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A Metric for Quantifying the Oscillatory Tendency of Consumer-Resource Interactions

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abstract: The oscillatory tendency of consumer-resource interactions is a key determinant of food-web persistence. Here, we develop a metric for quantifying oscillatory tendency that scales the positive feedback effects of saturating functional responses with the negative feedback effects of self-limitation. We use this metric to predict the oscillatory tendency of a pairwise interaction, tritrophic chain, and tritrophic web. This framework yields two key predictions. First, the oscillatory tendency of any food web increases with the number of trophic links with long handling times regardless of the magnitude of attack rates. Attack rates influence oscillatory tendency only when handling times are short. Second, the realized oscillatory tendency of a trophic link depends on how the product of the attack rate and handling time scales with the strength of self-limitation. Importantly, our metric allows calculations of the critical self-limitation strength at which a consumer-resource interaction moves from stable to oscillatory dynamics. Our data analysis reveals that the majority (77%) of interactions involve low attack rates and handling times, requiring only a modest level of self-limitation to suppress oscillations. Only 23% of the interactions exhibit a strong oscillatory tendency, consistent with previous findings, based on time-series data, that 30% of consumer-resource interactions in nature exhibit oscillations.

Keywords: consumer-resource oscillations, interaction strength, feedback, stability, self-limitation, saturating functional responses.

Introduction

Consumer-resource interactions (e.g., predation, herbivory, parasitism) constitute the building blocks of all natural communities. They have an inherent tendency to oscillate (Gurney and Nisbet 1998; Kot 2001; Murdoch et al. 2003), which can predispose species to stochastic extinction during periods of low abundances. Thus, the size and composition of food webs depend crucially on the oscillatory tendency of the consumer-resource links that constitute them.

Data suggest that at least 30% of consumer-resource interactions in nature tend to exhibit oscillations (Murdoch et al. 2002). Despite nearly a century of studies dating back to Lotka and Volterra (Lotka 1925; Volterra 1926; Rosenzweig and MacArthur 1963; Rosenzweig 1971; May 1972, 1976; DeAngelis et al. 1975; Brauer 1979; Vandermeer 1993; McCann et al. 1998; Murdoch et al. 2003), we still do not have a complete understanding of why some consumer-resource interactions tend to oscillate while others do not. Elucidating the factors that promote versus dampen oscillations is important not only in predicting the long-term persistence of food webs but also in addressing a broader array of questions involving the coevolution of antagonistic interactions (e.g., predator-prey, plant-herbivore, host-pathogen, pest-natural enemy) driven by an ecological selective environment of oscillatory population dynamics (Dieckmann et al. 1995; Marrow et al. 1996; Abrams 2000; Day et al. 2002; Gandon 2002; Gandon et al. 2008).

There have been two approaches to investigating the oscillatory dynamics of consumer-resource interactions. The first approach focuses on interaction strength, often quantified as the per capita attack rate of a consumer species on a given resource species (McCann et al. 1998; Berlow 1999; Berlow et al. 1999, 2004; McCann 2000; Neutel et al. 2002; Emmerson and Yearsley 2004; Christianou and Ebenman 2005; Rip et al. 2010). Higher per capita attack rates cause consumers to overexploit their resources, thus increasing the tendency for consumer-resource oscillations. In this viewpoint, the stability (quantified as variability in abundances) of consumer-resource interactions is determined solely by the consumer species' effect on resource species through their per capita attack rates. It has the advantage that the oscillatory tendency of a food web can be quantified in terms of an empirically measurable metric.

The second approach is based on coexistence theory

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(Chesson 2000). Long-term coexistence of consumer and resource species requires that the strength of intraspecific interactions exceed that of interspecific interactions. Specifically, self-limitation in resource and/or consumer species generate negative feedback (through density dependence) in their per capita growth rates, which in turn dampens consumer-resource oscillations. This is particularly important when consumers exhibit saturating (type II; Holling 1959) functional responses, which, because the per capita consumption rate increases with resource density at a decelerating rate, generate positive feedback in the resource species' per capita growth rate (Gurney and Nisbet 1998; Kot 2001; Murdoch et al. 2003). Unlike the interaction strength approach, which quantifies stability only in terms of variability, the coexistence approach quantifies stability in the mathematical sense as well (i.e., recovery from perturbations to steady state abundances) through its focus on both negative feedback arising from intraspecific interactions and positive feedback arising from interspecific interactions. While it has the advantage of scaling intra- and interspecific effects, the coexistence approach has the disadvantage that quantifying oscillatory tendencies requires analyzing dynamical models of species interactions, with the attendant problems of having insufficient data to parameterize the models.

Here, we propose a metric for assessing the oscillatory tendency of consumer-resource interactions that reconciles both approaches. It provides a more biologically realistic depiction of interaction strength by considering the consumer's functional response, which consists of the attack rate and handling time rather than the attack rate per se. It scales interspecific effects, mediated through the functional response, with intraspecific effects arising from self-limitation, thus providing an index of both the mathematical stability and the population variability of consumer-resource interactions. It thus retains the advantages of the interaction strength approach in providing an empirically quantifiable metric while overcoming the disadvantages of the coexistence approach by precluding the need for full-scale analyses of dynamical models.

Mathematical Framework

Background

Consumer-resource oscillations arise due to the time delay between the uptake of a resource by a consumer (mediated through its functional response) and the subsequent increase in the consumer population (mediated through the numerical response) via the conversion of energy consumed into reproduction. The initial delay in the consumer's numerical response to resource consumption allows the resource population to increase in abundance (the so-called prey escape phase of the consumer-resource cycle; Murdoch et al. 2003). Once the consumer's abundance increases, its impact on the resource population also increases. Unlike the resource species' positive effect on the consumer population (through providing energy for reproduction), which operates with a time delay, the consumer's negative effect on the resource (through mortality in the case of predation and reduction in performance in the case of herbivory) is instantaneous. Thus, increasing consumer abundance causes an immediate decrease in resource abundance. Resource overexploitation occurs when the decrease in resource abundance due to consumer-induced mortality exceeds the increase in resource abundance through reproduction, leading ultimately to a decline in both resource and consumer abundance. The higher the consumer species' attack rate, the greater the overexploitation of the resource by the consumer.

There are numerous studies showing that most consumer species (predators, herbivores, parasitoids) exhibit saturating (type II) functional responses (Hassell et al. 1976; Begon et al. 2005). Saturation occurs because of the time involved in handling and processing prey, a biological reality for the majority of heterotrophs. This raises the question of what role the handling time plays in generating consumer-resource oscillations. As is well known from consumer-resource theory (Gurney and Nisbet 1998; Kot 2001; Murdoch et al. 2003), saturating functional responses provide the biologically most realistic mechanism for inducing consumer-resource oscillations. When there is a handling time involved, the per capita consumption rate (functional response) increases with resource density at a decelerating rate, eventually saturating to a constant value. This means that consumers tend to underexploit the resource when it is abundant, thus generating positive feedback in the resource species' per capita growth rate. The longer the handling time, the stronger the positive feedback. Thus, quantifying interaction strength on the basis of the attack rate alone can underestimate the oscillatory tendency of consumer-resource interactions.

While incorporating the handling time into interaction strength can more accurately capture the oscillatory tendency of consumer-resource interactions, the focus on interspecific effects alone ignores the potential for the stabilizing (i.e., oscillation-damping) effects of resource and/or consumer self-limitation to counteract the destabilizing (i.e., oscillation-inducing) effects of high attack rates and/or handling times. A consumer species with a high attack rate and a long handling time will induce positive feedback in the resource species' per capita growth rate, leading to consumer-resource oscillations. However, self-limitation in the resource species will induce negative feedback in its per capita growth rate, which can dampen consumer-resource oscillations or eliminate them altogether. Thus, an accurate estimation of the oscillatory tendency of consumer-resource interactions requires a metric that scales the strength of interspecific effects with that of intraspecific effects. Here, we use dynamical models of consumer-resource interactions to develop such a metric. We analyze a series of community modules of increasing complexity: a pairwise interaction, a tritrophic food chain, and a tritrophic food web. Mathematica code used to conduct these analyses is provided in a zip file online.[1]

Pairwise Consumer-Resource Interaction

We begin with a pairwise consumer-resource interaction, as it constitutes the basic building block of all food webs. The dynamics are given by the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963; Rosenzweig 1971):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1-qR) - \frac{a_C RC}{1+a_C h_C R},$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = \frac{e_C a_C RC}{1+a_C h_C R} - d_C C, \tag{1}$$

where R and C are, respectively, the abundances of the resource and consumer species, r is the resource species' intrinsic growth rate, and q is the per capita competition coefficient (the inverse of resource carrying capacity), which quantifies the strength of resource self-limitation. The parameters a_C, e_C, h_C, and d_C depict, respectively, the consumer species' per capita attack rate, conversion efficiency, handling time, and per capita mortality rate.

Self-limitation in the resource species arises from intraspecific competition for limiting factors, such as space, water, and nutrients. It induces negative feedback in the resource species' per capita growth rate while the consumer species' saturating functional response induces positive feedback. To see the positive feedback effect, consider the case when resource self-limitation is weak or nonexistent (i.e., $q \approx 0$). Then the resource species' per capita growth rate is

$$\frac{1}{R}\frac{\mathrm{d}R}{\mathrm{d}t} = r - \frac{a_C C}{1+a_C h_C R}. \tag{2}$$

As resource abundance increases, the consumer's effect on the resource decreases and the resource species' per capita growth rate increases (fig. 1*a*). This positive feedback effect of the consumer on the resource is the direct result of the consumer's handling time (h_C), which causes the per capita consumption rate (functional response) to saturate to a constant value (a_C) at high resource densities. Hence, the consumer underexploits the resource when the resource is abundant, enhancing the resource species' ability to escape consumer control, leading to oscillations in both resource and consumer abundance.

Self-limitation in the resource species ($q > 0$) induces negative feedback in the resource species' per capita growth rate, i.e.,

$$\frac{1}{R}\frac{\mathrm{d}R}{\mathrm{d}t} = r(1-qR) - \frac{a_C C}{1+a_C h_C R}. \tag{3}$$

If the decrease in the resource species' per capita growth rate with increasing density due to self-limitation is stronger than the increase in the per capita growth rate with increasing density due to the consumer's saturating functional response (fig. 1*b*), the prey escape component of the consumer-resource cycle is suppressed, which in turn reduces the consumer's ability to overexploit the resource. The net effect is a dampening of consumer-resource oscillations. If negative feedback is sufficiently strong, it can eliminate oscillations altogether.

To illustrate how the interaction between negative and positive feedback effects determines the oscillatory tendency of the pairwise interaction, consider the stability of the consumer-resource equilibrium for the model (eq. [1]; details are provided in app. A; apps. A–D are available online). This point equilibrium is stable if

$$\frac{a_C h_C}{q} < \frac{e_C + h_C d_C}{e_C - h_C d_C}. \tag{4}$$

The important quantity is the metric $a_C h_C/q$ on the left-hand side, which scales the consumer's attack rate and handling time (the product of which determines the strength of positive feedback) with resource self-limitation (which determines the strength of negative feedback). It is this metric that determines whether the consumer-resource equilibrium is stable to perturbations in consumer and resource abundances. To see this, note that the right-hand side of equation (4), which has a minimum of 1 (when $h_C \rightarrow 0$ and/or $d_C \rightarrow 0$), increases much more slowly with an increase in the handling time compared with the left-hand side (fig. A1, app. A). Hence, the metric $a_C h_C/q$ dominates the stability condition. We can therefore derive a conservative condition for stability:

$$\frac{a_C h_C}{q} < 1, \tag{5}$$

which has the distinct advantage that it can predict the oscillatory tendency of the consumer-resource interaction on the basis of just three parameters.

To further illustrate the important role the metric $a_C h_C/q$ plays in determining the oscillatory tendency, we can calculate the critical resource equilibrium abundance be-

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[1] Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

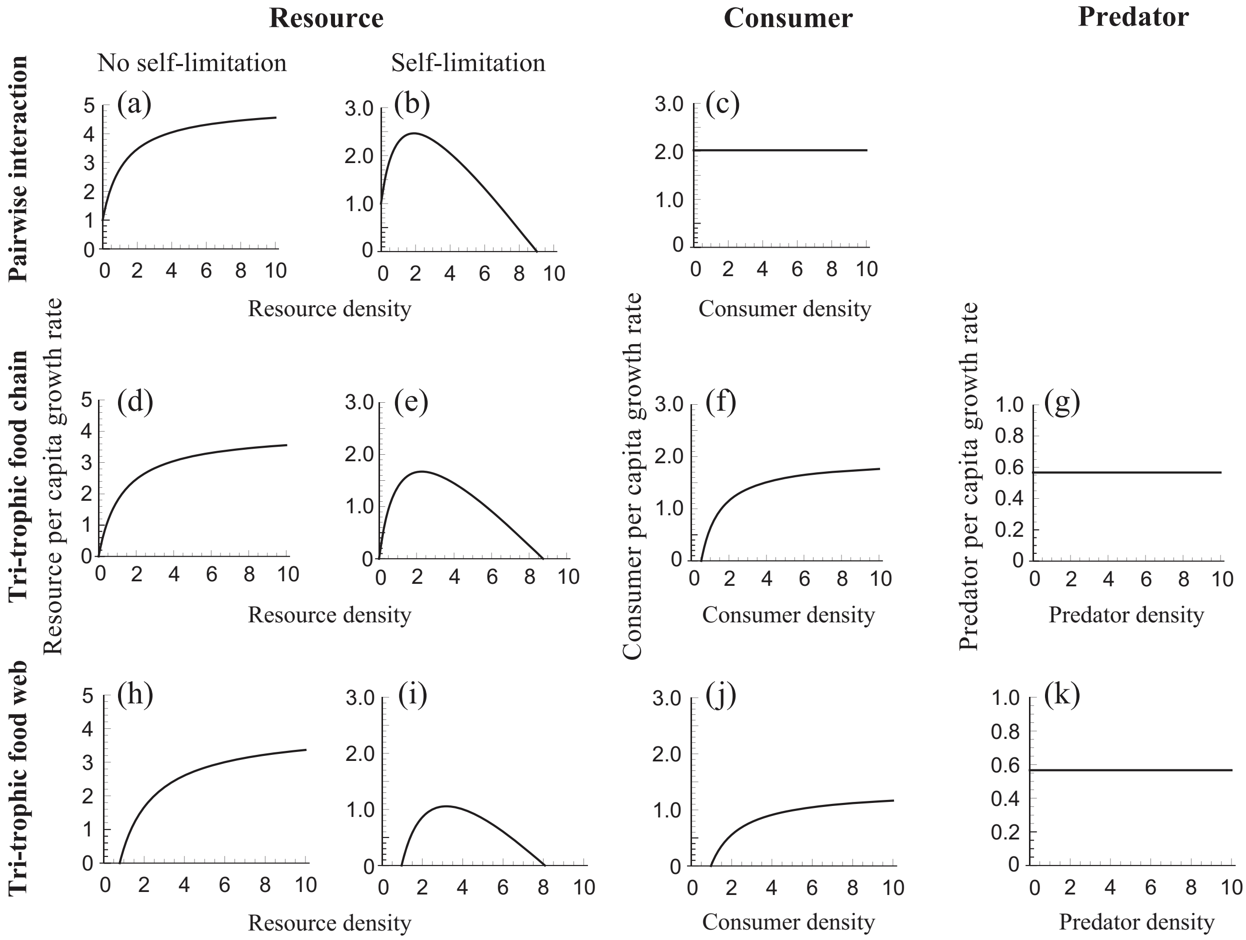

Figure 1: Negative and positive feedback effects on species' per capita growth rate in the pairwise interaction (*a*–*c*), tritrophic food chain (*d*–*g*), and tritrophic food web (*h*–*k*). When there is no self-limitation in the resource ($q = 0$; *a*, *d*, *h*), positive feedback due to the consumer's handling time causes the resource species' per capita growth to increase with increasing resource density. Self-limitation in the resource species ($q > 0$; *b*, *e*, *i*) counteracts this positive density-dependent effect, causing the resource's per capita growth rate to decrease with increasing resource density. The resource density at which the per capita growth rate switches from being positive to negative density dependent depends on the strength of resource self-limitation (q) and the consumer's attack rate (a_C) and handling time (h_C). In the tritrophic food chain and web, the predator's saturating functional response induces positive feedback in the consumer's per capita growth rate (*f*, *j*). The predator's per capita growth rate has no direct density-dependent feedback (*g*, *k*). Parameter values are $r = 5$, $q = 0.4$, $a_{C_1} = 2$, $a_{C_2} = 1$, $a_P = 0.5$, $h_{C_1} = h_{C_2} = h_P = 0.2$, $e_{C_1} = e_{C_2} = e_P = 0.2$, and $d_{C_1} = d_{C_2} = d_P = 0.1$.

low which the system moves from a stable equilibrium to limit-cycle oscillations (see app. A for details):

$$R_c > \frac{(a_C h_C/q) - 1}{2(a_C h_C/q)}. \tag{6}$$

As can be seen, this transition is determined entirely by the metric that scales the negative and positive feedback effects. Its magnitude determines the sign of R_c, and, hence, the oscillatory tendency of a given consumer-resource interaction. For instance, if positive feedback is stronger than negative feedback (i.e., $a_C h_C/q > 1$ and $R_c > 0$), the interaction has the potential to exhibit oscillations; if positive feedback is weaker than negative feedback (i.e., $a_C h_C/q < 1$ and $R_c < 0$), the consumer-resource equilibrium is stable when it is feasible.

If we nondimensionalize equation (1),

$$\frac{d\hat{R}}{d\hat{t}} = \hat{R}(1 - \hat{R}) - \frac{\hat{a}_C \hat{R}\hat{C}}{1 + \tau_C \hat{R}},$$

$$\frac{d\hat{C}}{d\hat{t}} = \frac{\hat{a}_C \hat{R}\hat{C}}{1 + \tau_C \hat{R}} - \hat{d}_C \hat{C}, \tag{7}$$

with the scaled quantities

$$\hat{R} = qR, \quad \hat{C} = \frac{qC}{e_C}, \quad \hat{t} = rt,$$

$$\hat{a}_C = \frac{e_C a_C}{rq}, \quad \hat{d}_C = \frac{d_C}{r}, \quad \tau_C = \frac{a_C h_C}{q}, \tag{8}$$

we see that the consumer attack rate and handling time scale naturally with the strength of resource self-limitation. This natural scaling makes τ_C an appropriate metric for quantifying the net effect of negative and positive feedback and, hence, the oscillatory tendency of the consumer-resource interaction.

It is instructive to consider how well the interaction strength metric (quantified as the per capita attack rate; see the review by Berlow et al. 2004) captures the oscillatory tendency of the pairwise consumer-resource interaction compared with τ_C. As shown in figure 2, high attack rates do not necessarily lead to oscillatory dynamics unless the handling time is long. Importantly, oscillations can occur even when the attack rate is low, provided the handling time is sufficiently long. Thus, the interaction strength metric consistently under- or overpredicts the tendency for oscillations compared with τ_C. This is because the interaction strength metric considers only the consumer's attack rate (a_C), whereas it is the handling time (h_C)—because it causes the functional response to saturate—that generates the positive feedback leading to oscillations. The attack rate serves only to mediate the strength of positive feedback. If the handling time is short, the product $a_C h_C$ is small, with the result that $\tau_C < 1$ and the consumer-resource interaction is unlikely to oscillate unless resource self-limitation is very weak.

Testing Model Predictions

To illustrate the importance of handling time in determining the oscillatory tendency of pairwise consumer-resource interactions, we now turn to data. We conduct two analyses. The first focuses on an insect host-parasitoid community studied by one of us (Amarasekare 2000*a*, 2000*b*, 2007, 2008). The second is a broader analysis, based on published data, of a large number of consumer-resource interactions spanning different taxa, habitat types, and feeding modes.

Insect Host-Parasitoid Community. We consider the interaction between an insect herbivore (the harlequin bug, *Murgantia histrionic*) and its egg parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*; see app. B for natural history details). Attack rates and handling times of both parasitoid species have been measured using functional response experiments (Kidd and Amarasekare 2012), and estimates of the bug's self-limitation strength are available from field studies (P. Amarasekare, unpublished data).

Notably, the two parasitoid species exhibit per capita attack rates of similar magnitude (*T. murgantiae*: 1.11 ± 0.03 eggs/female parasitoid/day, $P < .0001$; *O. johnsonii*: 1.32 ± 0.08 eggs/female parasitoid/day, $P < .0001$; $n = 6$ replicate experiments; Kidd and Amarasekare 2012), on the basis of which one might conclude that they exhibit comparable interaction strengths. However, the two species differ in the magnitude of their handling times, with *O. johnsonii* exhibiting a longer handling time (*T. murgantiae*: 0.015 ± 0.003 days, $P < .001$; *O. johnsonii*: 0.05 ± 0.08 days, $P < .0001$) and, hence, a more nonlinear functional response (Kidd and Amarasekare 2012).

We can use the data on attack rates and handling times to calculate the critical level of self-limitation (q_c) at which negative and positive feedback effects are exactly balanced (i.e., $\tau_C = 1 \Rightarrow q_c = ah$). (When resource self-limitation is below this value—i.e., $q < q_c$—the interaction moves from a stable point equilibrium to limit-cycle oscillations.)

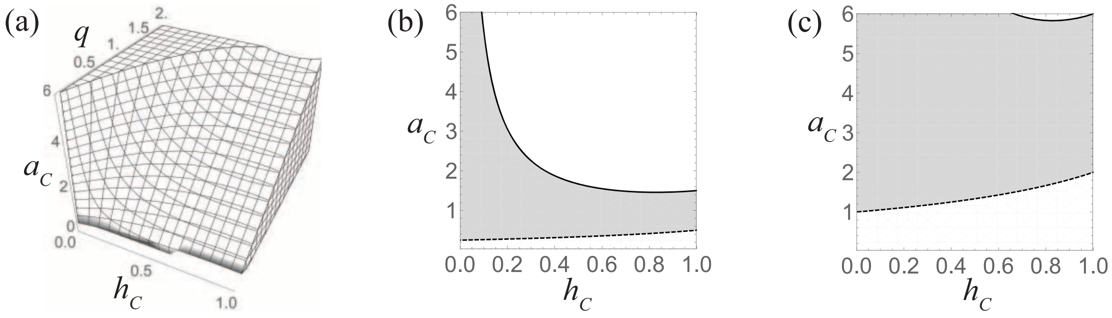

Figure 2: Stability (eq. [4]) and feasibility (eq. [A2]) boundaries for the pairwise consumer-resource interaction. *a* depicts the stability and feasibility boundaries as a function of the consumer's attack rate (a_C), handling time (h_C), and resource self-limitation (q); *b* and *c* depict two-dimensional slices of *a* for weak ($q = 0.5$; *b*) and strong ($q = 2.0$; *c*) self-limitation in the resource. In *b* and *c*, solid lines depict the stability boundary, and dashed lines depict the feasibility boundary. The gray area depicts the region of stable consumer-resource equilibrium. Parameter values are $e_C = 0.2$ and $d_C = 0.1$.

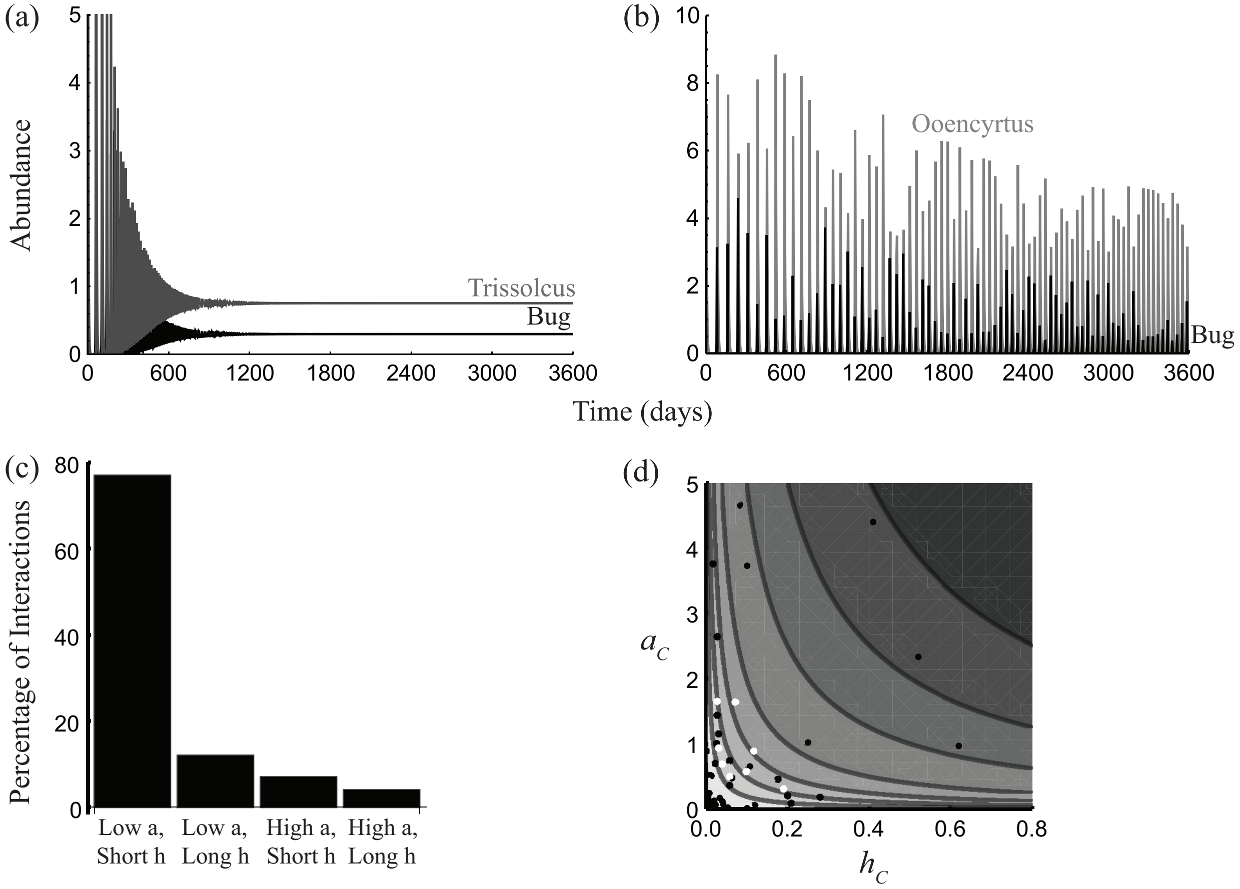

Figure 3: Results based on data from a host-parasitoid community (*a* and *b*) and a broader analysis based on published data (*c* and *d*). In the host-parasitoid community, dynamics of the harlequin with each parasitoid species, predicted from equation (1) parameterized with laboratory and field data, show that *Trissolcus murgantiae*, the parasitoid with a lower handling time, exhibits a stable interaction with the bug, while *Ooencyrtus johnsonii*, the parasitoid with the higher handling time, exhibits an unstable (oscillatory) interaction. Parameter values are $r = 0.85$/day and $q = 1/16$/individual for the bug; $a_C = 1.11$ eggs/female/day, $h_C = 0.015$ days, $e_C = 1$, and $d_C = 0.33$/day for *Trissolcus*; and $a_C = 1.32$ eggs/female/day, $h_C = 0.05$ days, $e_C = 1.82$, and $d_C = 0.25$/day for *Ooencyrtus*. *c* depicts the frequency distribution of attack rates and handling times for 57 species (see app. B for details), and *d* depicts the actual distribution of attack rates and handling time overlain on the contour plot depicting the critical value of q at which negative and positive feedback effects are exactly balanced (i.e., $\tau_C = 1$). Darker shades indicate greater values of q. Black circles represent predators, and white circles represent parasites.

The critical level of self-limitation is 0.017 for the pairwise interaction between the host and *T. murgantiae* and is 0.07 for the interaction between the host and *O. johnsonii*. Thus, we see that the species with the more nonlinear functional response (*O. johnsonii*) requires a higher level of resource self-limitation to suppress oscillations.

In this case, we actually have an estimate of the host species' self-limitation from field data, so we can calculate the relative strengths of negative and positive feedback experienced by each species. On the basis of field estimates of the bug's carrying capacity in the field (16 individuals; P. Amarasekare, unpublished data), $q = 1/16$, $\tau_C = 0.35$ for *T. murgantiae*, and $\tau_C = 1.05$ for *O. johnsonii*.

Since τ_C is less than 1 for *T. murgantiae* and is greater than 1 for *O. johnsonii*, we expect the interaction between the bug and *T. murgantiae* to exhibit damped oscillations toward a stable equilibrium and the interaction between the bug and *O. johnsonii* to exhibit persistent oscillations. We can test these predictions by parameterizing the full dynamical model 1 with data for each species and use numerical integration to generate the expected dynamics for each pairwise interaction. This exercise yields exactly the outcome predicted by the feedback metric: damped oscillations for *T. murgantiae* and persistent oscillations for *O. johnsonii* (fig. 3*a*, 3*b*).

The analysis of the host-parasitoid community yields two key results. First, the oscillatory tendency of the pairwise host-parasitoid interactions is determined by the balance between the host's self-limitation strength and the parasitoid's handling time. Second, the metric (τ_C) that scales positive and negative feedback effects can correctly predict the outcome of the full dynamical model.

Broader Analysis of Consumer-Resource Interactions. To determine whether the above findings generalize to other types of consumer-resource interactions (e.g., predator-prey), we used published data on attack rates and handling times for 57 species to calculate the critical level of self-limitation at which negative and positive feedback effects are exactly balanced (see app. B for details). These species include predators, herbivores, and parasitoids from both aquatic and terrestrial habitats, spanning a range of taxa from zooplankton, crustaceans, mites, insects, and fish. Two key insights emerge from this analysis. First, the distribution of attack rates and handling times is such that only two of 57 species (4%) have a high attack rate and a high handling time, a few (7%) have high attack rates and low handling times, several (12%) have low attack rates and high handling times, and an overwhelming majority (77%) have low attack rates and low handling times (fig. 3*c*). Second, as predicted by the feedback metric we have derived, the strength of self-limitation required for oscillations to be damped increases as the product of the attack rate and handling time increases (fig. 3*d*).

Pairwise consumer-resource interactions are a necessary starting point for investigating the oscillatory tendencies of consumer-resource communities because they form the basic building blocks from which more complex food webs are assembled. To get a complete understanding of the oscillatory tendencies of real communities, we need to build up from pairwise to multitrophic interactions that include indirect interactions between species. In what follows, we investigate whether the type of feedback metric we have derived for the pairwise interaction can also predict the oscillatory tendency of more complex community modules.

Tritrophic Food Chain

The dynamics of a tritrophic food chain consisting of a basal resource, an intermediate consumer, and a top predator are given by

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - qR) - \frac{a_C RC}{1 + a_C h_C R},$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = \frac{e_C a_C RC}{1 + a_C h_C R} - \frac{a_P CP}{1 + a_P h_P C} - d_C C, \qquad (9)$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{e_P a_P CP}{1 + a_P h_P C} - d_P P,$$

where P is the abundance of the predator and a_P, h_P, d_P, and e_P are, respectively, its per capita attack rate, handling time, mortality rate, and conversion efficiency. Other parameters are as defined above.

Table 1: Predictions about indirect effects on the potential for consumer-resource oscillations in the tritrophic food chain based on the relative strengths of negative and positive feedback

Species				Oscillatory tendency		Self-limitation	
Consumer		Predator					
a_C	h_C	a_P	h_P	R-C	C-P	Overall	q
Low	Low	Low	Low	Low	Low	1[a]	1[a]
Low	Low	High	Low	Low	Medium	2	2
High	Low	Low	Low	Medium	Low	2	2
High	Low	High	Low	Medium	Medium	3	3
Low	Low	Low	High	Low	High	4	4
Low	High	Low	Low	High	Low	4	4
High	Low	Low	High	Medium	High	5	5
Low	High	High	Low	High	Medium	5	5
Low	High	Low	High	High	High	5[b]	5[b]

Note: R-C, resource-consumer; C-P, consumer-predator.

[a] Oscillatory tendency and q lowest.

[b] Oscillatory tendency and q highest.

As with the pairwise interaction, the resource species' per capita growth rate has negative feedback due to resource self-limitation and positive feedback due to the consumer's saturating functional response (fig. 1*e*). Unlike in the pairwise interaction, the consumer's per capita growth rate now has positive feedback due to the predator's saturating functional response (fig. 1*f*). The predator's per capita growth rate has no direct density-dependent feedback (fig. 1*g*). Importantly, positive feedback in the resource's per capita growth rate makes the resource-consumer link oscillatory, while positive feedback in the consumer's per capita growth rate makes the consumer-predator link oscillatory. Whether oscillations in one or both links are damped is determined by direct negative feedback via resource self-limitation and indirect feedback through predation, which reduces positive feedback on the consumer's per capita growth rate, which in turn reduces positive feedback on the resource's per capita growth rate.

Nondimensionalizing equation (9) reveals that the parameters inducing negative and positive feedback scale naturally with each other (app. C). Now there are two feedback metrics: τ_C, which scales positive feedback effects due to the consumer's saturating functional response with resource self-limitation, and τ_P, which scales the positive feedback effects due to the predator's saturating functional response with resource self-limitation. Note that while τ_C scales the negative and positive feedback due to direct interactions between the resource and the consumer species, τ_P scales the positive feedback due to direct interactions between the consumer and predator with negative

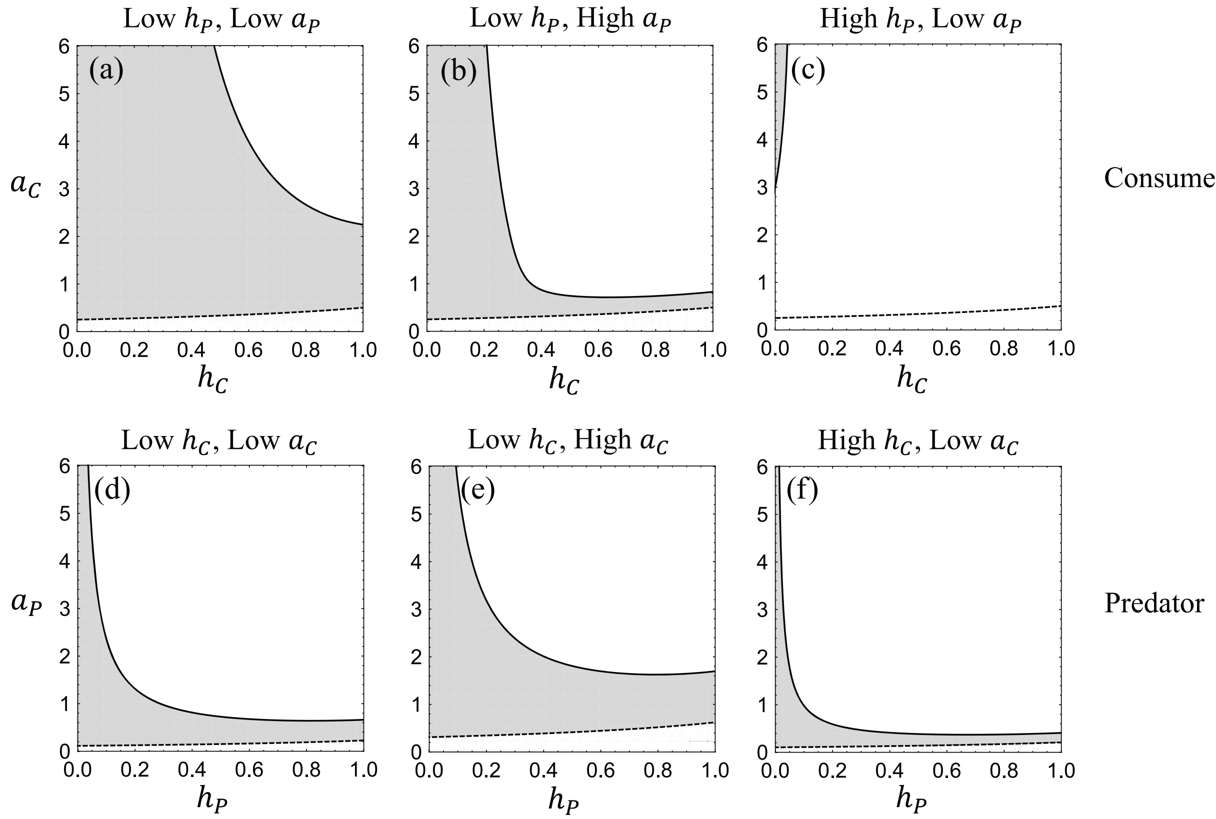

Figure 4: Stability boundary (see app. C for details) for the tritrophic food chain in terms of the functional response parameters for the consumer (*a*–*c*) and predator (*d*–*f*) for three cases in which oscillatory tendency is predicted to increase. Dashed lines depict the feasibility boundaries below which the consumer (*a*–*c*) or predator (*d*–*f*) becomes extinct, while solid lines depict the stability boundary beyond which oscillations occur. The gray area denotes the region of stable equilibrium. The panels depicted are for weak resource self-limitation ($q = 0.5$), but the qualitative outcomes are unaltered when resource self-limitation is strong ($q = 2.0$; see fig. C1, app. C) Parameter values are $e_C = e_P = 0.2$ and $d_C = d_P = 0.1$.

feedback arising from resource self-limitation that affects the predator only indirectly.

We can use the insights obtained from studying the pairwise interaction to predict the oscillatory tendency of the tritrophic food chain. The data analysis we have conducted shows that most consumer species fall into three categories: low attack rate and low handling time, high attack rate and low handling time, and low attack rate and high handling time. Combining this empirical knowledge with the theoretical insights obtained above, we can develop a set of predictions about the oscillatory tendency of resource-consumer-predator interactions and the strength of resource self-limitation required to dampen oscillations (table 1). The key general prediction is that oscillatory tendency—and the strength of resource self-limitation needed to counter it—should increase in the following order: low h and low a in consumer and predator < low h in both, high a in consumer or predator < high h in consumer or predator, low a in both < high h and low a in both.

The reasoning for this prediction is as follows. If the consumer and predator both have short handling times, oscillatory tendencies of both resource-consumer and consumer-predator links are low and the food chain overall has the lowest oscillatory tendency. Conversely, when both h_C and h_P are high, the food chain exhibits the strongest oscillatory tendency. If both species have short handling times but at least one species has a high attack rate, oscillatory tendency should be higher than when both species have low attack rates and handling times but lower than when both have low attack rates but one has a long handling time. In other words, the oscillatory tendency of the food chain increases with the number of links that involves a long handling time.

It is instructive to compare the above predictions with ones made on the basis of the interaction strength metric: a_C, a_P low < a_C or a_P high < a_C, a_P high, where oscillatory tendency increases with the number of links that have high attack rates.

Testing the above predictions by conducting a stability analysis of the tritrophic food chain (see app. C for details) yields two key results. First, consistent with our expectation, oscillatory tendency is greatest when both consumer and predator have long handling times and is least when both have short handling times, regardless of the magnitude of the attack rate (figs. 4, C1). Second, we observe a strong indirect effect of the predator. A shorter handling time in the predator has a stronger effect in lowering oscillatory tendency than a shorter handling time in the consumer (compare figs. 4*a*–4*c* and 4*d*–4*f*). This is because when the predator's handling time is short it has a stronger effect in suppressing consumer abundance, which in turn weakens the consumer's positive feedback effect on the resource's per capita growth rate and, hence, the oscillatory tendency of the resource-consumer link. This outcome highlights the importance of the predator's indirect effect on the resource species (quantified in terms of τ_P), which tends to stabilize (by reducing the potential for oscillations) the basal link of the food chain.

Because it does not take the effects of handling time into account, the interaction strength metric does not correctly predict the likelihood of oscillations when both species have attack rates of similar magnitude. For instance, low attack rates of both species does not imply low oscillatory tendency in resource-consumer and consumer-predator links unless the handling times of both species are also short. Similarly, high attack rates of both species do not imply a high oscillatory tendency unless the handling time of at least one species is long. Since data show that very few species exhibit high attack rates and long handling times, high attack rates in themselves are unlikely to signify a strong potential for oscillations in real consumer-resource communities. Indeed, as our analyses show (fig. 4), high attack rates and short handling times—a common combination in highly efficient predators and parasites—exhibit a lower oscillatory tendency than low attack rates and high handling times. Taken together, these findings underscore the importance of taking the handling time into account in evaluating the oscillatory tendencies of consumer-resource communities.

Empirical support for our predictions come from a naturally occurring tritrophic food chain (grass–grasshopper–wolf spider) studied by Schmitz (1993). Manipulations of nutrient input and spider density showed that nutrient limitation, which determines the strength of self-limitation and, hence, negative feedback in the resource (grass) species' per capita growth rate, had a stronger effect in regulating consumer (grasshopper) abundance than the consumer's handling time or predator (spider) density, which determines the strength of positive feedback. This is a case where a community that is potentially oscillatory when viewed only in terms of consumer and predator traits is stabilized (i.e., oscillations are damped) by strong self-limitation in the basal resource species.

Tritrophic Food Web

We next consider a tritrophic food web consisting of two consumer species competing for the basal resource, one of which is attacked by a top predator. A well-studied example of this food web involves two aphid species (*Acyrthosiphon pisum* and *Megoura viciae*) that share a common resource (*Vicia faba*) and a specialist parasitoid (*Aphidius ervi*) that attacks only *A. pisum* (van Veen et al. 2005). *Acyrthosiphon pisum* competitively excludes *M. viciae* in the absence of the parasitoid, and the *A. pisum*–*A. ervi* interaction exhibits oscillations in the absence of *M. viciae*. However, the full community exhibits stable dynamics (van Veen et al. 2005). Coexistence occurs because *A. pisum*'s susceptibility to parasitoid attack weakens its competitive effect on *M. viciae*, while *M. viciae* reduces the oscillatory tendency of the *A. pisum*–*A. ervi* interaction by lowering the parasitoid's search efficiency and, hence, its attack rate on *A. pisum*.

The dynamics of the tritrophic food web are given by the following:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - qR) - \frac{a_{C_1}RC_1}{1 + a_{C_1}h_{C_1}R} - \frac{a_{C_2}RC_2}{1 + a_{C_2}h_{C_2}R},$$

$$\frac{\mathrm{d}C_1}{\mathrm{d}t} = \frac{e_{C_1}a_{C_1}RC_1}{1 + a_{C_1}h_{C_1}R} - \frac{a_P C_1 P}{1 + a_P h_P C_1} - d_{C_1}C_1,$$

$$\frac{\mathrm{d}C_2}{\mathrm{d}t} = \frac{e_{C_2}a_{C_2}RC_2}{1 + a_{C_2}h_{C_2}R} - d_{C_2}C_2, \tag{10}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{e_P a_P C_1 P}{1 + a_P h_P C_1} - d_P P,$$

where C_1 and C_2 are the abundances of the two consumer species; a_{C_2}, h_{C_2}, and d_{C_2} are, respectively, consumer 2's attack rate, handling time, and mortality rate; and all other parameters are as in equations (1) and (9).

The resource species' per capita growth rate has negative feedback arising from resource self-limitation and positive feedback arising from the two consumer species' saturating functional responses (fig. 1*i*). As in the tritrophic food chain, the consumer's per capita growth rate has positive feedback due to the predator's functional response (fig. 1*j*). The per capita growth rates of the second consumer and predator (fig. 1*k*) have no direct density-dependent feedback. Importantly, whether oscillations due to positive feedback in the two resource-consumer links are dampened is determined by the strength of direct negative feedback due to resource self-limitation and by indirect feed-

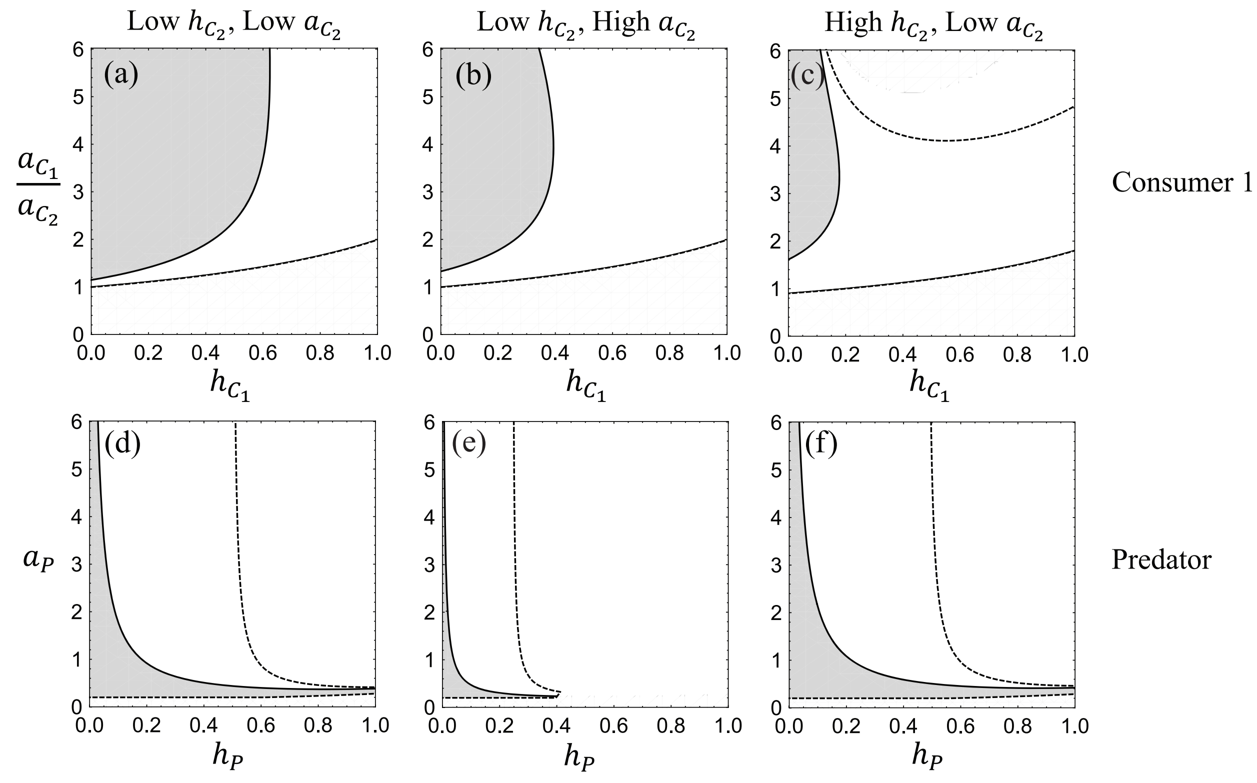

Figure 5: Stability boundary (see app. D for details) for the tritrophic food web in terms of the functional response parameters for consumer 1 (*a–c*) and the predator (*d–f*) for three cases based on consumer 2's functional response parameters. Dashed lines depict the feasibility boundaries below which the predator becomes extinct and above which consumer 1 becomes extinct, while solid lines depict the stability boundary beyond which oscillations occur. The gray area denotes the region of stable equilibrium. Note that feasibility requires that $a_{C_1} > a_{C_2}$, that is, consumer 1 is the superior competitor for the shared resource. The outcomes are qualitatively similar when resource self-limitation is strong and when the stability boundary is evaluated as a function of consumer 2's functional response parameters (see fig. D1, app. D). Parameter values are as in figure 4.

back through interspecific competition and predation, which may reduce or enhance the strength of positive feedback in the consumer's and predator's per capita growth rates.

Nondimensionalizing equation (10) (see app. D for details) reveals three feedback metrics, τ_{C_i} ($i = 1, 2$) and τ_P, which, respectively, scale consumer *i*'s and the predator's functional response parameters with the strength of resource self-limitation.

On the basis of the insights gained from studying the pairwise interaction and the tritrophic food chain, we expect oscillatory tendency of the tritrophic food web to increase in the following order: low *h* and low *a* in all species < low *h* in all species, high *a* in at least one species < high *h* in at least one species, low *a* in all species < high *h* and high *a* in all species.

We expect the food web to be least oscillatory when the two consumers and predator have short handling times and most oscillatory when all three species have long handling times. We also expect short handling times in all species and high attack rates in at least one species to be less oscillatory than a long handling time in at least one species and low attack rates in all species.

On the basis of interaction strength metric, we expect oscillatory tendency to increase in the following order: low *a* in all species < high *a* in one species < high *a* in all species.

Testing these predictions by conducting a local stability analysis (app. D) yields two key results. First, consistent with our expectations, oscillatory tendency is lowest when the two consumers and predator have short handling times and highest when all three species have long handling times, regardless of the magnitude of the attack rate (figs. 5, D1). For a given magnitude of the handling time in the two consumers, an increase in the predator's handling time leads to a large increase in oscillatory tendency (fig. 5*d*–5*f*). For a given magnitude of the predator's handling time, an increase in the handling times of the two consumers increases the oscillatory tendencies of the resource-consumer 1 and resource-consumer 2 links and, hence, that of the entire food web (fig. 5*a*–5*c*).

The second result pertains to indirect effects on oscillatory tendency mediated by the interaction between competition and predation. Counter to our expectations based on studies of the pairwise interaction and the tritrophic food chain, oscillatory tendency of the food web is lower when the attack rate of the consumer susceptible to predation (consumer 1 in our model) is relatively high (fig. 5*a*–5*c*). This is because an increase in consumer 1's attack rate increases its competitive effect on consumer 2, which in turn weakens the positive feedback effect that consumer 2 exerts on the resource. If the competitive superiority of consumer 1, a necessity for consumer coexistence given its greater susceptibility to the predator, involves a shorter handling time as well as a higher attack rate than in consumer 2, positive feedback on the resource is reduced even more, resulting in further reduction of the food web's oscillatory tendency.

These findings contrast with the prediction based on interaction strength that higher attack rates should always increase oscillatory tendency. This mismatch arises because the interaction strength metric does not consider the positive feedback effects arising from the handling time. The discrepancy between the predictions based on the interaction strength and feedback metrics underscores the importance of using the product of the attack rate and handling time, rather than the attack rate per se, to quantify the oscillatory tendency of food webs.

Discussion

Antagonistic interactions between consumers and resources can lead to oscillations in abundance, which can limit food-web persistence by predisposing species to stochastic extinction. Two approaches have been taken to investigate consumer-resource oscillations: interaction strength, which assesses consumers' effect on resources through their attack rates (McCann et al. 1998; Berlow 1999; Berlow et al. 1999, 2004; McCann 2000; Neutel et al. 2002; Emmerson and Yearsley 2004; Christianou and Ebenman 2005; Rip et al. 2010) and coexistence theory, which assesses the relative strengths of intraspecific (self-limitation) and interspecific (consumer-resource) interactions (Chesson 2000). Interaction strength is easily measurable but does not incorporate negative feedback due to self-limitation or positive feedback due to saturating functional responses. Coexistence theory incorporates both negative and positive feedback effects but requires data to parameterize dynamical models of species interactions.

Here, we develop a metric for assessing the oscillatory tendency of consumer-resource interactions that combines the advantages of both approaches. It incorporates the positive feedback effects of saturating functional response by considering the consumer's attack rate and handling time. It scales these positive feedback effects with negative feedback arising from self-limitation, thus allowing one to quantify both mathematical stability and population variability of consumer-resource interactions. Use of this metric to assess the oscillatory tendency of food-web modules ranging from a pairwise interaction to a tritrophic food web yields two key insights.

First, our analysis yields the general result that the oscillatory tendency of any food web will increase with the number of trophic links (e.g., resource-consumer, consumer-predator) that involve long handling times regardless of the magnitude of attack rates. This is because it is the handling time, rather than the attack rate, that generates the positive feedback leading to consumer-resource oscillations. The attack rate only serves to mediate the strength of positive feedback and has an overriding influence on the oscillatory tendency of a trophic link only when the handling time is short. As we have shown, quantifying the interaction strength in terms of the attack rate alone can lead to under- or overestimatation of the oscillatory tendency of a given food web, depending on the magnitude of the handling time. Since the vast majority of consumer species in nature tend to exhibit saturating functional responses (Hassell et al. 1976; Begon et al. 2005), incorporating handling time into measures of interaction strength is crucial if we are to realistically assess the oscillatory tendency of real food webs. This should not pose a problem in empirical measurements of interaction strength because attack rates are estimated using data from functional response experiments, which also allow for estimation of handling times.

The prediction that oscillatory tendency should increase with increasing handling time raises the issue of what constitutes high versus low attack rates and short versus long handling times. A high attack rate means a high per capita consumption rate per unit of time. On the basis of data from 57 species spanning a wide range of taxa, feeding modes, and habitats (see the supporting information, available online), the per capita attack rate ranged from 0.01 to 4.65 per day with a mode of 0.88 per day, and the handling time ranged from 0.001 to 0.62 days with a mode of 0.1 days. Thus, measured on a daily scale, a short handling time involves a matter of minutes, while a long handling time involves a matter of hours.

The second major insight to emerge from our analysis is the importance of scaling the positive feedback effects arising from consumers' functional responses with negative feedback effects due to self-limitation. While the product of the attack rate and handling time indicates the potential oscillatory tendency of a given resource-consumer link within a food web, the actual oscillatory tendency will depend on the strength of negative feedback, direct or indirect, arising from self-limitation in the resource and/or consumer. While attack rates and handling times are routinely quantified via functional response experiments, self-limitation strength is a more difficult quantity to measure, especially in field populations. The feedback metrics we develop, which scale each consumer's functional response parameters with resource self-limitation, provide a potential solution to this problem. If data on attack rates and handling times are available, one can calculate the critical level of self-limitation at which the interaction moves from exhibiting a stable point equilibrium to limit-cycle oscillations. The greater the magnitude of this critical value, the higher the potential for a given consumer-resource interaction to exhibit oscillations. On the basis of the data analysis we have conducted, which spans different taxa, habitat types, and feeding modes, the vast majority (77%) of consumer species in nature exhibit low attack rates and short handling times. This suggests that only a modest level of self-limitation would suffice to suppress consumer-resource oscillations. On the basis of these data, only 23% of the consumer-resource interactions studied have the potential to exhibit oscillations, which is consistent with the findings of an independent analysis, based on time-series data, that 30% of consumer-resource interactions in nature tend to exhibit oscillations (Murdoch et al. 2002).

Our analysis has focused on food webs in which self-limitation arises in the basal resource species. Effects of self-limitation on consumer species can be incorporated into the model by modifying the functional response so that it becomes a function of both resource and consumer density. Mechanisms such as interference competition in predators and parasitoids (Abrams 1980; Skalski and Gilliam 2001) that induce self-limitation in consumer species may provide additional negative feedback to counter the positive feedback effects of saturating functional responses.

In conclusion, our findings show that scaling the positive feedback effects arising from the saturating functional responses of consumers with the negative feedback effects arising from resource and/or consumer self-limitation provides a more accurate estimate of the oscillatory tendency of food webs than interaction strength measures based on the attack rate alone. The feedback metric we have developed provides a way to quantify the relative importance of negative and positive feedback processes without resorting to parameterizing and analyzing complex dynamical models. This metric has the advantage that it can be measured for any number of consumer-resource links within a food web, thus allowing for quantifying the oscillatory tendency of complex food webs with a large number of species.

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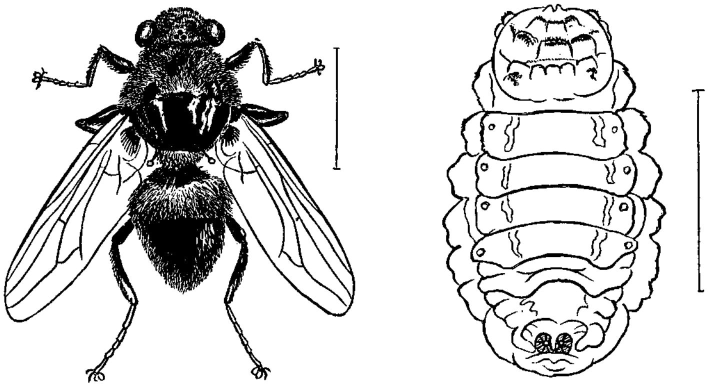

“The Bot-fly of the ox, *Hypoderma bovis* ... , is black and densely hairy, and the thorax is banded with yellow and white. The larva is found during the month of May, and also in summer, living in tumors on the back of cattle. When fully grown, which is generally in July, they make their way out and fall to the ground, and live in the puparium from twenty-six to thirty days, the fly appearing from May until September. It is found all over the world.” From “A Chapter on Flies” by A. S. Packard Jr. (*The American Naturalist*, 1869, 2:586–596).