

ARTICLE

Cascading benefits of mutualists' predators on foundation species: A model inspired by coral reef ecosystems

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Abstract

Multispecies mutualisms are embedded in a network of interactions that include predation, yet the effects of predation on mutualism function have not been well integrated into mutualism theory. Where predators have been considered, the common prediction is that predators reduce mutualist abundance and, as a consequence, decrease service provision. Here, we use a mathematical model of a predatory fish that consumes two competing coral mutualists to show that predators can also have indirect positive effects on hosts when they preferentially consume competitively dominant mutualists that are also lower in quality. In these cases, predation reverses the outcome of competition, allowing the higher quality mutualist to dominate and enhancing host performance. The direction and strength of predator effects depend on asymmetries in mutualist competition, service provision, and predation vulnerability. Our findings suggest that when the strength of predation shifts (e.g., due to exploitative harvest of top predators, introduction of new species, or range shifts in response to climate change), mutualist communities will exhibit dynamic responses with nonmonotonic effects on host service provision.

KEY WORDS

coral reefs, foundation species, Lotka–Volterra competition

INTRODUCTION

Mutualisms—reciprocally beneficial interactions between members of two or more species—hold great appeal to biologists. Whether mediated by service (e.g., pollinators bearing pollen from plant to plant) or resource (e.g., the nectar reward plants offer their pollinators), they capture our imagination. The study of mutualisms has evolved from initial research focused on pairwise positive–positive interactions between species, to a more recent focus on multispecies guilds—suites of mutualistic partners of potentially variable quality (Bronstein, 1994; Palmer et al., 2015; Stanton, 2003).

Additionally, mutualism biology has expanded to consider how mutualisms are embedded within the tangled web of complex species interactions that also include other ecological processes such as competition, nutrient limitation, and predation. For example, recent empirical studies have examined how predators may control mutualist populations and thereby alter partner availability and performance (see Knight et al., 2006). However, the majority of research linking trophic interactions and mutualisms has been empirical and the subject has received limited theoretical attention, restricting our general understanding of how

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predation can alter the services and performance of multispecies mutualisms.

Virtually all mutualisms are embedded in a trophic framework. For example, the ubiquitous plant–pollinator mutualism is shaped by herbivory and insectivory (Benoit & Kalisz, 2020; Knight et al., 2006), and predators can disrupt plant dispersal when they consume frugivores (Rogers et al., 2017). In general, predation on mutualists is expected to negatively affect host performance by reducing the abundance or behavioral activity of mutualists (Knight et al., 2006). For example, predation can reduce pollinator activity levels (Romero et al., 2011) and indirectly reduce plant fitness (Romero & Koricheva, 2011). However, it is possible to imagine alternate scenarios where predators have no effect or an indirect positive effect on the host, particularly when predation on a guild of competing mutualists is considered. For example, if predator-mediated coexistence favors the persistence of higher quality mutualists, indirect benefits to the mutualistic partners should be observed.

As the mutualism literature has grown, it has become increasingly clear that mutualists can vary tremendously in their level of service to the host (Brodie et al., 2009; Palmer et al., 2010), can compete or cooperate with one another to affect host performance (Johnson & Bronstein, 2019; Miller, 2007; Stanton, 2003), and that not all mutualists are equally impacted by predation (Brechbühl et al., 2010). Mathematical models can help us to predict how predators alter mutualist and host performance by integrating variable mutualist performance, competitive or cooperative interactions between mutualists, and variability in mutualists' susceptibility to predation.

Here, we use a mathematical model for multispecies mutualisms in a food web context that is inspired by a system of mutualistic coral-dwelling fishes that increase the growth of their coral hosts by excreting nitrogen-rich waste products into the nutrient-poor tropical waters where corals grow (Detmer et al., 2022; Holbrook et al., 2008). This increased growth of the coral in turn offers shelter for communities of coral-dwelling fish. Predation is a powerful force affecting the abundance of these coral reef fishes (Stier et al., 2017), but the effects of predators vary among the fish mutualists and can alter the outcome of competition among fish mutualists (Schmitt et al., 2009). While our model formulation is inspired by coral-dwelling fishes, our approach identifies a generalizable set of conditions under which higher trophic level may enhance mutualism performance. We particularly focus on the combinations of mutualist guild member quality, competitive strength, and susceptibility to predation that create scenarios with unexpected benefits cascading from higher trophic levels to mutualist hosts. Finally, given the context of our study system in an era of

defaunation (Dirzo et al., 2014), we discuss potential implications for conservation and management.

THE MODEL

To construct our mathematical model, we drew inspiration from a real biological system in which a multispecies mutualism is exposed to variable predation pressure (Figure 1). Tropical coral reefs are populated by dozens of fish species. Some of these species live on or among the interstices of branching corals where they receive protection from predation (Hixon, 1991). These coral-dwelling fishes excrete nitrogen-rich waste products, typically in the form of ammonium and/or urea (Allgeier et al., 2017), which can be taken up by the coral and are transferred to and used by the photosynthetic algae living inside of the coral animal's tissue (Holbrook et al., 2008; Muscatine et al., 1989). The photosynthate produced by these algae feeds the coral, stimulating coral growth.

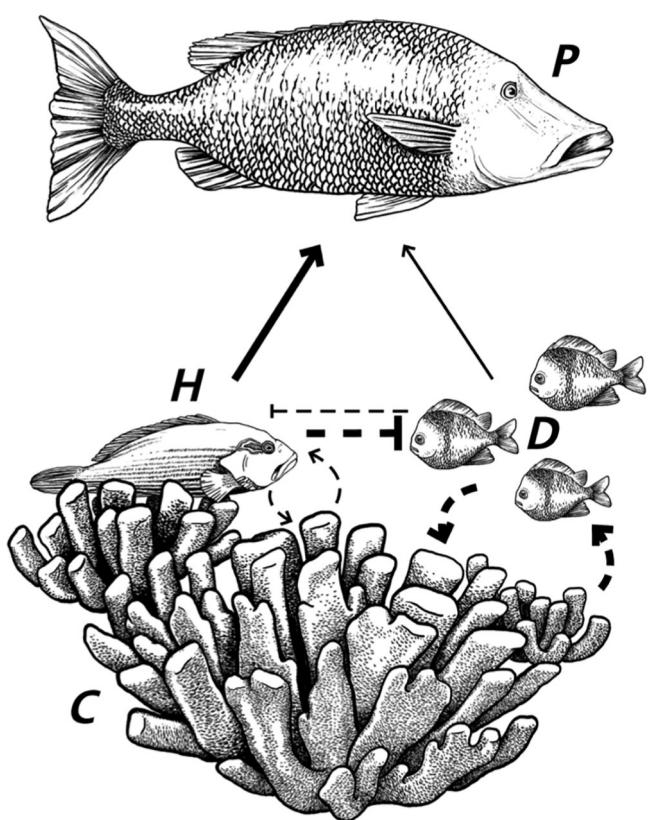


FIGURE 1 A model for the coral–fish–predator mutualism system. We model a population of corals *C* (here, one coral colony is shown for illustrative convenience) which hosts two coral-dwelling fishes: damselfish *D* and hawkfish *H*. Both fish species are vulnerable to predation by a mesopredator *P*, which is itself susceptible to fishing pressure. Depending upon the mutualists' traits, coral area exhibits divergent responses to increasing predator abundances. Illustration by Emma Vogan.

Benefits provided by two coral-dwelling fishes to corals are well studied in the lagoons surrounding the island of Moorea, French Polynesia. Both hawkfish (*Paracirrhites arcatus*) and yellow-tailed damselfish (*Dascyllus flavicaudus*) colonize branching colonies of the coral genus *Pocillopora*. While hawkfish—mesopredators that occasionally prey on damselfish—are the dominant competitors (Holbrook et al., 2011), corals that host damselfish grow significantly faster than those with hawkfish (Holbrook et al., 2008). Both fishes are preyed upon by transient predatory fishes (e.g., longface emperor *Lethrinus olivaceus*), though predation rates in Moorea are not well known and vary significantly across sites (Schmitt & Holbrook, 2007).

We represented the interaction between a population of corals (C), the associated populations of coral-dwelling damselfish (D) and hawkfish (H), and the predators of these fishes (P) using a system of four differential equations. (Symbols, their meanings and units, and their dimensionless equivalents are listed in Table 1.) We modeled corals as a population of individual coral colonies of age a living in an area with a finite carrying capacity C_T . If the areal extent of a colony of age a is given by $c(a,\tau)$, and the number of coral colonies in the age range $a \rightarrow a + da$ is given by $n(a,\tau)da$, then the total

area covered by corals at any time τ is given by the integral:

$$C(\tau) = \int_0^\infty c(a,\tau)n(a,\tau)da. \quad (1)$$

The change in coral area is determined by the balance between recruitment R , growth of existing corals G , and mortality M :

$$\frac{dC}{d\tau} = R(\tau) + G(\tau) - M(\tau). \quad (2)$$

We assumed that our model accounts for a sufficiently large coral population that we could approximate the population as closed, such that recruitment comes from corals within the population who have a per-area viable larval production rate β . (However, see Appendix S2 for the open recruitment case.) We assumed that larvae can only recruit onto space unoccupied by corals, such that:

$$R(\tau) = \beta C(\tau) \left(1 - \frac{C(\tau)}{C_T}\right). \quad (3)$$

Our growth function G must account for two processes: the intrinsic growth of corals (for which we assume a fixed specific [per area] growth rate of g_0) and

TABLE 1 Variables and parameters, their meanings and typical units, and rescaled versions.

Symbol	Meaning	Typical units	Rescaled version	Analysis values
Variables				
τ	Time	days	t	
C	Coral population area	m^2 coral	c	
D	Damselfish biomass	g dams	d	
H	Hawkfish biomass	g hawk	h	
P	Mesopredator biomass	g pred	p	
Parameters				
C_T	Carrying capacity of corals	m^2
β	Coral production of viable larvae	d^{-1}
g_0	Coral baseline areal extension rate	d^{-1}
g_D	Coral growth enhancement by damselfish	m^2 coral \times dams $^{-1}$ \times d^{-1}
g_H	Coral growth enhancement by hawkfish	m^2 coral \times hawk $^{-1}$ \times d^{-1}	ϵ	0–1
m	Coral mortality	d^{-1}	μ	0.9
r_D	Damselfish growth rate	d^{-1}	ρ_D	0.1
r_H	Hawkfish growth rate	d^{-1}	ρ_H	0.1
k_D	Per-coral damselfish carrying capacity	g dams \times m^2 coral $^{-1}$	κ_D	1
k_H	Per-coral hawkfish carrying capacity	g hawk \times m^2 coral $^{-1}$	κ_H	1
α_{DH}	Competitive effects of hawkfish on damselfish	g dams \times g hawk $^{-1}$
α_{HD}	Competitive effects of damselfish on hawkfish	g hawk \times g dams $^{-1}$	α	0–1
a_D	Attack rate of predators on damselfish	$d^{-1} \times g$ pred $^{-1}$
a_H	Attack rate of predators on hawkfish	$d^{-1} \times g$ pred $^{-1}$	ϕ	0–1

an acceleration in growth due to fertilization by coral-associated fishes. To model this growth acceleration, we must first account for the distribution of fishes on corals. We assume that, at any given time, all fish are associated with corals (Holbrook & Schmitt, 2003), and that the benefit to sheltering in a coral is related to that coral's size. We assume an ideal free distribution, which implies that the biomass of damselfish and hawkfish subpopulations associated with a coral of age a are given by:

$$d(a, \tau) = D(\tau) \frac{c(a, \tau)}{C(\tau)} \text{ and} \quad (4)$$

$$h(a, \tau) = H(\tau) \frac{c(a, \tau)}{C(\tau)}. \quad (5)$$

We assume that each fish excretes at a species-specific rate that leads to a per-fish acceleration in coral growth g_i (where i is D for damselfish or H for hawkfish). Thus, the growth rate of a coral cohort of age a is:

$$\begin{aligned} g(a, \tau) &= g_0 + g_D d(a, \tau) + g_H h(a, \tau) \\ &= g_0 c(a, \tau) + g_D D(\tau) \frac{c(a, \tau)}{C(\tau)} + g_H H(\tau) \frac{c(a, \tau)}{C(\tau)}. \end{aligned} \quad (6)$$

Integrating over the entire coral population, and assuming that corals can only grow into unoccupied space, we then have:

$$\begin{aligned} G(\tau) &= \int_0^\infty g(a, \tau) n(a, \tau) da \left(1 - \frac{C(\tau)}{C_T}\right) \\ &= \int_0^\infty n(a, \tau) \left(g_0 c(a, \tau) + g_D D(\tau) \frac{c(a, \tau)}{C(\tau)}\right. \\ &\quad \left.+ g_H H(\tau) \frac{c(a, \tau)}{C(\tau)}\right) da \left(1 - \frac{C(\tau)}{C_T}\right) \\ &= C(\tau) \left(g_0 + \frac{g_D D(\tau)}{C(\tau)} + \frac{g_H H(\tau)}{C(\tau)}\right) \left(1 - \frac{C(\tau)}{C_T}\right). \end{aligned} \quad (7)$$

Finally, we assume that corals have an age- and size-independent areal mortality rate m , such that $M(\tau) = mC(\tau)$.

Assembling these components, we can write the change in the area occupied by the coral population as:

$$\begin{aligned} \frac{dC}{d\tau} &= C(\tau) \left(\beta + g_0 + g_D \frac{D(\tau)}{C(\tau)} + g_H \frac{H(\tau)}{C(\tau)}\right) \left(1 - \frac{C(\tau)}{C_T}\right) \\ &\quad - mC(\tau). \end{aligned} \quad (8)$$

We model the dynamics of fish biomass using a modified Lotka–Volterra competition model. Both coral-dwelling

fishes rely on coral for habitat, so we assume that their carrying capacities scale with the area of available coral habitat with species-specific scalars k_D and k_H . This approach assumes that, as the coral population grows in areal occupancy, the physical structure (and interstitial space where fish dwell) scales proportionately. Damselfish and hawkfish populations grow toward their carrying capacities at the rates r_D and r_H , respectively. Because fish are represented in units of biomass, this growth could represent recruitment of new individuals and/or increases in biomass of existing members of the population. As with our coral population, we neglect external recruitment (but see Appendix S2). In addition to self-limitation through intraspecific competition, the fishes also compete with one another with competition coefficients α_{DH} and α_{HD} . Thus, for example, a hawkfish's perception of how much open space there is in a coral (e.g., as it approaches to settle) is determined by the abundance of both hawkfish and damselfish, scaled by competition coefficients. Both species are vulnerable to mortality due to predation with species-specific attack rates a_D and a_H .

$$\frac{dD}{d\tau} = r_D D \left(\frac{k_D C - D - \alpha_{DH} H}{k_D C}\right) - a_D DP, \quad (9)$$

$$\frac{dH}{d\tau} = r_H H \left(\frac{k_H C - H - \alpha_{HD} D}{k_H C}\right) - a_H HP. \quad (10)$$

Thus, in our formulation, fish are simultaneously competitors (for habitat provided by the coral) and indirect facilitators of one another via their beneficial impacts on the growth of the coral host.

We assume that predators integrate over large spatial and temporal scales and consume a diversity of prey of which hawkfish and damselfish are just one component. Therefore, their population dynamics are relatively unimpacted by the three other species (i.e., $dP/d\tau = 0$). However, the abundance of predators P may be altered by external pressures, such as fishing, so we explore the effects of variation in P in our analysis. In Appendix S3, we also consider the case in which the presence of the foundation species, coral, can alter predation rates either by increasing rates (because predators are drawn to regions of high prey habitat availability) or decreasing them (because coral structure provides shelter for prey to hide, decreasing predation success). Thus, we can write the full model:

$$\frac{dC}{d\tau} = (\beta C + g_0 C + g_D D + g_H H) \left(1 - \frac{C}{C_T}\right) - mC, \quad (11)$$

$$\frac{dD}{d\tau} = r_D D \left(\frac{k_D C - D - \alpha_{DH} H}{k_D C} \right) - a_D D P, \quad (12)$$

$$\frac{dH}{d\tau} = r_H H \left(\frac{k_H C - H - \alpha_{HD} D}{k_H C} \right) - a_H H P. \quad (13)$$

Note that, although the equation for coral growth at first glance appears to imply that the presence of fish could cause the spontaneous generation of coral (i.e., $dC/d\tau > 0$ if $D, H > 0$ even when $C = 0$), the fish themselves depend on coral as a source of habitat. Thus, because fish cannot persist in the absence of coral, this scenario does not arise in practice.

Though our model is inspired by a coral reef mutualism, slight modifications to our formulation could describe other goods-for-services mutualisms in which multiple mutualists compete for the service and are impacted by shared predators. Here, one partner guild (coral-dwelling fishes) provides a metabolic resource (N -rich waste products) in exchange for a partner's service (habitat provision by the coral). Similar systems include plant–pollinator mutualisms and plant defense mutualisms. Further, in our model, the predator (which does not respond dynamically to prey availability) acts as a fixed increase in mutualist per capita mortality; in this way, changes in predator abundance are similar to other changes in ecological regimes (e.g., reductions in food supply, shifts in disturbance intensity).

ANALYSIS

To reveal correlations between parameters that allow us to reduce our analysis to a few composite parameters, we use a change of variables to nondimensionalize the model (fully described in Appendix S1). First, we consolidate the two coral-dependent areal increase parameters β and g_0 into a single parameter r_C , which represents the capacity of a coral population for expansion in the absence of fish. By performing the change of variables $t = \tau r_C$, $c = C/C_T$, $d = (g_0 D)/(r_C C_T)$, $h = (\alpha_{DH} g_D H)/(r_C C_T)$, and $p = a_D P/r_C$, we can write the dimensionless model:

$$\dot{c} = (c + d + \epsilon h)(1 - c) - \mu c, \quad (14)$$

$$\dot{d} = \rho_D d \left(\frac{\kappa_D c - d - h}{\kappa_D c} \right) - dp, \quad (15)$$

$$\dot{h} = \rho_H h \left(\frac{\kappa_H c - h - \alpha d}{\kappa_H c} \right) - \phi h p, \quad (16)$$

where $\epsilon = g_H/(\alpha_{DH} g_D)$, $\mu = m/r_C$, $\rho_D = r_D/r_C$, $\rho_H = r_H/r_C$, $\kappa_D = (k_D g_D)/r_C$, $\kappa_H = (k_H \alpha_{DH} g_D)/r_C$, $\phi = a_H/a_D$, and $\alpha = \alpha_{DH} \alpha_{HD}$.

In our analysis, we pay special attention to three parameters that describe the relative traits of the two mutualist species: (1) ϵ , which represents the relative mutualist quality of hawkfish compared with damselfish, scaled by the competitive effects of hawkfish on damselfish; (2) α , which, following standard theory for Lotka–Volterra competition, is a measure of the relative strength of interspecific versus intraspecific population regulation of the two fish populations; and (3) ϕ , which represents the intensity of predation on hawkfish relative to damselfish.

In addition to these parameters, a few species-specific parameters remain: μ is the mortality rate of coral, and ρ_i and κ_i (where $i = \{D, H\}$) are the intrinsic growth rate and coral-dependent carrying capacity scalings of the fishes. In order to highlight the importance of competition and predation to our results, we consider the simplified case in which $\rho_D = \rho_H = \rho$ and $\kappa_D = \kappa_H = \kappa$, such that hawkfish and damselfish are identical except in their interspecific competitive ability, mutualist quality, and susceptibility to predation.

Note that the combination of our choice of dimensionless rescaling (which eliminates one of the competition coefficients) and our assumption that the carrying capacities of both fishes scale identically eliminate the possibility of competitive coexistence (in the absence of the predator) or of alternative stable states. This simplification allows us to draw biologically meaningful mathematical conclusions about our model. We comment briefly on the consequences of alternate assumptions in Appendix S1.

Predators may have either positive or negative effects on foundation species

Using numerical simulation, we observed two qualitatively different effects of increasing predatory fish abundance on coral area (Figure 2). We studied a scenario in which predator density increased at five-year intervals. In the absence of predators, our system was dominated by hawkfish, and damselfish were competitively excluded ($\alpha < 1$). Increasing predator abundance altered the outcome of competition by eliminating the hawkfish through predation ($\phi > 1$). In some scenarios, this also resulted in a decrease in coral area (Figure 2A) because the overall reduction in coral-dwelling fish biomass reduced the benefits to the corals, sensu Knight et al. (2006). However, when hawkfish were lower quality mutualists, a shift in competitive outcome could actually benefit the coral (Figure 2B) because, although total fish biomass on the head of coral was reduced, the biomass that remained produced greater growth enhancement of the coral. In both

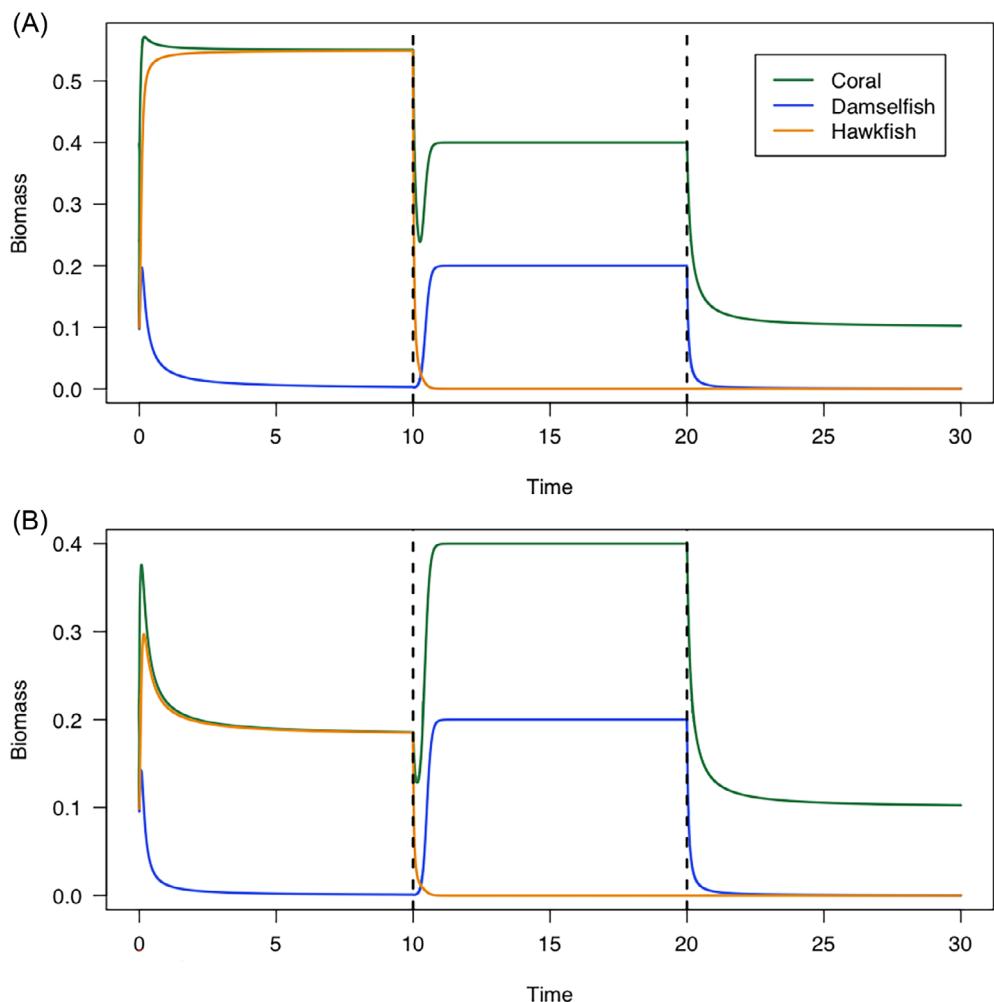


FIGURE 2 Dynamic response of corals and coral-dwelling fishes to changing predator biomass. (A) When hawkfish and damselfish are equally high-quality mutualists, an increase in predator abundance causes a decrease in coral equilibrium area (sensu Knight et al., 2006). (B) When damselfish are higher quality mutualists than hawkfish, corals benefit from intermediate predator biomass, but ultimately decline under sufficiently high predation regimes. Parameter values are $\gamma = \kappa_D = \kappa_H = 1$, $\rho_D = \rho_H = 0.1$, $\alpha = 0.5$, $\phi = 2$, and $\epsilon = 1$ for panel (A) and 0.1 for panel (B). Predators increase in abundance from $p = 0$ to $p = 0.05$ at year 5, and increase further to $p = 0.1$ at year 10 in both panels.

scenarios, continued increases in predator abundance ultimately had a negative effect on corals by completely suppressing coral-dwelling fish populations.

Conditions on indirect predator benefits

Under what conditions do these different scenarios emerge? We used graphical methods (see Appendix S1) to derive analytical relationships between relative competitive ability (α), relative mutualist quality (ϵ), and relative predator sensitivity (ϕ). We first discuss these results in the context of the hawkfish–damselfish system, before drawing broader conclusions about multispecies mutualisms with predation.

In order for predators to indirectly benefit the growth of foundation species, three criteria must be met:

1. Damselfish must be higher quality mutualists than hawkfish ($\epsilon < 1$).
2. Hawkfish must be stronger competitors than damselfish ($\alpha < 1$), such that damselfish are competitively excluded in the absence of predators.
3. Hawkfish must be more susceptible to predation than damselfish ($\phi > 1$).

More generally, predators mediate indirect benefits when their activity reduces the competitive dominance of a lower quality mutualist (Appendix S1: Figure S5). Predators do not benefit foundation species when:

1. they prefer the higher quality mutualist, because in this case predators reduce the population of the best partner and have a net negative effect on mutualist goods provisioning, or

2. they prefer the weaker competitor, because in this case predators do not alter the outcome of competition.

Of course, the relative magnitudes of trait differences (i.e., the relationship between α , ϵ , ϕ , and 1) affect the strength of predator effects. In addition to the three criteria described above, the mathematical condition for predator indirect facilitation (derived in Appendix S1) is:

$$\epsilon < \frac{\phi - 1}{\phi - \alpha}. \quad (17)$$

That is, the worse in quality the low-quality mutualist (here, hawkfish) is (i.e., the smaller ϵ is) or the less competitively dominant the hawkfish is (i.e., the closer α is to 1), the smaller the predator preference ϕ needs to be in order for the predator to indirect positive effects on the coral (Appendix S1: Figure S5).

The magnitude of predator benefits (in our system, the increase in coral growth relative to a predator-free environment) depends upon mutualist traits and predator abundance (Figure 3). We expect the strongest predator effects when $\alpha \approx 1$ (i.e., the two mutualists are of similar competitive strengths, so that little predation pressure is needed to tip the system from hawkfish-dominated to damselfish-dominated, with associated increases in nitrogen fertilization), $\phi \gg 1$ (i.e., the predator strongly prefers the hawkfish, so that little predator abundance is necessary to tip the system and thus the damselfish experience limited predation), and $\epsilon \ll 1$ (i.e., hawkfish are extremely poor mutualists, so that a flip from hawkfish- to damselfish-dominated heads of coral produces an extreme shift in mutualist benefits).

We emphasize, however, that regardless of the potential magnitude of predator benefits, there is a threshold of predator abundance beyond which these cascading benefits cease. This is because the predator is still a predator of all mutualists. Thus, sufficiently large numbers of predators suppress all mutualist populations and overall goods production. In our coral reef system, for example, a high abundance of mesopredators would eliminate hawkfish and also reduce damselfish populations, thus eroding the nutrient subsidy that supports coral growth. The predator abundance at which benefits cease (i.e., equilibrium coral abundance is equivalent to the no-predator case) is given by:

$$p_{\max} = \rho_D(1 - \epsilon). \quad (18)$$

In other words, the predator abundance at which benefits to the foundation species cease is a function of the speed at which the highest quality mutualist grows (e.g., in our system, faster growing damselfish provide benefits even

under high levels of predation) and the difference in mutualist quality between guild members (the larger the magnitude, the more predation can be sustained before overall negative effects become dominant).

The precise predator abundances at which benefits accrue are, of course, sensitive to the model's formulation. For example, when open recruitment is permitted (Appendix S2), external recruitment of the subdominant competitor can allow it to coexist with the dominant competitor even in the absence of the predator. This alters the baseline provision of benefits in the system into which a predator might enter, but our qualitative findings (that predators benefit foundation species when they favor a mutualist community composition that provides more benefits than the predator-free baseline) hold. Additional feedbacks between the foundation species and the predator (Appendix S3) can also constrain predator benefits. When the presence of coral draws additional predators, this can create a negative feedback in which increased coral abundance increases predation and reduces mutualistic benefits. This means the window over which predators indirectly benefit foundation species is narrower.

DISCUSSION

The effects of predation on ecosystem structure and function are highly dependent on the strength of competitive interactions between the species they consume (Chase et al., 2002; Chesson & Kuang, 2008). Yet we have a limited understanding of how the effects of predators cascade to affect ecosystems when their primary prey are guilds of competing mutualists. Because predators consume prey, their presence is generally thought to reduce benefits conferred by mutualist prey to their partners (Knight et al., 2006). However, here we show that under certain circumstances predators can in fact enhance the performance of multispecies mutualisms, with cascading impacts on the growth of foundation species. Our model predicts that the indirect benefits of predators on foundation species can occur under specific conditions: namely, when predators preferentially target a dominant competitor that is also a weaker mutualist. Under these circumstances, predators alter the outcome of competition in ways that enhance the overall delivery of mutualist goods. These results corroborate previous research documenting the importance of third-party species interactions in driving the performance of mutualist guilds (Palmer et al., 2015) and point to significant empirical opportunities to better integrate mutualisms into networks embedded with diverse sets of species interactions.

While our model offers somewhat counterintuitive predictions whereby predation on mutualists can increase

the performance of a foundation species, it also emphasizes the importance of context when predicting how multispecies mutualisms can integrate into our understanding of food web dynamics. Our findings corroborate the well-documented context-dependent nature of species interactions (Chamberlain et al., 2014) in at least three ways. First, we show that the effect of predators on coexistence of their mutualists depends on mutualist

competitive dynamics as well as the relative susceptibility mutualists have to predation. Second, we show that predators can have positive, negative, or little effect on the foundation species depending on the competitive interactions between mutualists, the relative susceptibility or mutualists to predation, and the benefits mutualists provide to the host. Third, we show that the effects of predators on mutualist communities depend on predation intensity. Even under circumstances where predators preferentially consume species that are dominant competitors but inferior partners, the positive effect of predators on foundation species only emerges at intermediate predation levels. In our dimensionless model, rescaled predator abundance is an amalgamation of actual predator biomass in the system (P), the attack rate of predators on damselfish (a_D), and the maximum nutrient enhancement of the coral's growth rate (g_1). Thus, a biological system that is more sensitive to predation could be one in which absolute predator abundance is elevated, in which damselfish vulnerability is increased, or in which coral growth is less dependent on nutrient enrichment.

These context dependencies suggest that, in order to predict how a change in predation pressure might later mutualist coexistence or the services provided by guilds of mutualists, we need significantly more empirical study of these systems. While predation on mutualists is common in nature, and various examples of predators altering mutualist abundance and host performance exist (reviewed in Knight et al., 2006), there is still much we do not know. Empirically, we know relatively more about

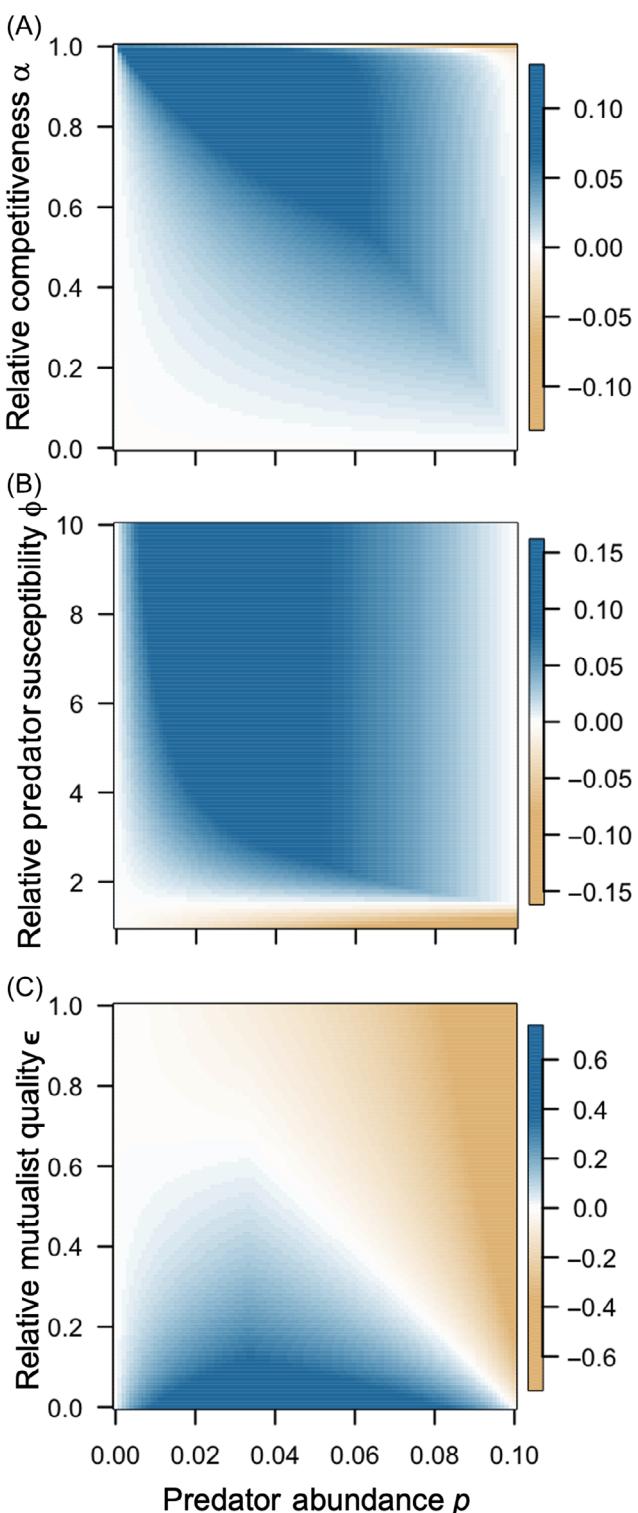


FIGURE 3 Effects of changes in mesopredator abundance (x-axis) and α (A), ϕ (B), and ϵ (C) on relative coral area. Changes in coral area are plotted on a log scale, such that negative numbers (brown) indicate declines and positive numbers (blue) indicate increases in coral area relative to a predator-free system. (A) As α approaches 1, the two mutualists become more and more equivalent competitors. Smaller amounts of predator are required to tip the system to dominance by the weaker competitor (and stronger mutualist), and the marginal gains in coral area are greater (blue color). (B) As ϕ increases, the lower quality, competitively dominant mutualist becomes more and more vulnerable to predation. As a consequence, less and less predator biomass is required to tip the system into dominance by the weaker competitor (and stronger mutualist), leading to greater gains in coral area. (C) As ϵ approaches 1, the mutualists become equivalent in quality. The higher in quality the low-quality mutualist is, the less beneficial predators may be (because their action to tip the system to dominance by the other mutualist has less and less of an impact on mutualist goods delivery). Parameter values are as listed in Figure 1B, with $\phi = 2$ and $\epsilon = 0.5$ for panel (A), $\alpha = 0.5$ and $\epsilon = 0.5$ for panel (B), and $\alpha = 0.5$ and $\phi = 2$ for panel (C). Colors are from the Manu package by Geoffrey Thomson, <https://g-thomson.github.io/Manu/>.

the relative quality of mutualists in diverse guilds (Stanton, 2003). We also know little about how mutualist quality covaries with competitive ability or predator susceptibility, two additional traits that qualitatively affect outcomes in our mathematical model. This empirical gap points to critical opportunities for future empirical research integrating mutualisms into diverse species interaction networks.

Trade-offs as mechanisms for coexistence of mutualists are relatively well studied, and there is a rich literature on trade-offs between competition between mutualists and partner quality. Specifically, the mutualism–partner quality trade-off has been reviewed empirically by Palmer et al. (2003) and is formalized theoretically most recently by Johnson and Bronstein (2019), which is grounded in the assumption that lower quality mutualists “save” resources and thus become better competitors (an underlying assumption of dozens of papers on mutualism stability). Similarly, trade-offs between competition and predation are well established in the theoretical (e.g., Holt et al., 1994; Kuang & Chesson, 2008) and empirical literature (Chase et al., 2002). However, covariance in all three factors remains poorly studied. It stands to reason that if trade-offs between competition and predation and competition and partner quality exist then a three-way covariance between competition, susceptibility to predation, and partner quality exists. While few published case studies exist, there is evidence for covariance in susceptibility to predation, competition, and in partner quality in the hawkfish–damselfish–coral system that inspired our model (Holbrook et al., 2011; Schmitt et al., 2009).

Our model also offers insight into the coral reef system that inspired it. While predation is a known driver of biodiversity on coral reefs (Stier et al., 2017), there has previously been a weak theoretical link between predation and the symbiotic interactions that power productive coral reef ecosystems living in otherwise nutrient-poor environments. One clear implication of our results is that the well-documented predation pressure on mutualistic fishes and invertebrates (Stier & Leray, 2014) may be critical to the maintenance of diversity within this system. A second implication is that variation in predation pressure across reefs may indirectly alter the growth and survival of coral if mesopredators shift the outcomes of competition toward higher quality mutualists (e.g., from hawkfish to damselfish). These outcomes may be further complicated by mutualist behavioral changes when predators create a “seascape of fear” (Laundré et al., 2014; Wirsing et al., 2008). For example, coral-dwelling fishes may spend more time hiding (and excreting) in the interstices of branching corals, further enhancing N deposition and fish benefits, when predators are present. Indeed, a more realistic accounting of fish behavior

(such as the territoriality of hawkfish that likely reduces their carrying capacity, i.e., $k_H < k_D$) might increase the range of parameter space over which predators have indirect benefits. The third implication of our model for coral reef ecosystem systems is that human impacts such as fishing that disproportionately remove predatory fishes from coral reefs may indirectly alter the performance of the coral. If fishing alters predation pressure on coral reefs either by reducing the abundance of large predatory fishes (Stallings, 2009) or increasing the abundance of highly carnivorous mesopredators, this may modify the dominant mutualist fish found in certain corals and restructure the services imbued by these diverse coral occupants. Additional research should consider how these potential shifts might integrate with ongoing research examining how fishing potentially alters the supply of nutrients from fishes to coral reefs (Allgeier et al., 2016). In extreme cases, these fisheries-induced shifts in mutualist identity and density may have significant consequences for the growth and survival of corals.

Although we expect the qualitative conclusions of our model to extend beyond coral–fish systems, the strength and even directionality of cascading predator effects depend upon the details of the system and the species interactions. For example, including open recruitment of mutualistic partners (see Appendix S2) can allow for coexistence of competing mutualists even in the absence of predation, although the model’s qualitative predictions (that predators strengthen the mutualism when they shift the numerical balance of the mutualists in favor of the higher quality partner) hold. Predator behavior can also influence outcomes: for example, if predators are drawn to patches of prey habitat, a positive feedback between the foundation species and predator abundance may erode mutualism benefits (see Appendix S3). Furthermore, our model assumes that the mutualistic species compete with one another for physical habitat space provided by the foundation species. Other types of interaction—including competition for consumable resources, neutral interactions, or even facilitation (Afekhami et al., 2014)—would produce different models and, presumably, different outcomes that are beyond the scope of the present study. For example, our model could be modified to allow for direct positive interactions between the mutualists, either by altering the signs of the competition coefficients or by introducing additional state variables describing resource exchange. Other effects of predator behavior could also be included, for example, by allowing mutualist benefits to the foundation species to depend upon predator abundance, mimicking the “landscape of fear.” Finally, we note that our model assumes that symbionts are strictly beneficial. However, an excess of mutualistic partners can be costly, including in coral–fish symbioses where modeling work suggests that excessive

nitrogen fertilization may drive coral-algal dysbiosis and bleaching (Detmer et al., 2022).

CONCLUSION

The idea that predation is a critical process governing the coexistence of species and altering the abundance of foundation species is central to our understanding of biological communities. Long-standing theories predict that predators can maintain the biodiversity in systems and by altering the abundance and behavior of prey they can alter the abundance of habitat-forming species. While the role of predation in modifying consumer-resource interactions is well established, the theoretical and empirical link between predation and diverse mutualist communities is in its infancy. The next step is to further characterize how predators interact with diverse guilds of mutualists in nature, paying particular attention to the covariance structure predation, competition, and the services mutualists provide. Moreover, the theory developed here provides a foundation to develop new models linking predation and mutualism, such as consideration for how predator-mutualist dynamics shift as the architecture of species interactions change in shape and the consequences for the resilience of natural systems.

AUTHOR CONTRIBUTIONS

Holly V. Moeller and Adrian C. Stier designed the research. All authors constructed and analyzed the mathematical model, drafted the manuscript, and contributed to revisions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study. Code (Moeller et al., 2022) is available from Zenodo: <https://doi.org/10.5281/zenodo.7168964>.

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Cascading benefits of mutualists' predators on foundation species: a model inspired by coral reef ecosystems

Holly V. Moeller, Roger M. Nisbet, and Adrian C. Stier

Ecosphere

Appendix S1

Nondimensionalization

Our dimensional set of equations is:

$$\frac{dC}{d\tau} = (r_C C + g_D D + g_H H) \left(1 - \frac{C}{C_T}\right) - mC \quad (\text{S1})$$

$$\frac{dD}{d\tau} = r_D D \left(\frac{k_D C - D - \alpha_{DH} H}{k_D C}\right) - a_D D P \quad (\text{S2})$$

$$\frac{dH}{d\tau} = r_H H \left(\frac{k_H C - H - \alpha_{HD} D}{k_H C}\right) - a_H H P \quad (\text{S3})$$

The key first decision that we make is to rescale time by the intrinsic growth rate of the coral r_C . (Note that this growth rate is the amalgamation of new recruitment and lateral extension.) Thus we employ the substitution $t = r_C \tau$. Simultaneously, we rescale coral by the maximum areal extent C_T via the substitution $C = cC_T$:

$$\frac{dc}{dt} = \left(c + \frac{g_D}{r_C C_T} D + \frac{g_H}{r_C C_T} H\right) (1 - c) - \frac{m}{r_C} c \quad (\text{S4})$$

$$\frac{dD}{dt} = \frac{r_D}{r_C} D \left(\frac{k_D C_T c - D - \alpha_{DH} H}{k_D C_T c}\right) - \frac{a_D}{r_C} D P \quad (\text{S5})$$

$$\frac{dH}{dt} = \frac{r_H}{r_C} H \left(\frac{k_H C_T c - H - \alpha_{HD} D}{k_H C_T c}\right) - \frac{a_H}{r_C} H P \quad (\text{S6})$$

This system of equations gives us a clue for our substitution for D . Let us define the dimensionless new state variable $d = (g_D D) / (r_C C_T)$ and substitute $D = (dr_C C_T) / (g_D)$. Simultaneously, we will define $h = (\alpha_{DH} g_D H) / (r_C C_T)$ and substitute $H = (h r_C C_T) / (\alpha_{DH} g_D)$:

$$\frac{dc}{dt} = \left(c + d + \frac{g_H}{\alpha_{DH} g_D} h \right) (1 - c) - \frac{m}{r_C} c \quad (\text{S7})$$

$$\frac{dd}{dt} = \frac{r_D}{r_C} d \left(\frac{k_D C_T c - \frac{r_C C_T}{g_D} d - \frac{\alpha_{DH} r_C C_T}{\alpha_{DH} g_D} h}{k_D C_T c} \right) - \frac{a_D}{r_C} d P \quad (\text{S8})$$

$$\frac{dh}{dt} = \frac{r_H}{r_C} h \left(\frac{k_H C_T c - \frac{r_C C_T}{\alpha_{DH} g_D} h - \frac{\alpha_{HD} r_C C_T}{g_D} d}{k_H C_T c} \right) - \frac{a_H}{r_C} h P \quad (\text{S9})$$

We can perform some simplifications (especially, cancelling C_T and dividing both numerator and denominator by r_C/g_D in the logistic terms for damselfish and hawkfish) to clean up these equations:

$$\frac{dc}{dt} = \left(c + d + \frac{g_H}{\alpha_{DH} g_D} h \right) (1 - c) - \frac{m}{r_C} c \quad (\text{S10})$$

$$\frac{dd}{dt} = \frac{r_D}{r_C} d \left(\frac{\frac{k_D g_D}{r_C} c - d - h}{\frac{k_D g_D}{r_C} c} \right) - \frac{a_D}{r_C} d P \quad (\text{S11})$$

$$\frac{dh}{dt} = \frac{r_H}{r_C} h \left(\frac{\frac{k_H \alpha_{DH} g_D}{r_C} c - h - \alpha_{HD} \alpha_{DH} d}{\frac{k_H \alpha_{DH} g_D}{r_C} c} \right) - \frac{a_H}{r_C} h P \quad (\text{S12})$$

Finally, we rescale our last dimensional variable, P , by substituting $P = r_C/a_D p$:

$$\frac{dc}{dt} = \left(c + d + \frac{g_H}{\alpha_{DH} g_D} h \right) (1 - c) - \frac{m}{r_C} c \quad (\text{S13})$$

$$\frac{dd}{dt} = \frac{r_D}{r_C} d \left(\frac{\frac{k_D g_D}{r_C} c - d - h}{\frac{k_D g_D}{r_C} c} \right) - dp \quad (\text{S14})$$

$$\frac{dh}{dt} = \frac{r_H}{r_C} h \left(\frac{\frac{k_H \alpha_{DH} g_D}{r_C} c - h - \alpha_{HD} \alpha_{DH} d}{\frac{k_H \alpha_{DH} g_D}{r_C} c} \right) - \frac{a_H}{a_D} h p \quad (\text{S15})$$

We now have eight dimensionless clusters of parameters. Let's replace them with new symbols representing these composites, where $\epsilon = g_H/(\alpha_{DH} g_D)$, $\mu = m/r_C$, $\rho_D = r_D/r_C$, $\rho_H = r_H/r_C$, $\kappa_D = (k_D g_D)/r_C$, $\kappa_H = (k_H \alpha_{DH} g_D)/r_C$, $\phi = a_H/a_D$, and $\alpha = \alpha_{DH} \alpha_{HD}$.

And, our dimensionless model is:

$$\frac{dc}{dt} = (c + d + \epsilon h) (1 - c) - \mu c \quad (\text{S16})$$

$$\frac{dd}{dt} = \rho_D d \left(\frac{\kappa_D c - d - h}{\kappa_D c} \right) - dp \quad (\text{S17})$$

$$\frac{dh}{dt} = \rho_H h \left(\frac{\kappa_H c - h - \alpha d}{\kappa_H c} \right) - \phi h p \quad (\text{S18})$$

It is convenient to rewrite the above equations using fish/coral ratios defined by $\delta = \frac{d}{c}$; $\gamma = \frac{h}{c}$ to obtain:

$$\frac{1}{c} \frac{dc}{dt} = (1 + \delta + \epsilon \gamma) (1 - c) - \mu \quad (\text{S19})$$

$$\frac{1}{c} \frac{dd}{dt} = -\frac{\delta (\rho_D (\gamma + \delta - \kappa_D) + p \kappa_D)}{\kappa_D} \quad (\text{S20})$$

$$\frac{1}{c} \frac{dh}{dt} = -\frac{\gamma (\rho_H (\alpha \delta + \gamma) + \kappa_H (p \phi - \rho_H))}{\kappa_H} \quad (\text{S21})$$

Note that these equations still describe the dynamics of *total* fish populations. The dynamics of damselfish and hawkfish *per coral* are given by:

$$\frac{d\delta}{dt} = \frac{c \frac{dd}{dt} - d \frac{dc}{dt}}{c^2} \quad (\text{S22})$$

$$\frac{d\gamma}{dt} = \frac{c \frac{dh}{dt} - h \frac{dc}{dt}}{c^2}. \quad (\text{S23})$$

A substantial simplification is available by initially assuming that the coral turnover rate is much faster than the population turnover rate for both fish populations, so that at all times after initial transient the coral area is close to a pseudo-equilibrium set by the instantaneous fish biomass per unit of coral area. This yields the following two-ODE approximation to our model:

$$\frac{1}{\delta} \frac{d\delta}{dt} = -\frac{(\gamma + \delta)\rho_D}{\kappa_D} + \rho_D - p \quad (\text{S24})$$

$$\frac{1}{\gamma} \frac{d\gamma}{dt} = -\frac{\rho_H(\alpha\delta + \gamma)}{\kappa_H} + \rho_H - p\phi \quad (\text{S25})$$

We have explored the robustness of this approximation with a wide, though far from comprehensive set of numerical studies, and found that the main limitation is that the initial transient in the coral dynamics may influence the long-term dynamics if the initial coral density is very small and the model has parameters that allow “founder effect”, i.e. the winner of the competition between fish species depends on initial conditions. The latter is beyond the scope of this paper. The value of the approximation is that all equilibrium states for the model can be calculated exactly by following 3 steps:

1. Find equilibrium value(s) for δ and γ from equations S24 and S25. These equations do not involve c .
2. Use equation S19 to calculate the equilibrium value of coral c using the equilibria (δ, γ) .

3. If needed, calculate h and d from the definitions of δ and γ .

It follows that *all equilibria for the full model can be computed, starting from isoclines in the $\delta - \gamma$ plane.* Less obviously, their qualitative local stability properties (i.e. stable or unstable) can also be assessed from the this phase plane, though the details of the approach to a stable equilibrium require simulations of the full 3D model.

To facilitate accessibility of the remaining analysis for the reader moving directly from the main text, we now drop explicit use of the δ and γ notation and label the axes of all isoclines d/c and h/c respectively.

Competitive Outcomes in a Predator-Free System

We can determine general relationships between these parameters that result in indirect benefits from predators by examining the effect of predators on the equilibrium abundance of hawkfish and damselfish. This is because the benefit (growth enhancement) to corals is a function of the weighted biomass of these fishes ($d + \epsilon h$).

We begin by considering the case in which predators are absent from the system ($p = 0$). This reduces the system to a Lotka-Volterra-esque competition model, with the exception that the carrying capacities of hawkfish and damselfish are proportional to coral area:

$$\dot{d} = \rho_D d \left(\frac{\kappa_{DC} - d - h}{\kappa_{DC}} \right) \quad (\text{S26})$$

$$\dot{h} = \rho_H h \left(\frac{\kappa_{HC} - h - \alpha d}{\kappa_{HC}} \right) \quad (\text{S27})$$

We compute the four zero net growth isoclines (ZNGIs) of the system by setting each ordinary differential equation equal to zero. From this we obtain:

$$d = 0 \quad \text{and} \quad \kappa_{DC} - d - h = 0 \quad (\text{S28})$$

which satisfy $\dot{d} = 0$, and:

$$h = 0 \text{ and } \kappa_H c - h - \alpha d = 0 \quad (\text{S29})$$

which satisfy $\dot{h} = 0$.

Assuming a non-zero coral area, we can express these equations in terms of fish biomass per unit of coral area (i.e., in terms of d/c and h/c), and then plot all four ZNGIs in the $d/c, h/c$ phase plane. As in the traditional Lotka-Volterra competition model, there are four possible non-trivial outcomes (Figure S1), excluding the trivial outcome in which $\kappa_D = \kappa_H$ and $\alpha = 1$, and therefore the species are equivalent to one another and all coexistence equilibria are neutrally stable. If if $\kappa_H \geq \kappa_D$, the hawkfish-only equilibrium is stable (Figure S1A), and $\kappa_D \geq \kappa_H/\alpha$, the damselfish-only equilibrium is stable (Figure S1B). When neither condition is satisfied, the interior coexistence equilibrium is stable (Figure S1C), and when both conditions are satisfied, the system exhibits bistability (Figure S1D).

Note that although these phase planes are similar to Lotka-Volterra two-species competition, and illustrate similar scenarios of competitive exclusion, coexistence, and alternate states, in reality these are two-dimensional approximations of a three-dimensional system as shown above. In particular, the effect of coral area is not captured in this projection, which represents the system in terms of fish density (per coral area). This approximation does not affect our assessment of the stability of the equilibria using the isoclines. However, in cases where the system is bistable and predators are present, the phase plane in $d/c, h/c$ space is insufficient to predict the dynamics of the system from a set of initial conditions. In particular, cases may arise in which two systems that begin with the same ratios of fish to coral, but different initial coral area, may follow different trajectories and arrive at different equilibria.

Using the mathematical relationship describing the effects of fish excretion on coral

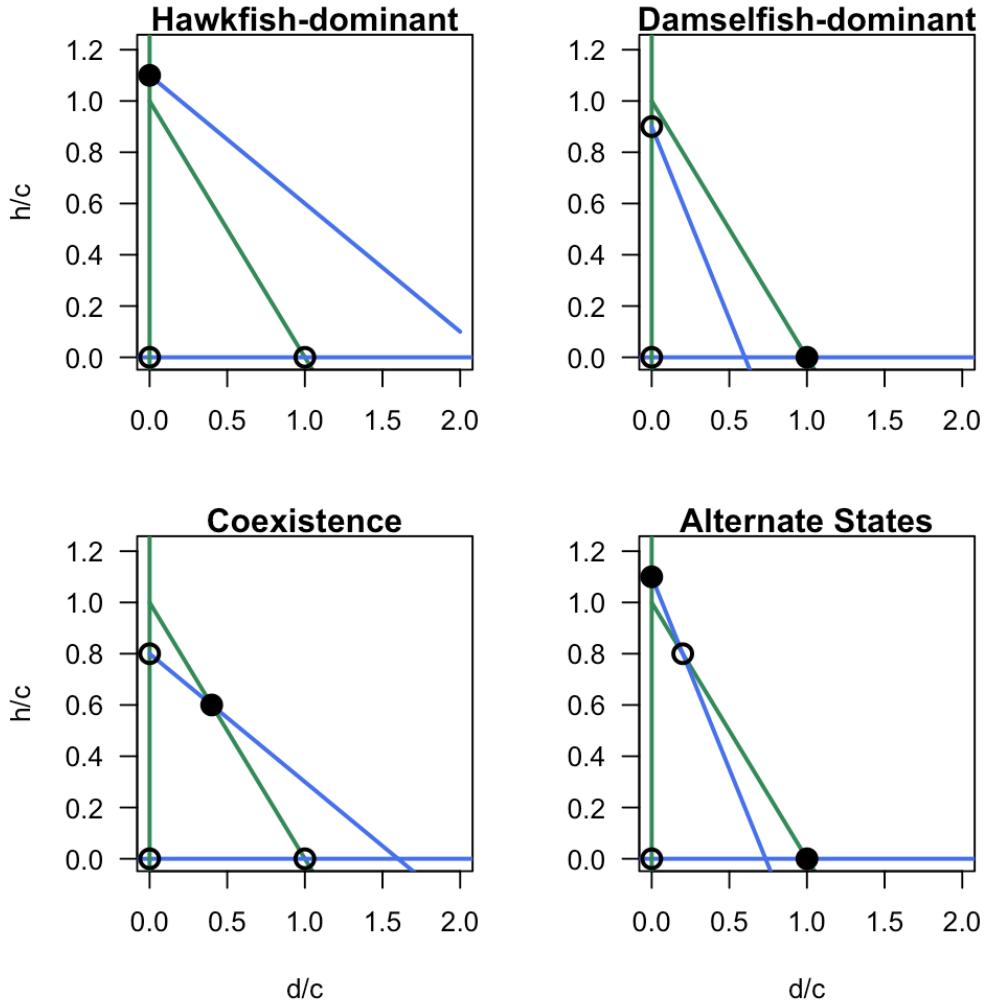


Figure S1: Zero-net growth isoclines (ZNGIs) showing four possible outcomes of competition: (A) Dominance by competitor one (hawkfish), (B) Dominance by competitor two (damselfish), (C) coexistence, and (D) alternative states. Green lines show the zero net growth isoclines for damselfish (i.e., $dc/dt = 0$), and blue lines show the zero net growth isoclines for hawkfish (i.e., $dh/dt = 0$). Parameter values are $\rho_D = \rho_H = \kappa_D = 1$, $\kappa_H = 1.1$ (panels A,D), $\kappa_H = 0.9$ (panel B), $\kappa_H = 0.8$ (panel C), $\alpha = 0.5$ (panels A,C), $\alpha = 1.5$ (panels B,D).

growth, we can also plot a line in hawkfish-damselfish space showing the combinations of hawkfish and damselfish that provide nutrient supplementation equivalent to hawkfish alone.

In this case, in the absence of predators, mutualist resource provision is done by only one mutualist. That is, in our system, coral growth enhancement occurs solely due to the nutrient excretion of hawkfish. The rescaled excretion rate of hawkfish is ϵ , and the rescaled per-coral carrying capacity of hawkfish is κ_H . Thus, at equilibrium, the amount of hawkfish per coral area is κ_H , and the amount of excretion received per coral area is $\epsilon\kappa_H$. We can contrast this predator-free mutualism goods production rate with the rate produced by any combination of hawkfish and damselfish per unit of coral area, which is given by:

$$\frac{d}{c} + \epsilon \frac{h}{c}. \quad (\text{S30})$$

Thus, there is a mutualism community equivalency line, given by

$$\epsilon\kappa_H = \frac{d}{c} + \epsilon \frac{h}{c} \quad (\text{S31})$$

which describes the combination of damselfish and hawkfish that produce the same amount of mutualist goods as are found in the hawkfish-only, predator-free equilibrium. We superimpose this line (in orange) on the phase plane in Figure S2.

Effects of predation on mutualist equilibrium

In order to derive conditions for which predators may indirectly enhance mutualisms, we focus on the case shown in Figure S1A (and expanded upon in Figure S2), in which the lower quality mutualist (hawkfish) is competitively dominant in the absence of predation.

When predators are present, they act to reduce the abundance of both mutualists. The extent of this reduction is shaped by ϕ , the predator's preference for hawkfish (the dominant competitor). Assuming non-zero coral area and writing our equations in terms of h/c and

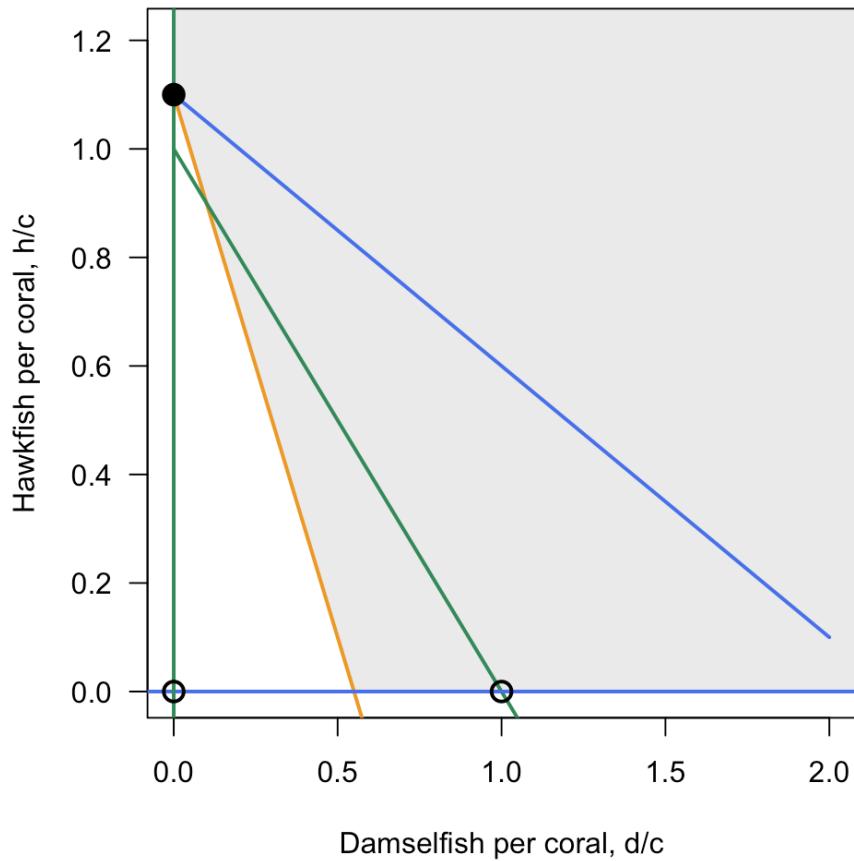


Figure S2: Phase plane for a hawkfish-dominated system. Green lines show the zero net growth isoclines for damselfish (i.e., $dc/dt = 0$), and blue lines show the zero net growth isoclines for hawkfish (i.e., $dh/dt = 0$). The orange line shows the mutualism-equivalency line: combinations of hawkfish and damselfish that produce the same level of goods (excrete the same amount of nitrogen) as hawkfish do at the predator-free equilibrium (filled black circle). When more damselfish and hawkfish exist per coral area than are given by the mutualism-equivalency line (gray shaded area), corals are expected to be larger than in the predator-free equilibrium because they are receiving greater N excretion from fish. Parameter values are $\rho_D = \rho_H = \kappa_D = 1$, $\kappa_H = 1.1$, $\alpha = 0.5$, and $\epsilon = 0.5$.

d/c , we obtain the four ZNGIs:

$$d = 0 \quad \text{and} \quad \kappa_D - \frac{d}{c} - \frac{h}{c} - \frac{p\kappa_D}{\rho_D} = 0 \quad (\text{S32})$$

$$h = 0 \quad \text{and} \quad \kappa_H - \frac{h}{c} - \alpha \frac{d}{c} - \frac{\phi p \kappa_H}{\rho_H} = 0 \quad (\text{S33})$$

From these equations and their effect on the system's equilibria, we can see that the overall effect of predators will be to reduce the abundances of both hawkfish and damselfish (Figure S3). The larger ϕ , the greater the differential effect on hawkfish. In particular, the hawkfish-only equilibrium will be destabilized once p has increased sufficiently to satisfy:

$$\kappa_D \left(1 - \frac{p}{\rho_D}\right) > \kappa_H \left(1 - \phi \frac{p}{\rho_H}\right). \quad (\text{S34})$$

Because $\kappa_H \geq \kappa_D$ (such that the hawkfish are competitively dominant to the damselfish), such a relationship can only be satisfied if:

$$1 - \frac{p}{\rho_D} > 1 - \phi \frac{p}{\rho_H} \quad (\text{S35})$$

or, by rearrangement, $\phi > \rho_H/\rho_D$. In the scenario in which $\rho_H = \rho_D = \rho$ (main text), ϕ must be greater than 1. In other words, absent biological differences in the species that affect growth rates, predators may only drive coexistence when the dominant competitor (hawkfish) are more sensitive to predation.

When the two diagonal ZNGIs intersect in the positive phase plane, coexistence is stable. The equilibrium abundance of hawkfish and damselfish can be computed by equating these ZNGIs. This internal equilibrium, which we designate (\hat{d}, \hat{h}) , is given by:

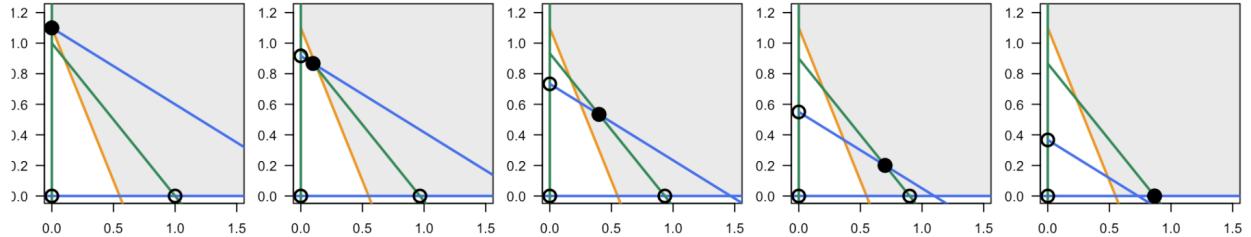


Figure S3: The presence of the predator alters equilibrium outcomes. Green lines show the zero net growth isoclines for damselfish (i.e., $dc/dt = 0$), and blue lines show the zero net growth isoclines for hawkfish (i.e., $dh/dt = 0$). The orange line shows the mutualism-equivalency line. When hawkfish are more sensitive to predation than damselfish ($\phi = 5$), increasing predator abundance (from left to right) qualitatively shifts the system's dynamics from hawkfish to damselfish dominated. Once predators are sufficiently abundant (panel C), they cause indirect benefits to the coral (note shift in stable equilibria, marked by filled black circles, from white to gray shaded region). Parameter values are $\rho_D = \rho_H = \kappa_D = 1$, $\kappa_H = 1.1$, $\alpha = 0.5$, $\epsilon = 0.5$, and $\phi = 5$. Predator abundances increase from 0 in increments of 0.00333 from left to right.

$$\hat{d} = c(1 - \alpha)^{-1} \left[\kappa_D \left(1 - \frac{p}{\rho_D} \right) - \kappa_H \left(1 - \frac{\phi p}{\rho_H} \right) \right] \quad (\text{S36})$$

$$\hat{h} = c\kappa_D \left(1 - \frac{p}{\rho_D} \right) - \hat{d} \quad (\text{S37})$$

We can plot this equilibrium in $d/c, h/c$ space, as well (Figure S4).

Conditions on predator-mediated mutualism enhancement

From Figure S4, we can see that whether predators can indirectly benefit mutualist hosts depends upon whether the system's trajectory as predator abundance increases (gray line) intersects with the mutualism-equivalency (orange) line. This intersection will always occur if, at the predator abundance when hawkfish are extirpated (Figure S4, point D), damselfish are more abundant than their hawkfish-equivalent (Figure S4, point E). Mathematically, this means that when $\hat{h} = 0$, \hat{d} must be greater than $\epsilon\kappa_H$.

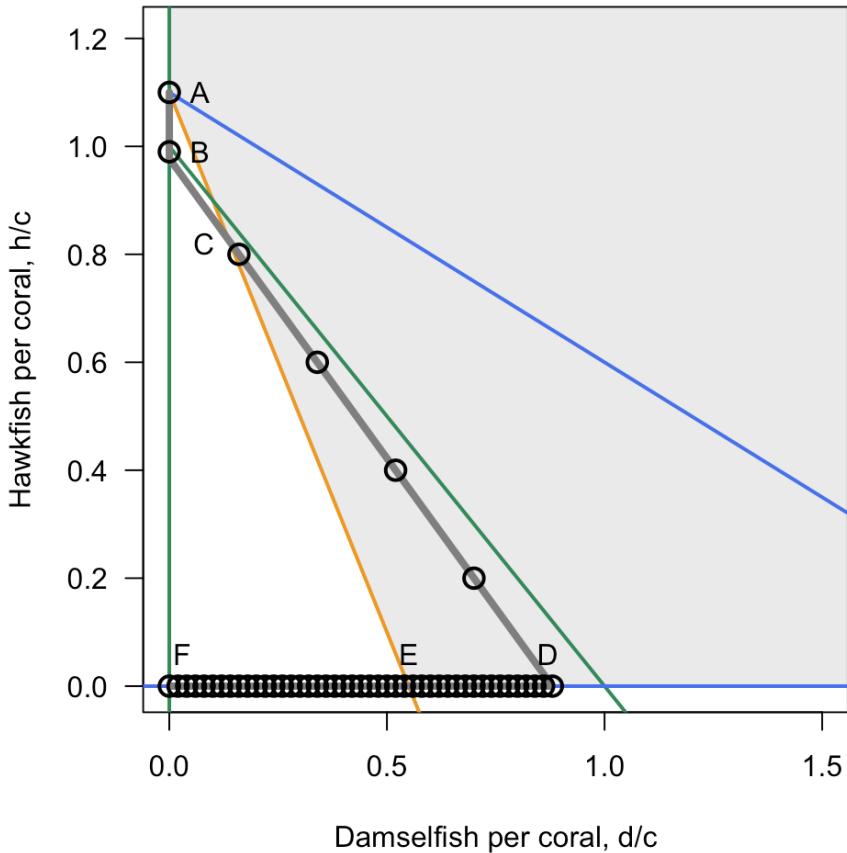


Figure S4: Phase plane for a hawkfish-dominated system. Green lines show the zero net growth isoclines for damselfish (i.e., $dc/dt = 0$), and blue lines show the zero net growth isoclines for hawkfish (i.e., $dh/dt = 0$) in a predator-free system. The orange line shows the mutualism-equivalency line, and the gray shaded area shows combinations of hawkfish and damselfish that produce coral growth enhancement relative to the predator-free equilibrium. The dark gray line shows the system's trajectory as predator abundance increases; black circles mark increases in predator abundance in increments of 0.002 from $p = 0$ to $p = 0.1$. A: At first, increases in predator abundance decrease the hawkfish population. B: When $p > 0.002$, the hawkfish population has been diminished so much that damselfish can begin to persist in the system. C: When $p > 0.00375$, predators have shifted the system towards damselfish so much that the coral receives indirect benefits (the system enters the shaded area of state space). D: Eventually, when $p > 0.012$, hawkfish have been extirpated; as the predator abundance increases, the damselfish population declines. E: Because $\phi_i = 5$, the damselfish are much less sensitive to predation than hawkfish, and so larger increases in predator abundance are needed to shift the system past the point at which predators no longer benefit corals. F: Ultimately, predators are so abundant that damselfish are extirpated as well. Parameter values as in Figure S2.

We first compute the critical predator abundance, p_{crit} , at which hawkfish have just been completely extirpated, and only damselfish are present in the system. We can find p_{crit} by equating the x-intercepts of the diagonal ZNGIs:

$$\kappa_D - \frac{p\kappa_D}{\rho_D} = \frac{1}{\alpha} \left[\kappa_H - \frac{\phi\kappa_H p}{\rho_H} \right]. \quad (\text{S38})$$

By solving for p we obtain

$$p_{crit} = \frac{\rho_H \rho_D (\kappa_H - \alpha \kappa_D)}{\rho_D \phi \kappa_H - \rho_H \alpha \kappa_D}. \quad (\text{S39})$$

We can substitute this value of p into either of the x-intercept expressions to determine the corresponding damselfish density (d_{crit}/c):

$$\frac{d_{crit}}{c} = \kappa_H \kappa_D \left[\frac{\phi \rho_D - \rho_H}{\rho_D \phi \kappa_H - \rho_H \alpha \kappa_D} \right]. \quad (\text{S40})$$

Because d_{crit}/c must be greater than $\epsilon \kappa_H$ in order for predators to confer indirect benefits, we have:

$$\epsilon < \kappa_D \left[\frac{\phi \rho_D - \rho_H}{\rho_D \phi \kappa_H - \rho_H \alpha \kappa_D} \right]. \quad (\text{S41})$$

Note that in the case $\rho_D = \rho_H$ and $\kappa_D = \kappa_H$ (as in the main text), this inequality simplifies to:

$$\epsilon < \frac{\phi - 1}{\phi - \alpha}. \quad (\text{S42})$$

Bounds on predator-mediated mutualism enhancement

We can also compute the threshold predator abundances at which the predators begin to produce benefits (p_{min} , i.e., the predator abundance at which the damselfish-hawkfish coexistence equilibrium produces more benefits than the hawkfish-only predator-free equilibrium, point C on Figure S4) and at which predators are so abundant that the mutualism's function

is lowered (p_{\max} , i.e., the predator abundance at which the hawkfish have been extirpated, and the damselfish population has fallen so low that it produces fewer benefits than the hawkfish-only predator-free equilibrium, point E on Figure S4).

We can find p_{\min} by computing the intersection between the mutualist-equivelency line (Figure S4, orange line) and the predator-mediated coexistence line (Figure S4, gray line):

$$\epsilon \kappa_H = \frac{\hat{d}}{c} + \epsilon \frac{\hat{h}}{c}. \quad (\text{S43})$$

By substitution, we obtain:

$$p_{\min} = \frac{(\kappa_H - \kappa_D)(1 - \alpha\epsilon)}{\frac{\kappa_H \phi}{\rho_H}(1 - \epsilon) - \frac{\kappa_D}{\rho_D}(1 - \epsilon\alpha)}. \quad (\text{S44})$$

Note that in the case $\rho_D = \rho_H$ and $\kappa_D = \kappa_H$ (as in the main text), p_{\min} simplifies to $p_{\min} = 0$. In other words, when hawkfish and damselfish share the same per-coral carrying capacity, an introduction of even a very small amount of predators will produce benefits for the coral.

We can find p_{\max} by studying the behavior of the dc/dt diagonal ZNGI in the absence of hawkfish (i.e., $h = 0$):

$$\kappa_D - \frac{d}{c} - \frac{p\kappa_D}{\rho_D} = 0. \quad (\text{S45})$$

p_{\max} is the predator abundance at which this ZNGI intersects the mutualist-equivelency line on the x-axis (Figure S4, point E). Mathematically, this means

$$\frac{d}{c} = \kappa_D - \frac{p\kappa_D}{\rho_D} = \epsilon \kappa_H. \quad (\text{S46})$$

Solving for p , we obtain:

$$p_{\max} = \rho_D \left(1 - \frac{\epsilon \kappa_H}{\kappa_D} \right). \quad (\text{S47})$$

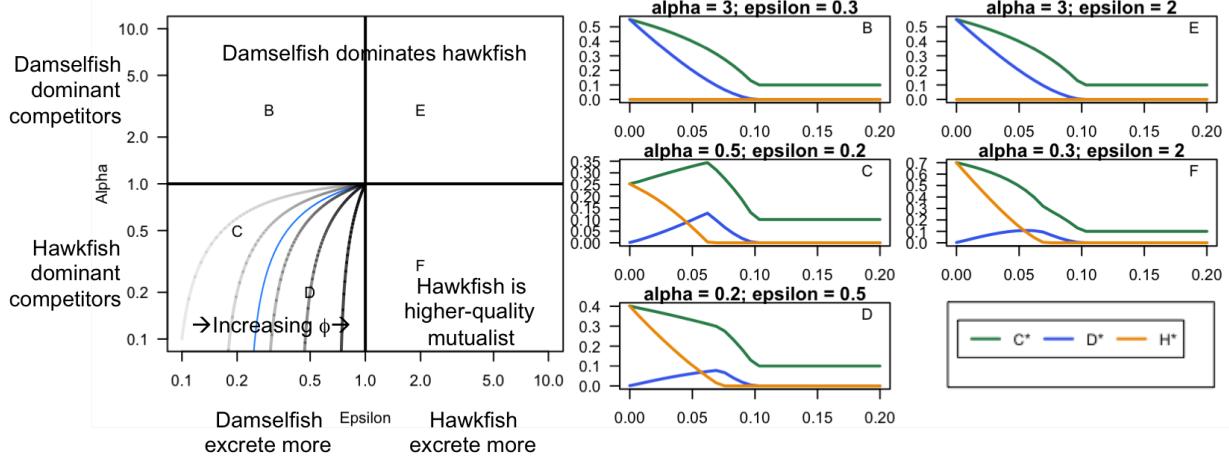


Figure S5: Regions of parameter space in which mesopredators indirectly benefit corals. (A): Predators benefit foundation species in one region of competition-excretion parameter space: under conditions when the higher-quality mutualist is also the weaker competitor (lower left quadrant). Even within this quadrant, the range of parameter space over which predators may confer benefits depends upon ϕ : As the predator's preference for hawkfish increases, the range over which these benefits occur increases. Panels B-F are bifurcation diagrams showing the effect of increasing predator abundance (x-axes) on equilibrium coral (green line), damselfish (blue line), and hawkfish (orange line) abundances for $\phi = 1.3$ (blue line on panel A) and $\alpha-\epsilon$ combinations indicated by the letters on panel A. For panels B and E, damselfish are dominant, so increases in predator abundance only remove this higher-quality mutualist and decrease coral abundance. For panel F, although increases in predators do cause a “switch” in competitive dominance from hawkfish to damselfish, because hawkfish are the higher-quality mutualists, this exacerbates coral decline. In panels C and D, a similar switch in competitive dominance occurs, but only in panel C does this result in an increase in coral area at intermediate predation levels. Parameter values are $\kappa_D = \kappa_H = 1$, $\mu = 0.9$, and $\rho_D = \rho_H = 0.1$.

We can represent the spectrum of possible outcomes graphically (Figure S5).

Cascading benefits of mutualists' predators on foundation species: a model inspired by coral reef ecosystems

Holly V. Moeller, Roger M. Nisbet, and Adrian C. Stier

Ecosphere

Appendix S2. Open Recruitment

Our model makes a number of assumptions about the structure of the coral and fish populations, including that they are closed to external recruitment, that all coral individuals share the same geometry, and that all fish biomass shares the same species-specific traits. Here, we test the impacts of the first assumption (that the populations are closed to external recruitment).

Open recruitment of corals

Suppose coral larvae recruit from outside the focal area and arrive at a rate I_C . Assuming that larval arrival is the same for any location within the coral habitat area, the dimensionless ODE for the coral becomes:

$$\dot{c} = i_C + (c + d + \epsilon h) (1 - c) - \mu c, \quad (\text{S1})$$

where $i_C = I_C / (C_T r_c)$.

The equations for hawkfish and damselfish dynamics remain unchanged, and, assuming that c is in pseudo-equilibrium, the logic from the preceding section based on the ZNGIs in the $d/c, h/c$ phase plane carries over. That is: although the equilibrium abundance of corals is altered by coral recruitment, the balance of hawkfish and damselfish per coral, and the

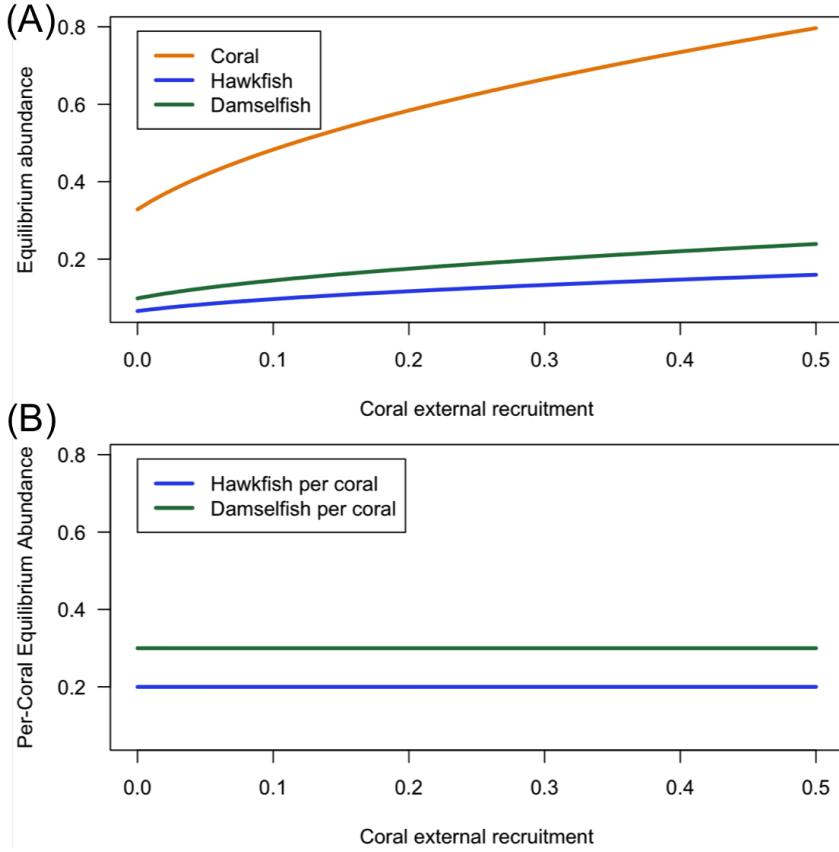


Figure S1: Effects of coral open recruitment. Although open recruitment increases the equilibrium abundances of coral, hawkfish, and damselfish (Panel A), the hawkfish-to-coral and damselfish-to-coral ratios remain constant (Panel B). For this simulation, the system is parameterized such that hawkfish are the dominant competitors, weaker mutualists, and most vulnerable to predation: $\kappa_D = \kappa_H = 1$, $\rho_D = \rho_H = 0.1$, $\mu = 0.9$, $\epsilon = 0.2$, $\alpha = 0.5$, $\phi = 1.3$, and $p = 0.05$.

impacts of predation on these population sizes, remains unchanged (Figure S1).

Open recruitment of fish

In contrast, allowing for open recruitment of fish can alter the equilibrium relative abundances of fish, especially because open recruitment prevents the competitive exclusion of one species.

Let us assume that the immigration rate of each fish species is proportional to patch

coral density:

$$I_d = i_D c \quad (\text{S2})$$

$$I_h = i_H c. \quad (\text{S3})$$

This gives the dimensionless system of ODEs:

$$\dot{d} = \rho_D d \left(\frac{\kappa_D c - d - h}{\kappa_D c} \right) - dp + i_D c \quad (\text{S4})$$

$$\dot{h} = \rho_H h \left(\frac{\kappa_H c - h - \alpha d}{\kappa_H c} \right) - \phi h p + i_H c. \quad (\text{S5})$$

As above, we will consider fish-to-coral ratios, and assume c is in pseudo-equilibrium so that we can determine the equilibria and their stability using the $d/c, h/c$ phase plane.

For either species, the presence of recruitment eliminates the 0 equilibrium, and causes the interior isocline to be non-linear. The damselfish interior isocline in $d/c, h/c$ phase space is given by:

$$\rho_D \frac{d}{c} \left(\frac{\kappa_D - d/c - h/c}{\kappa_D} \right) + i_D = 0, \quad (\text{S6})$$

and the hawkfish interior isocline is given by:

$$\rho_H \frac{h}{c} \left(\frac{\kappa_H - h/c - \alpha d/c}{\kappa_H} \right) + i_H = 0. \quad (\text{S7})$$

Thus, external recruitment impacts coexistence, even in the absence of predators (Figure S2). The most notable consequence is that, when the inferior competitor has open recruitment, it can no longer be competitively excluded by the dominant competitor. The larger the rate of open recruitment, the more the relative equilibrium abundance shifts in favor of the rapidly recruiting species.

This, of course, constrains the effects of predators on the system, but in similar qualitative

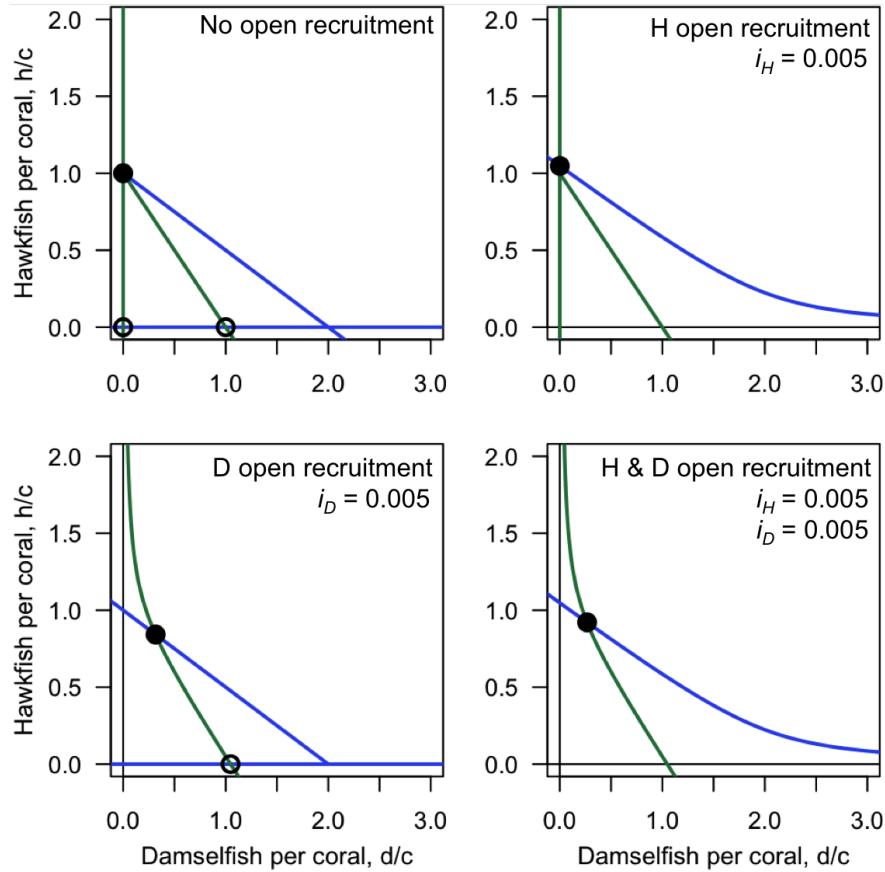


Figure S2: Effects of fish open recruitment. The inclusion of open recruitment for a fish species eliminates the 0 (axial) ZNGI and causes curvature of the internal ZNGI. When the weaker competitor (here: damselfish) has open recruitment, it can coexist with the dominant competitor even in the absence of predation. For this simulation, the system is parameterized such that hawkfish are the dominant competitors, weaker mutualists, and most vulnerable to predation: $\kappa_D = \kappa_H = 1$, $\rho_D = \rho_H = 0.1$, $\mu = 0.9$, $\epsilon = 0.2$, $\alpha = 0.5$, $\phi = 1.3$, and $p = 0.05$.

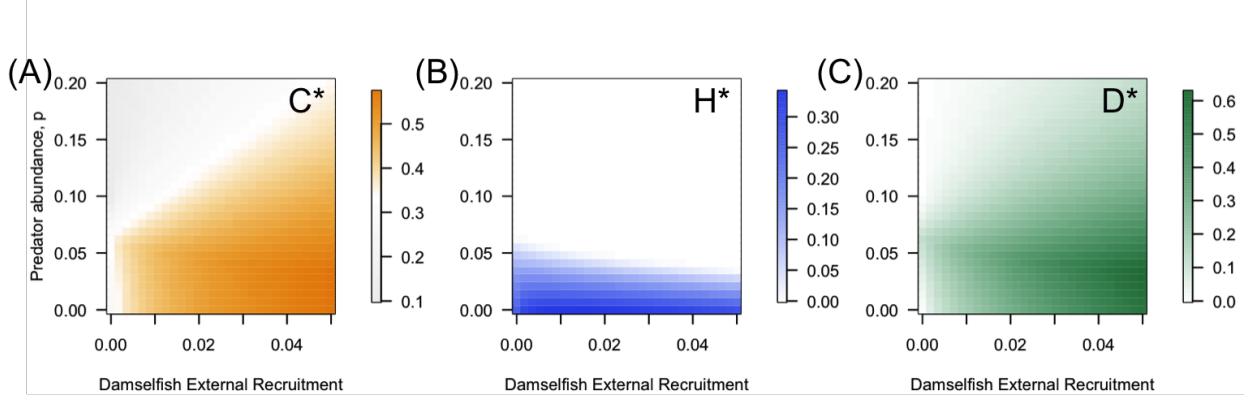


Figure S3: Interaction between damselfish open recruitment and predator abundance. Open recruitment of damselfish (here, the weaker competitor) promotes the coexistence of damselfish and hawkfish even in the absence of predation (along x-axis). As in the case without open recruitment (along y-axis), when predators drive a numerical shift towards higher damselfish abundance, there can be cascading benefits to coral. For this simulation, the system is parameterized such that hawkfish are the dominant competitors, weaker mutualists, and most vulnerable to predation: $\kappa_D = \kappa_H = 1$, $\rho_D = \rho_H = 0.1$, $\mu = 0.9$, $\epsilon = 0.2$, $\alpha = 0.5$, $\phi = 1.3$, and $p = 0.05$.

ways to the intuition that we have already developed (Figure S3). Open recruitment prevents the elimination of any species with an external propagule supply, even when predation is high. However, if the presence of predators causes a shift from low-quality mutualist to high-quality mutualist (following the mutualist benefit constraints outlined above), then predators can still have indirect positive effects on the foundation species by enhancing mutualistic benefits.

Cascading benefits of mutualists' predators on foundation species: a model inspired by coral reef ecosystems

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Appendix S3. Coral-Dependent Predators

In our model, we make several simplifying assumptions about predatory fish and their behavior. First, we assume that the total predator population size is fixed, because it is controlled at spatial and temporal scales that exceed our model. Second, we simplify the predator's role to a fixed predation rate (that is specific to damselfish or hawkfish) that does not depend upon habitat availability, fish behaviour, etc.

Here, we consider alternative assumptions. First, we consider the effect of habitat availability on predator abundance. Predators may be drawn to areas with high availability of prey habitat as likely hunting grounds. One simple way to represent this is by assuming that predator abundance increases with habitat availability. Here, scale this increase relative to C_0 , the abundance of coral in the absence of mutualistic coral-dwelling fishes. We express this as:

$$P = P_0 \left(\frac{C}{C_0} \right)^x. \quad (\text{S1})$$

Here, x is an exponent that scales the predator's sensitivity to coral availability. Note that in the main text, we have assumed that $x = 0$. Note that this formulation is only sensible when corals can persist in the absence of fishes ($C_0 > 0$).

Second, we can make the predator's attack rate a function of habitat availability. Damselfish and hawkfish use corals as shelter from predation, so one reasonable assumption is that attack success decreases with increasing coral cover (again, relativized to the abundance

of coral in the absence of fish):

$$a_i = \frac{a_{i,0}}{(C/C_0)^y}, \quad (\text{S2})$$

where i is D for damselfish or H for hawkfish. Again, in the main text, we have assumed that the scaling exponent $y = 0$.

Let's assume that the scaling exponents are the same for both hawkfish and damselfish. This means that we can write the predation term for each species as:

$$a_i IP = a_{i,0} P \left(\frac{C}{C_0} \right)^{x-y} = a_{i,0} P \left(\frac{C}{C_0} \right)^z \quad (\text{S3})$$

where the exponent z captures the modification of coral habitat on predation. If $z > 0$, the presence of corals has a net negative effect on mutualists by increasing the predation rate, and when $z < 0$, corals have a net protective benefit. Again, if $z = 0$, we recover the model used in the main text. Note that this implies that the main text model assumes that the positive and negative effects of corals on predation are balanced (rather than that neither positive nor negative effects occur).

Including non-zero values of z in the model means that we can no longer approximate the model's behaviour using phase planes. Instead, we used numerical simulation to explore the effects of varying z on the equilibrium abundances of corals, hawkfish, and damselfish. The dimensionless model that we used for these explorations is:

$$\dot{c} = (c + d + \epsilon h)(1 - c) - \mu c \quad (\text{S4})$$

$$\dot{d} = \rho_D d \left(\frac{\kappa_D c - d - h}{\kappa_D c} \right) - dp \left(\frac{c}{c_0} \right)^z \quad (\text{S5})$$

$$\dot{h} = \rho_H h \left(\frac{\kappa_H c - h - \alpha d}{\kappa_H c} \right) - \phi h p \left(\frac{c}{c_0} \right)^z \quad (\text{S6})$$

where $c_0 = 1 - \mu$.

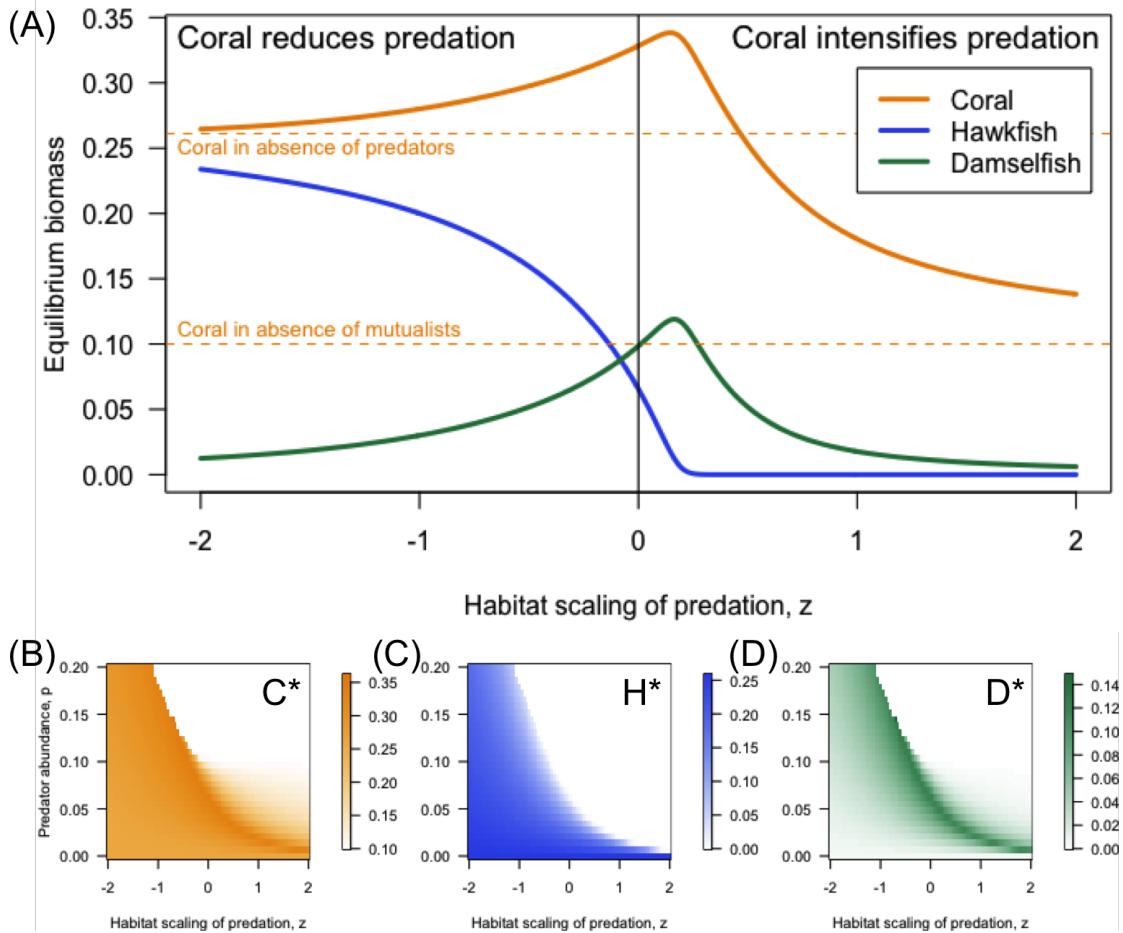


Figure S1: Including the effects of coral on predation. Panel A: When increases in coral cover act to protect coral-dwelling fishes (left side), reduced predation impacts shift mutualist populations towards the dominant competitor (hawkfish), resulting in reductions in coral biomass. (Note that as $z \rightarrow -\infty$, C^* approaches the equilibrium coral abundance in the absence of predators (upper dashed orange line).) In contrast, when coral cover attracts predators and intensifies predation (right side), predation drives down the total mutualist abundance. Eventually, the system asymptotes to a mutualist-free state (as $z \rightarrow \infty$, $C^* \rightarrow C_0$). For this simulation, the system is parameterized such that hawkfish are the dominant competitors, weaker mutualists, and most vulnerable to predation: $\kappa_D = \kappa_H = 1$, $\rho_D = \rho_H = 0.1$, $\mu = 0.9$, $\epsilon = 0.2$, $\alpha = 0.5$, $\phi = 1.3$, and $p = 0.05$. The black vertical line indicates the $z = 0$ case, which is the focus of the main text. Panels B-C: Equilibrium abundances of coral, hawkfish, and damselfish as a function of predator abundance p and habitat scaling z . Both high predation rates, and positive feedbacks of coral on predation lead to elimination of fish and reductions in coral biomass (white areas; upper right corners).

Following biological intuition, when coral acts as a predator attractant, this leads to a reduction in mutualist biomass and a cascading negative effect of predators on coral abundance (Figure S1). In the limit that $z \rightarrow \infty$, the system approaches a hawkfish- and damselfish-free state because of the intensification of predation. In the limit that $z \rightarrow -\infty$, the system approaches the predator-free state, and is dominated by the competitively dominant mutualist. When that competitively dominant mutualist is also the lower quality mutualist partner, this results in a reduced abundance of coral.