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Multiple time scales in consumer-resource interactions

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Arguments regarding the appropriate form for the rate at which consumers extract biomass from resource populations hinge on relative time scales of underlying processes. Some ecologists argue that, because differential equation models imply instantaneous rates of change, time scale arguments do not hold. Here we point out that this reasoning is fallacious. We define three natural time scales for consumer-resource interactions and demonstrate, using asymptotic methods of analysis, how relative differences in these scales lead to the formulation of models with qualitatively distinct dynamics. Further, we identify time scale and resource heterogeneity assumptions that constrain the R^* competition rule (i.e., the competitor that suppresses the resource to the lowest density excludes all other competitors), as well as clarify the dichotomy between Schoener's models of competition for overlapping and for partitioned resources.

1. Introduction

The relative merits of using discrete versus continuous time equations to model population processes is an important issue for both theoretical and applied population biologists because both approaches embody different kinds of approximations and implicit assumptions. Discrete-time difference equation models, for example, require that we pay careful attention to the sequencing of events such as such as survivorship and aging. Reversing such sequences could lead to fundamental changes in the stability properties of the population process being modeled (Wang & Gutierrez 1980).

Inherent in the formulation of continuous-time differential equation population models is the notion of instantaneous rates of change and how this notion determines the form of the functional response (Holling 1959) in Lotka-Volterra type prey-predator equations (Lotka 1925, Volterra 1926). Arditi and Ginzburg (1989), for example, have argued that when the time scale governing consumer behavioral processes is much faster than the time scale governing consumer demographic processes then a ratio-dependent functional response is most appropriate. Oksanen, Moen, and Lundberg (1992), on the other hand, criticized Arditi and Ginzburg's rationale for ratio-dependent extraction with the claim that time-scale considerations are invalid in differential equation models because "... differential equations only deal with instantaneous rates of change." In this same paper, Oksanen et al. continued their criticism with the statement that "One must either stick to instantaneous rates of change or switch from differential to difference equations."

Abrams (1994) following Oksanen *et al.*'s lead concluded (p. 1842/3) "A differential equation model measures instantaneous rates of change, not yearly averages ... Thus it is fundamentally incorrect to argue that the functional response in a differential equation model should reflect some time average of instantaneous processes." Through these arguments, Abrams links the fate of ratio-dependent models to an assessment of the suitability of differential equations as models of biological processes with disparate time scales. This is unfortunate since the two issues are entirely separate.

The relative merits of using difference versus discrete equations depends on the processes being modeled and the temporal resolution of interest (e.g., generation versus intergenerational, daily versus annual). In this paper, we focus on the question of how comparative rates of change of different process at particular time scales decisively effect the outcome of various population processes, such as competition, that are modeled using differential equations. We stress that this use of differential equations makes no statement about the relative merits of ratio versus pure resource dependence in the functional response. In general, we expect the functional response to have ratio-dependent characteristics when the consumer density is high relative to the resource density and to have resource-dependent characteristics when the consumer density is low relative to the resource density, as is evident in some functional forms that include the effects of interference competition (DeAngelis *et al.* 1975, Frazer & Gilbert 1976, Getz 1991, 1994 — for additional discussion on inteference competition *see* Arditi and Saïah 1992, Beddington *et al.*, 1975, Getz 1984, Gutierrez *et. al.* 1994, Ruxton & Gurney 1992).

The approach we take here is based on both deterministic and stochastic averaging methods in dynamical systems (Friedlin 1987, Sanders & Verhulst 1985) and is inspired by an application of deterministic averaging methods to a model of a consumer-resource system (Michalski *et al.* 1997). In carrying out our analysis, we also revisit the question of two consumers competing for a limiting resource. We demonstrate that the R^*rule (Hsu *et al.* 1977, Tilman 1990, Holt *et al.* 1994), which elucidates which of the two consumers competitively excludes the other, only applies to systems that satisfy the following criteria: the time scales of demographic change in the consumer and resource population are sufficiently longer or slower than the time scale at which the consumer encounters heterogeneity in the distribution of the resource to justify the application of asymptotic methods.

2. Instantaneous rates

We begin by examining the notion of instantaneous rates of change. In biological systems this notion is not as useful an abstraction as it is in the physical sciences. In both the physical and biological sciences rates are typically averages of discrete events. In the physical sciences, however, the process of ensemble averaging generally involves many orders of magnitude more objects, each with much less variation in their behavior, than in the biological sciences. Thus the coefficients of variation involved with ensemble averages are often inconsequential in physical systems (e.g., radioactive decay in kilograms of material or proportion of reactants in liters of solvent), but are invariably a sizable fraction of unity and sometimes greater than unity in ecological processes (e.g., *see* Hassell *et al.* 1991, Pacala & Hassell 1991).

While instantaneous refers to a particular moment or point in time, an average rate necessarily involves the notion of an interval rather than a point in time. To calculate a rate associated with a repeating event, we need to select an interval or unit of time and count the number of events occurring over that unit of time. By the above argument, all rates of repeated events, such as births and deaths in a population, are averages. Thus Oksanen *et al.*'s (1992) criticism of using average rates in differential equations is tantamount to criticizing any model, including any discrete time model, because it is an approximation to reality. Since all models are approximations of reality, this criticism is vacuous.

Thus the real issue is what model best captures the processes of interest. In the context of differential equation models, this raises the questions of what the appropriate time scales are over which to average events associated with the processes of interest. If the scale is too coarse, some of the faster processes that are central to the question at hand may be excluded. If the scale is too fine, the analysis may be overwhelmed with details, many of which may be irrelevant to analyzing the processes of interest. To analyze long term population trends in macro-fauna and perennial plants, we should typically choose an annual scale to calculate average birth and death rates, while within season distributions of individuals requires a monthly or even weekly time scale.

Further, the appropriateness of a differential versus a difference equation model depends on the system and on the phenomenon under consideration. For example, mortality related processes, including predation and some types of harvesting, are often best modeled by differential equation models, while births occurring over a short period of time during a seasonal cycle are best modeled using discrete equations. Sometimes it is most appropriate to combine these two approaches: for example, when modeling continuous harvesting in age-structured fisheries with annual spawning events (Getz & Haight 1989) and modeling discrete generation host-parasitoid interactions when parasitoids redistribute themselves within generations respect to the distribution of their hosts (Rohani *et al.* 1994).

3. Time scales

We now focus on the question of how time scales influence the form of observed extraction functions in consumer-resource interactions. In the absence of consumers, we assume that the dynamics of the resource population are governed by the differential equation

$$\frac{\mathrm{d}R}{\mathrm{d}t_r} = G(R, \alpha_0), \tag{1}$$

where R is the resource density, G is a function with a form that ensures the existence of a stable equilibrium when the resource is exploited by one or more populations of consumers, and t_r is time measured in units appropriate for characterizing the dynamics of the resource. The parameter α_0 is assumed to vary stochastically and to be distributed in time and according to some known probability density function. Generally, this stochasticity will reflect environmental effects on the resource.

We assume the dynamics of the consumer population at densities C_i, $i = 1, 2$, are determined by the processes of resource extraction at rates $f_i(\bullet)$ and conversion of resource into consumer biomass at rates $F_i(f_i)$ (Getz 1991, 1993, 1994, 1999). The extraction functions themselves will depend on the resource density R and, perhaps, on stochastic parameters α_i so that $f_i(\bullet) = f_i(R, \alpha_i)$, $i = 1, 2$. Before writing down equations describing the interaction between these two consumers and their resource, it is useful to explicitly identify three time scales (where scales refers to measures of rates per unit time): the consumer scale measured in units t_c, the resource scale measured in units t_r, and the patch scale measured in units t_p. The first two time scales, as elaborated below, respectively relate to the reproduction and growth dynamics of the consumer and resource (e.g., what is their characteristic doubling time when growing at low population densities). The third time scale relates to the temporal patchiness of resource due to external influences (e.g., t_p may be less than t_c if resource abundance is also influenced by long term climatic cycles and t_p may be greater than t_c if resources are transported in heterogeneous fluxes such as river flows). This temporal patchiness reflects variation at the time scale of the consumptive interaction between consumer and resource (i.e., does the consumer experience comparable or different densities of resource from one feeding bout to the next).

Because the extraction rate functions are assumed to be rates per unit consumer, the system of equations used to model two consumers exploiting the resource modeled by Eq. 1 normally take the form

$$\frac{\mathrm{d}R}{\mathrm{d}t_r} = G\big(R, \alpha_0(t_p)\big) - f_1\big(R, \alpha_1(t_p)\big)C_1 - f_2\big(R, \alpha_2(t_p)\big)C_2 \tag{2}$$

$$\frac{\mathrm{d}C_i}{\mathrm{d}t_c} = F_i\Big(f_i\big(R, \alpha_i(t_p)\big)\Big)C_i \qquad i = 1, 2. \tag{3}$$

Of course, we cannot solve Eqs. 2 and 3 until the time scales are specified.

The consumer scale is often the longest and represents the scale at which we can expect significant changes to occur in the densities of the two consumer populations due to the demographic processes of mortality and natality (this scale is typically measured in years for vertebrates). As mentioned above, the resource scale represents changes in the resource dynamics and may be of the same order as the consumer for the case of lions feeding on zebra or may be significantly faster in the case of catfish grazing on algae (Power 1984). In the latter case, the scale could be measured in terms of weeks.

Because of its externally driven nature, the patch time scale can be characterized by stochastic parameters $\alpha = (\alpha_0, \alpha_1, \alpha_2)$ which, as described in more detail in the examples considered below, are a measure of the heterogeneity of the resource as perceived or utilized by the consumers. For highly mobile or long lived consumers, this scale measures how rapidly individual consumers can smooth out temporal heterogeneities in the resources. This scale may also reflect the diurnal time scale of the searching behavior of consumers and could be measured in terms of hours. On the other hand, if the consumers are sessile or short lived, then heterogeneities in the resource, as perceived by the consumer, may be on a longer time scale than the resource dynamics itself. An example of this could be corals feeding on phytoplankton, aphids feeding on walnut trees, or spruce budworm feeding in balsam fir forests (Ludwig *et al.* 1978).

The population dynamics of the consumers is our primary concern, so we use their time scale as a reference and write $t_c = t$. With respect to this reference time scale, we use $t_r = t/\varepsilon$ and $t_p = t/\delta$ respectively to denote the resource dynamics and the patch interaction dynamics time scales. If we assume that the resource and patch interaction dynamics are significantly faster (i.e., shorter time scales) than the consumer dynamics, then this would be equivalent to assuming that $0 < \varepsilon << 1$ and $0 < \delta << 1$. For example, if the consumer, resource, and patch interaction dynamics time scales respectively have units of years, weeks, and hours, then $\varepsilon = 0.0192$ and $\delta = 0.000\,114$.

With these new time scales Eqs. 2 and 3 can be written as:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \frac{1}{\varepsilon}\left(G\left(R, \alpha_0\left(\frac{t}{\delta}\right)\right) - f_1\left(R, \alpha_1\left(\frac{t}{\delta}\right)\right) C_1 - f_2\left(R, \alpha_2\left(\frac{t}{\delta}\right)\right) C_2 \right) \quad (4)$$

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = F_i\left(f_i\left(R, \alpha_i\left(\frac{t}{\delta}\right)\right)\right) C_i \qquad i = 1, 2. \quad (5)$$

As ε and δ approach zero, we can approximate Eqs. 4 and 5 with a much simpler set of equations, by temporally averaging these equations over the probability distribution $p(\alpha)$ of the stochastic parameters α, provided a set of technical assumptions are met. These assumptions are (*see* Friedlin 1978): (i) the trajectories of the processes, $\alpha_i(t)$, are continuous with probability 1 or have only finitely many discontinuities of the first kind in any finite time interval; (ii) a probability density function, $p(\alpha)$, exists such that for any Borel set A and indicator function 1_{A}, the relationship $\lim_{t\to\infty} \frac{1}{t}\int_o^t 1_{\mathrm{A}}(\alpha(t))\mathrm{d}t = \int_A p(\alpha)\mathrm{d}\alpha$ holds.

The method by which we simplify Eqs. 4 and 5, in letting $\varepsilon \to 0$ and $\delta \to 0$, depends on whether $\varepsilon << \delta << 1$ or $\delta << \varepsilon << 1$. This ordering has critical consequences for the forms of extraction functions so derived. For example, if $\varepsilon << \delta << 1$, then on the δ time scale, we can solve Eq. 4 for the within patch "quasi-steady-state" (e.g. *see* Edelstein-Keshet 1988: section 7.2) density $\tilde{R}(\boldsymbol{C}, \alpha)$ in terms of the values of $\boldsymbol{C} = (C_1, C_2)$ and α. In this case, averaging over the variability in α as $\delta \to 0$ Eqs. 4 and 5 reduce to

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = \int p(\alpha) F_i\left(f_i\left(\tilde{R}(\boldsymbol{C}, \alpha), \alpha_i\right)\right) C_i d\alpha \qquad i = 1, 2 \quad (6)$$

On the other hand, for $\delta << \varepsilon << 1$, the effects of the stochastic patch interaction dynamics on the growth, extraction, and conversion functions must be averaged out for given resource and consumer levels. If we let $\delta \to 0$ for fixed ε Eqs. 4 and 5 reduce to

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \frac{1}{\varepsilon}\int p(\alpha)\left(G(R, \alpha_0) - f_1(R, \alpha_1)C_1 - f_2(R, \alpha_2)C_2 \right)\mathrm{d}\alpha \quad (7)$$

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = C_i \int p(\alpha) F_i\left(f_i(R, \alpha_i)\right)\mathrm{d}\alpha \qquad i = 1, 2. \quad (8)$$

Equating the right hand side of Eq. 7 to zero allows us to solve for the quasi-steady-state resource density $\tilde{R}(\boldsymbol{C})$ for any fixed value C. Letting $\varepsilon \to 0$ reduces models 7 and 8 to the single equation

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = C_i \int p(\alpha) F_i\left(f_i\left(\tilde{R}(\boldsymbol{C}), \alpha_i\right)\right)\mathrm{d}\alpha \qquad i = 1, 2. \quad (9)$$

Before continuing with a development of the theory in the context of two species competing for the same resources (which leads to a re-evaluation of the so called R^* rule — *see* Tilman 1990), it may be instructive to illustrate this asymptotic approach by demonstrating how Schoener's (1978) models of competition for partitioned and for overlapping resources arise out of time scale arguments respectively used to derive Eqs. 6 and 9.

4. Schoener's models

Consider the case where the functional responses f_i, $i = 1$and 2, are type I with no satiation (i.e.,$f_i = \alpha_i R$,) and the conversion functions F_i, $i = 1, 2$, have the linear form $F_i = a_i f_i - b_i$. Assume that the resource growth function in Eq. 1 has the form $G(R, \alpha_0) = \alpha_0 - \lambda R$ and α_0 is a stochastic input: for example, seeds falling on the ground with probability α_0 and subsequently removed at a constant rate λ (by fungi, bacteria, and incidental vertebrate and invertebrate consumers). Also assume that the remaining stochastic variables α_i, $i = 1, 2$, have either a value $\hat{\alpha}_i$ with probability p_i or are 0 with probability $(1 - p_i)$. Then for the case in which the resource dynamics are much faster than the patch interaction dynamics (i.e., $\varepsilon << \delta << 1$), the resource equilibrium

$$\tilde{R}(\boldsymbol{C}, \alpha) = \frac{\alpha_0}{\lambda + \alpha_1 C_1 + \alpha_2 C_2}$$

is obtained locally in each temporal patch before the heterogeneities across patches can be averaged out. After integrating this expression over the defined binomial probabilities Eq. 6 reduces to

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = \frac{a_i \overline{\alpha}_0 \hat{\alpha}_i p_i p_j C_i}{\lambda + \hat{\alpha}_i C_i + \hat{\alpha}_j C_j} + \frac{a_i \overline{\alpha}_0 \hat{\alpha}_i p_i (1 - p_j) C_i}{\lambda + \hat{\alpha}_i C_i} - b_i C_i \qquad (10)$$
$$i \neq j, \quad i, j = 1, 2$$

where $\overline{\alpha}_0$ is the average value of α_0

On the other hand, for the case in which the patch interaction dynamics are much faster than the resource dynamics (i.e., $\delta << \varepsilon << 1$), the resource equilibrium

$$\tilde{R}(\boldsymbol{C}) = \frac{\overline{\alpha}_0}{\lambda + p_1 \hat{\alpha}_1 C_1 + p_2 \hat{\alpha}_2 C_2}$$

is obtained globally after the heterogeneities across patches have been averaged out. Hence Eq. 9 reduces to

$$\frac{\mathrm{d}C_i}{\mathrm{d}t} = \frac{a_i \overline{\alpha}_0 \hat{\alpha}_i p_i C_i}{\lambda + p_i \hat{\alpha}_i C_i + p_j \hat{\alpha}_j C_j} - b_i C_i \qquad (11)$$
$$i \neq j, \quad i, j = 1, 2$$

Eqs. 10 and 11 are models proposed by Schoener (1978) that represent two consumers competing for a resource that they respectively (i) partition in time and space, and (ii) shared completely in space and time. Thus we see, in the context of resources exploited by consumers with relatively long demographic times scales, how differences in the time scales of the resource and consumptive interaction dynamics lead to fundamentally different types of consumer-resource interactions.

Eqs. 4 and 5, with the functions f_i, F_i, $i =1, 2$, and G as defined in this section, thus represent a two parameter (ε and δ) generalization of the Schoener models such that Eqs. 10 and 11 respectively represent two different specific cases that are obtained through appropriate limiting processes. Hence, by manipulating the particular values of the parameters ε and δ, one can obtain a competition model that represents a partial sharing and partial partitioning of the resource between the two competitors, where the degree of sharing and partitioning depends on the relative values of ε and δ.

5. The *R** rule

We now turn to the issue raised prior to the Schoener example of how the methods use to derive Eqs. 6 and 9 help address the question of the effects of time scales on the coexistence or competitive exclusion of two species exploiting the same temporally varying resource. For this purpose, we define the two quantities R_i^*, $i = 1, 2$, as the temporal average of the resource density when the resource is exploited solely by consumer i. In the absence of temporal heterogeneity, R_i^* corresponds to the resource density at the equilibrium of Eqs. 2 and 3 when the resource is exploited solely by consumer i (Hsu *et al.* 1977, Tilman 1990). When heterogeneity exists, the R_i^* are defined as follows. If the resource dynamics are much faster than the patch interaction dynamics (i.e., $\varepsilon << \delta << 1$) then

$$R_1^* = \int \tilde{R}\big((C_1^*, 0), \alpha\big) p(\alpha) \mathrm{d}\alpha,$$

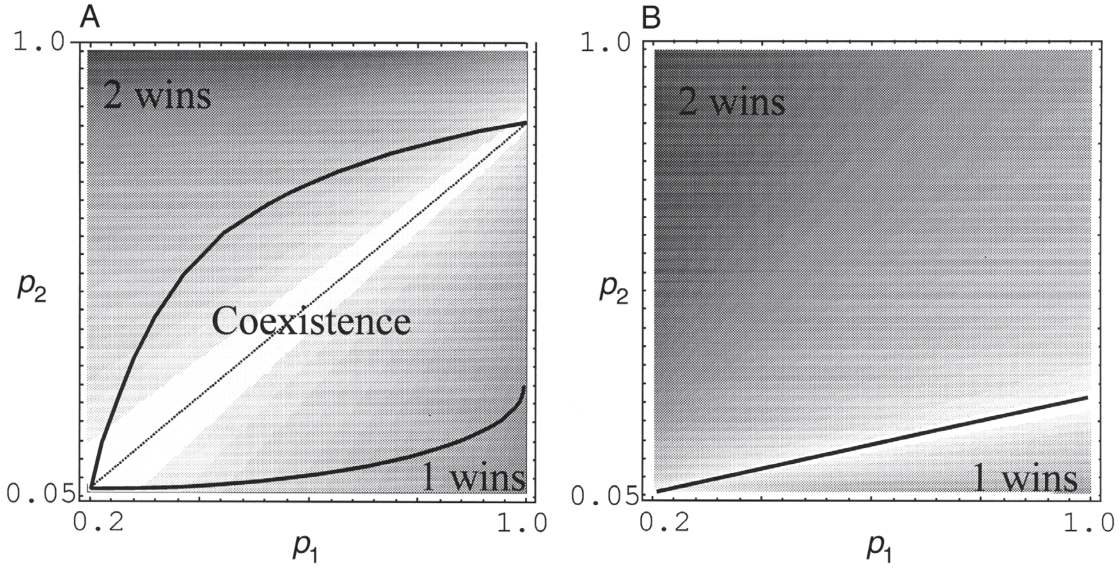

Fig. 1. Bifurcation diagrams are plotted for consumers modeled by Eqs. 4 and 5 with unsatiated type I intake functions and a linear conversion function in an extremely variable environment (i.e., Schoener's (1978) eqs. 10 and 11 with parameter values $a_1 = a_2 = 0.5$, $\hat{\alpha}_1 = 0.1$, $\hat{\alpha}_2 = 2.0$, $b_1 = 0.1$, $b_2 = 0.5$, $\bar{\alpha}_0 = 10$, and $\lambda = 1$). The horizontal and vertical axes respectively represent the probabilities p_1 and p_2 that consumers 1 and 2 are able to extract the resource at a maximal rate. The shading represents the values of $|\ln R_1^*/R_2^*|$, where the lighter shading corresponds to values closer to 1. Diagram *A* depicts the limiting situation for the case $\varepsilon << \delta << 1$. The dotted line represents points in the parameter space where $R_1^* = R_2^*$. Because the two competitors can coexist in part of the parameter space, ther R^* rule does not apply. Diagram *B* depicts the limiting case $\delta << \varepsilon << 1$. Because the solid line both represents points in the parameter space where $R_1^* = R_2^*$ and separates the regions where 1 and 2 win, it follows that the R^* rule applies.

where $(C_1^*, 0)$ is an equilibrium of Eq. 6. On the other hand, if the patch interaction dynamics are much faster than the resource dynamics (i.e., $\delta << \varepsilon << 1$) then $R_1^* = \tilde{R}\big((C_1^*, 0)\big)$, where $(C_1^*, 0)$ is now an equilibrium of Eq. 9. The same expressions apply with an appropriate change of subscript for R_2^*.

In the absence of variability, Hsu *et al.* (1977) and Tilman (1990) demonstrated that the consumer with the smaller R_i^* competitively displaces the other consumer. This result has been extended to systems where competition is apparent rather than direct (Holt *et al.* 1994). In the presence of variability, however, the existence of an R^*-like rule depends on the time scale of the variability. Specifically, if the variability defines the fastest time scale ($\delta << \varepsilon << 1$) an R^* rule still applies and its existence can be explained by the fact the patch variability is averaged out during the fastest time scale. After averaging, the dynamics is deterministic on the intermediate resource and slow consumer time scales and the classical R^* analysis applies (Hsu *et al.* 1977, Tilman 1990). The outcome of competition, however, still depends critically on the distribution of the variability, which must be taken into account before the region of parameter space in which consumer 1 or 2 wins can be calculated.

When the variability evolves at a slower time scale than the resource ($\varepsilon << \delta << 1$), the Schoener partitioned-resource model (Eq. 9) provides an example of an asymptotic analysis where consumers may coexist and, hence, an R^*-like rule no longer applies. Numerical simulations using Schoener's model (Eqs. 9 and 10) with specific parameter values (Fig. 1) illustrates the two cases in point (i.e., $\delta << \varepsilon << 1$ and $\varepsilon << \delta << 1$). Shading in Fig. 1 provides a graphic illustration of the failure of an R^*-like rule for the case $\delta << \varepsilon << 1$ (Fig. 1A) and the existence of an R^*-like rule for the case $\varepsilon << \delta << 1$ (Fig. 1B). Specifically, when the patch interaction dynamics are much faster than resource dynamics, so that heterogeneity is essentially smoothed out before consumption takes place (Fig. 1B), then the R^* rule applies and the boundary between the 1-winning and 2-winning regions is the line $R_1^*/R_2^* = 1$. When the resource dynamics are much faster than patch interaction dynamics, so that heterogeneity is only smoothed out after consumption has taken place (Fig. 1A), then the R^* rule no longer applies and a region of coexistence now appears in the parameter space under consideration. Interestingly, the line of *isosuppression* (the dotted line representing the points $R_1^*/R_2^* = 1$) is closer to the boundary of the region where 2 wins than where 1 wins. Further, coexistence occurs for much greater values of the ratio $R_1^*/R_2^* > 1$ than for values of the ratio $R_2^*/R_1^* > 1$.

6. Stochastic input

In deriving the Schoener equations, we made the assumption that the functional responses f_i, $i = 1$ and 2, are linear. More realistic functional responses include a notion of satiation: viz., $f_i = \alpha_i R$ for $R < \omega_i/\alpha_i$ and $f_i = \omega_i$. In this case, the analysis is more complicated and richer systems behavior is expected. We analyze this new case assuming, as we did in deriving the Schoener models, that the resource growth rate function has the same stochastic form $G(R, \alpha_0) = \alpha_0 - \lambda R$, and the conversion functions have the linear forms $F_i = a_i f_i - b_i$, $i = 1, 2$. To keep the analysis simple, we assume that only the resource input α_0 is a stochastic variable — that is, α_i, $i = 1, 2$ are constants — and is Gamma distributed in time: that is α_0 has the distribution function

$$f_{\gamma,v}(\alpha_0) = \frac{1}{\Gamma(v)}\gamma^v \alpha_0^{\;v-1} e^{-\gamma\alpha_0}, \qquad (12)$$

where Γ is the Gamma function. The mean μ and variance σ^2 of this distribution satisfy (Feller 1966)

$$\mu = \frac{v}{\gamma} \quad \text{and} \quad \sigma^2 = \frac{v}{\gamma^2}. \qquad (13)$$

Under the assumptions that consumer 1 satiates at lower resource densities than consumer 2 (i.e., $\omega_1/\alpha_1 < \omega_2/\alpha_2$ — *see* Fig. 2A) and that the resource variability evolves at the slower time scale $\varepsilon << \delta << 1$, the resource equilibrium

$$\tilde{R}(\boldsymbol{C}, \alpha) = \begin{cases} \dfrac{\alpha_0}{\lambda + \alpha_1 C_1 + \alpha_2 C_2} & \text{if } \alpha_0 \le A \\ \dfrac{\alpha_0 - \omega_1 C_1}{\lambda + \alpha_2 C_2} & \text{if } A \le \alpha_0 \le B, \\ \dfrac{\alpha_0 - \omega_1 C_1 - \omega_2 C_2}{\lambda} & \text{if } \alpha_0 \ge B \end{cases}$$

where

$$\begin{aligned} A &= \frac{\omega_1}{\alpha_1}\left(\lambda + \alpha_1 C_1 + \alpha_2 C_2\right) \\ B &= \frac{\omega_2}{\alpha_2}\left(\lambda + \alpha_2 C_2\right) + \omega_1 C_1 \end{aligned}$$

is obtained locally in each patch before the heterogeneities across patches can be averaged out. After integrating over the gamma distributed probabilities defined by Eq. 12, Eq. 6 becomes

$$\begin{aligned} \frac{\mathrm{d}C_1}{\mathrm{d}t} &= a_1 C_1 \int_0^A \frac{\alpha_0 \alpha_1}{\lambda + \alpha_1 C_1 + \alpha_2 C_2} p_{\gamma,v}(\alpha_0)\mathrm{d}\alpha_0 \\ &\quad + a_1 C_1 \int_A^\infty \omega_1 p_{\gamma,v}(\alpha_0)\mathrm{d}\alpha_0 - b_1 C_1 \\ \frac{\mathrm{d}C_2}{\mathrm{d}t} &= a_2 C_2 \int_0^A \frac{\alpha_0 \alpha_1}{\lambda + \alpha_1 C_1 + \alpha_2 C_2} p_{\gamma,v}(\alpha_0)\mathrm{d}\alpha_0 \\ &\quad + a_2 C_2 \int_A^B \frac{(\alpha_0 - \omega_1 C_1)\alpha_2}{\lambda + \alpha_2 C_2} p_{\gamma,v}(\alpha_0)\mathrm{d}\alpha_0 \\ &\quad + a_2 C_2 \int_B^\infty \omega_2 p_{\gamma,v}(\alpha_0)\mathrm{d}\alpha_0 - b_2 C_2 \end{aligned}$$

Note that after integrating over input heterogeneity, the intake rates of both consumers, when measured at the consumers' time scales, are no longer type I functional responses (i.e., linear until saturation is reached), but are smooth compensatory functions (i.e., type II functional responses). In this time scale scenario ($\varepsilon << \delta << 1$), coexistence is possible between an efficient consumer that produces a low R_i^* but satiates at low resource densities and a consumer that produces a higher R_i^* but satiates at a higher resource densities (i.e.,

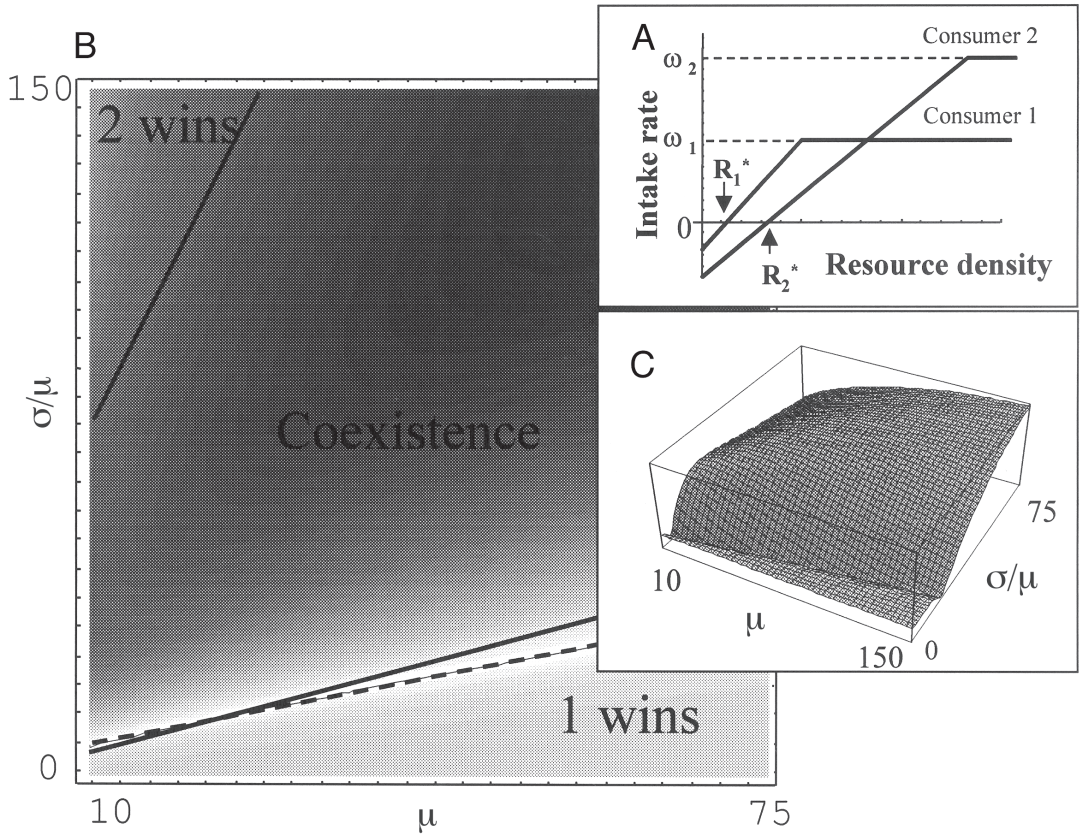

Fig. 2. The intake functions are plotted in terms of resource density (A). The bifurcation diagram contour (B) and surface plots (C) of the values of $|\ln R_1^*/R_2^*|$ for consumers with satiated type I extraction functions and linear conversion functions are plotted in terms of the mean μ and coefficient of variation σ/μ in an environment where the input of resources α_0 is Gamma distributed (*see* Eqs. 12 and 13). — A: Extraction function 1 applies to a consumer that produces a relatively low R_1^* but satiates at low resource densities, and extraction function 2 applies to a consumer that produces a higher R_2^* but satiates at higher resource densities than is the case for extraction function 1. — B: The horizontal and vertical axes respectively represent the mean resource input and the coefficient of variability of this input. The solid lines demarcate the coexistence from the exclusionary regions. The dashed line represents points in the parameter space where $R_1^* = R_2^*$. Parameter values in both plots are given by: $a_1 = a_2 = 0.4$, $\alpha_1 = \alpha_2 = 1.0$, $b_1 = 0.10$, $b_2 = 0.152$, $\omega_1 = 1.0$, $\omega_1 = 4.0$, and $\lambda = 1$.

their type I intake responses "cross") (Fig. 2A). When the variance of the resource input is high relative to the mean resource input, coexistence breaks down and the consumer with the higher satiation level dominates (Fig. 2B). When the variance of the resource input is low relative to the mean resource input, coexistence also breaks down and the consumer with the lower R_i^* dominates (Fig. 2B). As in Fig. 1, the quantity $|\ln R_1^*/R_2^*|$ is plotted (contour shading in 2B, surface plot in 2C) for different values of the the mean μ and coefficient of variation σ/μ of the Gamma distribution of α_0 (*see* Eqs. 12 and 13) to demonstrate that a R^* like rule does not apply. Further the line of isosuppression (dashed line in Fig. 2B) does not need to lie within the coexistence region.

In sharp contrast, as with the Schoener models, when the resource variability or patch interaction dynamics is faster than the demographic dynamics of the resource ($\delta << \varepsilon << 1$), the variability can be integrated out and analysis of the resulting deterministic model implies that the consumer with the lower R_i^* always dominates (Hsu *et al.* 1977, Tilman 1990).

7. Conclusion

Time-scale arguments if not explicitly incorporated into population models, are implicitly implied by the understanding that all parameters represent the average values of processes measured over appropriate intervals of time. Although we kept our analysis simple by allowing time-scale ratios to become infinite (i.e., letting $\varepsilon \to 0$ and $\delta \to 0$), approximation theory (Sanders & Verhulst 1985, Freidlin 1978) allows us to infer properties of models with finite but large time-scale ratios. In fact, coexistence of consumers partitioning a resource that has a finitely faster time-scale than the consumers has been obtained in the context of difference equation models (Loreau 1992).

Through the analysis presented here, we obtain insights into what types of time scales lead to the emergence of resource partitioning in consumers exploiting a patchily distributed resource. We also gained an understanding of the time-scale conditions under which an R^* rule for the coexistence of consumers applies to these systems. The first example considered here provides us with additional insights into the underlying difference between Schoener's (1978) two types of competitive interaction models. The second example provides some sense of the trade off the size of the mean and the variance around the mean in facilitating the coexistence of two competitors with satiating functional responses. Finally, our analysis suggests that diversity in competitive systems is maximized when heterogeneity evolves at an intermediate time scale and the coefficient of variation (i.e., σ/ν; *see* Fig. 2B) in the resource distribution is not too extreme.

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