

The shape of the spatial kernel and its implications for biological invasions in patchy environments

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Ecological and epidemiological invasions occur in a spatial context. We investigated how these processes correlate to the distance dependence of spread or dispersal between spatial entities such as habitat patches or epidemiological units. Distance dependence is described by a spatial kernel, characterized by its shape (kurtosis) and width (variance). We also developed a novel method to analyse and generate point-pattern landscapes based on spectral representation. This involves two measures: continuity, which is related to autocorrelation and contrast, which refers to variation in patch density. We also analysed some empirical data where our results are expected to have implications, namely distributions of trees (*Quercus* and *Ulmus*) and farms in Sweden. Through a simulation study, we found that kernel shape was not important for predicting the invasion speed in randomly distributed patches. However, the shape may be essential when the distribution of patches deviates from randomness, particularly when the contrast is high. We conclude that the speed of invasions depends on the spatial context and the effect of the spatial kernel is intertwined with the spatial structure. This implies substantial demands on the empirical data, because it requires knowledge of shape and width of the spatial kernel, and spatial structure.

Keywords: kurtosis; spread of disease; point patterns; spectral density; dispersal; invasion

1. INTRODUCTION

Both ecological and epidemiological studies are concerned with invasion of organisms, the mechanism and dynamics of which are essential components of numerous specific topics. These include the following: recolonization of habitats [1,2], migration in response to variations in climate [3,4], the spread of diseases [5–7] and invasion of alien species [8,9]. The rate of invasion is determined largely by the spatial spread of organisms, which is commonly modelled using some probability density distribution describing the probability of dispersal or infectious contacts as a function of distance. Here, we refer to these distributions as spatial kernels because that term has been used in both epidemiological (e.g. [6,10]) and ecological (e.g. [11,12]) studies. In the ecological literature, they are also known as dispersal kernels [3,13], redistribution kernels [14,15], dispersal curves [16] and displacement kernels [17,18], and in epidemiological publications they are sometimes called contact kernels [7,19].

Here, we focus on the importance of spatial kernel characteristics in spatially explicit settings. The spatial kernel can be characterized by its scale and shape, which are quantified by variance (v) and kurtosis (κ), respectively [17]. Dispersal of organisms that follow a random-walk process results in a Gaussian distribution [20], where $\kappa = 3$ or $\kappa = 2$ for one- and two-dimensional kernels, respectively [17,21]. In this study, we consider two-dimensional kernels, because most ecological and epidemiological dynamics occur in at least two-

dimensional landscapes. Figure 1 shows examples of spatial kernels with different scales and shapes.

For epidemiological studies, assumptions regarding the shape of the kernel should be derived from knowledge of how transmission occurs. For example, if transmission arises through direct contacts, the kernel should be based on the movement behaviour of the hosts. However, for many pathogens, transmission is mediated via a vector. If the movement of the vector resembles a random walk, a fair assumption is to model transmission with a Gaussian kernel [22]. Yet outbreak data [7] and studies of pathways that potentially mediate transmission [23] often reveal highly leptokurtic distributions. Furthermore, empirical studies in ecological settings show that dispersal frequently deviates from Gaussian distributions. A leptokurtic ($\kappa > 2$) distribution is usually observed for both plants [14,24] and animals [4,25], which implies a peak in density at short distances but at the same time a fat tail, indicating fairly frequent long-distance dispersers. A number of explanations have been proposed for leptokurtic dispersal, including population differences in dispersal abilities [26], temporal variation in the diffusion constant [27] and loss of individuals during dispersal [28].

Previous studies have focused on the shape of the kernel in relation to invasion speed. If Gaussian dispersal in a homogeneous and continuous space is assumed, the invasion can be modelled as a reaction–diffusion process, and the speed of the invasion will be given by the diffusion constant [8], which can be calculated from the kernel variance. Fat-tailed kernels are generally considered to result in faster invasion speed, and highly leptokurtic kernels that are exponentially unbounded may result in accelerating invasions [3,14,19]. In recent research, the centre of attention has moved further away from assumptions of

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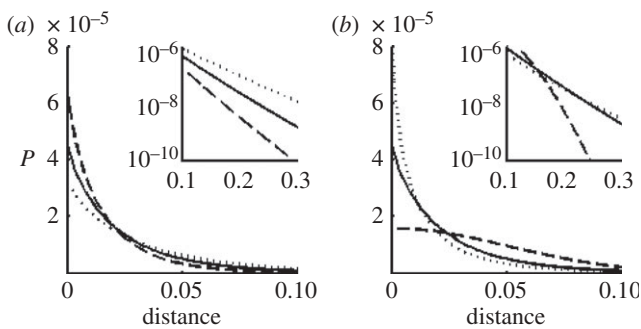


Figure 1. (a) Probability densities at distances from the source shown for shape/kurtosis (κ) and scale/variance (ν): $\kappa = 4$ and $\nu = 0.0025$ (dashed), $\nu = 0.005$ (solid) and $\nu = 0.01$ (dotted), respectively. (b) Corresponding probability densities for $\nu = 0.005$ and $\kappa = 2$ (dashed), $\kappa = 4$ (solid) and $\kappa = 6$ (dotted). The diagrams in the inserts in both (a) and (b) are the same as the main diagrams but at larger distances from the source and with a logarithmic y -axis.

homogeneous and continuous space, and is instead turning to heterogeneous landscapes [9,29]. In this paper, we take yet another step and focus on invasion of organisms in environments where the habitats or epidemiological units are best represented as discrete entities with a fixed spatial location. Examples of this are studies of livestock epidemics [6,30] and ecological invasions, where habitats and epidemiological units are regarded as isolated patches surrounded by a hostile matrix (as is done in metapopulation studies). Throughout this article, we refer to such habitats and epidemiological units as patches, hence using terminology that is perhaps more familiar to ecologists. Our aim here is to explore the impact of shape and scale of spatial kernels on the speed of biological invasion in patchy environments. The results may support both future research and the predictive power of estimated speed of invasions, which we presume can also depend on the spatial pattern of focal entities. Therefore, we introduce a novel method that uses a spectral density approach to incorporate spatial aggregation into point-pattern representations. Accordingly, we test whether the role of scale and shape depends on spatial structures such as aggregation in patchy landscapes. To exemplify what spatial patterns may be found, we also analyse relevant point-pattern data by applying a method developed from the approach described by Muggleston & Renshaw [31].

2. MATERIAL AND METHODS

In this study, we focused on invasion in spatially explicit, patchy landscapes. Such a strategy requires methods for representations of (i) the spatial distribution of patches, and (ii) the distance-dependent probability of colonization between patches. Patch distributions were generated and characterized using a novel technique based on Fourier transform, and the probability of colonization was modelled with spatial kernels characterized by their scale and shape, as described by Lindström *et al.* [17].

(a) Analysis and generation of point-pattern landscapes

Keitt [32] defined neutral landscapes for lattices as models in which the value at any point in the landscape can be

considered random, and he also emphasized that this does not exclude models with spatial autocorrelation. This neutral landscape definition can also be applied to point-pattern landscapes, where the distribution of points may deviate from random as long as the exact position of a point cannot be predicted. We refer to these as neutral point-pattern landscapes (NPPLs), and in this section we describe two measures that we designate contrast (δ) and continuity (γ), which can be used to characterize such landscapes. Technical details and mathematical explanations of these parameters are presented in electronic supplementary material, appendix A.

Continuity (γ) is a scale-free measure of spatial autocorrelation that is based on assumptions of self-similarity over multiple scales. Large values of γ indicate that nearby areas have similar density. By using Fourier transform as described by Muggleston & Renshaw [33], the point pattern can be represented by a series of sine and cosine terms, and γ is given by the negative slope of a linear regression fitted to the $\log(\text{frequency})$ versus $\log(\text{amplitude})$ of these elements. Readers familiar with time-series analysis may find it useful to interpret this measure as a two-dimensional point-pattern equivalent to the spectral colour parameter of 1/f-noise (for a review of 1/f-noise, see [34]).

Continuity determines whether areas with similar patch density are located near each other or are more scattered in the landscape. It does not, however, provide any information about the differences in patch density in the landscape, and thus we introduce contrast (δ), which is a normalized and a scale-free measure of density dispersion. Large values of δ reflect a substantial difference between sparse and dense areas. We measure contrast in the frequency domain, and this measure can be interpreted as a point-pattern equivalent of coefficient of variation. Figure 2 shows examples of NPPLs generated using different values of contrast and continuity. For further details regarding continuity and contrast and generation of NPPLs, see the electronic supplementary material. The assumption of self-similarity over scales in an NPPL is crucial to the use of a single continuity measure γ for spatial autocorrelation. To determine whether this assumption holds, we analyse some relevant empirical point-pattern data. These analyses also provide some estimates of what parameter values (of continuity and contrast) can be expected in studies in which our results have implications. The empirical data consist of distributions of two species of trees (*Quercus robur* (English oak) and *Ulmus glabra* (wych elm)) and farms (pig and cattle) in Sweden, all represented by their Cartesian coordinates. The data on *Ulmus* and *Quercus* were provided by the County Administrative Board of Östergötland and had been collected in a massive inventory of large and old trees [35]. The farm data were supplied by the Swedish Board of Agriculture and we used the same data as used for kernel estimation in Lindström *et al.* [23]. A more detailed analysis of the farm data has been reported by Nöremark *et al.* [36].

(b) The spatial kernel

In this study, we modelled the spatial kernel with a generalized normal distribution [37]. In Lindström *et al.* [17] this was extended to two-dimensional symmetrical kernels. Kernel density is given by

$$K(d) = \frac{e^{-(d/a)^b}}{S}, \quad (2.1)$$

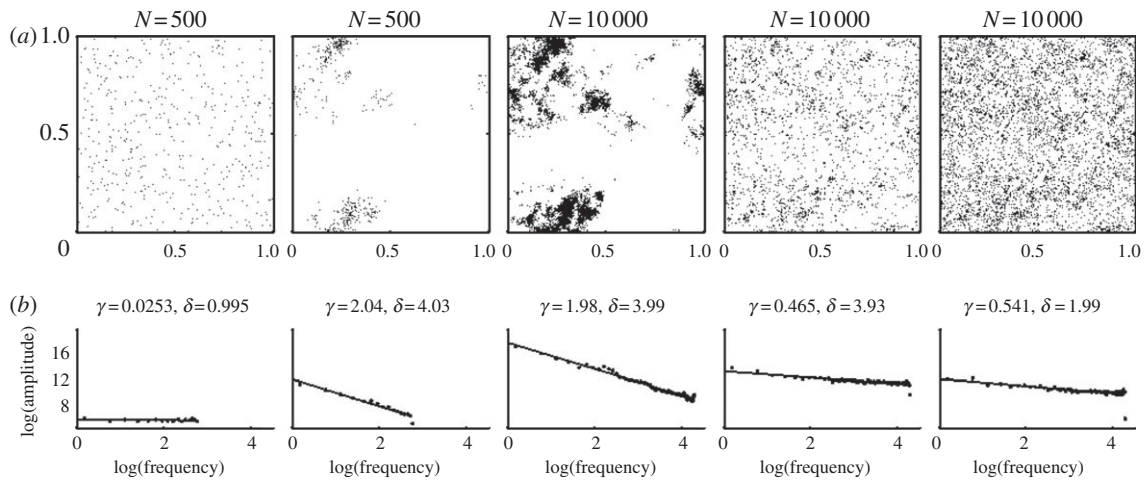


Figure 2. (a) Examples of spatial distributions of patches used in the simulation study and (b) their corresponding spectral densities with estimated continuity (γ) and contrast (δ).

where d is the distance, and a and b are parameters that regulate the scale and shape of the kernel. The kernel is normalized by S , as discussed further below. Note that equation (2.1) may have the shape of some well-known distributions, such as the normal distribution ($b = 2$) or the negative exponential ($b = 1$).

We focus on rotationally symmetric kernels and quantify scale and shape by two-dimensional variance and kurtosis, respectively, as defined by Clark *et al.* [21] and Lindström *et al.* [17]. As described in Lindström *et al.* [17], the two-dimensional variance (ν) is defined as the second moment and is a kernel measurement, which is perhaps more familiar to the empirical ecologist as expected net squared displacement. Kurtosis (κ) is a dimensionless quantity defined as the fourth moment divided by the square of the second moment, and in Lindström *et al.* [17] it was shown that for equation (2.1) ν and κ are given by

$$\nu = a^2 \frac{\Gamma(4/b)}{\Gamma(2/b)} \quad \text{and} \quad \kappa = \frac{\Gamma(6/b)\Gamma(2/b)}{(\Gamma(4/b))^2}, \quad (2.2)$$

where Γ is the gamma function.

In studies focused on continuous space, the spatial kernel usually describes the probability of dispersal events as a function of distance. Here, we instead consider invasion as a series of colonization events in discrete patches. Implementation of spatial kernels is somewhat less straightforward because the probability of colonization events is also influenced by the location of patches. Hence, the spatial kernel can be incorporated in different ways that correspond to different assumptions of the dispersal process. First, one may assume that every occupied patch overall has the same potential to colonize other patches. For instance, this may correspond to the assumption of animals dispersing actively without any mortality, or transmission of disease between farms through human-mediated contacts such as animal transports, given that the number of shipments does not depend on the farm location [23]. In these instances, the spatial kernel describes how much more probable the colonizations of nearby patches are as compared with the colonizations of distant patches, and we refer to this as relative density dependence. This is implemented by normalizing the spatial kernel by summation over all possible patches such that the colonization from patch j is

normalized over all patches $k \neq j$ by

$$S = \sum_{k=1}^{N-1} e^{-(d_{kj}/a)^b}, \quad (2.3)$$

where N is the number of patches.

Second, one may assume that the probability that one occupied patch will colonize another patch is a fixed probability that depends on between-patch distance and thus does not depend on the location of all other patches. This would correspond to situations where colonization is the result of a large number of passively dispersing (e.g. by wind) units, such as seeds or pathogens, and we refer to this as absolute density dependence. Equation (2.1) is then normalized by the following [17]:

$$S = 2\pi a^2 \Gamma(2/b)/b. \quad (2.4)$$

(c) Simulation

The effect of κ and ν on invasion was estimated by simulating invasions in NPPLs with a discrete time scale and the combination of parameters given in table 1. Some combinations of δ and γ could not be generated (figure 3), because it is not feasible to uphold a pattern with high spatial autocorrelation without any contrast in patch density. Starting at a random patch, we simulated invasions with 200 replicates of each parameter combination, considering both absolute and relative distance dependence. To reduce edge effects, we arranged the landscape such that the starting point was located in the centre of the NPPL; such arrangement is possible owing to the periodic nature of the Fourier transform.

(i) Probability of colonization

In the discrete time and space simulation model presented here, the probability (p) of colonization of an unoccupied patch by an occupied patch at a distance d in one time step is given by $p = RK(d)$, where $K(d)$ is the kernel from equation (2.1), normalized by equation (2.3) or (2.4), and R is a constant determining the colonization pressure. For relative distance dependence, we use $R = 0.1$, and, on average, an occupied patch will initially colonize one other patch every 10th time step. To achieve comparable results for absolute distance dependence, we use $R = 0.1/(N - 1)$, where N is the number of patches. Thereby, on average, we obtain the same probability of colonization as for relative

Table 1. Input parameters of the simulations and values used.

parameter	explanation	parameter values
δ	contrast of patch density	1, 2, 3, 4, 5
γ	continuity of patch density	0, 0.5, 1, 1.5, 2
N	number of patches	500, 10 000
ν	variance of kernel	0.0025, 0.005, 0.01
κ	kurtosis of kernel	2, 4, 6

distance dependence, if the distribution is random. In a non-random landscape, patches in sparse (dense) areas will have a lower (higher) probability to colonize other patches.

(ii) Simulation outputs and analysis

To address the current objective of investigating the importance of the shape of the spatial kernel for biological invasions in a spatially explicit context, we analysed two measurements of invasion speed. First, we investigated the time, T_1 , required to reach fixed proportions, p_1 , of occupied patches, and we used $p_1 = 10, 50$ and 90 per cent to acquire estimates at different stages of the invasion. Second, we analysed the speed, ψ , of spatial spread, defined as $\psi = d_1/t_1$, where d_1 is a fixed distance, and t_1 the number of time steps required to reach that distance. We analysed the results for $d_1 = 0.25$ (given relative to the unit square), a distance at which the influence of the edge effect is considered very small. For ψ , we present the results of both absolute and relative distance dependence.

The results were analysed with an ANOVA (type three) for each combination of landscape parameters, with the output parameters ψ and T_1 as dependent variable, and variance and kurtosis as categorical predictors. Since the outputs showed non-normal residuals, a Box-Cox transform [38] was performed for each analysis. The exact values of continuity and contrast varied between replicates, and therefore, these parameters were included as continuous covariables. The relative effect of kurtosis was calculated by $E_\kappa = MS_\kappa / (MS_\kappa + MS_\nu)$, where MS_κ and MS_ν are the mean sum of squares of κ and ν , respectively.

3. RESULTS AND DISCUSSION

(a) Simulations of invasion

Our results show that the shape of the dispersal kernel can have a substantial effect on the invasion speed, in terms of both the number of occupied patches (figure 3a) and the spatial range of the invasion (figure 3b). However, the extent of the impact depends on the spatial structure of patches, as well as assumptions regarding the dispersal process. The black areas in the diagrams in figure 3 indicate that the kernel shape is of limited importance, which is consistently found for random NPPLs (contrast = 1 and continuity = 0), indicating that the shape of the kernel has little influence when patches are randomly distributed.

Absolute distance dependence can best describe a colonization process involving an organism with a large number of propagules and passive dispersal (e.g. caused by wind). Under such assumptions, our results suggest that the shape of the spatial kernel can have a pronounced

impact on the invasion speed in non-random landscapes. The general pattern in our findings is that contrast is the characteristic that had the most extensive effect on the importance of kernel shape, whereas the influence of continuity was less apparent. In figure 3a,b, this can be seen as a more evident left-right shift instead of an up-down shift. Moreover, the importance of kernel shape changes during the course of invasion (figure 3a), with the most prominent effect being observed during the initial phases of invasion. High values for contrast result in groups of locally connected but regionally isolated patches, and colonization between such isolated groups is rare when dispersal is limited (i.e. variance is low). This is enabled by the occurrence of rare but long-distance events (described by the tail of the leptokurtic kernels). The importance of kurtosis decreases with higher continuity, at which the distribution of patches may locally resemble random distribution of patches, where kurtosis is of little consequence.

The relative distance dependence will correspond to colonization by actively dispersing individuals that are not affected by mortality, or to spread of disease between farms via human activities, if the number of contacts of infected premises is independent of its location. For example, the number of animal transports can be expected to be the same for geographically isolated farms as for those in dense areas [23]. Our results show that, for such organisms, kernel shape is unimportant relative to the kernel scale for all landscape characteristics (figure 3c). Hence, it is not essential to consider kernel shape in the context of invasions of organisms, when the colonization process follows the assumptions of relative distance dependence. Under such an assumption, the patch arrangement becomes less important, and, because the colonization pressure from each patch is the same, the invasion process may not be equally dependent on fat-tailed kernels to reach isolated patches. It might also be expected that dispersal can comprise both an active component and a more passive component that include mortality. Depending on the organism and its dispersal mechanism, it is possible that the invasion process will position the importance of kurtosis along the gradient between absolute and relative distance dependence in a given patchy landscape.

Factors other than distance can influence the dynamics, and this is particularly apparent for epidemiological invasions [30,39]. Here, we have used an admittedly simplified colonization model to represent both ecological invasions and spread of disease. This analogy between colonization in a metapopulation and spread of disease has been discussed and used in disease modelling, for example, by Vernon & Keeling [40] in their study of the spread of disease in a network representation. These investigators emphasized that the assumptions of a simplified colonization model may be too crude to capture the dynamics of any real invasion, but with such a model it is possible to test the effect of the contact structure. Our aim was to reduce the system so that the main characteristics considered in the study were landscape and dispersal, while excluding recovery/extinction and within-patch dynamics such as density dependence. We argue that our results regarding the importance of kurtosis and the interaction with landscape features will hold for more realistic models as well.

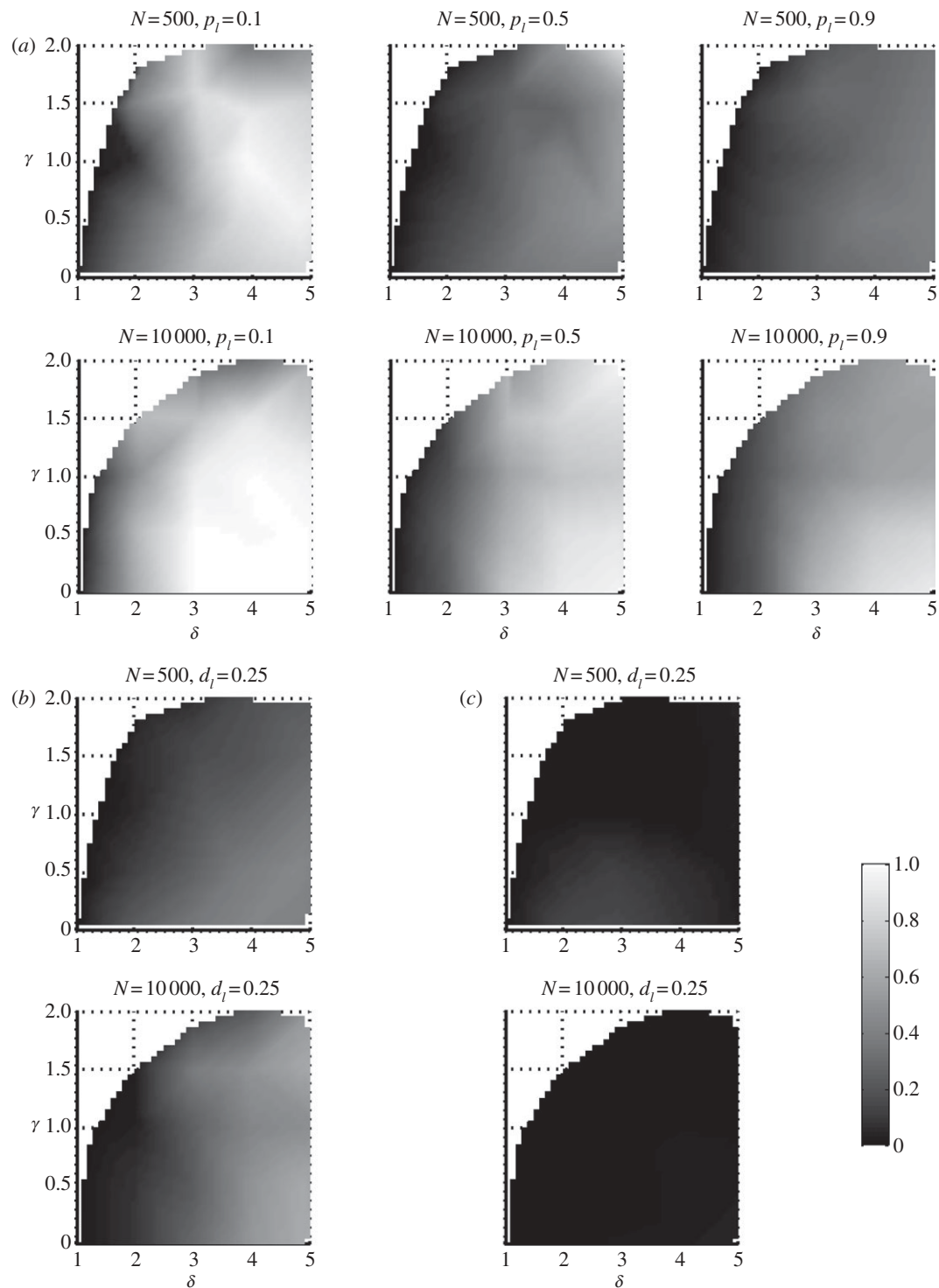


Figure 3. The relative importance of shape/kurtosis (κ) for time of invasion to reach proportions ($p_l = 0.1, 0.5$ and 0.9) of occupied patches with absolute distance dependence (a) and for spatial range expansion with absolute (b) and relative (c) distance dependence under two different landscape parameters: contrast (δ) and continuity (γ). Black areas indicate that κ is unimportant and that it is instead the variance of the dispersal kernel that determines the speed, and white areas signify that κ is highly important. The relative importance was calculated as $E_\kappa = MS_\kappa / (MS_\kappa + MS_\nu)$, where MS_κ and MS_ν are the mean sum of squares of κ and ν , respectively, from ANOVAs for each combination of δ and γ . Areas where the grid appears (for low δ and high γ) indicate that a point-pattern landscape could not be generated using the present method.

Previous studies have shown that spatial kernels without exponentially bounded tails lead to invasions where the speed of the spatial range expansion accelerates [14,19,41]. The cited investigations focused on travelling wave solutions and examined invasion as the speed of the wavefront. Such fronts cannot be observed in our spatially explicit and finite point-pattern landscape. Instead, we

studied spatial range expansion as time to a fixed distance, and thus we cannot draw many conclusions about accelerating invasions. However, when there are heavy tails, they can also be expected to occur in point-pattern landscapes. Yet, much larger landscapes and more replicates are required to assess acceleration, and consequently computational power may become a limiting factor.

An alternative is to turn to one-dimensional models of invasion, as has been done in many previous studies (e.g. [3,14]), although in that case it is necessary to consider that invasions in one and two dimensions may behave quite differently [19]. In addition, it might be cumbersome to relate the results of one-dimensional models to empirical patch distributions. In a patchy landscape, the last patches to be colonized are not necessarily those that are farthest from the initial point. Therefore, we evaluated both a direct measure of spatial speed and a measure of the time required for a specified proportion of patches to become colonized. For example, the spatial speed measure applies to when a disease will reach a specific area, while the proportion colonized relates to the number of infected units within an area. Inasmuch as the trends are very similar, only examples of the spatial range results are shown in figure 3.

(b) *Point-pattern landscapes*

To justify the linear model used for continuity and to demonstrate what landscape parameter values might be expected in areas where our results have implications, we used the method given in electronic supplementary material, appendix A to analyse relevant data. More precisely, we assessed the distribution of two species of deciduous trees (*Quercus robur* and *Ulmus glabra*). Trees of these species are important habitats for saproxylic insects. Many of these insect species are endangered, and limited dispersal has been proposed to be a major explanation for this situation [42,43]. Both of these tree species are also hosts for numerous lichens [44], and *Ulmus* is also of interest in epidemiological studies owing to the spread of Dutch elm disease (caused by the fungal pathogen *Ophiostoma ulmi*) [45]. We also examined the spatial distribution of pig and cattle farms in southern Sweden. The spatial distribution of farms has a marked impact on possible outbreaks of livestock diseases [6]. The continuity estimates are all fairly close to 1, while the contrast estimates are more variable, ranging from 1.29 for cattle farms to 4.9 for elm trees (figure 4). From figure 4, it can be seen that the estimated values of continuity and contrast of the empirical distributions (see §3b) lie within the range where kurtosis can have a substantial effect on invasion speed under absolute distance dependence. Hence, although it is not within the scope of this paper to compare invasions in tree and farms landscapes, it can be noted that the differences in contrast suggest that kernel shape is more important for invasions in the former.

The distribution of the analysed data and the estimated values of contrast (δ) and continuity (γ) indicate that the linear assumption in determining γ is also applicable for the analysis of empirical data. The linear relationship between \log (frequency) and \log (amplitude) implies that there is a spatial self-similarity over scales, which is the definition of a fractal process [46]. There are, however, many processes underlying the distributions of these point patterns. Furthermore, Halley *et al.*, p. 259 [46] point out that ‘Even an elephant appears linear if plotted on \log – \log axes’, and one should be careful when inferring fractality. Therefore, we refrain from drawing conclusions about the fractal properties of these distributions. Instead, we conclude that the analysed

patterns justify the assumptions of the NPPLs used in this study and that the measurements continuity and contrast may capture important landscape features.

Keitt [32] introduced spectral methods to landscape ecology and presented neutral landscapes for lattice models. By further developing the point-pattern representation offered by Muggleston & Renshaw [33] and the spectral mimicry of time series described by Cohen *et al.* [47], we were able to introduce the NPPL model. This method can be used to generate non-random landscapes with specific characteristics. The landscapes are characterized by their continuity, which is a measure of spatial autocorrelation, and by their contrast, which is a measure of the variability of patch density in the landscape. High contrast results in groups of locally connected but regionally isolated patches, and colonization between such isolated groups is rare when dispersal is limited (i.e. when there is low kernel variance).

The methods introduced here to generate and analyse point-pattern landscapes are based on spectral representation, which has become increasingly important in spatial data analysis. This approach is especially advantageous when studying spatial dependence in point-pattern processes, because, compared with other techniques, it may capture more complex dependencies. An example of this is anisotropy [48], which was not within the scope of our study but is a straightforward modification of the method.

(c) *Implications of our results*

Ecological and epidemiological processes occur in a spatial context. Our understanding of those processes and our ability to predict and control them depend on how well we can describe the spatial context, which includes both the spatial environment and the spatial behaviour of the processes themselves. Here, to study invasion, we used a patchy landscape as the spatial environment and a family of spatial kernels to model the distance dependence in the colonization process. The novel feature of our work is that we employed spatially explicit models, and we avoided the commonly applied assumption of homogeneous and continuous spatial structures, and instead focused on colonization in patchy landscapes. In that way, we were able to include the interplay between the spatial kernel and patchy landscapes. Our results indicate that, depending on the assumptions of distance dependence, this interaction may be very strong, and the findings also suggest that the spatial structure of the patches determines whether kernel shape will have a pronounced effect on the invasion speed. More specifically, the importance of shape of the spatial kernel is measured in relation to the scale of the spatial kernel and our results emphasize the importance of correct representation of both these features. Indeed, a vast array of topics, such as colonization of habitats, migrations in response to climate variations and spread of diseases, all occur in a spatial context in which the arrangement of patches is an obvious component [49], and thus we expect that our results can have implications in direct applications and in future research and investigations. The observation that the importance of kurtosis differs depending on the structure of the landscape suggests that both the speed of invasion and the methodology used to estimate that variable can differ

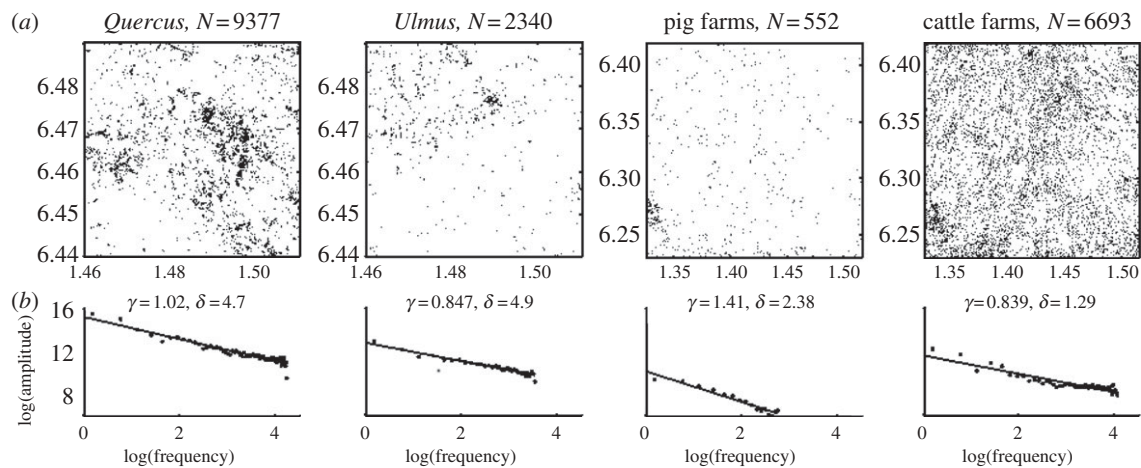


Figure 4. (a) Observed spatial distribution of N patches of oak (*Quercus*) and elm (*Ulmus*) trees and of pig and cattle farms (left to right) and (b) corresponding spectral densities with estimated continuity (γ) and contrast (δ). Data from Sweden.

between landscapes. In some landscapes, it may suffice to analyse the scale of the spatial kernel, whereas in other landscapes it will be necessary to assess the shape of the kernel. This also stresses the importance of developing empirical methods that correctly capture landscape structure.

Both variance and kurtosis are related to long-distance dispersal (LDD), and most studies of LDD (e.g. [50]) define this as either dispersal events beyond some fixed distance or some percentile of the tail. It should be kept in mind that these distances or percentiles are chosen by the researchers, and thus the measures of LDD are to some extent subjective, and comparison between studies may be difficult. We argue that dispersal is better described by analysis of the spatial kernel and its characteristics. Several investigations of dispersal in continuous space (e.g. [14,41,51]) have shown that the fat tail of the spatial kernel (reflected by kurtosis in our study) has an impact on invasion speed. However, to our knowledge, ours is the first investigation to focus on the importance of the kernel characteristics for invasions in patchy environments, applying both random and non-random distribution of patches. By using variance and kurtosis to describe the kernel, and testing the effect of these measures, it is possible to ascertain whether and when it will be essential to estimate these characteristics.

4. CONCLUSIONS

The impact of the spatial aspect on ecological and epidemiological theory is especially apparent when considering invasions and spread of disease. This aspect has two components, the landscape and the dispersal of organisms, which we have shown are entwined when the landscape structure is complex. Our observations also demonstrate that in many cases it will not suffice to assess the scale of the dispersal kernel, because the specific shape of the spatial kernel may be important as well. Yet, the influence of the scale of the kernel depends on the structure of the landscape, and hence it is also necessary to measure the structure. These conclusions emphasize that studying ecological and epidemiological spread in a spatial context places considerable demands on empirical details regarding dispersal, contact patterns and landscape structures.

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