Short communication

Application of compound interest laws in biology: Reunification of existing models to develop seed bank dynamics model of annual plants☆

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ABSTRACT

Reunification of widely-usedclassic models in ecology is a very important step for the field to grow. In this study, classic models based on compound interest law, which exists in many natural phenomena, were reunified, and a seed bank dynamics model of annual plants was developed.

We found an intrinsic relationship between the compound interest of unit period and density dependence, and the relationship was interpreted using evolutionary stability strategies of a single seed. Based on the relationship, a seed bank dynamic model of annual plants was constructed, and compound interest of the unit period and discrete-time dynamic processes, by which a new density-dependence based on the benefit balance of storage and investment (defined as the compound interest law) was derived.

Our model not only can be used to reunify the three classic models (Cohen's, Goldberg's, and Bulmer's) but can also support different levels of density dependence in the seed bank dynamics of annual plants. Our study has shown that the compound interest law interprets seed bank dynamics more clearly than the traditional power law, not only because there are close relationships between the compound interest law and the power laws in numerical simulations but also because the compound interest law can be directly interpreted by the evolutionary stability theory.

Our study provides new insight into the bet hedging theory and the life-history evolution of plants with seed banks by adding a compound interest term to the fitness function of annual plants. We suggest that if the interest rate of delaying growth can be defined by compensating for delayed growth, compound interest of the unit period will play an important role in biology and ecology.
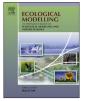
1. Introduction

Many natural phenomena follow the compound interest law. Compound interest has important applications in human society based on the benefit of storage and investment in economics (Almenberg and Gerdes, 2012). A compound interest model of annual growth and increases in dry weight was proposed by Blackman back to 1919 (Blackman, 1919). The law of compound interest has been used frequently in other fields, but its development in biological and ecological theory has been slow (Connolly et al., 2001; Erickson, 1976; Hember et al., 2012).

The key to compound interest research primarily lies in the organism's choice of interaction characteristics on different temporal and spatial scales (Fischer and Fiedler, 2002). Three formulas for compound interest exist in terms of different periods of time: (1) continuous compound interest e^{rt} (where r is the growth rate and t is the time) (Blackman, 1919; Shimojo et al., 2010); (2) compound interest of k periods $(1+r)^k$ (where r is the interest rate and k is the number of periods); continuous compound interest as well as compound interest for k periods has received more attention in evolutionary ecology (Weis et al., 2000); (3) compound interest of a unit period $(1+r/k)^k$ (where r is the interest rate and k is the amount of deposit interest added to the principal).

We found here that the storage compound interest of the unit period was more relevant to individual growth than are

other factors. However, this finding must be tested on theoretical grounds.

Seed dormancy is an important life cycle strategy that improves the sustainability of populations in fluctuating environmental conditions. Plant species growing in rapidly fluctuating environments must be preserved in permanent soil seed banks to prevent extinction (Gutterman, 2002). The possibility of seasons with zero seed production is low but not zero. This behavior is called delayed germination at the seed level. Seeds in any soil seed bank have only a limited chance of germination, even if the conditions for germination are perfect. Thus, soil seed banks must be permanent. Many different models have been used to illustrate this phenomenon from an evolutionary viewpoint (Cohen, 1966; Bulmer, 1984; Ellner, 1985; Gutterman, 2002; Kuang and Chesson, 2009).

An obvious trade-off exits between plant yield and germination (Rees, 1993, 1994). The first seed bank dynamic model of annual plants, called Cohen's model, was proposed in 1966 (Cohen, 1966).

$$S(t + 1) = S(t)[gf(gS(t))H(t) + (1 - g)(1 - d)], \tag{1}$$

where $S(t)$ is the number of seeds in the soil bank during season t; $H(t)$ is the average yield of each plant in season t; g is the total germination ratio; and d is the death rate of dormant seeds. $f(x)$ represents the density dependence function, and $x = gS(t)$ indicates the number of seeds surviving after competing for germination. The first seed bank dynamics model of annual plants was proposed without considering density dependence, which mean that $f(x) = 1$ in Eq. (1).

Cohen's model was gradually improved. Two main strategies have been used, both of which focus on density dependence. The first was proposed by Bulmer et al. (Bulmer, 1984; Ellner, 1985; Thomas, 1993; Valleriani, 2005; Tielbörger and Valleriani, 2005). $f(gS(t) = Q/[Q + gS(t)]$ in Eq. (1), where Q is the carrying capacity of the system, specifically the maximum density of adult plants supported by the environment. This equation is based on the reciprocal yield law, as first proposed by Shinozaki and Kira (Shinozaki and Kira, 1956; Firbank and Watkinson, 1985). The second strategy was proposed by Goldberg et al. (Goldberg, 1990; Kuang and Chesson, 2009). $F[gS(t)] = e^{-cS(t)}$ in Eq. (1), where c defines the total effect of competition on reproductive fitness of each individual. It is based on the exponent yield law, as proposed by Ricker (Ricker, 1954).

It is necessary to determine if there exists some intrinsic links among the three models. At present, the density-dependence law is mostly based on power laws (Farazdaghi and Harris, 1968; Holliday, 1960; Yoda et al., 1963; Watkinson, 1980; Antonovics and Levin, 1980; Deng et al., 2012) and the reciprocal yield law (see Appendices A and B for more details) (Willey and Heath, 1969; Hassell, 2000). There is an error in the reciprocal yield law, which is mentioned in Appendix A. There have been a lot of efforts to derive mechanistic explanations of these and related power laws in ecology (see Li et al. (2000) for some related discussion and references). There is still no good, general interpretation of these power laws, even they fit experimental data well (Antonovics and Levin, 1980; Deng et al., 2012).

We first noticed that compound interest of the unit period of one seed plays an important role in permanent soil seed banks. We tackled this idea, which was an extension of classic seed bank models, by adding a compound interest term to the fitness function of annual plants and constructed a seed bank dynamic model of annual plants for one seed, with compound interest of the unit period and discrete-time dynamic processes. Our results show that the density dependence can be interpreted by the evolutionary stability theory, mainly because one seed can choose germination or no germination so that there is an evolutionary stability strategy.

2. Model construction and derivation

Symbols and explanation of the model parameters and their derivation

$H(t) = H$ where H is the average yield of each plant during season t;
$S(t)$ is the number of seeds in the soil bank during season t;
S is the stable number of seeds in the bank;
g is the total germination ratio;
d is death rate of dormant seeds;
$f(x)$ represents the density dependence function;
$x, N = gS(t)$ indicates the number of surviving seeds after germination competition;
Q is the carrying capacity;
Y is the total yield of all plants in a season.
k is the amount of deposited interest added to the principal and the average of the occurrence of number of compensation (reproductive success) opportunities in a unit period.
a is the nongermination interest rate of nondormant seeds, which is based on seeds that can benefit from nongermination by preserving their chance of germination for some future date, when conditions may be more favorable.
C and D are constants in the power law.
b is a proportionality factor (dimensionless).

The relationships and intrinsic links between the three existing models are open to question. The density-dependence law must be experimentally determined, but no unified mechanism by which these laws may be interpreted has yet been published. Here, compound interest was important to the permanent soil seed banks. The intrinsic links between the three seed bank dynamic models of annual plants and the compound interest of density dependence as interpreted by the evolutionary stability strategies of one seed are shown.

It is hypothesized that the seed is homogeneous, the germination proportions have ceased to change, the germination ratio is evolutionarily stable, the soil seed bank is stable, and $S(t + 1) = S(t) = S$, and $H(t) = H$, where H is the average yield of each plant during the season t (Bulmer, 1984; Ellner, 1985).

g is the total germination ratio, and d is the death rate of dormant seeds. Here, we give another interpretation for g and d. $d(1 - g)$ is loss of soil seed bank in a cycle, $d(1 - g) + g$ is the germinating part, where $d(1 - g)$ can be seen as seeds die before becoming seedlings, and only g seeds become seedlings (see Fig. 1). So $d(1 - g)$ can also be defined as the death rate of germinated seeds.

Seeds benefit from germination, but they also benefit from not germinating. Thus, the germination decision of each seed should be considered.

Delaying germination and avoiding the risk of extinction in hedge bets theory essentially addresses the issue of how to maximize interest by storing seeds for future germination. Seed nongermination and economic storage interests are essentially the same. Seeds benefit from not germinating by preserving their chance of germination for some future date when conditions may be more favorable. Here, if the germination rate of one seed is 1, a is defined as the nogermination interest rate of nondormant seeds or interest rate. If the germination rate of one seed is g, then ga is interest rate of the seed.

The so-called interest, which can stimulate or inhibit seed production, is the potential future benefit. The interest rate of nondormant seeds is determined by the carrying capacity Q and the number of seeds in bank S. The optimized nongermination interest rate of nondormant seeds should be consistent with seed production. When Q is large, a low nongermination interest rate stimulates seed production. When S is large, large delays occur in germination,