

The community effects of phenotypic and genetic variation within a predator population

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Abstract. Natural populations are heterogeneous mixtures of individuals differing in physiology, morphology, and behavior. Despite the ubiquity of phenotypic variation within natural populations, its effects on the dynamics of ecological communities are not well understood. Here, we use a quantitative genetics framework to examine how phenotypic variation in a predator affects the outcome of apparent competition between its two prey species. Classical apparent competition theory predicts that prey have reciprocally negative effects on each other. The addition of phenotypic trait variation in predation can marginalize these negative effects, mediate coexistence, or generate positive indirect effects between the prey species. Long-term coexistence or facilitation, however, can be preceded by long transients of extinction risk whenever the heritability of phenotypic variation is low. Greater heritability can circumvent these ecological transients but also can generate oscillatory and chaotic dynamics. These dramatic changes in ecological outcomes, in the sign of indirect effects, and in stability suggest that studies which ignore intraspecific trait variation may reach fundamentally incorrect conclusions regarding ecological dynamics.

Key words: apparent competition; genetic variation; heritability; phenotypic variation; predator–prey interaction; quantitative genetics.

INTRODUCTION

Phenotypic variation is a ubiquitous feature of natural populations: individuals differ in size, morphology, physiology, and behavior. Such variation is an organizing theme of evolutionary biology. Genetic variation permits evolutionary response to selection, and environmental variance can facilitate invasion of novel habitats. In contrast, phenotypic variation has played a relatively minor part in the study of community ecology. Community ecologists have tended to treat species as homogeneous units, focusing on the dynamics of overall population size. These dynamics are modeled using populations' average demographic parameters (e.g., reproductive, death, and attack rates). However, the phenotypic variation found within populations may generate variance in ecological and demographic parameters. For example, behavioral differences among co-occurring California sea otters (*Enhydra lutris*) lead to differences in prey preference, energy income, and pathogen exposure (Tinker et al. 2008, Johnson et al. 2009). Such ecological variation can arise from among-individual differences in age (Polis 1984), sex (Shine 1989), morphology (Smith and Skúlason 1996, Bolnick et al. 2003) or experience (Estes et al. 2003). As a result

individuals typically use only a subset of their population's resource base (i.e., they are "individual specialists"). For example, at the population level *Trypoxylon albonigrum* wasps consume six genera of spiders, but individuals rarely use more than two genera (Araújo and New 2007).

Despite the high incidence of individual specialization (Bolnick et al. 2003), little is known about its ecological consequences for population and community dynamics. To what extent can ecologists safely use a population's mean ecological parameters (e.g., attack rates on various prey species) to understand population dynamics? Or, do we arrive at qualitatively different predictions by accounting for among-individual variation in these parameters? The few existing empirical studies suggest that intraspecific genetic variation (typically with unknown phenotypic effects) can substantially alter population size means and variances (Imura et al. 2003, Hughes et al. 2008, Agashe 2009, Becks et al. 2010). However, there is surprisingly little theory regarding the ecological effects of trait variation. A few papers have incorporated genetic variation into familiar ecological models of intraspecific competition (Doebeli 1996a, Bürger 2005, Schneider 2007), predation (Saloniemi 1993, Abrams and Matsuda 1997b, Abrams 2000), and parasitism (Doebeli 1996a, 1997, Abrams and Kawecki 1999). These models suggest that eco-evolutionary feedbacks alter both transient and equilibrium population sizes. Even without eco-evolu-

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tionary feedbacks, using average interaction strengths may be misleading due to Jensen's inequality (Okuyama 2008). However, such models have not typically provided analytical insight into the effects of ecological variation within species, nor clearly distinguished between the effects of environmental vs. genetic variance. Here, we investigate how intraspecific trait variation alters the dynamics of a classic ecological model of apparent competition.

Apparent competition is a fundamental community module that occurs when prey species share a common predator. Just as competitors reciprocally harm each other by suppressing a common resource, prey species may reciprocally harm each other by mutually subsidizing a shared predator (Holt 1977, Holt and Lawton 1993, 1994). These negatively reciprocal responses have been demonstrated empirically in a diversity of systems including plants sharing a common herbivore (Rand 2003, Rand et al. 2004), phytophagous insects sharing a common parasitoid (Mueller and Godfray 1997, Rott and Godfray 1998, Morris et al. 2001), game birds sharing parasites (Tompkins et al. 2000), and canopy trees sharing pathogens (Cobb et al. 2010). When prey are not resource limited or predation pressure is strong, apparent competition can lead to the exclusion of one of the prey species: dynamic monophagy (Holt and Lawton 1994). The only demonstration of this exclusionary dynamic comes from a multigenerational laboratory experiment with two stored product moth species that share a common parasitoid (Bonsall and Hassell 1997). While there is some limited evidence that dynamic monophagy occurs in the field (Zwölfer 1979), this evidence appears to be the exception rather than the rule (van Veen et al. 2006). Theory suggests several reasons for the limited empirical support for dynamic monophagy. Predator switching and nonequilibrium dynamics may promote coexistence (Abrams and Matsuda 1996, Abrams et al. 1998, Schreiber 2004), as can evolution of prey defenses (e.g., shifts into enemy-free space; Jeffries and Lawton 1984, Abrams and Chen 2002). We propose an additional and potentially general explanation: phenotypic variation in a predator's feeding strategies may limit the scope for dynamic monophagy.

Prior work on the evolution of a predator attacking two prey species has focused on the consequences of the ecological and evolutionary feedbacks on the phenotypic distribution and fitness of the predator (Wilson and Turelli 1986, Rueffler et al. 2006, Abrams 2006a, b). For example, using a single-locus selection model based on differential utilization of two prey species, Wilson and Turelli (1986) illustrated that there can be selection for polymorphic predators in which, surprisingly, the heterozygous individuals are the least fit. While providing important insights into the phenotypic diversification of consumers, these studies did not examine how evolution and phenotypic variation in the predator alter the ecological dynamics of apparent competition (see, however, Abrams and Kawecki 1999). To address this

limitation, we analyze the ecological and evolutionary dynamics of a predator with two prey using a quantitative genetics framework (Bürger 2000). Using quantitative genetics tools allows us to start with the familiar apparent competition model (when trait variation is near zero) and evaluate the effect of trait variation and of the heritability of this variation on the stability of species interactions, the creation of alternative states, and the magnitude and sign of indirect effects between prey species.

MODEL AND METHODS

We consider the dynamics of a predator population with density $P = P(t)$ consuming two prey species with densities $N_1 = N_1(t)$ and $N_2 = N_2(t)$, where t denotes time. Each of the predator's attack rates on the two prey species depends on the phenotypic value, x , of a quantitative trait. This trait is normally distributed with mean $\bar{x} = \bar{x}(t)$ and constant variance σ^2 , i.e., its density is

$$p(x, \bar{x}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(x - \bar{x})^2}{2\sigma^2}\right]$$

where the phenotypic variance has a genetic and an environmental component, $\sigma^2 = \sigma_G^2 + \sigma_E^2$. The predator's attack rate $a_i(x)$ on prey i is maximal at an optimal trait value $x = \theta_i$ and decreases away from this optimal trait value in a Gaussian manner, i.e.,

$$a_i(x) = \alpha_i \exp\left[-\frac{(x - \theta_i)^2}{2\tau_i^2}\right]$$

where α_i is the maximal attack rate and τ_i determines how steeply attack rate declines with distance from the optimal trait value. In effect, τ_i determines how phenotypically specialized a predator must be to use prey i .

This model is intended to mimic the common empirical situation in which quantitative trait variation in a predator influences individuals relative use of alternative resources. For example, in lake populations of threespine stickleback (*Gasterosteus aculeatus*), individuals preferentially consume either benthic insect larvae or limnetic zooplankton even when such prey are within meters of each other (Svanbäck and Bolnick 2007, Araújo et al. 2008, Bolnick and Paull 2009, Matthews et al. 2010). Within a given population, traits such as gill raker length or number are normally distributed, and individuals at different ends of this distribution tend to consume different prey types, in part because the trait influences handling times and attack rates (Robinson 2000).

Under these assumptions, the average attack rate on prey i is

$$\begin{aligned} \bar{a}_i(\bar{x}) &= \int_{-\infty}^{\infty} a_i(x) p(x, \bar{x}) dx \\ &= \frac{\alpha_i \tau_i}{\sqrt{\sigma^2 + \tau_i^2}} \exp\left[-\frac{(\bar{x} - \theta_i)^2}{2(\sigma^2 + \tau_i^2)}\right]. \end{aligned}$$

If predators have a linear functional response, convert the consumed prey into offspring with efficiencies e_i and experience a per-capita mortality rate d , then the fitness of a predator with phenotype x is

$$W(x, N_1, N_2) = \sum_{i=1}^2 e_i a_i(x) N_i - d$$

and the mean fitness of the predator population is

$$\begin{aligned} \bar{W}(\bar{x}, N_1, N_2) &= \int_{-\infty}^{\infty} W(x, N_1, N_2) p(x, \bar{x}) dx \\ &= \sum_{i=1}^2 e_i \bar{a}_i(\bar{x}) N_i - d. \end{aligned}$$

In the absence of the predator, each prey species exhibits logistic dynamics with intrinsic rates of growth r_i and carrying capacities K_i . Under these assumptions, the ecological and evolutionary dynamics of our system are

$$\frac{dN_i}{dt} = r_i N_i (1 - N_i/K_i) - P \bar{a}_i N_i \quad (1a)$$

$$\frac{dP}{dt} = P \bar{W} \quad (1b)$$

$$\frac{d\bar{x}}{dt} = \sigma_G^2 \frac{d\bar{W}}{d\bar{x}} \quad (1c)$$

where

$$\frac{d\bar{W}}{d\bar{x}} = \sum_{i=1}^2 \frac{e_i N_i \tau_i \alpha_i (\theta_i - \bar{x})}{(\tau_i^2 + \sigma^2)^{3/2}} \exp \left[-\frac{(\bar{x} - \theta_i)^2}{2(\tau_i^2 + \sigma^2)} \right]. \quad (2)$$

Lande (1976) derived Eq. 1c under the assumption that the distribution of phenotypes remains Gaussian. While epistasis or genotype-by-environment interaction can generate substantial deviations from a normal trait distribution, Turelli and Barton (1994) showed numerically that the normal approximation still gives remarkably accurate predictions for dynamics of the mean and variance of the trait value under a wide variety of assumptions. Under weak assumptions, even frequency-dependent disruptive selection maintains a nearly Gaussian trait distribution (Bürger and Gimelfarb 2004). However, many forms of selection will lead to changes in the genetic variance (Bürger 2000).

The feedbacks between the ecological and evolutionary dynamics of our model result in more diverse outcomes than are seen in the traditional apparent competition model, including alternative stable states, oscillatory or chaotic dynamics, and transient shifts in community structure (Fig. 1). To understand these behaviors, we begin by examining how phenotypic variation and functional resource differentiation alters the long-term dynamics of a predator–prey pair and develop an analytic criterion for prey coexistence. Using

a combination of analytic and numerical methods, we examine how predator trait variation and prey differentiation alter equilibrium abundances and generate alternative stable states for the three species system. We show that these equilibria determine the long-term dynamics whenever genetic variation of the predator trait is sufficiently small. Consequently, we conclude our analysis by examining how the higher levels of genetic variation generate nonequilibrium dynamics and circumvent transients of high extinction risk. Analytical details are presented in the Appendices.

RESULTS

Pairwise predator–prey dynamics

When there is only a single prey species, say species i , in the system and $\sigma_G > 0$, the mean predator phenotype evolves to $\hat{x} = \theta_i$ which maximizes \bar{W} . The predator coexists with the prey species provided that it can invade when the predator's reproductive number at the prey's carrying capacity is greater than 1, i.e.,

$$\frac{e_i K_i \alpha_i \tau_i}{d \sqrt{\sigma^2 + \tau_i^2}} > 1.$$

When this occurs, the predator–prey pair approaches a globally asymptotically stable equilibrium given by

$$\hat{N}_i = \frac{d \sqrt{\sigma^2 + \tau_i^2}}{e_i \alpha_i \tau_i} \quad (3a)$$

$$\hat{P}_i = r_i \frac{\sqrt{\sigma^2 + \tau_i^2}}{\alpha_i \tau_i} (1 - \hat{N}_i/K_i). \quad (3b)$$

Eq. 3 implies that increasing phenotypic variation of the predator reduces top-down control (i.e., \hat{N}_i increases with σ^2) and reduces the predator's reproductive number. In particular, when phenotypic variation is too great, the predator goes extinct. Intuitively, there is no advantage to phenotypic variation in the predator in the absence of trait variation of its prey. Trait variation is thus maladaptive and imposes a fitness load on the predator population.

Coexistence, apparent competition, and facilitation

To explore how a shared predator affects coexistence of the prey species, we assume that the predator persists and restrict our attention to the case where $\tau_1 = \tau_2$, and $\sigma_G > 0$. Conditions for predator persistence and coexistence conditions for the prey with $\tau_1 \neq \tau_2$ are presented in Appendix A. Without loss of generality, we also assume that $r_1/\alpha_1 > r_2/\alpha_2$. Under this assumption, prey 1 is the “superior” (apparent) competitor and always persists. On the other hand, prey 2 coexists with prey 1 provided that

$$\frac{r_2 \alpha_1}{\alpha_2 r_1} > \underbrace{\left(1 - \frac{\hat{N}_1}{K_1}\right)}_{\text{TDC}_1} \underbrace{\exp \left(-\frac{(\theta_1 - \theta_2)^2}{2(\sigma^2 + \tau^2)} \right)}_{C_1} \quad (4)$$

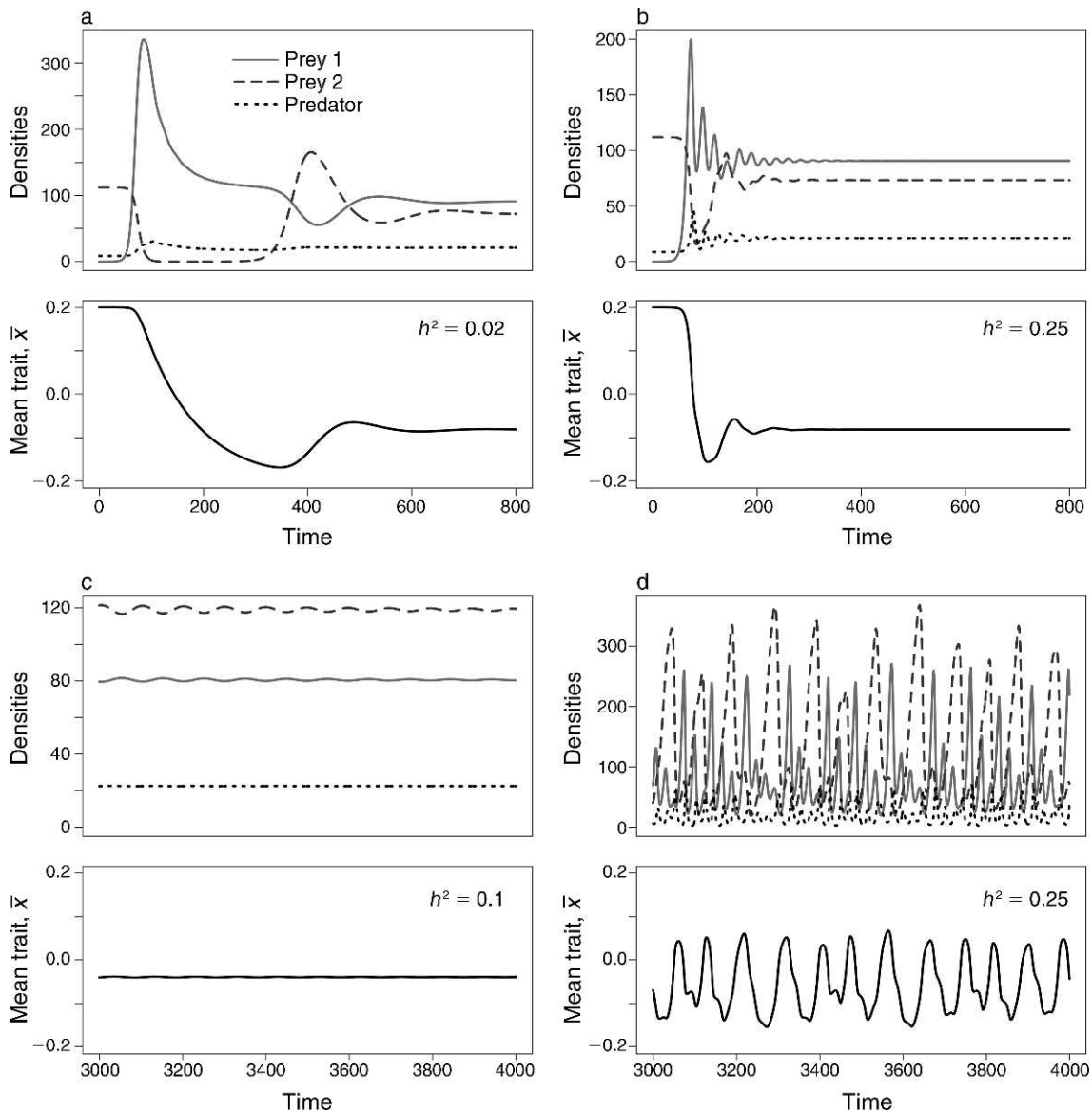


FIG. 1. Transient and oscillatory dynamics. In upper (respectively, lower) figures, population densities (respectively, the mean predator trait value) are plotted as functions of time. In panels (a) and (b), the dynamics following the invasion of the superior apparent competitor (prey 1) into the system are shown. Parameter values are $r_1 = 0.2$, $r_2 = 0.1$, $K_1 = K_2 = 500$, $\sigma^2 = 0.04$, $\tau_1 = \tau_2 = 0.1$, $-\theta_1 = \theta_2 = 0.2$, $e_1 = e_2 = d = 0.5$, and $\alpha_1 = \alpha_2 = 0.02$. The meaning of parameters is explained in *Model and Methods*. Different degrees of heritability $h^2 = \sigma_G^2 / \sigma^2$ result in alternative ecological transients. In panels (c) and (d), the long-term dynamics of the entire system for two levels of genetic variation are displayed. Parameter values are as in panel (a) except $\sigma^2 = 0.01$.

cf. Eq. A.1 in Appendix A. When the opposite inequality of Eq. 4 holds, the equilibrium (\hat{N}_1, \hat{P}_1) is stable and prey 2 can be displaced by the introduction of prey 1.

The right-hand side of the coexistence condition (Eq. 4) equals the product of two terms. The first term, TDC_1 , appears in the classical apparent competition theory (Holt 1977, 1987) and equals the reduction in the superior competitor's (prey 1) equilibrium abundance (below its carrying capacity) due to top-down control by the consumer. Intuitively, the greater the top-down

control, the more difficult it is for the inferior competitor (prey 2) to invade and/or persist. Greater top-down control occurs when the superior competitor has a large carrying capacity, or the predator has a high attack rate or is long lived (i.e., $1/d$ is large). The second term in Eq. 4, C_1 , represents the predator's cost (reduced attack rate on prey 2) due to specializing on prey 1 (the superior competitor). The greater this cost, the more likely the inferior competitor can increase when rare. This decomposition of the coexistence condition into the

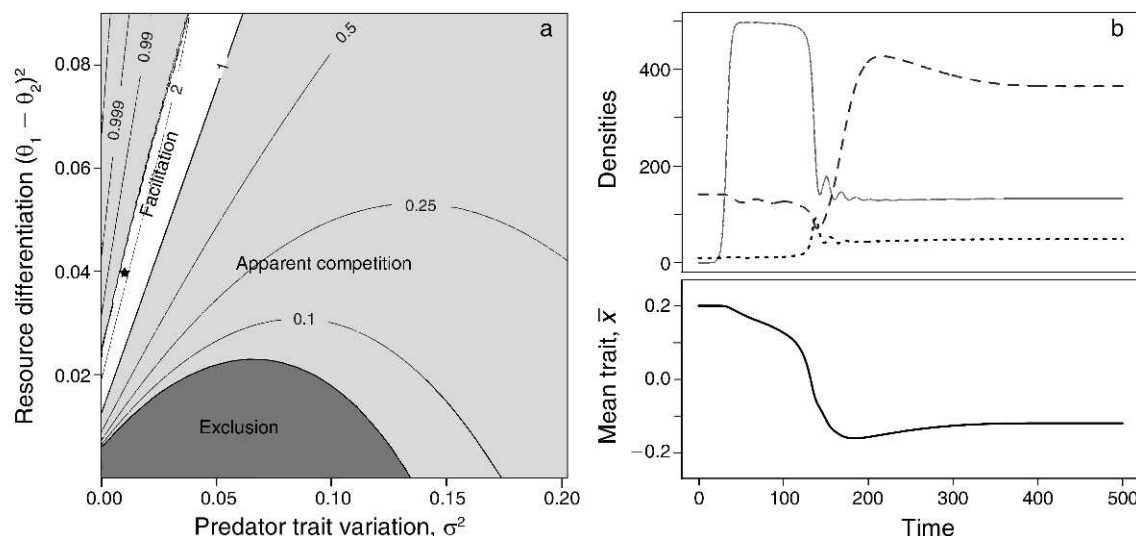


FIG. 2. Facilitation, apparent competition, and exclusion. In panel (a), the contours for the ratio of equilibrium densities of the inferior competitor (prey 2) with and without the superior competitor (prey 1) are plotted. In the region denoted “exclusion,” the invasion of the superior competitor leads to the exclusion of prey 2. In the region denoted “apparent competition” (respectively, “facilitation”), invasion of the superior competitor decreases (respectively, increases) the equilibrium abundance of prey 2. Panel (b) presents the system dynamics corresponding to facilitation for the parameter combination represented by the star in panel (a), i.e., $\sigma^2 = 0.01$, $(\theta_1 - \theta_2)^2 = 0.04$, and $\sigma_0^2 = 0.0025$. Key: solid gray line, prey 1; long-dash line, prey 2; short-dash line, predator (i.e., same as in Fig. 1a). Parameter values in all figures are $K_1 = K_2 = 500$, $e_1 = e_2 = d = 0.5$, $\alpha_1 = \alpha_2 = 0.01$, $\tau_1 = \tau_2 = 0.1$, $r_1 = 0.4$, and $r_2 = 0.1$.

two terms clarifies the relative roles of predator trait variation σ^2 and resource differentiation $(\theta_1 - \theta_2)^2$ on community structure (Fig. 2).

Resource differentiation reduces C_1 and has no effect on top-down control. Hence, increasing resource differentiation increases predator specialization on the superior competitor and thus increases the likelihood of inferior competitor persisting. Intuitively, when there is strong resource differentiation and the inferior competitor is rare, the predator evolves to specialize on the superior competitor and thereby ceases to be an effective predator of the inferior competitor, which is thus released from apparent competition.

The effects of predator trait variation on the coexistence condition are twofold. On the one hand, top-down control is diluted by predator trait variation, which imposes a fitness load on the predator. This dilution enhances the invasion of the inferior competitor. On the other hand, predator trait variation results in higher attack rates on the inferior competitor when the consumer is specializing on the superior competitor. This is because even when the predator is on average specialized on prey 1, high trait variance means some predators are still phenotypically well adapted to prey 2. These higher attack rates reduce the invasion rate of the inferior competitor. As a consequence of these trade-offs, the effects of apparent competition (exclusion or reduced N_2) can be greatest at intermediate levels of consumer trait variation (Fig. 2a).

When coexistence occurs, the introduction of the superior competitor into the predator–prey-2 system has

two countervailing effects on the equilibrium density of the resident inferior competitor. From the ecological perspective, the introduction of the superior competitor increases the long-term density of the shared predator. This increase suppresses the density of the inferior competitor. From the evolutionary perspective, the introduction of the superior competitor causes the predator's trait to evolve toward the optimal trait for the introduced species. This shift in the distribution of predator attack rates releases the inferior competitor from predation and thereby increases its density.

Depending on the relative strengths of these countervailing effects, the introduction of the superior competitor can either decrease or increase the equilibrium density of the inferior competitor. When the ecological effect dominates, we recover the prediction from classical apparent competition theory: the introduction of the superior competitor results in a reduction in the density of the inferior competitor (Fig. 1a and b and light gray region in Fig. 2a). However, when the evolutionary effect dominates, the introduction of the superior competitor results in a long-term increase in the density of inferior competitor (Fig. 2b). This facilitation occurs when there are intermediate levels of resource differentiation and predator trait variation is not too large (white region in Fig. 2a). When resource differentiation is small, there is minimal evolution of the consumer trait and limited evolutionary release of the inferior competitor from consumption. When resource differentiation is too large (relative to σ^2), there is a steep fitness valley between specializing on the inferior

and superior competitors. Hence, following the introduction of the superior competitor at low densities, there is minimal evolution of the predator trait. As a consequence, the invasion of the superior competitor has virtually no effect on the equilibrium density of the inferior competitor (e.g., less than a 1% reduction in density in Fig. 2a). However, a large change in the predator's trait or a large change in the abundance of the superior competitor can lead to predator specialization on the superior competitor and thereby facilitate the growth of the inferior competitor.

Alternative stable states

When there is sufficient resource differentiation, the ecological-evolutionary feedbacks can generate alternative stable states of the system. For example, if the system is highly symmetric (i.e., $r_1 = r_2$, $K_1 = K_2$, $\alpha_1 = \alpha_2$, $e_1 = e_2$, $\tau_1 = \tau_2$), then alternative stable states may arise whenever $(\theta_1 - \theta_2)^2 > \sigma^2 + \tau^2$. Intuitively, when resource differentiation is sufficiently greater than predator trait variation, evolution generates alternative states corresponding to the predator specializing on one or the other prey species. While finding general analytic criteria (without the assumption of strong symmetry) for the existence of alternative equilibrium states appears to be intractable, in Appendix B: *Determining the equilibria* and Appendix C we develop methods that reduce the multivariate problem of finding equilibria to a numerically tractable, univariate problem. In particular, these univariate problems depend only on a small set of compound parameters.

Fig. 3 illustrates the complex dependence of alternative states on predator trait variation. Low predator trait variation ($\sigma^2 < 0.0003$ in Fig. 3) produces two stable alternative states corresponding to specialization on a single prey species, though both are present. The predator achieves higher densities when this specialization occurs on the superior competitor. At both of these alternative states, the predator's trait lies at a local maximum of mean fitness \bar{W} . Intermediate predator trait variation ($0.0003 < \sigma^2 < 0.005$) generates a new stable alternative state corresponding to a generalist predator. Despite its stability, this equilibrium occurs at a local fitness minimum and, consequently, at this equilibrium disruptive selection occurs (see Appendix B: *Fitness minima and disruptive selection*). At higher levels of predator trait variation ($\sigma^2 > 0.005$), there are no alternative states (courtesy of saddle node bifurcations) and the predator tends to specialize on the superior competitor. Finally, consistent with our analysis in the Appendices, when phenotypic variation is too high ($\sigma^2 > 4.1$), the predator does not persist.

Transients and nonequilibrium dynamics

While the ecological and evolutionary dynamics eventually approach an equilibrium state whenever heritability is sufficiently low (see Appendix B: *Convergence*), this asymptotic behavior may be preceded by

long-term transients that can have significant implications for coexistence and exclusion. These transients correspond to the population dynamics tracking ecological quasi-equilibria as the predator trait slowly evolves. These transients are particularly pronounced following the introduction of the superior competitor (here, prey 1) into an evolved predator–inferior-competitor community. Even if the species ultimately coexist (i.e., Eq. 4 holds), this invasion may result in transient periods where prey 2 reaches low densities and is vulnerable to stochastic extinction. This vulnerability occurs whenever evolution causes the mean predator trait \bar{x} to pass through values such that

$$\frac{r_2}{a_2(\bar{x})} < \frac{r_1}{a_1(\bar{x})} \left(1 - \frac{\hat{N}_1(\bar{x})}{K_1} \right)$$

where $\hat{N}_1(\bar{x}) = d/(\tilde{a}_1(\bar{x})e_1)$ is the equilibrium abundance attained by prey 1 if the predator has mean trait value \bar{x} . This transient vulnerability is illustrated in Fig. 1a, in which evolution of the predator's trait causes the near-extinction of the inferior competitor, which later recovers when the predator evolves to specialize on the superior competitor. Higher levels of heritability result in the predator trait evolving more rapidly and thereby circumventing extinction risk (Fig. 1b and Appendix D).

More generally, following the invasion of the superior competitor, low heritability (for a given level of phenotypic variation) results in slow evolutionary dynamics that can generate transient facilitation, apparent competition or high extinction risk. Fig. 4a illustrates the community going through two forms of transients before reaching a final equilibrium state. Following its invasion, the superior competitor achieves high densities resulting in a weak transient increase in the predator (which is still specializing on prey 2) and a corresponding small decrease in the inferior competitor. After approximately time 400, the predator evolves to be a generalist (i.e., $\bar{x} = 0$), increases in density, and severely reduces the inferior competitor's density. During this transient phase, the inferior competitor is vulnerable to stochastic extinction. Finally around time 1000, the predator evolves to specialize on the superior competitor, releases the inferior competitor from predation, and the system converges to an equilibrium with a net increase in the inferior competitor's density.

Predator trait variation plays a key role in determining the temporal patterns of transients (Fig. 4b). For higher values of predator trait variation (e.g., $\sigma^2 \approx 0.06$) and starting with a predator specializing on the inferior competitor (i.e., $\bar{x} = 0.2$), the competitors can coexist on evolutionary time scales before the inevitable exclusion of the inferior competitor. This exclusion occurs despite the predator ultimately specializing on the superior competitor. At intermediate values of predator trait variation (e.g., $\sigma^2 = 0.0225$) and starting with a predator specializing on prey 2, the transients are as described in the preceding paragraph (Fig. 4b). Finally at low values of predator trait variation (e.g., $\sigma^2 = 0.0025$), there are

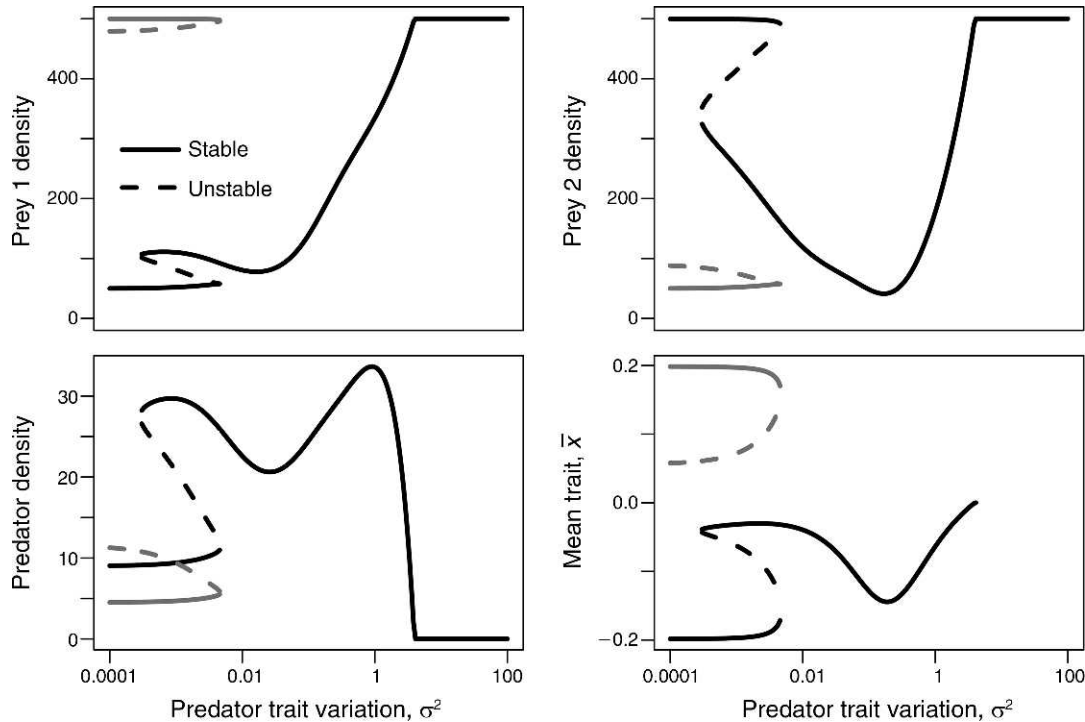


FIG. 3. Effects of predator trait variation on alternative ecological and evolutionary states. Equilibrium densities of predator, prey, and mean predator trait are plotted as functions of predator trait variance σ^2 . Only equilibria supporting all species are shown except for when the predator goes extinct, which occurs if $\sigma^2 > 4.1$. These equilibria always satisfy $\theta_1 < \bar{x} < \theta_2$. Locally stable and unstable equilibria are indicated by solid and dashed lines, respectively, and these stability properties hold provided σ_G^2 is sufficiently small (but positive). Depending on the initial conditions, trajectories converge to one of the (up to three) stable equilibria. Equilibria corresponding to high prey 1 density are indicated by gray lines. Parameter values are as in Fig. 1.

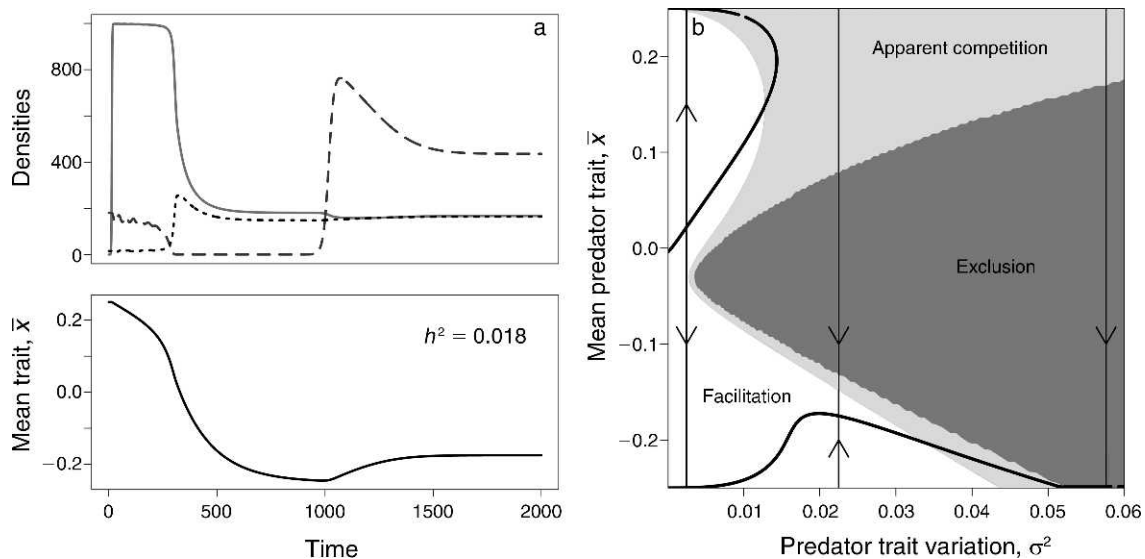


FIG. 4. Transients of exclusion, facilitation, and apparent competition. In panel (a), transient dynamics corresponding to $\sigma^2 = 0.0225$ and $\sigma_G^2 = 0.004$ are plotted. Key: solid gray line, prey 1; long-dash line, prey 2; short-dash line, predator (i.e., same as in Fig. 1a). In panel (b), a bifurcation diagram for prey 2 and \bar{x} is plotted for small h^2 . Thick solid lines correspond to the equilibrium values of the predator trait as a function of σ^2 . Stability of these equilibria are indicated by the arrows. Dark shaded, light shaded, and unshaded regions correspond to parameter–trait combinations where prey 2 (in the absence of trait evolution) goes extinct, persists at a reduced density, or persists at an enhanced density. Evolution of the predator trait results in different transients as the mean trait passes through these different regions of ecological quasi-equilibria. Parameter values are $r_1 = 1$, $r_2 = 0.1$, $K_1 = K_2 = 1000$, $\tau_1 = \tau_2 = 0.1$, $e_1 = e_2 = d = 0.5$, $\alpha_1 = \alpha_2 = 0.01$, $\theta_1 = -0.25$, and $\theta_2 = 0.25$.

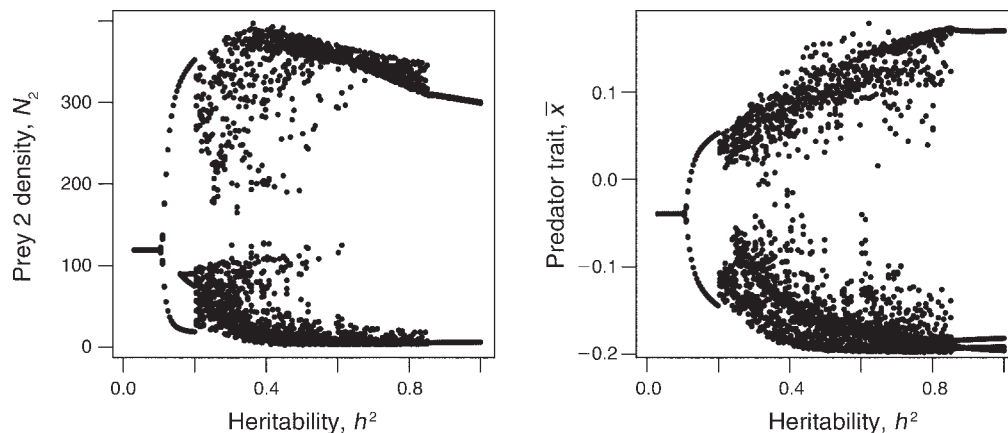


FIG. 5. Chaotic population dynamics due to increasing heritability. The figure presents bifurcation diagrams with respect to heritability, plotted for a fixed amount of phenotypic variation σ^2 . Simulations ran for 5000 time steps and sampled at all of the local maxima and local minima between time 4000 and 5000. Other parameter values are as in Fig. 1b.

no transients despite the final state of the system depending on the initial mean of the predator trait.

In addition to circumventing transients of high extinction risk, greater heritability (for a fixed level of phenotypic variation) can generate oscillatory and chaotic dynamics (Fig. 1c and d and Fig. 5). Since the ecological dynamics and the evolutionary dynamics, by themselves, always converge to a stable equilibrium, the nonequilibrium behavior arises from negative feedbacks between the ecological and evolutionary dynamics. When heritability is high, this evolutionary shift can occur on a time scale commensurate with the ecological dynamics. At lower heritabilities there is a greater separation of time-scales, whose effect is analogous to introducing lags into ecological dynamics. Finally at the lowest heritabilities, evolution is so slow as to be insensitive to short term ecological dynamics.

DISCUSSION

Two of Darwin's great insights were the importance of individual variation for evolutionary change and the complexity of indirect effects between species. While there has been extensive work regarding each of these insights separately, most theoretical work at their intersection focuses on the evolution of the mean trait value (Loeuille and Loreau 2005, Ingram et al. 2009), or focuses on how species interactions select for or against individual variation (Wilson and Turelli 1986). What has been largely missing is a consideration of how individual variation per se influences evolutionary and ecological dynamics (see, however, Lomnicki 1978, Doebeli 1996b, Hughes et al. 2008, Bolnick et al. 2011). To help fill this gap, we analyzed a model of two prey species sharing a predator with individual variation in the predator's trait. Our analysis reveals that introducing heritable trait variation leads to a remarkable diversity of new dynamical behaviors (e.g., alternative states, ecological transients of exclusion or facilitation, chaos). Moreover, trait variation can

substantially alter ecological outcomes and indirect effects, highlighting the importance of measuring individual variation in the field.

Apparent commensalism and mutualism

When prey species share a common predator, Holt (1977) showed that species sharing a common predator have reciprocally negative effects on each other under three broad assumptions: (1) the predator is strictly food limited, (2) the predator has a positive numerical response to each prey, and (3) the system settles into a point equilibrium. When any of these conditions are violated, these negative effects may become positive (Holt and Kotler 1987, Abrams and Matsuda 1996, Abrams et al. 1998). For instance, Abrams et al. (1998) found that for systems with oscillatory dynamics, the removal of one prey species often results in a decrease in mean abundance of the remaining prey species. Here, we show that despite the ecological dynamics satisfying all these assumptions of classical apparent competition theory, trait variation in predator populations can marginalize or even reverse the predictions of the classical theory.

We show that sufficient variation in predator attack rates can dilute top-down regulation and, thereby, reduce negative reciprocal effects between the prey. This dilution effect is purely ecological and follows from Jensen's inequality (Ruel and Ayres 1999) whenever predators experience limited trade-offs in capturing different prey species. More specifically, the predator attack rates are concave down functions of the predator trait whenever $(\theta_1 - \theta_2)^2 / \tau_1^2$ is sufficiently small. Such concave-down functions imply that when predators vary for the trait (around mean \bar{x}), mean attack rate is lower than for a homogeneous predator population with the same trait mean \bar{x} .

When there are sufficiently strong trade-offs in capturing different prey species, heritable variation in the predator attack rates can lead to apparent commensalism or mutualism between the prey species. At low

levels of trait variation, the ecological and evolutionary dynamics have alternative stable states corresponding to the predator preferentially attacking one of the prey species. Removing the non-preferred prey has a marginal effect on either prey species as it produces a marginal shift in the predators traits. In contrast, removing the preferred prey results in an evolutionary shift to specialize on the other prey, whose density then declines substantially. Thus, with respect to species removals, the species appear to exhibit commensalism. At intermediate levels of trait variation, however, apparent commensalism becomes apparent mutualism as the predator evolves to be a generalist for all initial conditions with both prey species present. Removal of one prey species always results in the long-term reduction of the other prey species as the predator evolves to specialize on the remaining prey species.

These latter indirect effects are analogous to what happens on behavioral time scales for optimally foraging predators (Abrams and Matsuda 1996, Abrams 1999, van Baalen et al. 2001). Optimal foraging theory implies that when the abundance of a preferred prey (i.e., an energetically more profitable prey item) falls below a threshold, optimally foraging predators switch to an alternative prey, either by including the alternative prey in their diet in a fine-grained environment or by moving to the alternative prey's habitat in a coarse-grained environment (Stephens and Krebs 1986). As in the case of low trait variation, indirect commensalism can occur in fine-grained environments due to the underlying asymmetry in the optimal foraging behavior. As in the case of intermediate trait variation, indirect mutualism can occur in coarse-grained environments as the predator always reduces its attack rate on the rare species.

Heritability, transients, and chaos

The equilibrium densities of our system are strongly dependent on predator trait variance, regardless of whether this variation is genetic or environmental. However, for a given level of phenotypic variation, the heritability of trait variation plays a fundamental role in transient dynamics and stability. We have shown that low levels of heritability ensure that the long-term dynamics equilibrate. However, the approach to this steady state may be preceded by long-term transients that fundamentally alter the structure of the community. For example, at intermediate levels of predator trait variation, the invasion of a superior (apparent) competitor may initially drive the inferior (apparent) competitor to arbitrarily low densities prior to an evolutionary release from apparent competition. The length of these transients tend to be inversely proportional to the heritability of the predator's trait: greater heritability produces shorter transients and lower risk of extinction. These transients on evolutionary time scales may exacerbate or diminish extinction risk due to transients

on ecological time scales (Holt and Hochberg 2001, Noonburg and Abrams 2005).

Even though greater heritability may circumvent transients of extinction risk, it can also generate oscillatory and chaotic dynamics. Negative feedbacks between ecological and evolutionary dynamics generate the oscillations: evolution of the predator to specialize on the more abundant species releases the other prey species from predation and, thereby, allowing the other prey species to become the more abundant species. These results are consistent with the general prediction that evolutionary destabilization of predator-prey interactions occurs most commonly when (1) there is a trade-off in capturing different prey phenotypes and (2) the predator and prey coevolve (Abrams and Matsuda 1997a, b, Abrams 2000).

Experimental work with rotifers and algae demonstrated that rapid evolution of prey trait can substantially alter predator-prey dynamics in natural systems (Yoshida et al. 2003, Hairston et al. 2005). For example, Yoshida et al. (2003) found that population cycles were driven by selection for resistant clones under intense predation, subsequent crashes in predator numbers, and non-resistant clones outcompeting resistant clones in the wake of these predatory crashes. Our results suggest that the rapid evolution of polyphagous predators may generate oscillatory or chaotic dynamics in natural systems due to similar ecological-evolutionary feedbacks.

Predator trait evolution

The few previous approaches to studying the evolution of a predator trait differ conceptually from the present one because they use adaptive-dynamics frameworks which assume asexual inheritance. Abrams (2006a, b) investigated when a consumer species feeding on two resources (which may have time-dependent growth rates) can evolve three distinct lines that differ in their capture success on the preys and can be interpreted as two specialists and one generalist. Implications of the evolution of the consumer for the resource species were not considered. Without explicit interbreeding between the different genotypes, such models are a closer approximation to multi-species dynamics than to within-population variation.

Rueffler et al. (2006) studied a related adaptive-dynamics model in which the consumer species evolves along a trait that determines the efficiency with which the two resources are transformed into fitness. Phenotypes are subjected to trade-offs, e.g., in their capture success. They found that for strong, or convex, trade-offs, and depending on the initial conditions, one specialist will evolve; for moderate trade-offs, there are three stable equilibria (either one of the specialists or a generalist at a branching point); for weak, or concave, trade-offs, there is a single convergence-stable generalist equilibrium. Earlier, Schreiber and Tobiason (2003) had

obtained similar results for consumers exploiting antagonistic, substitutable, or complementary resources.

The three outcomes described by Rueffler et al. (2006) also occur in our model. However, the phenotypic trade-offs emerging from our models on the predator trait are more complex than those *assumed* by Rueffler et al. (2006). They are not necessarily convex or concave but may be “wave-like” (see Appendix E). Consequently, the equilibrium structure in our model exhibits greater complexity and can not be inferred directly from the type of the trade-off (see Eqs. B.4 and B.5 in Appendix B). Moreover, unlike Rueffler et al. (2006), our results demonstrate that the transient dynamics, the stability properties of equilibria, as well as the existence of periodic or chaotic attractors, depend crucially on the genetic variation, i.e., the heritability, of the trait under selection. Thus, analyses only examining conditions for mutants invading homogeneous populations cannot capture the complexity of ecological systems exhibiting intraspecific variation.

Because it is well known that the genetic variance itself may evolve in response to selection (Bürger 2000), it would be a worthwhile enterprise to develop and explore genetic models that allow for the evolution of the genetic component of predator trait variation.

Implications and future directions

Our model illustrates the potentially very general point that ecological dynamics can be greatly altered by incorporating intraspecific variation. The classic apparent competition model predicts negative indirect effects between prey species and, under strong top-down control, exclusion of a prey species. By adding trait variation in the predator it becomes far easier for the prey species to coexist and in some situations even exhibit facilitation (the details depending greatly on particular parameter combinations). Such dramatic changes in outcomes suggests that studies which ignore trait variation may reach fundamentally incorrect conclusions. This is a sobering prospect, given (1) the long tradition of using species trait means in ecological models and (2) the ubiquity of ecologically significant trait variation within populations. Equally sobering is the potential complexity of how trait variation alters ecological dynamics. It would be nice to be able to say something straightforward like “variation increases the potential for coexistence,” but in truth the potential for species persistence depends on non-linear interactions between trait variation and other parameters (e.g., Fig. 2).

Given the potentially large effect of trait variation on ecological dynamics, it is urgent that empiricists and theoreticians alike increasingly consider intraspecific variation. For empiricists, this means getting a better understanding of the causes and magnitude of among-individual variance in ecologically significant phenotypic traits, interaction terms (prey use, competitive ability, pathogen resistance, predator evasion), and/or the

demographic parameters that arise out of interactions (growth, fecundity, survival). As our model shows, the heritability of such variation is also extremely important. Finally, we need more experiments that measure the population and community dynamic effects of intraspecific variation (Hughes et al. 2008). Interest in such experiments has skyrocketed recently, as it has become clear that intraspecific variation can have large effects. However, many of the existing studies manipulate genetic variation in place of known ecological traits (Agashe 2009).

For theoreticians, there are many possible ecological interactions whose properties are already well known, but which may benefit from reanalysis with trait variation in one or more species. This task is particularly challenging for food webs. In revisiting previous ecological models, it will be important to consider a variety of mechanisms of trait variation, from environmental noise to Mendelian or quantitative genetics. We believe our approach of partitioning quantitative variation into genetic and environmental components is particularly promising because it allows one to analytically separate the effects of trait variance *per se*, from the effects of heritable variation. Such analyses will allow more effective integration of eco-evolutionary feedbacks and direct effects of variation. This is not to say that trait variation will always have ecological effects, or that such effects will be large. But at the very least, ecologists need to develop an understanding of when trait variation may be important, and what its effects might be.

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APPENDIX A

Conditions for persistence of predator and prey species (*Ecological Archives* E092-133-A1).

APPENDIX B

Coexistence equilibria and their stability (*Ecological Archives* E092-133-A2).

APPENDIX C

Symmetric predation and the existence of alternative states (*Ecological Archives* E092-133-A3).

APPENDIX D

Supplementary figures on transient dynamics (*Ecological Archives* E092-133-A4).

APPENDIX E

Quantifying ecological trade-offs (*Ecological Archives* E092-133-A5).