Title

How interplay between positive and negative feedback influences the persistence of consumer-resource and mutualistic interactions

Author

Johnson, Christopher

Publication Date

2013

UNIVERSITY OF CALIFORNIA

Los Angeles

How interplay between positive and negative feedback influences the persistence of consumer-resource and mutualistic interactions

A dissertation submitted in partial satisfaction of the requirements

for the Degree of Doctor of Philosophy in Biology

by

Christopher Johnson

2013

ABSTRACT OF THE DISSERTATION

How interplay between positive and negative feedback influences the persistence of consumer-resource and mutualistic interactions

By

Christopher Johnson
Doctor of Philosophy in Biology
University of California, Los Angeles, 2013
Professor Priyanga A. Amarasekare, Chair

Investigating the mechanisms by which species persist within complex ecological communities and in variable environments is critical for understanding how biodiversity is maintained in the face of perturbations in the biotic (e.g., invasive species) and abiotic (e.g., climate change) environment. Persistence arises from the interplay between species interactions (e.g., consumer-resource, mutualism, competition) and species' responses to environmental variability. My objectives are to investigate the mechanisms promoting the persistence of consumer-resource (e.g., predator-prey) and mutualistic (e.g., plant-pollinator) interactions and to understand how species respond to environmental variation. From a theoretical perspective, I develop conceptual frameworks to investigate how tension between stabilizing negative feedback and destabilizing positive feedback affects the persistence of (*i*) consumer-resource and (*ii*) mutualistic interactions. (*i*) The stability of consumer-resource interactions arises from the tension between within-species interactions inducing negative feedback (e.g., resource self-limitation due to intraspecific competition) and between-species interactions inducing positive feedback (e.g., consumer overcompensation due to saturating functional responses). I derive an empirically quantifiable metric that incorporates positive and negative feedback effects, and thus, the net effect of within- and between-species interactions on a focal species' per capita growth rate. (*ii*) Mutualistic interactions are characterized by positive feedback that should make them extinction prone. Yet, mutualisms are widespread and persistent in nature. Empirical data suggests that competition for the benefits given by mutualistic partners may induce negative feedback. I develop a theoretical framework that incorporates competition for benefits within mutualistic interactions and find that competition for benefits alone promotes the assembly and persistence of mutualistic communities. Finally, I use a combination of theoretical and empirical approaches to investigate the population dynamics of the bordered plant bug (*Largus californicus*), a Hemipteran herbivore inhabiting the California coastal sage scrub. I find that both temperature and resource variation interact with development-induced delays in the operation of negative feedback to drive the observed dynamics. These frameworks yield testable predictions about the mechanisms promoting the persistence of consumer-resource and mutualistic interactions and the dynamics of species inhabiting variable environments. The results illustrate how considering positive and negative feedback effects offer key insights into the mechanisms underlying the generation and maintenance of biodiversity.

The dissertation of Christopher Johnson is approved.

Stephen P. Hubbell

James O. Lloyd-Smith

Van Maurice Savage

Priyanga A. Amarasekare, Committee Chair

University of California, Los Angeles

2013

To my mom and dad and my sister Andrea,

for your love and support

in all of my endeavors

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ACKNOWLEDGMENTS

First and foremost, I thank my adviser Priyanga Amarasekare for her tireless efforts and guidance over the past five years. She has been very generous with financial support, which gave me the opportunity to attempt ambitious research projects that otherwise would have been impossible. When my research was stymied, Priyanga helped me find my footing and pushed me to improve. Over the past five years, we have met on almost a weekly basis to discuss my research and I greatly value all of her insights and guidance. She has taught me to think more critically and quantitatively, and has made me a better writer and speaker. By her example, Priyanga showed me how to be both a good theoretician and a good biologist.

I owe much to my dissertation committee. Steve Hubbell kindly shared valuable perspectives and new ideas from his wealth of knowledge about ecology. Jamie Lloyd-Smith was a constant source of encouragement and sage advice and kindly wrote many letters of reference for me. He and Priyanga offered me TA positions for the graduate ecology course and Jamie allowed me to give a guest lecture, both of which were invaluable experiences for learning how to communicate quantitative ideas to students. Of my committee members, I worked most closely with Van Savage. Van provided invaluable comments on my papers and kindly allowed me to use an automatic video system to study the bordered plant bugs and its parasitoids. I also thank his former postdocs Tony Dell and Samraat Pawar for helping me with the video system. Special thanks to Van for writing a letter of reference for me when he was suffering from a very nasty flu bug; it helped me obtain a great postdoctoral position.

Financial support for my research has come from the following sources: NSF grant DEB-0717350 and a Complex Systems Scholar Grant from the James S. McDonnell Foundation to Priyanga Amarasekare, the U.S. Department of Education Graduate Assistantship in Areas of

National Need (GAANN) Grant, and the Linda Scott Brown Fund and a Research Grant from the Department of Ecology and Evolutionary Biology. I am grateful to the Department of Ecology and Evolutionary Biology for providing me with GAANN Fellowships in 2008 and 2010 and two Quarter Fellowships in 2013, and the Department of Biomathematics for providing me with the National Institutes of Health Systems and Integrative Biology (SIB) Grant in 2009. I would also like to acknowledge Drs. Thomas Huggins and Philip Rundel for two quarters of Graduate Student Research support in 2012 for a project on milkvetch population dynamics in the Mojave. I am grateful to the Denver Zoological Society for grants in 2011-2012 for conservation work stemming from research not included in my dissertation. I thank Kate McCurdy (Sedgwick Reserve), Cristina Sandoval (Coal Oil Point Reserve), and Lisa Stratton (Main Campus Reserve) for permission to work at their reserves. Chapter two is a version of: Johnson, C., Amarasekare, P. 2013. Competition for benefits can promote the persistence of mutualistic interactions. *Journal of Theoretical Biology* **328**, 54-64. I acknowledge the Journal of Theoretical Biology for permission to reprint (license: 3197330201681). P. Amarasekare is a coauthor of all chapters.

My research on the bordered plant bug could not have been done without the tireless efforts of many dedicated undergraduates at UCLA. Thank you to my ‘plant bug crew’: Erin Berlin, Kim Dolphin, Johanna Heyer, Britney Kim, Alice Leung, Jamie Lou Sabellon, and Jamie Eng. A special thanks to Renato Coutinho, a visiting Ph.D. student from the Instituto de Física Teórica, Universidade Estadual Paulista, São Paulo, Brazil, for his help in developing the variable delay models. R. Coutinho, E. Berlin, K. Dolphin, J. Heyer, B. Kim, A. Leung, and J. L. Sabellon are coauthors of Chapter 3: Effects of temperature and resource variation on insect population dynamics: the bordered plant bug (*Largus californicus*) as a case study. Finally, thank you to my lab mates Kenichi Okamoto and Maggie Simon for their helpful comments, advice, and support.

There are several people who were particularly influential during my undergraduate career at the University of Arizona whom I would like to thank. Dr. Betty Pierazzo, Planetary Science Institute, gave me one of my first opportunities to do scientific research. Betty passed away in 2011 from a rare form of cancer – she is sorely missed. I thank Dr. Paddy Orr, University College Dublin, for taking a chance on a student who knew little about paleoecology (and my UREKA friends for the great times in Ireland!). I thank Dr. Andy Cohen, University of Arizona, for mentoring me during my senior thesis and giving a broke college student a job as lab manager.

My heartfelt appreciation goes out to all of my friends for their support and encouragement during my time at UCLA. There are far too many people to name, but I must especially thank my amazing cohort: Julia Barske, Abigail Curtis, Greer Dolby, J. P. Drury, Zac Harlow, Julie Himes, Jim Holmquist, Claire Narraway, Sergio Nigenda, Rena Schweizer, Stephanie Steele, Marisa Tellez, and Jeff Wolf. We made memories that will last a lifetime and I greatly cherish each of your friendships. In addition, a special thank you to Sarah Joy Bittick, and her dog Sierra, for their companionship and for cheering me up when my spirits were low. Outside of academia, I must thank my good friends Danny Nuñez and Caitlin Palmer for always being there for me.

Finally, I would not be who I am today without the love and support of my family, especially my mom and dad, and my sister Andrea. It was my dad who instilled in me a love for science and the natural world. My mom taught me to be myself while thinking of others. My parents are a constant source of compassion and reassurance. My little sister is my inspiration and my hero. I would also like to acknowledge my grandmother, and my grandfather who passed away in 2011 while I was in the field – I love you both and miss you grandpa! My family means the world to me and I thank them from the bottom of my heart for all that they have done for me.

"*Nothing exists for itself alone, but only in relation to other*[*s*]" – Charles Darwin

VITA

Previous Degrees

B. S. (Ecology and Evolutionary Biology)	University of Arizona

Awards and Fellowships

Undergraduate

2004-2008	University of Arizona Achievement Award
2004-2008	University of Arizona Spirit of Discovery Scholarship
2007	University of Arizona College of Science Dean's List
2007	UREKA Internship, University College Dublin

Graduate

2008, 2010	UCLA Graduate Assistantship in Areas of National Need (GAANN) Fellowship
2009	UCLA Dept. of Biomathematics Systems and Integrative Biology Training Grant
2010	UCLA Dept. of Ecology and Evolutionary Biology Schechtman Teaching Award

Postgraduate

2013-2015	Science Foundation Arizona Bisgrove Postdoctoral Grant, University of Arizona

Research Grants

2008, 2010	UCLA Graduate Assistantship in Areas of National Need (GAANN) Grant
2009	UCLA Dept. of Ecology and Evolutionary Biology Linda Scott Brown Fund
2011, 2012	Denver Zoological Society, Conservation Biology Department
2012	UCLA Dept. of Ecology and Evolutionary Biology Research Grant

Publications

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Johnson, C., Coutinho, R., Berlin, E., Dolphin, K., Heyer, J., Kim, B., Leung, A., Sabellon, J. L. and Amarasekare, P. 2013. Effects of temperature and resource variation on insect population dynamics: the bordered plant bug (*Largus californicus*) as a case study. (In Review)

Johnson, C. and Amarasekare, P. 2013. A conceptual framework for quantifying the tension between positive and negative feedback within consumer-resource interactions. (In Review)

Presentations

Johnson, C. and Amarasekare, P. 2011. Mutualistic interactions generate both stability and long-term persistence. 96th Ecological Society of America Conference. 2011. Austin, TX.

Johnson, C. and Amarasekare, P. 2012. Species Coexistence in a host-multiparasitoid community: the interplay between biotic and abiotic environmental variation. 97th Ecological Society of America Conference. 2012. Portland, OR.

Johnson, C. and Amarasekare, P. 2013. Tension between positive and negative feedback determines the dynamics and long-term persistence of consumer-resource interactions. 98th Ecological Society of America Conference. 2013. Minneapolis, MN.

CHAPTER 1

An empirically quantifiable metric for how the tension between positive and negative feedback affects the stability of consumer-resource interactions

Abstract

Consumer-resource interactions are prone to oscillations in species' abundances that increase extinction risk due to stochastic events during periods of low abundance. Oscillations arise due to time delays between consumption and consumer reproduction, which can be amplified by processes that generate positive feedback (e.g., consumer overcompensation) and/or suppressed by processes that generate negative feedback (e.g., resource self-limitation). A challenge is to quantify how the tension between positive and negative feedback affects the stability of consumer-resource interactions. Interaction strength (often measured by the per capita attack rate) is a common metric for quantifying destabilizing effects of consumers due to resource overexploitation. Interaction strength, however, does not consider nonlinear functional responses or resource self-limitation. We derive an empirically quantifiable metric that incorporates both positive and negative feedback processes, and hence, the net effect of both within- and between-species interactions on a focal species' per capita growth rate. We use non-dimensional consumer-resource equations to identify how parameters that induce positive and negative feedback group together and use these scaling relationships to define a new metric. The metric we derive provides a more comprehensive assessment of the stability of consumer-resource modules (pairwise and multi-species) than does interaction strength. This improvement is because our metric includes the joint effects of the per capita attack rate and handling time (quantifying positive feedback) and resource self-limitation (quantifying negative feedback), while interaction strength is based solely on the per capita attack rate. Our results highlight the importance of considering feedback processes to predict the stability of consumer-resource interactions.

Introduction

Consumer-resource interactions (e.g., predation, herbivory, parasitism) often exhibit oscillations in species' abundances. While oscillations can in some cases facilitate coexistence (Armstrong and McGehee, 1980; Benincà et al., 2008; Hsu et al., 1978; Huisman and Weissing, 1999), they predispose species to stochastic extinction during periods of low abundance (Christianou and Ebenman, 2005; Ebenman and Jonsson, 2005; Lande, 1993; Law and Morton, 1993). A key issue is to identify factors that amplify oscillations and mechanisms by which they are dampened or bounded. Oscillations arise from time delays between consumption and consumer reproduction. Consumers induce destabilizing positive feedback (e.g., via overcompensation due to saturating functional responses) that can lead to resource overexploitation and amplify oscillations. Within-species interactions (e.g., resource self-limitation due to intraspecific competition) may induce stabilizing negative feedback that can dampen oscillations. It is the tension between positive and negative feedback that determines the persistence of consumer-resource interactions.

Theory has focused on how interaction strength affects the stability of consumer-resource communities (e.g., Berlow, 1999; Berlow et al., 2004, 1999; Christianou and Ebenman, 2005; Emmerson and Yearsley, 2004; McCann et al., 1998; McCann, 2000; Neutel et al., 2002; Rip et al., 2010). While there are many metrics for quantifying interaction strength (reviewed by Berlow et al., 2004), a commonly used measure of interaction strength is the per capita attack rate. The advantage of using the per capita attack rate as a measure of interaction strength is that it considers consumer overexploitation of resources (leading to consumer-resource oscillations); however, the per capita attack rate alone does not capture important factors such as resource self-limitation (which dampens consumer-induced oscillations) or handling times (which determine the nonlinearity of the functional response).

Strong consumer-resource interactions (characterized by high per capita attack rates) can enhance oscillations by amplifying time delays between consumption and consumer reproduction (if consumers have saturating functional responses). This can predispose species to stochastic extinction during periods of low abundances. Conversely, weak consumer-resource interactions (characterized by low per capita attack rates) can inhibit strong consumer-resource interactions, reducing the tendency for oscillations and the potential for stochastic extinction (Berlow, 1999; Berlow et al., 2004, 1999; Christianou and Ebenman, 2005; Emmerson and Yearsley, 2004; McCann et al., 1998; McCann, 2000; Neutel et al., 2002; Rip et al., 2010). These ideas have formed a basis for studying diversity maintenance in complex communities (e.g., Berlow, 1999; Berlow et al., 2004, 1999; McCann, 2000; Rip et al., 2010). A few recent studies, however, have challenged these ideas, predicting that strong interactions are stabilizing because they increase consumer-resource coupling (Allesina and Pascual, 2008; Allesina and Tang, 2012). Thus, there is ambiguity about how interaction strength affects the stability of consumer-resource interactions.

Here we build on previous work by considering how negative feedback processes that arise from interactions within species (e.g., self-limitation due to intraspecific competition) interact with positive feedback processes resulting from consumers' effects on resources to determine the stability and persistence of consumer-resource interactions. Our objective here is to derive an empirically quantifiable metric that captures the tension between positive and negative feedback processes, and thus, incorporates the net effect of both within- and between-species interactions on a focal species' per capita growth rate. We conclude by showing how this metric can be quantified empirically and suggest future empirical directions to test model predictions. While the ideas we build on are well known, synthesizing them in a common framework better predicts the conditions for the stability and persistence of consumer-resource interactions.

Mathematical Framework

We begin by analyzing the pairwise consumer-resource interaction (Fig. 1-1a) as it constitutes the basic building block from which more complex communities are assembled. We then proceed to investigate how these direct effects are affected by indirect interactions within more complex community modules (e.g., tri-trophic food chain and exploitative competition; Fig. 1-1b,c).

Pairwise Interactions

We use the well-known Rosenzweig-MacArthur Model (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971) to illustrate how quantifying the tension between positive and negative feedback provides new insights into the stability of pairwise consumer-resource interactions. The dynamics are given by:

$$\frac{dR}{dt} = rR(1 - qR) - \frac{a_C RC}{1 + a_C h_C R} \qquad (1)$$

$$\frac{dC}{dt} = C\left(\frac{e_C a_C R}{1 + a_C h_C R} - d_C\right)$$

where R and C are, respectively, the abundances of the resource and consumer species; r is the resource's intrinsic growth rate; q quantifies intraspecific competition within the resource (the inverse of the carrying capacity); and a_C, e_C, h_C, and d_C are, respectively, the consumer's per capita attack rate, conversion efficiency, handling time, and per capita mortality rate. Negative feedback arises due to self-limitation, which can in theory operate at any trophic level (e.g., resource self-limitation, predator interference). In simple consumer-resource models, negative feedback operates only on the resource's per capita growth rate because consumers are expected to be limited by their resources. Negative feedback is quantified as the strength of intraspecific competition (q) for background resources (e.g., space, water, nutrients). The positive feedback effect can be seen in the way that the resource's growth rate changes with resource density:

$$\frac{\partial\left(\frac{dR}{dt}\right)}{\partial R} = r(1-2qR) - \frac{a_C C}{(1+a_C h_C R)^2} \qquad (2)$$

If the resource is rare ($R \rightarrow 0$), the negative term in Eq. 2 increases ($a_C C/(1+a_C h_C R)^2 \rightarrow a_C C$), and the resource's growth rate increases more slowly (if $r > a_C C$). Conversely, if the resource is abundant, the negative term in Eq. 2 decreases (as the $a_C h_C R$ term in its denominator increases), and the resource's growth rate increases more rapidly. Thus, the consumer overexploits the resource when it is rare and underexploits the resource when it is abundant. This is a signature of positive feedback. Note that as the per capita attack rate increases, the consumer overexploits the resource to a greater degree when it is rare. Furthermore, as the per capita attack rate and/or handling time increase, the functional response becomes more nonlinear, and thus, saturates more slowly. As a result, the consumer underexploits the resource to a greater degree when it is abundant. In both cases, the positive feedback effects on the resource's per capita growth rate are more pronounced, which amplifies oscillations. The important point is that it is the *saturation* of the functional response that induces positive feedback. Therefore, the strength of positive feedback is determined by both the per capita attack rate and handling time.

We non-dimensionalize Eq. 1 to identify the parameter groupings that illustrate the tension between positive and negative feedback. We use the following substitutions:

$$\hat{t} = rt, \qquad \hat{R} = qR, \qquad \hat{C} = \frac{qC}{e_C}, \qquad \hat{a}_C = \frac{e_C a_C}{rq}, \qquad \tau_C = \frac{a_C h_C}{q}, \qquad \hat{d}_C = \frac{d_C}{r} \qquad (3)$$

We substitute these non-dimensional quantities into Eq. 1 and omit the hats for convenience. The substitutions yield the non-dimensional pairwise interaction:

$$\frac{dR}{dt} = R(1-R) - \frac{a_C RC}{1+\tau_C R} \qquad (4)$$

$$\frac{dC}{dt} = C\left(\frac{a_C R}{1+\tau_C R} - d_C\right)$$

Note that τ_C scales the parameters inducing positive feedback (a_C, h_C) with that which induces negative feedback (q). This scaling provides a natural metric for quantifying the tension between the two types of feedback processes (hereafter, we refer to this scaling as the 'feedback metric', which is quantified by τ_i, where i is the species inducing positive feedback). For instance, if τ_C is high, the functional response is more nonlinear, leading to increased positive feedback effects on the resource's per capita growth rate relative to negative feedback due to resource self-limitation. Conversely, if τ_C is low, the functional response is more linear, and negative feedback due to resource self-limitation counteracts positive feedback due to the saturating functional response.

Tri-trophic food chain

The pairwise interaction cannot depict feedback due to indirect interactions; thus, we incorporate additional species within the pairwise interaction. The tri-trophic food chain (e.g., resource – consumer – predator; Fig. 1-1b) is a key community module (Stouffer and Bascompte, 2010) and can exhibit various dynamical behaviors, such as stable equilibria, limit cycles, or chaos (Hastings and Powell, 1991; McCann and Yodzis, 1994; McCann et al., 1998). For the tri-trophic food chain model, we use the substitutions in Eq. 3 and the following scaled quantities:

$$\hat{P} = \frac{qP}{e_P}, \qquad \hat{a}_P = \frac{e_P a_P}{rq}, \qquad \tau_P = \frac{e_C a_P h_P}{q}, \qquad \varepsilon = \frac{e_C}{e_P}, \qquad \hat{d}_P = \frac{d_P}{r} \qquad (5)$$

The substitutions (with hats dropped for convenience) yield the non-dimensional system:

$$\frac{dR}{dt} = R(1-R) - \frac{a_C RC}{1+\tau_C R} \qquad (6)$$

$$\frac{dC}{dt} = C\left(\frac{a_C R}{1+\tau_C R} - \frac{a_P C}{1+\tau_P C} - d_C\right)$$

$$\frac{dP}{dt} = P\left(\frac{\varepsilon a_P C}{1+\tau_P C} - d_P\right)$$

where P is the abundance of the predator; a_p, τ_p, and d_p are, respectively, the predator's per capita attack rate, handling time, and per capita mortality rate; ε is the ratio of the consumer conversion efficiency to that of the predator; and all other variables and parameters are the same as before. Positive feedback arises within the resource (via the consumer's saturating functional response) and the consumer (via the predator's saturating functional response). Note that τ_P scales the parameters that induce positive feedback (a_P, h_P) within the consumer's per capita growth rate with that which induces negative feedback in the resource's per capita growth rate (q). We use the tri-trophic foodweb to investigate how indirect top-down effects of the predator influence the stability of the pairwise interaction. Whether the predator has a stabilizing or destabilizing effect will depend on how the predator modifies the interaction between the consumer and resource.

Exploitative competition module

We investigate indirect non-trophic interactions by incorporating a second consumer species within the tri-trophic food chain that competes with the initial consumer for the shared resource. We use the substitutions defined above (Eqs. 3, 5), which yield the non-dimensional system:

$$\frac{dR}{dt} = R\left((1-R) - \frac{a_{C_1}C_1}{1+\tau_{C_1}R} - \frac{a_{C_2}C_2}{1+\tau_{C_2}R}\right) \qquad (7)$$

$$\frac{dC_1}{dt} = C_1\left(\frac{a_{C_1}R}{1+\tau_{C_1}R} - \frac{a_P P}{1+\tau_P C_1} - d_{C_1}\right)$$

$$\frac{dC_2}{dt} = C_2\left(\frac{a_{C_2}R}{1+\tau_{C_2}R} - d_{C_2}\right)$$

$$\frac{dP}{dt} = P\left(\frac{\varepsilon a_P C_1}{1+\tau_P C_1} - d_P\right)$$

where C_1 and C_2 are the abundances of the two consumer species and all other variables and parameters are given before (Eqs. 4, 5). Note that positive feedback arises within the resource (via both consumer species' saturating functional responses) and consumer 1 (via the predator's saturating functional response). Whether or not interspecific competition has a stabilizing effect depends on how consumer 2 alters the interactions within the tri-trophic food chain.

Results

Pairwise interaction

Our goal is to understand how positive and negative feedback processes affect the stability of consumer-resource interactions. Two conditions must be met for persistence. First, species must maintain positive abundances, which is given by the feasibility boundary. Second, the interior equilibrium must be stable to perturbations of species' abundances, which is given by the stability boundary (where a transition from a stable steady state to oscillatory dynamics occurs; (Murdoch et al., 2003). The pairwise interaction (Eq. 1) is stable (see App. A for derivation) if:

$$\frac{h_C d_C}{e_C - h_C d_C} < \frac{a_C h_C}{q} < \frac{e_C + h_C d_C}{e_C - h_C d_C} \qquad (8)$$

where the lower and upper conditions are, respectively, the feasibility and stability boundaries. We find that the parameters inducing positive and negative feedback defined in τ_C group together to give the conditions under which stable coexistence occurs (Eq. 8; Fig. 1-2a). Feasibility requires that the per capita attack rate (a_C) be high enough that the consumer acquires sufficient resources to maintain a positive abundance. Stability requires that resource self-limitation (q) is sufficiently strong that negative feedback exceeds positive feedback due to the saturating functional response (quantified by $a_C h_C$). Thus, while interaction strength (as defined here) only considers the effects of the per capita attack rate, the feedback metric derived here considers the joint effects of the per capita attack rate and handling time (which determine the nonlinearity of the functional response) relative to the negative feedback effect of resource self-limitation.

The feedback metric (quantified here by τ_C) also gives the regions of the phase-plane diagram in which stable dynamics occur. In the pairwise interaction, the resource isocline is a quadratic function, the maximum of which is the stability boundary that divides the phase-plane into regions of stability (i.e., point equilibria) and instability (i.e., limit cycles). The critical resource abundance (R_{crit}) at which this transition occurs (see App. A for derivation) is given by:

$$R_{crit} = \frac{\tau_C - 1}{2\tau_C} \qquad (9)$$

The sign of R_{crit} depends on whether τ_C is greater than or less than 1. If positive feedback exceeds negative feedback (i.e., $a_C h_C > q$), then $\tau_C > 1$, and $R_{crit} > 0$ such that the phase-plane includes a region of instability (whether a given interaction is unstable depends on if the consumer's zero growth isocline lies within this region). Conversely, if negative feedback exceeds positive feedback (i.e., $a_C h_C < q$), then $\tau_C < 1$, and $R_{crit} < 0$ such that all feasible interactions are always stable. Thus, the feedback metric provides insights into consumer-resource dynamics by giving the region of the phase-plane diagram in which stable versus unstable dynamics can occur.

Given that the feedback metric is defined by the parameter grouping in the scaled handling time (Eq. 3), we want to know how handling time affects the feasibility and stability boundaries of the non-dimensionalized interaction (Eq. 4; see App. A for derivation), which are given by:

$$d_C(\tau_C + 1) < a_C < \tau_C d_C \frac{(\tau_C + 1)}{(\tau_C - 1)} \qquad (10)$$

Note that this condition is similar to Eq. 8 for the un-scaled pairwise interaction (Eq. 1).

Previous theory often uses the per capita attack rate as a measure of interaction strength (see Berlow et al., 2004 for other measures). Yet, handling time, which is not incorporated within interaction strength, determines the range of per capita attack rates under which stability occurs. As handling time increases, the critical per capita attack rate at which the stability boundary occurs (i.e., $\tau_C d_C(\tau_C+1)/(\tau_C-1)$; Eq. 10) declines sharply (Fig. 1-2b). This is because handling time determines the nonlinearity of the functional response, and hence, the strength of positive feedback. When the handling time is high enough that positive feedback overrides negative feedback, the stability boundary is exceeded, and oscillations occur. Note that the stability boundary asymptotes when $\tau_C = 1$ (Fig. 1-2b), which is the critical value of τ_C that determines whether the stability boundary occurs at a positive resource abundance (i.e., $R_{crit} = 0$) in the phase-plane diagram (Eq. 9). The important point is that the per capita attack rate alone is not sufficient to predict the stability of consumer-resource interactions. It is necessary to consider the joint effects of the per capita attack rate and handling time (positive feedback) relative to the strength of resource self-limitation (negative feedback).

Tri-trophic food chain

The tri-trophic food chain (Fig. 1-1b) can exhibit different dynamical behaviors, such as stable equilibria, cycles, or chaos (Boer et al., 2001, 1999; Hastings and Powell, 1991; McCann and Yodzis, 1994; McCann et al., 1998; Rinaldi and De Feo, 1999). Here we investigate how positive and negative feedback (mediated by top-down effects of the predator) alter the stability of the tri-trophic food chain. We derive the stability boundary, focusing on the positive feedback effects of the consumer and predator relative to the strength of negative feedback within the resource (i.e., τ_C, τ_P). The stability boundary (see App. B for derivation) is approximated by:

$$\tau_C < \frac{\alpha - 4 d_C d_P a_P \tau_P}{\beta + \delta \tau_P} \qquad (11)$$

To illustrate the mathematical structure of the stability boundary, we use the functions α, β, and δ to encapsulate parameter-rich terms (see App. B for full equation).

The question we want to address is how stability is affected by interaction strength (a_C, a_P; Fig. 1-3a,b) versus the feedback metric (τ_C, τ_P; Fig. 1-3c,d). We first explore two cases: (*i*) when positive feedback is weak relative to negative feedback (mathematically: $\tau_C, \tau_P < 1$) and (*ii*) when positive feedback is strong relative to negative feedback (mathematically: $\tau_C, \tau_P > 1$). If positive feedback is weak relative to negative feedback, stability occurs over a wide range of per capita attack rates (Fig. 1-3a); hence, interaction strength has fairly little effect on stability in this case.

Conversely, if positive feedback is strong relative to negative feedback, stability occurs only if the consumer's per capita attack rate is fairly high (Fig. 1-3b). In this case, however, when the interaction is stable, the consumer is extremely rare, and thus, vulnerable to stochastic extinction. This is because it underexploits the abundant resource (due to positive feedback via its saturating functional response) *and* is overexploited by the predator (due to positive feedback via its saturating functional response). The key point is that the stability regions under interaction strength (Fig. 1-3a,b) depend strongly on the feedback metric; i.e., stability occurs over a wide range of interaction strengths if $\tau_C, \tau_P < 1$, but only when the consumer is very rare if $\tau_C, \tau_P > 1$.

We find that the feedback metric (quantified here by τ_C and τ_P) is a good predictor of the stability of the tri-trophic food chain because stability only occurs when τ_C and τ_P are fairly low (Fig. 1-3c,d); i.e., positive feedback induced by the saturating functional responses of the consumer and predator species are weak relative to negative feedback due to resource self-limitation. We find that τ_P has a particularly strong effect on stability because it determines the predator's ability to inhibit the consumer's per capita growth rate, and thus, reduce positive feedback within the resource's per capita growth rate (via the consumer's saturating functional response). Increasing species' per capita attack rates (a_C, a_P) increases the region where stability occurs (Fig. 1-3c vs. 1-3d). This is because high per capita attack rates suppress the abundance of both the resource and consumer, which inhibits the per capita growth rates of the consumer and predator, respectively. This in turn reduces positive feedback induced by the consumer and predator via their saturating functional responses. Taken together, these results suggest that focusing on feedback processes (e.g., the joint effects of the attack rate and handling time relative to the strength of resource self-limitation) provides a more comprehensive assessment of the stability of the tri-trophic food chain than does focusing on interaction strength alone.

Exploitative competition module

We use the exploitative competition module (Fig. 1-1c) to explore how non-trophic interactions (e.g., interspecific competition) alter the feedback processes within trophic consumer-resource interactions. We derive the feasibility and stability boundary, focusing on the strength of positive feedback induced by each consumer species relative to the strength of negative feedback within the resource (i.e., τ_{C_1}, τ_{C_2}). The feasibility boundary (see App. C for derivation) is given by:

$$\frac{(a_{C_2}-\tau_{C_2}d_{C_2})\left(a_{C_1}d_P(a_{C_2}-\tau_{C_2}d_{C_2})+\left(a_{C_2}-d_{C_2}(\tau_{C_2}+1)\right)(\tau_P d_P-\varepsilon a_P)\right)}{d_{C_2}\left(a_{C_2}-d_{C_2}(\tau_{C_2}+1)\right)(\varepsilon a_P-\tau_P d_P)} < \tau_{C_1} < \left(\frac{a_{C_1}}{d_{C_1}}-\frac{a_{C_2}}{d_{C_2}}\right)+\tau_{C_2} \qquad (12)$$

The stability boundary (see App. C for derivation) is given by:

$$\tau_{C_1} < \frac{1}{R^*}\left(1+\frac{{a_{C_1}}^{2/3}(R^*)^{1/3}}{\epsilon^{1/3}{a_P}^{2/3}(P^*)^{1/3}}\right) \qquad (13)$$

where R^* and P^* are, respectively, the resource and predator equilibrium.

The question we want to address is how stability is affected by the consumers' interaction strength (a_{C_1}, a_{C_2}; Fig. 1-4a,b) versus the tension between negative feedback and positive feedback induced by the consumer species (τ_{C_1}, τ_{C_2}; Fig. 1-4c,d). If positive feedback is weak relative to negative feedback (τ_{C_1}, $\tau_{C_2} < 1$; Fig. 1-4a), stability occurs over a wide range of per capita attack rates (within the feasibility boundaries). Thus, interaction strength has relatively little effect on stability in this case. Conversely, if positive feedback is strong relative to negative feedback (τ_{C_1}, $\tau_{C_2} > 1$; Fig. 1-4b), stability requires that consumer 2's per capita attack rate is extremely low (i.e., its interspecific competitive effect is very weak). In this case, however, when the interaction is stable, consumer 2's abundance is extremely low (and thus, vulnerable to stochastic extinction). This is because it underexploits the shared resource (due to positive feedback via its saturating functional response) *and* suffers strong interspecific competition from consumer 1. The key point is that, similar to the tri-trophic food chain, the stability regions under interaction strength (Fig. 1-4a,b) depend strongly on the feedback metric; i.e., stability occurs over a relatively wide range of interaction strengths if τ_{C_1}, τ_{C_2} < 1, but only when consumer 2 is very rare if τ_{C_1}, τ_{C_2} > 1.

We find that the feedback metric is a good predictor of the stability of the interspecific competition module because stability requires that τ_{C_1} and τ_{C_2} are relatively low (Fig. 1-4c,d); i.e., positive feedback induced by the consumers' saturating functional responses is weak relative to negative feedback due to resource self-limitation. This is because if the consumers' functional responses are highly nonlinear, they induce strong positive feedback within the shared resource's per capita growth rate. Stability occurs over a wider range of τ_{C_1} than τ_{C_2} because the predator inhibits its per capita growth rate. Increasing the consumer species' per capita attack rate (i.e., a_{C_1}, a_{C_2}) increases the region in which stability occurs (Fig. 1-4c vs. 1-4d). This is because high consumer per capita attack rates suppress the abundance of the resource, which inhibits the consumers' per capita growth rates, and thus, reduces positive feedback due to their saturating functional responses. These results illustrate how considering the effects of indirect interactions on the stability of consumer-resource interactions are captured by a metric that quantifies the relative strengths of negative and positive feedback in addition to interaction strength alone.

Discussion

The stability of consumer-resource interactions results from the tension between positive feedback (e.g., due to saturating functional responses) and negative feedback (e.g., due to resource self-limitation). A widely used measure of interaction strength is the per capita attack rate. Thus, interaction strength considers top-down effects of consumers, but not self-limitation within resources or indirect interactions that can reduce the strength of top-down effects. We build on previous work by considering how negative feedback processes that arise from interactions within species (e.g., self-limitation due to intra-specific competition) interact with the positive feedback effects of consumers (e.g., saturating functional responses) to determine the stability of consumer-resource interactions. We derive an empirically quantifiable metric that captures the tension between positive and negative feedback, and hence, the net effect of within- and between-species interactions on a focal species' per capita growth rate.

Three key results emerge from this framework. The first pertains to the pairwise interaction. We find that the parameters inducing positive and negative feedback group together to determine the conditions under which stable coexistence occurs (Eq. 8; Fig. 1-2a). While interaction strength only considers the effects of the per capita attack rate, the feedback metric derived here considers the joint effects of the per capita attack rate and handling time (which determine the nonlinearity of the functional response) relative to negative feedback due to resource self-limitation. We then investigate feedback induced by indirect interactions within multi-species consumer-resource modules. The second result pertains to top-down effects within the tri-trophic food chain. Stability requires that τ_C and τ_P are relatively low (Fig. 1-3) such that positive feedback induced by the saturating functional responses of the consumer and predator are weak relative to negative feedback due to resource self-limitation. The third result pertains to community modules with both consumer-resource and competitive interactions. Stability requires that the handling time of the additional consumer (τ_{C_2}) be relatively low (Fig. 1-4c,d) because as its handling time increases, it induces stronger positive feedback within the shared resource, driving oscillations within both consumer species. The overarching result of this study is that focusing on the tension between positive and negative feedback (including feedback arising from indirect interactions) provides a more comprehensive metric for determining the stability of consumer-resource interactions than does considering interaction strength alone.

We present two empirical case studies as illustrative examples for how the theoretical framework developed here can be integrated with empirical systems. (*i*) We derive a metric for quantifying the tension between positive feedback induced by consumers' saturating functional responses (top-down effect) and negative feedback induced by resource self-limitation (bottom-up effect) on species' per capita growth rates. Empirical work could test model predictions by quantifying the relative strength of top-down and bottom-up effects within natural community modules (see review by Walker and Jones, 2001). For example, Schmitz (1993) manipulated nutrient input (bottom-up) and spider density (top-down) within a natural tri-trophic food chain (grass - grasshopper - wolf spider) and found that grasshopper abundance is regulated by strong bottom-up processes (resource limitation) relative to top-down effects (grasshopper handling time and spider density). These results are consistent with our model prediction that τ_C is low in stable interactions (i.e., negative feedback generated by bottom-up processes exceeds positive feedback induced by top-down processes). (*ii*) We use our theoretical framework to investigate how indirect feedback due to top-down effects and/or non-trophic interactions (e.g., interspecific competition) can modify direct feedback processes to determine the stability of community modules. The role of indirect effects on natural communities is an area of intense interest in ecology (see reviews by Borrett et al., 2010; Salas and Borrett, 2011). As an illustrative example of how the theoretical framework developed here could be integrated with an empirical study system, consider a community consisting of 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* (Frank van Veen et al., 2005). Note that this community represents the exploitative competition module. *A. 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*; yet, the full community exhibits stable dynamics (Frank van Veen et al., 2005). Coexistence occurs because parasitoid attack on *A. pisum* facilitates the persistence of *M. viciae*, while *M. viciae* stabilizes the *A. pisum* – *A. ervi* interaction by inhibiting the per capita attack rate of the parasitoid on *A. pisum* by reducing the parasitoid's search efficiency (Frank van Veen et al., 2005). Such empirical study systems could be used to test model predictions about how indirect interactions (e.g., interspecific competition between *A. pisum* and *M. viciae*: τ_{C_1}, τ_{C_2}; top-down effects of *A. ervi* on *A. pisum*: τ_P, τ_C) modulate the tension between positive and negative feedback processes to determine the stability of consumer-resource communities.

This study provides a conceptual framework for investigating the joint roles of bottom-up and top-down processes on species' per capita growth rates and provides a new metric that considers how the tension between positive and negative feedback influences the stability of consumer-resource interactions. The framework explicitly considers how indirect interactions (e.g., top-down effects of predators and non-trophic interspecific competition) modulate direct feedback processes. By incorporating the net effect of within- and between-species interactions on species' per capita growth rates, this metric provides a mechanistic way to investigate the stability and persistence of consumer-resource interactions.

Acknowledgments

We thank James Lloyd-Smith, Stephen Hubbell, and Van Savage for helpful comments that substantially improved the manuscript. This research was supported by NSF grant DEB-0717350 and a Complex Systems Scholar Grant from the James S. McDonnell Foundation to P.A.

Figures

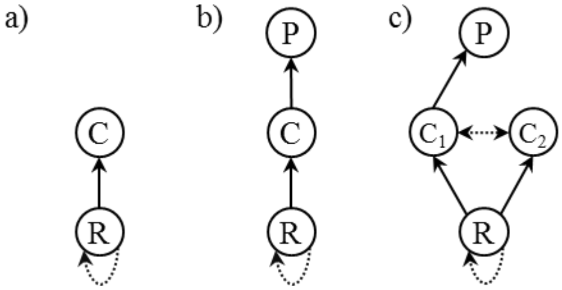

Figure 1-1. Schematics of the community modules: (panel a) pairwise interaction; (panel b) tri-trophic food chain; (panel c) exploitative competition: R is the resource, C_i are the consumer species (i = 1, 2), and P is the predator. Solid arrows indicate consumer-resource interactions, dashed lines with single-arrows indicate intraspecific competition, and dashed lines with double-arrows indicate interspecific competition.

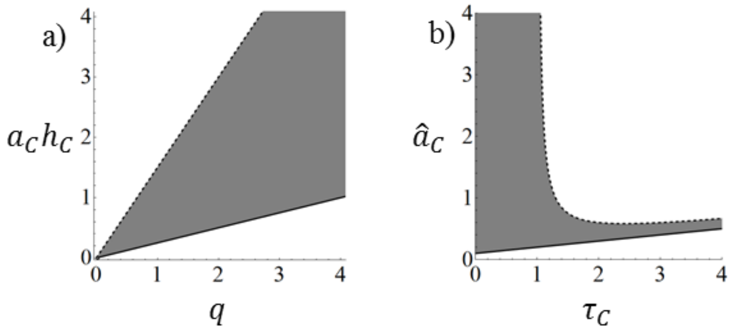

Figure 1-2. Parameter space diagrams for the pairwise consumer-resource interaction. Stable coexistence occurs within the gray regions; solid lines depict the feasibility boundary beyond which the consumer goes extinct; and dashed lines depict the stability boundary beyond which oscillations occur (see App. A). (Panel a) The parameters that induce positive and negative feedback group together to predict the conditions under which stable coexistence occurs. Stability requires that resource self-limitation (q) be sufficiently strong such that negative feedback counteracts positive feedback due to the saturating functional response (given by $a_C h_C$). (Panel b) Handling time, which is not incorporated within interaction strength, determines the range of the per capita attack rate under which stability occurs because the parameters jointly determine the nonlinearity of the functional response, and hence, the strength of positive feedback. Other parameters: $r = e_C = 1$, $h_C = 2$, $d_C = 0.1$.

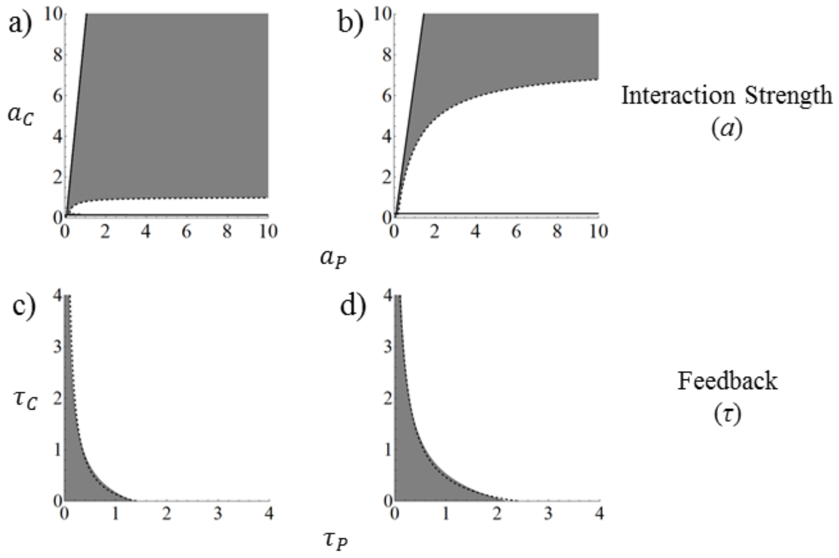

Figure 1-3. Parameter space diagrams for the tri-trophic food chain. Stable coexistence occurs within the gray regions, above which the predator goes extinct. Dashed lines indicate the stability boundary beyond which oscillations occur (see App. B). Panels (a,b) are for interaction strength: a) $\tau_C = \tau_P = 0.5$; b) $\tau_C = \tau_P = 1.2$. Panels (c,d) are for the feedback metric: c) $a_C = a_P = 1$; d) $a_C = a_P = 2$. While stability occurs over a wide range of interaction strengths (panels a,b), stability arises only if positive feedback is relatively weak compared to the strength of negative feedback (panels c,d). Other parameters: $\varepsilon = 1$, $d_C = d_P = 0.1$.

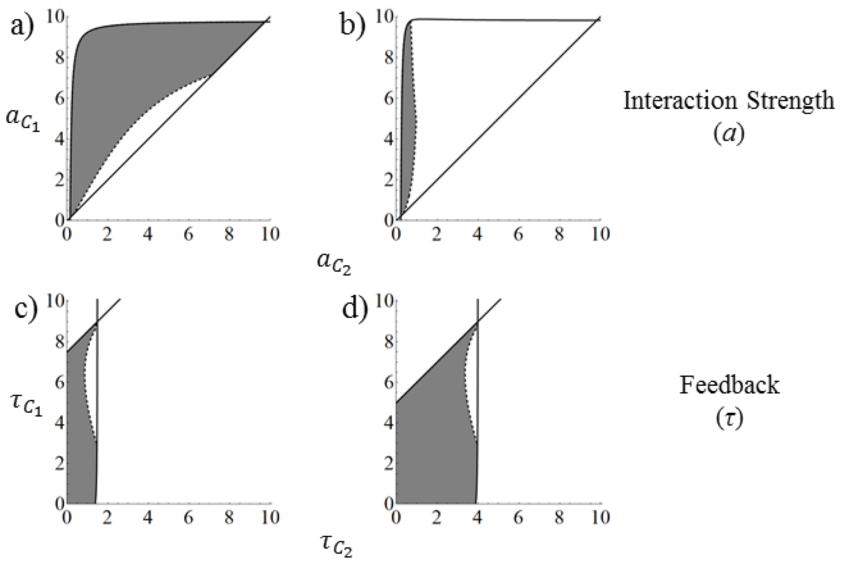

Figure 1-4. Parameter space diagrams for the exploitative competition module. Stable coexistence occurs within the gray regions and the dashed lines denote the stability boundary beyond which oscillations occur (see App. C). Panels (a,b) are for interaction strength: a) $\tau_{C_1} = \tau_{C_2} = 0.5$; b) $\tau_{C_1} = \tau_{C_2} = 1.2$. Panels (c,d) are for the feedback metric: c) $a_{C_1} = 1$, $a_{C_2} = 0.25$; d) $a_{C_1} = 1$, $a_{C_2} = 0.5$. In panels (a,b), consumer 2 goes extinct above the black curves, while consumer 1 and the predator go extinct beyond the black lines. In panels (c,d), consumer 1 and the predator go extinct above the upper black lines, while consumer 2 goes extinct beyond the vertical black lines. There are two key points. First, stability occurs over a fairly wide range of interaction strengths if positive feedback is relatively weak (i.e., $\tau_i < 1$; panel a), but requires that a_{C_2} is very small if positive feedback is somewhat strong (i.e., $\tau_i > 1$; panel b). Second, stability requires that τ_{C_1} and τ_{C_2} are relatively low (panels c,d); that is, positive feedback induced by the consumers' saturating functional responses is weak relative to negative feedback via resource self-limitation. Other parameters: $a_P = 1$, $\varepsilon = 1$, $d_{C_1} = d_{C_2} = d_P = 0.1$.

Supporting Information

Appendix A: *Pairwise consumer-resource interaction*

A.1 Equilibria

The un-scaled pairwise model (Eq. 1) yields three equilibria: the trivial equilibrium ($R^* = 0$, $C^* = 0$), a boundary equilibrium ($R^* = 1/q$, $C^* = 0$), and an interior equilibrium:

$$\left(R^* = \frac{d_C}{a_C(e_C - h_C d_C)}, C^* = \frac{r e_C(a_C(e_C - h_C d_C) - q d_C)}{a_C{}^2 (e_C - h_C d_C)^2}\right) \qquad \text{(A.1)}$$

The non-dimensionalized pairwise model (Eq. 4) yields three equilibria: the trivial equilibrium ($R^* = 0$, $C^* = 0$), a boundary equilibrium ($R^* = 1$, $C^* = 0$), and an interior equilibrium:

$$\left(R^* = \frac{d_C}{a_C - \tau_C d_C}, C^* = \frac{a_C - d_C(\tau_C + 1)}{(a_C - \tau_C d_C)^2}\right) \qquad \text{(A.2)}$$

A.2 Feasibility Boundary

Feasibility requires that both species increase in abundance when initially rare and the other species is at its equilibrium. In the un-scaled pairwise interaction (Eq. 1), when the resource is rare ($R \approx 0$), then $C^* = 0$ and the resource can increase in abundance when:

$$\frac{1}{R}\frac{dR}{dt} = r(1 - qR^*) - \frac{a_C C^*}{1 + a_C h_C R^*} = r > 0 \qquad \text{(A.3)}$$

When the consumer is rare (i.e., $C \approx 0$), then $R^* = 1/q$ and the consumer can increase when:

$$\frac{1}{C}\frac{dC}{dt} = \frac{e_C a_C R^*}{1 + a_C h_C R^*} - d_C = \frac{e_C a_C - d_C(q + a_C h_C)}{q + a_C h_C} > 0 \qquad \text{(A.4)}$$

Rearranging terms yields the consumer invasion criterion (Eq. 8) reported in section 3.1:

$$\frac{h_C d_C}{e_C - h_C d_C} < \frac{a_C h_C}{q} \qquad \text{(A.5)}$$

In the non-dimensionalized interaction (Eq. 4), the resource can always increase when rare:

$$\frac{1}{R}\frac{dR}{dt} = (1 - R^*) - \frac{a_C C^*}{1 + \tau_C R^*} = 1 > 0 \qquad \text{(A.6)}$$

When the consumer is rare (i.e., $C \approx 0$), then $R^* = 1$ and the consumer can increase when:

$$\frac{1}{C}\frac{dC}{dt} = \frac{a_C C^*}{1+\tau_C R^*} - d_C = \frac{a_C}{1+\tau_C} - d_C > 0 \qquad \text{(A.7)}$$

Rearranging terms yields the consumer invasion criterion (Eq. 10) reported in section 3.1:

$$d_C(1+\tau_C) < a_C \qquad \text{(A.8)}$$

A.3 Local Stability Analysis

The Jacobian matrix of Eq. 1 and Eq. 4 are, respectively, given by:

$$J = \begin{bmatrix} -rqR^* + \frac{a_C{}^2 h_C R^* C^*}{(1+a_C h_C R^*)^2} & -\frac{a_C R^*}{1+a_C h_C R^*} \\ \frac{e_C a_C C^*}{(1+a_C h_C R^*)^2} & 0 \end{bmatrix} \qquad \text{(A.9)}$$

$$J = \begin{bmatrix} -R^* + \frac{a_C \tau_C R^* C^*}{(1+\tau_C R^*)^2} & -\frac{a_C R^*}{1+\tau_C R^*} \\ \frac{a_C C^*}{(1+\tau_C R^*)^2} & 0 \end{bmatrix} \qquad \text{(A.10)}$$

To evaluate the stability of the interior equilibria, it is necessary to show that $A_1 = -Tr(J) > 0$ and $A_2 = Det(J) > 0$ (Routh-Hurwitz Criteria). Note that $A_1 = -J_{11}$ and $A_2 = -J_{12}J_{21}$ (because $J_{22} = 0$) and that A_2 is always positive because J_{12} is always negative and J_{21} is always positive. Thus, a sufficient condition for stability is $A_1 = -J_{11} > 0$.

A.4 Stability Boundary

A complex root with a zero real part ($\lambda = i\omega$) indicates a transition from damped oscillations to growing oscillations (Gurney and Nisbet 1998). Substituting this form into the characteristic equation and setting the imaginary parts to zero yields the stability boundary. For the pairwise interaction, the stability boundary is given by: $A_1 = 0$ (Murdoch et al., 2003). For the un-scaled interaction (Eq. 1), evaluating A_1 at the interior equilibrium yields the condition:

$$\frac{rd_C\left(qe_C-h_C(a_C(e_C-h_Cd_C)-qd_C)\right)}{e_Ca_C(e_C-h_Cd_C)} > 0 \qquad \text{(A.11)}$$

Rearranging terms and simplifying yields the stability boundary (Eq. 8) reported in section 3.1:

$$\frac{a_Ct_C}{q} < \frac{e_C+h_Cd_C}{e_C-h_Cd_C} \qquad \text{(A.12)}$$

For the non-dimensionalized interaction (Eq. 4), this condition is:

$$\frac{d_C\left(\tau_Cd_C(\tau_C+1)-a_C(\tau_C-1)\right)}{a_C(a_C-\tau_Cd_C)} > 0 \qquad \text{(A.13)}$$

Rearranging terms and simplifying yields the stability boundary (Eq. 10) reported in section 3.1:

$$a_C < \tau_Cd_C\frac{(\tau_C+1)}{(\tau_C-1)} \qquad \text{(A.14)}$$

A.5 Onset of oscillations

In the Rosenzweig-MacArthur Model, the resource isocline is a quadratic function, the maximum of which divides the parameter space into stable and unstable regions. This critical point is where the stability boundary occurs. We derive this critical point in Eqs. 1, 4 by differentiating the resource isocline with respect to *R*, setting it equal to zero, and solving for *R*:

$$R = \frac{a_Ch_C-q}{2a_Ch_Cq} \qquad \text{(A.15)}$$

Substituting R^* (Eq. A.1) and rearranging shows that this point lies on the stability boundary:

$$\frac{a_Ch_C}{q} = \frac{e_C+h_Cd_C}{e_C-h_Cd_C} \qquad \text{(A.16)}$$

For the non-dimensionalized model (Eq. 3), this critical point yields Eq. 9 in section 3.1:

$$R = \frac{\tau_C-1}{2\tau_C} \qquad \text{(A.17)}$$

Substituting R^* (Eq. A.2) and rearranging shows that this point lies on the stability boundary:

$$a_C = \tau_Cd_C\frac{(\tau_C+1)}{(\tau_C-1)} \qquad \text{(A.18)}$$

Appendix B: *Tri-trophic food chain*

B.1 Equilibria

The non-dimensionalized tri-trophic food chain (Eq. 5) yields four biologically-relevant equilibria: the trivial equilibrium ($R^* = 0$, $C^* = 0$, $P^* = 0$), the resource equilibrium ($R^* = 1/q$, $C^* = 0$, $P^* = 0$), the pairwise equilibrium (Eq. A.1), and an interior equilibrium:

$$\left(R^* = \frac{\varepsilon a_P(\tau_C-1)-\tau_P d_P(\tau_C+1)+\sqrt{\gamma}}{2h_C(\varepsilon a_P-\tau_P d_P)}, C^* = \frac{d_P}{\varepsilon a_P-\tau_P d_P}, P^* = \frac{\varepsilon\left((\tau_P d_P-\varepsilon a_P)(\tau_C+1)+2\tau_C d_P(a_C-\tau_C d_C)+\sqrt{\gamma}\right)}{2{\tau_C}^2 d_P(\varepsilon a_P-\tau_P d_P)}\right)$$

Where $\gamma = (\tau_P d_P - \varepsilon a_P)(4a_C\tau_C d_P + (\tau_C + 1)^2(\tau_P d_P - \varepsilon a_P))$

(B.1)

B.2 Feasibility Boundary

Note that the resource can always invade (see App. A) and the consumer's invasion criterion is given by Eq. A.7. The predator can increase in abundance when rare provided that:

$$\frac{1}{P}\frac{dP}{dt} = \frac{\varepsilon a_P C^*}{1+\tau_P C^*} - d_P = \frac{\epsilon a_P\left(a_C-d_C(\tau_C+1)\right)}{{a_C}^2+a_C(\tau_P-2\tau_C d_C)+d_C\left({\tau_C}^2 d_C-\tau_P(\tau_C+1)\right)} - d_P > 0 \qquad \text{(B.2)}$$

B.3 Local Stability Analysis

The Jacobian matrix of Eq. 5 is given by:

$$J = \begin{bmatrix} -R^* + \frac{a_C\tau_C R^* C^*}{(1+\tau_C R^*)^2} & -\frac{a_C R^*}{1+\tau_C R^*} & 0 \\ \frac{a_C C^*}{(1+\tau_C R^*)^2} & \frac{a_P\tau_P C^* P^*}{(1+\tau_P C^*)^2} & -\frac{a_P C^*}{1+\tau_P C^*} \\ 0 & \frac{\epsilon a_P P^*}{(1+\tau_P C^*)^2} & 0 \end{bmatrix} \qquad \text{(B.3)}$$

The tri-trophic food chain is stable provided that $A_1 = -\mathrm{Tr}(J) > 0$, $A_3 = -\mathrm{Det}(J) > 0$, and $A_1A_2 - A_3 > 0$ where $A_1 = -(J_{11} + J_{22})$, and $A_2 = -J_{12}J_{21} - J_{23}J_{32} + J_{11}J_{22}$, $A_3 = J_{11}J_{23}J_{32}$ (Routh–Hurwitz Criteria). Note that showing that $J_{11} < 0$ and $|J_{11}| > J_{22}$ proves that $A_1 > 0$

(because $J_{22} > 0$) and $A_3 > 0$ (because $J_{23}J_{32} < 0$). Stability requires that negative feedback within the resource exceeds (*i*) positive feedback induced by the consumer within the resource ($J_{11} < 0$) and (*ii*) positive feedback induced by the predator within the consumer ($|J_{11}| > J_{22}$).

B.4 Stability Boundary

Our goal is to derive the critical consumer handling time (τ_C) at which the stability boundary (given by $A_1A_2 - A_3 = 0$) occurs as illustrated in Fig. 1-3. While it is possible to derive an analytical solution for the stability boundary, it is sufficiently complex to render further analyses intractable. Thus, we fit a nonlinear function to the stability boundary plotted on the τ_P vs. τ_C parameter space plot (see Fig. 1-3). This yields the condition (Eq. 11) reported in section 3.2:

$$\tau_C < \frac{\alpha - 4d_C d_P a_P \tau_P}{\beta + \delta\tau_P} \qquad \text{(B.4)}$$

where $\alpha = 4d_C d_P({a_C}^2(2 + a_P) + a_C(4 + 2a_P + {a_P}^2)d_C + 4a_P d_P)$, $\beta = 2(a_C - 1)(4 + a_C(2 + a_P)){d_C}^2$, and $\delta = (a_P + 2(1 - a_C + a_P)d_P)$.

Appendix C: *Exploitative competition module*

C.1 Equilibria

The non-dimensionalized exploitative competition module (Eq. 6) has six biologically-relevant equilibria: the trivial equilibrium, resource equilibrium ($R^* = 1/q$), *R – C₁* and *R – C₂* equilibria (Eq. A.1; $C = C_1, C_2$), tri-trophic equilibrium (*R – C₁ – P*; Eq. B.1), and an interior equilibrium:

$$\left(R^* = \frac{d_{C_2}}{\rho}, {C_1}^* = \frac{d_P}{\varepsilon a_P - \tau_P d_P}, {C_2}^* = \frac{\varepsilon a_P \varphi_2\left(a_{C_2} - d_{C_2}(1+\tau_{C_2})\right) - a_{C_1} d_P \rho^2}{\varepsilon a_P \varphi_2 \rho^2}, P^* = \frac{d_{C_2}\varphi_1 - a_{C_2} d_{C_1}}{a_P \varphi_2}\right) \quad \text{(C.1)}$$

where $\varphi_i = a_{C_i} + d_{C_i}\left(\tau_{C_j} - \tau_{C_i}\right)$ and $\rho = a_{C_2} - \tau_{C_2} d_{C_2}$.

C.2 Feasibility Boundary

The resource can always invade (see App. A). Consumer 1 can invade the *R – C₂* interaction if:

$$\frac{1}{C_1}\frac{dC_1}{dt} = \frac{a_{C_1}R^*}{1+\tau_{C_1}R^*} - \frac{a_P P^*}{1+\tau_P {C_1}^*} - d_{C_1} = \frac{d_{C_2}\left(a_{C_1} + d_{C_1}(\tau_{C_2} - \tau_{C_1})\right) - a_{C_2} d_{C_1}}{a_{C_2} + d_{C_2}(\tau_{C_1} - \tau_{C_2})} > 0 \quad \text{(C.2)}$$

Consumer 2 can invade the *R – C₁ – P* tri-trophic interaction if:

$$\frac{1}{C_2}\frac{dC_2}{dt} = \frac{a_{C_2}R^*}{1+\tau_{C_2}R^*} - d_{C_2} = \frac{a_{C_2}\left(\tau_P d_P(1-\tau_{C_1}) + \varepsilon a_P(\tau_{C_1}-1)\right) + \sqrt{\gamma}}{\tau_P d_P\left(\tau_{C_2} - \tau_{C_1}(\tau_{C_2}+2)\right) + \varepsilon a_P\left(2\tau_{C_1} + \tau_{C_2}(\tau_{C_1}-1)\right) + \tau_{C_2}\sqrt{\gamma}} - d_{C_2} > 0$$

where $\gamma = (\tau_P d_P - \varepsilon a_P)(4 a_{C_1}\tau_{C_1} d_P + \left(\tau_{C_1} + 1\right)^2(\tau_P d_P - \varepsilon a_P))$

(C.3)

Solving Eqs. C.2, C.3. for τ_{C_1} yields the invasion criterion (Eq. 12) reported in section 3.3:

$$\frac{(a_{C_2} - \tau_{C_2} d_{C_2})\left(a_{C_1} d_P(a_{C_2} - \tau_{C_2} d_{C_2}) + \left(a_{C_2} - d_{C_2}(\tau_{C_2}+1)\right)(\tau_P d_P - \varepsilon a_P)\right)}{d_{C_2}\left(a_{C_2} - d_{C_2}(\tau_{C_2}+1)\right)(\varepsilon a_P - \tau_P d_P)} < \tau_{C_1} < \left(\frac{a_{C_1}}{d_{C_1}} - \frac{a_{C_2}}{d_{C_2}}\right) + \tau_{C_2} \quad \text{(C.4)}$$

Note that the predator can invade the *R – C₁* pairwise interaction if Eq. B.2 (see App. B) holds.

C.3 Local Stability Analysis

The Jacobian matrix of Eq. 6 is given by:

$$J = \begin{bmatrix} -R^* + \frac{a_{C_1}\tau_{C_1}R^*{C_1}^*}{\left(1+\tau_{C_1}R^*\right)^2} + \frac{a_{C_2}\tau_{C_2}R^*{C_2}^*}{\left(1+\tau_{C_2}R^*\right)^2} & -\frac{a_{C_1}R^*}{1+\tau_{C_1}R^*} & -\frac{a_{C_2}R^*}{1+\tau_{C_2}R^*} & 0 \\ \frac{a_{C_1}{C_1}^*}{\left(1+\tau_{C_1}R^*\right)^2} & \frac{a_P\tau_P{C_1}^*P^*}{(1+\tau_P{C_1}^*)^2} & 0 & -\frac{a_P{C_1}^*}{1+\tau_P{C_1}^*} \\ \frac{a_{C_2}{C_2}^*}{\left(1+\tau_{C_2}R^*\right)^2} & 0 & 0 & 0 \\ 0 & \frac{\epsilon a_P P^*}{(1+\tau_P{C_1}^*)^2} & 0 & 0 \end{bmatrix} \qquad \text{(C.5)}$$

A four-species module is stable provided that: $A_1 > 0$, $A_3 > 0$, $A_4 > 0$, $A_2A_3 - A_1A_4 > 0$, and $A_1A_2A_3 - {A_3}^2 - {A_1}^2A_4 > 0$ where $A_1 = -(J_{11} + J_{22})$, $A_2 = -J_{12}J_{21} - J_{13}J_{31} - J_{24}J_{42} + J_{11}J_{22}$, $A_3 = J_{22}J_{13}J_{31} - J_{11}J_{24}J_{42}$, and $A_4 = J_{13}J_{31}J_{24}J_{42}$ (Routh–Hurwitz Criteria). While it is possible to derive an analytical solution for these conditions, they are sufficiently complex to render further analyses intractable. We therefore make the simplifying assumption that $\tau_P \approx 0$ such that $J_{22} \approx 0$. Under this assumption: $A_1 = -J_{11}$, $A_2 = -J_{12}J_{21} - J_{13}J_{31} - J_{24}J_{42}$, $A_3 = -J_{11}J_{24}J_{42}$, and $A_4 = J_{13}J_{31}J_{24}J_{42}$. Note that showing that $J_{11} < 0$ proves that $A_1 > 0$, $A_3 > 0$ (because $J_{24}J_{42} < 0$), and $A_4 > 0$ (because $J_{13}J_{31} < 0$ and $J_{24}J_{42} < 0$). Furthermore, we find that ${A_3}^2 \approx 0$ (because J_{24} and J_{42} are both relatively small, and thus, A_3 is small and ${A_3}^2$ is very small); thus, $A_1A_2A_3 - {A_3}^2 - {A_1}^2A_4 \approx A_1(A_2A_3 - A_1A_4)$. Thus, for the exploitative competition module to be stable, it is sufficient to show that $J_{11} < 0$ and $A_2A_3 - A_1A_4 > 0$ (i.e., the stability boundary).

C.4 Stability Boundary

We solve the equation $A_2A_3 - A_1A_4 = 0$ in terms of consumer 1's handling time (τ_{C_1}), which yields the stability boundary (Eq. 13) reported in section 3.3:

$$\tau_{C_1} < \frac{1}{R^*}\left(1 + \frac{{a_{C_1}}^{2/3}(R^*)^{1/3}}{\epsilon^{1/3}{a_P}^{2/3}(P^*)^{1/3}}\right) \qquad \text{(C.6)}$$

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CHAPTER 2

Competition for benefits can promote the persistence of mutualistic interactions

Abstract

Mutualistic interactions are characterized by positive feedback that should cause interacting species to go extinct when rare. However, data show mutualistic interactions to be common and persistent. Previous theory predicts persistence provided that mutualistic species are regulated by factors external to the mutualistic interaction (e.g., limiting background resources). Empirical data suggest that competition for the benefits provided by mutualistic partners could be a source of negative feedback that allows for population regulation, but there is little, if any, theoretical exploration of this mechanism. Here we develop mathematical models to investigate whether competition for benefits *alone* can allow the persistence of obligate mutualistic interactions. We consider the role of trade-offs in persistence, specifically, trade-offs between benefits acquired versus given and between competition for access to partners (competitive ability) and benefit acquisition. We find that competition for benefits alone is sufficient to promote the persistence of pairwise interactions and the assembly of a three-species community module from an initially pairwise interaction. We find that a trade-off between benefits acquired versus given reduces opportunities for cheating (i.e., a species that acquires significantly more benefits than it gives drives its partner extinct), while a trade-off between competitive ability and benefit acquisition facilitates persistence when it is weak, but constrains persistence when it is strong. If both trade-offs operate simultaneously, persistence requires each species acquire sufficient benefits to avoid being cheated by its partners, but not so much that it loses its competitive ability. The key finding is competition for benefits is a biologically-realistic mechanism for the persistence of mutualistic interactions and the assembly of complex modules from initially pairwise interactions.

Introduction

Mutualistic interactions are characterized by positive density-dependence (i.e., species' per capita growth rates decline with decreasing abundance), which should increase their risk of extinction and cause them to be quite rare in nature. Empirical data, however, suggest otherwise. Mutualisms are ubiquitous in nature, and many mutualistic interactions exhibit long-term persistence (Boucher *et al.*, 1982, Bawa, 1990, Bronstein, 1994, Jordano, 2000 and Bascompte and Jordano, 2007). This represents a paradox: long-term persistence suggests that negative density-dependent mechanisms, which cause the per capita growth rate to increase with decreasing abundance, are counteracting the positive density-dependent mechanisms that cause species to go extinct when rare. The challenge for theory has been to identify the sources of negative density-dependence that ensure long-term persistence. In previous models that do not consider stochasticity or spatial dynamics, negative density-dependence is incorporated via a self-limitation term that is independent of the mutualistic interaction, which is considered to arise from intra-specific competition for limiting background resources (e.g., nutrients, water, nest-sites, etc.) causing density-dependent mortality (Gauss and Witt, 1935, May, 1973, Vandermeer and Boucher, 1978, Goh, 1979, Travis and Post, 1979, Heithaus *et al.*, 1980, Addicott, 1981, Soberon and Martinez del Rio, 1981, Gilpin *et al.*, 1982, Wells, 1983, Wolin and Lawlor, 1984, Wolin, 1985, Pierce and Young, 1986, Wright, 1989, Hernandez, 1998, Ferrière *et al.*, 2002, 2007, Holland *et al.*, 2002, Bronstein *et al.*, 2004, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine 2010, Fishman and Hadany, 2010, Lee and Inouye, 2010, 2011, Wang and Wu, 2011 and Wang *et al.* 2012). Henceforth, we will refer to this source of negative density-dependence as intra-specific competition for background resources. In these models, therefore, the source of negative density-dependence (competition for background resources) is decoupled from the source of positive density-dependency (mutualism). As such, the theory is built on the assumption that population regulation occurs independently of the mutualistic interaction itself.

There is widespread empirical evidence that individuals compete for the benefits provided by mutualistic partners (see reviews by Addicott, 1985, Palmer *et al.*, 2003 and Mitchell *et al.*, 2009). Yet, very few studies have investigated whether competition for benefits *alone* can provide the negative density-dependence necessary for persistence (Jones *et al.*, 2012). Nearly all the studies that consider competition for benefits also include a density-dependent mortality term attributed to competition for background resources. This makes it is difficult to disentangle the role of competition for benefits in promoting persistence from that of competition for background resources externally-induced self-regulation.

There are two recent studies of note that incorporate intra-specific competition for benefits. Ferrière *et al.* (2002) investigated the evolutionary dynamics of mutualism, in which different mutualist phenotypes (e.g., mutualist and 'cheater' phenotypes) engage in intra-specific competition for benefits. However, the model incorporates both competition for mutualistic benefits and competition for background resources. Therefore, it is difficult to determine what effect competition for benefits *per se* has on persistence. Morris *et al.* (2003) consider interactions between a plant and a pollinator/seed parasite and an exploiter species. The pollinator/seed parasite engages in intra-specific competition for benefits. However, the plant species engages in intra-specific competition for a background resource (suitable sites) and not for benefits. The model also incorporates inter-specific competition for benefits, but such competition occurs between a mutualist and an exploiter species rather than between mutualist species and competition is asymmetric: the mutualist has a competitive effect on the exploiter but not vice-versa. Because the model includes mutualistic-parasitic and consumer-resource interactions and because the nature of intra-specific competition is different for the two mutualistic species (e.g., competition for benefits vs. background resources), it is difficult to elucidate what role competition for benefits plays in promoting persistence. As this summary of previous work shows, there is no theory that explicitly investigates whether competition for benefits can allow the persistence of mutualistic interactions in the absence of competition for background resources or other species interactions.

Here, we investigate whether competition for benefits *alone* can provide sufficient negative density-dependence to allow the persistence of two- or three-species modules. While processes external to the mutualistic interaction (e.g., competition for limiting background resources) may play a role in regulating mutualistic interactions, our goal here is to investigate the role of competition within the context of the mutualistic interaction itself in promoting persistence. We explicitly consider trade-offs between acquiring versus giving benefits and between an individual's ability to compete for access to partners (competitive ability) and its ability to acquire benefits once it obtains a partner (benefit acquisition). Our approach yields testable predictions about the conditions under which competition for benefits *alone* can allow the persistence of pairwise interactions and the assembly of more complex community modules.

Background

Previous models of mutualistic interactions are based on either modified Lotka-Volterra competition models or, more recently, modified consumer-resource models (e.g., Holland *et al.*, 2002, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine 2010, Fishman and Hadany, 2010 and Wang *et al.* 2012). In both cases (but see Dean, 1983 and Morris *et al.*, 2003), the dynamics of obligate pairwise interactions (e.g., between a plant and animal species) are given by the following generalized model:

$$\frac{dP}{dt} = P\big(r_P - I_P P + f_P(A,P)\big) \qquad (1)$$

$$\frac{dA}{dt} = A\big(r_A - I_A A + f_A(P,A)\big)$$

where P and A are, respectively, the abundances of the plant and animal species; r_i is the intrinsic growth rate of species i ($i = P, A$); I_i is the strength of density-dependent mortality (assumed to arise via intra-specific competition for background resources), and the function f_i, which is akin to a functional response in consumer-resource interactions, describes the rate at which species i acquires benefits from species j.

The model given by Equation (1) has three features of note. First, the obligate nature of the interaction is represented in terms of a negative intrinsic growth rate (i.e., $r_i < 0$). Hence, species go extinct if they cannot acquire sufficient benefits to overcome the deficit between births and deaths. Second, persistence requires both a source of negative density-dependence (depicted by the density-dependent mortality term) *and* non-linear rates of benefit acquisition (see App. B). Without a source of negative density-dependence, the interior equilibrium is unstable (Fig. 2-1a) and species either increase without bound (if $f_P(A,P) > |r_P|$ and $\mathrm{f_A(P,A)} > |\mathrm{r_A}|$) or go extinct. Likewise, if species experience self-limitation (via competition for background resources), but acquire benefits at a constant rate (i.e., f_i is linear), the interior equilibrium is unstable and the only outcomes are unbounded growth (if $f_P(A) > |r_P| + I_P P$ and $f_A(P) > |r_A| + I_A A$) or extinction (Fig. 2-1a; e.g., Gauss and Witt, 1935, May, 1973, Vandermeer and Boucher, 1978, Goh, 1979, Travis and Post, 1979, Heithaus *et al.*, 1980, Addicott, 1981, Gilpin *et al.*, 1982, Wolin and Lawlor, 1984 and Wolin, 1985). Modified competition models with self-limitation and non-linear rates of benefit acquisition result in non-linear zero-growth isoclines and two interior equilibria: an unstable equilibrium (a saddle) at low density and a stable equilibrium at high density (Fig. 2-1b; e.g., Addicott, 1981, Wolin and Lawlor, 1984, Wolin, 1985, Pierce and Young, 1986, Hernandez, 1998, Ferrière *et al.*, 2002, 2007 and Bronstein *et al.*, 2004). Likewise, modified consumer-resource models with self-limitation and saturating rates of benefit acquisition (i.e., f_i is a declining function of partner density) result in a stable equilibrium at high density (Fig. 2-1b; e.g., Soberon and Martinez del Rio, 1981, Wells 1983, Wright, 1989, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Thébault and Fontaine 2010 and Fishman and Hadany, 2010). Several recent models have modified the functional response (f_i) to capture the costs of mutualism, which results in one or two unstable interior equilibria (depending on whether mutualism is uni-directional or bi-directional), but these models still require a density-dependent mortality term to obtain a stable interior equilibrium (e.g., Holland *et al.*, 2002, Holland and DeAngelis, 2009, 2010 and Wang *et al.* 2012). The important point is that persistence is impossible without the density-dependent mortality term, which phenomenologically represents intra-specific competition for background resources.

The third feature of note is that the source of negative density-dependence (density-dependent mortality) is decoupled from the source of positive density-dependence (mutualism). This decoupling means that persistence is determined by the strength of density-dependent mortality arising from factors external to the mutualistic interaction, rather than by the properties of the mutualistic interaction. If the mutualistic interaction is itself a source of negative density-dependence, persistence will not be contingent on self-limitation induced by external factors such as competition for resources. This is the issue that we investigate here.

Mathematical Framework

We use the mathematical framework for consumer-resource interactions (e.g., Holland *et al.*, 2002, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine 2010, Fishman and Hadany, 2010 and Wang *et al.*, 2012) as a starting point to develop a framework in which competition for mutualistic benefits is the only source of negative density-dependence. We begin with a pairwise interaction because it represents the basic building-block of mutualistic communities and serves as a starting point for investigating how more complex communities are assembled. We consider obligate, rather than facultative, mutualisms because they represent the 'worst-case scenario', i.e., species go extinct in the absence of their mutualistic partners. We envision an interaction between a plant species and its pollinator or seed-disperser for illustrative purposes, but our model applies broadly to other mutualistic interactions.

Pairwise mutualistic interaction

Consider a plant species that relies on an animal species for pollination and/or seed dispersal and provides the animal species with a resource that it cannot otherwise obtain (e.g., nectar, fruit). The dynamics of such an obligate interaction are given by the following generalized model:

$$\frac{dP}{dt} = P\big(r_P + g(P,A)\big) \qquad (2)$$

$$\frac{dA}{dt} = A\big(r_A + h(A,P)\big)$$

where P and A are, respectively, the abundances of the plant and animal species; r_i is the intrinsic growth rate of species i ($i = P, A$), and $g(P,A)$ and $h(A,P)$ are, respectively, the per capita rates at which the plant and animal species acquire benefits.

In nature, the benefits available to a given mutualist (e.g., the amount of nectar available to pollinators) are limited. Because our goal is to disentangle the role of intra-specific competition for benefits from intra-specific competition for background resources, we assume that species are limited primarily by mutualistic benefits rather than by external resources. Let m_{AP} be the per capita rate at which the animal species acquires benefits from an individual plant; thus, $m_{AP}P$ quantifies the per capita rate at which benefits are acquired from the plant population at any given time. We consider the per capita rate of benefit acquisition to be a saturating function of the abundance of the species that gives the benefits, i.e., $m_{AP}P/(1+m_{AP}\tau_A P)$ where τ_A is the benefit handling time. Intra-specific competition for benefits reduces the rate at which individuals acquire benefits. Let $\propto_A$ quantify the competitive effect of a single animal individual on another animal individual in a population (measured in units of per individual animal squared). Thus, $\alpha_A A$ gives the competitive effect of a single animal individual on the animal population and $\alpha_A A^2$ gives the cumulative strength of intra-specific competition for benefits within the animal species. The per capita rate at which the animal species acquires benefits from the plant species is therefore given by $h(A,P) = m_{AP}P/(1+m_{AP}\tau_A P+\alpha_A A^2)$. We can use the same argument to derive the per capita rate at which the plant species acquires benefits from the animal species as $g(P,A) = m_{PA}A/(1+m_{PA}\tau_P A+\alpha_P P^2)$.

These functions are qualitatively similar to the Beddington-DeAngelis functional response (Beddington, 1976, DeAngelis *et al.*, 1975), which describes interference competition in consumer-resource interactions. The key difference is that the term describing competition for benefits is a function of mutualist abundance squared, while the consumer interference term in the Beddington-DeAngelis functional response is a linear function of consumer abundance. Thus, the terms describing intra-specific competition for benefits (i.e., $\alpha_A A^2$ and $\alpha_P P^2$) are more akin to intra-specific competition terms in Lotka-Volterra competition models, in which species compete for implicit resources. The functional responses (i.e., $g(P, A)$ and $h(A, P)$), however, are based on consumer-resource theory. Hence, our framework incorporates competition for benefits without within the same framework of recent models of mutualistic interactions (e.g., Holland *et al.*, 2002, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine 2010, Fishman and Hadany, 2010 and Wang *et al.* 2012).

Our model has three key features. First, each species' intrinsic growth rate is negative (i.e., $r_i < 0$) due to the obligate nature of the interaction. Because the magnitude of r_i describes the rate at which species *i* goes extinct in the absence of the benefits it receives from species *j*, we refer to r_i as the extinction tendency of species *i*. Second, note that m_{ij} is a trait of both species (i.e., it includes both the rate at which species *j* produces benefits and the rate at which species *i* acquires benefits), and is analogous to an attack rate in consumer-resource interactions. For brevity, we refer to m_{ij} as the benefits acquired by species *i*. Third, competition for benefits is incorporated into the species' benefit acquisition response (akin to a functional response in consumer-resource models). The dynamics of a pairwise mutualistic interaction with competition for benefits is given by:

$$\frac{dP}{dt} = P\left(r_P + \frac{m_{PA}A}{1+m_{PA}\tau_P A+\alpha_P P^2}\right) \qquad (3)$$

$$\frac{dA}{dt} = A\left(r_A + \frac{m_{AP}P}{1+m_{AP}\tau_A P+\alpha_A A^2}\right)$$

The key feature of our model that distinguishes it from previous work is that intra-specific competition for benefits is the only source of negative density-dependence. Hence, the mutualistic interaction is the source of both positive and negative density-dependence.

We first investigate whether competition for benefits alone is sufficient to allow the persistence of obligate pairwise interactions. We then determine the conditions under which a new species can invade the pairwise interaction, leading to a three-species community module.

Assembly of community modules

The invading species can be a plant or an animal species. Without loss of generality, we consider a plant species that invades and competes with a resident plant over the benefits provided by a shared animal partner. For example, the invasive dandelion (*Taraxacum officinale*) competes with the native dandelion (*T. japonicum*) for the attention of shared pollinators (Kandori *et al.*, 2009). Similarly, fireweed aphids (*Aphis varians*) compete with ant-tended aphids (*Cinara sp.*) for protection by ants (*Formica fusca*, *F. cinerea*) (Addicott, 1978, Cushman and Addicott, 1989 and Breton and Addicott, 1992). The dynamics of the three-species interaction are given by:

$$\frac{dP_R}{dt} = P_R\left(r_{P_R} + \frac{m_{P_RA}A}{1+m_{P_RA}\tau_{P_R}A+\alpha_{P_R}{P_R}^2+\alpha_{P_RP_I}P_I}\right) \qquad (4)$$

$$\frac{dP_I}{dt} = P_I\left(r_{P_I} + \frac{m_{P_IA}A}{1+m_{P_IA}\tau_{P_I}A+\alpha_{P_I}{P_I}^2+\alpha_{P_IP_R}P_R}\right)$$

$$\frac{dA}{dt} = A\left(r_A + \frac{m_{AP_R}P_R+m_{AP_I}P_I}{1+m_{AP_R}\tau_{AP_R}P_R+m_{AP_I}\tau_{AP_I}P_I+\alpha_AA^2}\right)$$

where P_I, P_R, and A are, respectively, the abundances of the invader plant species, the resident plant species, and the animal species scaled by their respective carrying capacities. There are two features to note. First, all species have negative intrinsic growth rates ($r_i < 0;\ i = P_R, P_I, A$). This is because the two plant species are completely dependent on the animal partner and the animal species' persistence requires that at least one plant species be present in the community. Second, there is now intra- *and* inter-specific competition for benefits; with $\alpha_{P_iP_j}$ specifying the competitive effect of plant species j on plant species i (measured in units of per individual of species *j*). The population-level effect of inter-specific competition for benefits of plant species *j* on plant species i is given as the product of the per capita competition coefficient and the abundance of species *j* (i.e., $\alpha_{P_iP_j}P_j$), as is the standard form in competition models.

The role of trade-offs on persistence and community assembly

In many species, energetic, physiological, and/or other constraints lead to trade-offs between life history traits. We investigate how persistence is influenced by two types of trade-offs that are likely to be important in mutualistic species: a trade-off between (i) benefits acquired and benefits given and (ii) between competitive ability and benefit acquisition.

Trade-off between benefits acquired and benefits given

For mutualistic species in nature, producing benefits (e.g., nectar) comes at an energetic cost. One could envision a situation in which providing benefits to a mutualistic partner comes at the cost of reduced survival and/or reproduction (Ferrière *et al.*, 2002, 2007, Bronstein *et al.*, 2004 and Holland *et al.*, 2004). We incorporate this trade-off into the model (Eqs 3, 4) by making the intrinsic growth rate of each species a function of the ratio of benefits given versus received, i.e., $\hat{r}_i = r_i\left(\sum_j m_{ji} / \sum_j m_{ij}\right)$ where $\hat{r}_i$ is the intrinsic growth rate with the trade-off. Thus, an increase in the rate at which a species gives benefits to its partner (i.e., m_{ji} increases), comes at the cost of an increased extinction tendency (i.e., r'_i becomes more negative). We use a linear form for purposes of illustration, but more complex forms can easily be incorporated into the model. This trade-off can arise in the pairwise interaction and three-species community module. Note that because this trade-off does not depend on species' abundances, it is not a source of negative density-dependence.

Trade-off between benefit acquisition and competitive ability

In mutualistic species, greater energy allocation to competition for access to partners may come at the cost of acquiring fewer benefits (or vice-versa). For example, a plant species may allocate energy towards large, colorful flowers to attract pollinators away from competitors, thus increasing its competitive ability, at the cost of reduced energy allocation towards pollen production, thus reducing the rate at which it acquires benefits (pollen transfer). We incorporate this trade-off into the three-species community module (Eq. 4) by modifying the rate of benefit acquisition of plant species *i* (m_{P_iA}). For this trade-off to occur, the rate of benefit acquisition must first be directly related to the strength of inter-specific competition for benefits. We assume that m_{P_iA} decreases as the strength of inter-specific competition for benefits increases (i.e., $\widehat{m}_{P_iA} = m_{P_iA}\left(1 - \alpha_{P_iP_j}P_j\right)$ where $\widehat{m}_{P_iA}$ is the rate of benefit acquisition with the trade-off). The trade-off is incorporated into this function by making inter-specific competition a function of the rate at which species *i* acquires benefits relative to that of its competitor *j* (i.e., m_{P_iA}/m_{P_jA}). Thus, this trade-off is incorporate into the model as: $\widehat{m}_{P_iA} = m_{P_iA}\left(1 - \left(m_{P_iA}/m_{P_jA}\right)\alpha_{P_iP_j}P_j\right)$. Hence, when species *j* allocates more towards acquiring benefits relative to species *i* (i.e., m_{P_iA}/m_{P_jA} decreases), its competitive effect on species *i* becomes weaker and species *i* is able to acquire more benefits. Because it involves inter-specific competition, this trade-off can only operate in community modules of three or more species.

Results

Pairwise mutualistic interaction

We find that competition for benefits alone is sufficient to allow the persistence of obligate pairwise mutualistic interactions. We first report results in the absence of any trade-offs. In the absence of any negative density-dependence, the tight inter-dependence between species leads to an Allee effect. If the initial species' abundances are below a critical threshold defined by an unstable interior equilibrium (a saddle; Fig. 2-1a; App. A), positive density-dependence (i.e., per capita growth rates decrease with declining abundance) causes extinction. If the initial abundances exceed this threshold, species abundances increase indefinitely. Thus, when there are no negative density-dependent mechanisms operating, extinction is the only stable outcome.

With competition for benefits, an interior equilibrium becomes feasible such that there now exist alternative stable states (extinction and persistence) separated by a saddle (Fig. 2-1b). This occurs because competition for benefits causes benefit acquisition rates (functions g and h in Eq. 2) to decline with increasing species abundance, which causes each species' per capita growth rate to decrease as its abundance increases and leads to a non-linearity in the species' zero-growth isoclines (Fig. 2-1b). Importantly, this non-linearity in species' zero-growth isoclines is an outcome of the model that arises naturally from the negative density-dependent mechanism (competition for benefits). Whether species can persist in the long-term depends on their initial abundances. Below we explain how this dependence can lead to different outcomes.

When both partners are rare, competition for benefits is weak and negative density-dependence is insufficient to overcome positive density-dependence. Because neither species can acquire sufficient benefits from its rare partner to overcome its extinction tendency (r_i), species' per capita growth rates decline as their abundances decrease and both partners go extinct.

When both species are abundant, intra-specific competition for benefits is strong and causes each species' per capita growth rate to decline as its abundance increases. Thus, the negative density-dependence due to intra-specific competition for benefits outweighs the positive density-dependence due to the Allee effect, allowing both partners to attain a steady state with positive abundances (Fig. 2-1b; App. A).

An interesting outcome ensues when one species is abundant and the other is rare. In this case, competition for benefits is intermediate in strength and the outcome depends on the tension between positive density-dependence in the rare partner and negative density-dependence in the abundant partner. Because of this tension, the interaction stands on the knife-edge between persistence and extinction and a small difference in the initial abundances of the partners can lead to fundamentally different outcomes (Fig. 2-2a,b). The initially rare partner increases in abundance due to weak intra-specific competition for the large amount of benefits provided by the abundant partner. As the rare partner increases, increased intra-specific competition leads to stronger negative density-dependence. At the same time, the initially abundant partner decreases in abundance due to strong intra-specific competition for the small amount of benefits provided by the rare partner. As the abundant partner declines, decreased intra-specific competition leads to weaker negative density-dependence. Persistence occurs when the rare partner increases above a level that allows the abundant partner to increase (Fig. 2-2a). Above this threshold, negative density-dependence is stronger than positive density-dependence for each partner, allowing them both to persist. Extinction occurs when the abundant partner declines below a level that prevents the rare partner from increasing (Fig. 2-2b). Below this threshold, positive density-dependence is stronger than negative density-dependence and both species go extinct.

As the above analyses show, the relative strengths of positive and negative density-dependence when species are abundant versus rare is the key to understanding how competition for benefits alone allows for the persistence of pairwise mutualistic interactions.

Role of trade-offs on the persistence of pairwise interactions

An important question is how a trade-off between benefits acquired versus given alters the above results for pairwise interactions (Ferrière *et al*., 2002, 2007, Bronstein *et al*., 2004 and Holland *et al*., 2004). The main difference is that the trade-off causes the extinction of interactions in which one species gains significantly more benefits than does its partner (i.e., a ‘cheater’; Fig. 2-3). Here, cheaters are species that acquire significantly more benefits than they give, as opposed to species that acquire benefits without reciprocating at all (e.g., Morris *et al*., 2003 and Bronstein *et al*., 2003). Extinction occurs because the cheater causes the abundance of its partner to fall below the Allee threshold. This suggests that a trade-off between benefits acquired versus given should reduce opportunities for cheating. Note that the trade-off between competitive ability and benefit acquisition can only operate in interactions involving three or more species.

Assembly of community modules

The key finding is that competition for benefits alone is sufficient to allow the assembly of more complex modules from simple pairwise interactions. Below we explain how this comes about.

Invasibility

The conditions under which a second plant species can invade the pairwise interaction between a resident plant and animal species are as follows. The invader can increase from initially small numbers if it can maintain a positive per capita growth rate when the resident plant-animal pair is at equilibrium. Invasion occurs when $m_{P_I A}A^* > |r_{P_I}|\left(1 + m_{P_I A}\tau_{P_I}A^* + \alpha_{P_I P_R}{P_R}^*\right)$ where ${P_R}^*$ and A^* are, respectively, the equilibrium abundances of the resident plant and animal species (Fig 4a). The invading plant species will increase when rare if it acquires sufficient benefits to overcome both its extinction tendency (i.e., $r_{P_I} < 0$) *and* the effects of inter-specific competition for benefits from the resident plant (i.e., $\alpha_{P_I P_R} {P_R}^*$), despite the saturating rate at which it acquires benefits (i.e., $1 + m_{P_I A} \tau_{P_I} A^*$). Otherwise, the initial pairwise plant-animal interaction cannot be invaded by a second plant (or by extension, an animal) species. The invader species is more likely to establish with an increase in its benefit acquisition rate relative to its extinction tendency (i.e., $m_{P_I A}/r_{P_I}$) and/or a reduction in its handling time (τ_{P_I}) or the strength of inter-specific competition for benefits of the resident species ($\alpha_{P_I P_R}$).

Stable Coexistence

In order for a third species to successfully integrate into an existing two-species community, it must invade *and* coexist with the resident species. Coexistence requires mutual invasibility, i.e., each plant species must be able to increase in abundance when it is rare and its competitor is at equilibrium with the animal species. Mutual invasibility occurs when $m_{P_I A} A^* > |r_{P_I}|\left(1 + m_{P_I A} \tau_{P_I} A^* + \alpha_{P_I P_R} {P_R}^*\right)$ and $m_{P_R A} A^* > |r_{P_R}|\left(1 + m_{P_R A} \tau_{P_R} A^* + \alpha_{P_R P_I} {P_I}^*\right)$, where P_I^* is the equilibrium abundance of the invader plant. Mutual invasibility is possible when both species acquire sufficient benefits to overcome their respective extinction tendencies *and* the effects of inter-specific competition for benefits, despite saturating rates of benefit acquisition. Coexistence occurs when inter-specific competition for benefits in both species is relatively weak compared to the rates at which each species acquires benefits and is more likely to occur with a reduction in both species' handling times. The resident excludes the invader when its inter-specific competitive ability is relatively strong compared to the rate at which the invader acquires benefits (Fig. 2-4a). However, if the invader acquires sufficient benefits to increase in abundance when rare *and* is a relatively strong competitor for benefits, the invader excludes the resident and forms a new pairwise interaction with the animal species. Coexistence further requires that all species' abundances exceed their respective Allee thresholds (i.e., species are locally, but not globally, stable to perturbations of their equilibrium abundances).

An interesting point to note is that coexistence can occur even when the invader acquires fewer benefits than does the resident (i.e., $m_{P_I A} < m_{P_R A}$). In extreme cases, the invader can even persist in a three-species web when it would go extinct in a pairwise interaction. This occurs because the resident plant keeps the animal sufficiently abundant to compensate for the low rate at which the invader plant acquires benefits. Hence, the resident may indirectly facilitate the invader and thus promote coexistence.

Role of trade-offs in community assembly

We next investigate how the above results on invasibility and coexistence are influenced by trade-offs between (i) benefits acquired and given and (ii) competitive ability and benefit acquisition both when they operate separately versus simultaneously. When there is a fitness cost to giving benefits, the invader must acquire greater benefits to become established than it would in the absence of the trade-off (Fig. 2-4b vs. 2-4a). This is because the invader must acquire sufficient benefits to overcome competition from the resident as well as its greater extinction tendency (i.e., $r_{P_I} \ll 0$) due to providing more benefits than it receives.

When a trade-off between competitive ability and benefit acquisition operates, invasion is much less likely to occur compared to when there is no trade-off (Fig. 2-4c vs. 2-4a). When inter-specific competition from the resident is relatively weak, however, we get a counter-intuitive result: the invader is more likely to establish when the trade-off is weak than when it is strong. This is because the strength of competition for benefits from the resident (i.e., $\alpha'_{P_I P_R}$)

determines the outcome of invasion. When the trade-off is relatively weak, coexistence is possible because the resident species is superior at acquiring benefits, but the invader species is the superior competitor for benefits. For instance, the invader is better at competing for the attention of the shared partner species, but the resident is able to acquire greater benefits per interaction with the shared partner species. When the trade-off is relatively strong, the species that is the superior competitor for benefits deprives the other species of its advantage in acquiring benefits, resulting in competitive exclusion. The superior competitor, because of its greater ability to attract the mutualistic partner, preempts the benefits that the inferior competitor (who is more efficient at acquiring benefits once an encounter with a partner ensues) could have otherwise acquired. Thus, the trade-off leads to a priority effect where the species that is better able to attract a mutualistic partner gains an initial advantage by depriving its competitor from sufficient access to the mutualistic partner.

When both trade-offs operate simultaneously, the invader cannot establish when it acquires significantly fewer benefits or greater benefits than the resident (Fig. 2-4d). When the invader acquires significantly fewer benefits than the resident, the trade-off between benefits acquired versus given dominates and extinction occurs because the invader experiences a greater deficit between benefits acquired versus given, and thus a greater extinction tendency (i.e., r_{P_I} is more negative). In other words, the invader is unable to acquire sufficient benefits to compensate for the benefits it gives to the partner species and is thus ‘cheated’ by its partner. In this case, the invader is eliminated by its partner. Thus, this trade-off reduces both the persistence of pairwise partners and the coexistence of species competing for shared partner species. When the invader acquires more benefits than the resident, the trade-off associated with competitive ability and benefit acquisition dominates and extinction occurs because the resident is the superior competitor for benefits and competitively excludes the invader. In contrast to the previous case, the invader is now eliminated by its competitor. The key result is that coexistence requires that a species acquire an intermediate level of benefits such that it is neither cheated by its partner nor competitively excluded by a superior competitor for benefits.

Comparison with previous work

In previous models, negative density-dependence arises from a density-dependent mortality term, which is attributed to intra-specific competition for background resources. Hence, negative density-dependence arises from a source external to the mutualistic interaction and is therefore decoupled from the positive density-dependence that is inherent in the mutualistic interaction. In contrast, when competition is for benefits, positive and negative density-dependence arise from the mutualistic interaction itself.

We illustrate this point by comparing our framework with a model in which negative density-dependence arises from external factors (Eq. 1 with $f_P(A,P) = m_{PA}A/(1+A)$ and $f_A(P,A) = m_{AP}P/(1+P)$; e.g., Holland *et al.*, 2002, Okuyama and Holland, 2008, Bastolla *et al.*, 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine 2010, Fishman and Hadany, 2010 and Wang *et al.* 2012. The key finding is that for a given intrinsic growth rate (r), species requires greater rates of benefit acquisition (m) to persist when self-limitation arises from a process external to the mutualistic interaction, such as competition for background resources (i.e., I in Eq. 1), than when self-limitation arises from competition for benefits (i.e., α in Eqs. 3,4), even when $I = \alpha$ (Fig. 2-5). We illustrate this difference by considering the plant species in a pairwise interaction. We derive the minimum value of $m_{PA}A$ (i.e., the total benefits acquired from the animal species) required for the per capita growth rate of the plant species to be positive (i.e., $(dP/dt)/P > 0$). We do this by solving $r_P - I_P P + m_{PA}A/(1 + m_{PA}\tau_P A) > 0$ (competition for background resources) and $r_P + m_{PA}A\,/(1 + m_{PA}\tau_P A + \alpha_P P^2) > 0$ (competition for benefits) for $m_{PA}A$. When competition is for background resources, this condition is: $m_{PA}A > (|r_P| + I_P P)/(1 - \tau_P I_P P - |r_P|\tau_P)$. When competition is for benefits, it is: $m_{PA}A > |r_P|(1 + \alpha_P P^2)/(1 - |r_P|\tau_P)$. The difference in outcomes can be illustrated as follows. If the minimum value of $m_{PA}A$ is equal in both models, then: $(|r_P| + I_P P)/(1 - \tau_P I_P P - |r_P|\tau_P) = |r_P|(1 + \alpha_P P^2)/(1 - |r_P|\tau_P)$, which simplifies to: $I_P/(1 - \tau_P I_P P - |r_P|\tau_P) = |r_P|\alpha_P P$ (note that the left-side of this condition is when competition is for background resources and the right-side is when competition is for benefits; see App. C). The plant species can persist only if it can acquire sufficient benefits to increase when rare (i.e., when $P \approx 0$). Thus, for the minimum value of $m_{PA}A$ to be equal in both models *and* be sufficient for the plant species to increase when rare, requires that: $I_P/(1 - |r_P|\tau_P) \approx 0$. Since $I_P \neq 0$, the minimum value of $m_{PA}A$ must always be greater when competition is for background resources (as in previous models) than when competition is for benefits (as in our framework). This is because in previous models self-limitation via intra-specific competition for background resources is decoupled from the mutualistic interaction *and* persistence requires the inclusion of a saturating function for benefit acquisition (App. B). In our model, competition for benefits is intrinsic to the mutualistic interaction and thus directly leads to the decline in the rate of benefit acquisition as species increase in abundance. It should be noted that saturating rates of benefit acquisition are an input in previous models that is necessary to generate non-linear zero growth isoclines and a stable interior equilibrium, while in our case, non-linear zero growth isoclines are a natural outcome of the model resulting from the interplay between competition and mutualism.

Discussion

Mutualistic interactions represent a paradox: they are characterized by positive density-dependence, but data demonstrate long-term persistence, suggesting that negative density-dependent mechanisms are at play. The challenge for theory has been to identify biologically-realistic sources of negative density-dependence. One source of negative density-dependence which theory has not adequately explored is competition for the benefits provided by mutualistic partners (Jones *et al*., 2012). Here we develop a mathematical model to investigate the role of competition for benefits in the persistence of mutualistic interactions. Our approach differs from previous work in that we consider intra- *and* inter- specific competition, both of which occur for the benefits received from a mutualistic partner. Inter-specific competition ensures that inferior competitors for benefits are excluded, but the fact that both positive and negative density-dependence arise from the mutualistic interaction itself ensures that even weakly interacting partners (i.e., those that acquire relatively few benefits from one another) can persist in the long-term. While it is possible that factors such as competition for background resources play a role in regulating mutualistic interactions, our work shows that mechanisms external to the mutualistic relationship are not necessary for persistence. Indeed, we find that competition for benefits alone can allow the long-term persistence of pairwise mutualistic interactions as well as the assembly of more complex modules. Thus, our model provides a parsimonious resolution to the paradox of how mutualistic species persist despite their inherent tendency to go extinct when rare.

An important aspect of our framework is the explicit consideration of trade-offs that affect both persistence and community assembly. This analysis leads to two key results. First, a trade-off between benefits acquired and benefits given can reduce persistence by eliminating cheaters (partners that acquire far more benefits that they give). This trade-off is interesting because it imposes an ecological constraint on the evolution of cheating (e.g., Ferrière *et al*., 2002, 2007, Bronstein *et al*., 2004 and Holland *et al*., 2004). It also suggests the possible role of indirect interactions in more complex modules that may lead to a transition between mutualism and antagonism (Holland *et al*., 2002, Holland and DeAngelis, 2009, 2010, Wang *et al*., 2011).

A second key result is that when a trade-off between benefit acquisition and competitive ability operates, invasion is more likely when the trade-off is weak than when the trade-off is strong. Coexistence occurs when the trade-off is weak because one species is slightly better at competing for access to partners, while the other species is slightly better at acquiring benefits once an interaction with a partner ensues. Competitive exclusion occurs when the trade-off is strong because of an asymmetry in the trade-off: the superior competitor has an extra advantage because it exerts a preemptive effect, i.e., by attracting more mutualistic partners it undermines its competitor's advantage in acquiring greater benefits once a partner is encountered.

When the two trade-offs operate simultaneously, coexistence requires that a species acquire sufficient benefits relative to those it gives to overcome its extinction tendency, but not in such excess that it is excluded by a superior competitor for benefits. A key insight to emerge from this analysis is that persistence is most likely at intermediate levels of benefit acquisition. This result offers an intriguing parallel to consumer-resource models in which biodiversity is maximized at intermediate productivity (e.g., Holt and Polis, 1997). In consumer-resource models, biodiversity is reduced by limited resources at low productivity and by strong consumer control at high productivity. In our model, persistence is reduced by limited benefits at low levels of benefit acquisition and by strong competition for benefits at high levels of benefit acquisition.

An important question in applying these ideas to real communities is how prevalent competition for benefits is likely to be in nature and how relevant our results are to real mutualistic communities. Empirical evidence suggests that competition is quite common (see reviews by Addicott, 1985, Palmer *et al.*, 2003 and Mitchell *et al.*, 2009). Examples include competition for pollinators (e.g., Levin and Anderson, 1970, Mosquin, 1971, Waser, 1978, Bawa, 1980, Zimmerman, 1980, Campbell, 1985, Campbell and Motten, 1985, Waser and Fugate, 1986, Bell *et al.*, 2006 and Pauw and Bond 2011), seed dispersers (e.g., Ruhren and Dudash, 1996, Alcantara *et al.*, 1997, Alcantara and Rey, 2003, Saracco, 2005 and Rodriguez-Perez and Traveset, 2010), or ant protectors (e.g., Addicott, 1978, Cushman and Addicott, 1989, Cushman and Whitham, 1991, Breton and Addicott, 1992, Fischer and Shingleton, 2001, Ness and Bronstein 2004, Morris *et al*., 2005, Ness *et al*., 2009). It also suggests that natural mutualistic communities are characterized by weak interactions (Bascompte *et al*., 2006 and Bascompte and Jordano, 2007). For instance, Bascompte *et al.* (2006) analyzed the distribution of interaction strengths (termed 'mutual dependence') of 26 plant-animal networks, quantified by the fraction of all visits to a plant species from a given animal species (quantified here by m_{PA}) and the fraction of all visits from an animal species to a given plant species (quantified here by m_{AP}). Regardless of the type of mutualism, the frequency distribution of interaction strength (dependences) shows mostly weak interactions with only a few strong interactions (Bascompte *et al*., 2006). A key outcome of our mathematical framework is that mutualistic species can persist even when there are low rates of benefit acquisition (m) for a given intrinsic growth rate (r). This is because competition for benefits occurs within the mutualistic interaction itself, while competition for background resources is decoupled from the mutualistic interaction. Thus, our framework, based on competition for mutualistic benefits, provides a potential explanation for the preponderance of weakly interacting mutualistic communities in nature.

Indeed, the biological significance of our theory lies in its ability to generate testable predictions about the conditions under which persistence verses competitive exclusion may arise in natural mutualistic communities. As illustrative examples, we present two empirical case studies which relate to the theory we develop here. First, consider the case in which fireweed aphids (*Aphis varians*) engage in intra-specific competition with conspecifics and inter-specific competition with ant-tended aphids (*Cinara sp.*) for the protection benefits provided by ant mutualists (*Formica fusca* and *Formica cinerea*) (Addicott, 1978, Cushman and Addicott, 1989 and Breton and Addicott, 1992). The benefits acquired by individual fireweed aphids declined as the number of conspecifics increases (Breton and Addicott, 1992). Also, the presence of neighboring ant-tended aphids significantly reduced the number of ants tending fireweed aphid populations, resulting in increased risk of extinction (Cushman and Addicott, 1989). Second, consider the so-called "Dandelion War" in Japan (Kandori *et al*., 2009 and references therein), in which the invasive dandelion *Taraxacum officinale* has been competitively displacing the native dandelion *T. japonicum* across Japan over the past few decades. There is growing concern that the native species will ultimately go extinct. The invasive *T. officinale* attracts more pollinator visits than the native *T. japonicum*, likely because it produces more nectar; as a result, the native species suffers reduced seed set in the presence of the invasive species (Kandori *et al*., 2009). These data suggest that competition for benefits may be an important determinant of exotic species' ability to invade and displace native species. Importantly, the mathematical framework we have developed can predict the conditions under which competitive exclusion may occur; namely, that species with a greater ability to attract mutualistic partners will have a competitive advantage and exclude its competitor. This is consistent with observations that fireweed aphids experience increased extinction risk in the presence of ant-tending aphids and that the invasive *T. officinale* attracts more pollinators and, as a result, is displacing the native *T. japonicum* in Japan.

The work presented here suggests several important future directions. First, the models we have developed are deterministic. Investigating the effects of environmental stochasticity in driving species' abundances below their extinction (Allee) thresholds, and the role of demographic stochasticity in enhancing the tendency to go extinct when rare are important future directions. Second, exploring how negative density-dependence generated by competition for benefits leads to the assembly of complex mutualistic communities is an important next step. Particularly important in this regard is to determine whether competition for benefits allows community modules to assemble in such a way that they lead to the nested structure observed in natural mutualistic communities (Bascompte *et al*., 2003 and Bascompte and Jordano, 2007).

Our findings have potential implications for the conservation and restoration of mutualistic communities. If mutualistic partners are rare, such as in the case of pollen limitation in plants due to a scarcity of pollinators, our model predicts that plant species with greater abilities to attract pollinators (i.e., superior competitors for the attention of mutualistic partners) will be better able to persist. If such species are invaders rather than natives, then native plant species will suffer a greater extinction risk. Indeed, there is growing concern that invasive species may be competitively displacing native mutualists by attracting shared partners (e.g., McKey, 1988, Brown and Mitchell, 2001, Brown *et al*., 2002, Traveset and Richardson, 2006, Jakobsson *et al*., 2009, Kawakami *et al*., 2009, Keuffer *et al*., 2009 and Kaiser-Bunbury *et al*., 2010). Thus, if competition for benefits is an important mechanism for diversity maintenance in real communities, native mutualists may be at greater risk of extinction than was previously thought.

Acknowledgments

We thank Van Savage, Samraat Pawar, and Tony Dell and two anonymous reviewers for helpful comments on the manuscript. This research was supported by NSF grant DEB-0717350 to P.A.

Figures

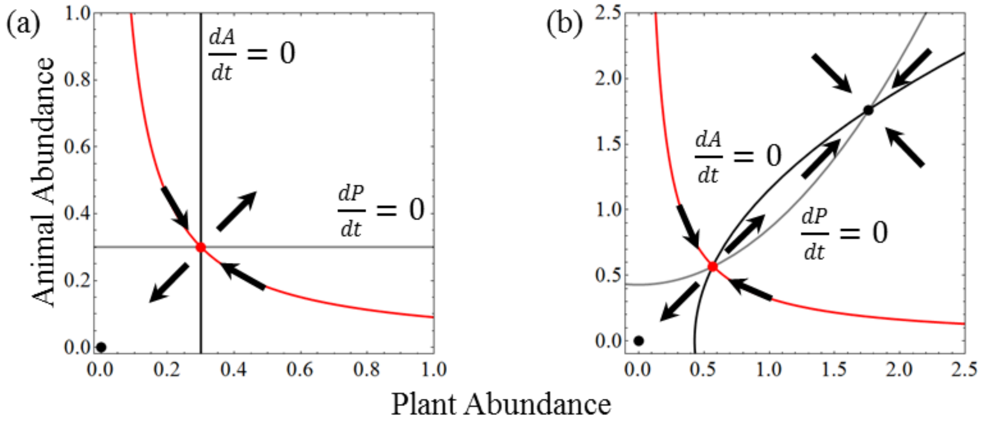

Figure 2-1. Phase plots for pairwise mutualistic dynamics (equation 3). The gray line is the zero growth isocline for the plant species and the black line is the zero growth isoclines of the animal species. The black circles represent stable equilibria and red circles represent unstable equilibria. The red line is the separatrix that represents the Allee threshold. (a) Without a source of negative density-dependence parameter, extinction is the only stable equilibrium. (b) When competition is for benefits, stable persistence is possible provided the abundances of both speces exceed the Allee threshold. Other parameters: $r_P = r_A = -0.3$; $m_{PA} = m_{AP} = 1$; $\tau_P = \tau_A = 1$; $\alpha_P = \alpha_A = 1$

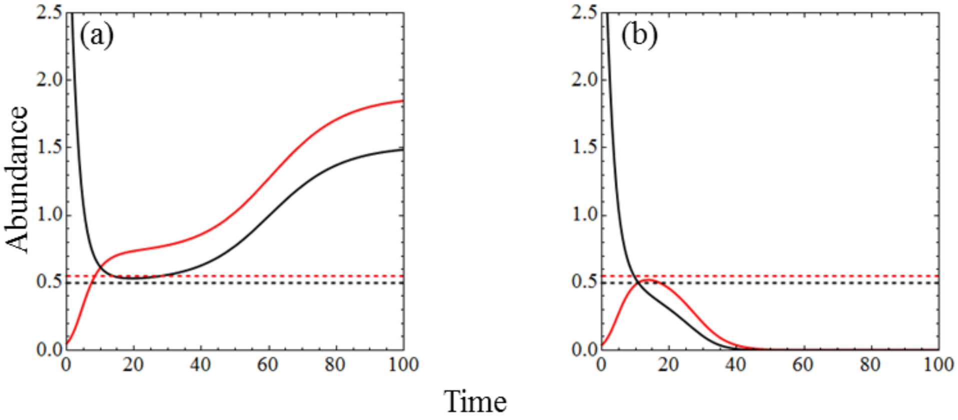

Figure 2-2. Time series plots for the pairwise mutualistic interaction when one partner is rare and the other is abundant. The red line is the initially rare partner and the black line is the initially abundant partner. The dashed red line is the threshold abundance of the rare partner. If the rare species exceeds this threshold, the abundant species can increase. The dashed black line is the threshold abundance of the abundant species. If the abundant species delines below this threshold, the rare species cannot increase. The initial abundance of the rare partner is only 1% greater in panel (a) than in panel (b). (a) When the rare partner increases above its threshold, negative density-dependence is stronger than positive density-dependence for both partners and the species persist. (b) When the abundant partner declines below its threshold, positive density-dependence is stronger than negative density-dependence for both partners and the species go extinct. Parameter values: $r_P = -0.2$; $r_A = -0.3$; $m_{PA} = m_{AP} = 0.75$; $\tau_P = \tau_A = 1$; and $\alpha_P = \alpha_A = 1$. Initial abundances: (a) $P = 0.05$ and $A = 3$; (b) $P = 0.04$ and $A = 3$.

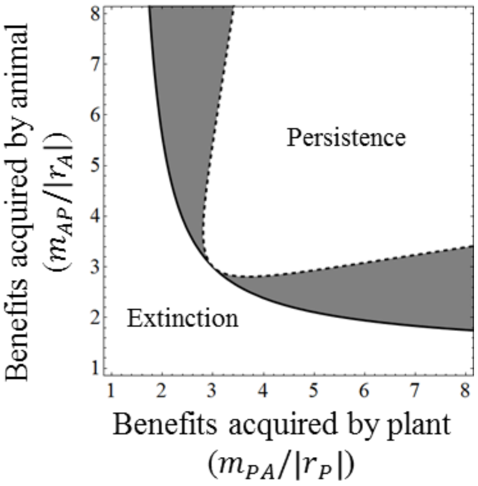

Figure 2-3. Effect of a trade-off between benefits acquired versus given on the persistence of an obligate pairwise mutualistic interaction (Eq. 3), plotted as the ratio of the benefit acquisition rate to the intrinsic growth tendency (i.e., $m_{ij}/|r_i|$) of the animal species against that of the plant species. The solid line divides the parameter space into regions where exinction and persistence occur without the trade-off . The dashed line is the threshold above which persistence occurs with the trade-off and the grey area is the region of the parameter space eleminated by the trade-off. The trade-off constrains persistence by eliminating interactions in which one species (i.e., a cheater) acquires more benefits from its partner than it gives in return. Other parameter values: $r_P = r_A = -0.2$; $\tau_P = \tau_A = 1$; and $\alpha_P = \alpha_A = 1$.

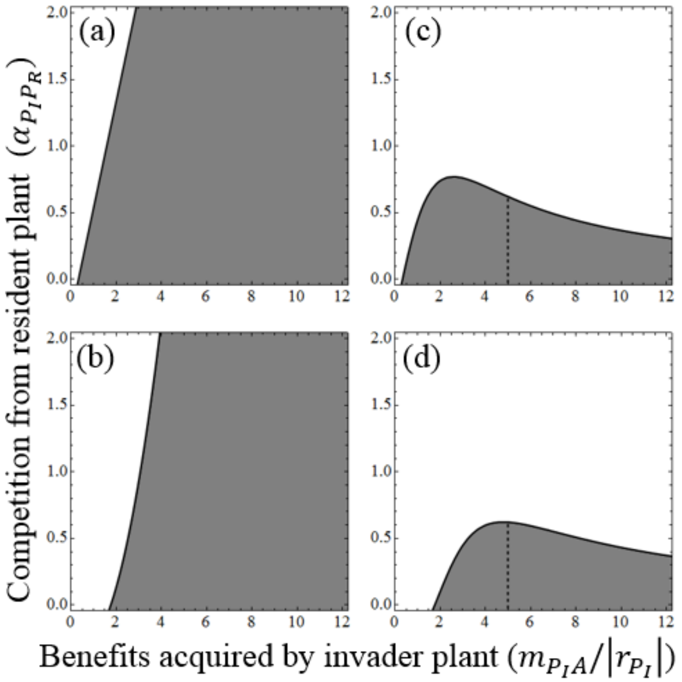

Figure 2-4. Effects of a trade-off between (i) benefits acquired versus given (panels b and d) and (ii) benefit acquisition and competitive ability (panels c and d) on community assembly (Eq. 4), plotted as the strength of inter-specific competition for benefits on the invader plant species from the resident plant species (i.e., $\alpha_{P_I P_R}$) against ratio of the benefit acquisition rate to the intrinsic growth rate of the invader plant species (i.e., $m_{P_I A}/|r_{P_I}|$). The black line divides the parameter space into regions where invasion (gray region) and exinction (white region) occur. The dashed lines in panels (c) and (d) show the benefits acquired by the resident plant for comparison purposes. (a) In the absence of any trade-off, invasion occurs if inter-specific competition for benefits from the resident species is relatively weak compared to the rate at which the invader species acquires benefits from the shared animal parnter. (b) A trade-off between benefits acquired versus given contrains persistence because the invader must acquire greater benefits to invade than without the trade-off. (c) A trade-off between benefit acquisition and competitive ability facilitates persistence at intermediate levels of benefit acquisition, but constrains persistence at high levels of benefit acquisition. (d) When both trade-offs operate, persistence is constrained to intermediate levels of benefit acquisition. Other parameter values: $r_{P_R} = r_{P_I} = r_A = -0.2$; $m_{P_R A} = m_{A P_R} = m_{A P_I} = 1$; $\tau_{P_R} = \tau_{P_I} = \tau_A = 1$; and $\alpha_{P_R} = \alpha_{P_I} = \alpha_A = \alpha_{P_R P_I} = 1$.

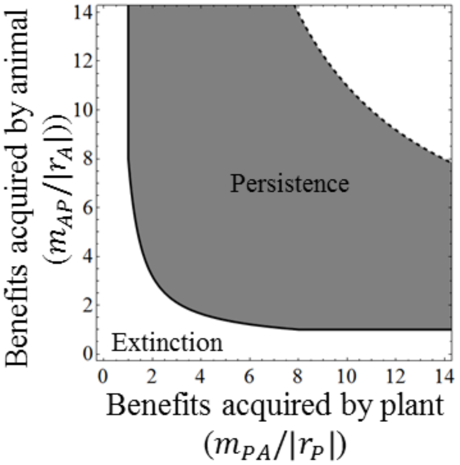

Figure 2-5. Persistence of pairwise mutualistic interactions in our model and in previous models, plotted as the ratio of the benefit acquisition rate to the intrinsic growth rate (i.e., $m_{ij}/|r_i|$) of the animal species against that of the plant species. In previous models (Eq. 1), persistence occurs in the region above the dashed line, while extinction occurs in the region below the dashed line. In our model (Eq. 3), persistence occurs in the region above the solid line, while extinction occurs in the region below the solid line. The key point is that for a given intrinsic growth rate (*r*), our model allows for the persistence of species with lower rates of benefit acquisition (*m*) than in previous models (gray region). Note that for comparison purposes, the strength of competition for background resources in previous models is eqivalent to the strength of competition for benefits in our model (i.e., $I = \alpha$); hence, *all parameters are the same in both models*. Other parameter values: $r_P = r_A = -0.2$; ; $\tau_P = \tau_A = 1$; and $\alpha_P = I_P = \alpha_A = I_A = 1$.

Supporting Information

The following Supporting Information is available for this article online.

Appendix A: Equilibria and stability analysis of models in which mutualistic species compete for benefits

Pairwise interaction:

The pairwise model yields three equilibria: the trivial equilibrium (P_0^*, A_0^*) = (0, 0) and two interior equilibria:

$$P_{1,2}{}^* = \frac{r_P m_{AP} - r_A m_{PA} + m_{PA} m_{AP} \pm \sqrt{(r_A m_{PA} - r_P m_{AP} + m_{PA} m_{AP})^2 + 4 r_A m_{PA}{}^2 m_{AP}}}{2 m_{PA} m_{AP}} \qquad \text{(A.1)}$$

$$A_{1,2}{}^* = \frac{r_A m_{PA} - r_P m_{AP} + m_{PA} m_{AP} \pm \sqrt{(r_P m_{AP} - r_A m_{PA} + m_{PA} m_{AP})^2 + 4 r_P m_{AP}{}^2 m_{PA}}}{2 m_{PA} m_{AP}}$$

where P_1, A_1 and P_2, A_2 are, respectively, the low and high-abundance interior equilibria. The Jacobian matrix of Eq. 3 is given by:

$$\begin{bmatrix} r_P + m_{PA} A^*(1 - 2P^*) & m_{PA} P^*(1 - P^*) \\ m_{AP} A^*(1 - A^*) & r_A + m_{AP} P^*(1 - 2A^*) \end{bmatrix} \qquad \text{(A.2)}$$

The eigenvalues of the Jacobian matrix evaluated at the trivial extinction equilibrium are: $\lambda_{1,2} = r_P, r_A$. As both r_P and r_A are always negative, $\lambda_{1,2}$ are always negative and the trivial equilibrium is always stable.

To evaluate the stability of the two interior equilibria, it is necessary to show that the Jacobian matrix evaluated at each equilibrium has both a negative trace and a positive determinant (Routh-Hurwitz Criteria). The trace of the simplified Jacobian matrix is $-P^* A^*(m_{PA} + m_{AP})$, which is always negative because m_{PA}, m_{AP}, P^*, and A^* are always positive. The determinant of the simplified Jacobian matrix is $m_{PA} m_{AP} P^* A^*(P^* + A^* - 1)$ and is positive if $P^* + A^* > 1$. When evaluated at the interior equilibria (Eq. A.1), this condition becomes:

$$\frac{-b_P \pm \sqrt{{b_P}^2 - 4ac_P} - b_A \pm \sqrt{{b_A}^2 - 4ac_A}}{2a} > 1 \qquad \text{(A.3)}$$

where: $a = m_{PA}m_{AP}$; $b_P = r_Am_{PA} - r_Pm_{AP} + m_{PA}m_{AP}$; $b_A = r_Pm_{AP} - r_Am_{PA} + m_{PA}m_{AP}$; $c_P = r_Am_{PA}$; and $c_A = r_Pm_{AP}$. This inequality (Eq. A.3) can be simplified by noting that $-(b_P + b_A) = 2m_{PA}m_{AP} = 2a$. Applying this substitution for each interior equilibrium yields:

$$-\left(\sqrt{{b_P}^2 - 4ac_P} + \sqrt{{b_A}^2 - 4ac_A}\right) > 0 \ \text{(low-abundance equilibrium)} \qquad \text{(A.4)}$$

$$\left(\sqrt{{b_P}^2 - 4ac_P} + \sqrt{{b_A}^2 - 4ac_A}\right) > 0 \ \text{(high-abundance equilibrium)}$$

The square root terms must always be positive for the interior equilibria to be feasible, so the determinant will only be positive for the high-abundance interior equilibrium. Thus, if feasible, the low-abundance interior equilibrium is always a saddle and the high-abundance interior equilibrium is always locally stable.

Three-species community module:

The model of a three-species community module yields seven equilibria: the trivial equilibrium (stable); a low-abundance (unstable) and high-abundance (stable) equilibrium associated with a pairwise interaction between the resident plant and animal species; a low-abundance (unstable) and high-abundance (stable) equilibrium associated with a pairwise interaction between the invader plant and animal species; and a low-abundance (unstable) and high-abundance (stable) equilibrium associated with three species coexistence. The eigenvalues at the trivial equililibrium are $\lambda_{1,2,3} = r_{P_R}, r_{P_I}, r_A$, which are always negative, so the equilibrium is always stable. Although it is possible to derive analytical solutions for the equilibria, they are sufficiently complicated to render the stability analysis intractable. We therefore evalutate stability by using phase diagrams.

Appendix B: Equilibria and stability analyses of models with density-dependent mortality

The purpose of this appendix is to show that both density-dependent mortality *and* a saturating rate of benefit acquisition are required for long-term persistence in previous models of mutualistic interactions. We present variations of the basic model (Eq. 1 in main text) as separate cases and investigate long-term persistence by determining in each case whether the model yields a stable interior equilibrium.

Pairwise interaction:

Case 1: The dynamics of a pairwise mutualistic interaction without a source of negative density-dependence and with a linear rate of benefit acquisition are given by:

$$\frac{dP}{dt} = P(r_P + m_{PA}A) \qquad \text{(B.1)}$$

$$\frac{dA}{dt} = A(r_A + m_{AP}P)$$

The model yields two equilibria: the trivial equilibrium and an unstable interior equilibrium: $(P_0^*, A_0^*) = \left(\frac{|r_A|}{m_{AP}}, \frac{|r_P|}{m_{PA}}\right)$ (B.2).

Case 2: The dynamics of a pairwise interaction without a source of negative density-dependence and with a saturating rate of benefit acquisition are given by:

$$\frac{dP}{dt} = P\left(r_P + \frac{m_{PA}A}{1+A}\right) \qquad \text{(B.3)}$$

$$\frac{dA}{dt} = A\left(r_A + \frac{m_{AP}P}{1+P}\right)$$

The model yields two equilibria: the trivial equilibrium and an unstable interior equilibrium: $(P_0^*, A_0^*) = \left(\frac{|r_A|}{m_{AP}-|r_A|}, \frac{|r_P|}{m_{PA}-|r_P|}\right)$ (B.4).

Case 3: With density-dependent mortality and a linear rate of benefit acquisition (e.g. May 1976; Vandermeer & Boucher 1978; Goh 1979; Heithaus *et al.* 1980), the dynamics of the pairwise interaction are given by:

$$\frac{dP}{dt} = P(r_P - I_P P + m_{PA} A) \qquad \text{(B.5)}$$

$$\frac{dA}{dt} = A(r_A - I_A A + m_{AP} P)$$

The model yields two equilibria: the trivial equilibrium and an unstable interior equilibrium: $(P_0{}^*, A_0{}^*) = \left(\frac{m_{PA}|r_A| + I_A|r_P|}{I_P I_A - m_{AP} m_{PA}}, \frac{m_{AP}|r_P| + I_P|r_A|}{I_P I_A - m_{AP} m_{PA}}\right)$.

Case 4: The dynamics of the pairwise interaction with density-dependent mortality and a saturating rate of benefit acquisition (e.g. Okuyama & Holland 2008; Thébault & Fontaine 2010; Holland & DeAngelis 2010), are given by:

$$\frac{dP}{dt} = P\left(r_P - I_P P + \frac{m_{PA} A}{1+A}\right) \qquad \text{(B.6)}$$

$$\frac{dA}{dt} = A\left(r_A - I_A A + \frac{m_{AP} P}{1+P}\right)$$

The model yields three equilibria: the trivial equilibrium and a low- (unstable) and high- (stable) interior equilibria (analogous to Fig. 2-1b). Although it is possible to derive analytical solutions for the interior equilibria, they are sufficiently complicated to render the stability analysis intractable.

Case 5: In Ferriére e*t al.* (2002), the dynamics of the pairwise interaction with density-dependent mortality and competition for benefits, are given by:

$$\frac{dP}{dt} = P(r_P - I_P P + m_{PA} A(1 - P)) \qquad \text{(B.7)}$$

$$\frac{dA}{dt} = A(r_A - I_A A + m_{AP} P(1 - A))$$

The model yields three equilibria: the trivial equilibrium and a low- (unstable) and high- (stable) interior equilibria (analogous to Fig. 2-1b). While it is possible to derive analytical solutions for the interior equilibria, they are sufficiently complicated to render the stability analysis intractable.

Case 6: In Morris e*t al.* (2002), the dynamics of a plant – pollinator/seed parasite interaction with competition for benefits in the pollinator/seed parasite and competition for a background resource in the plant species, are given by:

$$\frac{dP}{dt} = P(r_P + m_{PA}A(1 - P)(1 - A)) \qquad \text{(B.8)}$$

$$\frac{dA}{dt} = A(r_A + m_{AP}P(1 - A))$$

The model yields three equilibria: the trivial equilibrium and a low- (unstable) and high- (stable) interior equilibria (analogous to Fig. 2-1b, but the plant species' isocline is unimodal). Although it is possible to derive analytical solutions for the interior equilibria, they are sufficiently complicated to render the stability analysis intractable.

Three-species community module:

The dynamics of a three-species community with density-dependent mortality and a saturating rate of benefit acquisition are given by:

$$\frac{dP_I}{dt} = P_I\left(r_{P_I} - I_{P_I}P_I + \frac{m_{P_IA}A}{1+A}\right) \qquad \text{(B.9)}$$

$$\frac{dP_R}{dt} = P_R\left(r_{P_R} - I_{P_R}P_R + \frac{m_{P_RA}A}{1+A}\right)$$

$$\frac{dA}{dt} = A\left(r_A - I_AA + \frac{m_{AP_I}P_I}{1+P_I} + \frac{m_{AP_R}P_R}{1+P_R}\right)$$

The model of a three-species community module yields seven equilibria: the trivial equilibrium (stable); a low-abundance (unstable) and high-abundance (stable) equilibrium associated with a pairwise interaction between the resident plant and animal species; a low-abundance (unstable) and high-abundance (stable) equilibrium associated with a pairwise interaction between the invader plant and animal species; and a low-abundance (unstable) and high-abundance (stable) equilibrium associated with three species coexistence. The invasion criterion for this model is: $r_{P_I} + \frac{m_{P_I A} A^*}{1+A^*} > 0$, which if A^* is relatively large, tends towards: $m_{P_I A} > \left|r_{P_I}\right|$. Therefore, extinction only occurs in the extreme case where a species cannot acquire sufficient benefits to overcome its inherent tendency to go extinct (see the discussion section in the main text for details). Although it is possible to derive analytical solutions for the equilibria they are too cumbersome to allow a stability analysis.

Appendix C: Comparison between our framework and previous models

The purpose of this appendix is to show that for a given intrinsic growth rate (*r*), species requires greater rates of benefit acquisition (*m*) to persist in previous models than in our framework, even when $I = \alpha$ (Fig. 2-5). We illustrate this difference by deriving the minimum value of $m_{PA}A$ required for the plant to have a positive per capita growth rate (i.e., $(dP/dt)/P > 0$) in a pairwise interaction. We do this by solving $r_P - I_P P + m_{PA}A/(1 + m_{PA}\tau_P A) > 0$ (previous model) and $r_P + m_{PA}A\,/(1 + m_{PA}\tau_P A + \alpha_P P^2) > 0$ (our model) for $m_{PA}A$:

$$m_{PA}A > (|r_P| + I_P P)/(1 - \tau_P I_P P - |r_P|\tau_P) \quad \text{(C.1; previous model)}$$

$$m_{PA}A > |r_P|(1 + \alpha_P P^2)/(1 - |r_P|\tau_P) \quad \text{(C.2; our model)}$$

If the minimum value of $m_{PA}A$ is the same in both models, then:

$$(|r_P| + I_P P)/(1 - \tau_P I_P P - |r_P|\tau_P) = |r_P|(1 + \alpha_P P^2)/(1 - |r_P|\tau_P) \quad \text{(C.3)}$$

Cross multiplying yields:

$$(|r_P| + I_P P)(1 - |r_P|\tau_P) = |r_P|(1 + \alpha_P P^2)(1 - \tau_P I_P P - |r_P|\tau_P) \quad \text{(C.4)}$$

Which simplifies to:

$$I_P P = |r_P| \alpha_P P^2 (1 - \tau_P I_P P - |r_P| \tau_P) \tag{C.5}$$

Rearranging terms so that all terms associated with the previous model are on the left side of the equation and all terms associated with our model are on the right side of the equation yields to simplification reported in the main text:

$$I_P / (1 - \tau_P I_P P - |r_P| \tau_P) = |r_P| \alpha_P P \tag{C.6}$$

The plant species can persist only if it can acquire sufficient benefits to increase when rare (i.e., when $P \approx 0$); hence, this condition becomes:

$$I_P / (1 - |r_P| \tau_P) = 0 \tag{C.7}$$

Thus, $I_P / (1 - |r_P| \tau_P) \approx 0$ for the minimum value of $m_{PA} A$ to be equal in both models *and* be sufficient for the plant species to increase when rare. Since $I_P \neq 0$, the minimum value of $m_{PA} A$ must always be greater in previous models than it is in our framework. Thus, persistence requires a lower rate of benefit acquisition (*m*) for a given value of *r* in our framework.

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CHAPTER 3

Effects of temperature and resource variation on insect population dynamics: the bordered plant bug (*Largus californicus*) as a case study

Abstract

In species with complex life cycles, population dynamics are the result of developmental time delays that cause delays in the operation of negative feedback processes (e.g., intraspecific competition), which lead to intrinsically generated cycles, and seasonal forcing due to abiotic environmental variation (e.g., temperature). Elucidating how the interplay between density-dependent dynamics and environmental variability affects population dynamics is important, not only in understanding how species persist in variable environments, but also in predicting species' responses to perturbations in their typical biotic and abiotic environment. Here we investigate this issue in the bordered plant bug, a *Hemipteran* herbivore inhabiting the California coastal sage scrub community.

In the bordered plant bug, juvenile developmental is comparable to adult longevity, which theory predicts should be near the stability boundary between stable (non-oscillatory) dynamics verses delayed feedback cycles. However, field populations show high variability in adult density, suggesting that seasonal environmental variation may play a role in generating the observed population dynamics.

We investigate whether variability in adult density is the result of density-dependent dynamics interacting with seasonal variation in temperature and resource availability. We develop a stage structured delay model which contains mechanistic descriptions of the temperature responses of life history traits (reproduction, development, mortality) and in which fecundity is affected by both intraspecific competition and temporal variation in resource

availability. We parameterize the model with experimental data on the temperature responses of life history and competitive traits and compare model dynamics with independent field data.

We report two key results. First, we find that intraspecific competition is strongest at temperatures that are optimal for reproduction. To our knowledge, this is the first time that a unimodal temperature response of intraspecific competition has been demonstrated empirically. Second, we find that while temperature and resource variability can each interact with development-induced delays in self-limitation to generate population fluctuations, it is the interaction between all three factors that generate the pattern of dynamics observed in the field. Our results highlight the importance of considering how multiple environmental factors interact with nonlinear density-dependent processes to generate patterns of population dynamics observed in nature.

Introduction

A long-standing challenge in ecology is to understand the mechanisms that drive species' population dynamics. In organisms with complex life cycles, time delays due to juvenile development lead to delays in the operation of negative feedback processes (e.g., intraspecific competition), which can generate population cycles (Gurney et al. 1983, Nisbet and Gurney 1983, Murdoch and Walde 1989, Gurney and Nisbet 1998, Murdoch et al. 2003). Intrinsic density-dependent dynamics can be modulated by species' responses to variability in the abiotic (e.g., temperature) and/or abiotic (e.g., resource availability) environment. For instance, temperature variation directly affects the population dynamics of ectotherms via the temperature responses of their underlying life history traits (Van der Have 2002, Ragland and Kingsolver 2008, Kingsolver 2009, Kingsolver et al. 2011, Amarasekare and Sifuentes 2012). Understanding how the interplay between density-dependent dynamics and environmental variability affects population dynamics is important for determining the mechanisms by which species persist in variable environments and for predicting how species may respond to atypical environmental variability. Here we use the bordered plant bug (*Largus californicus*), a Hemipteran herbivore inhabiting the California coastal sage scrub, as a model system to investigate this issue.

We begin by describing the population dynamics and natural history of the bordered plant bug as well as background data on the study system. Based on these data, we then consider two hypotheses for the observed population dynamics, which we investigate by developing stage structured delay differential equation (DDE) models that are parameterized with experimental data. Finally, we compare model dynamics with independent field time-series data.

Materials and Methods

Study system

Population dynamics

We have been studying the bordered plant bug at the Main Campus Reserve of the University of California, Santa Barbara. This population is essentially a closed system because the reserve is a small (150 *m* by 250 *m*) region of coastal bluffs enclosed by the Pacific Ocean and a lagoon within a highly urbanized area. The population was monitored in 1986 by Booth (1990) and we censused the same population 25 years later in 2011 (see App. S1 for census protocols).

The bordered plant bug has a stage structured life cycle consisting of eggs, five nymphal instars, pre-reproductive adults, and reproductive adults. All life stages exhibit fluctuations in density (Coefficient of Variation: 1986) nymphs: 2.6, adults: 1.3; 2011) nymphs: 2.2, adults: 1.5). We observe a distinctive pattern in the dynamics of the adult stage: adults are extremely abundant during the summer and fall, but are completely absent in late-spring and late-summer (Fig. 3-1). Our objective here is to explain this pattern in adult density.

Theory predicts that species with stage structured life cycles will exhibit cycles if juvenile development (τ_J) is long relative to adult longevity (τ_A) (Murdoch et al. 2003). For example, the flour beetle (*Tribolium castaneum*) has a developmental period of 93.4 days and an adult lifespan of 127.5 days ($\tau_J/\tau_A = 0.7$) (Howe 1956, Soliman and Lints 1975) and adult density is remarkably stable when resources are plentiful (Costantino and Desharnais 1991). In contrast, California red scale (*Aonidiella aurantii*) has a developmental period of ~40 days and an adult lifespan of ~33 days ($\tau_J/\tau_A = 1.2$) and exhibits delayed feedback cycles (Murdoch et al. 1987). We find that the bordered plant bug has a developmental period of 80 $\pm$ 4.8 days and an adult lifespan of 81 $\pm$ 6.2 days at 23°C ($\tau_J/\tau_A = 1.0$). Hence, the bordered plant bug is an interesting case study because it lies near the stability boundary between where we would expect to see stable (i.e., non-oscillatory) dynamics verses cycles (Murdoch et al. 2003).

Natural History

The bordered plant bug consumes a variety of plant species (Booth 1990), but mainly feeds on bush lupine (*Lupinus arboreus*) at this site (unpublished data). Bugs are attacked by an egg parasitoid (*Gryon largi*), a parasitoid wasp (*unidentified species*), and a tachinid fly (*Trichopoda pennipes*). Our goal here is to understand the factors that drive plant bug population dynamics. As a first step, we investigate the bottom-up processes (resource variation) and environmental factors (temperature variation) that influence plant bug population dynamics in the absence of top-down effects from its natural enemies.

Background Data

Environmental variability

Two environmental factors that are likely to influence plant bug dynamics are temperature and resource variation, which we quantify by fitting functions to data (Fig. 3-2). Monthly temperature data was obtained from the Western Regional Climate Center (http://www.wrcc.dri.edu/). Temperature, $T(t)$, (in units of degrees Kelvin) is given by the following function:

$$T(t) = m_T - a_T \cos(2\pi t/365 - s_T) \qquad (1)$$

where m_T is the mean temperature, a_T is the amplitude of annual temperature variation, s_T is the shift in the cosine function, and t is the day of the year. Separate temperature functions were fit to monthly temperature data from 1986 and 2011, which coincide with the censuses (Fig. 3-2a,b).

Because plant bugs mainly consume new stems, flowers, and seed pods (Booth 1990), the availability of the preferred resource varies seasonally based on the phenology of bush lupine. Resource availability dramatically increases at the end of January following the winter rains (Harrison et al. 1986) and remains high until the end of the flowering season in July (Kittelson and Maron 2000) when bush lupine wilts and drops its seed pods (Strong et al. 1995).

We assessed resource availability in the field by determining the percent leaf-cover of 25 marked bush lupine shrubs during each census point. Shrubs were scored as follows: 3 (>80% leaf-cover), 2 (50-80% leaf-cover), 1 (20-50% leaf-cover), and 0 (<20% leaf-cover). Average leaf-cover during each census point was calculated by the sum of each shrubs' score divided by the maximum possible score of 75 (i.e., a score of 3 x 25 shrubs). Thus, leaf-cover varies from 0 (i.e., the average shrub has <20% leaf-cover) to 1 (i.e., the average shrub has >80% leaf-cover). We quantify resource availability by fitting phenomenological sinusoidal functions to the leaf-cover data obtained in the field. Resource availability, $Q(t)$, is given by the following functions:

$$Q(t) = \frac{1}{4}\left(\frac{|q_1(t)|}{q_1(t)} + 1\right)\left(\frac{|q_2(t)|}{q_2(t)} + 1\right) q_1(t) \qquad (2)$$

$$q_1(t) = -\cos\left(\cos\left(\pi\cos\left(\frac{\pi t}{365} - \frac{4\pi}{3}\right)\right)\right)$$

$$q_2(t) = -\cos\left(\pi\cos\left(\frac{\pi t}{365} - \frac{4\pi}{3}\right)\right)$$

where $q_1(t)$ gives the resource availability during the growing/flowering seasons and $q_2(t)$ defines the period of the year when resource availability is low. Note that $Q(t) = 0$ when $q_1(t)$ or $q_2(t)$ are negative (resource availability is low); $Q(t) = q_1(t)$ when both functions are positive (resource availability is high); and $Q(t)$ varies between 0 (few resources) and 1 (plentiful resources). We find that $Q(t)$ captures the resource availability determined in the field (Fig. 3-2c).

Laboratory experiments

To investigate how environmental variability affects plant bug population dynamics, we quantify the temperature responses of life history and competitive traits in laboratory experiments at four constant temperatures (18°C, 23°C, 26°C, and 30°C). Cultures of field-collected adult plant bugs were maintained at each temperature treatment and monitored daily. Per capita fecundity (b) was quantified as the eggs laid per adult density per time. Egg clutches were placed in new containers within the same temperature treatment. Upon hatching, nymphs were monitored daily. The development rate of each life stage i (τ_i) was quantified as the inverse of the stage duration (i.e., the average time for individuals from one life stage to develop into the next stage). The pre-reproductive stage is defined to be from when a female molts into an adult until she oviposites. Mortality (d_i) was quantified by $d_i = -\ln(s_i)/\tau_i$ where s_i is the stage-specific survivorship (i.e., the proportion of individuals that survived from one life stage to the next). See App. S2 for further details about experiment methodologies. Using data from these experiments, we now discuss the temperature responses and density-dependence of life history and competitive traits.

Temperature responses of life history traits

The mechanistic basis of life history trait responses to temperature is well-understood in the absence of competition (Van der Have 2002, Ragland and Kingsolver 2008, Angilletta 2009, Kingsolver 2009, Kingsolver et al. 2011). The per capita birth rate of most ectotherms exhibits a symmetric and unimodal response to temperature that is well-described by a Gaussian function:

$$b(T) = b_{T_{opt}} e^{-\frac{\left(T-T_{opt,b}\right)^2}{2{s_b}^2}} \qquad (3)$$

where b_{Topt} is the maximum reproductive rate, which is attained at an optimal temperature $T_{opt,b}$, s_b is the variability about the optimum, and T is temperature (in degrees Kelvin). We find that in laboratory experiments (see App. S2), fecundity exhibits a unimodal response to temperature with data providing a significant fit to a Gaussian function (Eq. 3, Fig. 3-3a). Reproduction is therefore greatest at intermediate temperatures and declines at higher and lower temperatures. The optimum temperature for reproduction is 23.9 $\pm$ 0.3°C, which is near the maximum temperature experienced by plant bugs in the field (1986: 24.3°C, 2011: 24.0°C; Fig. 3-2a,b).

In ectotherms, development rate (m) and mortality (d) exhibit monotonic temperature responses (Gillooly et al. 2001, Savage et al. 2004) given by the Boltzmann-Arrhenius function:

$$k_j(T) = k_{j,T}\, e^{A_{j,k}\left(\frac{1}{T_{j,k}} - \frac{1}{T}\right)} \qquad (4)$$

where $k_j(T)$ is the trait value (i.e., $k_j = m_j, d_j$) of life stage j at temperature T, $k_{j,T}$ is the trait value at a reference temperature $T_{j,k}$, and $A_{j,k}$ is the Arrhenius constant, which measures the temperature sensitivity of the trait; i.e., how fast the trait changes with increasing temperature. We find that development rate and mortality increase monotonically with temperature in a manner described by the Boltzmann-Arrhenius function (Eq. 4, Fig. 3-3b,c). Egg development is more sensitive to temperature (greater Arrhenius constant) than are nymphs or pre-reproductive adults (Fig. 3-3b). In contrast, nymphs suffer the greatest mortality and are most sensitive to temperature (Fig. 3-3c) because 1st and 2nd instars have extremely high mortality rates and are particularly sensitive to temperature (see Table 3-S1), likely since these stages are the first to be mobile, feed, and molt.

Density-dependence of life history traits

Density-dependence may arise via the effects of competition on fecundity, development, or mortality. Fecundity is predicted to decrease with increasing adult density with empirical data commonly found to fit an exponential function: $f(A) = be^{-\alpha A}$ (Gurney and Nisbet 1998, Murdoch et al. 2003), where $f(A)$ gives fecundity at adult density A, b is the reproductive rate in the absence of competition, and α describes the decline in fecundity with increasing adult density (i.e., the per capita competitive effect). We find that fecundity declines as adult density increases with data providing a significant fit to this exponential function (Fig. 3-4a).

The development rate is also predicted to decrease with increasing density (Van der Have and de Jong 1996, Van der Have 2002), while mortality is predicted to increase with density (Murdoch et al. 2003). We quantify the effects of density on development and mortality using a linear ($c_J(J) = k_J + \alpha_J J$) and nonlinear ($c(J) = k_J e^{\alpha_J J}$) function where $c_J(J)$ depicts the density-dependence of trait k (i.e., $k = m$, d), J is the density of the life stage at which competition arises, k_J is the trait value in the absence of competition, and α_J is the per capita competitive effect. We find that density has no effect on either development rate (Fig. 3-4b) or mortality (Fig. 3-4c).

Temperature response of competitive traits

There are currently no empirical data on the temperature response of competitive traits; however, theory suggests two hypotheses for how temperature may affect the strength of competition. First, metabolic scaling theory acknowledges that competition is likely a unimodal function of temperature, but focuses on the part of the curve in which the strength of competition increases monotonically with temperature (Savage et al. 2004). Second, ecological theory predicts that competitive traits exhibit a unimodal response to temperature such that competition is strongest near the optimal temperature for reproduction (Begon et al. 2005).

We quantify the temperature response of competition, $\alpha(T)$, by fitting the function $be^{-\alpha A}$ to data on adult fecundity in laboratory experiments at four constant temperatures (see App. S2; Fig. 3-S1a). We find that the strength of competition is a unimodal function of temperature with data providing a significant fit to a Gaussian function (Eq. 3; Fig. 3-5). Thus, competition is strongest at intermediate temperatures ($T_{opt,\alpha} = 23.3 \pm 0.3$ °C) near the optimum for reproduction ($T_{opt,b} = 23.9 \pm 0.3$ °C) and declines at both higher and lower temperatures.

Conceptual Framework

Based on these background data, we make the following hypotheses about the distinctive pattern observed in adult density in the field (i.e., adults are extremely dense during the summer and fall, but are completely absent in late-spring and late-summer; Fig. 3-1).

1. Adult density results from nonlinear dynamics due to time delays (in development) in the operation of negative feedback (e.g., self-limitation via intraspecific competition), which occur even in the absence of extrinsic environmental factors.
2. Adult density results from the interplay between nonlinear dynamics (due to developmental time delays) and environmental forcing driven by:
   - *(a)* abiotic variability (seasonal temperature variation)
   - *(b)* biotic variability (seasonal resource variation)
   - *(c)* abiotic *and* biotic variability (seasonal temperature *and* resource variation).

If density results from nonlinear dynamics via time delays in the operation of negative feedback, we expect to see stable (non-oscillatory) dynamics if adult longevity is high relative to juvenile development and delayed feedback cycles if otherwise (Murdoch et al. 2003). If density results from the interplay between nonlinear dynamics and environmental variation in temperature and/or resource availability, we expect more complex dynamics due to seasonal forcing interacting with density-dependent population dynamics. To determine whether it is this interplay that drives the observed dynamics, we need to develop a theoretical framework that integrates both time delays in the operation of negative feedback and the effects of seasonal environmental forcing.

Mathematical Framework

We develop a stage structured delay-differential equation (DDE) model to investigate plant bug population dynamics. DDE models provide a natural way to describe the dynamics of species with stage structured life cycles (Gurney et al. 1983, Nisbet and Gurney 1983, Gurney and Nisbet 1998, Murdoch et al. 2003). The model is mechanistic because it incorporates temperature response functions for all parameters and explicitly considers variability in developmental delays due to temperature variation. We parameterize the model with data from laboratory experiments and use the parameterized model to generate predictions about plant bug population dynamics under our two hypotheses. We then compare the predicted time-series with those observed in the field. Although motivated by the biology of the bordered plant bug, the models can be easily modified to investigate the dynamics of other ectotherms that inhabit variable environments.

The model incorporates 8 life stages: eggs (*E*), five nymphal instars (N_i; $i = 1,\ldots,5$), pre-reproductive adults (*P*), and reproductive adults (*R*). All rates vary according to the ambient temperature ($T(t)$; Eq. 1). The dynamics of the stage structured DDE model are given by:

$$\frac{dE(t)}{dt} = b\big(T(t)\big)\,Q(t)\,R(t)\,e^{-\alpha(T(t))R(t)} - g_E(t) - d_E\big(T(t)\big)\,E(t) \qquad (5)$$

$$\frac{dN_i(t)}{dt} = g_{N_{i-1}}(t) - g_{N_i}(t) - d_{N_i}\big(T(t)\big)\,N_i(t)$$

$$\frac{dP(t)}{dt} = g_{N_5}(t) - g_P(t) - d_P\big(T(t)\big)\,P(t)$$

$$\frac{dR(t)}{dt} = g_P(t) - g_R(t) - d_R\big(T(t)\big)\,R(t)$$

where $b(T(t))$ is the temperature response of reproduction, $Q(t)$ gives the effect of resource variability on fecundity ($Q(t) = 1$ if resource availability remains constant or $Q(t)$ is a sinusoidal function (Eq. 2) if resource availability varies seasonally); $\alpha(T(t))$ is the temperature response of competition, $g_j(t)$ describes maturation through stage j ($j = E, N_1,\ldots,N_5, P$; note that N_0 is the egg stage and $g_R(t)$ is adult senescence), and $d_j(t)$ is the mortality of stage j. There are two key points about the model. The first pertains to the effects of resource variation, $Q(t)$, on bug dynamics. We assume that resource availability predominantly affects reproduction (and not development and mortality) because fecundity is the only trait to exhibit density-dependence in laboratory experiments (Fig. 3-4). As we were unable to directly quantify how fecundity varies with resource availability, we assume that the estimates of fecundity in the laboratory are the maximum values possible in the field (i.e., when resources are plentiful; $Q(t) = 1$) since bugs were given food *ad libitum* in laboratory experiments. Thus, fecundity varies linearly with resource availability; e.g., if $Q(t) = 0.5$, fecundity is half of the predicted value due to temperature alone; i.e., 0.5 $b(T(t))$.

The second key point pertains to development rates. Because development is temperature-dependent, stage duration is not constant over time, and hence, time delays are variable. Note that we do not consider variation in development rates between individuals; however, we expect such variation to be small relative to the variation in development rates due to temperature. We use the following maturation functions based on theory on stage structured models with dynamically varying time delays (Gurney et al. 1983, Nisbet and Gurney 1983):

$$g_E(t) = b\big(T(t')\big)Q(t')R(t')e^{-\alpha\left(T(t')\right)R(t')}\,\frac{m_E\big(T(t)\big)}{m_E\big(T(t')\big)}\,s_E(t) \text{ where } t' = t - \tau_E(t) \qquad (6)$$

$$g_j(t) = g_{j-1}\left(t - \tau_j(t)\right)\frac{m_j\big(T(t)\big)}{m_j\Big(T\big(t-\tau_j(t)\big)\Big)}\,s_j(t)$$

where

$$\frac{ds_j(t)}{dt} = s_j(t)\left(\frac{m_j\big(T(t)\big)\,d_j\Big(T\big(t-\tau_j(t)\big)\Big)}{m_j\Big(T\big(t-\tau_j(t)\big)\Big)} - d_j\big(T(t)\big)\right) \qquad (7)$$

$$\frac{d\tau_j(t)}{dt} = 1 - \frac{m_j\big(T(t)\big)}{m_j\Big(T\big(t-\tau_j(t)\big)\Big)}$$

Note that $s_j\,(t)$ describes through-stage survivorship of stage j and $\tau_j\,(t)$ gives the time delay due to the development of stage j. Maturation of eggs to 1st nymphal instars at time t (i.e., $g_E\,(\mathrm{T},t)$) is a function of the rate at which eggs were laid a time $\tau_E\,(t)$ ago and the survivorship through the egg stage (i.e., $\mathrm{s}_E\,(t)$). Maturation of successive nymphal stages and pre-reproductive adults (i.e., $g_j\,(\mathrm{T},t)$) are functions of the rate at which individuals mature from the previous life stage and through-stage survivorship. The ratio $m_j\,(T(t))/m_j\,(T(t'))$ determines how temperature affects maturation (i.e., if temperature increases over the duration of life stage j, this ratio is greater than one, and more individuals survive through the stage, while if temperature decreases over the stage duration, this ratio is less than one, and fewer individuals survive through the stage). Note that survivorship, $s_j\,(t)$, and developmental time delays, $\tau_j\,(t)$, are time-varying differential equations (see Nisbet and Gurney 1983; App. S3 for further details). Models are compared for goodness-of-fit with the census data using Akaike's Information criterion, $\mathrm{AIC_C}$ (Table 3-1).

Results

Hypothesis 1: Adult density results from nonlinear dynamics due to time delays (in development) in the operation of negative feedback

To predict bug dynamics in the absence of temperature and resource variability, we evaluated the stage structured model (Eq. 5) in a constant environment (i.e., $T(t) = m_T$ and $Q(t) = 1$). In sharp contrast to the patterns in adult density observed in the field, the model predicts a transient period of damped oscillations followed by a stable steady state in the long-term (Fig. 3-6a,b). Oscillations arise from time delays (due to development) in the operation of negative feedback (due to intraspecific competition). Note that the model predicts much greater bug densities than are observed in the field (Fig. 3-6i,j) because, in the model, adults reproduce throughout the year.

Hypothesis 2: adult density results from the interplay between density-dependent population dynamics and environmental variability.

(a) Seasonal temperature variation

Seasonal temperature forcing causes fluctuations in density with a period of roughly one year (Fig. 3-6c,d). Because the mortality of 1st and 2nd nymphal instars is most sensitive to increasing temperature (Table 3-S1), their densities are greatest in the winter (November – January) when mortality is reduced due to low temperatures. As a result, successive nymphal stages peak in density during the spring (February – April) and adult density is greatest during the summer (May – July) when temperatures approach the optimum for reproduction.

Comparing the predicted time series with field census data reveals two mismatches. First, the model predicts that nymphs are present in the winter, when in the field nymphs are completely absent during winter. Second, the predicted densities of all life stages are much greater than is observed in the field. These mismatches are likely due to the model assumption that resources remains plentiful year-round, which would allow adults to reproduce, and nymphs to survive, throughout the year. Thus, temperature variation alone does not explain the observed dynamics.

(b) Seasonal resource variation

A model with resource variability but no seasonal temperature variation (i.e., $T(t) = m_T$) captures the gross patterns observed in the field, but greatly underestimates bug density (Fig. 3-6e,f). Overwintering adults reproduce in February when resource availability increases (Fig. 3-2c). This initial juvenile cohort develops during the spring (February – April) and adults reproduce during the summer (June – July). Reproduction ceases in August as resource availability declines (Fig. 3-2c). The second juvenile cohort develops during the summer/fall (June – September) and matures into adults by October. While this model captures the overall trend in plant bug dynamics, it greatly underestimates density such that extinction occurs within a few years. Extinction occurs because adults cannot maintain sufficient density after overwintering to replace themselves the following year, perhaps signifying an important role for seasonal temperature variation. The key point is that this model predicts that seasonal variation in resource availability determines the period of the year in which reproduction occurs, and hence, when nymphal stages are present. Resource variation alone, however, does not explain the observed bug densities, likely because reproduction is limited to a subset of the year, while mortality remains fairly high year-round.

(c) Seasonal temperature and resource variation

The full model with variability in temperature and resource availability captures both the qualitative pattern of population dynamics and the range of bug densities observed in the field (Fig. 3-6g,h). Adults cannot reproduce during the fall or winter (September – January) due to insufficient resource availability (Fig. 3-2c); thus, nymphs are not present in the winter (November – January). Overwintering adults suffer reduced mortality due to low temperatures, and thus, survive long enough to reproduce when resource availability increases in February following the winter rains (Fig. 3-2c) and before senescing by April. The initial juvenile cohort develops in the spring (February – May) and matures into adults by June. Reproduction ceases in August as resource availability declines following the flowering seasons (Fig. 3-2c) and adults have senesced by September because of increased mortality due to elevated summer temperatures. The second juvenile cohort develops in late-summer (July – September) and has matured into adults by October. Bug densities are greater in the second cohort because reproduction is greatest in the summer as temperatures approach the optimum for reproduction. There are two key model results. First, bug densities are driven by both resource availability (via its effects on fecundity) and temperature (via the temperature responses of reproduction, development, and mortality). Second, bug dynamics arise from both resource availability (which determines the periods of the year in which reproduction occurs) and temperature (which determines stage duration via the temperature responses of development and mortality). Thus, the model predicts that plant bug population dynamics arise from the interplay between nonlinear dynamics and environmental variation in temperature and resource availability.

Discussion

In species with complex life cycles, juvenile development leads to time delays in self-limitation that can generate intrinsic population cycles (Murdoch et al. 2003). Environmental variability (e.g., in temperature, resource availability) can interact with such delays, leading to patterns of population dynamics that deviate from those expected under intrinsic density-dependent dynamics. Understanding how environmental variability interacts with time delays is important for predicting population dynamics not only under typical environmental regimes, but also under atypical environmental perturbations due to natural or anthropogenic factors. Here we investigate this issue in the bordered plant bug (*Largus californicus*), a Hemipteran herbivore inhabiting the California coastal sage scrub community, as a model system.

The bordered plant bug has a stage structured life cycle consisting of eggs, five nymphal instars, pre-reproductive adults, and reproductive adults. Adult longevity is roughly equal to the juvenile developmental period, which theory predicts should lead to either stable (i.e., non-oscillatory) dynamics or cycles (Murdoch et al. 2003). Yet, field census data shows high variability in adult density, suggesting that environmental factors may have a strong influence on the dynamics. Our objective here is to explain the observed patterns in adult density.

We report two key results. The first result pertains to the joint effects of temperature and intraspecific competition on fecundity. We find that the effects of competition on fecundity are strongest at intermediate temperatures near the optimum for reproduction and decline at both lower and higher temperatures. Thus, competition suppresses reproduction the furthest at the temperatures at which reproduction is greatest. To our knowledge, this is the first time that a unimodal temperature response of intraspecific competition has been demonstrated in an empirical system. The second result pertains to population dynamics. We find that while both temperature and resource availability interact with density-dependent dynamics to induce population fluctuations, it is the interplay between intrinsic population dynamics and seasonal temperature *and* resource variation that generates the distinctive pattern in adult density observed in the field. Bug densities and population dynamics arise from seasonal variation in both resource availability (which determines when reproduction occurs and affects the magnitude of fecundity) and temperature (via the temperature responses of life history and competitive traits).

A few studies have investigated the effects temperature and resource variation on population dynamics using a combination of mathematical models and either laboratory experiments or field manipulations. We discuss four key previous studies. (*i*) Ritchie (1996) developed a non-delay model with temperature-dependent parameters and resource limitation which predicts that species suffer increased mortality and reduced density under elevated temperatures. Model predictions were validated by field experiments on grasshoppers under three thermal treatments. (*ii*) Ritchie (2000) studied grasshopper dynamics in the field in response to nitrogen addition and found that temperature has a greater effect on grasshopper density than does resource variation.

(*iii*) Reigada and Godoy (2006) studied the effects of larval density on the dynamics of the fly *Chrysomya megacephala* at two temperatures in a laboratory environment and found that fecundity declines with increasing density and/or temperature, which may lead to a transition from a two-point limit cycle to a stable equilibrium. (*iv*) Law and Belovsky (2010) studied the effects of density and temperature on the dynamics of the grasshopper *Camnula pellucida* in the field. They found that peak survival in low-density treatments occurs at higher temperatures than for high-density treatments, indicating that the strength of intraspecific competition varies with temperature; however, the temperature response of competition was not determined. Previous studies incorporate only a few (2-3) temperatures, do not quantify the temperature responses of life history or competitive traits, and fail to link data with realistic models that explicitly consider temperature effects on the developmental delays that characterize ectotherm life cycles. We have developed a mechanistic mathematical framework that incorporates measurable temperature response functions for all parameters, explicitly considers variability in developmental delays due to temperature variation, and is well-linked with independent field census data.

The work presented here suggests several important future directions. Here we discuss two possible future directions, the first of which relates to host-parasitoid interactions. This study underscores the important roles of bottom-up processes (resource availability) and environmental factors (temperature) on species' dynamics. It does not, however, consider the effects of top-down processes such as natural enemies, which are important to gain a full understanding of how temperature and other environmental factors affect this insect community. Intriguingly, a model with both temperature and resource variation captures the overall patterns observed in nature, but tends to overestimates bug density (Fig. 3-6g,h), perhaps signifying a key role for natural enemies in suppressing plant bug density. Thus, we suggest that future work should incorporate natural enemies within the mathematical framework described here. The bordered plant bug and its parasitoids are a useful study system for investigating host-parasitoid dynamics in variable environments because plant bugs are attacked by multiple natural enemies, some of which parasitize different host life stages and some that parasitize similar host life stages.

The second future direction we discuss here pertains to predicting how ectotherms respond to atypical environmental variability, which is an important issue in conservation given projected temperature variation due to climate change (Bale et al. 2002, Walther et al. 2002, Root et al. 2003, Parmesan 2006, Kingsolver 2009, McMahon et al. 2011, Kingsolver et al. 2011). Here we model plant bug dynamics under temperature regimes determined in the field. An important future direction is to use this framework to predict species' dynamics under various temperature regimes predicted under different climate change scenarios (IPCC 2007). This framework is particularly amenable to investigating the effects of climate change on ectotherm dynamics because all parameters are empirically determined functions of temperature and other forms of variation (e.g., increasing mean and/or variance) can be easily incorporated within the model.

In conclusion, this study serves as a first step towards investigating how the interplay between intrinsic dynamics and extrinsic environmental variability affect ectotherm population dynamics. It also provides a conceptual foundation for future research on the dynamics of host-parasitoid communities and species' responses to atypical environmental perturbations.

Acknowledgements

We would like to thank Lisa Stratton at the Main Campus Reserve of the University of California, Santa Barbara, and Dr. Cristina Sandoval at the Coal-Oil Point Natural Reserve for access to field sites. This research was supported by NSF grant DEB-0717350 and a Complex Systems Scholar Grant from the James S. McDonnell Foundation to P.A.

Figures.

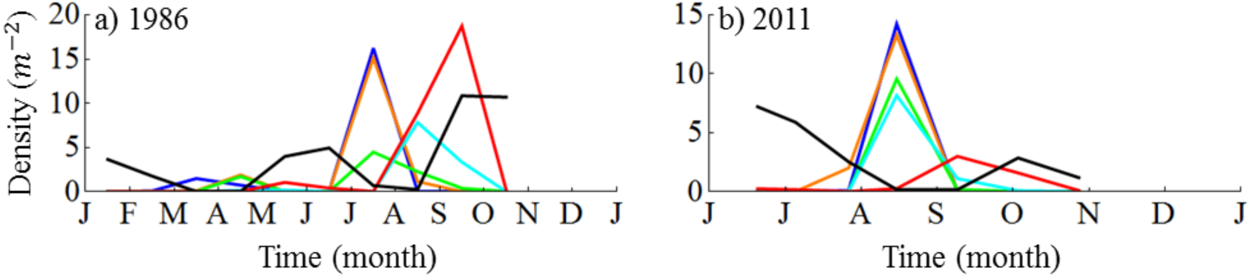

Figure 3-1. Time-series plots show the density of plant bug life stages (1st instar (blue line), 2nd instar (orange line), 3rd instar (green line), 4th instar (cyan line), 5th instar (red line), and adults (black line)) from the Main Campus Reserve at the University of California, Santa Barbara. Panel (a) is census data collected by Booth (1990) from January to October, 1986, and panel (b) is data that we collected from May to November, 2011 (see App. S1 for census protocols).

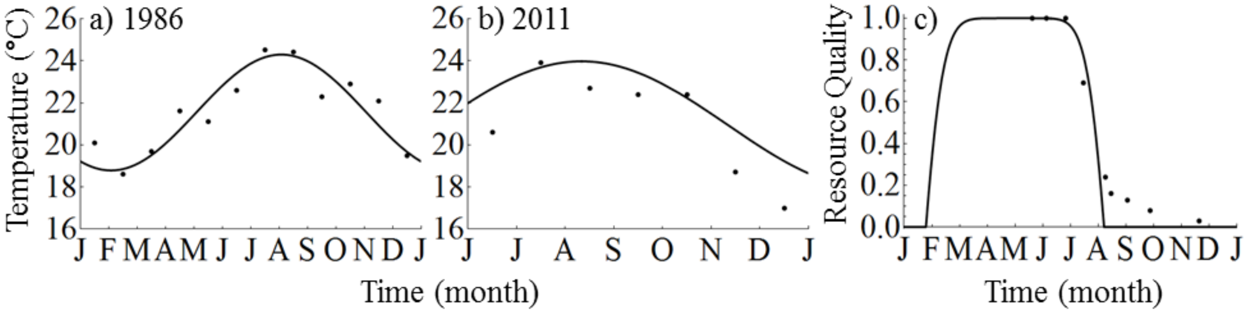

Figure 3-2. Seasonal variation in temperature and resource availability are quantified by fitting functions to data on monthly temperatures in 1986 (a) and 2011 (b), and to field data on resource availability (c). Temperature functions are fit via nonlinear regression: (a) 1986 (m_T = 294.5 ± 0.3, $p < 0.001$, a_T = 2.8 ± 0.4, $p < 0.001$; s_T = 0.2π ± 0.04π, $p < 0.001$; $n = 12$); (b) 2011 (m_T = 294.0 ± 0.4, $p < 0.001$, a_T = 3.0 ± 0.5, $p < 0.001$; s_T = 0.2π ± 0.05π, $p < 0.001$; $n = 12$). Resource availability is determined by the percent leaf-cover of 25 marked bush lupine shrubs.

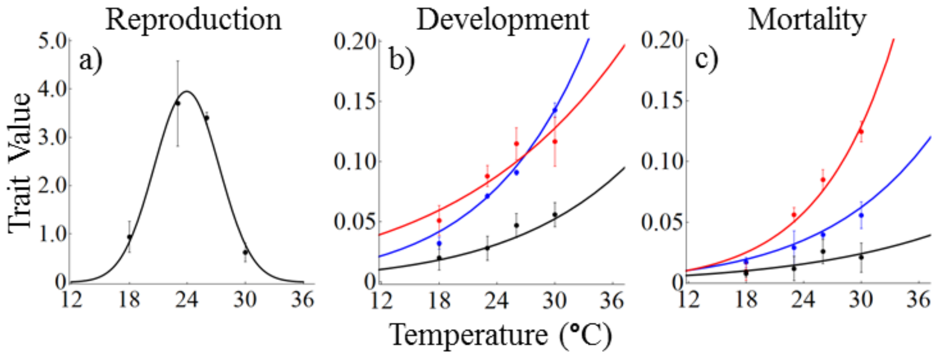

Figure 3-3. Temperature responses of life history traits. Reproduction (panel a) is described by a Gaussian function (Eq. 3), while development (panel b) and mortality (panel c) are described by the Boltzmann-Arrhenius function (eq. 4). Panel (a): reproduction (nonlinear regression: b_{Topt} = 4.0 ± 0.2, $p = 0.04$, $T_{opt,b}$ = 296.9 ± 0.3, $p < 0.05$; s_b = 3.4 ± 0.4, $p < 0.05$; $n = 4$ temperatures). Development (panel b): eggs (blue; nonlinear regression: $m_{E,T}$ = 0.07 ± 0.1, $p = 0.04$, $T_{E,m}$ = 296.3 ± 0.3, $p = 0.01$; $A_{E,m}$ = 10,000 ± 1,100, $p = 0.07$; $n = 4$ temperatures); nymphs (red; nonlinear regression: $m_{\bar{N},T}$ = 0.08 ± 0.01, $p < 0.001$, $T_{\bar{N},m}$ = 295.5 ± 1.0, $p = 0.002$; $A_{\bar{N},m}$ = 5,600 ± 1,100, $p = 0.02$; $n = 4$ temperatures); and pre-reproductive adults (black; nonlinear regression: $m_{E,T}$ = 0.03 ± 0.002, $p = 0.06$, $T_{A,m}$ = 294.6 ± 1.0, $p = 0.03$; $A_{A,m}$ = 7,700 ± 1,200, $p = 0.10$; $n = 4$ temperatures). Mortality (panel c): eggs (blue; nonlinear regression: $d_{E,T}$ = 0.03 ± 0.001, $p = 0.02$, $T_{E,d}$ = 297.0 ± 0.2, $p = 0.01$; $A_{E,d}$ = 8,500 ± 500, $p = 0.04$; $n = 4$ temperatures); nymphs (red; nonlinear regression: $d_{\bar{N},T}$ = 0.05 ± 0.01, $p = 0.03$, $T_{\bar{N},d}$ = 295.9 ± 1.3, $p = 0.003$; $A_{\bar{N},d}$ = 12,000 ± 2,700, $p = 0.05$; $n = 4$ temperatures); and adults (black; nonlinear regression: $d_{E,T}$ = 0.012 ± 0.004, $p = 0.06$, $T_{A,d}$ = 295.3 ± 3.8, $p = 0.03$; $A_{A,d}$ = 6,400 ± 2,300, $p = 0.07$; $n = 4$ temperatures). See Table 3-S1 for further details.

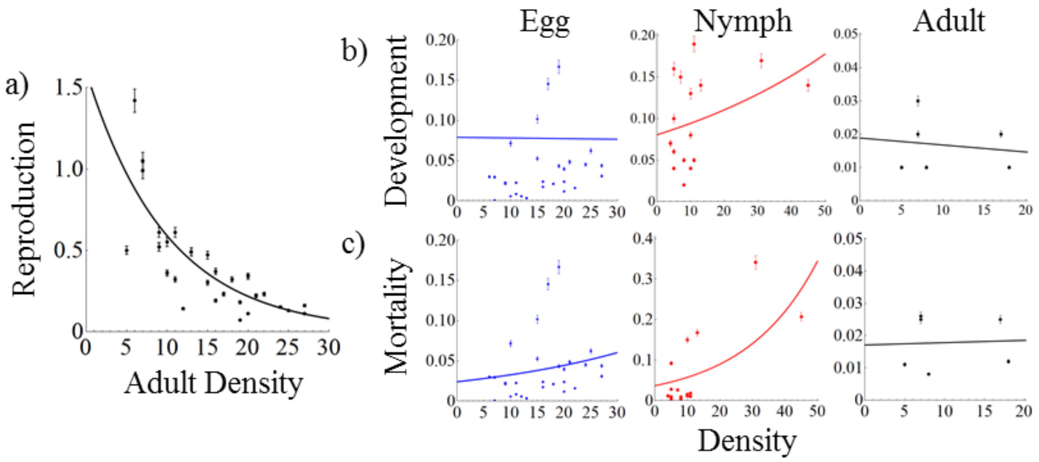

Figure 3-4. Density-dependence of life history traits. Panel (a): reproduction declines with adult density, likely due to intraspecific competition: $f(A) = be^{-\alpha A}$ where b is reproduction and α is the strength of intraspecific competition (nonlinear regression: b = 1.6 ± 0.3, $p < 0.001$; α = 0.010 ± 0.002, $p < 0.001$, n = 33). We determine whether density has an effect on development and/or mortality by whether the per capita competitive effect (α_J) provides a significant fit to the data. Panel (b): density does not have a significant effect on development: eggs (left panel; linear regression: p = 0.95; nonlinear regression: p = 0.95, n = 33); nymphs (middle panel; linear regression: p = 0.95; nonlinear regression: p = 0.08, n = 17); and pre-reproductive adults (right panel; linear regression: p = 0.78; nonlinear regression: p = 0.80, n = 6). Panel (c): density does not have a significant effect on mortality: eggs (left panel; linear regression: p = 0.28; nonlinear regression: p = 0.20, n = 33); nymphs (middle panel; linear regression: p = 0.40; nonlinear regression: p = 1, n = 12); and adults (right panel; linear regression: p = 0.93; nonlinear regression: p = 0.93, n = 6).

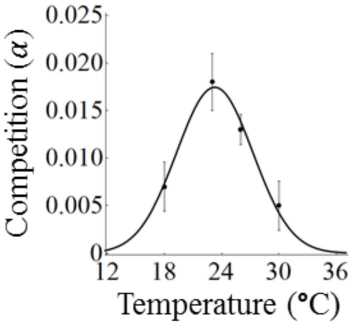

Figure 3-5. Temperature response of competitive traits. Competition (quantified by the decline in fecundity with adult density) exhibits a unimodal response to temperature, which is well-described by a Gaussian function (Eq. 3) (nonlinear regression: $\alpha_T = 0.02 \pm 0.001$, $p = 0.04$, $T_{opt,\alpha} = 296.3 \pm 0.3$, $p = 0.04$; $s_\alpha = 5.7 \pm 0.5$, $p = 0.05$; $n = 4$ temperatures).

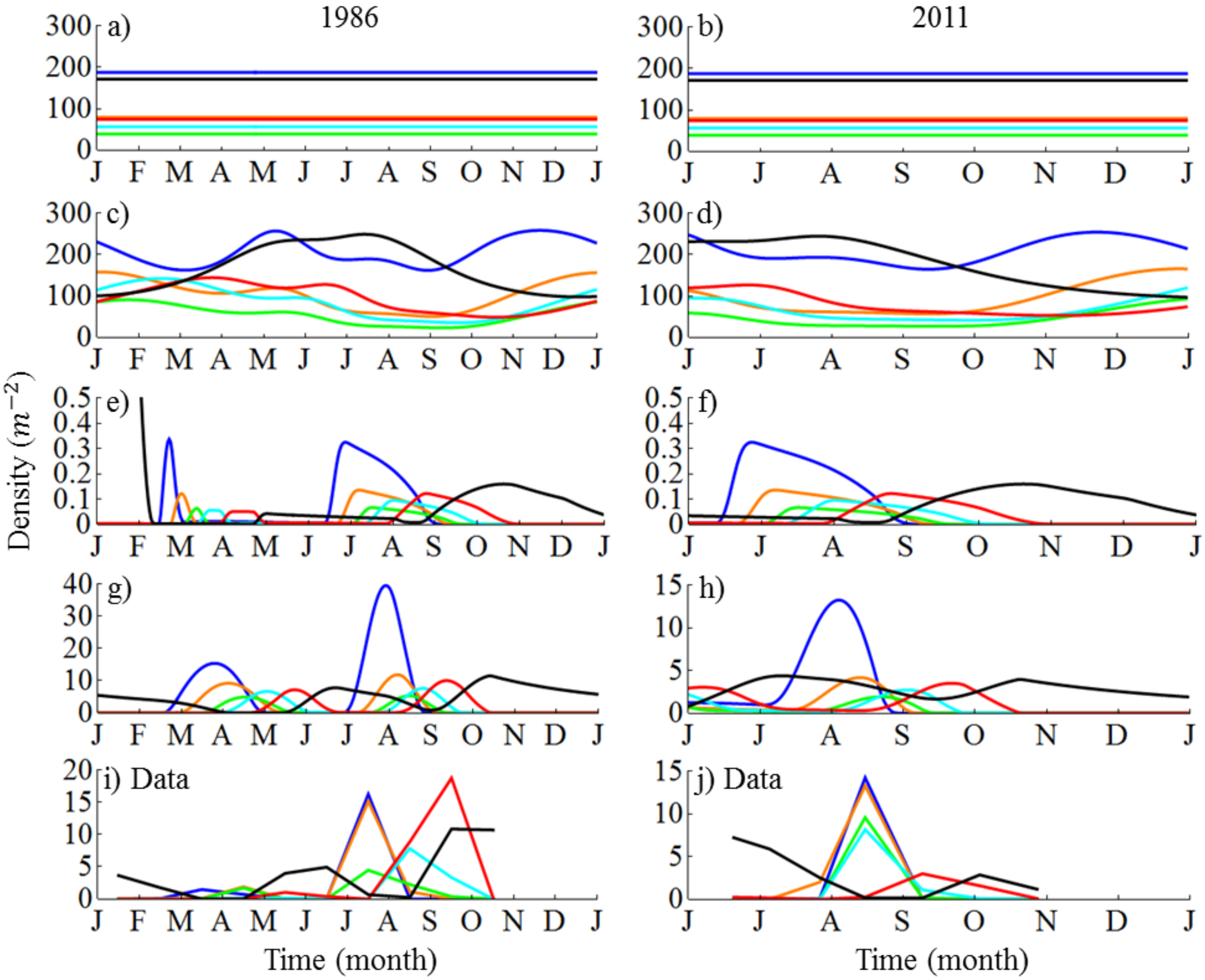

Figure 3-6. Plant bug population dynamics predicted by stage structured DDE models: 1st instar (blue), 2nd instar (orange), 3rd instar (green), 4th instar (cyan), 5th instar (red), and adults (black). Left panels show model predictions for the 1986 census period and right panels show model predictions for the 2011 census period: panels (a, b): constant environment (no temperature or resource variation), panels (c, d): seasonal temperature variation, panels (e, f): seasonal resource variation, panels (g, h): seasonal temperature *and* resource variation, panels (h, i): census data.

Table 3-1

Goodness-of-fit of stage structured DDE models to census data using Akaike's Information Criterion (AIC_C) corrected for small sample size and large number of parameters. Note that 18 parameters come from the basic model (without temperature or resource variation; Eq. 5), 40 parameters come from the temperature variation function (Eq. 1) and the temperature response functions (Eqs. 3,4), and 4 parameters come from the resource availability function (Eq. 2).

Model	**Parameters**	**AICc (1986)**	**AICc (2011)**
(*1*) No temperature or resource variation	18	85.4	64.4
(*2a*) Temperature variation	58	103.7	72.5
(*2b*) Resource variation	22	22.6	13.0
(*2c*) Temperature and resource variation	62	19.6	10.5

Supporting Information

The following Supporting Information is available for this article online.

Appendix S1: *Census protocols*

Bordered plant bug density was recorded on the Main Campus Reserve of the University of California, Santa Barbara, in 1986 and 2011. Booth (1990) performed monthly censuses from August, 1985, to October, 1986, by recording the number of individuals of each life stage along a 300 m by 0.5 m trail. We converted these counts to density by dividing the number of bugs by (300 x 0.5) m^2. We censused the same plant bug population from June to December, 2011, at roughly two-week intervals during the summer (June – September) and monthly intervals in the fall/winter (October – December). Because plant bugs were predominantly aggregated on/around bush lupine shrubs, we quantified the average number of bugs per shrub from 25 marked shrubs. For comparison purposes, we converted our data to density by calculating the average cover area of each of the 25 shrubs (unpublished data). Because our census techniques differ from Booth (1990), there may be biases when comparing the two datasets. For example, our census may overestimate bug densities relative to Booth (1990) because we did not include the areas between shrubs where bug densities are typical lower. Despite these differences in census protocol, bug populations exhibit qualitatively similar dynamics during both census periods. Furthermore, our goal is not necessarily to compare the two censuses, but rather to use the census data to motivate and validate mathematical models to investigate how environmental variability influences plant bug population dynamics. Note that egg density was not recorded as eggs are extremely difficult to find in the field. Census data from November – December are excluded from the analysis because accurate counts were not possible as adults overwinter within the leaf-litter and soil.

Appendix S2: *Experiment methodologies*

We quantified the temperature responses of reproduction, development, mortality, and intraspecific competition at four constant temperatures (18°C, 23°C, 26°C, and 30°C). All temperature treatments were conducted in incubators or walk-in chambers with a photoperiod of 12L:12D and a relative humidity of 40% ± 10%. Laboratory cultures of field-caught adult plant bugs were maintained in 19 x 14.2 x 9.3 cm rectangular plastic containers with wire mesh on the top for ventilation and observed every day. Several large pieces of fresh green iceberg lettuce were placed in each container every other day, so the bugs could feed. Egg clutches were removed to minimize the effects of cannibalism and the numbers of eggs per clutch were counted. Eggs were reared in 5 x 5 x 8.2 cm rectangular plastic containers with mesh caps for ventilation. Once the eggs hatched and the first instar nymphs emerged, small pieces of iceberg lettuce were placed in each container daily so the nymphs could feed. The nymphs were monitored every day for molts and/or deaths, which were removed from the containers. Due to extremely high mortality of 1st and 2nd instar nymphs, particularly at 18°C and 30°C, the experiment was repeated using field-caught 2nd through 5th instar nymphs. Cultures of 4th and 5th instar nymphs were maintained at all four temperatures, while cultures of 2nd and 3rd instar nymphs, which were much rarer in the field, were only maintained at 23°C and 26°C. Nymphs were allowed to acclimatize before molts and/or deaths were recorded. Cultures were maintained until the final individual in each container had recruited into the adult life stage and senesced or until all individuals had expired.

For each temperature, we quantified reproduction and intraspecific competition by fitting data to the function: $b(A) = b_0 e^{-\alpha A}$ where $b(A)$ gives per capita reproduction; b_0 is the reproductive rate, α describes intraspecific competition, and A is the adult density (Fig. 3-S2).

For each life stage, we quantified survivorship (the number of individuals that molt from a given stage divided by the number of individuals which recruited into the stage) and stage duration (the average number of days for an individual to develop to the next stage). Development is given by the inverse of stage duration and mortality is determined as follows. Survivorship (s_i) is given by $s_i = e^{-d_i \tau_i}$ where d_i and τ_i are, respectively, the mortality and stage duration of life stage i (see Gurney and Nisbet 1998 for derivation); solving for mortality yields: $d_i = -\ln(s_i)\,/\tau_i$. The pre-reproductive period is defined as the average number of days from when a female molts into an adult until she reproduces (oviposites). Finally, adult cohorts were observed to exhibit high survivorship until a certain age, at which point individuals rapidly senesce. To capture this phenomena, we quantify the rate of senescence as the inverse of the average adult life-span. The temperature responses of each trait (reproduction, development, mortality, and intraspecific competition) were quantified by fitting phenomenological functions to data from the laboratory cultures. The temperature responses of reproduction and competition, as well as development and mortality of the egg, average nymphal, and adult stages are given in Fig. 3-3 in the main text. Development and mortality of each nymphal stage are given in Table 3-S1.

Appendix S3: *DDE Model Description*

We develop a delay-differential equation (DDE) model in Python (http://www.python.org/) using the pyDDE solver (http://users.ox.ac.uk/~clme1073/python/PyDDE/) to numerically solve the system of delay-differential equations. The temperature responses of reproduction, development, mortality, and competition are incorporated into the model via the functions defined in the main text (see Methods). Seasonal variation in temperature and resource variability are incorporated into the model via Eqs. 1,2.

Initial History

An initial history function, which defines bug dynamics before time $t = 0$, is implemented as follows. The model begins on January 1st of a given year and we define the initial history to be the preceding 60 days (i.e., November – December). Because only adults overwinter and adults do not reproduce in the winter, we set the densities of all developmental stages (i.e., eggs, nymphal instars, pre-reproductive adults) to be 0 throughout the initial history. Since only adult mortality occurs during the initial history, we can use a non-delay model to describe adult density over the initial history. Adult density (R) over the initial history is given by: $\frac{dR}{dt} = -d_R R$ where d_R is adult mortality. Solving this equation yields: $R(t) = R_0 e^{-d_R t}$ where R_0 is the adult density at the beginning of the initial history (i.e., at time $t = -60$). We define the initial adult density (i.e., on January 1st at time $t = 0$) to be $R(0) = 5$, which approximates the density observed in January, 1986 (Booth 1990). Our results are robust to small changes in the initial adult density. We calculate adult density at the beginning of the initial history by solving $R(t)$ for R_0; i.e., $R_0 = R(0)e^{d_R t}$, which yields: $R_0 = 9.1$. As temperatures are roughly constant during the initial history, we set temperatures in the initial history to be $T(t) = m_T - a_T$ (see Eq. S1).

Note that since maturation is not possible until after the eggs are laid, we set $g_j(T,t) = 0$ for each stage j at time $t = 0$ (see Eqs. 2,3 in main text). Also, as through-stage survivorship, $s_j(t)$, and the developmental time delay, $\tau_j(t)$, of each stage j are time-varying differential equations, we must set their initial conditions. We set $s_j(0) = e^{-d_j(T[0])/m_j(T[0])}$ and $\tau_j(0) = 1/m_j(T[0])$ where $m_j(T[0])$ and $d_j(T[0])$ are, respectively, the temperature responses of development and mortality at temperature T quantified at time $t = 0$ (see Eqs. 4,5 in main text).

DDE Model

Because the dynamics each life stage can only unfold after a time delay associated with the development of all previous life stages, we must define when each life stage first develops. Thus, the model evaluates each successive delay-differential equation in Eq. 1 after a time delay equal to the cumulative developmental periods of all previous stages. We demonstrate how the model works using the first 4 life stages (i.e., $E, N_1 - N_3$) as illustrative examples. The model evaluates the latter 4 stages (i.e., N_4, N_5, P, R) in a similar manner, but the algorithms for each successive stage become progressively more complex due to the iterative nature of the model.

We assume that adults begin laying eggs after a time t_{init}. Here $t_{init} = 0$ (i.e., adults begin laying eggs on January 1st) as we do not know when eggs are first laid in the field. Hence, $\frac{dE}{dt}$ is evaluated when $t > t_{init}$. Eggs begin to hatch (i.e., $\frac{dN_1}{dt}$ is evaluated) when $t > t_{init} + \tau_E(t)$ where $\tau_E(t)$ is the time delay due to egg development. From this time onward, we quantify $g_E(T,t)$ via Eq. 2. When $t > t_{init} + \tau_E(t) + \tau_{N_1}(t)$ where $\tau_{N_1}(t)$ is the time delay due to N_1 development, N_2 individuals begin to recruit (i.e., $\frac{dN_2}{dt}$ is evaluated). From this time onward, $g_{N_1}(T,t)$ is calculated by first quantifying $g_E\left(T, t - \tau_{N_1}(t)\right)$ via Eq. 2 and then plugging this value into $g_{N_1}(T,t)$ via Eq. 3. When $t > t_{init} + \tau_E(t) + \tau_{N_1}(t) + \tau_{N_2}(t)$ where $\tau_{N_2}(t)$ is the time delay due to N_2 development, N_3 individuals begin to recruit (i.e., $\frac{dN_3}{dt}$ is evaluated). From this time onward, $g_{N_3}(T,t)$ is calculated by quantifying $g_E\left(T, t - \tau_{N_1}\left(t - \tau_{N_2}(t)\right) - \tau_{N_2}(t)\right)$ via Eq. 2 and plugging this value into $g_{N_1}\left(T, t - \tau_{N_2}(t)\right)$ and finally into $g_{N_2}(T,t)$ via Eq. 3. This algorithm is repeated for the latter life stages (i.e., N_4, N_5, P, R), which for purposes of brevity are not included here.

The full model incorporates a system of 8 delay-differential equations (Eq. 1), which describe the dynamics of each life stage, and 16 differential equations, which give through-stage survivorship, $s_j(t)$, and the developmental time delay, $\tau_j(t)$, of each stage (Eqs. 4,5)**.** Note that in the model analysis (Fig. 3-6), the dynamics of the egg stage are not given because there is no census data of egg density in the field. Furthermore, as it is impossible to distinguish between pre-reproductive (P) and reproductive (R) adults in the field, the two life stages are combined into a single adult class (A). Lastly, while this model is fairly complex due to the large number of life stages, the framework we have developed here can be easily collapsed to model the population dynamics of any ectotherm whose life history is characterized by stage structure.

Supplementary Figures

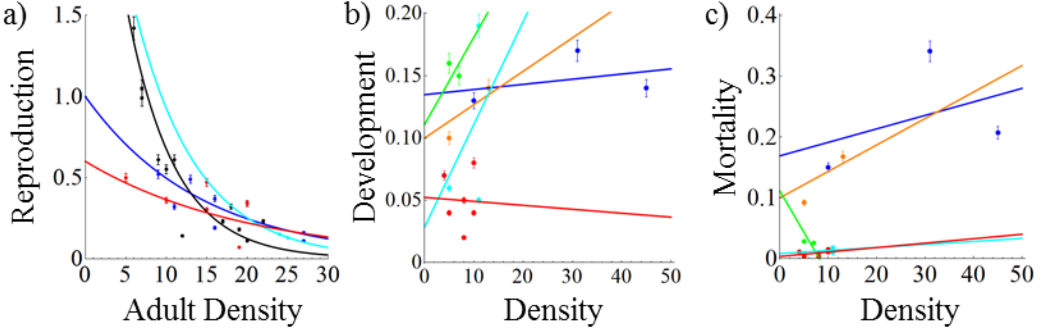

Figure 3-S1. Panel (a) shows fecundity as a function of adult density at four temperatures: 18°**C** (blue), 23°**C** (black), 26°**C** (cyan), and 30°**C** (red). Per capita reproduction is given by: $f(A) = be^{-\alpha A}$ where b is the reproductive rate and α describes intraspecific competition (see Fig. 3-4a): 18°**C** (nonlinear regression: $b = 0.94 \pm 0.32$, $p = 0.03$; $\alpha = 0.007 \pm 0.003$, $p = 0.04$, $n = 9$); 23°**C** (nonlinear regression: $b = 3.7 \pm 0.9$, $p = 0.002$; $\alpha = 0.018 \pm 0.003$, $p < 0.001$, $n = 13$); 26°**C** (nonlinear regression: $b = 3.4 \pm 0.1$, $p = 0.001$; $\alpha = 0.013 \pm 0.002$, $p = 0.001$, $n = 4$); and 30°**C** (nonlinear regression: $b = 0.62 \pm 0.20$, $p = 0.02$; $\alpha = 0.005 \pm 0.003$, $p = 0.14$, $n = 7$). Panel (b) shows nymphal development as a function of density (see Fig. 3-4b): 1st instar (linear regression: $p = 0.77$; nonlinear regression: $p = 0.79$, $n = 3$); 2nd instar (linear regression: $p = 0.23$; nonlinear regression: $p = 0.19$, $n = 2$); 3rd instar (linear regression: $p = 0.18$; nonlinear regression: $p = 0.17$, $n = 2$); 4th instar (linear regression: $p = 0.52$; nonlinear regression: $p = 0.56$, $n = 4$); and 5th instar (linear regression: $p = 0.95$; nonlinear regression: $p = 0.93$, $n = 6$). Panel (c) shows nymphal mortality as a function of density (see Fig. 3-4b): 1st instar (linear regression: $p = 0.74$; nonlinear regression: $p = 0.79$, $n = 3$); 2nd instar (linear regression: $p = 0.31$; nonlinear regression: $p = 0.15$, $n = 2$); 3rd instar (linear regression: $p = 0.10$; nonlinear regression: $p = 0.60$, $n = 2$); 4th instar (linear regression: $p = 0.53$; nonlinear regression: $p = 0.53$, $n = 4$); and 5th instar (linear regression: $p = 0.40$; nonlinear regression: $p = 0.32$, $n = 6$).

Supplementary Tables.

Development				
Stage	Parameter Estimates			n
	$m_{i,T}$	$T_{i,m}$	$A_{i,m}$	
N_1	$m_{N1,T} = 0.13 \pm 0.006$ $p = 0.03$	$T_{N1,m} = 297.6 \pm 1.0$ $p = 0.03$	$A_{N1,m} = 4{,}140 \pm 600$ $p = 0.006$	4
N_2	$m_{N2,T} = 0.10$	$T_{N2,m} = 296.0$	$A_{N2,m} = 10{,}500 \pm 300$ $p < 0.001$	2
N_3	$m_{N3,T} = 0.11$	$T_{N3,m} = 296.0$	$A_{N3,m} = 11{,}900 \pm 200$ $p = 0.003$	2
N_4	$m_{N4,T} = 0.06 \pm 0.01$ $p = 0.12$	$T_{N4,m} = 295.9 \pm 1.2$ $p = 0.03$	$A_{N4,m} = 14{,}200 \pm 2{,}800$ $p = 0.12$	4
N_5	$m_{N5,T} = 0.04 \pm 0.002$ $p = 0.03$	$T_{N5,m} = 295.8 \pm 0.4$ $p = 0.01$	$A_{N5,m} = 9{,}000 \pm 700$ $p < 0.05$	4
Mortality				
Stage	Parameter Estimates			n
	$d_{Ni,T}$	$T_{Ni,d}$	$A_{Ni,d}$	
N_1	$d_{N1,T} = 0.15 \pm 0.002$ $p = 0.008$	$T_{N1,d} = 296.2 \pm 0.2$ $p = 0.006$	$A_{N1,d} = 10{,}800 \pm 500$ $p = 0.03$	4
N_2	$d_{N2,T} = 0.09$	$T_{N2,d} = 296.0$	$A_{N2,d} = 17{,}800 \pm 700$ $p < 0.001$	2
N_3	$d_{N3,T} = 0.03$	$T_{N3,d} = 296.0$	$A_{N3,d} = 2{,}200 \pm 300$ $p = 0.002$	2
N_4	$d_{N4,T} = 0.009 \pm 0.001$ $p = 0.06$	$T_{N4,d} = 295.5 \pm 1.2$ $p = 0.03$	$A_{N4,d} = 6{,}900 \pm 1{,}700$ $p = 0.16$	4
N_5	$d_{N5,T} = 0.005 \pm 0.001$ $p = 0.13$	$T_{N5,d} = 290.9 \pm 0.7$ $p = 0.03$	$A_{N5,d} = 8{,}180 \pm 1{,}770$ $p = 0.14$	4
Adult Senescence				
A	$m_{A,T} = 0.010 \pm 0.002$ $p < 0.05$	$T_{A,m} = 295.3 \pm 1.6$ $p < 0.001$	$A_{A,m} = 7{,}000 \pm 2{,}000$ $p = 0.04$	4

Table 3-S1. Parameter estimates for the temperature responses of development and mortality of the nymphal life stages and adult senescence. All parameters were estimated via nonlinear regression (see main text for details). Note that *n* indicates the number of temperatures at which laboratory cultures were maintained.

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