Armstrong–McGehee mechanism revisited: Competitive exclusion and coexistence of nonlinear consumers

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ABSTRACT

A number of mechanisms have been proposed to explain the coexistence of species engaging in exploitative competition. The Armstrong–McGehee mechanism relies on different levels of nonlinearity in functional response between competing consumers and their ability to avoid competitive exclusion through temporal resource partitioning during endogenously generated fluctuations. While previous studies have mainly focused on cases where one consumer has nonlinear functional response and the other consumer has linear functional response, our study assessed coexistence and competitive exclusion under a more realistic scenario with two nonlinear consumers. Using analytical and numerical methods we found that the potential of coexistence of the two consumers decreases with increasing nonlinearity in the more linear species; increasing nonlinearity in the more nonlinear species, however, resulted in non-monotonic changes in the parameter space allowing coexistence. When coexistence potential is quantified under the presupposition that each consumer must be able to persist with the resource by itself, coexistence becomes consistently less likely with increasing similarity of the functional responses of the two consumers. Our results suggest that the Armstrong–McGehee mechanism is unlikely to operate as the sole coexistence-promoting mechanism in communities with generally nonlinear consumer–resource interactions. However, its role as a module in more complex systems and in synergy with other factors remains to be established.

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1. Introduction

Defining the conditions under which competing species can coexist has a long history in theoretical ecology. When two or more species compete for concrete resources ("exploitative competition") the conditions for steady-state coexistence are quite stringent. In essence, only as many consumer species as there are resources can stably coexist. While two or more species compete for concrete resources ("exploitative competition") the conditions for steady-state coexistence are quite stringent. In essence, only as many consumer species as there are resources can stably coexist. However, the observation that many more species coexist in the real world than would be suggested by the handful of mineral resources

that ultimately limit the growth of primary producers at the base of food webs (Hutchinson, 1961). Subsequent theoretical work has attempted to reconcile the competitive exclusion principle with naturally observed patterns of coexistence by relaxing the assumptions under which coexistence must occur. These attempts have focused on effectively eliminating competition through segregation of competitive forces across space ("metapopulations"; Levins, 1969; Richards et al., 2000) or time ("storage effect"; Chesson, 2000; Chesson and Warner, 1981; Descamps-Julien and Gonzalez, 2005) or have explored the consequences of relaxing the assumption of steady-state coexistence.

In our paper we are concerned with the latter case and provide an analysis of coexistence in a fluctuating two-consumer–one-resource system. Our study follows a long tradition of theoretical investigations of coexistence in this most basic module of...
exploitative competition. In this scenario, resource fluctuations provide periodically recurring conditions that lead to alternating competitive superiority of one of the two competitors and thereby facilitate coexistence. This mechanism has been shown, in principle, to allow two consumers to coexist on a single resource, both for exogenously forced and endogenously generated oscillations (Abrams, 2004; Armstrong and McGehee, 1980; Hsu et al., 1978a, 1978b; Koch, 1974). The endogenous case is of particular interest because it provides a mechanism by which coexistence could arise from within the consumer–resource system itself without environmental stochasticity or forcing. Because of the great influence of the classical Armstrong and McGehee (1980) paper describing this mechanism of coexistence due to endogenous cycles, we refer to it as the “Armstrong–McGehee mechanism”.

Previous investigations into the conditions for coexistence in the oscillating two-consumer–one-resource system postulate a linear resource uptake function (functional response) for one of the consumers while the other consumer has a saturating (Holling type II; Holling, 1959) functional response. A nonlinear functional response is a necessary condition for coexistence because it provides the potential for endogenous stable limit cycles in the consumer–resource system and, after coupling, the second consumer can be entrained into these cycles. A saturating nonlinear functional response also enables the “linear consumer” to enjoy higher growth rates at high resource concentrations during the cycles while the “nonlinear consumer” is superior at periods of low resources (although this could also be accomplished with two linear functional responses). Multiple studies have established that coexistence and mutual invasion of competitors is possible in such linear–nonlinear systems and that the parameter space allowing coexistence increases with the degree of relative nonlinearity of the Holling type II function (Abrams and Holt, 2002; Hsu et al., 1978b). In a number of more recent papers (Abrams and Holt, 2002; Abrams, 2004; Abrams et al., 2003) the authors found a substantial parameter bandwidth of coexistence, which led them to conclude that relative nonlinearity may have been discarded prematurely as a coexistence-generating mechanism.

Nonlinear, saturating functional responses of the Holling type II are widespread in nature (Jeschke et al., 2004) and are likely a much more realistic representation of consumer–resource interactions in nature than the linear functional responses used in Lotka–Volterra frameworks. The traditional approach that couples a linear consumer with a nonlinear one to a shared resource is therefore a rather special and extreme case in a universe of coupled consumer cases that vary in the relative nonlinearity of their functional responses. In this paper we use analytical and numerical methods to investigate the more general case of two nonlinear consumers. The nonlinear–nonlinear system is analytically richer than the linear–nonlinear system because each of the two consumers can either cycle or stably coexist with the resource in the absence of the other consumer. In determining the potential for coexistence we thus need to distinguish the cases where one consumer–resource module is stable and the other is not, plus the case where both are unstable. We also use numerical simulations to determine the fraction of the parameter space for which coexistence is actually achieved (“realized coexistence”).

Our goal is to establish a relationship between coexistence – potential or realized – and the degree of relative nonlinearity between the consumers’ functional responses. While it is fairly obvious that involvement of one linear consumer maximizes the potential for coexistence, the rate at which the potential diminishes with gradual changes of nonlinearity has not been formally established. Moreover, it is not a foregone conclusion that maximum differences in the relative nonlinearity of the consumers also maximize the potential for coexistence; highly nonlinear functional responses can diminish the parameter space in which consumers can successfully exploit their resource and this effect may interfere with the competitive relationship of the two consumers. Hence, a formal theoretical analysis of coexistence under variable relative nonlinearity is necessary to determine the true potential of the Armstrong–McGehee mechanism for promoting coexistence in natural communities.

2. Methods

We focus on a modified Armstrong–McGehee system (Armstrong and McGehee, 1980) with two consumers and one biotic resource. Both consumers have saturating (Holling Type II) functional responses; the resource grows logistically when the consumers are absent:

\[
\frac{dP}{dt} = R\left[f\left(1 - \frac{P}{R}\right) - \frac{C_1P_1}{1 + h_1C_1R} - \frac{C_2P_2}{1 + h_2C_2R}\right]
\]

(1.1)

\[
\frac{dP_1}{dt} = P_1\left(\frac{B_1C_1R - D_1}{1 + h_1C_1R}\right)
\]

(1.2)

\[
\frac{dP_2}{dt} = P_2\left(\frac{B_2C_2R - D_2}{1 + h_2C_2R}\right)
\]

(1.3)

The coupled differential equations represent the rate of change of the three state variables in the system: resource \( R \), consumer 1 \( P_1 \), and consumer 2 \( P_2 \), respectively. \( r \) and \( K \) denote the intrinsic population growth rate and carrying capacity of the resource; \( h_i \), \( B_i \), \( C_i \), and \( D_i \) denote the handling time, conversion efficiency, attack rate, and mortality rate of the corresponding consumer. Let \( t' = t, R' = R/K, P_1' = P_1/[BK], a_i = B_iC_iK, b_i = KC_ih_i \) and \( d_i = D_i/r \) (i = 1, 2). With the primes dropped, the system can be simplified to (Abrams and Holt, 2002):

\[
\frac{dR}{dt} = R\left((1 - R) - \frac{a_1P_1}{1 + b_1R} - \frac{a_2P_2}{1 + b_2R}\right)
\]

(2.1)

\[
\frac{dP_1}{dt} = P_1\left(\frac{a_1R}{1 + b_1R} - d_1\right)
\]

(2.2)

\[
\frac{dP_2}{dt} = P_2\left(\frac{a_2R}{1 + b_2R} - d_2\right)
\]

(2.3)

Here \( a_i \) is a scaling parameter which determines proportionally the growth rate of \( P_i \) conditional on the resource level \( R \) and \( b_i \) while \( b_i \) can be interpreted as a measure of the nonlinearity of the corresponding functional response; smaller \( b_i \) indicates that the functional response reaches half saturation at higher resource level. When one of the \( b_i \) values is zero, the functional response of the corresponding consumer degenerates into a linear one, and the system is equivalent to the one studied by Armstrong and McGehee (1980).

We evaluated the coexistence of the two consumers as a twodimensional coexistence bandwidth (Abrams and Holt, 2002; Armstrong, 1976), i.e., range of parameter space allowing coexistence. Here we portrayed coexistence bandwidth on the \( d_1-d_2 \) plane (i.e., mortality rates of the two consumers), as they determine the dynamics of the system when the functional responses are fixed (Abrams and Holt, 2002). We analyzed the effect of nonlinearity in functional responses \( (b_1 \) and \( b_2 \)) both for the “potential region of coexistence”, which is defined by analytical criteria fulfilling the necessary conditions for coexistence (see Section 3.1), and the “realized region of coexistence”, which can only be obtained with numerical simulations. Without loss of generality, we assume throughout our paper that \( b_1 > b_2 \) (the special case where \( b_1 = b_2 \) can never sustain stable coexistence; see Section 3.2). To establish the relationship between relative nonlinearity \( (b_i) \) and the realized range of coexistence, we investigated
A successful invasion requires that the long-term per-capita growth rate of the invader invades a system which undergoes stable limit oscillations, as described by (Armstrong and McGehee, 1980). On the other hand, when the abundance of the invading consumer, and the resource levels are assessed to determine if each of the consumers was able to invade the system with the other consumer and the resource. If so, this combination was classified as coexistent (Armstrong and McGehee, 1980; McGehee and Holt, 2002; Armstrong and McGehee, 1980; McGehee and Holt, 2002). However, we have evaluated multiple starting points with different levels of functional response and always reached stable equilibrium as its limit, successful establishment of the invader requires that the system went through enough cycles in 2500 time steps for the criterion of mutual invasion. When the other consumer is absent. If Fig. 2 (500 time steps) or extreme oscillatory cycles for which the cycle maxima and minima were deemed to have reached limiting dynamics, while the dynamics of systems with CV > 0.05 (84 cases out of 1368) were individually plotted and examined. Our analysis showed that systems with high CV had either long oscillatory periods (> 500 time steps) or extreme oscillatory cycles for which the cycle maxima and minima were not always well captured with discrete time steps; however, we found no case in which the system had not approached limiting dynamics by time step 7501, we assessed the coefficients of variation (CV) among the maximal as well as the minimal resource levels within the five 500 time-step segments from 7501 to 10,000 for each parameter combination with oscillatory limiting dynamics. Systems with CV<0.05 among both the maxima and the minima were deemed to have reached limiting dynamics, while the dynamics of systems with CV < 0.05 were typically plotted and examined. The area of the potential region of coexistence was calculated by (Armstrong and McGehee, 1980). For each (b1−b2) parameterization at each grid point on the d1−d2 plane, the inequalities corresponding to the limiting dynamics of the two one-consumer–one-resource systems were assessed to determine if each of the consumers was able to invade the system with the other consumer and the resource. If so, this parameter combination was scored as ‘coexistence.’ The area of the realized region of coexistence for a specific (b1−b2) combination was then calculated as (number of d1−d2 combinations allowing coexistence)×(area of rectangular region allowing each consumer to persist with the resource)/10,000. While the area under the nonlinearities (bi) of the functional response is essential for the Armstrong–McGehee mechanism to operate, coexistence may also depend on a, which influences the growth rate of P, as well as its equilibrium P1* (see Section 3.1). To evaluate the effect of a on coexistence, we followed a similar procedure as our analyses for b, a1 and a2 were allowed to vary independently from 1 to 5 at intervals of 0.5, while b1 and b2 were fixed at either b1 = 10 and b2 = 0, where consumer 2 has a linear functional response and always reaches stable equilibrium as its limiting dynamics with the resource, or b1 = 10 and b2 = 3, where both consumers have the potential to oscillate. For each parameter combination (a1, a2, b1, b2), the rectangular region on the d1−d2 plane allowing each consumer to persist with the resource when the other consumer is absent (see Section 3.1) was partitioned into 10,000 grid points, where realized coexistence was assessed with the criterion of mutual invasion. All simulations were carried out in R 2.12.2 (R Development Core Team, 2011) (code is available at: https://github.com/weecology/AM_coexistence). Differential equations were solved with package ‘deSolve’ (Soetaert et al., 2010), parallel computing was achieved with packages ‘snow’ (Tierney et al., 2011) and ‘ foreach’ (Revolution Analytics, 2011), and 3-D plots were constructed with packages ‘lattice’ (Sarkar, 2008) and ‘gridExtra’ (Auguie, 2011).
This condition can be interpreted as follows: when the resource level is at carrying capacity, the per capita mortality rate of consumer 2 is a smaller fraction of its per capita growth rate compared to that of consumer 1. The inequality ensures that consumer 2 is competitively dominant over consumer 1 at high resource levels. \(d_1 - d_2\) combinations in the region above this line lead to the exclusion of consumer 2.

3. \(d_2 \geq \frac{a_2}{d_1/d_1 - b_1 + b_2}\)

This condition implies that the minimal resource requirement of consumer 1, \(R^*_1\), is higher than the minimal resource requirement of consumer 1, \(R^*_1\), which gives an advantage to consumer 1 when the resource level is low. For \(d_1 - d_2\) combinations above the curve, consumer 1 is inferior to consumer 2 under all resource conditions and will eventually be excluded.

Taken together, the three conditions define a bounded region in the \(d_1 - d_2\) parameter space (Fig. 1), which gives the necessary but not sufficient conditions for coexistence; any \(d_1 - d_2\) combination outside the boundary will always lead to the exclusion of at least one consumer.

The analytical boundaries derived by Hsu et al. (1978b) provide an effective means to delimit the parameter space where coexistence is possible. The region of potential coexistence can be refined even further by allowing for the dynamical behavior of each consumer when the other consumer is absent. In a simpler system with the resource and only one of the two consumers, the limiting dynamics depends on the per capita mortality rate of the consumer, \(d_1\), with respect to its functional response (Armstrong and McGehee, 1980). When \(d_1\) is high, both the resource and the consumer oscillate with decreasing magnitudes through time and eventually converge on their equilibrium density. \(R^*_1 = d_1/(a_1 - b_1d_1)\) and \(P^*_1 = (1 - R^*_1)(1 + b_1R^*_1)/a_1\). Note that condition 1 ensures that the equilibrium density of the resource and the consumer exists and is positive. With decreasing \(d_1\), the stability of this equilibrium declines, and the system undergoes a Hopf bifurcation at \(d_1 = a_1(b_1 - 1)/[b_1(b_1b_1 + 1)]\) for \(b_1 > 1\). For \(d_1\) values below this critical value, the limiting dynamics of the system is oscillation with fixed period and magnitude, instead of stable equilibrium. When \(b_1 \leq 1\), i.e., when the functional response of the consumer is close to linear, a biologically meaningful bifurcation point does not exist, and the system always converges to stable equilibrium.

Consequently, the rectangular region defined by condition 1 can be divided into four sub-regions, assuming for now that both \(b_1\) and \(b_2\) are larger than 1 (Fig. 1). In sub-region A, consumer 2 approaches equilibrium when consumer 1 is absent, while consumer 1 oscillates when consumer 2 is absent. In sub-region B, both consumers approach stable equilibrium when the other consumer is absent. In sub-region C, both consumers oscillate. In sub-region D, consumer 1 approaches stable equilibrium while consumer 2 oscillates. Sub-regions A and C disappear if \(b_1 \leq 1\), while sub-regions B and D disappear if \(b_2 \leq 1\).

Under the assumption that \(b_1 > b_2\), it can be shown analytically that the region of potential coexistence defined by the above three conditions never overlaps with sub-region D (see Appendix). Thus coexistence cannot be achieved if the more linear consumer (i.e., consumer 2) undergoes oscillatory dynamics while the more nonlinear consumer (i.e., consumer 1) approaches stable equilibrium when each of them is the sole consumer in the system; in such cases, consumer 1 is always excluded. The remaining three sub-regions are all traversed by the region of potential coexistence, which implies that coexistence is at least hypothetically possible in them if the above three analytical conditions are fulfilled. However, in sub-region B where both consumer species are at stable equilibrium with the resource (when the other consumer is absent), the system behaves in a similar way to a system where both consumers have linear functional responses, and the competitive exclusion principle applies. Assume that the two consumers differ in \(R^*\), which is always the case in nature given that they represent two different species. If a small number of the consumer with high \(R^*\) is added to a system where the other consumer with high \(R^*\) is in equilibrium with the resource, the added consumer (invader) will increase in abundance, because the equilibrium resource density is above what is required for it to maintain zero-growth. However, if conversely a small number of the consumer with high \(R^*\) is added to a system where the other consumer with low \(R^*\) is in equilibrium with the resource, the invader will decrease in abundance and be outcompeted by the resident consumer, because the resource level is too low for it to grow. This implies that mutual invasion cannot be achieved in sub-region B where the limiting dynamics of both consumers are stable equilibrium. Coexistence can thus only be attained in the bounded region of potential coexistence defined by the above three conditions where it traverses sub-regions A or C, which we will refer to as potential region of coexistence. Note however that this refined analytical boundary still gives the necessary but not sufficient conditions for coexistence; competitive outcome for parameterizations within the bounded region can only be examined numerically.

3.2. The effect of functional response nonlinearity on potential region of coexistence

Since we now know the analytical form of the curves defining the region of potential coexistence, we can directly assess the effect of \(b_1\) and \(b_2\) on the parameter space allowing for potential coexistence. The area of this region can be computed as the difference of the integrals of the upper and lower bound curves of the shaded area in Fig. 1; integration is with respect to \(d_1\) and across the range from 0 to \(a_1(b_1 - 1)/[b_1(b_1b_1 + 1)]\) (i.e., the division

![Fig. 1. The potential region of coexistence of the modified Armstrong-McGehee system, defined as coexistence bandwidth. The upper bound corresponds to condition 2, while the lower bound corresponds to condition 3. The two dashed lines intercept at the maximal value of \(d_1\) and \(d_2\) given by condition 1, while the horizontal and vertical solid lines divide the rectangular region into four sub-regions differing in the limiting dynamics of the two consumers (see text for details). Coexistence is only possible within the shaded region between the two bounds overlapping with sub-regions A and C.](image)
between sub-regions A/C and sub-regions B/D:

\[ A_{\text{potential}} = \frac{a_1a_2(b_1-1)(b_1+b_2)}{2(b_1-b_2)(b_2+1)b_1^2} + \frac{a_1a_2}{(b_1-b_2)^2} \ln \frac{b_1b_2+2b_1-b_2}{b_1(b_1+1)} \]  

(5)

Because the analytical boundaries are functions of \(a_1\), \(a_2\), \(b_1\), and \(b_2\), the area of the bounded region \(A_{\text{potential}}\) is determined by the shape of the functional responses of the two consumer species. While \(A_{\text{potential}}\) increases proportionally with \(a_1\) and \(a_2\), the effect of the nonlinearity measure of the functional responses, \(b_1\) and \(b_2\), is more complex (Fig. 2a). Increasing \(b_1\) raises the level of resource density required for consumer 2 to maintain its population when consumer 1 is absent, thus reduces the range of \(d_2\) that may lead to coexistence. Moreover, the upper and lower bounds of the potential coexistence region shift towards each other when \(b_2\) approaches \(b_1\), and eventually collapse into a single line when \(b_2\) and \(b_1\) are equal, completely eliminating the possibility of coexistence of the two consumers. Therefore, assuming that \(b_1 > b_2\), the region of potential coexistence expands if the difference between the functional responses of the two species is increased by lowering the nonlinearity of the functional response of the more linear species (i.e., \(b_2\)) while keeping the shape of the functional response of the more nonlinear species (i.e., \(b_1\)) constant. This is consistent with Abrams and Holt’s statement (Abrams and Holt, 2002) that significant differences in functional response are essential to achieve coexistence. Such effect is most apparent when \(b_2\) is low.

Conversely, if the difference between the two functional responses is increased by increasing \(b_1\) while keeping \(b_2\) constant, the potential coexistence region follows a unimodal trajectory, first expanding then shrinking with increasing \(b_1\) values. This behavior is largely explained by the fact that the range of \(d_1\) allowing coexistence runs from zero to \(a_1/[b_1-1]/[b_2(b_2+1)]\) (i.e., from origin to the vertical line dividing sub-regions A/C and B/D), which has a similar unimodal dependence on \(b_1\). This leading effect becomes somewhat attenuated by an enlargement along the vertical dimension of the region of coexistence with increasing \(b_1\) (Fig. 3a–c), causing the dependence of the area of the potential coexistence region on \(b_1\) to be less steep than suggested by the attainable range of \(d_1\). In general, our analysis supports the notion that differences in the shape of the functional responses promote coexistence; however it should be added as a disclaimer that increasing the difference does not necessarily and consistently lead to an expanded coexistence bandwidth (otherwise the maximum of the plane in Fig. 2a would need to be at \((b_1,b_2)=(10,0)\)).

3.3. The realized region of coexistence and its dependence on functional response nonlinearity

As we have previously emphasized, the potential region of coexistence reflects the necessary yet not the sufficient conditions for coexistence. The realized region of coexistence, which is inevitably smaller, was obtained by evaluating grid points for mutual invasion within the rectangular area consisting of sub-regions A–D on the \(d_1–d_2\) phase plane (see Section 2 for details). The realized coexistence region is similar in shape to the potential region in that it has a unimodal relationship with \(b_1\) and decreases
monotonically as $b_2$ increases (Fig. 2b). The decline in realized coexistence with increasing $b_1$ is less steep than that of potential coexistence (Fig. 2a), implying that the realized region takes up a larger proportion of the potential region as $b_1$ increases. This observation is confirmed by the pattern of the ratio between the realized region and the potential region, which follows a monotonically increasing trajectory as $b_1$ increases (Fig. 2c). Conversely, the effect of $b_2$ on the ratio is hump-shaped, with the ratio decreasing with $b_2$ across the larger part of the $b_2$ axis, which is presumably due to the abrupt appearance of the Hopf bifurcation for the limiting dynamics of $P_2$ at $b_2=1$.

Fig. 3 demonstrates how potential and realized areas of coexistence manifest and change for concrete parameter values. As $b_1$ increases (Fig. 3a–c), the potential coexistence region first expands then shrinks, showing the non-monotonic trajectory; the divergence between the upper and lower bounds of the region, however, consistently increases. The realized coexistence region, on the other hand, expands towards the upper bound as $b_1$ increases and takes up a higher proportion of the potential region, resulting in a less steep decline when $b_1$ is large.

Similarly, changes in $b_2$ affect the coexistence region set by $d_2$ (i.e., the height of the rectangular area consisting of sub-regions A and C) and the shape of the bounds. However, under the assumption that $b_1 > b_2$, increasing $b_2$ diminishes the difference in nonlinearity of the functional response between the two consumers, leading to convergence instead of divergence of the upper and lower bounds of the potential coexistence region. Thus, in this case, the two effects work in synergy as $b_2$ increases, which results in a monotonically decreasing relationship between the area of the potential region and $b_2$. Moreover, when $b_2$ is larger than 1, increasing $b_2$ leads to the expansion of sub-region C with respect to sub-region A. Because the consumer with stable equilibrium as its limiting dynamics in sub-region A (i.e., consumer 2) also has a higher requirement for resource for any parameterization within the bounded potential region of coexistence in this sub-region, the other consumer with oscillatory behavior (consumer 1) is always able to invade (see Eq. (1)); thus the realized region always matches the lower bound of the potential region in sub-region A. However, in sub-region C, where both species undergo oscillations as limiting dynamics, the outcome of the invasion is determined by Eq. (4) instead of by the average resource density alone. Under these conditions, consumer 1 is not necessarily capable of invading the simplified system with consumer 2 and the resource even though $R_1^*$ is lower than $R_2^*$, causing the realized range to detach from the lower bound of the potential region in this sub-region. As the proportion of sub-region C increases with $b_2$ for $b_2 > 1$, the ratio between the realized and the potential regions declines.

3.4. The effect of scaling parameters $a_1$ and $a_2$ on coexistence

Both the potential and the realized regions of coexistence increase with $a_1$ and $a_2$ regardless of the limiting dynamics of the consumers (Figs. 4 and 5). While the potential region of coexistence scales proportionally with $a_i$ (Eq. (5); Figs. 4a and 5a), numerical analyses suggest that the effect of $a_i$ on the realized region of coexistence is generally not linear, except in the special case of $a_2$ when the limiting dynamics of consumer 2 with the resource is stable across the $d_2$ parameter space (i.e., $b_2≤1$; Fig. 4c and d). Here the linear relationship can be explained by the fact that in the stable system with the resource and consumer 2, the equilibrium resource level is $R_i^* = d_j/(a_i - b_jd_j)$, which does not

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change as long as \(d_2\) is proportional to \(a_2\); thus the invasibility of such a system with respect to consumer 1 remains unchanged. On the other hand, when consumer 2 invades the system with the resource and consumer 1, its long-term growth rate scales linearly with \(a_2\) (assuming again that \(d_2\) is proportional to \(a_2\); Eq. (4)) with its sign unaffected, indicating that the invasibility of the system with respect to consumer 2 does not change either. Therefore in this special case where the limiting dynamics of consumer 2 is stable equilibrium, the coexistence bandwidth expands/shrinks along the \(d_2\) axis proportionally to changes in \(a_2\).

In all other cases, the realized region of coexistence is not entirely proportional to changes in \(a_1\) or \(a_2\). However, it is worth noting that the deviation from linearity is relatively small. For instance, the ratio between the realized and potential regions of coexistence declines from 0.41 to 0.34 with \(a_1\) varying from 1 to 5 and \(a_2\) fixed at 1 when \(b_1 = 10\) and \(b_2 = 3\) (Fig. 5c), which is much more subtle compared to the effect of \(b_1\) and \(b_2\) (Fig. 2).

4. Discussion

It has long been recognized that relative nonlinearity of consumer functional responses potentially facilitates coexistence of species that compete for the same resource (Armstrong and McGehee, 1980; Hsu et al., 1978a, 1978b; Koch, 1974). Most previous studies have focused on the special and extreme case where one of two competing species has a linear functional response while the other has a nonlinear functional response (Abrams and Holt, 2002; Abrams, 2004; Abrams et al., 2003; Armstrong and McGehee, 1980; Wilson and Abrams, 2005) (but see Hsu et al., 1978b; Keener, 1983; Smith, 1982). It is immediately obvious that involving a linear consumer maximizes the effect of a coexistence-enhancing mechanism in a two-consumer–one-resource system because, at high resource levels, the linear consumer will be a superior competitor to any competitor with a curved, saturating functional response. Yet, in the Armstrong–McGehee system a number of different mechanisms contribute to the balance between coexistence and competitive exclusion and the conditions determining their relative dominance and their interaction are not always obvious. The objective of our study was to provide a more general and systematic examination of the potential for coexistence of two consumer species through the Armstrong–McGehee mechanism. We considered the more natural case where both consumer species were allowed to have saturating functional responses, with varying degrees of relative nonlinearity.

Under this scenario, three principal consequences of the relative curvatures (or nonlinearities) of the consumers’ functional responses play a role in determining coexistence bandwidth in the system. First, the curvature determines the effectiveness of resource exploitation and, because resource exploitation translates to consumer growth rate, competitive superiority at low versus high resource concentrations. For coexistence to be possible effectiveness needs to trade off over the range of resource concentrations encountered (i.e., one consumer is better at high resource concentrations, the other at low ones). Second, nonlinearity opens the door for unstable dynamics. The degree of functional response curvature determines the location of the Hopf bifurcation that separates stable from oscillatory dynamics. In the two-consumer–one-resource system, at least one of the two
consumers needs to display oscillatory dynamics, or else competitive exclusion will occur. The fact that in our general case both consumers can cycle adds complexity to the traditional Armstrong–McGehee system. Finally, curvature of the functional response also determines the coexistence criteria for each consumer alone with the resource (i.e., in the absence of the other consumer). Strong curvature sets more stringent limits on the amount of mortality that the consumer can sustain without becoming extinct. Our paper attempted to clarify the conditions for coexistence as they arise from the interplay of these mechanisms.

Our results are largely consistent with previous studies (Abrams and Holt, 2002; Litchman and Klausmeier, 2001) in that substantial difference in the shape of functional response between the two species is essential for coexistence. In our framework, nonlinearity arises from relative increases in the $b$-values of the functional responses, which signify that half-saturation occurs at lower resource concentrations (to be precise, Monod’s half-saturation $k_s = 1/b$). In particular, coexistence is drastically reduced with increasing $b_2$ (index “2” always indicating the less nonlinear functional response) when $b_1$ is high and $b_2$ is low, i.e., when the functional response of one of the consumers is very nonlinear while the functional response of the other consumer is close to linear (Fig. 2d). On the other hand, a high degree of nonlinearity indicates long handling time, which reduces the efficiency of the corresponding consumer and makes it harder for it to persist even when the other consumer is absent. Thus, when the potential of coexistence is expressed as the area in the $d_1-d_2$ parameter space that can support the more nonlinear consumer (Fig. 2a and b). It is interesting to note that this result also holds for the classical case in which one of the consumers has a linear functional response (i.e., $b_2=0$).

We translated results from early analytical studies (Hsu et al., 1978a, 1978b; also see Smith, 1982) into our analytical framework and combined them with our analyses of potential for mutual invasion. This allowed us to define necessary (but not sufficient) conditions for coexistence on the $d_1-d_2$ plane (Fig. 1). Subsequent numerical simulations showed to what degree these analytical procedures provide realistic estimates of true patterns of coexistence and competitive exclusion in the two-consumer–one-resource system. On one hand, the analytically and numerically derived regions of coexistence match quite well in that they display similar trends of expansion and contraction as the nonlinearity of the two consumers varies (Fig. 2). On the other hand, the proportion of the potential region that reflects realized coexistence remains well below 100 percent (Fig. 2c) and the predictive power of the potential region appears to depend strongly on the conditions leading to coexistence (Fig. 3). The only case in which the bounds of the predicted and realized coexistence fully align is the lower bound in sub-region A (Fig. 3). Because the limiting dynamics of consumer 2 with the resource is stable in sub-region A, consumer 1 is able to invade such system provided that $R_1^* < R_2^*$, which is satisfied by any $d_1-d_2$ combination above the lower bound of the potential region. The condition no longer holds when the limiting dynamics of both consumers is oscillatory (sub-region C). Here, neither consumer is able to fully exploit the periods of high resource levels during the oscillation generated by the other consumer so that mutual invasion becomes more

**Fig. 5.** Effect of scaling parameters $a_1$ and $a_2$ on (a) region of potential coexistence, (b) region of realized coexistence, (c) the ratio between the two, and (d) the proportion of the full rectangular region (A+B+C+D) taken up by the region of realized coexistence. $b_1$ and $b_2$ are fixed at 10 and 3, respectively.
difficult. Consequently, we observe an abrupt transition between the two sub-regions, with the realized region increasingly detaching from the lower bound the potential region. The upper bound of the realized region represents the condition for consumer 2 to successfully invade and is largely influenced by the dynamics of consumer 1. As the nonlinearity of consumer 1 increases, the divergence between the potential and realized regions in their upper bounds diminishes (Fig. 3a–c), presumably due to increasing dissimilarity between the two consumers which makes it easier for consumer 2 to invade.

While $b_1$ and $b_2$ represent the nonlinearity of the functional responses, $a_1$ and $a_2$ act as scaling parameters that determine the growth rate of the consumers at a given resource level. Our results show that $a_1$ and $a_2$ mainly affect coexistence bandwidth through linearly expanding or shrinking the $d_1$–$d_2$ parameter space that allows each consumer to persist with the resource when the other consumer is absent (condition 1; Figs. 4 and 5). Though the realized region of coexistence is not strictly proportional to $a_1$ (Figs. 4b and 5b), the deviation from linearity is small even with considerable shift in $a_1$ (Figs. 4c,d and 5c,d). Moreover, substantial difference in nonlinearity is required for coexistence regardless of the $a$-values. Thus the effect of $a_1$ on coexistence, while interesting, is relatively unimportant compared to the effect of $b_1$.

A condition essential for coexistence (and derived from the classical Lotka-Volterra framework of competition) is that each species limit their own growth more than they limit the growth of other species; in other words, intraspecific competition needs to be more intense than interspecific competition, thus giving less abundant species an advantage and preventing competitive exclusion (Chesson, 2000). In the Armstrong–McGehee system with a nonlinear consumer and a linear consumer competing for the same self-renewing resource, coexistence is achieved by endogenous fluctuations of the resource and a trade-off between the two consumers to more efficiently exploit resource at different levels. This trade-off is akin to the theory of r–K selection (Kneitel and Chase, 2004; MacArthur and Wilson, 1967), or gleaner-opportunist trade-off (Litchman and Klausmeier, 2001; Kremer and Klausmeier, in this issue), where one species benefits from high reproductive rate in a good environment, while the other species benefits from high tolerance to harsh environment. We demonstrated in our study that such a mechanism can still operate to facilitate coexistence in a system with two nonlinear consumers. However, a species with saturating functional response is neither as effective at exploiting high resource levels nor at dampening existing resource fluctuations as a species with linear functional response. Consequently, the degree to which the Armstrong–McGehee mechanism can promote coexistence diminishes as the relative nonlinearity (or the trade-off in life history traits) between the two species decreases.

Relative nonlinearity as a mechanism promoting coexistence has a long history in theoretical ecology and there is evidence from laboratory experiments that environmental fluctuation enhances coexistence of competitors (e.g., Descamps-Julien and Gonzalez, 2005; Grover, 1988). Yet, empirical evidence that unambiguously demonstrates operation of Armstrong—McGehee-like mechanisms in natural systems has yet to be found. The fact that coexistence bandwidth is greatly reduced when the functional response of both species deviates from linear suggests that the Armstrong–McGehee mechanism is unlikely to be detected in most ecological systems where the intake rates of consumers saturate with resource density. Moreover, it has been shown that the mechanism has limited contribution to coexistence when the level of resource partitioning is high (Abrams and Holt, 2002). We thus presume that relative nonlinearity is most likely to significantly contribute to coexistence in systems where competitors have both high niche overlap and high divergence in life-history traits. While the requirement may sound stringent, it is not uncommon for species in the same guild to employ drastically different strategies (e.g., Brown and Davidson, 1977; Christensen and Whitham, 1993; Hochberg and Lawton, 1990). Such systems may be the most promising candidates for the Armstrong–McGehee mechanism to be detected in nature.

Another way in which relative nonlinearity may contribute to coexistence is through its conjugate effect with other biotic or abiotic factors. It has been demonstrated that the effect of relative nonlinearity can be enhanced by exogenous temporal variation (Abrams, 2004), predator switching (Kimbrel and Holt, 2005), and predation (Kuang and Chesson, 2008). Incorporating detailed biological information such as age structure into the model has also been shown to interact with relative nonlinearity and generate oscillatory cycles with smaller amplitudes (McCauley et al., 2008) than they typically occur in the original system where resource population can drop to extremely low levels and thus may be too sensitive to perturbation to maintain long-term persistence (Abrams and Holt, 2002; Upadhyay, 2009). One factor that is of particular interest is exogenous temporal variation in resource level, which can promote coexistence when the relative strength of intra- and inter-specific competition varies with resource fluctuation (Chesson and Hnuty, 1997). This effect has been extensively studied both theoretically (Abrams, 2004; Chesson and Hnuty, 1997; Chesson and Warner, 1981; Hsu, 1980) and experimentally (Descamps-Julien and Gonzalez, 2005; Narwani et al., 2009). Moreover, it has been demonstrated that trade-offs in life-history traits, which are essential for difference in functional response and endogenous cycles, can arise from divergent evolution induced by a fluctuating environment (Tachikawa, 2008; Kremer and Klausmeier, in this issue). When both exogenous and endogenous cycles are present, however, they can interact in complicated ways with non-additive effect, where the two cycles may either reinforce for interfere with each other (Abrams, 2004). It thus remains an open question how our findings of the effects of relative nonlinearity on coexistence apply when endogenous fluctuations generated by relative nonlinearity operate in conjugate with other processes in more complex ecological systems. While it is beyond the scope of our study, this question should prove a fruitful area for future investigation.

5. Conclusion

We confirmed the validity of the Armstrong–McGehee mechanism of relative nonlinearity in promoting coexistence for the scenario of two consumers with nonlinear functional responses. In agreement with previous studies the range in parameter space allowing coexistence is generally reduced when the difference in curvature between the two functional responses decreases. This implies that the mechanism is unlikely to make significant contributions to coexistence in the absence of other conjugate mechanisms that occur in more complex food webs. Future studies should explore the potential of enhanced coexistence through the interaction of the Armstrong–McGehee mechanism with such conjugate mechanisms.

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Appendix A. Supporting information

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References


