



Interplay between habitat subdivision and minimum resource requirement in two-species competition

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ABSTRACT

This paper explores the effects of increasing spatial subdivision of habitat on competition between two species. An increase in the degree of subdivision without any increase in the total amount of resources in the environment leads to smaller patch sizes, and thus, fewer individuals supported per patch. This fact suggests that when the degree of subdivision is high, the minimum resources that an individual must obtain before reproduction become important. Competition equations derived from first-principles that incorporate the minimum resource requirement are employed to investigate the effects of spatial subdivision and how these effects depend on the minimum requirements of the two species, type of resource competition such as scramble or contest, and spatial aggregation level of individuals. The results show that increased subdivision leads to changes in “effective fecundities” of the species, and consequently, affects their competitive superiority. Species coexistence is promoted at intermediate subdivision levels, especially if there is a trade-off between the minimum resource requirement and inherent fecundity. The range of subdivision in which coexistence occurs depends on the spatial aggregation of individuals and inequality in competitive ability between the species.

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1. Introduction

Population and community dynamics are manifestations of processes operating at the individual-level, and thus, one of the central problems in ecology is understanding the relationship between individual-level processes and population-level phenomena. In general, considering that individuals interact locally, any spatial structure of a habitat that affects their distribution or dispersal will influence the population or community dynamics. Theory suggests that when a habitat or resource is subdivided into many patches among which two competing species are distributed independently in a clumped manner, species coexistence can be promoted (Atkinson and Shorrocks, 1981; Ives and May, 1985). However, there has been some controversy about the type of the aggregation that is sufficient for coexistence, and this issue has been addressed extensively (Green, 1986; Chesson, 1991; Heard and Remer, 1997; Hartley and Shorrocks, 2002). It has been suggested that the variation caused by laying eggs in clutches among patches alone is insufficient for species coexistence. Independent negative binomial variation with a constant k has strong effects on coexistence, but this means that the species respond independently to a spatially varying environment. Hence this outcome is a form of habitat partitioning (Chesson, 2012). Compared with the extensive study on the effects of aggregation, however, the effects of increasing the

level of spatial subdivision have been less explored. What effects does increasing the subdivision while maintaining the aggregation level constant have on species coexistence?

The effects of subdivided resources or habitats have been explored in various situations. Environmental changes due to human activities cause habitat fragmentation at the regional scale. It has been suggested that the effects of pure habitat fragmentation without habitat loss on biodiversity are often positive (Fahrig, 2003). Many insects exploit ephemeral and discrete resources (for example, dung, carrion, and dead wood), and the aggregation model of coexistence suggests that the coexistence of two competing species can be promoted in such a patchy environment if the species are distributed independently in a clumped manner (Atkinson and Shorrocks, 1981; Ives and May, 1985; Ives, 1988; Sevenster, 1996; Hartley and Shorrocks, 2002). Empirical studies have reported that the outcome of competition and the overall metrics of species diversity depend significantly on the degree of spatial aggregation and patch size (e.g., Kneidel, 1985; Sevenster and Van Alphen, 1996; Toda et al., 1999; Andresen, 2002; Woodcock et al., 2002; Yamashita and Hijii, 2003; Horgan, 2005; Krasnov et al., 2006). Toquenaga and Fujii (1990), and Toquenaga et al. (1994) experimentally investigated competition between two species of bean weevils by using different sizes of beans. These weevils competed for resources in beans (patches) during their larval stage, and the competitive outcome depended on the size of the beans used.

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Table 1
Competition equations.

Type	Competition equations	Eq.
(S, S)	$x_{t+1} = b_1 x_t \left(1 + \frac{x_t}{\lambda_1}\right)^{-\lambda_1 - 1} \left(1 + \beta_{21} \frac{y_t}{\lambda_2}\right)^{-\lambda_2}$	(7a)
	$y_{t+1} = b_2 y_t \left(1 + \frac{x_t}{\lambda_1}\right)^{-\lambda_1} \left(1 + \frac{y_t}{\lambda_2}\right)^{-\lambda_2 - 1}$	(7b)
(C, C)	$x_{t+1} = b_1 x_t \int du q_1(u) \left\{1 + Q_1(u) \frac{x_t}{\lambda_1}\right\}^{-\lambda_1 - 1} \left\{1 + Q_2(u) \frac{y_t}{\lambda_2}\right\}^{-\lambda_2}$	(16a)
	$y_{t+1} = b_2 y_t \int du q_2(u) \left\{1 + Q_1(u) \frac{x_t}{\lambda_1}\right\}^{-\lambda_1} \left\{1 + Q_2(u) \frac{y_t}{\lambda_2}\right\}^{-\lambda_2 - 1}$	(16b)
(C, S)	$x_{t+1} = b_1 \left\{1 - \left(1 + \frac{x_t}{\lambda_1}\right)^{-\lambda_1}\right\} \left(1 + \beta_{21} \frac{y_t}{\lambda_2}\right)^{-\lambda_2}$	(20a)
	$y_{t+1} = b_2 y_t \left(1 + \frac{x_t}{\lambda_1}\right)^{-\lambda_1} \left(1 + \frac{y_t}{\lambda_2}\right)^{-\lambda_2 - 1}$	(20b)
	Here,	
	$b_i = b'_i e^{-s_i n / R_0}$,	(9)
	$\beta_{21} = (1 - e^{-\beta'_{21} s_2 n / R_0}) / (1 - e^{-s_2 n / R_0})$,	(10)
	$Q_i(u) = \int_u^\infty du' q_i(u')$.	(15)
	For S and C2 species,	
	$x_t = (1 - e^{-s_1 n / R_0}) X_t / n$ or $y_t = (1 - e^{-s_2 n / R_0}) Y_t / n$.	(8)
	For C1 species,	
	$x_t = X_t / n$ or $y_t = Y_t / n$.	(17)

S, scramble competition; C, contest competition (C1, contest-1; C2, contest-2).

The above experimental results suggest the importance of patch size in species competition. In general, increasing the spatial subdivision while keeping the total amount of resources fixed leads to fewer resources per patch (smaller patch sizes). When a habitat is highly subdivided, a patch can support only a small number of individuals. This suggests that the minimum resources that an individual needs to obtain to survive until the reproductive period (Łomnicki, 1988) become important at high degrees of subdivision. If two competing species differ in this threshold, there can be a situation where one species with a larger threshold cannot reproduce in a small patch owing to resource shortage, but the other species with a smaller threshold can. However, the minimum resource requirement has not been considered in most competition models in patchy habitats, where the maximum number of individuals supported by a patch (patch carrying capacity) has often been given by a continuous rather than a discrete number (Atkinson and Shorrocks, 1981; Ives and May, 1985; Pearman and Wilbur, 1990). Fujii (1965) considered the effects of spatial subdivision on population dynamics by developing an equation that incorporates integer numbers of patch carrying capacity, but he did not extend the model to interspecific competition. The minimum resource requirement has also been incorporated into some individual-based models to describe population dynamics (Johst et al., 2008, 2013). Toquenaga et al. (1994) used individual-based models to consider the effects of patch size on competition between contest and scramble species of bean weevils. Game-theoretical models have also discussed the effects of patch size on the evolution of competition strategies in terms of payoff matrices (e.g., Smith and Lessells, 1985). Interspecific competition models incorporating the minimum resource requirement have been developed in a first-principles manner, but the role of the minimum requirement in competition has not been discussed (Anazawa, 2012b). The effects of increasing spatial subdivision on interspecific competition in systems with the minimum resource requirement remain insufficiently understood. In particular, the relationship between subdivision and spatial aggregation as a factor affecting competition is poorly understood.

This paper explores the effects of increasing spatial subdivision on competition between two species by using first-principles competition equations developed by Anazawa (2012b). More specifically, the dependence of these effects on the minimum resource requirements of the two species, type of resource competition such as scramble or contest (Nicholson, 1954; Anazawa, 2010), and spatial aggregation level of individuals is investigated. These discrete-time competition equations describing the population dynamics of two competing species are extensions of site-based models (Sumpter and Broomhead, 2001; Johansson and Sumpter, 2003;

Brännström and Sumpter, 2005a, b, 2006; Anazawa, 2009, 2010, 2012a; Gotzen et al., 2011) and Fujii's model (Fujii, 1965), which are derived from first-principles by modeling resource competition within patches among individuals and subsequently computing averages over all possible spatial configurations of individuals and resources among patches. One advantage of the first-principles equations is that they can be used to deal with interspecific competitions of various types (scramble vs. scramble, contest vs. contest and contest vs. scramble). Another advantage is that they allow us to understand the effects of increased subdivision without relying on simulations. This is because population-level key parameters of the equations are provided as simple analytic functions of the minimum resource requirement and patch number through which the effects of increasing patch number can be understood clearly.

In Section 2, I summarize these competition equations, and in Section 3, I use them to explore the effects of increasing subdivision on interspecific competition. Increased subdivision leads to changes in the “effective fecundities” of the species, and consequently, affects their competitive superiority. Species coexistence is promoted at intermediate subdivision levels, especially when there is a trade-off between the minimum resource requirement and inherent fecundity, suggesting the possibility of a coexistence mechanism mediated by the new trade-off. The biological rather than mathematical mechanism as to how subdivision level affects resource availability and species coexistence is explained in Section 3.3.

2. First-principles competition equations

The analysis here will be based on three sets of competition equations summarized in Table 1, which were derived in Anazawa (2012b) from first-principles. Eqs. (7) and (20) in this table are from Table 2 and Eqs. (16) and (15) are from Table 4 in Anazawa (2012b). Note that x , y , $Q_1(u)x$, and $Q_2(u)y$ in this paper stand for \hat{x} , \hat{y} , $D_1(u)x$, and $D_2(u)y$ in Anazawa (2012b), respectively. Table 2 summarizes the key parameters and functions. This section summarizes the basic framework, the underlying assumptions of these equations, and outlines of their derivations.

2.1. Site-based framework

Consider two species that compete for a common resource during their larval stage in a habitat consisting of n patches or resource sites (n is very large). The larvae compete for resources while staying in their natal patch. At the end of the larval stage, only those larvae that have obtained a sufficient amount of resources become adults and lay eggs by moving among the patches.

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