



Demographic stochasticity alters the outcome of exploitation competition

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ARTICLE INFO

Article history:

Received 28 July 2014

Accepted 31 October 2014

Available online 11 November 2014

Keywords:

R^* rule

Armstrong–McGehee mechanism

Coexistence

Competitive reversal

ABSTRACT

Temporal variability in resource density is one of the mechanisms that facilitate coexistence between competitors. This study examines whether demographic stochasticity as a source of resource fluctuation can facilitate coexistence. The dynamics of a deterministic model (without demographic stochasticity) and a stochastic individual-based model (with demographic stochasticity) are compared. The deterministic model is an exploitation competition module consisting of two consumer species and one resource. The Gillespie algorithm is used to simulate demographic stochasticity in the corresponding individual-based model. The parameters of the models are chosen to represent cases where the deterministic model shows competitive exclusion according to the R^* rule and exhibits only stable equilibrium dynamics based on any combinations of the species. The analysis of the individual-based model shows that demographic stochasticity induces persistent population cycles between a consumer and the resource (i.e., when one of the consumers is absent), and this resource fluctuation allows the two consumers to coexist. Coexistence becomes possible through emerging tradeoffs that allow an inferior species (predicted by the deterministic model) to become competitively dominant (e.g., deviation of the R^* rule). These tradeoffs are useful for interpreting apparently contradicting empirical observations.

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1. Introduction

Competition is a key species interaction in ecological processes, and much has been studied about the fate of competition as well as the mechanisms that allow coexistence among competitors. The R^* rule, for example, is a fundamental result that predicts the outcome of competition (Tilman, 1982). In short, when multiple consumers are exploiting one limiting resource, a species that can deplete the resource to the lowest level and can sustain itself will exclude all the other competitors (more explicitly described below). This result indicates the difficulty of coexistence among competitors. In response, a substantial body of research has been conducted to understand mechanisms that allow competitors to coexist (e.g., Paine, 1966; Levin, 1970; Armstrong and McGehee, 1980; Chesson and Warner, 1981; Glover, 1997; Bolker and Pacala, 1999; Chesson, 2000).

Temporal variability is one of the mechanisms of coexistence and is also the topic of this study. Consider, there are two consumer species competing for the same resource where R_i^* is the equilibrium resource density when the resource and consumer species i are left alone ($i=1,2$). The R^* rule predicts that species 1 wins (i.e., species 2 is excluded) when $R_1^* < R_2^*$, and species 2 wins when $R_2^* < R_1^*$,

corresponding with the verbal description above. The Armstrong–McGehee mechanism poses a possibility for these two species to coexist (Armstrong and McGehee, 1980). For example, even when $R_1^* < R_2^*$, if the equilibrium associated with R_1^* is unstable (i.e., the resource and consumer species 1 will exhibit cyclic dynamics), the cyclic dynamics can create a tradeoff (i.e., species 1 is dominant when the resource level is low, and species 2 is dominant when the resource level is high) for the two species to coexist (see Abrams and Holt, 2002; Wilson and Abrams, 2003; Xiao and Fussmann, 2013, for conditions where the mechanism is more likely to operate).

The Armstrong–McGehee mechanism is a coexistence mechanism generated by endogenous population cycles. It is also known that resource oscillation caused by exogenous factors can allow the two competitor species to coexist (Smith, 1981). Thus, cyclic dynamics are generally thought to facilitate the coexistence of consumers. Stochasticity and discreteness (of individuals) are also factors that can induce population cycles even when corresponding deterministic models predict a stable equilibrium (Turchin, 2003; McKane and Newman, 2005; Okuyama et al., 2011). This study examines whether it is possible for two competitors to coexist when both R_1^* and R_2^* are stable in the deterministic model but cyclic dynamics are induced by demographic stochasticity. Previous studies that examined the importance of stochasticity and discreteness focused on whether their inclusion may expand or shrink the coexistence region predicted by the deterministic model (Anderies and Beisner, 2000; Wilson and Abrams, 2003).

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By adopting a different focus, this study provides new insights into the importance of demographic stochasticity in exploitation competition. First, a deterministic model of exploitation competition is described. Next, the corresponding individual-based model (IBM) that includes demographic stochasticity is introduced. The differences in dynamics between the two models are discussed with respect to the R^* rule and the Armstrong–McGehee mechanism.

2. The models

2.1. Deterministic model

A community consisting of two consumers and one resource is considered. In the absence of the consumers, the resource population grows logistically. The dynamics of the population densities of the consumers (N_1 and N_2) and the resource (R) are described by

$$\frac{dR}{dt} = R \left(r \left(1 - \frac{R}{K} \right) - \frac{a_1 N_1}{1 + a_1 h_1 R} - \frac{a_2 N_2}{1 + a_2 h_2 R} \right) \quad (1)$$

$$\frac{dN_1}{dt} = N_1 \left(\frac{b_1 a_1 R}{1 + a_1 h_1 R} - m_1 \right) \quad (2)$$

$$\frac{dN_2}{dt} = N_2 \left(\frac{b_2 a_2 R}{1 + a_2 h_2 R} - m_2 \right) \quad (3)$$

where r is the intrinsic rate of increase of the resource, K is the carrying capacity of the environment, a_i is the attack rate of consumer i , h_i is the handling time of consumer i , b_i is the conversion efficiency of consumer i , and m_i is the mortality rate of consumer i .

2.2. Individual-based model

The deterministic model (Eqs. (1)–(3)) is translated into an IBM using the Gillespie algorithm (Gillespie, 1976). In IBM, the three species exist in discrete numbers (R, N_1, N_2) for a given time. The number of each species changes according to the following eight events: (1) birth of the resource ($u_1 = rR$), (2) death of the resource due to intraspecific interaction ($u_2 = qR^2$), (3) death of the resource due to consumption by species 1 ($u_3 = a_1 RN_1 / [1 + a_1 h_1 R]$), (4) death of the resource due to consumption by species 2 ($u_4 = a_2 RN_2 / [1 + a_2 h_2 R]$), (5) birth of species 1 ($u_5 = b_1 a_1 RN_1 / [1 + a_1 h_1 R]$), (6) death of species 1 ($u_6 = m_1 N_1$), (7) birth of species 2 ($u_7 = b_2 a_2 RN_2 / [1 + a_2 h_2 R]$), and (8) death of species 2 ($u_8 = m_2 N_2$). The quantities, u_1, \dots, u_8 , describe the rates at which the respective event takes place and are derived from the deterministic model (Eqs. (1)–(3)). The algorithm is an exact procedure for numerically simulating the deterministic model by introducing inherent stochasticity (Gillespie, 1977). In this formulation, Eq. (1) was rearranged such that $q = r/K$, but this reparametrization does not affect the deterministic model.

Each of the eight events will change the density of the species as follows. Consider, the current densities to be (R, N_1, N_2) . Then events 1–8 will result in $(R+1, N_1, N_2)$, $(R-1, N_1, N_2)$, $(R-1, N_1, N_2)$, $(R-1, N_1, N_2)$, (R, N_1+1, N_2) , (R, N_1-1, N_2) , (R, N_1, N_2+1) , and (R, N_1, N_2-1) , respectively. The probability that event i takes place is $u_i / (u_1 + \dots + u_8)$. At each event, time is incremented by a random variate from an exponential distribution whose rate parameter is $u_1 + \dots + u_8$.

3. Analysis

In the absence of species 2, the equilibrium is described by $(R_1^*, N_1^*, 0)$ in the deterministic model. In the absence of species 1, the equilibrium is described by $(R_2^*, 0, N_2^*)$. Thus, according to the R^* rule, when $R_1^* < R_2^*$, species 2 will be excluded when the three species are initially present. However, when $(R_1^*, N_1^*, 0)$ is not stable, the resource and species 1 may exhibit limit cycle behavior, and coexistence among the three species may be possible according to the Armstrong–McGehee mechanism.

The default parameter values are $K=1000$, $r=2$, $a_1=0.001$, $a_2=0.001$, $b_1=1$, $b_2=1$, $h_1=1$, and $h_2=0$. In addition, default R^* s are set as $R_1^*=150$, and $R_2^*=151.5$, and the values of m_1 and m_2 are determined accordingly. The effect of each parameter is also examined (e.g., sensitivity analysis). This study considers whether dynamics generated by demographic stochasticity affect the competitive interaction. Thus, in the entire parameter space including the sensitivity analysis, the considered situation corresponds with $R_1^* < R_2^*$ and both $(R_1^*, N_1^*, 0)$ and $(R_2^*, 0, N_2^*)$ are stable in the deterministic model. In other words, the Armstrong–McGehee mechanism does not operate and no coexistence mechanism is known for the deterministic model. In terms of the fate of competition, no further analysis of the deterministic model is required (i.e., species 2 is excluded).

IBM is studied by simulation. The initial densities are always $(R_1^*, (N_1^* + N_2^*)/2, (N_1^* + N_2^*)/2)$ computed by the deterministic model, but the densities are rounded to make them discrete. Each simulation runs for 15,000 time units; this corresponds with more than 16×10^6 events in the Gillespie algorithm. The length of the time unit is chosen because, in the corresponding deterministic model, it takes 5000–6000 time units until N_2 becomes less than 1 around the default parameter values (see Results section). Thus, when IBM persists for 15,000 time units, the two competitors are considered to coexist.

4. Results

When only one of the consumer species is present, although both $(R_1^*, N_1^*, 0)$ and $(R_2^*, 0, N_2^*)$ are stable in the deterministic model, IBM exhibits persistent cycles (Fig. 1).

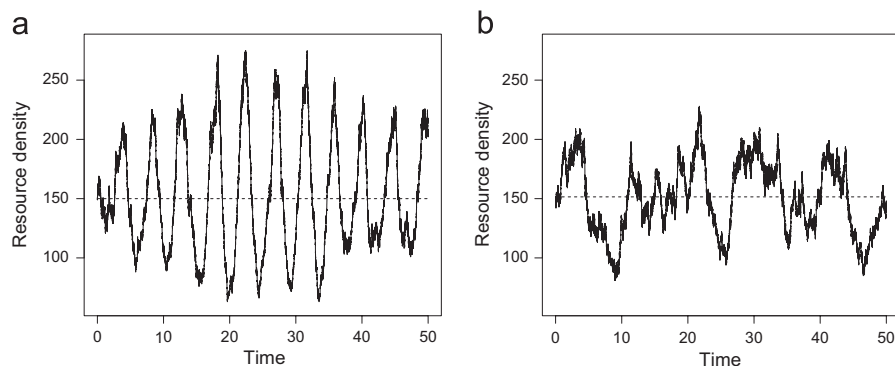


Fig. 1. Representative dynamics of the resource based on IBM. (a) $N_2 = 0$, and (b) $N_1 = 0$. The initial values for (a) and (b) are $(R_1^*, N_1^*, 0)$ and $(R_2^*, 0, N_2^*)$, respectively. The dotted lines indicate the dynamics based on the deterministic model. The default parameter values are used.

At the default parameter values, the deterministic model predicts that species 2 is competitively excluded according to the R^* rule. On the other hand, IBM shows that coexistence is readily possible. The prediction from the deterministic model (Eqs. (1)–(3)) and a typical result from IBM are shown in Fig. 2. The dynamics based on IBM are fundamentally different from the deterministic prediction (i.e., it is not stochasticity simply slowing down the rate of extinction).

Coexistence is possible because tradeoffs emerge along the parameters (Fig. 3), whereas such tradeoffs do not exist in the deterministic model. For example, as h_1 increases, competitive reversal occurs (species 2 wins although $R_1^* < R_2^*$). Similarly, when $R_2^* - R_1^*$ is small, even when $R_1^* < R_2^*$, species 2 dominates. These results are fundamentally different from the prediction of the R^* rule and indicate that the R^* rule does not apply when stochasticity and discreteness are considered. Relative expressions in b_1 and b_2 also affect the outcome of competition. In general, when $b_1 > b_2$, species 2 wins, and when $b_2 > b_1$, species 1 wins (Fig. 4).

5. Discussion

This study demonstrated the important ways by which demographic stochasticity can alter the outcome of exploitation competition. Although the entire parameter space corresponds with the situation where species 2 is excluded in the deterministic model (Eqs. (1)–(3)), the corresponding IBM showed rich dynamics where coexistence as well as competitive reversal is possible. These results suggest that discreteness and stochasticity play important roles in the fate of exploitation competition, and the result based on deterministic models, such as the R^* rule, must be interpreted carefully based on the assumptions.

There are tradeoffs between the two consumers along the examined parameters, K , h_1 , b_1 , and b_2 , and coexistence is possible when neither species is dominant (e.g., at the transition of the dominance). Among the parameters, the result based on b_1 and b_2 most clearly describe the effect of demographic stochasticity. This is because changes in b_1 and b_2 do not affect the phase-plane diagram (i.e., the predator and prey isoclines) because R_1^* and R_2^*

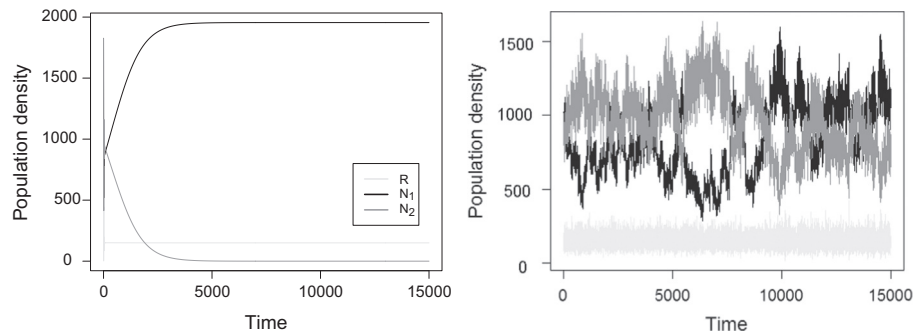


Fig. 2. Population dynamics based on the deterministic model (left) and IBM (right). The default parameters and the initial values are used. Color key: light grey (R), black (N_1), and dark grey (N_2).

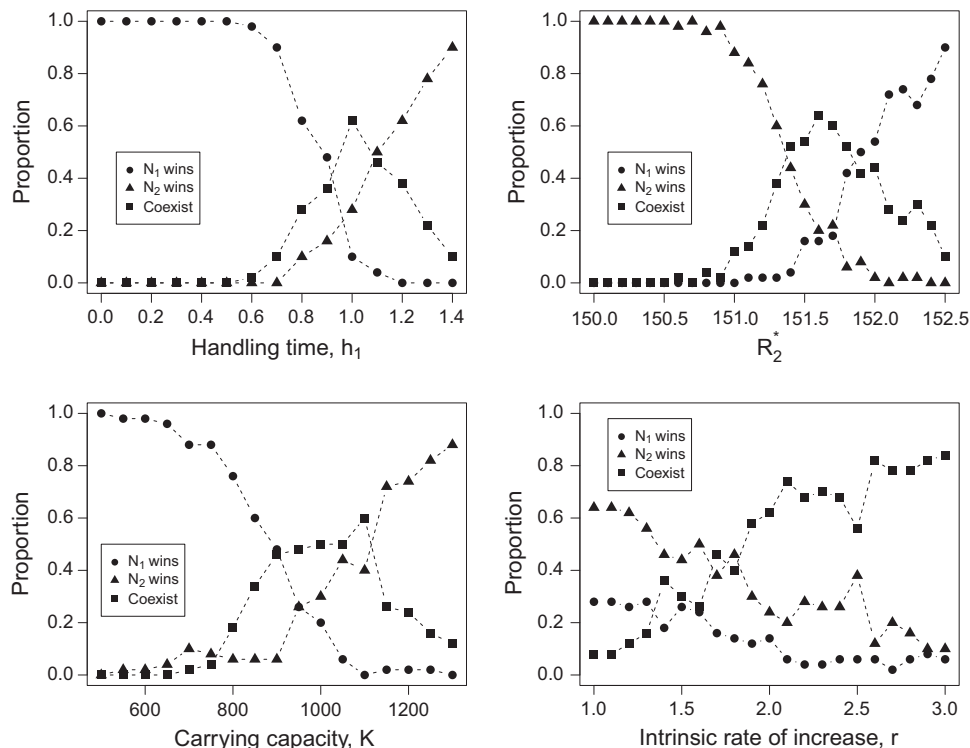


Fig. 3. Sensitivity analysis based on h_1 , R_2^* , K , and r . Proportions of the three outcomes are shown. The default parameters are used except for the one in question. Proportions are computed based on 50 replications.

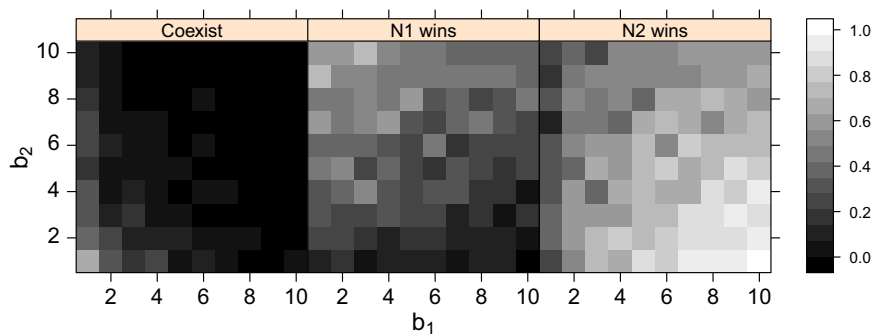


Fig. 4. Sensitivity analysis based on b_1 and b_2 . For each combination of b_1 and b_2 , the proportion of respective outcomes is described by the color key. The default parameters are used. Proportions are computed based on 50 replications.

are fixed. Therefore, further changing their values does not change the prediction of the deterministic model. Other parameters change the shape of the isoclines such that changing their values will also change other quantities. For example, h_1 changes the shape of the prey isocline, thus changing the equilibrium density of the predator, N_1^* . Further increasing h_1 also makes $(R_1^*, N_1^*, 0)$ unstable in the deterministic model. As a result, the interpretation of a change is more difficult, i.e., confounded with relatively more details. With regard to b_1 and b_2 , an increase in b_i ($i=1,2$) is compensated by increase in m_i . Therefore, a large b_i indicates that species i has a high turnover. Fig. 4 shows that species with a high turnover is competitively inferior, which is consistent with the conventional succession theory where species with high reproduction and short generation times can first colonize an open space but are then replaced by species with long generation times (Houston and Smith, 1987).

Competitive reversal is an important result of this study. Abrams and Wilson (2004) showed an inferior competitor (i.e., one with a higher R^*) can be competitively dominant when there are two patches. The present study showed the limitation of the R^* rule without using multiple patches, and thus the result is relevant to wider cases. For example, the gleaner-opportunist tradeoff directly relates to the coexistence mechanisms based on cyclic dynamics discussed above (e.g., Glover, 1990; Litchman and Klausmeier, 2001). It is a tradeoff between R^* and r_{\max} where r_{\max} for consumer species i may be represented by $(dN_i/dt)/(1/N_i)$ when the resource level is high. Species with low R^* and r_{\max} are gleaners, and those with high R^* and r_{\max} are opportunists. Gleaners dominate where environments are static, and opportunists dominate in highly variable environments. However, this study showed that species with identical R^* and/or r_{\max} can be variable in important individualistic ways (e.g., the same R^* results with many demographic parameter combinations). Furthermore, while having a large r_{\max} is generally considered a positive trait, large r_{\max} (corresponding with a large b_i in this study according to the above definition) makes the species competitively inferior in this study. Using the same r_{\max} definition, Kirk (2002) experimentally tested competition between a gleaner and an opportunist by artificially introducing resource fluctuation, and found that gleaners always won regardless of the level of fluctuation. The identity of each species, i.e., gleaner or opportunist, is more multidimensional and is hidden in the two numbers: R^* and r_{\max} .

Previous studies that examined the importance of stochasticity and discreteness in the Armstrong-McGehee mechanism focused on evaluating how the coexistence prediction by the deterministic model expands or shrinks when stochasticity is incorporated (Anderies and Beisner, 2000; Wilson and Abrams, 2003). On the other hand, this study entirely considers the situation where coexistence through the Armstrong-McGehee mechanism is impossible in the deterministic model. Therefore, the focus of this

study and the previous studies is different, and apparently inconsistent conclusions are reached. For example, Wilson and Abrams (2003) found that competitive reversal is rarely possible, and impossible in a nonspatial case, which most closely corresponds with this study, because of the different parameter space considered. The limitations of a specific study based on specific parameters should be considered in model analysis. Nevertheless, although dimensional analysis and rescaling of parameters are powerful approaches for attaining more general results by reducing parameters (Edelstein-Keshet, 1988; Stephens and Dunbar, 1993), this study showed that explicit consideration of original parameters can have important implications in the light of demographic stochasticity.

This study used the Gillespie algorithm to examine the effect of demographic stochasticity. Although the model is described as individual-based, the model considered here is arguably not a true IBM (or the strengths of IBMs are not utilized). This is because the model assumed that all individuals within a species are identical, as assumed in the original model (Eqs. (1)–(3)). However, the fact is that individuals are variable, and potential demographic stochasticity is influenced by such variability. Even in the case of the simple model, e.g., predators are either handling a captured prey or searching for a prey at a given moment (Okuyama, 2009, 2012). More fundamentally, predators have variable foraging success simply by chance (Okuyama, 2013). Such individual identity is intentionally ignored in this study so that the comparison with the original model can be solely attributed to stochasticity. However, real demographic stochasticity is much richer than the stochasticity introduced by the Gillespie algorithm, partly as a result of such individual identities. Given that a simple consideration of demographic stochasticity revealed rich tradeoffs, further detailed examinations of demographic stochasticity with explicit consideration of individualism are likely to result in important mechanisms that determine the fate of competition modules and other general ecological communities.

Acknowledgments

I thank anonymous reviewers for their comments. This study was supported by the Ministry of Science and Technology of Taiwan through research Grant Nos. 99-2628-B-002-051-MY3 and 102-2311-B-002-038-MY3.

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