GOBY - SHRIMP MUTUALISM: COSTS AND BENEFITS OF OBLIGATE VERSUS FACULTATIVE STRATEGIES

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Abstract. We model the mutualism interactions between gobies and shrimp based on recent experimental work on the shrimp *Alpheus floridans* and the facultative and obligate gobies *Ctenogobius saepepallens* and *Nes longus* in the Bahamas. We show that the model is consistent with observations, and suggest that obligate mutualism may favour rapid speciation in gobies due to their restricted spatial range. We calculate the resilience of the goby-shrimp systems to evaluate the robustness of the mutualist interactions to parameter choices. While experimental evidence has noted the ubiquity of obligation in gobies, our theoretical investigation predicts the ubiquity of facultative mutualism in shrimp despite the many obligate mutualism strategies open to them. Future experimental work might be usefully directed at evaluating the ubiquity of facultative versus obligate interactions of shrimp in goby - shrimp mutualist populations, and examining whether facultative and obligate strategies are correlated with food availability.

Key words. obligate mutualism, facultative mutualism, cost-benefit, tradeoff, explicit resource accounting

1. Introduction.

We consider the dynamics of a goby and a shrimp population based primarily on the field study of Lyons [20] in the Bahamas, but see also Thompson et al.[31]. The goby and shrimp engage in a mutualist relationship, that may be facultative or obligate, where each shrimp constructs a burrow that can accommodate both the shrimp and its goby partner. The shrimp provides protection for the goby from its predators (mainly groupers), allowing the goby to forage for food with a refuge in close proximity. The goby provides warnings to the shrimp, signalling when it is unsafe to leave the burrow to forage for food due to the presence of predators. In certain cases the shrimp may utilise the goby's faeces as its sole source of food, and then the goby exclusively defecates inside the burrow. Lyons speculated that the increased costs of an obligate lifestyle must be balanced by the significant advantages enjoyed by both the goby and the shrimp populations. We investigate that speculation in this study.

A key to understanding mutualisms is to understand the cost/benefit payoff or tradeoff involved in the interaction between the mutualist partners. Lyons [20] measured the improved life expectancy of gobies when they behave in an obligate manner. He also notes that they spend a majority of their time hiding in burrows, but does not quantify this. Lyons also asks what is the cost/payback to the goby for becoming obligate, i.e. is the significant reduction in mortality for obligate gobies staying close to, and hiding in, a particular shrimp burrow (that is observed by Lyons) offset by a reduction in feeding due to reduced grazing time and range. Lyons [20] does not measure the costs and benefits that accrue to the shrimp for changes in its behaviour (which appear to be more complex than the options available to the gobies). The shrimp may feed on plankton/detritus outside its burrow, in which case the goby provides a protection; or it may feed both outside and inside its burrow on plankton and goby faeces; or may feed exclusively inside its burrow solely on goby faeces. Each of these options involves different costs and benefits which will have different eco-evolutionary implications.

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To robustly consider tradeoffs, we need a measure of costing that is compatible with the benefits of obligate behaviour The model we propose here is both simple enough to understand, and yet we can compare with data. We use a linear cost/benefit analysis that balances costs and benefits related to the changes in behaviour of the gobies and shrimp spending more time in their burrow versus more time outside and foraging over a larger area. We use this model to examine several aspects of the goby - shrimp interaction, in particular Lyons' [20] suggestion that over 90% of goby species are obligate on their shrimp partners. This raises the question of whether obligate mutualism provides the gobies with an eco-evolutionary advantage that is reflected in the ubiquity of obligate mutualism among gobies, or whether the constriction of spatial movement associated with obligate mutualist relationships drives speciation among those gobies that are obligate.

All living populations must resolve the competing imperatives to increase their sustainable population size, by maximising their growth rate and/or minimising their mortality rate, and to ensure the reliable availability of their food supply by "farming" their resources (nutrients or populations) that they rely upon to grow. These imperatives are resolved in an ecosystem in which the equilibrium point where all populations coexist is stable and resilient. Resilience measures the rate at which the system will return to its previous state after a perturbation. Populations in a highly resilient ecosystem will maintain reliable sustainable food supplies even in environments that are subjected to substantial perturbations.

We take as 'canonical species' the obligate goby *Nes longus* and the facultative goby *Ctenogobius saepepallens*, together with the shrimp *Alpheus floridans*. We build a computational simulation model for these interactions to see if resilience of the system varies with facultative or obligate behaviours. We examine the ubiquity of obligate and facultative mutualist interactions between gobies and shrimp by examining the properties of ecologically-realistic instantiations of our model, defined with randomly generated parameter values over appropriately defined ranges. We randomly sample large numbers of parameter choices to model our systems, extract the ecologically relevant ones, and then categorise which parameters lead to higher resilience or diversity. Despite constraining the parameter space sampled to minimise unrealistic parameter combinations, only around 8% of the random parameter sets sampled produce valid ecosystems that have positive finite equilibrium populations, of which around 63% have stable equilibriums and 27% have persistent population oscillations. We classify each valid instance of the model according to the type of its mutualist interactions (obligate or facultative). We examine the tradeoffs in each case and how they relate to overall properties of the system such as its resilience and the equilibrium partitioning of biomass to identify cost-benefit interactions and consider our results in the context of Lyons' [20] observations that obligate goby species are much more common in the field.

2. A Mutualist Model for Gobies and Shrimp.

Gobies and shrimp are marine shallow water heterotroph populations that have a mutualist relationship which we model by the inclusion and explicit accounting of finite resources for each population. Gobies consume zooplankton such as copepods and utilise shrimp burrows for shelter from grouper, their primary predators. In return, the gobies either provide food for the shrimp by defecating inside the burrow, where the shrimp feeds on the faeces, or alert the shrimp to safe feeding conditions outside the burrow by waving their caudal fins. The shrimp dig and maintain the burrows that provide shelter for both themselves and the gobies.

The goby x_2 and the shrimp x_3 populations and their interactions are modelled in their simplest form consistent with experimental results. We use the Lotka-Volterra models [19, 33] in the CN framework [6] as the basis for our modelling approach and adopt the standard notation for the parameters and their signs. We accept that this may lead to interactions being somewhat counterintuitive to some readers, but suggest that the benefits of casting the model in this general framework outweighs the convenience of writing a specific model just for this single application. (Note that using more complicated forms of interactions such as the commonly used saturating Holling Type II and III forms does not qualitatively change our results.)

We reserve x_1 for the aggregated plankton species that the goby, and potentially the shrimp, populations feed on. The goby and shrimp populations may depend upon each other to survive via protection mutualisms, and both populations may feed on a common resource, the plankton x_1. The goby population x_2 only feeds on the plankton population x_1, and this is represented by the simplest grazing term $-a_{21}x_1x_2$ (where $a_{21} < 0$). The shrimp population may also feed on the plankton x_1 or may feed on goby faeces, which are proportional to x_2. These processes are represented by the terms $a_{31}x_1x_3$ and $a_{32}x_2x_3$ respectively, where $a_{31} < 0$ and $a_{32} < 0$.

Either population may receive a mutualist benefit from the presence of the other that reduces its mortality, which we represent with $r_i(1 - M_i(x_j))x_i$, where r_i is the usual density-independent heterotroph mortality coefficient $(i, j = 2, 3; i \neq j)$, and $M_i(x_j)$ is the mutualist protection benefit that x_i derives from x_j. We use $M_2(x_3) = \mu_2(x_3/[x_3 + \epsilon_2])$ for the reduction in goby mortality due to shrimp and $M_3(x_2) = \mu_3 x_2$ for the reduction in shrimp mortality due to gobies. We chose values for μ_2 and ϵ_2 consistent with that measured by Lyons [20] (see Supplementary Material for details). We also include the usual density-dependent mortality terms $a_{22}x_2^2$ and $a_{33}x_3^2$ which include predation losses to un-modelled higher trophic levels. The generic interaction term $a_{23}x_2x_3$ is usually positive, reflecting that the sequestration of a fraction of the total resources by the shrimp population results in fewer resources being available for the goby population (see Table 1 for further details).

Collecting these process terms, and writing them in a per-capita rate form provides the following equations that determine the population sizes :

$$\begin{aligned} \dot{x}_2 &= x_2 f_2(x_1, x_2, x_3) = x_2(r_2[1 - M_2(x_3)] - a_{21}x_1 - a_{22}x_2 - a_{23}x_3), \\ \dot{x}_3 &= x_3 f_3(x_1, x_2, x_3) = x_3(r_3[1 - M_3(x_2)] - a_{31}x_1 - a_{32}x_2 - a_{33}x_3). \end{aligned} \tag{1}$$

Our explicit, exact resource cycling and accounting framework requires that we include an equation that describes the availability of resources, in this case plankton x_1, for the gobies x_2 and shrimp x_3 to feed on, and an equation that describes the availability of nutrients N, the resource for x_1. We use x_1 to capture a combined plankton population (i.e. comprising phytoplankton, mixotrophic plankton, and zooplankton). The plankton population dynamics are determined by r_1, the net growth rate on the limiting nutrient N, its density-dependent mortality rate a_{11}, and the coefficients a_{12} and a_{13} that represent its losses to grazing by x_2 and x_3 respectively:

$$\begin{aligned} \dot{x}_1 = x_1 f_1(x_1, x_2, x_3, N) &= x_1(r_1 N - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 - \hat{a}_{13}x_3), \\ &= x_1(r_1(1 - x_1 - x_2 - x_3) - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 - \hat{a}_{13}x_3), \\ &= x_1(r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3). \end{aligned} \tag{2}$$

Here we incorporate the plankton population's growth dependence on the limiting nutrient N. New interaction coefficients are introduced above to simplify the notation, so that $a_{ij} = r_i + \hat{a}_{ij}$. Note that the limiting nutrient N is typically dissolved inorganic nitrogen together with decaying organic matter and we take $N = N_T - x_1 - x_2 - x_3$ to represent the cycling of the limiting nutrient within the study site. Here we assume that the scaled total nutrient $N_T = 1$ is constant over the experimental period (i.e. there is no net immigration or emigration, or net influx or efflux of limiting inorganic nutrient across the boundary). Flows of all other resources such as sunlight, water, oxygen and other nutrients, are not restricted.

Table 1
Summary of parameter roles that determine facultative / obligate interactions.

Parameter	Role
a_{21}	Rate of goby grazing on plankton - reduced if foraging range is reduced
a_{23}	Cost incurred by goby in obtaining a mutualist benefit from the shrimp - metabolic cost of providing warnings to the shrimp or cost of reduced foraging range
μ_2	Maximum magnitude of mortality reduction of gobies due to provision of burrows by shrimp
ϵ_2	Half-saturation constant for mortality reduction due to availability of burrows
a_{31}	Rate of shrimp grazing on plankton - zero if shrimp feeds only on goby faeces
a_{32}	Cost of obtaining mutualism benefit from gobies or rate of shrimp feeding on goby faeces
μ_3	Maximum magnitude of mortality reduction of shrimp due to warnings from gobies

The goby population may have a facultative mutualism interaction with the shrimp, in which case it receives a benefit of reduced mortality due to the presence of the shrimp, but may survive in the absence of shrimp (for example, *C. saepepallens*); or be obligate on the shrimp, in which case the condition that it cannot grow in the absence of shrimp holds (here *N. longus*). We express these conditions formally so that we can check parameter relations in the model that ensure that the various populations are acting in obligate versus facultative mode. These formal definitions are facilitated by the theoretical framework that we have used to develop the model. This is described in detail in [6], and while less intuitive than a model written specifically for this scenario, it has the benefit of utilising results known to hold in the framework, and provides a general context for the interpretation of the results (see also Supplementary Material).

The shrimp population may receive a reduced mortality rate similarly to the goby if the goby signals to it when it is safe to feed outside the burrow, or may remain in the burrow and fed solely on goby faeces. The equation describing the dynamics of the shrimp population allows the shrimp to be a facultative or obligate mutualist similarly to the goby (Lyons [20] noted the shrimp could be facultative or obligate, but did not classify their role in his experiments). The shrimp is a facultative mutualist if it has an alternative food source to the goby faeces, in this case the plankton population x_1, that it can survive on when the goby is absent (suppose $x_2 = 0$ and x_3 is in an environment rich in plankton ($x_1 = 1$), then $f_3|_{x_1=1} > 0$). Otherwise, the shrimp is obligate on the goby, and this may occur in several ways. If the shrimp remains in its burrow and depends solely on the goby faeces for its food, then it has a parameter profile similar to a predator of the goby, so that x_3 grows when there is an abundance of the goby x_2, formally $f_3|_{x_2=1} > 0$, and as the shrimp does not feed on plankton, formally defined as $f_3|_{x_1=1} < 0$. If the shrimp feeds on plankton solely and is obligated on the goby to provide a protection mutualism that reduces its susceptibility to predation, then the shrimp per capita growth rates are (i) negative when there are no goby present and there is an abundance of plankton but (ii) positive for a value x_2^{**} of the goby population at which it provides sufficient protection that the shrimp population can survive. In this case $a_{32} \geq 0$. Finally, if the shrimp both grazes on plankton outside the burrow and feeds on goby faeces inside the burrow, but can survive on neither in the absence of the goby population it has the properties that $f_3|_{x_1=1} < 0$, $f_3|_{x_2=1} < 0$, and $f_3|_{x_1^{**}+x_2^{**}=1} > 0$ where x_2^{**} is again a critical goby population size that allows shrimp survival. The parameter relationships that define these trophic strategies are listed in Table 2.

Facultative mutualist interactions in contrast are straight forward: if either population can exist in the absence of the other then they are facultative. This occurs if either population can survive on the plankton alone: for the goby this is the case if $a_{21} < r_2 < 0$ and for the shrimp if $a_{31} < r_3 < 0$, irrespective of other parameter values. These are the simple tests we use to classify the goby and shrimp populations as facultative or obligate - for the purposes of this manuscript we do not differentiate between the types of obligation. See the Supplementary Material for an explicit derivation of the parameter ranges that determine the extent of the facultative and obligate behaviour for each of the goby and shrimp populations. We again note that while the parameter values may vary if different functional forms are used to represent the mutualist dependencies $M_2(x_3)$ and $M_3(x_2)$, the qualitative results do not critically depend on the specific functional forms used, as is the case for some models of mutualism (for example, see Bazykin [2]).

2.1. Resilience.

We wish to calculate the resilience (R) of the equilibrium state where all populations coexist for each of the four potential population interactions:

- Facultative gobies and facultative shrimp;
- Obligate gobies and facultative shrimp;
- Facultative gobies and obligate shrimp; and
- Obligate gobies and obligate shrimp.

The measure of resilience we use is defined after DeAngelis [7] as the negative of the real part of the dominant eigenvalue (λ_D, the most positive one) of the equilibrium point where all living populations coexist:

$$R = -\text{real}\{\lambda_D(x_1^*, x_2^*, x_3^*)\}. \tag{3}$$

An equilibrium at any point in the model's ecospace (which we have normalised by population abundances, so that $N_T = 1$, and $0 \leq x_1^*, x_2^*, x_3^* \leq 1$) may have a range of resiliences associated with it. More than one parameter set can determine a point in the ecospace, and each parameter set will cause the point to have a different resilience. In order to explore the resilience of the model we need to vary all parameters suitably in ranges that can produce valid ecosystem models and investigate a number of parameter sets for each point in the ecospace. Although DeAngelis' definition of resilience is only relevant for stable equilibrium points, we include the 'resiliences' of unstable points in our analysis to elucidate the relative ubiquity of stable and unstable equilibria in the ecospace.

2.2. Parameter Space Search. The parameter space for the search was constrained to optimise the probability that a randomly generated parameter set had each population functioning in the manner desired (for example, x_1 always had properties of an autotroph), that mass balance principles of predation were always respected (i.e. the predator could not gain more mass than the prey lost), and that the populations could not 'borrow' from the nutrient pool. To achieve this the constraints listed in Table 2 were imposed on the parameter search. To simplify the interpretation of the results of the parameter search we restricted μ_2 and ϵ to small ranges that reflected the changes in mortality observed by Lyons [20], and μ_3 to small values. Changes in goby and shrimp mutualist behaviour may be determined simply by considering r_2 and r_3 in relation to a_{21} and a_{31} respectively.

Table 2
Summary of constraints for the parameter space.

Constraint	Implication of the Parameter Constraint
$r_1 = 1$	Ensures x_1 can grow on inorganic nutrient
$1 < a_{11}, a_{12}, a_{13} < 2$	Ensures x_1 always functions as a mixotroph
$-1 < r_2 < 0$	Ensures x_2 always functions as a heterotroph
$0.5 < \mu_2 < 1$	Implements a reduction in mortality of x_2 due to protection by x_3 of the order measured by Lyons [20]
$0 < \epsilon < 0.001$	Implements a reduction in mortality x_2 due to protection by x_3 of the order measured by Lyons [20]
$-a_{12} < a_{21} < 0$	Ensures x_2 predation on x_1 respects mass balance
$0 < a_{22} < 1$	Implements density-dependent mortality for x_2
$0 < a_{23} < 2$	Restricts the mutualism interaction between x_2 and x_3 to protection effects on density-independent mortality
$-1 < r_3 < 0$	Ensures x_3 always functions as a heterotroph
$0.05 < \mu_3 < 0.10$	Implements a reduction in mortality of x_3 due to protection by x_2
$-a_{13} < a_{31} < a_{13}$	Ensures x_3 predation on x_1 respects mass balance and allows x_3 to feed solely on x_2 faeces
$-a_{23} < a_{32} < a_{23}$	Ensures x_3 consumption of x_2 faeces respects mass balance but also allows x_3 to feed solely on x_1
$0 < a_{33} < 1$	Implements density-dependent mortality for x_3

The equilibrium population sizes were calculated analytically for each parameter set (see Supplementary Material for details) and each model defined by a parameter set was deemed valid if the equilibrium value of each population and the equilibrium nutrient was between zero and one. Ten million randomly generated parameter sets drawn from the space defined in Table 2 were evaluated, of which approximately 8% resulted in valid models. The location and resilience of the internal equilibrium point was calculated for each of the valid parameter sets. The valid parameter sets were allocated to one of four potential goby - shrimp interactions (facultative - facultative, facultative - obligate, obligate - facultative, or obligate - obligate) on the simple basis of whether each could survive in the absence of the other. The goby was classified as facultative if $r_2 > a_{21}$, otherwise it was obligate. Similarly, the shrimp was classified as facultative if $r_3 > a_{31}$, otherwise it was obligate.

3. Results. The parameter search found 803,131 valid models, that is, about 8% of randomly selected sets produced ecologically sensible solutions. Figure 1 shows the distributions of the resiliences of the coexistence equilibrium point for each classification of the mutualism interaction. The facultative goby - facultative shrimp case accounts for about three-quarters of the valid parameter sets, and its distribution of resiliences dominates the overall distribution (see Supplementary Material). The least common case found in the parameter search was the obligate goby - obligate shrimp case, which accounted for only about 0.5% of valid parameter sets, followed by the facultative goby - obligate shrimp interaction which accounted for about 11% of valid parameter sets. This is despite the parameter search ranges resulting in obligate behaviour being equally as likely as facultative as the parameter ranges were symmetrical. Both of the obligate shrimp cases had much smaller maximum resiliences, and fewer cases of near-maximum resiliences, than the two facultative shrimp cases. The obligate goby - facultative shrimp case (around 13% of cases) had both the greatest maximum resilience and the greatest proportion of cases of near-maximum resiliences (see Table 3), with a strongly left-skewed third mode compared to the facultative goby - facultative shrimp case.

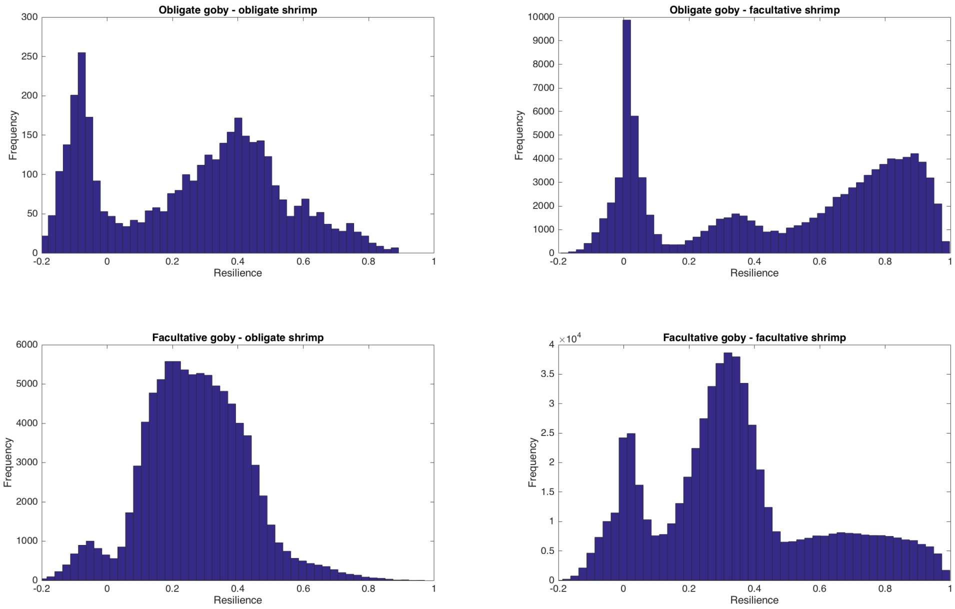

Fig. 1. *Distributions of resiliences for the obligate goby and obligate shrimp (top left,* $n = 3,838$*), the obligate goby and facultative shrimp (top right,* $n = 101,420$*), the facultative goby and obligate shrimp (bottom left,* $n = 90,498$*), and the facultative goby and facultative shrimp (bottom right,* $n = 607,375$*).*

The distributions of resilience in each of the four cases may be characterised crudely based on the intersections of the modal distributions, as low ($R < 0.15$), medium ($0.15 < R < 0.5$) and high ($R > 0.5$). The partitioning of equilibrium points between these resiliences is given in Table 3. The obligate goby - facultative shrimp system has the greatest proportion of its systems in the high resilience mode, with over 55%, more than double the fraction of any other system. The facultative goby - facultative shrimp systems could potentially have similarly high resiliences, although a smaller fraction of these systems had high resiliences. However, as there were many more parameter sets found in this category, the probability of facultative goby - facultative shrimp or obligate goby - facultative shrimp being a high resilience system appear similar.

Table 3
Partitioning of equilibrium points among resiliences.

Interaction	Low	Medium	High
Obligate goby - obligate shrimp (OO)	36%	47%	17%
Facultative goby - obligate shrimp (FO)	21%	73%	6%
Obligate goby - facultative shrimp (OF)	30%	15%	55%
Facultative goby - facultative shrimp (FF)	22%	55%	23%

We noted above that as different parameter sets can define the same equilibrium point in the system's ecospace each point can have multiple resiliences, and that there may not necessarily be a simple relationship between equilibrium population sizes and resilience. Figure 2 supports this observation and suggests three relationships between population size and resilience correlated with the three modes of resiliences apparent in Figure 1. Each panel of Figure 2 has a horizontal lobe of points extending along the equilibrium population axis with resiliences near zero, where there is no relationship between population size and resilience. However, each figure also has many more solutions which reveal either a relatively weak relationship between population size and resilience (the middle mode in Figure 1 and the middle lobe in Figure 2) or a potentially strong relationship (the upper lobes) The boundaries of these lobes represent optimal tradeoff regimes where the goby and shrimp populations can trade the benefits of increased sustainable population size against the costs of reduced system resilience. Note that the lowest trophic level, the plankton, does not have to trade these options off - it increases the system resilience when it increases its sustainable population size.

This provides a few broad rubrics: systems with relatively large lower trophic level populations (i.e. the classic 'trophic pyramid') tend to be more resilient than systems with relatively small lower trophic levels; and conversely, resilient systems tend to have relatively small populations in the higher trophic levels. There appears to be no correlation between the total sustainable biomass in the system and resilience (Figure 2(d)). Figure 2 also reveals that the most common systems we found were low resilience systems with x_1^* between 0.2 and 0.4, and with a total living biomass between 0.5 and 0.8-0.9.

TABLE 4

Correlation coefficients between parameters, resilience and/or equilibrium population size. Data for these correlations were included if all the goby and shrimp populations were in optimal trade-off regimes: $|R-(1-x_2^*)| < 0.1$ *and* $|R-(1-x_3^*)| < 0.1$ *for facultative shrimp, and if* $|R-(1-1.25x_2^*)| < 0.1$ *and* $|R-(1-2x_3^*)| < 0.1$ *for obligate shrimp.*

Interaction	OG - OS ($n = 17$)	FG - OS ($n = 94$)	OG - FS ($n = 14,458$)	FG - FS ($n = 27,450$)
r_2 v a_{21}	0.71	0.75	0.75	0.90
r_3 v a_{31}	0.95	0.82	0.88	0.92
a_{11} v x_1^*	-0.97	-0.96	-0.97	-0.97
R v x_2^*	-0.75	-0.79	-0.72	-0.85
R v x_3^*	-0.66	-0.77	-0.54	-0.54

The boundaries which constrain the plankton resilience-population relationship and along which the higher trophic level populations optimise the competing interests of maximising their equilibrium population size and maximising system resilience are shown by the dashed lines in Figure 2. When data for both facultative and obligate strategies are combined, as in Figure 2, the tradeoff between resilience and sustainable population size is slightly more expensive for shrimp ($R \approx 1 - 1.67x_3^*$) than for gobies ($R \approx 1 - 1.45x_2^*$). However, the tradeoffs are sensitive to whether the shrimp are facultative or obligate. For facultative shrimp, the compromise for the goby is $R \approx 1 - x_2^*$, and similarly for the shrimp $R \approx 1 - x_3^*$. For obligate shrimp, the goby tradeoff is $R \approx 1 - 1.25x_2^*$, and for the shrimp the compromise is $R \approx 1-2x_3^*$, although these regressions are based on fewer data points. An interesting implication of the goby resilience distribution in Figure 2 is that very small equilibrium populations of gobies (say, smaller than 0.05) produce either very low or very high, but not intermediate, resilience systems, unlike shrimp for which small equilibrium populations can be associated with systems of any resilience but most commonly produce systems of intermediate resilience.

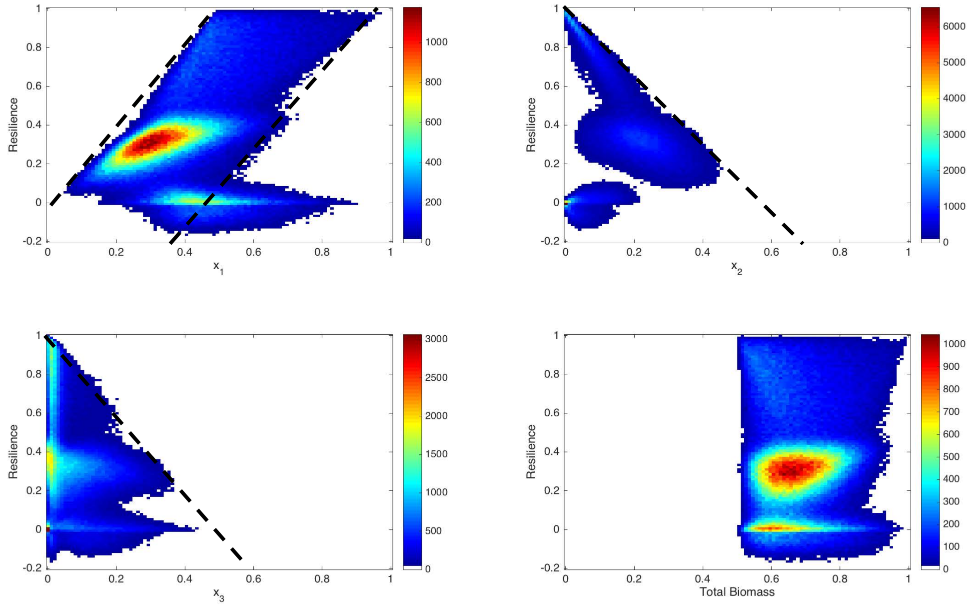

FIG. 2. *Scatter plots of resiliences for the goby and shrimp systems. Resilience vs:* x_1^* *(top left);* x_2^* *(top right);* x_3^* *(bottom left); and total equilibrium biomass* $x_1^* + x_2^* + x_3^*$ *(bottom right),* ($n = 803,131$)*. Colours show the number of parameter sets that resulted in each population - resilience combination. The dashed lines show optimal resilience-population tradeoffs (see text for details).*

The lowest trophic level, the plankton x_1, is not constrained by such a trade-off, but the distribution of valid systems is constrained by two resilience-population relationships: $R \approx 2x_1^*$ on the left and $R \approx 2x_1^* - 1$ on the right. Between these bounds resilience is not necessarily strongly affected by population size, with maximum resiliences being achievable with x_1^* populations between 0.5 and 1, and minimum resiliences occurring for x_1^* values between 0 and 0.5. The x_2^* and x_3^* trade-offs occur along the left diagonal side of the scatter of x_1^* points in Fig 2) the increase in system resilience with increasing plankton population is approximately $R = 2x_1^*$. Along this line, the system resilience does not increase after $x_1^* = 0.5$, indicating that $x_1^* = 0.5, R = 1$ is an optimal point for the competing interests of the goby and shrimp populations to potentially maximise their equilibrium size (so $x_2^* + x_3^* \approx 0.5$) while maintaining the resilience of the system near its maximum (in this case $R = 1$). However, this does not appear to be an achievable outcome for the system, as $x_2^* + x_3^* \approx 0.5$ produces resiliences of $R \approx 0.5$.

Table 4 shows a summary of high correlations between parameters, resilience and/or equilibrium population size for parameter sets that were near the trade-offs for gobies and shrimp. The data in Table 4 reveal strong negative correlations between resilience and the equilibrium population sizes of x_2 and x_3. Note that there is no correlation between x_1^* and R as the optimal trade-offs for x_2 and x_3 lie in a region of the solution space where R is insensitive to x_1^* (see Fig 2). In this part of the parameter space the plankton's density-dependent mortality rate a_{11} is a primary determinant of the x_1^* population size rather than higher trophic level grazing (a_{21} and a_{31}). However, for the goby and shrimp populations, a_{21} and a_{31} are involved in key trade-offs with r_2 and r_3 respectively.

The trade-offs that the goby and shrimp populations make in order to service their objectives of maximising their steady-state populations while maintaining a resilient ecosystem are apparent in Fig 3. This plot shows the correlation between r_2 and a_{21}, and r_3 and a_{31} for obligate goby - facultative shrimp and facultative goby - facultative shrimp interactions for parameter sets for which both populations were near the optimal trade-off regimes: $|R - (1 - x_2^*)| < 0.1$ and $|R - (1 - x_3^*)| < 0.1$. Scatter plots for systems with obligate shrimp are not shown as these cases did not have sufficient data points to reveal a robust relationship ($n = 17$ for obligate gobies and $n = 94$ for facultative gobies).

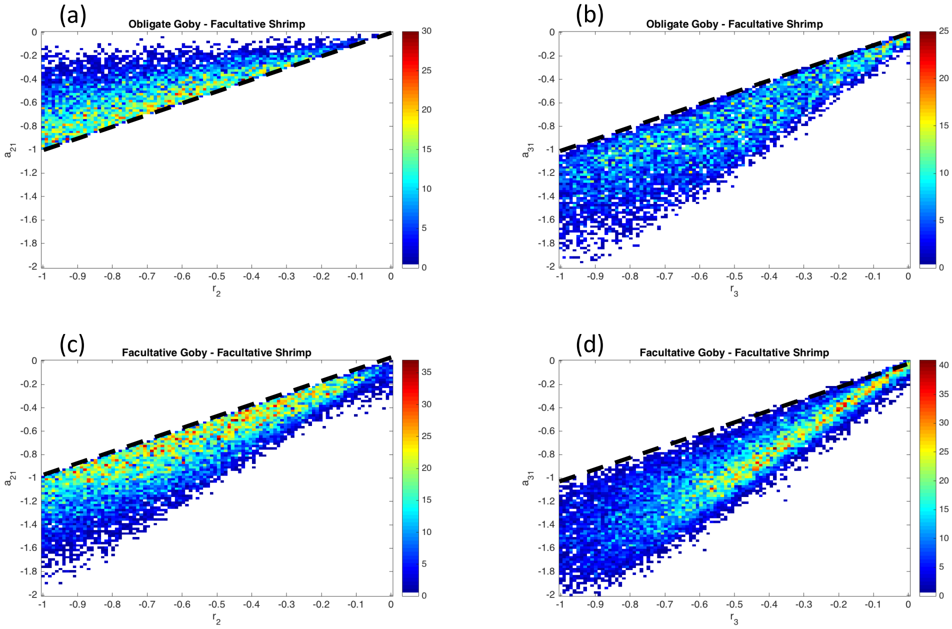

Fig. 3. *Scatter plots of* r_2 *versus* a_{21}*, and* r_3 *versus* a_{31} *for the obligate goby - facultative shrimp system (panels (a) and (b) respectively,* $n = 14,458$*), and* r_2 *versus* a_{21}*, and* r_3 *versus* a_{31} *for the facultative goby - facultative shrimp system (panels (c) and (d) respectively,* $n = 27,450$*). Colours show how many parameter sets resulted in each trade-off. Points above the dashed lines* $r_2 = a_{21}$ *or* $r_3 = a_{31}$ *in each panel are obligate interactions and those below are facultative interactions for the goby (panels (a) and (c)) and the shrimp (panels (b) and (d)). Data were included in these plots if both* x_2 *and* x_3 *populations were in optimal trade-off regimes:* $|R - (1 - x_2^*)| < 0.1$ *and* $|R - (1 - x_3^*)| < 0.1$.

The key trade-offs that both populations make in each case in Figure 3 is of their density-independent mortality rate (r_2 or r_3) against their per capita rate of plankton consumption (a_{21} or a_{31}). In all cases, these parameters are positively correlated - if r_2 is reduced for example, a_{21} is reduced in the tradeoff. Trade-offs between the density-independent mortality rates (r_2 or r_3) and the density-dependent mortality rates (a_{22} or a_{33}) or their interaction coefficients (a_{23} or a_{32}) were not evident in the analysis. The imperatives for trade-offs appear to be much stronger for the shrimp than for the goby, with the correlation coefficients between r_3 and a_{31} being much stronger (0.99 in both cases) than the correlation coefficients between r_2 and a_{21} (0.75

and 0.88 respectively) in each case.

The cases for the obligate goby are distributed throughout the available space, but are mostly concentrated near $a_{21} = r_2$, that is, along the facultative/obligate boundary. The facultative goby cases are also distributed throughout the available space, but again are more common near the facultative/obligate boundary. The goby parameters are more common either side of the dividing line that differentiates facultative interactions from obligate, suggesting that either strategy optimises the goby trade-offs equally well. There appears to be little pressure on the goby to be strongly facultative or strongly obligate - most goby cases cluster around the line $r_2 = a_{21}$ where the goby has the flexibility to adapt its mutualist strategy with small parameter changes. There also appears to be little difference in the ubiquity of small versus large parameter values, with cases distributed approximately uniformly along the facultative/obligate boundary.

The shrimp parameter set distributions are different to the goby: low values of r_3 and a_{31} are more common than large values whether the shrimp are facultative or obligate. Further, when the gobies are obligate (Figure 3b) they are more dense near the boundary $r_3 = a_{31}$ that divides facultative from obligate shrimp, but are more densely clustered near the parameter search boundary $a_{31} = 2r_3$ when the gobies are facultative (Figure 3d). The points in this latter region are points that lie along the left edge of the plankton-resilience scatter in Figure 2, for which all three population-resilience relationships $R = 2x_1^*$, $R = 1 - x_2^*$, and $R = 1 - x_3^*$ hold.

The other side of the parameter space, near $r_3 = a_{31}$, where the obligate goby - facultative shrimp systems are more common, involves only tradeoffs between the goby and the shrimp ($R = 1 - x_2^*$, and $R = 1 - x_3^*$) and are not constrained by the plankton-resilience relationship. This suggests a benefit to the shrimp of being strongly facultative in low plankton regimes, and presents an interesting rubric. Facultative goby - facultative shrimp systems have more parameter combinations that result in high resilience but occur in regions with low sustainable plankton population regimes, where resilience increases as the lowest trophic level population increases. In contrast, obligate goby - facultative shrimp systems have fewer parameter combinations that lead to high resilience but occur in high sustainable plankton population regimes, where resilience is not correlated with changes in the lowest trophic level population.

4. Discussion.

The modelling framework we have used to simulate mutualism interactions between gobies and shrimp allows us to identify points of maximum resource levels for each population and use those points to define parameter relationships that determine whether the goby is in a facultative or obligate mutualist relationship with the shrimp and *vice versa*. It also allows us to constrain the parameter space that we randomly search and to eliminate unrealistic ecosystems from our analysis, for example systems in which populations 'borrow' resources from the environment.

Only around 8% of the ten million random parameter sets we sampled from the parameter space resulted in valid ecosystem models. Models with obligate shrimp had lower maximum resiliences than models with facultative shrimp, and were relatively rare, an interesting result given the number of obligate strategies proposed or documented for shrimp. Models in which the gobies and the shrimp were both facultative were about six times more common than the obligate goby - facultative shrimp interaction, most often reported for real systems. Obligate-facultative mutualist interactions presumably originate from mutualist interactions that are initially facultative-facultative and one of Lyons' [20] key questions was what is the payoff that the goby obtains that results in it becoming obligate on the shrimp.

The answer may lie in the distribution of the resiliences of the various systems. We find three modes of resilience among the valid systems found by our random parameter search: low ($R \approx 0$); medium ($R \approx 0.3$); and high ($R \approx 1$). Based on the scalings used in the model, the low resilience systems equate to ecosystems that take months to recover from perturbations while the high resilience systems equate to ecosystems that take days to recover. The low resilience mode in all scenarios, is not correlated with sustainable population size, while the second mode appears weakly correlated with population size. The third mode has a complex relationship with sustainable population sizes, and dominates the distribution of resiliences for the obligate goby - facultative shrimp scenario, accounting for over half of the valid cases, more than double the fraction of high resilience cases for other scenarios. The distributions of resiliences in the other three scenarios are dominated by the second mode, which account for 47 - 73% in these systems. While facultative-facultative systems are more abundant, and consequently account for most of the high-resilience systems, the obligate-facultative interaction has a high mode that is strongly skewed in favour of high resilience systems. This suggests that the payoff for the gobies transitioning from facultative to obligate mutualists may be that it produces more stable ecosystems that maintain its food, reproductive and protector populations at more predictable levels.

The relationships between system resilience and the sustainable x_2^* and x_3^* populations supports our conjecture that there may be two conflicting self-organising principles at work in these systems. Each higher trophic level population is trying to maximise its sustainable population and sequester the greatest fraction of resources in the system that it can. However, at the system level this strategy results in low resilience systems, in which all populations are more susceptible to extinction because small perturbations in the environment to which they have adapted can lead to large, long-lasting departures from the equilibrium state [28, 22]. This results in destabilisation of the food sources for all populations. This may drive trade-offs that the goby and shrimp populations make in order to achieve a compromise state somewhere between maximising their own sustainable population and ensuring a sufficient and reliable food supply.

Our analyses suggest that the major trade-offs that the gobies and shrimp make are their density-independent mortality rates (r_2 and r_3 respectively) against their rates of predation on the plankton (a_{21} and a_{31} respectively). Here we see differences between the goby and shrimp trade-offs. The sustainable goby populations are more dense in the vicinity of the trade-off $r_2 = a_{21}$, and although there are almost twice as many cases of facultative gobies as obligate gobies, both distributions are clustered around the same trade-off, and are distributed roughly uniformly along all values of $-1 < r_2 = a_{21} < 0$. This suggests there may be little advantage to the goby to be strongly facultative or strongly obligate, but an advantage to be positioned so that it can change its mutualist strategy with small behavioural changes.

The shrimp in contrast has clear mutualism interaction modes associated with goby behaviour. When the goby is obligate, the shrimp trade-offs are distributed near to the tradeoff $r_3 = a_{31}$, but when the gobies are facultative, the shrimp tradeoffs are most dense near the trade-off $r_3 = 2a_{31}$. Small magnitude values are also more common than large in this case. The differences between these strategies are profound. The latter, with the facultative goby, represents a model with low sustainable plankton populations, in which the optimisation of the resilience of the system is subject to three constraints. Here, system resilience is positively correlated with the sustainable plankton population and negatively correlated with the sustainable goby and shrimp populations. In contrast, the majority of the facultative shrimp models with obligate gobies have sustainable plankton populations, and occur in a region of parameter space where resilience is subject to only two constraints - resilience increases if the sustainable goby and shrimp populations reduce, but is unaffected by changes in the sustainable plankton population.

5. Conclusion.

Our analysis of this goby-shrimp model of mutualist behaviour suggests that obligate goby behaviour allied to facultative shrimp behaviour may be a preferred outcome (of the four possible interactions examined) as it is associated with the highest system resilience. This modelling outcome is consistent with the observation that over 90% of goby species are obligate on their shrimp partners [20]. Lyons [20, 21] data shows that obligate gobies tend to stay closer to their shrimp burrows and do not forage as far as facultative gobies. Such behaviour may make obligate goby populations more susceptible to speciation, leading to lots of obligate goby species. This does not mean that the total biomass of obligate gobies is greater than the total biomass of facultative gobies.

Further, facultative goby behaviour with facultative shrimp behaviour is an easily achievable state, with 75% of valid random parameter sets representing this interaction. This is a common state in regimes where the resilience of the system correlates with the sustainable biomass of the lowest trophic level. While systems with facultative goby and facultative shrimp had an approximately symmetric high resilience mode, in contrast to the strongly left-skewed high resilience mode of the obligate goby - facultative shrimp system, and had a small fraction of valid systems in the mode (23% versus 55%), it also had the potential for very high resilience systems and had many more high resilience systems (around 17% of all valid systems, versus 7% for the obligate - facultative system).

Two interesting questions now arise that might be determined empirically. First, the distribution of goby trade-offs most commonly falling in the region of parameter space where the goby can easily shift between facultative and obligate behaviour, suggests that goby behaviours in the wild may need to be categorised differently. In particular, the fraction of total goby *biomass* that is in an obligate relationship with shrimp needs to be estimated and compared with the number of goby *species* that are in obligate relationships with shrimp. Second, the role of the plankton populations that potentially support both the goby and shrimp populations might be compared with the ubiquity of obligate-facultative and facultative-facultative interactions. Our results predict that the former may be more common in regions with abundant plankton populations that serve as food for both gobies and shrimp, and the latter may be more common in regions where low plankton biomass dictates that predator populations need to utilise all available food sources.

A recurring issue in the empirical investigation of living systems to evaluate the veracity of theoretical predictions is to what extent the assumptions made in developing the theoretical model conflict with the real world. Here, we have abstracted the real world to its simplest form, and represent the interaction of the populations with their environment and other populations (through the r_i, and M_i and a_{ij} respectively) only by the sign and magnitude of the interaction. This provides a reasonable approximation to the actual system if we empirically study real systems that are relatively undisturbed. We also make one approximation, that the mass of the limiting nutrient is conserved within the system; recall the model system is open to flows of all other nutrients and energy. The approximation that 100% of the limiting nutrient is recycled, while it prevents the use of the model to simulate the effects of changes in nutrient supply, is reasonable as most living systems recycle in excess of 90% of their limiting nutrient [32]. We consider that the results and predictions that we articulate here are relevant to, and testable in, real natural systems. We also note that the assumption of conservation of mass makes models written in this framework especially suitable for mesocosm experiments, which are generally sealed and in which the mass of all nutrients is conserved.

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REFERENCES

[1] Allee, W. C. and E. S. Bowen, *Studies in animal aggregations: mass protection against colloidal silver among goldfishes.*,The Journal of Experimental Biology, 61, 185-207, 1932.

[2] Bazykin, A. D., *Nonlinear dynamics of interacting populations.* World Scientific, Singapore. 1998.

[3] Boucher, D. H., *The Biology of Mutualism*, Croom Helm, London, 1985.

[4] Bronstein, J.L., *Mutualism*, Oxford University Press, New York, 2015.

[5] Case, T. J., *An illustrated guide to theoretical ecology.* Oxford University Press, New York. 2000.

[6] Cropp, R.A. and J. Norbury, *Population interactions in ecology: a rule-based approach to modelling ecosystems in a mass-conserving framework*, SIAM Review, 57, 437-465, 2015.

[7] DeAngelis, D., *Energy Flow, Nutrient Cycling, and Ecosystem Resilience.* Ecology 61(4): 764-771. 1980 .

[8] Dean, A. M., *A simple model of mutualism.*, The American Naturalist, 121, 409-417, 1983.

[9] Graves, W. G., B. Peckham and J. Pastor, *A bifurcation analysis of a differential equations model for mutualism*, Bulletin of Mathematical Biology, 68, 1851-1872, 2006.

[10] Gross, K., *Positive interactions among competitors can produce species-rich communities.* Ecology Letters 11: 929?936. 2008.

[11] Holland, J. N. and D. L. DeAngelis, *A consumer-resource approach to the density-dependent population dynamics of mutualism*, Ecology, 91, 1286-1295, 2010.

[12] Johnson, N. C., *Mutualisms and ecosystem-level processes.* in Bronstein, J.L. (ed) Mutualism. pp 221-238, 2015.

[13] Johnson, C. A., and P. Amarasekare, *Competition for benefits can promote the persistence of mutualist interactions.* Journal of Theoretical Biology 328:54-64. 2013.

[14] Kang, Y., R. Clark, M. Makiyama, and J. Fewell, *Mathematical modeling on obligate mutualism: Interactions between leaf-cutter ants and their fungus garden.* Journal of Theoretical Biology 289:116-127. 2011.

[15] Kot, M., *Elements of Mathematical Ecology*, Cambridge University Press, Cambridge, UK, 2001.

[16] Levin, S., *The Princeton Guide to Ecology*, Princeton University Press, Oxford, UK. 2012.

[17] Loreau, M., *Evolutionary processesin ecosystems.* Encyclopedia of Global Environmental Change Vol. 2: The Earth System: Biological and Ecological Dimensions of Global Environmental Change. (eds. H.A. Mooney and J. Canadell) pp 292-297. (2002).

[18] Loreau, M., *From Populations to Ecosystems.* Princeton University Press, Woodstock, Oxfordshire. 2010. p80.

[19] Lotka, A.J., *Elements of Physical Biology*, Wilkins and Kilkins, Baltimore, 1925.

[20] Lyons, P.J., *The benefit of obligate versus facultative strategies in a shrimp-goby mutualism.*, Behavioral Ecology and Sociobiology, 67, 737-745, 2013.

[21] Lyons, P.J., *Competition by obligate and facultative mutualists for partners in shrimp-goby associations.* Environmental Biology and Fisheries, 97: 1347-1352. 2014.

[22] Mari, L. and R. Casagrandi and A. Rinaldo and M. Gatto, *A generalized definition of reactivity for ecological systems and the problem of transient species dynamics.* Methods in Ecology and Evolution, 8, 1574?1584. 2017.

[23] May, R.M., *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ, 1973.

[24] May, R. M., *Models for Two Interacting Populations.* Pages 49-70 in R. M. May, editor. Theo-

retical Ecology: Principles and Applications. Blackwell Scientific Publications, Oxford. 1976.

[25] May, R.M., *Theoretical Ecology: Principles and Applications*, Blackwell Science Inc, Princeton, Oxford, UK, 1981.

[26] Molles, M., *Ecology: Concepts and Applications*, McGraw-Hill Education,New York, 2014.

[27] Murray, J.D., *Mathematical Biology* Springer-Verlag, Berlin, 2001, p99.

[28] Neubert, M.G. and H. Caswell, *Alternatives to resilience for measuring the responses of ecological systems to perturbations.* Ecology, 78, 653-665. 1997.

[29] Pastor, J., *Mathematical Ecology of Populations and Ecosystems*, Wiley-Blackwell, Chichester, 2008.

[30] Ricklefs, R.E. and R. Relyea, *Ecology: the economy of nature*, W.H. Freeman, New York, 2014.

[31] Thompson, A.R., R.M. Nisbet and R.J. Schmitt, *Dynamics of mutualist populations that are demographically open.* Journal of Animal Ecology. 75: 1239-1251. 2006.

[32] Vitousek, P. M., and P. A. Matson, *Nutrient cycling and biogeochemistry.* Pages 330-339 in S. Levin, editor. The Princeton Guide to Ecology. Princeton University Press, New Jersey. 2012.

[33] Volterra, V., *Variations and fluctuations of the numbers of individuals in animal species living together.* Reprinted in 1931 in Chapman, R.N. *Animal Ecology* McGraw Hill, New York, 1925.

[34] Wetzel, R., *Limnology* (Third Edition), Academic Press, San Diego. 2001. p 828.

[35] Wright, D. H., *A simple, stable model of mutualism incorporating handling time.* The American Naturalist 134:664-667. 1989.

7. Supplementary Material.

7.1. Obligation. Consider an obligate mutualist population x_i that consumes a single resource $R_i = x_h$ and is obligated on the presence of another population x_j $(j \neq h, i)$ to be able to grow. The maximal point of the consumed resource for the population x_i lies at a vertex of E, where $x_h = 1$ and all other populations, including the population supplying the service to the obligated population, are zero. The population cannot grow there because its obligating population is zero, hence we include the obliging population x_j as a pseudo-resource $\hat{R}_i = \phi_i(x_h, x_j))$ on the line $x_h + x_j = 1$. The pseudo-resource must have the properties that:

- $\hat{R}_i = 0$ when the resource $x_h = 0$,
- $\hat{R}_i = 0$ when the obliging population $x_j = 0$,
- $\hat{R}_i > 0$ when $0 < x_h, x_j < 1$,
- $\hat{R}_i$ collapses to R_i when there is no obligation of x_i on x_j.

Many functions, including Holling Type II ($\phi_i(x_h, x_j) = x_h \frac{x_j}{x_j+\epsilon_j}$) and Holling Type III ($\phi_i(x_h, x_j) = x_h \frac{x_j^2}{x_j^2+\epsilon_j}$), where $\epsilon_j \geq 0$ is a half-saturation constant that measures the degree of the obligation of x_i on x_j capture these properties of $\hat{R}_i$, although other functions may be used. The point of maximum pseudo-resource $\hat{R}_i^{**} = \max(\phi_i(x_h, x_j))$ lies somewhere on the line $x_h + x_j = 1$. In order for the obligated population x_i to have valid ecological properties its life function f_i must satisfy the condition that $f_i|_{\hat{R}_i^{**}} > 0$ and $f_i|_{\hat{R}_i=0} < 0$.

The heterotroph mutualist system, (1) and (2), always has an unstable equilibrium point at the origin $C_0 = \{0, 0, 0\}$ with eigenvalues of:

$$\lambda_1 = r_1 > 0, \quad \lambda_2 = r_2 < 0, \quad \text{and,} \quad \lambda_3 = r_3 < 0, \tag{4}$$

where the signs of the eigenvalues hold for all heterotrophs, that is, they are the same for all mutualism strategies of x_2 and x_3. The origin is always an unstable saddle point in these systems as the autotroph population is always able to grow as λ_1 is always positive. The system also has an autotroph-only equilibrium point at:

$$C_1 = \{x_1^* = \frac{r_1}{a_{11}}, x_2^* = 0, x_3^* = 0\}. \tag{5}$$

This point always lies on the x_1 axis within E, and the eigenvalues of this point are always:

$$\lambda_1 = -r_1 < 0, \quad \lambda_2 = r_2 < 0, \quad \text{and,} \quad \lambda_3 = r_3 < 0. \tag{6}$$

This point is always stable when ϵ_1 and ϵ_2 are greater than zero (i.e. when the x_2 and x_3 populations are obligate upon each other). The only other equilibrium point of the model that influences its dynamics is the coexistence point $C_2 = \{x_1^* \neq 0, x_2^* \neq 0, x_3^* \neq 0\}$. Evaluating the location of this point algebraically is complicated and uninformative, so we calculate it numerically if we need it. Our parameter constraints do not guarantee that this interior coexistence equilibrium point will exist in E. It may not exist in E, or it may exist in E and be unstable, in which case it is likely that all three populations do not coexist, a circumstance which is not the subject of this analysis and will not be considered here. However, if C_2 does exist in E and it is stable, a separatrix dividing the basins of attraction of the two stable equilibrium points C_1 and C_2 must exist. This requires that solving the system $f_1 = 0; f_2 = 0; f_3 = 0$ results in two distinct equilibrium points for $C-2$, one stable and one unstable (that lies between C_1 and the stable C_2 point) and introduces an Allee effect [1] which imposes minimum sustainable population sizes on x_2 and x_3.

7.2. Parameter Values. The facultative goby case is defined by the conditions that it can survive solely on plankton (i.e. $f_2|_{x_1=1} > 0$) and that it may receive a benefit from the shrimp (i.e. $a_{23} < 0$ if benefits exceed costs). The obligate goby case is represented by the conditions that it cannot survive on plankton alone (i.e. $f_2|_{x_1=1} < 0$) but relies on a reduction in mortality due to a protection mutualism provided by the shrimp for the population to be able to grow (i.e. $f_2|_{x_1^{**}+x_3^{**}=1} > 0$ where x_3^{**} is a critical size of the shrimp population that provides sufficient benefits (burrows) that the goby population can survive). In this case, a_{23} may take either sign: if $a_{23} < 0$ the goby receives a mutualist benefit from the shrimp in addition to its reduced mortality (benefits exceed costs), or if $a_{23} > 0$ there is no additional mutualist benefit, or the cost of accessing the benefit exceeds the benefit. For simplicity, here we will assume no unspecified mutualist benefits so that $a_{23} > 0$. These conditions define simple parameter relationships, in particular between r_2 and a_{21} that allow us to succinctly differentiate facultative from obligate mutualist gobies (see Table 5).

We use the saturating Holling Type III function $M_2(x_3) = \mu_2(x_3^2/[x_3^2 + \epsilon_2])$ to quantify the effect that the presence of the shrimp population has on the mortality of the goby population as measured experimentally by Lyons [20]. This captures the properties that when the shrimp population is very low, and there are very few burrows within close range of each goby, the addition of an extra burrow does not improve the goby's chances of evading predation much. Similarly, when the shrimp population is high, and each goby has many burrows nearby, the addition of an extra burrow does not improve the goby's chances of evading predation much.

We use the linear Holling Type I function $M_3(x_2) = \mu_3 x_2$ to quantify the effect that the presence of the shrimp population has on the mortality of the goby population.

The obligate mutualism cases are more complicated, and these interactions are defined in Table 5.

TABLE 5
Summary of parameter conditions for obligate interactions.

Pop.	Interaction	Parameter Relations
Goby	Relies on mortality reduction from availability of burrows provided by shrimp	$r_2 < a_{21} < 0$ and $a_{21}x_1^{**} < r_2[1-M_2(x_3^{**})] < 0$ for some $0 < x_1^{**}, x_3^{**} < 1$ where $x_1^{**} + x_3^{**} = 1$
Shrimp 1.	Feeds solely on goby faeces	$a_{31} \geq 0$ and $a_{32} < r_3 < 0$
Shrimp 2.	Feeds on plankton and relies on mortality reduction from goby warnings	$r_3 < a_{31} < 0$ and $a_{31}x_1^{**} < r_3[1-M_3(x_2^{**})] < 0$ for some $0 < x_1^{**}, x_2^{**} < 1$ where $x_1^{**} + x_2^{**} = 1$
Shrimp 3.	Feeds on both plankton and goby faeces and relies on mortality reduction from goby warnings	$r_3 < a_{31} < 0$, $r_3 < a_{32} < 0$, and $(a_{31}x_1^{**} + a_{32}x_2^{**}) < r_3[1 - M_3(x_2^{**})] < 0$ for some $0 < x_1^{**}, x_2^{**} < 1$ where $x_1^{**} + x_2^{**} = 1$

Obligate option (1) for the shrimp in Table 5 is analogous to the obligation a predator has on its prey, although in this case the shrimp feeds on the goby faeces so the goby population is not reduced by the shrimp population, but the size of the shrimp population is constrained by the size of the goby population. In obligate options (2) and (3), the shrimp may feed exclusively on plankton (2) or both plankton and goby faeces (3), but in both cases relies on a reduction in mortality due to a protection mutualism provided by the goby. (Figure 4) reveals three distinct modes of resilience: a mode centred near $R = 0$, a larger normally distributed mode centred on about $R = 0.3$, and a broad left-skewed mode that extends almost to $R = 1$.

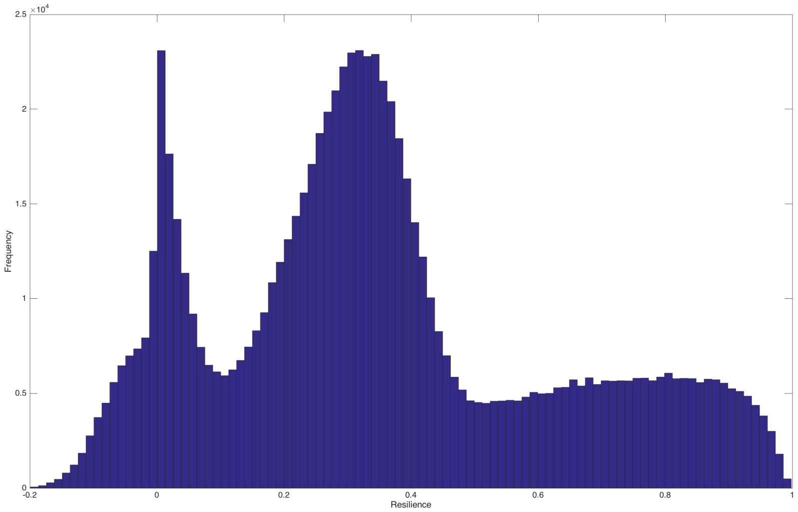

FIG. 4. *Distributions of resiliences for all goby - shrimp systems (*$n = 803,131$*).*

7.3. Parameter Relationships. The explicit accounting of limiting resources defines the finite ecospace (E) that contains all the valid states of populations in the model. E explicitly shows the resource(s) for each heterotroph population (as these are other populations), but also implicitly shows the resource for the autotroph population due to the relation that $N = 1 - x_1 - x_2 - x_3$ [6]. This explicit representation of finite resources allows us to impose simple constraints of the per capita growth functions (f_i). These are simply that populations must be able to grow when their resources are maximal ($f_i|_{R_i=1} > 0$) and cannot grow when they have no resources ($f_i|_{R_i=0} < 0$). These provide parameter relationships which must be respected if the populations and model are to be ecologically sensible, that is they constrain the values that the parameters r_i and a_{ij} for $i, j = 1, 2, 3$ may take.

The plankton population x_1 is an ecologically-sensible population only if its parameters have the relationship:

$$0 < r_1 < a_{11}, a_{12}, a_{13}. \tag{7}$$

Here, r_1 is the net density-independent per capita growth rate of x_1 on inorganic nutrient, which is a population net term of the positive phytoplankton rate of photosynthesis and the negative zooplankton density-independent mortality rate. a_{11} is the plankton population's density-dependent mortality rate, and a_{12} (a_{13}) is the grazing parameter for x_2 (x_3) on x_1.

The goby population x_2 may have a facultative or obligate mutualism relationship with the shrimp population x_3. If it is facultative, the goby life function f_2 is subject to the usual conditions $f_2|_{R_2=1} > 0 > f_2|_{R_2=0}$ and the mutualism benefit is defined by $a_{23} < 0$. Assuming that the population is always subject to some density-dependent mortality these conditions provide the parameter relationship:

$$a_{21} < r_2 < a_{23} < 0 < a_{22}. \tag{8}$$

However, if the goby is obligate on the shrimp and cannot survive without it, the goby must have the properties that:

- $f_2|_{x_1=1} < 0$,
- $f_2|_{x_3=1} < 0$,
- $f_2|_{x_2=1} < 0$,
- $f_2|_{x_1=x_2=x_3=0} < 0$,
- $f_2|_{x_1+x_3=1} > 0$ when $x_1 \neq 0 \neq x_3$.

Analogous conditions hold for the shrimp population.

7.4. Equilibrium Points.

The equilibrium population sizes for each parameter set were calculated from the equations:

$$\begin{aligned}
x_1^* &= -\frac{a_{12}x_2^* + a_{13}x_3^* - r_1}{a_{11}}, \\
x_2^* &= \frac{a_{11}r_3 - a_{31}r_1 - (a_{11}a_{33} - a_{13}a_{31})x_3^*}{a_{11}a_{32} - a_{12}a_{31} + M_2 a_{11} r_3}, \qquad (9)\\
&\alpha x_3^{*3} + \beta x_3^{*2} + \gamma x_3^* + \delta = 0,
\end{aligned}$$

where:

$$\begin{aligned}
\alpha &= \frac{a_{13}a_{21}}{a_{11}} - a_{23} + \frac{a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33}}{a_{11}a_{32} - a_{12}a_{31} + \mu_2 a_{11} r_3} + \frac{a_{12}a_{13}a_{21}a_{31}}{a_{11}^2 a_{32} - a_{11}a_{12}a_{31} + \mu_2 a_{11}^2 r_3}, \\
\beta &= r_2 - \mu_1 r_2 - \frac{a_{21}r_1}{a_{11}} - \frac{a_{11}a_{22}r_3 + a_{12}a_{21}r_3 + a_{22}a_{31}r_1}{a_{11}a_{32} - a_{12}a_{31} + \mu_2 a_{11} r_3} - \frac{a_{12}a_{21}a_{31}r_1}{a_{11}^2 a_{32} - a_{11}a_{12}a_{31} + \mu_2 a_{11}^2 r_3}, \\
\gamma &= \frac{\epsilon a_{13}a_{21}}{a_{11}} - \epsilon a_{23} + \frac{\epsilon a_{11}a_{22}a_{33} - \epsilon a_{13}a_{22}a_{31}}{a_{11}a_{32} - a_{12}a_{31} + \mu_2 a_{11} r_3} + \frac{\epsilon a_{12}a_{13}a_{21}a_{31}}{a_{11}^2 a_{32} - a_{11}a_{12}a_{31} + \mu_2 a_{11}^2 r_3}, \\
\delta &= \epsilon r_2 - \frac{\epsilon a_{21}r_1}{a_{11}} - \frac{\epsilon a_{11}a_{22}r_3 + \epsilon a_{12}a_{21}r_3 + \epsilon a_{22}a_{31}r_1}{a_{11}a_{32} - a_{12}a_{31} + \mu_2 a_{11} r_3} - \frac{\epsilon a_{12}a_{21}a_{31}r_1}{a_{11}^2 a_{32} - a_{11}a_{12}a_{31} + \mu_2 a_{11}^2 r_3}.
\end{aligned}$$

The roots of x_3^* are obtained numerically and then substituted to calculate x_2^* and then x_1^*.