

TILMAN'S (1994) MODELS OF COMPETITION AND BIODIVERSITY: CRITICAL COMMENTS

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ABSTRACT. Comparative analysis between Tilman's models (1994) of competition and biodiversity (based on Levin's logistic equation (1969)) and the classical Lotka-Volterra competition models reveals that the major difference is the omission of the mortality rate in the logistic terms in the Levins-Tilman models. This falsifies the equation $r = b - d$ (r = intrinsic growth rate, b = rate of reproduction/colonization, d = death rate) and results in an over-estimation of the logistic growth reduction per individual present in the system. Consequently, population growth is reduced to zero before the carrying capacity of the system is reached.

1. INTRODUCTION

In 1994 Tilman presented a mathematical model for the maintenance of biodiversity involving species competing for space and a common limiting resource, as, for instance, nitrogen-limited plants. The theory relates to a decade of work on the dynamics and diversity of natural and experimental grass lands by Tilman and his co-workers (Lit. refs. see Tilman 1994 [14]). According to the general Volterra model [17], with the specific consideration of the critical resource density for maintenance (Tilman 1982 [11], Tilman et al. 1984 [15], Tilman 1987 [12], Walker 1993 [19]), the superior competitor for the resource should replace all other species. In these models, though, the resource, i.e. mass/energy, determines the dynamics of the system.

The 1994-model, on the other hand is based on Levins' 1969-model of site occupation by single, sessile species. In Levins' model, space

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is the only determinant, while in Tilman's two- and multi-species models, limiting resource enters as an additional factor.

The challenging feature of Levins' single-species model is that, although it consists of a deterministic, logistic growth equation, the species cannot occupy the entire space available (and physiologically suitable!), in contrast to the classical logistic growth equation (Verhulst 1838 [16]), according to which growth stops when the space is fully occupied. Hence, a second species can invade the empty space of the first one, and a third the space not colonizable by the second one, and so on. Thus runs Tilman's argument. Thus, biodiversity is warranted by mathematical determinism, while the Volterra models predict non-equilibrium coexistence (Paine and Levine 1981 [8]) as a result of random destruction and random invasions.

In this paper, the single-species and the two-species models only, will be discussed. The basic, biophysical assumptions will be critically considered, and comparison between Levins' (1969) and Verhulst's (1838) logistic models must reveal the exact difference of biophysical interpretation between the two. This, in turn, should allow for a precise understanding of the two-species model. The choice between the classical (Verhulst-Volterra) models and the Levins-Tilman models can then be based on the biological reasonableness as it emerges from mathematical and biophysical considerations.

2. PRESENTATION OF THE MODEL AND DISCUSSION

2.1. The single-species model (Levins 1969, Tilman 1994).

Given is an area of n equal space cells or sites, physiologically suitable for the growth of a given, sessile species. The maximum rate of propagule fixation per parent in the as yet unoccupied area is defined as colonization rate = c . Individuals die and thus, liberate space cells at the specific rate m = mortality rate. From these parameters, the portion of occupied sites, N/n , can be calculated for any one time. Although the growth equation is a differential equation, it is important to note that the model is based on particulate, distinct units in space and in time. The space cell encloses the whole of a single individual, and nothing but a single individual, and space cells must be vacated, before they can be recolonized. In principle, $c =$

rate of space occupation, and m = rate of space evacuation. By definition, an occupied site coincides with a live individual.

For positive population growth, the condition

$$(1) \quad c > m$$

must be realized. The equation for the growth of the fraction of space cells occupied ($p = \frac{N}{n}$) reads:

$$(2) \quad \frac{dp}{dt} = cp(1-p) - mp$$

According to Tilman's explanation, the actual rate of colonization is proportional to the fraction p of the area occupied and thus produces propagules, and to $1-p$, that is, to the fraction of the area that can still accept colonizers. The equation may be simplified to

$$\frac{dN}{dt} = c(1-p)N - mN \quad \text{or to} \quad \frac{d}{dt} = c(1-p) - m$$

Growth reduces to zero ($\frac{d}{dt} = 0$) when

$$(3) \quad p = 1 - \frac{m}{c} = \hat{p}$$

Therefore \hat{p} can only reach 1, i.e. the whole area can only be fully occupied, when $m = 0$, or $c = \infty$, both of which are unreasonable assumptions. The portion $1 - \hat{p}$ is thus available for foreign invading species.

Before analysing the equations, we will consider the biophysical status of sessile organisms. They are prevalently characterized by a vertical axis with – often apical – branches, which expand to umbrella-like structures, such as hydroids, sessile polychaetes, trees and many herbs, etc. The reason being, that their essential resource (light for plants, food particles for aquatic animals) arrive generally from above. Hence, running around would not increase the rate of resource capture, while expansion of the resource-capturing surface (leaves, branches, tentacles, etc) optimizes the rate of resource absorption (Walker 1987 [18]). Because the model site, i.e. space cell, coincides with the three-dimensional, umbrella-shaped structure of the adult individual, propagules (seeds, spores, buds, etc) germinate, as a rule, underneath the umbrella-like branches long before the adult individual dies. As, in the model, m = the rate of liberalization of cells, while c = the rate of colonization of thus evacuated cells, the

realistic systems approach a rate of $m = 0$ and $c = \infty$. Indeed, sessile organisms have a strong tendency of vegetative reproduction via buds and stolons, which results in colonial structures and in extended areas of single species occupation. A tree, we may remember, is, botanically speaking, a colony. Moreover, saplings of trees with heavy seeds wait for decades till the mother tree falls over. Every botanist and marine biologist is familiar with more or less extended areas occupied by single species. This means that the assumption of phase-spatial discreteness, and the resulting definitions of the parameters c and m , are biologically unrealistic. After all, the continuity of any living system relies on the overlap of generations: offspring must be reproduced before the adult dies.

A further difficulty is the arbitrariness of the size of the model. Where does the patch end and the monoculture begin? In principle, an area of a single cell (or site in Tilman's terminology) which is occupied is, mathematically speaking, a monoculture.

Adjusting (3) to these boundary conditions, such that $n = \widehat{N} = 1$, and hence $\widehat{p} = \frac{\widehat{N}}{n} = 1$, leads of necessity to $m = 0$. In a peculiar way, m seems to be a function of p rather than viceversa. Comparing eq. (2) with the classical logistic growth equation may resolve the problem.

The classical logistic equation is

$$(4) \quad \frac{dN}{dt} = (r - aN)N$$

where N = number of individuals in a given population; r = species-specific, intrinsic growth rate, and a = species-specific reduction of growth per individual present in the population; a is the logistic brake of growth. For $\frac{dN}{dt} = 0$, $r = a\widehat{N}$, and, as $r = b - d$, b being the birth rate and d being the death rate, the condition for zero growth may be written in this form:

$$(5) \quad b - a\widehat{N} - d = 0$$

The equivalent form of (3) in the Levins-Tilman model, where $\widehat{p} = \frac{\widehat{N}}{n}$, writes:

$$(6) \quad c - \frac{c}{n}\widehat{N} - m = 0$$

and we see that $\frac{c}{n}$ should be equivalent to the logistic term a in (5). As a fraction of the growth rate r , a in (5) includes the death rate. In fact, $a = \frac{b-d}{\hat{N}}$ according to its very definition. On the other hand, $\frac{c}{n}$ as colonization rate, cannot include the death rate, again, by the very definition as given in the model. Yet, if $\frac{c}{n}$ is resolved according to (6), it is necessarily a function of m , i.e. the equation contradicts the definition of the term.

It stands to reason that the logistic brake is reduced in the measure individuals are dying. The logistic term is expressed in terms of population growth, not in terms of recruitment alone (b and c respectively). Hence, the biophysically correct model must contain the death rate in its logistic term. Correcting (6) accordingly, we write:

$$(7) \quad c - \left(\frac{c - m}{n} \right) \hat{N} - m = 0$$

Consequently, $\hat{N} = n$, that is, the population grows until all n sites of the area are occupied, without any necessity of additional conditions pertaining to c , the colonization rate, and to m , the death rate. Furthermore, the model applies to the boundary condition where $N = n = 1$, and hence, renders arbitrary definition of the system's size unnecessary.

Evidently, the introduction of the mortality rate into the logistic term (7) necessitates modification of the basic growth equation (2) of the model. Combining the terms m and c in (2) to the maximum growth rate $m - c$ (in analogy to the intrinsic growth rate $r = b - d$) introduces m into the logistic term in (7). (2) transforms into (8) below:

$$(8) \quad \frac{dp}{dt} = (c - m)p(1 - p)$$

meaning that growth $(c - m)$ is realized in proportion to the fraction of the area occupied (p , and hence contributes to growth), but is reduced in proportion to the diminishing colonizable area ($(1 - p)$, logistic term). $\frac{dp}{dt} = 0$ when $p = \frac{\hat{N}}{n} = 1$, i.e. when all sites are occupied.

Thus, even under the unrealistic assumption that sites get colonized *after* the death of its occupant, the necessary introduction of the death rate into the logistic term results in the colonization of the

whole area by populations of single species, provided only that the rate of propagule settlement is larger than the death rate ($b > d$, $c > m$). It is, in fact, not understandable, why a species with a positive growth rate should not be able to occupy its whole area, unless one accepts probabilistic events, which, however, are not considered in the Levins-Tilman model.

2.2. The two-species model. Tilman's 1994-two-species model is presented by his equations (3.1) and (3.2) (Tilman 1994 [14]). The basic assumption is, that this system is nitrogen-limited, and species 1 ($= (N_1)$) is the better nitrogen competitor: whenever propagules of (N_1) settle on sites occupied by species (N_2), (N_1) will replace (N_2), while the reverse process cannot occur. The population of (N_1) therefore, grows entirely unaffected by species (N_2). However, Tilman's equation (3.1) will be substituted by our (8) with the altered logistic term. The growth rate of (N_2) is diminished as sites get occupied by both species (logistic terms) as well as by the invasion of sites already occupied by (N_2), i.e. by the term $-p_2p_1c_1$. Here again, we argue that this invasion rate is diminished by the mortality rate of (N_1). The invasion term, therefore, is amended to read $-p_2p_1(c_1 - m_1)$. Surely, the fraction of invaders, $p_1p_2c_1$ is also subject to its own death rate m_1 . The growth equations of the two species then read:

$$(9) \quad \frac{dp_1}{dt} = (c_1 - m_1)p_1(1 - p_1)$$

$$(10) \quad \frac{dp_2}{dt} = (c_2 - m_2)p_2(1 - p_2 - p_1) - (c_1 - m_1)p_1p_2$$

For reasons of biophysical explanation let us set $(c_i - m_i) = r_i$ as species-specific growth rate under unlimited conditions, while $p_i = \frac{N_i}{n}$ as formerly noted; furthermore, we write the equations for the populations N_1 and N_2 , that is, we multiply both equations, (9) and (10), by n . Thus,

$$(11) \quad \frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1}{n}\right) N_1$$

$$(12) \quad \frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2}{n} - \frac{N_1}{n}\right) N_2 - r_1 \frac{N_1}{n} N_2$$

where $-\frac{r_2}{n}(N_2 + N_1)$ = reduction of growth r_2 as result of sites already occupied, while the second term in (12) stands for the reduction of r_2

as the result of the invasion by (N_1) of sites occupied by the species (N_2). Note that equations (10) and (12) pass through a state of zero growth when the rate of invasion equals the growth of population (N_2) in absence of invasion (first term of the equations). However, owing to superior nitrogen competitiveness, (N_1) continues to invade, and the growth rate $\frac{dN_2}{dt}$ becomes negative.

Equations (11) and (12) conform to the traditional Lotka-Volterra model of two competing species, and may be written as ¹⁾

$$(13) \quad \frac{dN_1}{dt} = r_1 N_1 - a_1 N_1^2$$

$$(14) \quad \frac{dN_2}{dt} = r_2 N_2 - a_2 N_2^2 - b_1 N_1 N_2$$

The omission of the term $-b_2 N_2 N_1$ in (13) is due to the initial assumption that the growth of species (N_2) has no effect on the growth of (N_1), hence $b_2 = 0$. Invasion of species (N_2) by species (N_1) is incorporated in the coefficient b_1 in eq. (13).

The attractive feature of Tilman's (1994) model (amended to include the death rate in the logistic terms) is, that it lends itself to a detailed analysis of the growth dynamics of the two species, as well as to an independent verification of the biophysical significance of the a_i - and b_i -coefficients.

Retaining the initial assumptions that $r_i > 0$, and that each individual present in the system occupies a single site of a total of n available sites, and furthermore, choosing the initial population numbers $N_1^{(0)}$ and $N_2^{(0)}$ such that both species still coexist when all n sites are occupied, the growth dynamics allows to identify three different phases (Fig. 1):

¹In eq. (14) the b_i -coefficients are not to be confused with b = birth rate in eq. (5)

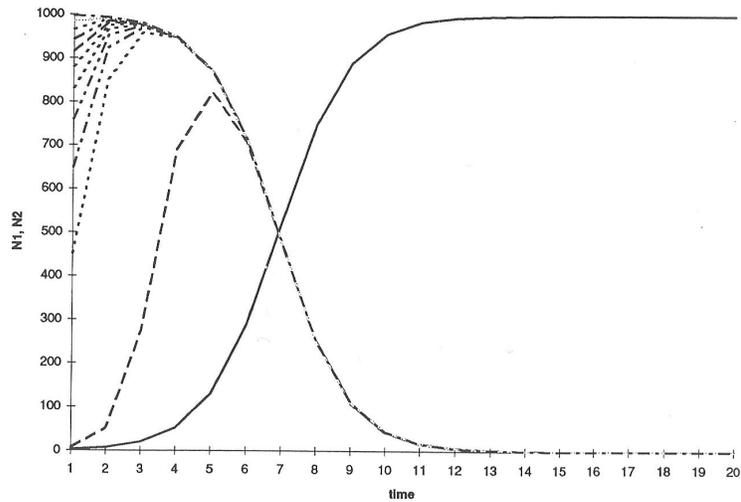


FIGURE 1. Invasion of species (N_2) by species (N_1). N_1 , N_2 = respective numbers of individuals in the course of time. Various broken lines: for species (N_2) with different, initial numbers at time zero. Single, solid line: for species (N_1) with a single individual at time zero. $n = 1000$. Intrinsic growth rates: $r_2 = 2r_1 = 2$. The three phases mentioned in the text are different for the various (N_2)-curves, and hence, are not shown in the figure.

During the first phase $N_1 + N_2 < n$, and both species coexist despite the invasion of species (N_2) by species (N_1).

During the second phase (=Phase II), all n sites are occupied by both species, that is, $N_1 + N_2 = n$, however, owing to invasion, (N_1) grows at the expense of (N_2).

During the third phase, the whole space is occupied by (N_1), that is, $N_1 = n$.

Making no further assumptions as to the nature of the a_i - and b_i -coefficients in (13) and (14) than those mentioned above, Phase II allows to identify their magnitude and their biophysical significance.

During Phase II the following conditions are valid:

1. $n - N_1 = N_2$, and
2. $\frac{dN_1}{dt} = -\frac{dN_2}{dt}$.

Substituting these values in eq. (14), we write:

$$\frac{d(n - N_1)}{dt} = r_2(n - N_1) - a_2(n - N_1)^2 - b_1N_1(n - N_1)$$

Setting $-d(n - N_1)/dt = dN_1/dt$ and resolving, we find:

$$\frac{dN_1}{dt} = -(r_2n - a_2n^2) + (r_2 - 2a_2n + b_1n)N_1 + (a_2 - b_1)N_1^2$$

Comparing this last equation to eq. (13), we find that

1. $(r_2 - a_2n^2) = 0$,
2. $(r_2 - 2a_2n + b_1n) = r_1$,
3. $(a_2 - b_1) = -a_1$.

From these three expressions, we determine the values of the coefficients:

$$a_1 = \frac{r_1}{n}, \quad a_2 = \frac{r_2}{n}, \quad b_1 = \frac{r_1 + r_2}{n}.$$

Biophysically speaking, the coefficients express growth permitted per empty site, or, in the negative, growth reduction per site occupied. This result confirms the correctness of Tilman's (1994) model, provided it includes the death rate in the logistic terms: substituting these values in eqs. (13) and (14) renders them identical with eqs. (11) and (12). As the a_i - and b_i -coefficients stand for mean growth per site, it is irrelevant whether propagules settle before or after the death of an occupant. This accommodates vegetative reproduction and – nota bene – invasion as well.

3. CONCLUSIONS

The difference between the classical logistic equations (Verhulst 1838; Volterra 1926; Lotka 1932) and the Levins (1969)-Tilman (1994) models is the omission of the mortality rate (m) in the logistic terms in the latter.

The logistic terms express the reduction of population growth ($r = b - m$; b for birth rate) as a function of the increasing number of consumer individuals under space- and/or resource-limited conditions. Eventually population growth ($\frac{dN}{dt}$) is reduced to zero and (neglecting time lags) the population just maintains itself at the carrying capacity of the limiting factor. Evidently, the logistic brake of population growth is attenuated in the measure individuals die and thus liberate space and/or resource for new recruits. Omission of the mortality rate in the logistic terms means over-estimation of the growth reduction per individual added to the system. As a consequence, the population reaches zero growth before the available space/resource sets the limit to growth.

In the Tilman-models the colonization rate c is the rate of propagule fixation in "adult sites". As such, c is equivalent to the birth rate b in the classical models, and $c - m = r$ stands for the species- and system-specific maximum population growth under unlimited conditions. Omission of the mortality rate in the logistic terms distorts the relation between the parameters c and m in the equation $c - m = r$. With increasing number of species within the competitive system, each with its specific distortion $r_i \neq c_i - m_i$ in the logistic terms, the numerical discrepancy of the c_i and m_i values within and between species attain specific values which, presumably, may or may not, allow for stable coexistence. Whence the "surprising predictions" discussed in Tilman's (1994) paper, which, indeed, are not understandable, if one argues in biophysical terms.

Under the assumption that – for reasons of biophysical reality – the mortality rate must be included in the logistic terms, deterministic, stable coexistence of species in Tilman's (1994) spatial competition models is fiction, and this is probably true for all models based on Levins' (1969) equation of logistic growth. The problems arising from the omission of the mortality rate in the logistic terms would at least need explicit consideration.

The distortion $r \neq c - m$, furthermore, is responsible for the inconsistency of the boundary conditions of eqs. (2), (3) and (6) i.e. for the case $\hat{N} = n = 1$ and hence, $m = 0$, while inclusion of m in the logistic term resolves this mathematical problem.

The interesting aspect of Tilman's (1994) models is that they include both, space- and resource-limitation in the same set of equations, and that they allow to differentiate between mere space occupation and invasion. Thereby space limitation (n available sites) enters the equations explicitly, whereas the winner of resource competition is determined by initial assumption: (N_1) can invade population (N_2), while the reverse process is not permitted. In other words, the systems' outcome is determined by the physiological capacity of maintenance (the winner can subsist on lower resource densities, Tilman 1988), and not by the species-specific growth rates (r_i). From the biophysical point of view, this is the most important aspect of the models.

Lastly, as Tilman (1994) discusses biodiversity of tropical forests (Hubbell and Foster 1986), and the authors of the present article are studying amazonian forest systems, the following comments are presented for consideration.

The amazonian rain forest is structured at the order of magnitude of hectares. The Amazon Basin is dissected by tenths of thousands of smallest streams which join to larger rivers. The streams' catchment areas have their plateau with patchwise clay and sandy soils and podzolization processes in between, besides steep slopes and flat stream valley bottoms with hydrological and solar radiation gradients. There is little tree species overlap between these various areas. Furthermore, there are geological differences on larger scale, and there are the inundation forests of rivers with different water chemistry ([1], Sioli 1984 [9]).

Vital competition processes occur primarily along the vertical axis (nutrient input with rain and from herbivory in the canopy, (Franken et al. [2]; solar radiation, Marques Filho 1994 [7]). Hence, resources are mostly compartmentalized and are not open to general competition (Walker 1987 and 1993 [18], [19]).

There were dry periods during the last 60'000 years with isolated forest refugia, from which the rain forests spread repeatedly over

the Amazon Basin during the more humid periods. Today's forest, therefore, is relatively young (Iriondo and Latrubesse [4]).

The generation periods of trees range between several decades, while mutation rates in eucaryotes are ca. 1-5 per haploid genome and per mitosis; that is, selection is slow and diversification is relatively fast. As the more recent climate presents no vital stress, forms diverge while functions persist.

Hence, everything is in favour of biodiversity, despite the fact that single species may colonize their whole area if nothing prevents them from doing so.

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