

A framework for analyzing the robustness of movement models to variable step discretization

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Abstract When sampling animal movement paths, the frequency at which location measurements are attempted is a critical feature for data analysis. Important quantities derived from raw data, e.g. travel distance or sinuosity, can differ largely based on the temporal resolution of the data. Likewise, when movement models are fitted to data, parameter estimates have been demonstrated to vary with sampling rate. Thus, biological statements derived from such analyses can only be made with respect to the resolution of the underlying data, limiting extrapolation of results and comparison between studies. To address this problem, we investigate whether there are models that are robust against changes in temporal resolution. First, we propose a mathematically rigorous framework, in which we formally define robustness as a model property. We then use the framework for a thorough assessment of a range of basic random walk models, in which we also show how robustness relates to other probabilistic concepts. While we found robustness to be a strong condition met by few models only, we suggest a new method to extend models so as to make them robust. Our framework provides a new systematic, mathematically founded approach to the question if, and how, sampling rate of movement paths affects statistical inference.

Keywords animal movement · random walk · sampling rate · discretization · GPS data · parameter estimation

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1 Introduction

To learn about animal movement behaviour, researchers across the world collect increasing amounts of data for many different species. When tracking an animal, e.g. via GPS-based telemetry, locations are measured at discrete times, and the rate and regularity of measurements are critical features. From raw location data we can estimate classic movement characteristics such as mean square displacement, measures of directional persistence or tortuosity, and travel distance (Turchin 1998; Codling et al 2008; Rowcliffe et al 2012). These quantities can vary largely when derived from movement data with different temporal resolutions (Ryan et al 2004; Codling and Hill 2005; Nouvellet et al 2009; Rowcliffe et al 2012). When we fit a movement model to data to perform statistical inference, the temporal resolution of the sampling can both affect parameter estimates and result in erroneous inference such as misclassified behavioural states (Breed et al 2011; Postlethwaite and Dennis 2013). Generally, sampling a continuous path of an animal at discrete intervals can lead to various degrees of information loss (Turchin 1998).

A few studies used fine-scale movement data to empirically estimate correction factors to adjust measured travel distances according to the sampling interval (Pépin et al 2004; Ryan et al 2004). While this is a first approach to understand the influence of sampling interval on measured travel distance, it is unclear whether results can be generalized from these studies to other species and systems. Another approach has been to simulate movement according to correlated random walks or velocity jump processes to estimate relationships between the resolution of a discretized path and common movement characteristics, such as apparent speed and angular deviation. In this way, Bovet and Benhamou (1988) and Benhamou (2004) defined sinuosity as a measure of a path's tortuosity that is independent of the discretization. While these studies used "spatial sampling", that is a rediscrretization of a path based on a certain step length, Codling and Hill (2005) extended the approach to "temporal sampling", where discretization is based on a fixed time interval. In addition to sinuosity, Codling and Hill (2005) also investigated the relationship between apparent speed and sampling interval. Both relationships break down when the observed angular deviation becomes large, either due to high tortuosity of the underlying movement or a relatively large sampling time step (Bovet and Benhamou 1988; Codling and Hill 2005). An extension of this work has recently been provided by Rosser et al (2013), who more closely investigated the full distributions of relative apparent speed and apparent angle change. All these studies demonstrate that movement characteristics are highly sensitive to path discretization but also that, unless discretization becomes too coarse, changes may be described by functional relationships. However, analyses of this kind are still lacking for other movement parameters, e.g. parameters that describe selective behaviour with respect to the environment.

One may think that the best solution to avoid undersampling and information loss is to take measurements at high rates to approximate a continuous path as best as possible. However, this is often not feasible, because limited battery life of tagging devices gives rise to a tradeoff between sampling frequency and total sampling time span (Mills et al 2006; Breed et al 2011). In addition, oversampled movement paths can be problematic in data analysis, because they lead to strong and long-lasting au-

to correlations and require the processing of very long time series (Benhamou 2004). Also, very frequent fix attempts can reduce GPS transmitter efficiency (measured as total number of successful locations obtained during the deployment time) (Mills et al 2006), and noise can become very large compared to the actual signal, especially if animals are resting or moving slowly (Ryan et al 2004). It is therefore important to choose measurement rates appropriately to the behavioural scale of interest. Even if we decide about sampling rates with care, it remains a problem that results are often tied to the data's resolution of a particular study. Generalizing or transferring results as well as comparison between different studies is limited (Tanferna et al 2012; Postlethwaite and Dennis 2013).

Here, we introduce a new theoretical framework for analyzing the robustness of movement models to varying resolutions of temporal discretization. In our paper, we formally define robustness as a specific property of a model. Generally speaking, we consider a model to be robust if it can be applied validly to movement data with different temporal resolutions, thus allowing consistent statistical inference. While we do not require important movement characteristics expressed in model parameters to be the same across sampling rates, we ask for them to vary systematically in a way that allows translation of results between resolutions. Because our framework is defined at the level of the model, it is more general than previous approaches that consider individual movement characteristics.

Our idea of movement model robustness is related to the formal concept of robustness in statistics, which explicitly acknowledges that statistical models usually simplify and approximate the processes that generate observations. Robust statistical methods aim at safeguarding results against misspecified model assumptions (Hampel 1986; Huber and Ronchetti 2009). Here, in case of movement models, we may consider the temporal resolution of a model as an assumption. Sometimes, a suitable resolution can be determined by scale considerations, for example when modelling inter-patch movement at the patch level (Benhamou 2013). If, in contrast, we are interested in the finer behavioural rules of the inter-patch movement, for example, compared to intra-patch movement, it may be less clear which resolution to choose because regularly sampled locations do not necessarily correspond to an individual's decision points (Turchin 1998). Here, we investigate whether there are movement models that are robust to the choice of sampling rate. We emphasize, however, that this type of robustness is only biologically meaningful across a range of resolutions that are all within the scale of the behaviour of interest.

We present the new framework in terms of random walk models with independently and identically distributed steps. Many contemporary movement models have surpassed these classical random walk models in complexity, e.g. including persistent movement and additional components to describe environmental effects (e.g., Rhodes et al 2005; McClintock et al 2012). Still, here we focus on basic random walks to introduce the new concept of robustness of movement models to temporal discretization and to put it in context with other established ideas in probability theory and movement ecology. Our aim is to provide the first step towards a rigorous theory of robustness of movement models by working out fundamental results at the level of simple random walks that are analytically tractable. This will provide a basis for future work including more realistic random walk models. Ultimately, our goal is to

understand how we can use models' robustness properties to mitigate effects of data collection rate on statistical inference about movement behaviour and in particular parameter estimates.

Our paper is organized as follows. In section 2 we describe the set-up of our study, after which we follow with two introductory example models that illustrate our framework. We then give formal definitions of two types of robustness that vary in their strength of requirements but also benefits. In section 3, we analyze robustness properties of one-dimensional models. We present models that are robust, suggest a way to construct robust models from non-robust models and relate robustness to the probabilistic concept of infinite divisibility. In section 4, we extend results about robustness to two-dimensional models, in particular models with radially symmetric step densities. Our framework provides a new systematic, mathematically founded approach to analyze if, and how, sampling rate of movement paths influences movement parameters and inference results. Here, we provide a first analysis at the fundamental level of simple random walks. We conclude our paper by discussing future steps towards application of the new concept to biologically relevant models.

2 The robustness framework

2.1 Temporal resolution of random walks

Random walks have a long history as animal movement models. They are useful as a basis for deriving partial-differential equation models for population distributions (Patlak 1953; Skellam 1951), for building simulation models for moving individuals (Kaiser 1976; Jones 1977), and for developing metrics that summarize movement characteristics (Kareiva and Shigesada 1983). Although models have become more complex to include behavioural mechanisms such as territorial defense (Moorcroft and Lewis 2006; Potts et al 2013) or resource selection (Mckenzie et al 2012; Potts et al 2014), to describe temporally switching behaviour (Morales et al 2004; McClintock et al 2013), and to account for stochasticity of the measurement process (Patterson et al 2008; Breed et al 2012), random walks remain at the root of many movement models (Börger et al 2008; Smouse et al 2010).

The classic random walk model for movement is a stochastic process $\{\mathbf{X}_t, t \in \mathbb{N}\}$, where the location $\mathbf{X}_t \in \mathbb{R}^2$ of an organism for each time index $t \in \mathbb{N}$ is given as a sum of independently identically distributed (i.i.d.) steps (Klenke 2008). That is,

$$\mathbf{X}_t = \mathbf{x}_0 + \sum_{i=1}^t \mathbf{S}_i, \quad (1)$$

where \mathbf{x}_0 is the (fixed) start location of the movement path, and \mathbf{S}_i is the vector, that is the step, between location \mathbf{X}_{i-1} and \mathbf{X}_i . Note that here we use \mathbf{S} to denote steps and \mathbf{X} to denote locations, which are sums of steps. In the statistical literature, often \mathbf{S} is used for sums of random variables. However, we have chosen our notation according to the movement context. For a graphical clarification of our notations refer to Fig. 1. The random walk models an observed movement path, that is a series of locations $\underline{\mathbf{x}} = \{\mathbf{x}_0, \mathbf{x}_1, \mathbf{x}_2, \dots\}$, where $\mathbf{x}_t \in \mathbb{R}^2$, measured at regular time intervals. For some

types of movement data paths can only be sampled irregularly. For example, when tracking marine mammals, individuals must surface to allow location measurements. To connect such data to discrete-time random walk models, hierarchical models such as state-space models can be used (Jonsen et al 2005; Breed et al 2012).

As a convenient way for systematically studying varying temporal discretization of movement data, we can mimic different sampling rates of movement paths via subsampling. The n th subsample of \mathbf{x} consists of every n th location, that is $\mathbf{x}_n = \{\mathbf{x}_0, \mathbf{x}_n, \mathbf{x}_{2n}, \dots\}$. As n increases, the temporal resolution of the data becomes coarser. Note that $\mathbf{x}_1 = \mathbf{x}$ is the original time series. If \mathbf{x} is modelled by the process $\{\mathbf{X}_t, t \in \mathbb{N}\}$, then the subsample \mathbf{x}_2 , which consists of every second location of the original time series, is correctly described by the subprocess $\{\mathbf{X}_{2t}, t \in \mathbb{N}\}$. In general, the subprocess may have a different probability distribution than the original process. However, there is a simple relationship between the two processes. For the subprocess we have $\mathbf{X}_{2t} = \mathbf{x}_0 + \sum_{i=1}^{2t} \mathbf{S}_i = \mathbf{x}_0 + \sum_{i=1}^t \tilde{\mathbf{S}}_{i,2}$, for steps $\tilde{\mathbf{S}}_{i,2} = \mathbf{S}_{2i-1} + \mathbf{S}_{2i}$; refer to Fig. 1. Note that \mathbf{X}_{2t} is the t -th element in the subprocess $\{\mathbf{X}_{2t}, t \in \mathbb{N}\}$ and the $2t$ -th element in the original process $\{\mathbf{X}_t, t \in \mathbb{N}\}$. More generally, for an arbitrary subprocess, we have

$$\mathbf{X}_{nt} = \mathbf{x}_0 + \sum_{i=1}^{nt} \mathbf{S}_i = \mathbf{x}_0 + \sum_{i=1}^t \tilde{\mathbf{S}}_{i,n}, \quad (2)$$

for the larger steps $\tilde{\mathbf{S}}_{i,n} = \sum_{j=0}^{n-1} \mathbf{S}_{ni-j}$. Therefore, the distribution of \mathbf{X}_{nt} is based on steps that are themselves sums of steps of the original process. We remind that for a random walk with i.i.d. steps, all \mathbf{S}_i have the same distribution, however, their sum may generally have a different distribution.

If a movement model were robust to changes in temporal resolution, the same model should be able to describe validly both a path \mathbf{x} and its subsample \mathbf{x}_n . As we have described above, in a random walk model the distributions of the steps define the process. If the steps $\{\mathbf{S}_i, i \in \mathbb{N}\}$ and $\{\tilde{\mathbf{S}}_{i,n}, i \in \mathbb{N}\}$ for a range of subsampling indices $n \in \mathbb{N}$ can be described by the same probability model, with appropriate adjustment of model parameters, then we consider the model to be robust to varying temporal discretization within that range.

2.2 Two illustrative examples

We illustrate the concept of robustness with two simple examples. For simplicity, we consider one-dimensional models. First, for an example of a robust model, we assume that all steps S_j have identical normal distribution, with zero mean and variance σ^2 , which we denote by $S_i \sim \mathcal{N}(0, \sigma^2)$. Because the model is in one dimension, the normal distribution models both the distance and direction (right or left) of a step. A step density centred at zero means that steps to the right and left have the same probability. Because sums of independent random variables with normal distribution have again a normal distribution with summed means and variances, it follows that the location X_t is normally distributed as well, $X_t \sim \mathcal{N}(x_0, t\sigma^2)$. The steps $\tilde{S}_{i,2}$ of the subsampled process $\{X_{2t}, t \in \mathbb{N}\}$ are sums of two normally distributed random variables and therefore we have $\tilde{S}_{i,2} \sim \mathcal{N}(0, 2\sigma^2)$ and $X_{2t} \sim \mathcal{N}(x_0, 2t\sigma^2)$. Thus, the

probability distributions that describe the original and the subsampled process are both normal with the same mean but different variances. However, the variances are related through a simple linear function. Therefore, we can make inference using the subsampled data and process and simply divide the estimated variance by 2 to obtain an estimate of the variance of the original process. Conversely, we can multiply the variance obtained using the original process by 2 to obtain the valid variance for the coarser process. This also works analogously for $n > 2$. Because of this property, the random walk model with normally distributed steps is robust.

For a counter example of robustness, we consider steps that have Laplace distribution, which is also termed double-exponential distribution. The Laplace distribution, similar to the Normal distribution, is symmetric, however it is more peaked and has slightly heavier tails than the Normal distribution. It commonly serves as a one-dimensional (or marginal, in two-dimensional models) redistribution kernel in models for dispersing organisms (Neubert et al 1995). We assume that steps S_i are i.i.d. Laplace distributed with location parameter zero, i.e. the density is centred at zero, and scale parameter σ , that is $S_i \sim \text{Laplace}(0, \sigma)$. Consequently, the location X_t is distributed as a sum of Laplace distributions. Sums of Laplace distributed random variables are not as simple or well-known as the previous Normal example. Still, we can employ characteristic functions to look into this case further. The characteristic function (ch.f.) of a random variable X is defined by the expectation $\phi_X(u) = E(e^{iuX})$. Characteristic functions uniquely define distributions. The ch.f. for the above step distribution is given by

$$\phi_{S_i}(u) = \frac{1}{1 + \sigma^2 u^2}. \quad (3)$$

Characteristic functions have the convenient property that summing independent random variables corresponds to multiplying their characteristic functions (Klenke 2008). The steps of the subsampled process, $\tilde{S}_{i,2} = S_{2i-1} + S_{2i}$, consequently have ch.f.

$$\phi_{\tilde{S}_{i,2}}(u) = \phi_{S_i}(u)^2 = \frac{1}{1 + (\sqrt{2}\sigma)^2 u^2 + \sigma^4 u^4}. \quad (4)$$

This function cannot be expressed as the characteristic function of any Laplace distribution, which would have to be of the form $e^{i\mu t}(1 + \sigma^2 u^2)^{-1}$ for some location parameter $\mu \in \mathbb{R}$ and scale $\sigma > 0$. With a bit more work, one can also compare probability density functions. The steps S_i of the original process have the Laplace density

$$f_{S_i}(s) = \frac{1}{2\sigma} e^{-\frac{|s|}{\sigma}}. \quad (5)$$

The density of the sum of two such random variables can be calculated as convolution of the individual densities,

$$f_{\tilde{S}_{i,2}}(s) = \int_{\mathbb{R}} f_{S_i}(v) f_{S_i}(s-v) dv. \quad (6)$$

This results in (refer also to Kotz et al 2001)

$$f_{\tilde{S}_{i,2}}(s) = \frac{1}{4\sigma^2} e^{-\frac{|s|}{\sigma}} (\sigma + |s|), \quad (7)$$

which we cannot write in form of $f_{S_i}(s)$ by transforming the parameters. We conclude that the step distribution for the subsampled process does not belong to the same family of distributions as the original process, namely the Laplace family. This means that if we fit the original model with Laplace distributed steps to both \mathbf{x} and \mathbf{x}_2 , the resulting parameter estimates are not truly comparable. If, however, instead we fit a different model to \mathbf{x}_2 that uses densities (7), the parameter σ describes the same quantity as in the original model. Therefore, the model that has Laplace distributed steps is not robust against varying temporal resolution; but see section 3.2.

2.3 Formal definition of robustness

We now define robustness formally. We have seen above that the step distributions play an essential role for the robustness of random walk models. In the Laplace example, the characteristic function has been a convenient tool to analyze step distributions of random walk models. Therefore, we use them in our definitions of robustness. For a two-dimensional model, the ch.f. of a step $\mathbf{S}_i \in \mathbb{R}^2$ is $\phi(\mathbf{u}) = E(e^{i\mathbf{u} \cdot \mathbf{S}_i})$ for $\mathbf{u} \in \mathbb{R}^2$, where \cdot denotes the scalar product of vectors. For our purpose we highlight the parameters of a distribution as auxiliary variables of the ch.f. by writing $\phi(\mathbf{u}; \boldsymbol{\theta})$ for model parameters $\boldsymbol{\theta} \in \Theta$.

We provide two definitions of robustness that vary slightly in the strength of their requirements. In principle, we consider a model to be robust if step distributions of the subprocesses belong to the same class of distributions as those of the original process. Because characteristic functions uniquely define distributions, we can formulate this idea rigorously by requiring the characteristic functions of original and coarser steps to have the same functional form.

Definition 1 (Semi-robustness) Let $\phi(\mathbf{u}; \boldsymbol{\theta})$ be the characteristic function of the i.i.d. steps in a random walk movement model, where $\boldsymbol{\theta} \in \Theta$ is the vector of model parameters. The movement model is *semi-robust* if for every $n \in \mathbb{N}$ there exists a function $g_n : \Theta \rightarrow \Theta$ such that

$$\phi(\mathbf{u}; \boldsymbol{\theta})^n = \phi(\mathbf{u}; g_n(\boldsymbol{\theta})). \quad (8)$$

As we have mentioned before, summing independent random variables (here, steps in a random walk) corresponds to multiplying their respective characteristic functions. In our random walk models, steps are identically distributed. Therefore, the LHS of equation (8) is the ch.f. of the sum of n steps and therefore defines the distribution for the steps $\tilde{\mathbf{S}}_{i,n}$ of the model for the n th subsample. The RHS of the equation is the ch.f. of the steps S_i , however with transformed parameters. Therefore, semi-robustness requires that subsamples of the random walk are defined by the same step distribution up to a known parameter transformation. The parameter transformation g_n is an important part of the definition, because it allows us to scale up model parameters to a coarser discretization. Say, our model represents a temporal discretization τ , that is τ is the time interval between two locations. If our model is semi-robust, we know that it is also valid for any discretization $n\tau$, $n \in \mathbb{N}$, with parameter $g_n(\boldsymbol{\theta})$.

If we want to be able to compare results of studies that use different temporal resolutions for their models more generally, we also need to be able to translate parameters downwards, that is to a finer discretization. The following definition characterizes models that can be scaled both upwards and downwards.

Definition 2 (Robustness) A semi-robust movement model is *robust* if the function g_n in Definition 1 is bijective, that is both one-to-one and onto.

This definition allows scaling upwards just as before. Additionally, we can translate the parameter θ to a finer scale $\frac{1}{n}\tau$. The surjectivity of g_n guarantees that there exists an inverse image $\psi = g_n^{-1}(\theta) \in \Theta$, which is unique by injectivity. Therefore, $\phi(\mathbf{u}; \psi)$ defines a valid characteristic function, and by property (8) we have

$$\phi(\mathbf{u}; \psi)^n = \phi(\mathbf{u}; g_n(\psi)) = \phi(\mathbf{u}; \theta). \quad (9)$$

This means that there is a valid sub-model for the discretization $\frac{1}{n}\tau$ with parameter vector ψ .

The introductory example model with Normally distributed steps is robust. The transformation for the only model parameter, the standard deviation σ , is $g_n(\sigma) = \sqrt{n}\sigma$. The second example with Laplace distributed steps is neither robust nor semi-robust since property (8) is not met. In section 3.2, we will see that it is possible to embed the Laplace model within an extension so as to make it robust.

3 One-dimensional models

In the following we look further into the question which random walk models are robust. First, we focus on one-dimensional models, that is random walks on the real line. These models can play a role in situations where movement is naturally limited, e.g. movement within a stream or along a river bank. Also, univariate step distributions arise as marginals of two-dimensional movement- or dispersal kernels; see section 4.2. After presenting classes of robust models, we describe the relationship of robustness with the probabilistic concept of infinite divisibility. With this, we hope to deepen the reader's understanding of robustness and to set robustness apart from other concepts.

3.1 Robust random walk models

To find robust models, we look for steps with probability distributions that are closed under summation. Such a property ensures semi-robustness, which is a necessary condition for robustness. Whether a semi-robust model is also robust depends largely on the parameter space for which the step distribution is well-defined. A straightforward example is given by distributions, whose ch.f. can be expressed as some function raised to a power, where the power is a model parameter. In such a case, taking the ch.f. to the power n simply corresponds to multiplying the power parameter by n . Thus, we can define a parameter transformation g_n that multiplies the power parameter by n , while all other parameters remain unaffected. We obtain semi-robustness

as long as the product of power parameter and n still belongs to the model parameter space. For robustness, we additionally require that the parameter transformation is invertible, which means that we need to be able to divide the power parameter by any $n \in \mathbb{N}$ and still remain within the valid parameter space. Therefore, the definition of the parameter space of a distribution is key to whether a model is semi-robust or robust.

Theorem 1 *Consider a one-dimensional random walk movement model with i.i.d. steps that have characteristic function of the form $\phi(u; \boldsymbol{\theta}) = h(u; \boldsymbol{\theta}_1)^{\theta_2}$ for some function $h: \mathbb{R} \times \Theta_1 \rightarrow \mathbb{C}$ and model parameters $\boldsymbol{\theta} = (\boldsymbol{\theta}_1, \theta_2) \in \Theta_1 \times \Theta_2$. If the parameter space is such that $n\Theta_2 = \{n\theta_2; \theta_2 \in \Theta_2\} \subset \Theta_2$ for all $n \in \mathbb{N}$, the model is semi-robust. If additionally $\frac{1}{n}\Theta_2 \subset \Theta_2$ for all $n \in \mathbb{N}$, then the model is robust.*

Proof We define the parameter transformation as $g_n(\boldsymbol{\theta}) = g_n(\boldsymbol{\theta}_1, \theta_2) = (\boldsymbol{\theta}_1, n\theta_2) \in \Theta_1 \times \Theta_2$. Then, trivially, we have $\phi(u; \boldsymbol{\theta})^n = h(u; \boldsymbol{\theta}_1)^{n\theta_2} = \phi(u; g_n(\boldsymbol{\theta}))$, and semi-robustness follows. Let $\frac{\theta_2}{n} \in \Theta_2$ for all $n \in \mathbb{N}$ and all $\theta_2 \in \Theta_2$. Then for each $\boldsymbol{\theta}$ we have a unique inverse image $g_n^{-1}(\boldsymbol{\theta}) = (\boldsymbol{\theta}_1, \frac{\theta_2}{n})$, which lies within the valid parameter range. Therefore, the model is robust.

For such models, the parameter transformation only affects the parameter that constitutes the power in the ch.f. For example, consider i.i.d. steps S_i that have Gamma distribution with shape $\kappa > 0$ and scale $\sigma > 0$. Note that the support of the Gamma density is only the positive real line, so movement steps are always into the same direction (to the right). The Gamma distribution has the well-known property that a sum of independent Gamma random variables, all having the same scale parameter, again has a Gamma distribution (Casella and Berger 2002). The ch.f. of the Gamma distribution is $\phi(u; \kappa, \sigma) = (1 - \sigma iu)^{-\kappa}$. Therefore, we directly obtain $\phi(u; \kappa, \sigma)^n = (1 - \sigma iu)^{-n\kappa} = \phi(u; n\kappa, \sigma)$. Hence, the summation affects the shape parameter, and we have $g_n(\kappa, \sigma) = (n\kappa, \sigma)$. Because the Gamma distribution is defined for all positive shapes $\kappa \in \mathbb{R}^+$, the transformation g_n is invertible, and we conclude that steps with Gamma distribution lead to robust models.

The chi-squared distribution is a special case of the Gamma distribution for a scale $\sigma = 2$ and shape $\kappa = \frac{k}{2}$ for degrees of freedom $k \in \mathbb{N}$. The ch.f. is

$$\phi(u; k) = (1 - 2iu)^{-\frac{k}{2}}. \quad (10)$$

The n th power of ϕ is still a ch.f. of a chi-squared distribution with degrees of freedom $nk \in \mathbb{N}$, and therefore a model with chi-squared steps is semi-robust. However, for an arbitrary $k \in \mathbb{N}$, the fraction $\frac{k}{n}$ is a rational but not necessarily a natural number. Thus, the second condition of Theorem 1 is not satisfied. For more examples of distributions that meet the conditions of Theorem 1, see table 1. Note that there are also discrete distributions that belong to the group of distributions described in the theorem (e.g. the binomial, Poisson and negative-binomial).

Another class of distributions that are suitable as step distributions for robust models is given by the family of stable distributions (Samorodnitsky 1994; Nolan 1997; Klenke 2008). The stable distributions comprise a four-parameter family of distributions, which we denote by $\mathcal{S}(\alpha, \beta, \sigma, \mu)$, with index of stability $0 < \alpha \leq 2$,

skewness $-1 \leq \beta \leq 1$, scale $\sigma > 0$ and location $\mu \in \mathbb{R}$. Note that the scale parameter does not necessarily correspond to the variance of the distribution, which is in fact infinite for most stable distributions. Only for certain values of α and β , do stable distributions have closed-form density functions. However, for any parameter values, we can define a stable distribution uniquely by its characteristic function. There are multiple ways to parameterize stable distributions, which differ slightly in the interpretation of the parameters σ and μ . Here we use the form of the ch.f. provided in Nolan (1997),

$$\phi(u; \alpha, \beta, \sigma, \mu) = \begin{cases} \exp[i\mu u - \sigma^\alpha |u|^\alpha (1 - i\beta \tan(\frac{\pi\alpha}{2}) \text{sign}(u))], & \alpha \neq 1 \\ \exp[i\mu u - \sigma |u| (1 + i\beta \text{sign}(u) \ln |u|)], & \alpha = 1. \end{cases} \quad (11)$$

The most famous example of a stable distribution is the Normal distribution for $\alpha = 2$. Using the above parameterization of the stable distribution, the mean and variance of the Normal distribution are μ and $2\sigma^2$, respectively. For $\alpha = 2$, the term including the parameter β vanishes. For $\alpha = 1$ and $\beta = 0$, the Cauchy distribution is another well-known case, for which a closed-form density is known. While the Normal and Cauchy distribution are symmetric, the Lévy distribution for $\alpha = \frac{1}{2}$ and $\beta = 1$ is an example of a stable distribution with skewed density function (Samorodnitsky 1994).

Theorem 2 *A one-dimensional random walk movement model with i.i.d. steps is robust if steps are distributed according to the stable law $\mathcal{S}(\alpha, \beta, \sigma, \mu)$, i.e. have characteristic function (11).*

Proof We can easily verify that the ch.f. of the stable distribution satisfies property (8). We have

$$\phi(u; \alpha, \beta, \sigma, \mu)^n = \begin{cases} \exp[i(n\mu)u - (n^{\frac{1}{\alpha}}\sigma)^\alpha |u|^\alpha (1 - i\beta \tan(\frac{\pi\alpha}{2}) \text{sign}(u))], & \alpha \neq 1 \\ \exp[i(n\mu)u - (n\sigma) |u| (1 + i\beta \text{sign}(u) \ln |u|)], & \alpha = 1. \end{cases} \quad (12)$$

Therefore, we choose $g_n(\alpha, \beta, \sigma, \mu) = (\alpha, \beta, n^{\frac{1}{\alpha}}\sigma, n\mu)$. It is easy to see that g_n is a bijection of the parameter space, leaving α and β unchanged and being monotone on $\mathbb{R}^+ \times \mathbb{R}$ in the last two arguments. Therefore, stable steps distributions lead to robust models.

We have just seen that if we sum n steps, each having stable distribution $S_i \sim \mathcal{S}(\alpha, \beta, \sigma, \mu)$, the sum is again stable according to

$$\tilde{S}_{i,n} \sim \mathcal{S}(\alpha, \beta, n^{\frac{1}{\alpha}}\sigma, n\mu). \quad (13)$$

In fact, stable distributions are a family of distributions that have been constructed to have this special summation property. Equivalently to defining a stable distribution by its characteristic function, we can also say a random variable S has stable distribution if the sum of independent copies of S is a scaled and shifted version of S , that is if we have

$$\sum_{i=1}^n S \stackrel{d}{=} a_n S + b_n \quad (14)$$

for some $a_n > 0, b_n \in \mathbb{R}$, where $\stackrel{d}{=}$ stands for equality in distribution (Samorodnitsky 1994; Kotz et al 2001). In fact, the only choice for a_n is $a_n = n^{\frac{1}{\alpha}}$ (Samorodnitsky 1994). Because the location X_t is a sum of steps, $X_t = x_0 + \sum_{i=1}^t S_i$, the distribution of the location X_t is also stable,

$$X_t \sim \mathcal{S}(\alpha, \beta, t^{\frac{1}{\alpha}} \sigma, x_0 + t\mu), \quad (15)$$

for any $t \in \mathbb{N}$. The analogue holds for the locations of the subsampled process $\{X_{nt}, t \in \mathbb{N}\}$,

$$X_{nt} \sim \mathcal{S}(\alpha, \beta, n^{\frac{1}{\alpha}} t^{\frac{1}{\alpha}} \sigma, x_0 + nt\mu). \quad (16)$$

The parameters α and β remain unchanged under summation. The parameter β determines skewness, with $\beta = 0$ corresponding to a symmetric density, and therefore a stable distribution $\mathcal{S}(\alpha, 0, \cdot, \cdot)$ is also termed α -symmetric stable distribution.

A special case is given by models that have starting location $x_0 = 0$ and step distribution $S \sim \mathcal{S}(\alpha, 0, \sigma, 0)$. These specific stable distributions are symmetric with centre at zero, and they lead to

$$X_t \sim \mathcal{S}(\alpha, 0, t^{\frac{1}{\alpha}} \sigma, 0) \quad (17)$$

and

$$X_{nt} \sim \mathcal{S}(\alpha, 0, n^{\frac{1}{\alpha}} t^{\frac{1}{\alpha}} \sigma, 0). \quad (18)$$

Therefore, X_{nt} is a scaled version of X_t , that is we have

$$X_{nt} \stackrel{d}{=} n^{\frac{1}{\alpha}} X_t, \quad (19)$$

which means that the random walk $\{X_t, t \in \mathbb{N}\}$ is self-similar (Samorodnitsky 1994).

Also, the probability density function of the step distribution, $p_S(s)$, is related to the density of the summed steps $\tilde{S}_{i,n}$ via a scaling property (see Appendix A or refer to Klafter et al (1995)),

$$p_{\tilde{S}_{i,n}}(s) = \frac{1}{n^{\frac{1}{\alpha}}} p_{S_i} \left(\frac{s}{n^{\frac{1}{\alpha}}} \right). \quad (20)$$

This specific random walk is called a Lévy flight (Klafter et al 1995). Note that this (original) definition of a Lévy flight is different from a Lévy walk. In contrast to Lévy flights, where jumps between locations occur instantaneously or during a fixed time interval, a Lévy walk is based on a continuous-time random walk, describing the movement of an organism at constant speed between reorientation events (Klafter et al 1995). In this description, the emphasis lies on waiting times, which follow a scaling law. In the movement literature, the two terms are often used interchangeably (Reynolds and Rhodes 2009; James et al 2011). Note that because of the different assumptions, data are processed slightly different in a Lévy walk analysis, where usually steps (as we have defined them here) are combined as “moves” as long as directional changes between them remain under a certain threshold (Plank et al 2013). This type of post-processing has recently been mentioned as possibly problematic (Benhamou 2013), and it is not suitable for our framework.

Although stable step distributions are predestined to lead to robust models, robustness is a more general concept. In terms of the characteristic function ϕ of S ,

the summation property (14) is $\phi(u)^n = e^{iub_n} \phi(a_n u)$, or simply $\phi(u)^n \propto \phi(a_n u)$. In comparison, the robustness property (8) is a weaker condition.

It means that the sum of n i.i.d. steps has the same distribution as a single step up to adjusted parameter values according to a known function g_n . In the case where steps have stable distribution, the function g_n affects the scale and location parameter of a distribution. However, distributions may have other types of parameters that can be affected. For example, in the above case of Gamma distributed steps, summation of steps results in a modified shape parameter. In contrast, scaling a Gamma distributed random variable by a constant c leads to a Gamma distribution with same shape κ but adjusted scale $c\sigma$. Therefore, the Gamma distribution is not stable, and the resulting random walk does not exhibit self-similarity. However, the random walk model with Gamma distributed steps is robust.

3.2 Robust model extensions

As we have seen in Theorem 1, a step distribution having ch.f. that is the power of some function leads to a semi-robust or robust model, depending on the definition of the parameter space. This leads to the idea that we can obtain robustness by embedding a distribution into a larger family of distributions by adding an additional power parameter. Starting with a ch.f. $\phi(u; \boldsymbol{\theta})$, $\boldsymbol{\theta} \in \Theta$, we can augment the model parameters by $k \in \mathbb{N}$, that is we define a new parameter vector $\bar{\boldsymbol{\theta}} = (\boldsymbol{\theta}, k) \in \Theta \times \mathbb{N}$. We can then define a new distribution via the ch.f. $\psi(u; \bar{\boldsymbol{\theta}}) = \phi(u; \boldsymbol{\theta})^k$. For $k \in \mathbb{N}$ we know that ψ is again a ch.f., because by construction it is the ch.f. of a distribution of a sum of k independent random variables. Because $nk \in \mathbb{N}$ for all $n, k \in \mathbb{N}$, and according to Theorem 1, a step distribution with ch.f. $\psi(u; \bar{\boldsymbol{\theta}})$, where k is simply one of the model parameters, leads to a semi-robust random walk model with $g_n(\boldsymbol{\theta}, k) = (\boldsymbol{\theta}, nk)$. To go a step further and construct a robust model, the range of the parameter k would need to include positive rational numbers. However, for $k \neq \mathbb{N}$, we have in general no guarantee that ψ is again the ch.f. of a distribution

As an illustration of these ideas, consider the Laplace distribution. The Laplace distribution with mean zero and scale parameter $\sigma > 0$ has ch.f.

$$\phi(u; \sigma) = \frac{1}{1 + \sigma^2 u^2}. \quad (21)$$

We have seen above that a model with Laplace distributed steps is not robust. However, we can define a new family of distributions via the ch.f.

$$\psi(u; \sigma, k) = \frac{1}{(1 + \sigma^2 u^2)^k}, \quad (22)$$

where $k \in \mathbb{N}$. This is the ch.f. of the sum of k independent Laplace random variables and therefore a valid ch.f. Using this distribution for steps and treating k as a regular model parameter, we have constructed a semi-robust model. In this particular case, where we extend the Laplace distribution, the function ψ in equation (22) is also a valid ch.f. for any non-negative, real $k \in \mathbb{R}_{\geq 0}$ (Kotz et al 2001). It corresponds to a generalized asymmetric Laplace distribution with location parameter zero and

symmetry parameter being zero (and hence being symmetric); see also table 1. This generalized Laplace distribution is not widely known, however, it has found several applications. In particular, it has been used in financial modelling, where it is also known as variance gamma model (Madan and Seneta 1990; Seneta 2004). A movement model with step distribution determined by the ch.f. (22) for $k \in \mathbb{R}_{\geq 0}$ is robust.

For applications in which likelihood functions play an important role, e.g. for statistical inference, a remaining question is whether we can find the corresponding probability density function for the ch.f. ψ . In principle, the probability density function of a distribution can be calculated as inverse Fourier transform of the characteristic function (Klenke 2008). Alternatively, for $k \in \mathbb{N}$, the density of ψ can be obtained as the convolution of the k single step densities. Both methods can be difficult or may not result in a closed-form density. However, for the above example of the generalized asymmetric Laplace distribution, a density function is available in terms of a Bessel function (Kotz et al 2001). In the symmetric case with location parameter zero, the density that corresponds to the ch.f. ϕ in equation (22) is

$$f(x) = \frac{1}{\sqrt{\pi}(k-1)!} 2^{-k+\frac{1}{2}} \sigma^{-k-\frac{1}{2}} |x|^{k-\frac{1}{2}} K_{k-\frac{1}{2}}\left(\frac{|x|}{\sigma}\right), \quad (23)$$

where $K_{k-\frac{1}{2}}(x)$ is a modified Bessel function of the third kind. This formula is valid for any $k \geq 0$. For the case where we restrict k to the non-negative integers, $k \in \mathbb{N}_0$, the Bessel function $K_{k-\frac{1}{2}}(x)$ has a closed form (Kotz et al 2001, Appendix B), and we can alternatively write

$$f(x) = \frac{e^{-\frac{|x|}{\sigma}}}{\sigma(k-1)! 2^k} \sum_{j=0}^{k-1} \frac{(k-1+j)!}{(k-1-j)! j!} \cdot \frac{\left(\frac{|x|}{\sigma}\right)^{k-1-j}}{2^j}. \quad (24)$$

This density function can be used for likelihood-based inference, and both σ and k can be estimated simultaneously. While the new parameter k may take the role of a nuisance parameter, it allows the distribution to be more flexible. Most importantly, estimates of σ become comparable across different temporal resolutions; see Fig. 2.

3.3 Robustness and infinite divisibility

Robustness is related to the probabilistic concept of infinite divisibility. Roughly speaking, a distribution is infinitely divisible if it can be expressed as the distribution of a sum of independent random variables. More precisely, in terms of the characteristic function ϕ of a distribution, ϕ is infinitely divisible if for every $n \in \mathbb{N}$, there exists another ch.f. ϕ_n such that $\phi(u) = \phi_n(u)^n$ (Steutel and Van Harn 2004; Klenke 2008). It is important that ϕ_n is not just any function but the ch.f. of a random variable. An example of an infinitely divisible distribution is the Normal distribution with mean $\mu \in \mathbb{R}$ and standard deviation $\sigma \in \mathbb{R}^+$. Its ch.f. is

$$\phi(u; \mu, \sigma) = e^{i\mu u - \frac{1}{2}\sigma^2 u^2}. \quad (25)$$

We can choose $\phi_n(u) = \phi(u; \frac{\mu}{n}, \frac{\sigma}{\sqrt{n}})$, which is the ch.f. of another Normal distribution with mean $\frac{\mu}{n} \in \mathbb{R}$ and standard deviation $\frac{\sigma}{\sqrt{n}} \in \mathbb{R}^+$. In general, many of the commonly known distributions are infinitely divisible.

Both concepts, robustness and infinite divisibility, are linked to sums of random variables. However, the two concepts are not the same. The Laplace distribution is infinitely divisible, however, the factors of the ch.f. do not again correspond to Laplace distributions. Instead, the ch.f. of a zero-mean Laplace distribution can be factored as follows (Kotz et al 2001),

$$\phi(u) = \frac{1}{1 + \sigma^2 u^2} = \left[\left(\frac{1}{1 - i\sigma u} \right)^{\frac{1}{n}} \left(\frac{1}{1 + i\sigma u} \right)^{\frac{1}{n}} \right]^n = \phi_n(u)^n. \quad (26)$$

Each factor ϕ_n is the ch.f. of a random variable that is a difference between two i.i.d. Gamma random variables (Kotz et al 2001). This second example highlights that a distribution can be infinitely divisible but, as a step distribution, does not lead to a robust model. This is due to the fact that infinite divisibility only requires the existence of random variables that sum up to the variable in question. Robustness additionally requires that the summands belong to the same distribution as the original, only with modified parameter values. On the other hand, the converse is true and every robust random walk model of the form that we consider here must have infinitely divisible step distribution.

Theorem 3 *Let S_i , $i \in \mathbb{N}$, denote the i.i.d. steps of a random walk movement model. If the step distribution leads to a robust model, then S_i is infinitely divisible. The converse is not true, that is not every infinitely divisible step distribution leads to a robust model.*

Proof Let $\phi(u; \boldsymbol{\theta})$, with $\boldsymbol{\theta} \in \boldsymbol{\Theta}$, be the ch.f. of a single step S_i . Let $n \in \mathbb{N}$, and let g_n be the parameter transformation given by robustness. Because g_n is bijective, we can define a unique $\boldsymbol{\psi} := g_n^{-1}(\boldsymbol{\theta}) \in \boldsymbol{\Theta}$ and choose $\phi_n(u) := \phi(u; \boldsymbol{\psi})$. It follows that

$$\phi_n(u)^n = \phi(u; \boldsymbol{\psi})^n = \phi(u; g_n(\boldsymbol{\psi})) = \phi(u; g_n(g_n^{-1}(\boldsymbol{\theta}))) = \phi(u; \boldsymbol{\theta}), \quad (27)$$

which shows infinite divisibility. As a counter example for the converse, we have seen above that the Laplace distribution is infinitely divisible but a model with Laplace distributed steps is not robust.

In the preceding proof, the bijectivity, and in particular the surjectivity, of the transform g_n is crucial for the existence of ϕ_n . Therefore, semi-robustness is not a sufficient criterion for infinite divisibility. Consider the Binomial distribution, which is discrete and not typically used as distribution for movement steps. Still, it serves as a counter example for a distribution that is not infinitely divisible, yet as step distribution leads to a semi-robust model. For its ch.f. is $\phi(u; p, n) = (1 - p + pe^{iu})^n$ for $p \in [0, 1]$ and $n \in \mathbb{N}$, and therefore meets the first, but not the second, condition of Theorem 1. On the other hand, as a distribution with bounded support, namely $\{k \in \mathbb{N}, k \leq n\}$, it is not infinitely divisible (Steutel and Van Harn 2004).

Even if a model both is semi-robust and has infinitely divisible step distribution, it does not follow that it is robust. Consider the model with chi-squared distributed

steps. As we have seen in section 3.1, this model is semi-robust but not robust. Still, the chi-squared distribution is a special case of the Gamma distribution and thus infinitely divisible; compare table 1. The reason for the model not being robust is that the summands, which a chi-squared random variable can be decomposed into, are generally Gamma and not again chi-squared random variables. This examples highlights that the definition of the model parameter space is an important consideration for robustness. If instead of the chi-squared distribution, which is embedded in the Gamma distribution, we directly use the Gamma distribution as probability model for steps, we immediately obtain a robust model.

We have used the same idea in section 3.2 to embed the Laplace distribution within the more comprehensive generalized Laplace distribution. Although the Laplace distribution is infinitely divisible, Laplace distributed steps lead to neither a robust nor a semi-robust model. If we define the extension described by the ch.f. (22) for $k \in \mathbb{N}$, we obtain a random walk model that is semi-robust. If we go even further and define the extension for $k \in \mathbb{R}_{\geq 0}$, the resulting model is robust.

From these considerations we can conclude that robust random walk models lie within the intersection of semi-robust models and models with infinitely divisible steps, however, they do not constitute the entire intersection; see Fig. 3.

4 Two-dimensional models

4.1 Radially-symmetric step densities

Many applications of movement modelling, especially those that consider movement of terrestrial animals, require the use of two-dimensional models. We then often describe steps by their length and bearing, which corresponds to describing a vector in polar coordinates. Accordingly, instead of assigning a distribution to steps directly, we compose step distributions of a step length distribution and a distribution for the bearing. From these, we can obtain a step distribution (i.e. a distribution for the two-dimensional vector) by taking into account the transformation from polar coordinate formulation to euclidean space. Let $\mathbf{S} = \begin{pmatrix} S_1 \\ S_2 \end{pmatrix} \in \mathbb{R}^2$ be the two-dimensional step. Then we denote by

$$R = \sqrt{S_1^2 + S_2^2} \quad (28)$$

the step length, which is the length of the vector in polar coordinates, and let $p_R(r)$ be the step length distribution. Let $p_\Gamma(\gamma)$ denote the distribution of the bearing. Note that, in accordance with common usage, we use capital letters for random variables and small letters for their realizations. The transformation between the two coordinate systems is given by $S_1 = R \cos \Gamma$ and $S_2 = R \sin \Gamma$. Assuming that step length and bearing distributions are independent, we obtain as step density

$$p_{S_1, S_2}(s_1, s_2) = \frac{1}{\sqrt{s_1^2 + s_2^2}} \cdot p_R(\sqrt{s_1^2 + s_2^2}) \cdot p_\Gamma(\text{Arg}(s_1 + is_2)), \quad (29)$$

where $\text{Arg}(\cdot)$ denotes the principle argument of a complex number. The factor $(\sqrt{s_1^2 + s_2^2})^{-1}$ is due to the coordinate system transformation.

A classic assumption for simple random walk models is that bearings have uniform distribution on the interval $(-\pi, \pi]$, which leads to a bearing density $p_\Gamma(\gamma) = \frac{1}{2\pi}$ (Bartumeus et al 2005; Smouse et al 2010; James et al 2011). If movement is assumed to be persistent in its direction, we may release this assumption and use a von Mises or wrapped Cauchy distribution instead. In case of a correlated random walk, a non-uniform bearing distribution would be centred around the bearing of the previous step. In a biased random walk, the bearing distribution would have a (possibly time-varying) location parameter that represents a global tendency towards a certain direction or goal location (Morales et al 2004; McClintock et al 2013; Benhamou 2013). Here, we only consider models with uniform bearing distribution.

and therefore step densities of the form

$$p_{S_1, S_2}(s_1, s_2) = \frac{1}{2\pi\sqrt{s_1^2 + s_2^2}} \cdot p_R(\sqrt{s_1^2 + s_2^2}). \quad (30)$$

This density function is radially symmetric, and we can simply write

$$p_{S_1, S_2}(r) = \frac{1}{2\pi r} p_R(r) \quad (31)$$

for $r = \sqrt{s_1^2 + s_2^2}$. Note that we distinguish the radius density p_R and radially-symmetric step density p_{S_1, S_2} via the subscript.

The radial symmetry of the density (30) enables us to compute its ch.f. via a Hankel transform. The Hankel transform of order ν of a function $f(r)$ for $r \geq 0$ is given by the integral

$$\mathcal{H}_\nu\{f\}(u) = \int_0^\infty r f(r) J_\nu(ru) dr, \quad (32)$$

where J_ν denotes the Bessel function of the first kind of order ν (Piessens 2000). The ch.f. of a two-dimensional random vector with joint density (31) can be calculated as

$$\phi(\mathbf{u}) = 2\pi \mathcal{H}_0\{p_{S_1, S_2}\}(\|\mathbf{u}\|). \quad (33)$$

For details about the calculation, see Appendix B. Because ϕ only depends on the norm of \mathbf{u} and hence is radially symmetric as well, we also use the notation $\phi(\|\mathbf{u}\|)$. Hankel transforms have been computed for a variety of functions, which in the following simplifies our analysis of characteristic functions for two-dimensional step distributions.

4.2 Robust two-dimensional models

In the following, we look for robustness among two-dimensional models. A direct way of verifying robustness is via the two-dimensional ch.f. according to Definition 1 or 2. In the case where the step distribution has a radially symmetric density function, it depends on the step distribution $p_{S_1, S_2}(r)$ whether the Hankel transform in formula (33) can be readily obtained or not. Alternatively, we can draw on our previous results for one-dimensional models.

Theorem 4 Consider a random walk model with two-dimensional steps that have radially symmetric density of the form (30). If the marginal step distribution, given by the density $p_{S_1}(s_1) = \int_{-\infty}^{\infty} p_{S_1, S_2}(s_1, s_2) ds_2$, leads to a (semi-) robust model in one dimension, then the two-dimensional model is (semi-) robust as well.

Proof Let $\phi(\|\mathbf{u}\|; \boldsymbol{\theta})$ denote the radially symmetric ch.f. of the two-dimensional steps, where $\boldsymbol{\theta} \in \Theta$ are the model parameters. The ch.f. of the marginal density is

$$\begin{aligned} \int_{-\infty}^{\infty} e^{iu_1 s_1} p_{S_1}(s_1) ds_1 &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{iu_1 s_1} p_{S_1, S_2}(s_1, s_2) ds_1 ds_2 \\ &= \phi(\|\mathbf{u}\|; \boldsymbol{\theta}) \Big|_{u_2=0} = \phi(|u_1|; \boldsymbol{\theta}) =: \phi_{S_1}(u_1; \boldsymbol{\theta}) \end{aligned} \quad (34)$$

Let $n \in \mathbb{N}$. By assumption, there exists a function g_n such that

$$\phi_{S_1}(u_1; \boldsymbol{\theta})^n = \phi_{S_1}(u_1; g_n(\boldsymbol{\theta})). \quad (35)$$

Because of the previous calculations, we also have $\phi(|u_1|; \boldsymbol{\theta})^n = \phi(|u_1|; g_n(\boldsymbol{\theta}))$. Replacing u_1 by $\|\mathbf{u}\|$ yields semi-robustness for the two-dimensional model. The parameter transformation is the same for the two-dimensional and the marginal one-dimensional model, therefore if the one-dimensional model is robust, the same holds for the two-dimensional one.

With this result, we have established a link between one- and two-dimensional models. The correspondence of the characteristic functions given in equation (34) allows us to compute the ch.f. of the radially symmetric two-dimensional model directly from the ch.f. of the one-dimensional model, and vice versa. Whether it is easier to obtain the two-dimensional ch.f. via the Hankel transform of the two-dimensional density or via the ch.f. of the one-dimensional marginal depends on which of the two densities is available. From the two-dimensional ch.f., in turn, we can calculate the two-dimensional, radially symmetric step density via an inverse Hankel transform, which is self-reciprocal.

To demonstrate these relationships, we now present three example models and their robustness properties.

Example 1 (Exponential step length) A common step length distribution used for movement analyses is the exponential distribution (Smouse et al 2010; DeMars et al 2013), which has density $p_R(r) = \frac{1}{\lambda} e^{-\frac{r}{\lambda}}$. Using this in the step density (31), we obtain

$$p_{S_1, S_2}(r) = \frac{1}{2\pi\lambda r} e^{-\frac{r}{\lambda}}. \quad (36)$$

The Hankel transform of order zero is given by $\mathcal{H}_0\{p_{S_1, S_2}\}(u) = \frac{1}{2\pi} (1 + \lambda^2 u^2)^{-\frac{1}{2}}$ (Piessens 2000), and thus the ch.f. is

$$\phi(\|\mathbf{u}\|; \lambda) = \frac{1}{\sqrt{1 + \lambda^2 \|\mathbf{u}\|^2}} \quad (37)$$

From this, we can already see that the exponential step length model, where $\lambda > 0$ is the only parameter, is neither robust nor semi-robust. The marginal of the density p_{S_1, S_2} is

$$p_{S_1}(s_1) = \frac{1}{\lambda\pi} K_0\left(\frac{|s_1|}{\lambda}\right), \quad (38)$$

where K_0 denotes the Bessel function of the second kind of order zero. The ch.f. of the marginal is $\phi(u; \lambda) = (1 + \lambda^2 u^2)^{-\frac{1}{2}}$. This is in fact the ch.f. of a generalized (asymmetric) Laplace distribution with location and asymmetry parameters being zero, and with scale λ and power $k = \frac{1}{2}$, which we have seen before to be robust; compare section 3.2 and Table 1. Therefore, if we embed the exponential step length model in an extended model with step characteristic function

$$\phi(\|\mathbf{u}\|; \lambda, k) = \frac{1}{(1 + \lambda^2 \|\mathbf{u}\|^2)^k}, \quad (39)$$

for $k \in \mathbb{R}_{\geq 0}$, we obtain a robust model with the two parameters $\lambda > 0$ and $k \in \mathbb{R}_{\geq 0}$. In the one-dimensional case, we could obtain the density from the ch.f. (22) via an inverse Fourier transform. However, the two-dimensional step density needs to be computed from (39) as an inverse Hankel transform. Unfortunately, the inverse Hankel transform of order zero of the function (39) is not readily available.

Example 2 (Heavy-tailed step length distribution) In one dimension, we have seen that stable step distributions lead to robust models. An example of a stable distribution with closed-form density function is the Cauchy distribution. According to Theorem 4, we can therefore construct a robust two-dimensional model by finding the two-dimensional density (31) that has the Cauchy density as marginal. We can achieve this via the identity of characteristic functions established in (34). From the ch.f. of the Cauchy distribution, we obtain a corresponding two-dimensional ch.f. $\phi(\|\mathbf{u}\|; \sigma) = e^{-\sigma\|\mathbf{u}\|}$. Applying an inverse Hankel transform according to the identity (33), we obtain (Piessens 2000)

$$p_{S_1, S_2}(r) = \frac{\sigma}{2\pi(\sigma^2 + r^2)^{\frac{3}{2}}}. \quad (40)$$

According to (31), this results in a step length density for the two-dimensional models as follows

$$p_R(r) = \frac{\sigma r}{(\sigma^2 + r^2)^{\frac{3}{2}}}. \quad (41)$$

The variance does not exist for this density, and the density is heavy-tailed. More precisely, the tail is of order $\frac{1}{r^2}$, that is we have

$$\frac{\sigma r}{(\sigma^2 + r^2)^{\frac{3}{2}}} = \mathcal{O}\left(\frac{1}{r^2}\right), \quad (42)$$

as $r \rightarrow \infty$. We will later see that the step distribution in this example is a special case of a bivariate stable distribution. Because of its relation with the univariate Cauchy, it is also known as bivariate (isotropic) Cauchy (Achim and Kuruoglu 2005; Nadarajah and Kotz 2007).

Example 3 (Normally distributed steps, or Rayleigh step length distribution) The Normal distribution is another special case of a stable distribution. Its radially symmetric two-dimensional version with mean zero is the bivariate Normal distribution with covariance matrix $\begin{pmatrix} \sigma^2 & 0 \\ 0 & \sigma^2 \end{pmatrix}$, having density

$$p_{S_1, S_2}(r) = \frac{1}{2\pi\sigma^2} e^{-\frac{r^2}{2\sigma^2}}, \quad (43)$$

and ch.f. $\phi(\|\mathbf{u}\|; \sigma) = e^{-\frac{1}{2}\sigma\|\mathbf{u}\|^2}$. The corresponding step length distribution with density

$$p_R(r) = \frac{r}{\sigma^2} e^{-\frac{r^2}{2\sigma^2}} \quad (44)$$

is a Rayleigh distribution with scale parameter $\sigma > 0$. As we can easily see from the ch.f. and also via Theorem 4, this model with Normally distribution steps is robust.

In the latter two examples, the step distributions are special cases of bivariate stable distributions. Analogously to one-dimension, an α -stable random vector $\mathbf{S} \in \mathbb{R}^2$, $0 < \alpha \leq 0$, by construction has the property

$$\sum_{i=1}^n \mathbf{S} \stackrel{d}{=} n^{\frac{1}{\alpha}} \mathbf{S} + \mathbf{b}_n \quad (45)$$

for some $\mathbf{b}_n \in \mathbb{R}^2$ (Samorodnitsky 1994). If \mathbf{S} is elliptically contoured, its ch.f. is

$$E(e^{i\mathbf{u}\cdot\mathbf{S}}) = \exp\left(i\mathbf{u}\cdot\boldsymbol{\mu} - (\mathbf{u}^T \Sigma \mathbf{u})^{\frac{\alpha}{2}}\right) \quad (46)$$

for location vector $\boldsymbol{\mu} \in \mathbb{R}^2$ and positive definite shape matrix Σ (Nolan 2013). From this form of the ch.f., we can easily see that the n th power is again the ch.f. of an α -stable random vector, with location vector $n\boldsymbol{\mu}$ and shape matrix $n^{\frac{2}{\alpha}}\Sigma$. Therefore, we immediately obtain the following theorem.

Theorem 5 *A two-dimensional random walk model with elliptically contoured steps \mathbf{S} that have bivariate stable distribution, i.e. have ch.f. (46), is robust.* \square

The bivariate Normal distribution with mean $\boldsymbol{\mu}$ and a general covariance matrix

$$\Sigma = \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}, \quad (47)$$

where ρ is the correlation, is an example of such a bivariate stable distribution for $\alpha = 2$. If \mathbf{S} is not only elliptically contoured but even radially symmetric with location $\boldsymbol{\mu} = 0$, the ch.f. (46) simplifies to

$$\phi(\|\mathbf{u}\|; \alpha, \sigma) = e^{-\sigma^\alpha \|\mathbf{u}\|^\alpha}, \quad (48)$$

for $\sigma > 0$. Example 2 and 3 were special cases for $\alpha = 1$ and $\alpha = 2$, respectively.

As in the univariate case, closed-form expressions for the density of bivariate stable distributions are available only for some special cases, e.g. the examples we have presented above. However, there are results that allow simulation of random

variables with stable distributions. For an α -stable, radially symmetric stable random vector \mathbf{S} , we have

$$\mathbf{S} \stackrel{d}{=} \sqrt{AT} \mathbf{U}, \quad (49)$$

where \mathbf{U} is a random vector with uniform distribution on the unit circle, T is a chi-squared random variable with degrees of freedom 2, and A is a univariate stable random variable, $A \sim \mathcal{S}(\frac{\alpha}{2}, 1, 2\sigma^2(\cos \frac{\pi\alpha}{4})^{\frac{2}{\alpha}}, 0)$ (Nolan 2013). Thus, to obtain a bivariate stable random vector, it is enough to generate a univariate stable random variable. For this, an algorithm is available (Weron 1996), which has been implemented in the R package ‘stabledist’ (Wuertz et al 2013). This package also provides numerical calculations of density and cumulative distribution functions.

5 Discussion

We presented a new way of classifying movement models according to their robustness against changes in temporal discretization. After providing a formal definition for movement model’s robustness, we explored which models have this property. Our definition emphasizes a systematic transformation of model parameters between temporal resolutions. This ensures that, if a model is robust, we can fit it to movement data with varying time intervals between locations, and we know how to translate model parameters between resolutions. Conversely, if a model is not robust, any results we derive from it are tied to its particular temporal resolution, and thus comparison of studies is difficult if they use data obtained at different sampling rates.

The question of robustness may already arise at a fundamental level when interfacing models with data. If a model is not robust, then it cannot use data with a particular temporal resolution to make inferences about movement behaviours at higher and lower resolutions. This is of particular concern in movement ecology, because sampling schemes for animal movement data are often subject to logistical constraints. For example, limited battery life of GPS devices often leads to lower sampling rates in favour of longer total time spans. The resolutions thus imposed on data may be very different than those for behavioural or ecological questions about movement. If a model is not robust, then it may still be semi-robust, which means that inference can be made at lower but not at higher resolution. Because the conditions for robustness and semi-robustness are rather stringent, it appears that many existing movement models may fail in this regard.

Previous approaches to the problem have been empirical or based on simulations. Several studies used fine-scale movement data with sampling intervals of a few minutes (Pépin et al 2004; Postlethwaite and Dennis 2013) or even a few seconds (Ryan et al 2004). These data were subsampled at various scales to obtain empirical relationships between the sampling interval and measured or inferred movement parameters. Such investigations have demonstrated that the sampling interval can have a strong effect on results from movement analyses. However, each of these studies is based on a specific species within a particular environment, and it is unclear whether the obtained relationships and possible correction factors can be transferred to other species and systems. Also, fine-scale movement data is rarely available, and therefore we need a more general method that relates sampling rates to movement parameters.

As an alternative to using very fine movement data, another approach has been to simulate synthetic data from movement models, such as correlated random walks, and to subsample these. Movement characteristics, such as apparent angular deviation and apparent speed, were then calculated for varying discretization of the simulated movement paths to establish relationships, which can be used to derive discretization-independent measures such as sinuosity (Bovet and Benhamou 1988; Benhamou 2004; Codling and Hill 2005; Rosser et al 2013). In this approach, the focus lies on preserving movement characteristics across varying resolution. In contrast, our robustness definitions operate at the level of the model. However, if a model is robust, this implies that model parameters follow a relationship with the sampling interval. The parameter transformation g_n in our robustness definition takes a similar role as the relationship between, e.g. angular deviation and sampling interval in Codling and Hill (2005).

In our investigations, we found that robustness is a rather strong condition for a model. This is in line with previous empirical results that highlight the sensitivity of movement characteristics to the sampling interval. For one-dimensional models, we encountered two groups of step distributions that lead to robustness. First, Theorem 1 established robustness for distributions whose characteristic function is a simple power function. Among the common distributions, those that meet this condition have support $\mathbb{R}_{\geq 0}$ and therefore only allow steps into positive direction. Such models can be applicable in situations where movement experiences external forces, such as movement within strong water currents (Luschi et al 2003) or wind-driven dispersal (de la Giroday et al 2011). The second class of step distributions that lead to robust models are the stable distributions. If steps have α -symmetric stable distribution $\mathcal{S}(\alpha, 0, \sigma, 0)$, the resulting random walk is a Lévy flight (Klafter et al 1995). In our analysis of two-dimensional models, we found few robust models. It is, again, mainly the stable distributions that constitute examples of robust models. Stable distributions are fat-tailed and do not have second (and higher) moments, the Normal distribution for $\alpha = 2$ being the only exception. To circumvent this problem, the related Lévy walk was introduced (Klafter et al 1995).

On the one hand, Lévy walks may be attractive models because of their scale-invariance and optimality in certain foraging situations (Viswanathan et al 1999). On the other hand, it is highly debated whether Lévy walks are suitable models for movement and fit empirical data (Benhamou 2007; James et al 2011; Edwards 2011; Pyke 2015). A major point of controversy arises from the difficulty of inferring processes from patterns. Although movement patterns may fit Lévy walks, the underlying process does not necessarily need to be a Lévy walk but may be due to more complex behaviour (Benhamou 2007; Plank et al 2013). Interestingly, the risk of misidentifying a (composite) correlated random walk as Lévy walk is strongly affected by the data sampling scheme and whether higher dimensional data is projected on a lower dimension (Plank and Codling 2009; Codling and Plank 2011). The debate on Lévy walks further concerns statistical methods that are used to detect Lévy walk behaviour in data (White et al 2008; Edwards 2011). Even the application of Lévy walks within optimal foraging theory as Lévy foraging hypothesis has been met with scepticism (Pyke 2015).

In our paper, we are merely interested in the question if there are models that are robust to changes in sampling rates, and which models these are. Because of the complexity of the issue, we here concentrated on investigating this question for basic random walks. Because we assume that our random walks have i.i.d. steps, this excludes correlated random walks, in which the direction of a step depends on the direction of the previous step. We restrict our analysis of two-dimensional models further to radially symmetric step densities, which also excludes biased random walks. Even among these rather simple models, we found few that are robust. This foreshadows that robustness may be rare, if existent at all, among more complex models. But many contemporary models include forms of behavioural mechanisms beyond the mere random walk and will likely continue to become more sophisticated (Holyoak et al 2008; Smouse et al 2010; Fagan et al 2013). This means that most analyses of movement data to date are restricted to the temporal resolution of each study, limiting extrapolation of results and comparison between studies. Here, we have proposed a new fundament for analyzing movement models' robustness to varying sampling rates. Our analysis of simple random walks serves to illustrate the new framework and to provide a first step towards a mathematical rigorous treatment of the problem. An important next step will be to extend the framework to more complex and biologically realistic models that include temporal or spatial heterogeneities.

We suggest that a path for further investigation lies in continuing to look for robust extensions of models. The results we have presented here about robust random walk models need not be exhaustive. In Example 1, we have shown that the two-dimensional model with exponential step length is not robust but can be extended to a robust model with an additional parameter (the power of the ch.f.). This would be similar to the one-dimensional example in section 3.2, where we demonstrated a robust extension to the Laplace model. If we would use this extended model and during statistical inference estimate the power parameter together with all other parameters, we would be using a robust model. Such an extension is, in theory, also possible for other models. Unfortunately, although we may be able to straightforwardly construct the characteristic function of such a robust extension, it can be more difficult to derive the bivariate step density. To overcome this problem, one could fall back on numerical solutions. For example, one could solve the inverse Hankel transform of equation (39) numerically and embed this process into an inferential optimization routine such as likelihood maximization or an MCMC algorithm.

Another avenue for future research will be to release the strict conditions of robustness. In our definition presented here, the parameter transformation g_n is a key element. It assures that we can systematically translate results about model parameters between analyses using different sampling rates. The works by Pépin et al (2004) and Codling and Hill (2005) tried to establish such a transformation empirically for some specific movement quantities. The relationships they found were able to correct for different sampling rates to some extent. This suggests that although our robustness is a strong condition on a model, there may be models that are approximately robust within certain ranges of sampling intervals. Often, we do not wish to compare data analyses with widely varying sampling intervals. When we analyze movement, we always have to be aware of the behavioural scale of interest, as the behavioural processes may vary across scales (Yackulic et al 2011; Fleming et al 2014). Also, the

same movement path may be appropriately described by different models (e.g. ballistic or diffusive) when viewed at different scales. However, it may be a reasonable goal to compare movement analyses with sampling intervals within, e.g. a range of a few hours. Within such a reasonable range, an approximate type of robustness may be sufficient.

Therefore, a useful extension of the robustness framework presented here is a definition of approximate robustness, which does not require the model distributions to be exactly the same across resolutions but only approximately. We provide such a definition in Schlägel and Lewis (2015), in which we also make a step from simple random walks to spatially-explicit random walks that include a resource-selection component. Our present paper already demonstrates that analytical calculations become technically involved as soon as we move to two-dimensional models. Therefore, to include more biological realistic models in our robustness analysis, it is necessary to branch out to numerical as well as Monte Carlo (i.e. simulation) methods. For example, a challenge for future investigations of more complex models will be to identify a suitable parameter transformation g_n as required by the robustness definition. For this, simulations can be used, relating parameter estimates to the subsampling amount n , similar to the approach by Benhamou (2004) and Codling and Hill (2005).

We have put forward a new mathematical rigorous approach to address the question how sampling rate of movement data affects statistical inference and whether models, a key tool for analyzing movement data, can be robust to varying sampling rates. While our analysis here focuses on simple random walks, we hope to encourage further research built on this theoretical basis. We have presented our new framework of robustness to temporal resolution in the context of movement ecology. However, random walks serve as models for movement also in other areas than ecology, for example cell movement during physiological processes (Dickinson and Tranquillo 1993) or blood vessel growth, termed angiogenesis (Plank and Sleeman 2003). Therefore, our framework could be interesting to these fields as well.

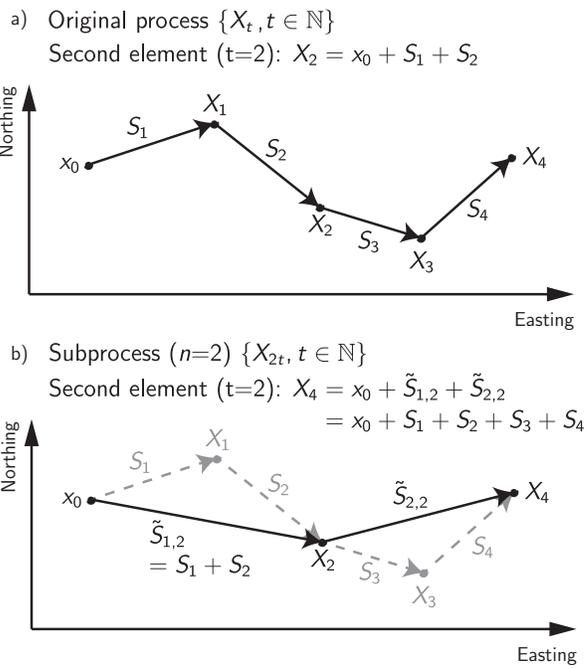


Fig. 1 Schematic of locations and steps between locations for a) an original process and b) its subprocess for $n=2$. The original process consists of steps S_i , whereas the subprocess has steps $\tilde{S}_{i,2}$, which are sums of the original steps

Table 1 List of distributions, which as random walk step distributions lead to semi-robust or robust models. The table indicates which of these distributions are also robust or infinitely divisible. We do not include any statements about infinite divisibility for two-dimensional models as we have not discussed this in our paper

Distribution	Ch.f. $\phi(u)$	Parameter space	Semi-rob.	Rob.	Inf. div.
Continuous distributions with support \mathbb{R}					
Normal	$e^{iu\mu - \frac{1}{2}\sigma^2 u^2}$	$\mu \in \mathbb{R}, \sigma \in \mathbb{R}^+$	✓	✓	✓
Cauchy	$e^{iu\mu - \sigma u }$	$\mu \in \mathbb{R}, \sigma \in \mathbb{R}^+$	✓	✓	✓
Lévy	$e^{iu\mu - \sigma u ^{\frac{1}{2}}(1-i\text{sign}(t))}$	$\mu \in \mathbb{R}, \sigma \in \mathbb{R}^+$	✓	✓	✓
Laplace extension	$\left(\frac{1}{1+\sigma^2 u^2}\right)^k$	$\mu \in \mathbb{R}, \sigma \in \mathbb{R}^+, k \in \mathbb{N}$	✓	✗	✓
Generalized asymmetric Laplace	$\frac{e^{iu\mu}}{(1+\sigma^2 u^2 + i\nu u)^k}$	$\mu, \nu \in \mathbb{R}, \sigma, k \in \mathbb{R}_{\geq 0}$	✓	✓	✓
Continuous distributions with support \mathbb{R}^2					
Bivariate Cauchy	$e^{-\sigma\ u\ }$	$\sigma \in \mathbb{R}^+$	✓	✓	
Bivariate Normal	$e^{-\frac{1}{2}\sigma\ u\ ^2}$	$\sigma \in \mathbb{R}^+$	✓	✓	
Continuous distributions with support $\mathbb{R}_{\geq 0}$					
Gamma	$\frac{1}{(1-\sigma u)^\kappa}$	$\sigma \in \mathbb{R}^+, \kappa \in \mathbb{R}^+$	✓	✓	✓
Chi-squared	$\frac{1}{(1-2u)^{\frac{k}{2}}}$	$k \in \mathbb{N}$	✓	✗	✓
Discrete distributions					
Poisson	$e^{\lambda(e^{iu}-1)}$	$\lambda \in \mathbb{R}_{\geq 0}$	✓	✓	✓
Bionomial	$(pe^{iu} + (1-p))^n$	$p \in [0, 1], n \in \mathbb{N}_0$	✓	✗	✗

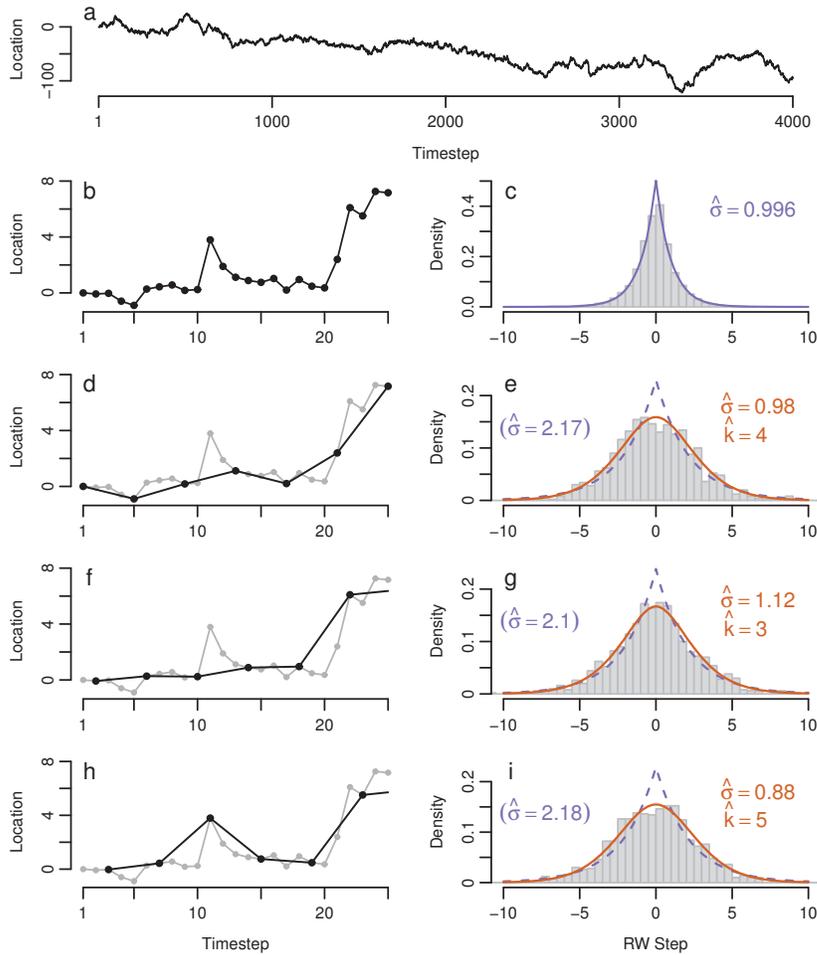


Fig. 2 Inference results when using the Laplace model versus the generalized Laplace model. **Panel a:** Simulated 1D-random walk with Laplace distributed steps with mean zero and scale $\sigma = 1$. **Panel b:** Excerpt of panel a for time steps 1 to 25. **Panel c:** Histogram of realized steps of the random walk, fitted with a Laplace distribution with mean zero. The estimate of the scale σ is denoted by $\hat{\sigma}$. **Panels d, f, h:** We subsampled the random walk, taking every 4th location. The panels show the original random walk (in grey) and the subsample (in black). We obtain different subsamples, depending on the starting location of the subsampling procedure. The three panels start the subsampling at x_1 , x_2 , and x_3 , respectively. Each subsampled path is 1000 time steps long. **Panels e, g, i:** Histograms of realized steps of the subsampled paths. Each histogram corresponds to the subsample to its left. Steps were fitted with a Laplace distribution (dashed purple line) and with a generalized Laplace distribution as given in equation (24) (red solid line). The generalized Laplace model accounts for the subsampling with its additional parameter k (here $k = 4$) and is thus the correct model. When fitted to the subsampled random walks, k was estimated simultaneously with σ . The estimate of k varies for the different subsamples, reflecting the stochasticity of the data, but it is always close to 4. When using the generalized Laplace model, estimates of the scale σ are valid estimates for the scale of the original random walk as well. In contrast, the scale estimate from the simple Laplace model (given in parenthesis) cannot validly represent the original scale and naturally overestimates σ .

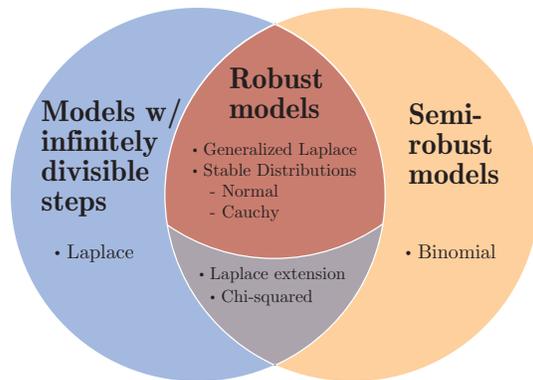


Fig. 3 Graphic depiction of the relationships between semi-robust and robust models and models with infinitely divisible step distributions. Each section contains examples from the text for step distributions that lead to the type of model

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A Scaling property for a step density with symmetric stable distribution

Here, we present a short calculation that shows the scaling property given in equation (20) for a step density $p_S(s)$ when $S \sim \mathcal{S}(\alpha, 0, \sigma, 0)$. The ch.f. of S is $\phi(u) = \exp(-\sigma^\alpha |u|^\alpha)$. From this, the density of S can be obtained via an inverse Fourier transform,

$$p_S(s) = \int_{-\infty}^{\infty} \exp(-ius) \phi(u) du. \quad (50)$$

Analogously, we calculate the density of the summed steps $\tilde{S}_{i,n} = \sum_{j=0}^{n-1} S_{ni-j}$ as

$$p_{\tilde{S}_{i,n}}(s) = \int_{-\infty}^{\infty} \exp(-ius) \phi(u)^n du = \int_{-\infty}^{\infty} \exp(-ius) \exp(-\sigma^\alpha n |u|^\alpha) du. \quad (51)$$

A substitution, $t = n^{\frac{1}{\alpha}} u$, yields

$$p_{S_{t,n}}(s) = n^{-\frac{1}{\alpha}} \int_{-\infty}^{\infty} \exp(-i n^{-\frac{1}{\alpha}} s) \exp(-\sigma^{\alpha} |t|^{\alpha}) dt = \frac{1}{n^{\frac{1}{\alpha}}} p_S\left(\frac{s}{n^{\frac{1}{\alpha}}}\right). \quad (52)$$

B Characteristic function of a radially symmetric random vector

Here, we provide details about the link between the characteristic function of a radially symmetric random vector and the Hankel transform as stated in equation (33). The ch.f. of the two-dimensional random vector \mathbf{S} with density (30) is given by

$$\phi(\mathbf{u}) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{i\mathbf{u} \cdot \mathbf{s}} p_{S_1, S_2}(s_1, s_2) ds_1 ds_2. \quad (53)$$

Because the density is radially symmetric, we switch to polar coordinates via $s_1 = r \cos \gamma$ and $s_2 = r \sin \gamma$, where the angle γ is chosen such that the vector \mathbf{u} has angle zero. The determinant of the Jacobian for this transformation is $|J| = r$. The dot product of the vectors \mathbf{u} and \mathbf{s} can be written as $\mathbf{u} \cdot \mathbf{s} = \|\mathbf{u}\| r \cos \gamma$. With this, we obtain

$$\phi(\mathbf{u}) = \int_0^{\infty} \left(\int_0^{2\pi} e^{i\|\mathbf{u}\| r \cos \gamma} d\gamma \right) p_{S_1, S_2}(r) r dr. \quad (54)$$

The symmetry of the cosine allows us to simplify the inner integral as follows,

$$\int_0^{2\pi} e^{i\|\mathbf{u}\| r \cos \gamma} d\gamma = 2 \int_0^{\pi} e^{i\|\mathbf{u}\| r \cos \gamma} d\gamma = 2\pi J_0(\|\mathbf{u}\| r), \quad (55)$$

where J_0 denotes the Bessel function of the first kind. The last equation follows from an integral representation of the Bessel function (Abramowitz and Stegun 1964, 9.1.21). With this, the characteristic function becomes

$$\phi(\mathbf{u}) = 2\pi \int_0^{\infty} p_{S_1, S_2}(r) r J_0(\|\mathbf{u}\| r) dr. \quad (56)$$

The integral is the Hankel transform of order zero of the density $p_{S_1, S_2}(r)$ evaluated at $\|\mathbf{u}\|$.