



# The relative importance of relative nonlinearity and the storage effect in the lottery model



Chi Yuan\*, Peter Chesson

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, United States

## ARTICLE INFO

### Article history:

Received 2 November 2013

Available online 22 August 2015

### Keywords:

Variable environment  
Species coexistence  
Relative nonlinearity  
The storage effect  
Stabilizing mechanism  
Equalizing mechanism

## ABSTRACT

Although it is likely that many coexistence mechanisms contribute to maintenance of species diversity, most approaches to understanding species coexistence proceed as if only one mechanism would be present. In studies of species coexistence in a temporally fluctuating environment, the storage effect, believed to be the most important coexistence mechanism, has been the focus. Although a different coexistence mechanism—relative nonlinearity—is also predicted to arise frequently with environmental variation, its effect has been overshadowed by the storage effect. The relatively nonlinear growth rates on which the mechanism depends arise simply from differences in life history traits. Many kinds of temporal variation can then interact with these nonlinearity differences to create the relative nonlinearity coexistence mechanism. Much is unknown about when this mechanism is important and its total neglect is not justified. Here, we use the lottery model to provide a much needed quantitative assessment of the relative and combined effects of relative nonlinearity and the storage effect. Our analysis takes advantage of recently developed techniques for quantifying coexistence mechanisms when multiple mechanisms operate in concert. We find that relative nonlinearity is able to contribute substantially to species coexistence in the lottery model when two conditions are satisfied: (1) species must differ greatly in their adult death rates, (2) sensitivity of recruitment to environmental variation must be greater for species with larger adult death rates. In addition, relative nonlinearity has a critical role in compensating for a weakened storage effect when there is high correlation between species in their responses to the varying environment. In some circumstances relative nonlinearity is stronger than the storage effect or is even the sole mechanism of coexistence.

© 2015 Elsevier Inc. All rights reserved.

## 1. Introduction

It has often been remarked that in any diverse natural community, multiple mechanisms of coexistence are likely to operate simultaneously (Amarasekare, 2007, 2009; Kuang and Chesson, 2010). The diversity present is thus not expected to have a single cause, but many approaches to understanding species coexistence both in nature and in models proceed as if only one mechanism would be present. Methods of analyzing systems to understand the separate contributions of different mechanisms, and the interactions between them, are needed both theoretically and empirically. In particular, theoretical studies have not generally had good means of defining and understanding contributions of different mechanisms to the central question of species

coexistence. Here we study the lottery model where two general mechanisms of species coexistence can contribute to diversity maintenance, and show how techniques for quantifying species coexistence (Chesson, 1989, 1994, 2003, 2008) can disentangle relative and absolute contributions of the different mechanisms when multiple mechanisms are present. These techniques have been applied previously to understand contributions to species coexistence from jointly acting competition-based and predation-based coexistence mechanisms (Chesson and Kuang, 2010; Kuang and Chesson, 2010). However, in the lottery model we study the contributions of two competition-based coexistence mechanisms. The lottery model provides a simple theoretical example of how stable species coexistence can occur in a fluctuating environment, but the relative and joint contributions of the separate mechanisms have not previously been elucidated. Fluctuating environments have provided challenges to theoretical and empirical understanding while also being proposed from time to time as the explanation for high diversity in systems with limited opportunities for traditional coexistence mechanisms, such as resource

\* Corresponding author.

E-mail addresses: [cyuan@email.arizona.edu](mailto:cyuan@email.arizona.edu) (C. Yuan), [pchesson@u.arizona.edu](mailto:pchesson@u.arizona.edu) (P. Chesson).

partitioning, to operate (Hutchinson, 1961; Grubb, 1977; Sale, 1977; Levins, 1979; Scheffer et al., 2003; Hiltunen et al., 2008).

A unified theoretical approach to coexistence in temporally varying environments has revealed two broad classes of fluctuation-dependent coexistence mechanism, the storage effect, and relative nonlinearity (Chesson and Warner, 1981; Chesson, 1994, 2000, 2008). The storage effect arises from interactions between fluctuations in the physical environment and fluctuations in the intensity of competition. It provides advantages to a species perturbed to low density by allowing the species to escape competition at times when the environment favors it, but does not favor its competitors. The outcome is recovery from low density and hence species coexistence. The mechanism relative nonlinearity is named from the requirement that different species have different nonlinear responses to competition. If competition fluctuates over time, Jensen's inequality (Needham, 1993) means that the long-term growth rates, which are time averages of short-term growth rates, will be affected differently for different species (Armstrong and McGehee, 1980; Chesson, 2000; Kuang and Chesson, 2008). Relative nonlinearity promotes coexistence when species drive fluctuations in competition in directions that favor their competitors. The coexistence mechanism thus involves both the relatively nonlinear growth rates and differences between species in their contributions to fluctuations in competition.

Coexistence by relative nonlinearity can result from endogenous fluctuations in population densities (Armstrong and McGehee, 1980; Adler, 1990; Abrams and Holt, 2002; Kuang and Chesson, 2008; Kang and Chesson, 2010) and from external environmental fluctuations that drive fluctuations in population densities (Chesson, 1994, 2000, 2003, 2008). In difference equation models for species with seasonal reproduction, relatively nonlinear growth rates arise simply from differences between species in life-history traits (Chesson, 1994, 2003). In such models, fluctuations in competition are often driven by fluctuations in environmental factors (Chesson, 1994), although endogenously driven fluctuations have also been considered (Kuang and Chesson, 2008). In both cases, coexistence is possible from relative nonlinearity. When fluctuations in competition are driven by environmental fluctuations, as in the lottery model studied here, the storage effect is present too. As the storage effect has been predicted to be the more important coexistence mechanism (Chesson, 1994), the role of relative nonlinearity has often been ignored. Moreover, empirical studies of coexistence in a variable environment have focused almost exclusively on the storage effect even though a reasonable expectation is that relative nonlinearity is present too (Chesson, 2003).

Both Chesson (1994) and Abrams and Holt (2002) point out that it is difficult for relative nonlinearity alone to maintain coexistence of more than two species competing for single resource whether fluctuations are endogenous in origin or due to temporal environmental variation. However, Abrams and Holt (2002) show that relative nonlinearity can have a coexistence promoting effect comparable to the resource partitioning in the case of two competing species, and Chesson (2003) suggests that relative nonlinearity might still be important in multispecies systems through its interactions with other mechanisms even though alone it is not effective in stabilizing coexistence of more than two species on one fluctuating resource. The case of relative nonlinearity with multiple resources has not been studied extensively, but general considerations in Chesson (1994) suggest that the complex nonlinearities possible in multiple resource systems have strong potential to promote coexistence. Indeed, one example of relative nonlinearity with multiple resources and endogenous fluctuations was found to strongly promote coexistence of phytoplankton species (Huisman and Weissing, 1999, 2002). More study of the potential for coexistence by relative nonlinearity with multiple

resources is certainly needed, but no less important is a better understanding the role of relative nonlinearity in the single resource case when other mechanisms are present. As models of recruitment variation that lead to the storage effect coexistence mechanism generally also permit relative nonlinearity, it is essential to understand what the relative contribution of relative nonlinearity to coexistence might be. It is also important to know if relative nonlinearity can make a strong contribution to coexistence in multiple species cases when other mechanisms are present even though alone it is unlikely to permit coexistence of more than two species. Without this understanding, the almost exclusive focus on the storage effect in models of recruitment variation may be seriously misleading.

The lottery model for iteroparous perennials has been an important model for understanding the role of environmental variation in species coexistence. It has been used for perennial plants such as forest trees, and marine space holding organisms such as coral reef fishes or benthic invertebrates (Chesson and Warner, 1981; Comins and Noble, 1985; Hatfield and Chesson, 1997; Hubbell, 2001; Kelly and Bowler, 2002). The model is in fact closely related to the model commonly used in neutral theory to define dynamics within a forest stand (Hubbell, 2001). However, as implemented here, it is far from neutral. Environmental fluctuations cause recruitment to vary from year to year. Persistent adult stages buffer population growth against unfavorable times, permitting the storage effect to be present. At the same time, species differences in adult death rates enable relative nonlinearity to be present. These features mean that these two mechanisms are nearly always present together and their contributions to coexistence are not independent. Indeed, below we show that important factors contributing to the strength of relative nonlinearity also crucially determine the strength of the storage effect. As parameters are changed, relative nonlinearity often changes in a contrasting way to the storage effect, which makes relative nonlinearity more important when the storage effect is weak. We determine the conditions that allow relative nonlinearity to be stronger than the storage effect. These conditions are identified using approximate formulae for mechanism strength, backed up by simulations. Our results show when relative nonlinearity might be important in natural systems providing a guide for empirical studies.

## 2. Methods

### 2.1. Relative nonlinearity and the storage effect in the lottery model

The lottery model (Chesson and Warner, 1981) describes community dynamics of iteroparous perennial species. Two distinct life stages, juveniles and adults, are considered. Each year, adults reproduce, and the resulting number of juveniles varies stochastically overtime, driven by the varying physical environment. Juveniles require open space to establish and mature as adults. Space is assumed to be limited, becoming available only with adult death. Juveniles compete for this space to recruit as adults. Success of a species in this competition for space is assumed proportional to the total number of juveniles produced during a given recruitment period. After maturation to an adult, the survival of an individual is assumed to be insensitive to both the varying physical environment and competition.

The model is specified by the following difference equation for the dynamics of  $n$  perennial species:

$$N_j(t+1) = \left\{ 1 - \delta_j + \left[ \sum_{k=1}^n \delta_k N_k(t) \right] \frac{\beta_j(t)}{\sum_{k=1}^n \beta_k(t) N_k(t)} \right\} N_j(t) \quad (1)$$

$j = 1, \dots, n.$

Download English Version:

<https://daneshyari.com/en/article/4502299>

Download Persian Version:

<https://daneshyari.com/article/4502299>

[Daneshyari.com](https://daneshyari.com)