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Self-thinning rule: a causal interpretation from ecological field theory

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Abstract

The self-thinning rule relates plant mass to plant density in crowded, even-aged stands by a power-law equation with an exponent $-3/2$. The rule is widely accepted as an empirical generalization and quantitative rule that applies across the plant kingdom. It has been called the only law in plant ecology. But the evidence supporting it has recently come under critical scrutiny. The theoretical and empirical bases for the density–mass boundary have been questioned. Here we use ecological field theory and statistical mechanics to show how the stochastic nature of ecological interactions among individuals, due to spatial field effects such as the availability of neighborhood resources at the microscopic level, leads to self-thinning at the macroscopic level. The self-thinning rule emerges as a natural result of our theoretical approach. Puzzling experimental data that contradict the rule are also explained.

Keywords: Ecological field theory; Self-thinning rule; Emerging property; Spatial patterns; Statistical physics

1. Introduction

The $-3/2$ power rule of self-thinning (also called the $-3/2$ power rule or Yoda's law) relates average plant biomass to density when density-dependent mortality occurs, such that populations decline in density as biomass increases. Let $\bar{M}$ and n be the mean plant biomass and density (stems per unit area). The self-thinning rule is described by a power function,

$$\overline{M} = \zeta n^{\gamma}$$

where ζ and γ are constants and are referred to as the thinning coefficient and exponent, respectively. The γ has been claimed to take the value approximately $-3/2$ (Yoda et al., 1963; Harper, 1977; Hutchings, 1983; Westoby, 1984). An equivalent relationship also exists between the stand biomass (e.g. total biomass for all plants), B, and density, $B = \xi' n^{\vartheta}$, where $\vartheta = \gamma + 1$ and is approximately $-1/2$. Existing theories explain self-thinning from geometric, allometric and dynamic growth arguments (Sprugel, 1984; Zeide, 1987; Weller, 1987a,b; Lonsdale, 1990; Burrows, 1991; Adler, 1996; Enquist et al., 1998; Franco and Kelly, 1998), but they lack a specific mechanism. We show that self-thinning results from individual

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interactions, which also explain the variability in experimental data.

To grasp the mechanistic essence of the self-thinning phenomena requires a thorough understanding of the relationship between spatial interactions among individuals and spatial arrangements of these individuals. Spatial interaction has to be defined and described on an individual physiological level, while spatial arrangement which leads to the spatial pattern of a population we see only has a meaning on the population level.

Most empirical studies on spatial patterns in ecology focus on the statistical analysis of field samples and remotely sensed data (Pielou, 1977; Turner and Gardner, 1991). These studies generally do not address the intrinsic causality of the pattern. Therefore, they can not explain why patterns change with abiotic conditions or the traits of individuals. Nor can they offer mechanistic insight about the self-thinning processes.

Spatial patterns can arise as a consequence of interactions among component individuals. These interactions result from such processes as growth and competition for space and other resources. Ecological field theory (EFT) quantifies the effect of an individual on its neighbors using geometric zones of influence that surround individual plants (Wu et al., 1985; Sharpe et al., 1986; Walker et al., 1989; Mou et al., 1993). It provides the basis for a methodology to analyze spatial interactions among plants of different size, function and growth-form in models of population and community dynamics. An ecological field (or zone of influence) is generated by a living entity, or, by an abiotic process that affects a living entity including the physical space occupied by and the surrounding space influenced by the entity's presence and activities.

In the original EFT, Wu et al. (1985) proposed a concept called interference potential as a measure of the effect neighboring plants have on a newly germinated seedling. Here we extend the concept of interference potential and propose a measure for the competition between two grown-up neighboring individuals. Furthermore, we will demonstrate a straightforward way to derive the self-thinning rule from EFT and statistical mechanics.

2. Methods

In our model, the presence of an individual plant alters the availability of neighborhood resources. Neighboring plants interact with each other through their spatial zones of influence. The influence of one or more plants through its effect on neighborhood resources can be described by the intensity of ecological fields. The field intensity is characterized by two parameters: the 'origin' field intensity and its influence domain. The 'origin' field intensity I_0 is calculated at the plant origin 0 and is defined as

$$I_0 = 1 - \frac{\text{actual relative growth rate of the plant}}{\text{potential relative growth rate of the plant}} \tag{1}$$

A relative growth rate is defined as

$$\frac{\mathrm{d}M}{M\mathrm{d}t},$$

where M is the biomass of an individual. The idea under this definition is that a plant alters the availability of resources in its neighborhood. An influence field arises only when resources are scarce and has an effect on growth. It is similar to Newton's action and reaction law. We express the effect of a plant on resources by measuring its reaction, i.e. the effect of resource level on plant growth. When all resources are sufficiently abundant, the plant has no significant influence on its neighborhood, such that $I_0 = 0$. When all resources are extremely limited, the plant, although still alive, has a growth rate near zero and exerts the greatest impact on the availability of its neighborhood resources. In this case, $I_0 = 1$. The influence domain (D) about a plant is defined as the distance over which one plant may alter the resources or microclimate of the plant community. Thus, the field intensity $I(r)$ at a distance r away from the plant origin 0 can simply be expressed as a Gaussian influence function (Zou and Wu, 1995):

$$I(r) = I_0 \exp\left(-\frac{r^2}{2D^2}\right) \tag{2}$$

Eq. (2) describes the influence of a plant on its neighborhood resources when there are no other plants around.

When the domains of two individuals overlap, they interact with each other. Then an interaction intensity Π is generated. Consider two individuals 'A' and 'B' located at r_A and r_B, respectively. According to Eq. (2), the influence on the neighborhood resources is described by functions

$$I_A(r-r_A)I_B(r-r_B) \text{ and } I_B(r-r_B)$$

for plant 'A' and 'B', respectively. We define the overlap of their influence by:

$$O_{AB}=\int_0^\infty I_A(r-r_A)I_B(r-r_B)\mathrm{ds} \tag{3}$$

where ds is the area element at the point r. The phase volume of function I_A which is not overlapped by I_B is defined as the complement of overlap O_{AB} with respect to individual 'A', that is,

$$\begin{aligned} O_{AB}^A &= \int_0^\infty I_A(r-r_A)[I_A(r-r_A)-\kappa_{AB}I_B(r-r_B)]\mathrm{ds} \\ &= O_{AA}-\kappa_{AB}O_{AB} \end{aligned} \tag{4}$$

where $O_{AA}=\int_0^\infty I_A(r-r_A)I_A(r-r_A)ds$, and κ_{AB} represents the different interaction effect if A and B are different species. The parameter κ_{AB} is positive for suppressive interactions and negative for facilitative interactions. Similarly we can describe the complement of individual 'B' as:

$$O_{AB}^B=O_{BB}-\kappa_{BA}O_{AB} \tag{5}$$

The interaction intensities of individual 'B' on individual 'A'(Π_{AB}) and individual 'A' on individual 'B'(Π_{BA}) are defined:

$$\Pi_{AB}=\kappa_{AB}\frac{O_{AB}}{O_{AB}^A} \quad \text{and} \quad \Pi_{BA}=\kappa_{BA}\frac{O_{AB}}{O_{AB}^B} \tag{6}$$

Generally, the interaction intensity on an individual 'i' caused by another individual 'j' which is located at distance r_{ij} can be expressed as:

$$\Pi_{ij}(r_{ij})=\frac{\kappa_{ij}\exp\left[-\dfrac{r_{ij}^2}{2(D_i^2+D_j^2)}\right]}{\left[\dfrac{I_{oi}(D_i^2+D_j^2)}{2I_{oj}D_j^2}\right]-\kappa_{ij}\exp\left[-\dfrac{r_{ij}^2}{2(D_i^2+D_j^2)}\right]} \tag{7}$$

where I_{oi}, I_{oj}, D_i and D_j are maximum influence intensities and domains for individuals 'i' and 'j', respectively.

A spatial pattern is defined to be stable if its nearest-neighbor distribution and average interaction intensity do not change over a specific time period. Whenever there is an overlap in spatial influence, neighboring individuals experience an interaction intensity. The tolerance of an individual for interaction intensity should have an upper limit (Harper, 1977; Tilman, 1988; Huston and DeAngelis, 1994). Above that limit, the individual can not survive. Therefore, the average interaction intensity of a pattern should also have an upper limit. Below this limit, all individuals in the pattern can grow with a low probability of mortality and additional individuals can recruit into the distribution. When plant growth causes the average interaction intensity, $\overline{\Pi}$, to reach its upper threshold $\overline{\Pi}_0$, compensatory behavior, such as self-thinning mortality, occurs, such that the average interaction intensity remains below the upper threshold, $\overline{\Pi}_0$. Therefore, one constraint for a stable spatial pattern is that the $\overline{\Pi}$ must equal $\overline{\Pi}_0$. Note that $\overline{\Pi}_0$ is a system constant and depends on the integrated effect of all factors that influence plant growth such as the total availability of resources, environmental conditions, and spatial distribution of individuals.

If there are N individuals in a stand and the interaction intensity on the i-th individual is Π_i, then for a stable pattern, the average interaction intensity, must be:

$$\overline{\Pi}=\frac{1}{N}\sum_{i=1}^{N}\Pi_i=\overline{\Pi}_0=\text{constant} \tag{8}$$

This constraint, however, does not guarantee that individuals are arranged over the entire land area to utilize resources most efficiently. To develop an additional constraint, we use the concept of the nearest-neighbor area πr_i^2 of the i-th individual (Wu et al., 1985; Zou and Wu, 1995). The average nearest-neighbor area of a stand is also determined by growth and therefore by the availability of resources and environmental factors. For constant resource and environmental conditions, the nearest-neighbor distribution becomes stable, and the average nearest-neighbor area is given by:

$$\overline{A} = \frac{1}{N} \sum_{i=1}^{N} \pi r_i^2 = \overline{A}_0 = \text{constant} \tag{9}$$

Eqs. (8) and (9) provide two mathematical constraints for stable spatial processes. Constant $\overline{\Pi}$ describes the repulsive (negative) interaction among individuals, while constant $\overline{A}$ represents the aggregate tendency of these individuals.

Let $n(r_\alpha)$ be the number of individuals whose nearest neighbors are within distances

r_α to $r_\alpha + \Delta r$,

where r_α ($\alpha = 1, 2, \ldots, k$) represents all possible nearest-neighbor distances observable in the spatial pattern. If we let $q(r_\alpha) = n(r_\alpha)/N$, the set $\{q(r_\alpha)\}$ ($\alpha = 1, 2, .., k$) specifies the nearest-neighbor distribution of the spatial pattern. We can rewrite Eqs. (8) and (9) in terms of $q(r_\alpha)$:

$$\overline{\Pi} = \sum_{\alpha=1}^{k} q(r_\alpha)\Pi(r_\alpha) = \overline{\Pi}_0 = \text{constant} \tag{10}$$

$$\overline{A} = \sum_{\alpha=1}^{k} q(r_\alpha)\pi r_\alpha^2 = \overline{A}_0 = \text{constant} \tag{11}$$

Statistical mechanics is a microscopic theory corresponding to a macroscopic one: thermodynamics. In so-called Predictive Statistical Mechanics, it is viewed as statistical inference based on incomplete information, but not as physical theory. On the basis of the principle of maximum entropy, the probability distribution is determined by maximizing entropy under the constraints of known information. Then all the thermodynamic quantities can be calculated (Wu, 1997). We can recall extremal entropy properties of some probability distributions we are familiar with. For example, uniform distribution has maximum entropy among all distributions with bounded support, exponential distribution has maximum entropy among all distributions concentrated on the positive halfline and possessing finite expectations, and normal distribution is the law with maximum entropy among all distributions with finite variances (e.g. see Gnedenko and Korolev, 1996). Because of its central place in the foundation of statistical mechanics, the maximum entropy formalism is perhaps the most familiar procedure for obtaining distribution functions of both common and complex statistical problems. Because of its power and elegance there has been considerable interest in identifying suitable constraints that would permit the application of variational technique to a wider set of systems (Robledo, 1999).

Among the possible set of $q(r_\alpha)$, the one that maximizes information entropy corresponds to the most probable distribution and the most likely to be observed in ecological systems. For each possible nearest-neighbor distribution, we can express the corresponding information entropy H as follows:

$$\mathrm{H}(q(r_1), q(r_2), \ldots, q(r_k)) = -K \sum_{\alpha=1}^{k} q(r_\alpha) \log(q(r_\alpha)) \tag{12}$$

where K is a positive constant. To maximize information entropy under constraints Eqs. (10) and (11) and the normalization condition

$$\sum_{\alpha=1}^{k} q(r_\alpha) = 1 \tag{13}$$

We introduce the Lagrange multipliers β and ε in the conventional manner. Following standard mathematical procedures (Wu, 1997), the most probable nearest-neighbor distribution is given by:

$$q(r_\alpha) = C r_\alpha \exp(-\beta \Pi(r_\alpha) - \varepsilon \pi r_\alpha^2) \tag{14}$$

where C is a normalization constant. Comparing the above equation with the nearest-neighbor distribution for dimensionless points (Pielou, 1977), the constant ε is interpreted as the number density n (individuals per unit area). Parameter β is controlled by available resources and environmental conditions. The role of β in the nearest-neighbor distribution is tantamount to temperature in Boltzmann's distribution of thermodynamic systems (Zou and Wu, 1995). Although Eq. (14) is for individuals of the same species having similar size, it can be adjusted for a community of multiple species and sizes by using a weighted nearest-neighbor distribution of the form in Eq. (14).

When a population reaches its carrying capacity, the average interaction intensity approaches a maximum value $\overline{\Pi}_0$:

$$\overline{\Pi} = \sum_{\alpha=1}^{k} Cr_\alpha \exp(-\beta\Pi(r_\alpha) - n\pi r_\alpha^2)\Pi(r_\alpha) \to \overline{\Pi}_0 = \text{constant} \quad (15)$$

This equation provides a dynamic equilibrium relationship between biomass accumulation and the density of the population. To simplify our computation, we treat individuals in a population as having similar sizes and the nearest-neighbor distances as a continuum. Then Eq. (7) becomes

$$\Pi(r) = \frac{\exp(-r^2/4D^2)}{1-\exp(-r^2/4D^2)} \quad (16)$$

The most probable nearest-neighbor distribution, Eq. (14), is then expressed as:

$$q(r) = Cr \exp(-\beta\Pi(r) - n\pi r^2) \quad (17)$$

and the corresponding average interaction intensity becomes:

$$\int_0^\infty q(r)\Pi(r)dr = \overline{\Pi}_0 = \text{constant} \quad (18)$$

The interaction intensity in Eq. (16) decreases rapidly as r increases. This implies that the influence domain D is only significant at small r. For small r, $\Pi(r)$ can be approximated by:

$$\Pi(r) = \begin{cases} \dfrac{4D^2}{r^2} - 1 & \text{if } r < 2D \\ 0 & \text{otherwise} \end{cases} \quad (19)$$

When r is near zero, r^2 can be ignored in comparison with r^{-2}. Changing variable r to y by letting

$$y^2 = \frac{r^2}{4\beta D^2},$$

the integral in Eq. (18) then can be simplified to:

$$\int_0^\infty q(r)\Pi(r)dr \approx C\int_0^{2D}\left(\frac{4D^2}{r^2} - 1\right)\exp(-4\beta D^2/r^2)rdr = 4CD^2\int_0^{\beta^{-1/2}}\left(\frac{\exp(-y^{-2})}{y} - \beta y \exp(-y^{-2})\right)dy = \overline{\Pi}_0 \quad (20)$$

The normalization constant C can be determined from

$$\int_0^\infty q(r)dr = 1$$

which yields

$$\int_0^\infty q(r)dr \approx C\left[\int_0^{2D} \exp(-4\beta D^2/r^2)rdr + \int_{2D}^\infty \exp(-n\pi r^2)rdr\right] = C\left[4\beta D^2 c_1 + \frac{\exp(-4n\pi D^2)}{2n\pi}\right] \quad (21)$$

where c_1 is a constant that only depends on β:

$$c_1 = \int_0^{\beta^{-1/2}} e^{-y^{-2}} y dy.$$

For the first-order approximation, the normalization constant C can be expressed as:

$$C \approx \frac{2n\pi}{1 - 4n\pi b D^2} \quad (22)$$

where $b = 1 - 2\beta c_1$. Evaluating the integral in Eq. (20) yields:

$$\overline{\Pi}_0 = \frac{8n\pi h D^2}{1 - 4n\pi b D^2} \quad (23)$$

where $h = c_{-1} - \beta c_1$ with $c_{-1} = \int_0^{\beta^{-1/2}} y^{-1} e^{-y^{-2}} dy$.

Rearranging Eq. (23), we obtain

$$n = \frac{\overline{\Pi}_0}{4\pi(2h + b\overline{\Pi}_0)} D^{-2}. \quad (24)$$

3. Results

Because biomass accumulation for most tall plants is three-dimensional, the influence domain D is roughly proportional to $\overline{M}^{1/3}$ (Walker et al., 1989). Eq. (24) thus becomes:

$$\overline{M} = \sqrt{\left(\frac{\overline{\Pi}_0}{4\pi(2h + b\overline{\Pi}_0)}\right)^3 * n^{-3/2}} \quad (25)$$

Eq. 25 is the traditional $-3/2$ self-thinning rule

$$\left(\gamma = -3/2 \text{ and } \zeta = \sqrt{\left(\frac{\overline{\Pi}_0}{4\pi(2h + b\overline{\Pi}_0)}\right)^3}\right)$$

For two-dimensional growing plants (ground-cover plants) or some sessile animals, the influence domain or territory may be proportional to the average biomass of the population, or $D^2 \propto \overline{M}$. Therefore, the thinning rule becomes:

$$\overline{M} = \frac{\overline{\Pi}_0}{4\pi(2h + b\overline{\Pi}_0)} * n^{-1} \tag{26}$$

Here $\gamma = -1$ and

$$\zeta = \frac{\overline{\Pi}_0}{4\pi(2h + b\overline{\Pi}_0)}.$$

Other power-law relationships can easily be established based on different biomass and influence domain functions in the framework of fractal geometry. For example, we can let $D \propto \overline{M}^{1/\eta}$. For the case of the -4/3 power rule derived from dynamic growth model (Burrows, 1991) and allometric scaling model (Enquist et al., 1998), the space filling property of biomass is $\eta = 8/3 < 3$ (dimensions), which gives

$$\zeta = \left(\frac{\overline{\Pi}}{4\pi(2h + b\overline{\Pi}_0)}\right)^{4/3}.$$

Therefore, we have accomplished the derivation of a generalized self-thinning rule for the different thinning exponents found in the ecological literature (the upper and lower limit bounds are -1 and $-3/2$, respectively) (Yoda et al., 1963; Harper, 1977; Hutchings, 1983; Sprugel, 1984; Westoby, 1984; Zeide, 1987; Weller, 1987a,b; Lonsdale, 1990; Burrows, 1991; Adler, 1996; Enquist et al., 1998; Franco and Kelly, 1998). In previous theories, the thinning coefficient ζ was not given ecological meaning. In our approach, ζ is a function of average interaction intensity in a population, and serves as a system-level constraint that generates the self-thinning phenomenon. This result may well serve as a starting point for further theoretical and experimental work toward the understanding of self-thinning patterns and processes.

4. Discussion

The real ecological goal is to elucidate the underlying processes — the interactions among individuals and between species — that generate such patterns. The theoretical analysis given above incorporates a field concept in physics, in terms of interaction intensity, to derive the $-3/2$ self-thinning rule. When a stand reaches its carrying capacity, the average interaction intensity becomes a constant, which results in self-thinning. During the self-thinning phase, the average nearest neighbor area changes continuously until the entire distribution becomes stable. Our result generates a new testable explanation for the underlying processes for this spatial pattern. It emerges from ecological interactions among individuals (or local spatial field effects). This explains the different empirically derived thinning exponents that have puzzled ecologists and challenged the generality of the rule. Similar to other macroscopic patterns, such as turbulence and critical phenomena (Bramwell et al., 1998), including the so-called theory of self-organized criticality (Bak, 1996), we have demonstrated that the observed power-law distribution that characterizes self-thinning can result from interactions among individuals at the microscopic level. Further studies are needed to understand the underlying reasons behind such similarities, and their consequences for the behavior of complex systems. Finally our approach provides a novel, systematic method for modeling the macro-ecological dynamics of a large collection of interacting micro-ecological agents or units.

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