



Aggregation dynamics explain vegetation patch-size distributions



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ABSTRACT

Vegetation patch-size distributions have been an intense area of study for theoreticians and applied ecologists alike in recent years. Of particular interest is the seemingly ubiquitous nature of power-law patch-size distributions emerging in a number of diverse ecosystems. The leading explanation of the emergence of these power-laws is due to local facilitative mechanisms. There is also a common transition from power law to exponential distribution when a system is under global pressure, such as grazing or lack of rainfall. These phenomena require a simple mechanistic explanation. Here, we study vegetation patches from a spatially implicit, patch dynamic viewpoint. We show that under minimal assumptions a power-law patch-size distribution appears as a natural consequence of aggregation. A linear death term also leads to an exponential term in the distribution for any non-zero death rate. This work shows the origin of the breakdown of the power-law under increasing pressure and shows that in general, we expect to observe a power law with an exponential cutoff (rather than pure power laws). The estimated parameters of this distribution also provide insight into the underlying ecological mechanisms of aggregation and death.

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1. Introduction

Vegetation patch-size distributions have been under intense study in recent years (Scheffer et al., 2009; Kéfi et al., 2011; Rietkerk et al., 2004; Oborny and GyörgySzabó, 2005; Manor and Shnerb, 2008). It has been shown that a power-law provides a good fit to the patch-size distribution under a robust range conditions, however there are marginal cases to this. Kéfi et al. (2007) analysed patch-size distributions in semi-arid vegetation in the Mediterranean and found that there was not only a power-law distribution evident in the patch-size distribution, but also a truncated exponential term, when the system was under increased grazing pressure. Similar power-law distribution phenomena have also been detected in a number of other ecosystems including mussel beds (Guichard et al., 2003) and marine benthic diatoms (Weerman et al., 2012). These phenomena of a power-law distribution transitioning to an exponential distribution under increasing stress have recently shown to be robust, where diverse ecological models are able to reproduce these results (Kéfi et al., 2011).

The leading explanation of this power-law pattern formation in ecology is due to local interactions driving the large-scale

behaviour (Pascual et al., 2002; Roy et al., 2003). Scanlon et al. (2007) supported this explanation through the use of numerical simulation of spatially-explicit models of vegetation growth combined with a global effect on the population density interpreted as the amount of rainfall or other global processes. The local positive feedback process driving the patch formation is through facilitation of neighbourhood sites that increase the birth rate and decrease the death rate (Manor and Shnerb, 2008). This explanation does not answer how a power-law forms at the patch level, whether it is due to a competition effect between larger clusters dominating the landscape or an aggregation of smaller clusters. There is also an open question of how patches aggregating together drive these observed patterns.

Models of aggregation and fragmentation have been considered in other areas in ecology such as the size of fish schools (Niwa, 1998) and marine diatoms (Jackson, 1990). Aggregation phenomena have been more generally studied in the Physical sciences (Aldous, 1999), including processes such as polymerisation (Ziff, 1980), coagulation of aerosols (Koch and Friedlander, 1990) and flocculation (Danov et al., 1994). Although these examples include clusters that may diffuse, aggregation phenomena may also be considered in the case where clusters are immobile (Krapivsky et al., 1998). Aggregation of vegetation clusters, however, has not been previously considered as an explicit driving force of the evolution of the patch-size distribution. Our novel contribution here is to apply established theory of aggregation dynamics to the system of

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vegetation clusters and derive a new model of aggregation with global death that is applicable to vegetation dynamics.

In this article, spatially implicit models of vegetation clusters are investigated by considering how patches form and aggregate. The general conditions under which a power-law distribution is expected to emerge are explored as well as when there is a breakdown of the power law distribution due to an exponential truncation. By adopting a patch-centric viewpoint, the impact of aggregation on the resulting distribution along with other processes may be studied directly. This represents a powerful new approach to understanding the origin of these distributions, by explicitly modelling the patch-size dynamics without the need to infer the patch-size distribution from a spatially explicit model (Manor and Shnerb, 2008).

Further, the connection between the power-law exponents and the persistence of the distribution in this model are explored. We begin by defining a novel model of aggregation with linear death and then deriving an asymptotic solution when the death rate is small. This analytic result is compared to a simulation study of vegetation with local and global growth properties subjected to a global disturbance. For small disturbance, the power law exponent closely matches the exponent expected from the model. The conclusion is that the power-law clustering observed in many vegetation ecosystems may simply be an aggregation effect and the exponential truncation observed when there is increased stress is due to an increase in the linear death rate of clusters.

2. Theory

The idea developed here is to model the patches themselves as opposed to an individual spatial site as is done in probabilistic cellular automata (Hogeweg, 1988; Balzter et al., 1998). We denote $c_k(t)$ as the density of patches of size k at time t , where time is taken to be continuous. A continuous model of patch-sizes can be studied, however for the present k shall take positive integer values only, $k \in \{1, 2, \dots\}$. A kernel of aggregation gives the rate at which patches of size i and j aggregate together to form a patch of size $i + j$, this kernel is denoted $K(i, j)$. Finally it is assumed there is a constant rate at which patches of size 1 or monomers enter the system. These assumptions are general and can include many different phenomena, including static clusters and diffusing monomers (Krapivsky et al., 1998). The governing master equation, also known as the Smoluchowski equation (VonSmoluchowski, 1916) is then

$$\frac{d}{dt}c_k = \frac{1}{2} \sum_{i+j=k} K(i, j)c_i c_j - \sum_{j \geq 1} K(j, k)c_j c_k + \delta_{k,1}, \quad (1)$$

where $\delta_{k,1}$ is the Kronecker-delta function that is 1 when $k = 1$ and 0 otherwise. For convenience, time has been re-scaled such that the rate at which aggregation occurs is 1. It is instructive to imagine a single unit or monomer coming into contact with a cluster and calculating the rate at which this occurs for larger as opposed to smaller clusters. If $a > 0$ then, assuming the size of the monomer is negligible, the monomer rate equation is $K(i) = i^{-a}$. This means smaller clusters are favoured and the growth rate reduces as clusters grow larger in size. An ecological explanation of this could be due to the self-limitation through competition a larger cluster experiences with itself, thus reducing its potential for growth. Smaller clusters have more space and thus can grow at a quicker rate.

When $a < 0$, larger clusters are favoured for growth compared with smaller clusters, this can be seen as a form of the Allee effect (Stephens and Sutherland, 1999). In the regime when $a < 0$, small clusters are more susceptible to environmental perturbation and as such, have a lower propensity for growth. At the other length scale,

larger clusters of vegetation are able to regulate their environment more and thus have greater resources for growth (An example species where this holds is ribbed mussels (Bertness and Grosholz, 1985), where larger clusters provide protection and shelter for new mussels). This example of an Allee effect can be demonstrated by again considering the rate at which single units of vegetation aggregate to a cluster. If $i > j$, then $K(1, i) = 1 + i^{-a} > 1 + j^{-a} = K(1, j)$ i.e. the rate at which a larger patch recruits new growth is greater than for a smaller patch. A value for a then can give an indication of whether there is strong small cluster growth at the expense of large clusters forming or if the converse holds.

An alternative explanation of the aggregation exponent a is due to the edge effects of a cluster. A single individual vegetation unit aggregates to a cluster proportional to the edge of that cluster. If all clusters are non-fractal then it would be expected that a vegetation unit aggregates at rate $i^{1/2}$, since the length of a non-fractal object scales as a square root with its area. For a general fractal cluster with boundary dimension d , it would be expected that an individual unit scales as $i^{1/d}$.

Various properties are desirable for the kernel. Firstly symmetry, where the rate at which patches of size i and j aggregate does not depend on the ordering of the patches i.e. $K(i, j) = K(j, i)$. Secondly, scaling homogeneity, where the rate at which patches of a certain size aggregate scales by some factor $K(mi, mj) = m^\lambda K(i, j)$. The simplest kernel that satisfies these conditions is the constant kernel $K(i, j) = 1$, corresponding to the case where $\lambda = 0$. When this form of kernel is assumed, the tail-solution (for large k) has the simple form (Hayakawa, 1987)

$$c_k \sim \frac{1}{\sqrt{4\pi}} \frac{1}{k^{3/2}}. \quad (2)$$

The tail of the patch-size distribution is a power law with exponent $3/2$, where the power law nature of the solution is a consequence of the injection term (where births of patch size one enter the system) and the non-linear aggregation term in the equation. The equation can be solved analytically for more general kernels of the type

$$K(i, j) = i^{-a} + j^{-a}. \quad (3)$$

This type of kernel also admits an analytic solution in the large patch-size limit (Krapivsky et al., 1999, 2010) with a steady state distribution of the form where

$$c_k \sim Ck^{-\tau} \quad (4a)$$

$$\tau = \frac{3-a}{2}, \quad C = \sqrt{\frac{1-a^2}{4\pi}} \cos\left(\frac{\pi a}{2}\right). \quad (4b)$$

For a steady state to exist we require $-1 < a < 1$ and hence the scaling exponent can be found on the interval $\tau \in (1, 2)$. The dynamics of the equation can be assessed by defining the cross-over time, which is the time taken for a density of patches of a certain size to reach its asymptotic value. The cross-over time for a patch of size k_* to the steady state solution c_{k_*} is found to take the form $t = (k_*)^z$ where $z = (1+a)/2$. The scaling of the cross-over time and the patch-size exponent can be related by the simple linear equation $\tau = 2 - z$. This gives a linear relationship between the static exponent at stationarity and its dynamic exponent.

A real vegetation system is not purely defined by an aggregation process however. In particular in the previous example there is no death either of single vegetation units or patch clusters. Death may lead to changes in the exponent of the stationary distribution and so it is important to include in any model of vegetation clustering. It is also assumed that a death event does not lead to fragmentation of

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