}], \end{aligned} \quad (3)$$

d_0 and c_0 are the baseline diffusion and advection coefficients associated with $\lambda(\mathbf{x}) = 1$. Solving for the transient UD on our realistic landscape unfolded a complex series of space-use patterns that clearly illustrated the group's behavioral adaptation to resource availability (Fig. 3). For a brief period, two distinct UD 'nuclei' appeared: one at \mathbf{x}_u , and the other at a site some distance away (Fig. 3d).

Next, we introduced linear landscape elements to the model. In this scenario, the group faces a set of identically shaped, equally spaced movement barriers, a configuration that resembles a transecting roadway with multiple overpasses. The landscape is thus further divided into permeable and nonpermeable regions. The domain becomes $\Omega = \{\mathbf{x} | \mathbf{x} \in \Omega_T\}$, where Ω_T denotes the permeable region that is contiguously traversable. A zero-flux boundary condition was imposed on both the outer and the inner boundaries $d\Omega_T$.

From the results (Fig. 4), we observed the potential of movement barriers in creating situations where, at times (Fig. 4d), the spread of likely locations (90% probability contour) covers nearly a fourth of the landscape. Since an animal's travel time often correlates with its exposure to predation and other hazards [63], our predictions of transient UD can help inform management decisions on where and how to build movement corridors to maximize the survivorship of the target individuals.

Case study 3: integrating space-use and population dynamics

PDEs are most appropriate for modeling continuous-time space-use patterns of individuals in an environment

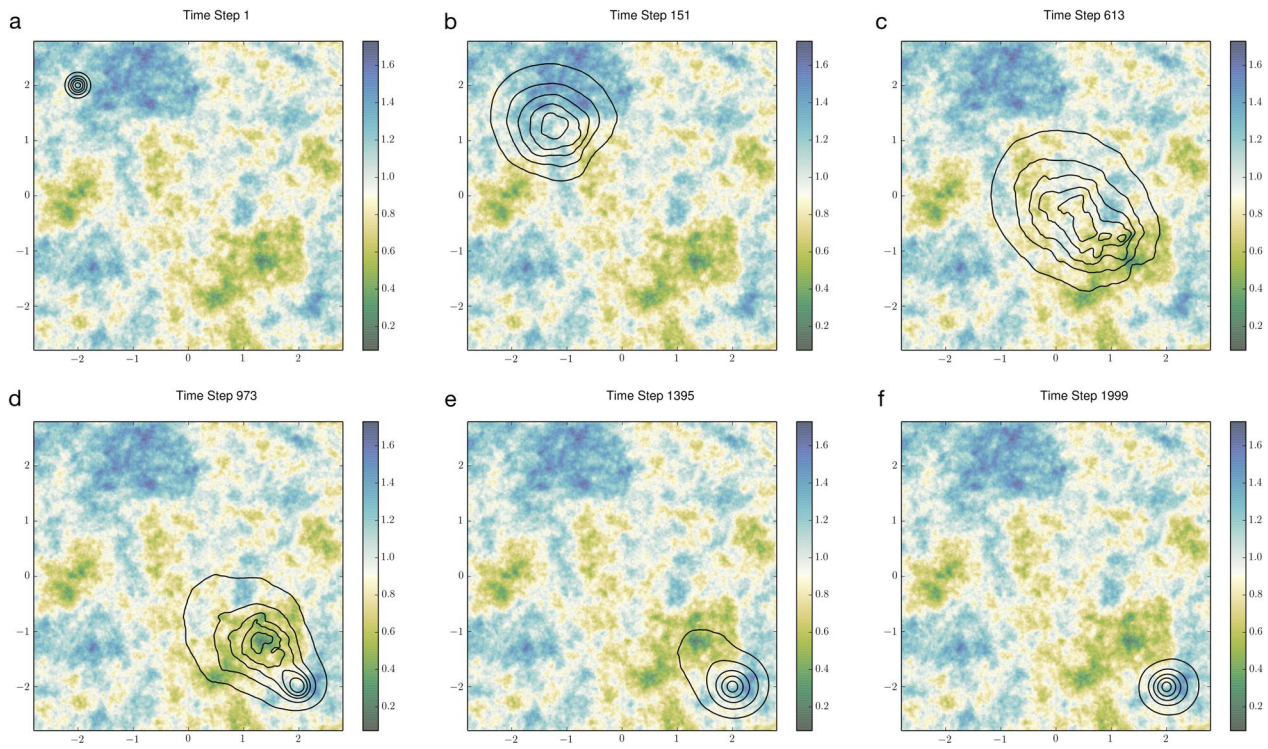


Fig. 3 Transient space-use dynamics over the course of home range relocation on a 2D heterogeneous landscape. The movement mechanism follows a Fokker-Planck equation with spatially dependent advection and diffusion terms. A point attractor is situated in the lower-right corner (2, -2). Black lines show contour levels of the individual's UD at 10%, 30%, 50%, 70%, and 90% probabilities. The color gradient illustrates the spatial distribution of local movement speed (a negative proxy for local resource availability), generated as a Gaussian field with an exponential variogram model (partial sill = 0.05, spatial correlation range = 25). The individual was assumed to slow down to forage in resource-rich patches (green) and speed up in resource-poor patches (blue)

where the locations of movement attractors, deterrents, corridors, and barriers are either constant or vary over time in a deterministic manner. However, at a population scale, discrete stochastic events often occur due to demographic processes (e.g., births, deaths) and disease outbreaks (e.g., infection, recovery), which can lead to changes in individual movement behavior at random times and locations; moreover, future population-scale events might, in turn, be altered by these very changes [39, 64]. To capture such feedback, we introduced a hybrid method that iteratively models transient UD in response to the simulated outcomes of a spatial agent-based model (ABM), while simultaneously simulating the ABM based on system conditions established by the transient UD.

We demonstrated this approach by considering a house-to-house vaccination campaign at the onset of a novel outbreak. The model assumes that the vaccine is being distributed across a two-dimensional landscape via diffusive movement of a single unit of healthcare personnel from a central point of deployment \mathbf{x}_u . To enhance vaccination coverage, personnel movement was guided by two simple rules: 1) slow down in areas with

many susceptible individuals to vaccinate, and 2) withdraw from areas with high disease prevalence, i.e., where infected individuals are numerous. The personnel's UD is governed by the following equation:

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = d_0 e^{-S(\mathbf{x}, t)} \nabla^2 u(\mathbf{x}, t) - c_0 I(\mathbf{x}, t) \nabla \cdot [u(\mathbf{x}, t) \tanh(\alpha |\mathbf{x} - \mathbf{x}_u|) \vec{\mathbf{x}}] \quad (4)$$

d_0 and c_0 are baseline rates of diffusion and advection. $S(\mathbf{x}, t)$ and $I(\mathbf{x}, t)$ represent the local densities of susceptible and infected individuals at time t , respectively. These densities are obtained by convolving the spatial distribution of agents for each disease status with a bivariate normal contact kernel.

As $u(\mathbf{x}, t)$ evolves over time, transmissions occur stochastically between infected and susceptible individuals at times $t = t' = (i - 1)\tau$, where $i = 1, 2, \dots, n$ and τ is the interval between consecutive ABM time steps. The probability that a susceptible individual becomes infected is given by:

$$\varphi(\mathbf{x}, t') = 1 - \exp[-\delta I(\mathbf{x}, t')], \quad (5)$$

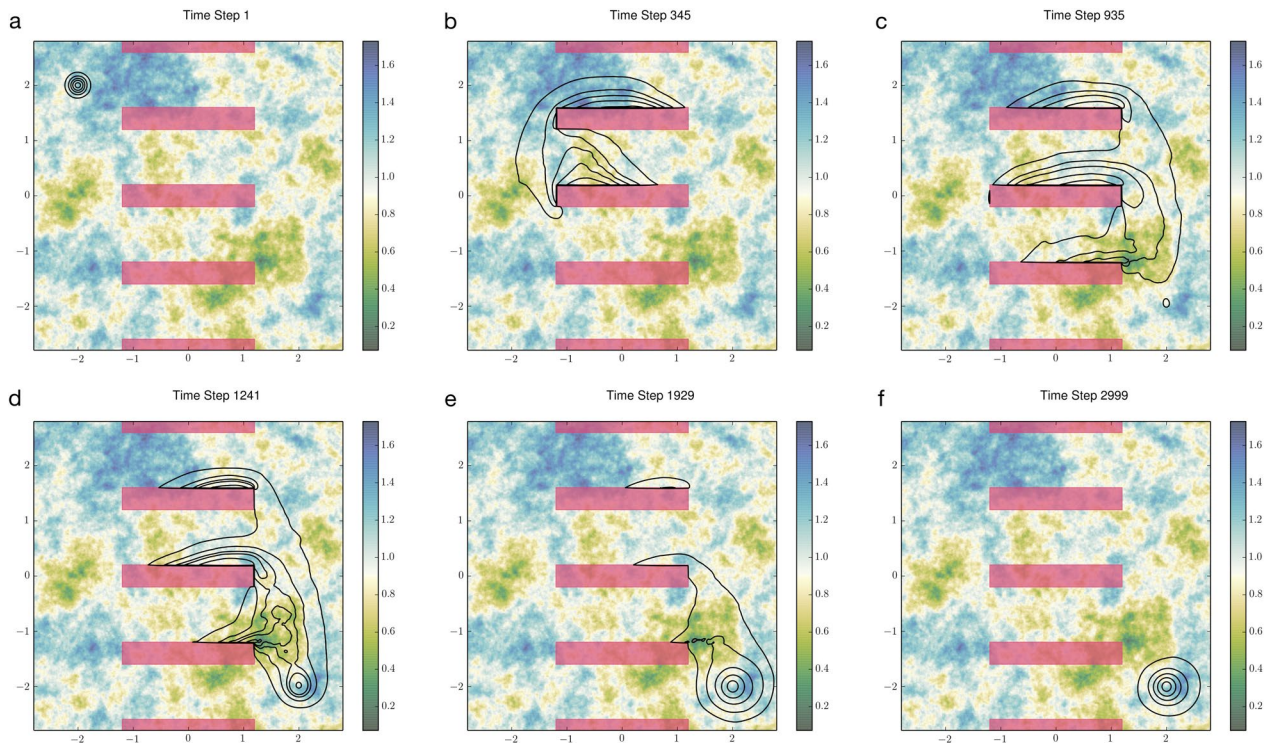


Fig. 4 Same model as Fig. 3 except for the inclusion of linear landscape elements. Passages are partially obstructed by a set of impermeable barriers (red) that open onto multiple movement corridors of equal widths. Notably, we observed the existence of parallel realities where, for long periods of time, the individual is just as likely to be found trapped somewhat near its initial location as at its expected destination given by the steady-state UD

where δ denotes the rate of transmission per infectious contact. If the individual remains uninfected, they are subsequently vaccinated with probability $\omega(\mathbf{x}, t')$, which increases with both vaccine efficacy ε and $u(\mathbf{x}, t')$, used here as a proxy for vaccine access:

$$\omega(\mathbf{x}, t') = 1 - \exp[-\varepsilon u(\mathbf{x}, t')]. \quad (6)$$

For computational simplicity, we assumed that the expected local wait time for vaccination is independent of the local density of susceptible individuals.

We simulated the discrete events described by Eqs. (5) and (6) while simultaneously solving Eq. (4) over smaller-sized time steps. The ABM outputs and the transient solutions $u(\mathbf{x}, t)$ are thus tightly coupled. Our results demonstrate that a deployment strategy outlined by the above two rules can create a protective “bubble” where vaccination efforts are concentrated and disease transmissions are inhibited (Fig. 5). Combining a Fokker–Planck equation with an ABM in this manner allows us to forecast outcomes for various management strategies across diverse epidemiological contexts [32]. Crucially, this hybrid approach enables the evaluation of behaviorally complex management theories. For example, it can

be used to assess whether forming a defensive perimeter with vaccinators is more effective at containing an outbreak than preemptively dispatching healthcare teams to already affected regions to halt epidemic progression.

Discussion

In this paper, we developed a novel modeling approach that leverages existing computational tools to unmask the elusive transient solutions of classical space-use models. Our approach is intuitive, self-contained, and does not require high-level programming proficiency. We demonstrated its ability to not only advance theory in movement ecology but also to address emerging ecological and epidemiological questions.

Transient space-use dynamics merit closer attention in the movement modeling literature. In systems where the space-use patterns of one or multiple individuals are in spatiotemporal flux, transient UD may yield greater ecological insights than traditional UD concepts rooted in steady-state assumptions. Even from a purely graphical standpoint, they impart far more information, exposing complex spatial patterns and a more elaborate sequence of events. We posit that this new dynamical perspective

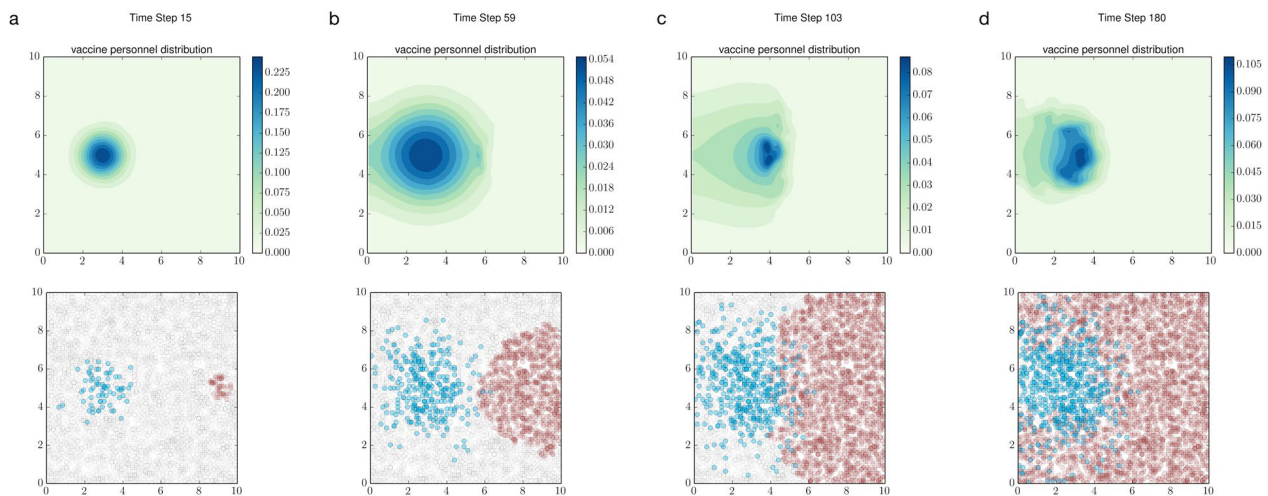


Fig. 5 Behaviorally adaptive vaccine deployment characterized by expending more control effort in high-needs neighborhoods and withdrawing from already infected regions. Top row: The blue surfaces depict the transient UD of the vaccination personnel in response to local disease prevalence. Bottom row: Susceptible, vaccinated, and infected individuals are shown in white, blue, and red, respectively

will have far-reaching implications across a wide range of disciplines concerned with organismal movement.

For instance, incorporating transient animal space-use dynamics can significantly enhance models of disease spread in wildlife populations. New methods that infer dynamic contact networks from animal movement trajectories, such as MoveSTIR and related frameworks [27, 65], have already laid the groundwork for mapping transient UD to transmission opportunities (see Vargas-Soto [29]). Building on these works could lead to identification of hotspots, hot hosts, and hot time windows that disproportionately influence disease outbreaks [27]. Moreover, because transient UD may be functions of environmental variables, these models could eventually reveal where large-scale outbreaks originate or how they are driven by host habitat conditions.

Transient space-use analysis also applies to the field of wildlife management. Consider the translocating of bears that are prone to human conflicts (e.g., [66]). The strategy's effectiveness has been debated as bears often resettle poorly, experiencing high mortality rates or attempting to return to their original place of capture. By predicting transient UD, managers can better anticipate the frequency of hazard (e.g., road) encounters and estimate the likelihood of a successful translocation.

In this paper, we have limited our case studies to centralized movement governed by a single fixed-point attractor (e.g., a den site or a base of deployment). In natural systems, however, many point attractors can coexist, and individuals may spend considerable time traveling among them. Our approach can be generalized to model such scenarios (e.g., multi-nucleic home ranges), where

the expected space-use pattern could represent a mixture of multiple transient UD driven by different directional preferences. In addition, sensory noise and ecological perturbations, two outcomes of global environmental changes, can keep an individual's UD in a perpetual state of transience. The consequences of this type of spatial instability on biodiversity and public health should be further investigated. Finally, we can apply our approach to other classes of PDEs: for instance, in reaction-advection-diffusion equations, it could yield more accurate predictions of the ecological dynamics of invasive pest animals.

Transient space-use analysis typically requires a well-defined set of mechanistic assumptions. However, the latter can be difficult to ascertain. Thus, a key challenge, and an incipient area of research, is to fit mechanistic models to the copious empirical movement data currently available. Recently, Potts and Schlögel [22] developed a method to parameterize classical space-use models using step-selection analyses of animal tracking data. The fitted parameters capture an animal's tendency to move toward or away from specific spatial features, reflecting actual movement mechanisms. In principle, one can then solve the resultant models with our approach to obtain the transient UD, thereby integrating empirical data with real-time predictions. At the moment, this method is constrained by its assumption that each movement step represents an immediate response to local cues (e.g., conspecific markings), instead of being part of a continuous trajectory shaped by long-term objectives (e.g., home range relocation). As such, it is incompatible with space-use models that include distant attractions or repulsions.

To take full advantage of transient space-use analysis, a continuous-time, multi-modal extension of step-selection analysis that accommodates remotely guided movements, as proposed by Wang et al. [67], may be necessary.

Space-use models are also fitted to movement data in hierarchical Bayesian models used to study population and disease spread, [68–70]. There, forecasts are typically generated by statistically estimating the parameters of a PDE and then solving the equation over time through manual numerical integration (e.g., [19]). Perhaps due to the difficulties involved in this process, the movement mechanisms are often highly simplified (e.g., limited to random movement). When models incorporate fine-scale environmental heterogeneity, more complex techniques, such as homogenization [18], are required, which can further deter non-expert users. Our approach to solving PDEs can enhance this hierarchical Bayesian framework in terms of both accessibility and inferential power. For instance, nesting a FiPy script that solves for transient UD inside its Markov chain Monte Carlo (MCMC) algorithm could eliminate much of the technical burden associated with numerical analysis, enabling predictions of ecological spread under complex and realistic movement mechanisms.

Conclusions

Transient space-use analysis can lead to reevaluations of foundational ecological concepts such as home range and territory, prompting a shift in definitions from static to dynamic constructs that more accurately reflect biological realities. It can also facilitate the integration of dynamical models developed across different spatiotemporal scales and open many new avenues of research, from exploring the links between demographic shifts and territorial spacing to examining how illness-induced behavioral changes modulate disease dynamics. By recognizing the interdependence between individual space-use dynamics and broader system-level processes, we can markedly improve our predictions of complex biological systems and formally establish movement ecology as a critical element of future ecological and epidemiology theories.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-025-00538-5>.

Additional file 1.

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Author contributions

YT conceived and designed the research. YT developed the model and analyzed the results. YT drafted the initial manuscript and generated the visualization. VG reviewed and compared existing numerical tools. All authors contributed to writing and editing.

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Availability of data and materials

Core code for generating the figures is available at <https://doi.org/https://doi.org/10.5281/zenodo.10871588>.

Declarations

Competing interests

The authors declare no competing interests.

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