# A Symmetric Intraguild Predation Model for the Invasive Lionfish and Native Grouper

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**Abstract**

Lionfish are top-level venomous predators native to the Indo-Pacific Ocean. Over the past decade, the species *Pterois volitans* and *P. miles* have become established throughout most of the western Atlantic Ocean, where they drastically impact coral reef communities. Overfishing of native species, such as grouper, who share their niche with lionfish may be the reason for the lionfish's success; research has suggested that at high density, groupers can act as a lionfish biocontrol. To determine if competition or predation is the mechanism behind lionfish suppression, we construct a symmetric intraguild predation model of lionfish, grouper, and prey. Thus, we assume lionfish and grouper compete for prey in addition to consuming juveniles of the other species. Holling type I functional responses are used to represent fecundity and predation. We conduct an equilibrium stability analysis and bifurcation analysis of the general model, and find that the system is able to coexist in an equilibrium or sustainable oscillations. After estimating parameter ranges, simulations and a sensitivity analysis indicate the parameters most influential to lionfish growth rate. The implied control strategies are then tested by varying harvesting and predation rates.

## 1 Introduction

Two species of lionfish, the red lionfish (*Pterois volitans*) and the devil firefish (*P. miles*), are invasive to the western Atlantic Ocean and Caribbean. Both are native to the Indo-Pacific, with *P. volitans* occupying the Indian Ocean and *P. miles* occupying the western Pacific and eastern Indian Ocean. The first Atlantic lionfish were reported in 1985 off the eastern coast of southern Florida [21], presumably originating from aquarium releases [24,32]. Since then, the populations have rapidly colonized the western coast of the United States, the Caribbean, and are spreading into the Gulf of Mexico [1]. Genetic analysis has shown a strong founder effect in Atlantic lionfish populations, i.e. low genetic diversity, and suggest a minimum of three female *P. volitans* and one female *P. miles* initiated the invasion [13].

*P. volitans* and *P. miles* are physically similar and were once considered a single species. Schultz (1986) first distinguished them as separate species based on physical characteristics including number of pectoral and anal fin rays, length of pectoral fins, and size of markings

[34]. It is not known if hybridization occurs, but no differences in their reproductive biology have been found [23] and where their ranges overlap, their distinguishing meristics may be shared and differentiation requires DNA analysis [13]. Furthermore, 93% of the lionfish in the Atlantic are *P. volitans* [13], making small differences negligible. Therefore, we consider both species to be functionally identical and refer to them collectively as "lionfish".

In their native ecosystems, lionfish play a comparatively minor role [2] and are solitary [10]. They have been observed hiding in the reefs instead of swimming in open water; this may be due to limited resources and increased mortality [12]. Their reported densities range from 80 fish/ha in the Red Sea [11] to 2.2 fish/ha in Palau [12]. However, they are flourishing in their invaded habitat, where densities of up to 450 fish/ha have been recorded [24]. Native prey species do not recognize the lionfish as a predator, while most predator species do not recognize the lionfish as prey. Lionfish are also able to fill the ecological niche left vacant by overfishing of competing species in the snapper-grouper complex (snappers, groupers, porgies, triggerfish, jacks, tilefishes, grunts, spadefishes, wrasses, and sea basses) [24]. Since lionfish evolved as part of the Indo-Pacific ecosystem, we suspect competing species, even if overfished, may be better adapted to stabilize their populations.

Lionfish spread is accomplished through dispersal in the egg and larval stages by water current; water depth, salinity, and temperature have little influence, although survival is limited by these factors [15]. Adult lionfish are stationary and territorial [10].

Cowen *et al.* [9] developed a connectivity model for damselfish in the Caribbean which has been shown to be applicable to lionfish dispersal patterns [24]. They have spread northwards up the eastern coast of the US and southwards to the Bahamas and Caribbean and are migrating west into the Gulf of Mexico. In the worst-case scenario, lionfish spread will be limited only by the (current) minimum survivable temperature of 10° C [18]. The spatial spread has been modeled in more detail by Johnston and Purkis (2011) [15] who developed a computational GIS, cellular automata model for the lionfish invasion, using publicly-available data on lionfish sightings around the western Atlantic.

Lionfish control has been limited to harvest. Several mathematical models have been developed to study the potential efficacy of harvesting. Morris *et al.* (2011) [22] developed a Leslie matrix model of lionfish populations, divided between larvae, juveniles, and adults. Elasticity analysis showed lionfish growth rate was most sensitive to adult and juvenile survival parameters, and it was found that 27% of adult lionfish would need to be removed monthly; as expected, additional harvesting of juveniles would reduce this percentage. Barbour *et al.* (2011) [4] used an age-structured fishery model to determine an annual harvest between 35 and 65% is required to overfish the population, although this was highly dependent on the size of lionfish associated with 50% harvest vulnerability.

Lionfish are generalist consumers [2,8] and prey proportions reflect local abundance [28]. Their diet comprises mostly teleost fish, but also crustaceans and a small percentage of mollusks [21, 28]. Lionfish are known to consume economically-important species including Nassau grouper and yellowtail snapper, although in low frequency [21].

In their native habitat, cornetfish have been recorded as consumers of lionfish [6], but in the Atlantic, lionfish are not thought to have many natural predators, although a wounded lionfish is known to have been consumed by a green moray eel [16]. Lionfish lay their eggs in mucous sacks containing up to 20,696 eggs [20], which are thought to be repulsive to predators [25]. Furthermore, predators typically avoid lionfish, who do not display a flight response when confronted with potential predators [20, 31], but spread their pectoral fins to increase their apparent size [20]. When large serranids were offered both lionfish and pinfish prey, only 7.6% of trials resulted in a consumed lionfish, whereas 75% resulted in a consumed pinfish [20]. Cannibalism has also been suggested as a cause of mortality [11], although it is primarily documented in aquarium fish and its occurrence in the wild is unknown [20].

Although the rates of grouper–lionfish consumption may be small, grouper at high density have been shown to suppress lionfish populations [12, 27]. Although competition for resources might be the mechanism behind this, Mumby *et al.* suggest that predation is more likely, since grouper are known to have consumed lionfish [19, 20], the larger grouper likely consumes larger prey than most lionfish, and grouper generally exhibit predatory responses towards smaller predators [27].

Based on this research, we conclude that interspecific interactions play a substantial role in the outcome of the ecosystems invaded by lionfish. We consider two cases: no direct predation between lionfish and grouper but competition for shared prey, and the additional effect of grouper predation on lionfish and lionfish on grouper. The latter is an example of symmetric intraguild predation (IGP).

Polis *et al.* (1989) [30] defined intraguild predation as predation occurring between members of the same "guild", or community of species that exploit the same resources. The authors classified IGP into four main types, depending on the direction of predation (symmetric or asymmetric) and age structure of the population (important or relatively unimportant). Holt and Polis (1997) [14] analyzed several models of asymmetric IGP, where the IGprey species depends on the resource, and the IGpredator species depends on both IGprey and resource.

The outline of this paper is as follows. In Section 2, we develop a three-species symmetric IGP model with two predators: lionfish and grouper. These species compete for the resource species, as well as predate directly on each other. Our model analysis is in Section 3, where we first nondimensionalize the model to simplify its structure and reduce the number of parameters, and then conduct an equilibrium existence, stability analysis, and bifurcation analysis. Simulation results are given in Section 5 and the sensitivity analysis is presented in Section 4 and . Our concluding remarks and discussion are found in Section 6.

## 2 Model Description

The general model is a system of three ODEs describing the populations of two predator species ($P_1$ and $P_2$) and a shared resource/prey species ($R$). Following Polis *et al.* (1989) [30], we assume symmetric intraguild predation (IGP) occurs between the predators. We do not assume equal strength of interaction on each species. "Lionfish" are defined as the *P. volitans/miles* complex, "grouper" are defined as members of the family *Serranidae*, and "prey" is defined as the collection of other species consumed by both.

In this general model, we do not explicitly model the age or size structure of any population. Thus, we have three variables representing the densities of each species over time. A diagram of the interactions in our system is given in Figure 1. We define "removal" as deaths due to natural causes or to human harvesting.

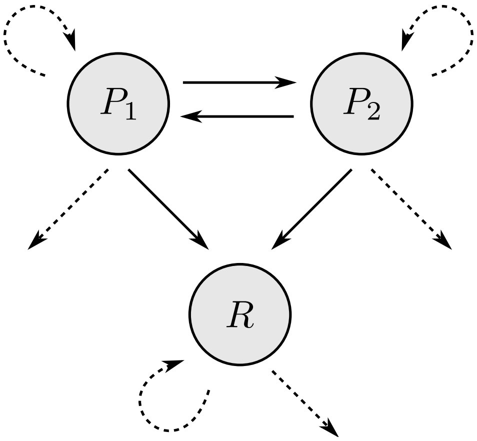

**Figure 1:** Conceptual model of general three-population model with symmetric intraguild predation. Solid lines represent predation dynamics (with arrows pointing towards prey); dotted loops represent fecundity and dotted lines represent mortality (natural deaths and harvesting).

As the analysis of this type of model is novel, we use the simplest functional response, Holling type I. This implies predator consumption increases at a linear rate with increasing prey density: handling time is negligible, search time is inversely proportional to prey density, and predators do not satiate. Density-independent predation rates are suitable for recently-introduced populations, whereas more established population would be better modeled with density-dependence [4].

In addition, the structure of this model implies that all members of the same class (lionfish, groupers, or prey) are the same size and are physiologically and behaviorally equivalent, with no differences in resource consumption and processing.

The equations in our model are

$$P_1' = P_1\left[c_1\left(a_1R + b_1m_2P_2\right) - b_2P_2 - d_1\right], \tag{1a}$$

$$P_2' = P_2\left[c_2\left(a_2R + b_2m_1P_1\right) - b_1P_1 - d_2\right], \tag{1b}$$

$$R' = R\left[r\left(1 - \frac{R}{K}\right) - a_1P_1 - a_2P_2\right]. \tag{1c}$$

This is a system of three variables which deterministically gives the populations of each class at time $t$. The predators are $P_1$ (corresponding to lionfish density) and $P_2$ (grouper density). The prey/resource density is given by $R$.

The parameters in the model and their units and values for the lionfish–grouper system are given in Table 1. We assume predator $i$ consumes the resource at a constant per capita rate $a_i$, and consumes the other predator at a similar rate $b_i$. Since the predators consumed may be larger than the resource, we introduce a mass scaling factor $m_i$ which rescales the size of the predators consumed in terms of the size of the prey (e.g. if predator 1 consumes predator 2, which is twice as large as its usual prey, then $m_2 = 2$). The total biomass consumed by predator $i$ is then converted into predator $i$ biomass by the constant $c_i$.

Both predators suffer from a removal rate $d_i$, which accounts for both natural mortality and harvesting. We account for prey mortality in their carrying capacity $K$ and maximum per capita growth rate $r$ and assume the prey species are not subject to harvesting.

Parameter values were obtained from the available literature on lionfish and grouper, with prey carrying capacity $K$ derived from other parameters and assumed grouper–prey equilibrium populations. Details of the derivation are provided in Appendix A.

| Parameter | | Units | Estimate | Reference |
|---|---|---|---|---|
| $a_1 R$ | Per capita prey predation rate of $P_1$ | $(P_1 \times \text{yr})^{-1}$ | 0.05 | Estimated |
| $b_1 P_2$ | Per capita intraguild predation rate of $P_1$ | $(P_1 \times \text{yr})^{-1}$ | 0.000897 | [20, 28] |
| $c_1$ | Biomass conversion factor of $P_1$ | $P_1 \times R^{-1}$ | 0.02 | Estimated |
| $d_1$ | Removal rate of $P_1$ | $\text{yr}^{-1}$ | 0.22 – 0.72 | [4, 17] |
| $m_1$ | Mass scaling factor of $P_1$ | $R \times P_1^{-1}$ | 110.625 | [7, 8, 20, 28] |
| $a_2 R$ | Per capita prey predation rate of $P_2$ | $(P_2 \times \text{yr})^{-1}$ | 0.045 | [5, 17] |
| $b_2 P_1$ | Per capita intraguild predation rate of $P_2$ | $(P_2 \times \text{yr})^{-1}$ | 0.00269 – 0.00375 | [7] |
| $c_2$ | Biomass conversion factor of $P_2$ | $P_2 \times R^{-1}$ | 0.0175 | [5, 17] |
| $d_2$ | Removal rate of $P_2$ | $\text{yr}^{-1}$ | 0.22 – 0.72 | [17] |
| $m_2$ | Mass scaling factor of $P_2$ | $R \times P_2^{-1}$ | 6.77 | [8, 28, 33] |
| $r$ | Maximum prey growth rate | $\text{yr}^{-1}$ | 0.447 | [5] |
| $K$ | Prey carrying capacity | $R$ | 1056 | [17] |

**Table 1:** Parameter definitions, units, and values in our model. Ranges on $d_1$ and $d_2$ represent varying rates of harvesting from 0 to 0.5. Ranges on $b_2$ signify uncertainty in our estimate as serranids may learn or be taught to consume lionfish [2].

We close this section by noting that in the case that $b_2 = 0$ (i.e. $P_2$ does not prey on $P_1$), our model (1) simplifies to the asymmetric Lotka-Volterra IGP model proposed by Holt and Polis (1997) [14]. The IGpredator species consumes both prey and the IGprey species, which may consume only prey. Assuming Holling type I responses and logistic growth in the prey results in the system

$$\begin{aligned}
\frac{dP}{dt} &= P(b'a'R + \beta\alpha N - m'),\\
\frac{dN}{dt} &= N(abR - m - \alpha P),\\
\frac{dR}{dt} &= R(r(1 - R/K) - aN - a'P),
\end{aligned}$$

where the IGpredator $P$ is $P_1$, the IGprey $N$ is $P_2$, and $R$ is the resource species. This implies the parameter substitutions

$$a = a_2,\ a' = a_1,\ b = c_2,\ b' = c_1,\ m = d_2,\ m' = d_1,\ \alpha = b_1,\ \beta = c_1 m_2,$$

where $r$ and $K$ represent the same quantities in the logistic growth of the prey.

This model has five equilibria: trivial, coexistence, prey-only, IGpredator and prey, and IGprey and prey. Holt and Polis summarize the biological requirements for their existence and stability, and discuss similarities and contradictions between these conditions. The coexistence equilibrium is found to exhibit limit cycles when unstable, with cycles of increasing magnitude farther away from the stability threshold. Thus, although coexistence is mathematically predicted, these oscillations would likely result in extinction of one or more species due to natural population fluctuations.

## 3 Model Analysis

The analysis of the system (1) is greatly simplified by nondimensionalization. Let $P_1 = \frac{r}{a_1}x$, $P_2 = \frac{r}{a_2}y$, $R = Kz$, and $t = \frac{1}{r}\tau$. Then

$$\begin{aligned}
\frac{dx}{d\tau} &= x\left[\frac{c_1a_1K}{r}z + \left(\frac{c_1b_1m_2}{a_2} - \frac{b_2}{a_2}\right)y - \frac{d_1}{r}\right], \\
\frac{dy}{d\tau} &= y\left[\frac{c_2a_2K}{r}z + \left(\frac{c_2b_2m_1}{a_1} - \frac{b_1}{a_1}\right)x - \frac{d_2}{r}\right], \\
\frac{dz}{d\tau} &= z\left[1 - x - y - z\right].
\end{aligned}$$

The remaining parameters can be grouped into dimensionless nonnegative constants,

$$\begin{aligned}
A_1 &= \frac{c_1a_1K}{r}, & A_2 &= \frac{c_1b_1m_2}{a_2}, & A_3 &= \frac{b_2}{a_2}, & A_4 &= \frac{d_1}{r}, \\
A_5 &= \frac{c_2a_2K}{r}, & A_6 &= \frac{c_2b_2m_1}{a_1}, & A_7 &= \frac{b_1}{a_1}, & A_8 &= \frac{d_2}{r}.
\end{aligned} \tag{2}$$

The parameters $A_1$ and $A_5$ represent the per capita increase in $x$ and $y$ respectively due to consumption of $z$, while $A_2$ and $A_6$ represent the same due to intraguild consumption of $y$ and $x$ respectively. Mortality for $x$ and $y$ is caused by IGP at per capita rates $A_3$ and $A_7$ respectively, and by natural death or harvesting at rates $A_4$ and $A_8$.

This gives the dimensionless system

$$\frac{dx}{d\tau} = x\left[A_1z + (A_2 - A_3)y - A_4\right], \tag{3a}$$

$$\frac{dy}{d\tau} = y\left[A_5z + (A_6 - A_7)x - A_8\right], \tag{3b}$$

$$\frac{dz}{d\tau} = z\left[1 - x - y - z\right]. \tag{3c}$$

As was determined for the asymmetric IGP model [14], the symmetric IGP system has five possible equilibria, denoted $E_i = (x, y, z)$ for $i = 0, 1, 2, 3, 4$:

$$\begin{aligned}
E_0 &= (0,0,0), & E_3 &= \left(0, 1 - \frac{A_8}{A_5}, \frac{A_8}{A_5}\right), \\
E_1 &= (0,0,1), & E_4 &= (x^*, y^*, z^*), \\
E_2 &= \left(1 - \frac{A_4}{A_1}, 0, \frac{A_4}{A_1}\right),
\end{aligned}$$

where

$$x^* := \frac{X}{D} = \frac{B_1(A_5 - A_8) + A_1A_8 - A_4A_5}{A_5B_1 + A_1B_2 - B_1B_2}, \tag{4a}$$

$$y^* := \frac{Y}{D} = \frac{B_2(A_1 - A_4) + A_4A_5 - A_1A_8}{A_5B_1 + A_1B_2 - B_1B_2}, \tag{4b}$$

$$z^* := \frac{Z}{D} = \frac{A_4B_2 + A_8B_1 - B_1B_2}{A_5B_1 + A_1B_2 - B_1B_2}, \tag{4c}$$

and

$$B_1 = A_2 - A_3 \quad \text{and} \quad B_2 = A_6 - A_7.$$

$B_1$ and $B_2$ represent the net benefit or loss caused by IGP on predators 1 and 2 respectively. A positive value indicates that the reproductive benefit of predation on the other species outweighs the mortality caused by predation by that species. A negative value indicates the converse.

In theory, symmetric IGP allows both predators to coexist in the absence of the prey species, since they can both feed on each other. However, this equilibrium, $\left(\frac{A_8}{B_2}, \frac{A_4}{B_1}, 0\right)$, only exists if $B_1, B_2 > 0$, which implies

$$(c_1 m_2)(c_2 m_1) > 1. \tag{5}$$

The quantities in parentheses represent the conversion of grouper into lionfish and lionfish into grouper respectively. However, biomass conversion efficiency cannot be equal to or greater than 1, as this would imply no waste in energy use and all energy devoted to reproduction. Therefore, it is biologically impossible for this inequality to be satisfied, and therefore, this equilibrium cannot exist.

In order to analyze the stability of the five equilibria, we determine the Jacobian of the rescaled system (3), which is

$$\mathcal{J}(x,y,z) := \begin{bmatrix} A_1 z + B_1 y - A_4 & B_1 x & A_1 x \\ B_2 y & A_5 z + B_2 x - A_8 & A_5 y \\ -z & -z & 1 - x - y - 2z \end{bmatrix}. \tag{6}$$

We now begin a detailed feasibility and stability analysis of the five equilibria.

### 3.1 Trivial Equilibrium

The trivial equilibrium $E_0 = (0,0,0)$ always exists. We evaluate the Jacobian (6) at the trivial equilibrium and obtain

$$\mathcal{J}(E_0) = \begin{bmatrix} -A_4 & 0 & 0 \\ 0 & -A_8 & 0 \\ 0 & 0 & 1 \end{bmatrix},$$

which has eigenvalues $-A_4, -A_8$ and 1. Since $E_0$ has both negative and positive eigenvalues, it is a saddle point. However, when restricted to the invariant $xy$ plane, both eigenvalues are negative, indicating stability.

Biologically, $E_0$ represents the extinction of all three classes; it is unstable because the prey is able thrive without the presence of predators.

A phase diagram of the case $z = 0$ is illustrated in Figure 2.

### 3.2 Prey Equilibrium

Equilibrium $E_1 = (0,0,1)$ is always feasible. The Jacobian at this equilibrium is

$$\mathcal{J}(E_1) = \begin{bmatrix} A_1 - A_4 & 0 & 0 \\ 0 & A_5 - A_8 & 0 \\ -1 & -1 & -1 \end{bmatrix},$$

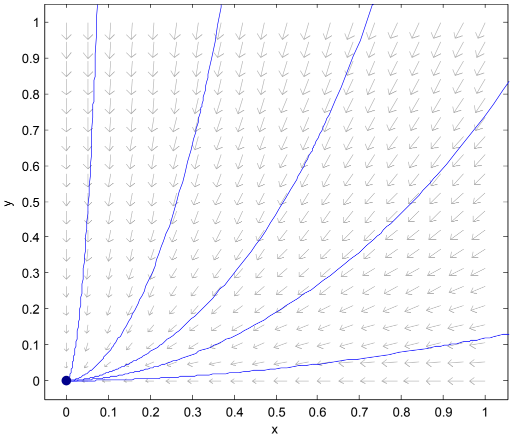

**Figure 2:** Phase portrait of the system in the $z = 0$ plane. The only equilibrium is the trivial equilibrium $E_0$, which is globally asymptotically stable.

which has eigenvalues $A_1 - A_4, A_5 - A_8$, and $-1$. The third eigenvalue indicates stability with respect to perturbations in prey population, as is expected for logistic growth. Stability of this equilibrium depends on the first two eigenvalues, i.e. we must have $A_1 < A_4$ and $A_5 < A_8$. In terms of our original parameters (2), this is

$$c_1 a_1 K < d_1 \quad \text{and} \quad c_2 a_2 K < d_2.$$

Biologically, this condition prevents either predator species from invading the equilibrium, since their death rate would exceed their maximum birth rate due to eating only prey.

### 3.3 Predator 1 and Prey Equilibrium

Equilibrium $E_2 = \left(1 - \frac{A_4}{A_1}, 0, \frac{A_4}{A_1}\right)$ exists if $A_1 > A_4$, i.e. $c_1 a_1 K > d_1$. From Section 3.2, this indicates that Predator 1 would be able to invade the prey-only equilibrium $E_1$, since its maximum growth rate due eating resource only would be larger than its death rate.

The Jacobian evaluated at this equilibrium is

$$\mathcal{J}(E_2) = \begin{bmatrix} 0 & \dfrac{B_1(A_1 - A_4)}{A_1} & A_1 - A_4 \\ 0 & \dfrac{B_2(A_1 - A_4) + A_4 A_5 - A_1 A_8}{A_1} & 0 \\ -\dfrac{A_4}{A_1} & -\dfrac{A_4}{A_1} & -\dfrac{A_4}{A_1} \end{bmatrix},$$

with eigenvalues

$$-\frac{A_4 \pm \Delta_{E_2}}{2A_1}, \quad \frac{B_2(A_1 - A_4) + A_4 A_5 - A_1 A_8}{A_1},$$

where

$$\Delta_{E_2} = \sqrt{A_4^2 - 4A_1 A_4 (A_1 - A_4)}.$$

If this equilibrium exists, then $A_1 - A_4 > 0$, so $A_4 > \Delta_{E_2}$, assuring the first two eigenvalues have negative real part. Stability of this equilibrium depends on the third eigenvalue, which can be written as $\frac{Y}{A_1}$, where $Y$ is defined as in (4b). This is negative if

$$Y < 0. \tag{7}$$

To derive a biological interpretation of (7), we rewrite it in terms of the original parameters to obtain the stability condition

$$\left(\frac{c_1 a_1 K - d_1}{r}\right)\left(\frac{c_2 m_1 b_2 - b_1}{a_1}\right) < \frac{c_1 a_1 K d_2}{r^2} - \frac{c_2 a_2 K d_1}{r^2},$$
$$\frac{r}{a_1 d_2}\left(\frac{c_1 a_1 K}{d_1} - 1\right)(c_2 m_1 b_2 - b_1) < \frac{c_1 a_1 K}{d_1} - \frac{c_2 a_2 K}{d_2}.$$

For ease of interpretation, we set $d = d_1 = d_2$ and assume $r = a_1 d$ in order to make the scaling factor 1. This gives

$$(c_1 a_1 K - d)(c_2 m_1 b_2 - b_1) < c_1 a_1 K - c_2 a_2 K.$$

This implies that the difference in maximum birth rates of $P_1$ and $P_2$ due to prey consumption (i.e. the difference in their utilization of the prey) must be greater than the maximum net growth rate of $P_1$ multiplied by the benefit of IGP for $P_2$. This latter quantity represents the maximum predation rate of $P_2$ on $P_1$, reduced by the mortality rate of the former.

### 3.4 Predator 2 and Prey Equilibrium

The equilibrium $E_3 = \left(0, 1 - \frac{A_8}{A_5}, \frac{A_8}{A_5}\right)$ exists if $A_5 > A_8$, i.e. $c_2 a_2 K > d_2$. Analogously to the interpretation in Section 3.3, this indicates that populations of Predator 2 can invade $E_1$ and stabilize at $E_3$.

The Jacobian evaluated at $E_3$ is

$$\mathcal{J}(E_3) = \begin{bmatrix} \dfrac{B_1(A_5 - A_8) + A_1 A_8 - A_4 A_5}{A_5} & 0 & 0 \\ \dfrac{B_2(A_5 - A_8)}{A_5} & 0 & A_5 - A_8 \\ -\dfrac{A_8}{A_5} & -\dfrac{A_8}{A_5} & -\dfrac{A_8}{A_5} \end{bmatrix},$$

The eigenvalues are

$$-\frac{A_8 \pm \Delta_{E_3}}{2A_5}, \quad \frac{B_1(A_5 - A_8) + A_1 A_8 - A_4 A_5}{A_5},$$

where

$$\Delta_{E_3} = \sqrt{A_8^2 - 4A_5 A_8 (A_5 - A_8)}.$$

As in the previous case, existence of $E_3$ implies that the first two eigenvalues have negative real part. Stability of this equilibrium depends on the third eigenvalue, which can be written as $\frac{X}{A_5}$, where $X$ is defined as in (4a). This is negative if

$$X < 0. \tag{8}$$

This has an interpretation analogous to that given for the condition (7): $P_2$'s superiority in prey utilization must be greater than the maximum predation rate of $P_1$ on $P_2$, reduced by the mortality rate of the former.

### 3.5 Coexistence Equilibrium

$E_4$ is the three-species coexistence equilibrium. Its components are obtained by solving the linear system that results from (3),

$$\begin{bmatrix} 0 & B_1 & A_1 \\ B_2 & 0 & A_5 \\ -1 & -1 & -1 \end{bmatrix} \begin{bmatrix} x^* \\ y^* \\ z^* \end{bmatrix} = \begin{bmatrix} A_4 \\ A_8 \\ -1 \end{bmatrix}, \tag{9}$$

for $x^*$, $y^*$, and $z^*$. This gives the components in (4).

**Theorem 1.** *If the equilibrium components defined in* (4) *are positive, then the coexistence equilibrium exists and is unique.*

*Proof.* Assuming $x^*$, $y^*$, $z^* > 0$, then $X$, $Y$, $Z$, and $D$ must have the same sign. Since the determinant of the matrix in the system (9) is $D$, it is not zero, so the system is nonsingular. Therefore, it has a unique solution which is the coexistence equilibrium $E_4$. ☐

Further examination of the requirements for existence of $E_4$ shows two cases in which $z^* := \frac{Z}{D}$ is positive:

(A1) $Z, D > 0$

(A2) $Z, D < 0$

Assuming one of these cases to hold, then from (3a) and (3b), it follows that

$$x^* = \frac{A_8 - A_5 z^*}{B_2} \quad \text{and} \quad y^* = \frac{A_4 - A_1 z^*}{B_1}. \tag{10}$$

The quantities $A_8 - A_5 z^*$ and $A_4 - A_1 z^*$ represent the respective growth rate of Predators 1 and 2 at equilibrium, assuming no IGP occurs and they are dependent solely on the prey species. The quantities $B_1$ and $B_2$ represent the net benefit (if positive) or loss (if negative) that IGP causes for Predators 1 and 2 respectively.

Note that we cannot have both $B_1 > 0$ and $B_2 > 0$, as this would imply the contradiction (5). Therefore, assuming $z^* > 0$ by either (A1) or (A2) being satisfied, there are three possible cases for existence of $E_4$:

(B1) $B_1, B_2 < 0,\ \frac{A_4}{A_1} < z^*,\ \frac{A_8}{A_5} < z^*$
Neither predator benefits from IGP and both depend on the prey species.
As a consequence of $B_1, B_2 < 0$, it follows from (4c) that $Z$ must be negative, and so by existence, $X, Y, D < 0$.

(B2) $B_1 < 0 < B_2,\ \frac{A_4}{A_1} < z^*,\ \frac{A_8}{A_5} > z^*$
Predator 2 benefits from IGP and cannot be maintained by the prey species alone, while Predator 1 suffers from IGP and depends on the prey species.

(B3) $B_2 < 0 < B_1,\ \frac{A_4}{A_1} > z^*,\ \frac{A_8}{A_5} < z^*$
Predator 1 benefits from IGP and cannot be maintained by the prey species alone, while Predator 2 suffers from IGP and depends on the prey species.

The cases (B2) and (B3) are analogous and simply reverse the roles of Predator 1 and Predator 2 in the system.

Now that the conditions for its existence have been expressed, we consider the stability of $E_4$.

**Theorem 2.** *$E_4$ is locally asymptotically stable iff $D > 0$ and*

$$A_1\left(\frac{Z}{Y} - B_2\right) + A_5\left(\frac{Z}{X} - B_1\right) > 0.$$

*Proof.* From (10) and the fact that $1 - x^* - y^* - z^* = 0$, which follows from (3c), the Jacobian evaluated at the coexistence equilibrium is

$$\mathcal{J}_4 := \mathcal{J}(E_4) = \begin{bmatrix} 0 & B_1x^* & A_1x^* \\ B_2y^* & 0 & A_5y^* \\ -z^* & -z^* & -z^* \end{bmatrix}.$$

$\mathcal{J}_4$ is used to implement the Routh-Hurwitz criterion, which is necessary and sufficient to determine the equilibrium's stability. This requires $w_1, w_2, w_3, w_4 > 0$, where the quantities are defined as

$$\begin{aligned} w_1 &= -\det(\mathcal{J}_4), \\ &= x^*y^*z^*(A_5B_1 + A_1B_2 - B_1B_2) \\ &= x^*y^*z^*D, \\ w_2 &= -\text{trace}(\mathcal{J}_4), \\ &= z^* > 0, \\ w_3 &= M_{11} + M_{22} + M_{33}, \\ &= z^*(A_1x^* + A_5y^*) - B_1B_2x^*y^*, \\ w_4 &= w_2w_3 - w_1, \\ &= z^*\left[z^*(A_1x^* + A_5y^*) - x^*y^*(A_1B_2 + A_5B_1)\right], \\ &= \frac{XYZ}{D^3}\left[A_1\left(\frac{Z}{Y} - B_2\right) + A_5\left(\frac{Z}{X} - B_1\right)\right], \end{aligned}$$

where $M_{ii}$ is the $(i,i)$ minor of matrix $\mathcal{J}_4$.

Due to the structure of $\mathcal{J}_4$, the stability of $E_4$ depends only on $w_1, w_4 > 0$. It is obvious that $w_2 > 0$ is implied by existence. The inequality $w_4 > 0$ implies

$$A_5y^*z^* + A_1x^*z^* > A_1B_2x^*y^* + A_5B_1x^*y^*,$$

and since $w_1 > 0$ implies

$$A_1B_2x^*y^* + A_5B_1x^*y^* > B_1B_2x^*y^*,$$

it follows that

$$A_5 y^* z^* + A_1 x^* z^* > B_1 B_2 x^* y^*.$$

This is exactly the condition $w_3 > 0$. Therefore, stability requires only $w_1, w_4 > 0$. Assuming existence, $w_1 > 0$ if and only if $D > 0$. The condition $w_4 > 0$ is equivalent to

$$A_1 \left( \frac{Z}{Y} - B_2 \right) + A_5 \left( \frac{Z}{X} - B_1 \right) > 0.$$

□

Since the numerators and denominators of the equilibrium components $x^*$, $y^*$, and $z^*$ must have the same sign, the following must be true for stability:

$$X, Y, Z, D > 0. \tag{11}$$

Note that (11) contradicts the existence case (A2). Similarly, if the case (B1) holds, then $Z, D < 0$, which implies instability. Therefore, stability is only possible if (A1) holds and either (B2) or (B3) holds. In this case, $X, Y > 0$ is needed in order to satisfy $w_1 > 0$.

### 3.6 Discussion of Existence and Stability Conditions

The conditions for existence and stability of each equilibrium are summarized in Table 2. These results indicate a number of possible combinations of equilibrium dynamics.

| Eq. | Existence | Stability |
|---|---|---|
| $E_0$ | always | never |
| $E_1$ | always | $A_1 < A_4$ and $A_5 < A_8$ |
| $E_2$ | $A_1 > A_4$ | $Y < 0$ |
| $E_3$ | $A_5 > A_8$ | $X < 0$ |
| $E_4$ | $X, Y, Z, D > 0$ or<br>$X, Y, Z, D < 0$ | $X, Y, Z, D > 0$ and<br>$A_1 \left( \frac{Z}{Y} - B_2 \right) + A_5 \left( \frac{Z}{X} - B_1 \right) > 0$ |

**Table 2:** Summary of conditions for existence and stability.

Three conclusions relating the dynamics of the boundary equilibria to those of the coexistence equilibrium follow from these results.

**Theorem 3.** *If either $E_2$ or $E_3$ exist, then $E_1$ is unstable.*

*Proof.* Stability of $E_1$ requires $A_1 < A_4$ and $A_5 < A_8$. However, this exactly contradicts the existence conditions for $E_2$ and $E_3$ respectively. Therefore, $E_1$ cannot be stable if either $E_2$ or $E_3$ exist. □

**Theorem 4.** *If $E_2$ and $E_3$ exist simultaneously, then they must both have the same stability in order for $E_4$ to exist.*

*Proof.* Suppose both $E_2$ and $E_3$ exist. If $E_2$ is stable and $E_3$ is unstable, then $X > 0$ and $Y < 0$. This implies $\frac{X}{D}$ and $\frac{Y}{D}$ have opposite signs; thus, at least one of the components of $E_4$ is negative, implying $E_4$ does not exist. An analogous argument holds for the case $E_2$ unstable and $E_3$ stable. □

**Theorem 5.** *If at least one of the boundary equilibria $E_2$ and $E_3$ is stable, then $E_4$ cannot be stable. That is, stability of $E_4$ prevents stability of $E_2$ and $E_3$.*

*Proof.* If $E_2$ is stable, then $Y < 0$. If $E_3$ is stable, then $X < 0$. In either case, existence of $E_4$ then implies that $X, Y, Z, D < 0$. However, this contradicts the stability condition $w_1$. The backwards direction is evident. □

In addition, we can prove the existence of a Hopf bifurcation. We first present a lemma on the roots of a special cubic polynomial.

**Lemma 1.** *If $B > 0$ and $C = AB$, then the polynomial $\lambda^3 + A\lambda^2 + B\lambda + C = 0$ has the root $-A$ and a pair of purely imaginary roots $\pm\sqrt{B}i$.*

*Proof.* Assuming $C = AB$, we have

$$\begin{gathered}
\lambda^3 + A\lambda^2 + B\lambda + AB = 0 \\
(\lambda + A)\lambda^2 + (\lambda + A)B = 0 \\
(\lambda + A)(\lambda^2 + B) = 0
\end{gathered}$$

This implies $\lambda_1 = -A$ and $\lambda_{2,3} = \pm\sqrt{B}i$. □

**Theorem 6.** *Let $\epsilon = (D + B_1B_2)x^*y^* - z^*(A_1x^* + A_5y^*)$ and assume $E_4$ exists and $D > 0$. Then $E_4$ is locally asymptotically stable if $\epsilon < 0$. If $\epsilon > 0$, then $E_4$ is unstable and a stable limit cycle appears.*

*Proof.* The characteristic equation in the eigenvalues of $E_4$ is

$$\lambda^3 + z^*\lambda^2 + \left[z^*(A_1x^* + A_5y^*) - B_1B_2x^*y^*\right]\lambda - Dx^*y^*z^* = 0. \tag{12}$$

We set $w_4 = -z^*\epsilon$, which implies the definition

$$\epsilon = (D + B_1B_2)x^*y^* - z^*(A_1x^* + A_5y^*). \tag{13}$$

Then we can express $z^*$ in terms of $\epsilon$,

$$z^* = \frac{(D + B_1B_2)x^*y^* - \epsilon}{A_1x^* + A_5y^*} := f(\epsilon).$$

Rewrite (13) as

$$z^*(A_1x^* + A_5y^*) - B_1B_2x^*y^* = Dx^*y^* - \epsilon.$$

The characteristic equation (12) can then be written as

$$\lambda^3 + f(\epsilon)\lambda^2 + (Dx^*y^* - \epsilon)\lambda - Dx^*y^*f(\epsilon) = 0.$$

We will use $\epsilon$ as the bifurcation parameter. In the case that $\epsilon = 0$, we have

$$\lambda^3 + f(0)\lambda^2 + Dx^*y^*\lambda - Dx^*y^*f(0) = 0.$$

From Lemma 1, this has one negative root $\lambda_1 = -f(0)$ and a pair of purely imaginary roots $\lambda_{2,3} = \pm\sqrt{Dx^*y^*}$. If $\epsilon < 0$, then we have $w_4 > 0$, so $E_4$ is stable and all eigenvalues have negative real part. If $\epsilon > 0$, then we have $w_4 < 0$, so $E_4$ is unstable and $\lambda_{2,3}$ have positive real part.

If $\epsilon \neq 0$, let the eigenvalues be denoted $\lambda = a(\epsilon) + b(\epsilon)i$, with $a(0) = 0$ and $b(0) = \sqrt{Dx^*y^*} \neq 0$. To show a Hopf bifurcation occurs, we further need to show that the condition

$$\frac{da(\epsilon)}{d\epsilon}\Big|_{\epsilon=0} = a'(0) \neq 0,$$

is satisfied. We implicitly differentiate the characteristic equation with respect to $\epsilon$ to obtain

$$3\lambda^2\lambda' + f'(\epsilon)\lambda^2 + 2f(\epsilon)\lambda\lambda' - \lambda + (Dx^*y^* - \epsilon)\lambda' - Dx^*y^*f'(\epsilon) = 0,$$

and evaluate it at $\epsilon = 0$, giving

$$3\lambda^2\lambda' + f'(0)\lambda^2 + 2f(0)\lambda\lambda' - \lambda + Dx^*y^*\lambda' - Dx^*y^*f'(0) = 0.$$

We know $\lambda(0) = b(0)i$ and $\lambda^2(0) = -b^2(0) = -Dx^*y^*$. Since $\lambda'(0) = a'(0) + b'(0)i$, we have

$$\begin{aligned} -3Dx^*y^*\big[a'(0) + b'(0)i\big] - f'(0)Dx^*y^* + 2f(0)b(0)\big[a'(0)i - b'(0)\big] \\ -b(0)i + Dx^*y^*\big[a'(0) + b'(0)i\big] - Dx^*y^*f'(0) = 0. \end{aligned} \tag{14}$$

Setting the real terms of (14) equal to 0 and imaginary terms equal to 0 yields the system

$$\begin{aligned} -2Dx^*y^*a'(0) - 2f'(0)Dx^*y^* - 2f(0)b(0)b'(0) = 0, \\ -2Dx^*y^*b'(0) + 2f(0)b(0)a'(0) - b(0) = 0, \end{aligned}$$

which can be written in matrix form as

$$\begin{bmatrix} -2Dx^*y^* & -2f(0)b(0) \\ 2f(0)b(0) & -2Dx^*y^* \end{bmatrix} \begin{bmatrix} a'(0) \\ b'(0) \end{bmatrix} = \begin{bmatrix} 2f'(0)Dx^*y^* \\ b(0) \end{bmatrix}.$$

By Cramer's rule,

$$a'(0) = \frac{-4D^2(x^*y^*)^2f'(0) + 2f(0)b^2(0)}{4D^2(x^*y^*)^2 + 4f^2(0)b^2(0)}.$$

The denominator of $a'(0)$ is positive since its first term is positive and its second term is nonnegative. In order to have $a'(0) = 0$, we would need the numerator to be zero, which implies

$$\begin{aligned} f(0)b^2(0) - 2D^2(x^*y^*)^2f'(0) = 0, \\ Dx^*y^*z^* - 2D^2(x^*y^*)^2f'(0) > 0, \end{aligned}$$

Since $f'(0) = -\frac{1}{Ax^* + A_5y^*} < 0$, this is always positive. Therefore, $a'(0) \neq 0$. $\square$

We illustrate this theorem with two examples. Figure 3 shows a trajectory in the case that $E_2$ and $E_3$ are unstable but $E_4$ is stable. In this case, the solution trajectory to the coexistence equilibrium point. However, when $E_4$ becomes unstable, as shown in Figure 4, a limit cycle is born, which is due to the Hopf bifurcation. Similarly, the transition from Figure 5 to Figure 6 illustrates the existence of a Hopf bifurcation as $E_4$ becomes unstable while $E_2$ remains nonexistent and $E_3$ is unstable.

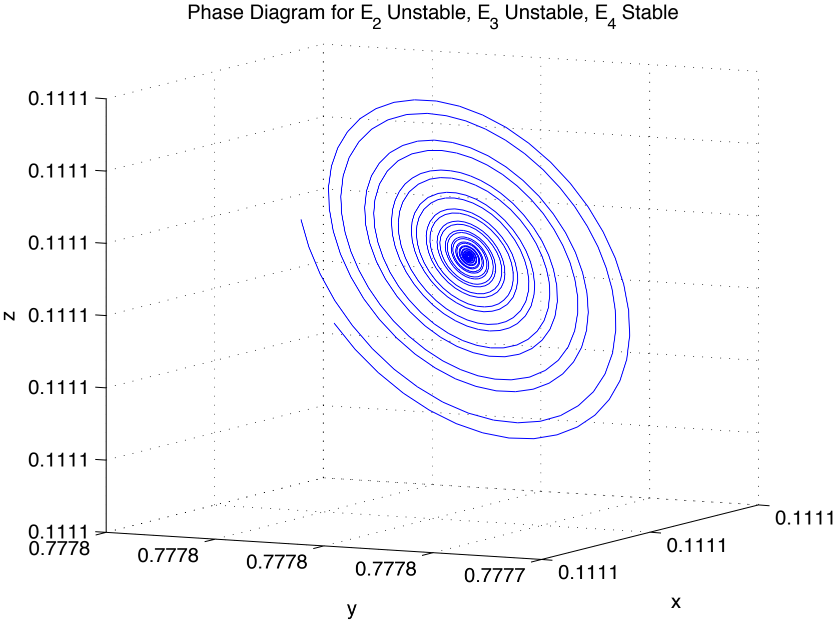

**Figure 3:** Two solutions spiral towards the stable coexistence equilibrium $E_4$. In this case, $E_1$, $E_2$, and $E_3$ and are unstable. Parameters used: $A_1 = 1.0, A_2 = 1.0, A_3 = 0.5, A_4 = 0.5, A_5 = 5.0, A_6 = 1.5, A_7 = 2.0, A_8 = 0.5$.

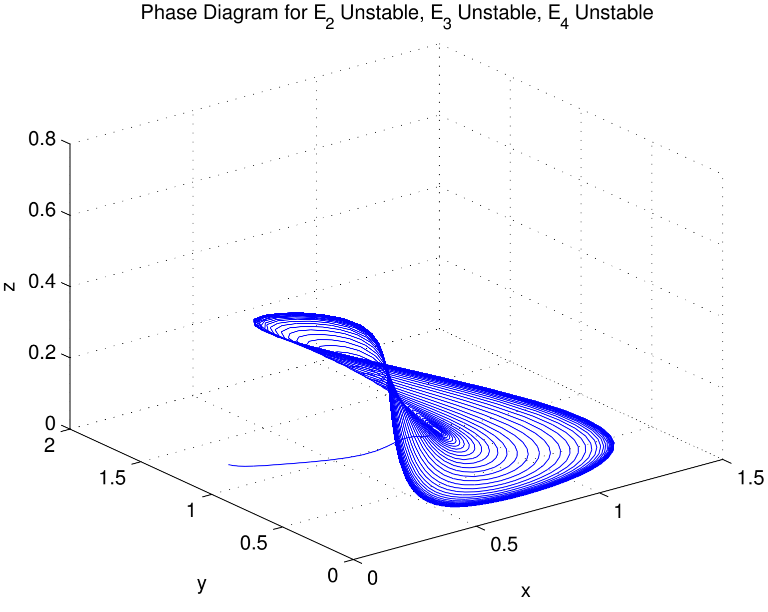

**Figure 4:** A stable limit cycle is born when $E_4$ becomes unstable. As in Figure 3, $E_1$, $E_2$, and $E_3$ are unstable. Parameters used: $A_1 = 1.0$, $A_2 = 1.5$, $A_3 = 0.5$, $A_4 = 0.5$, $A_5 = 5.0$, $A_6A = 0.8$, $A_7 = 2.0$, $A_8 = 0.5$.

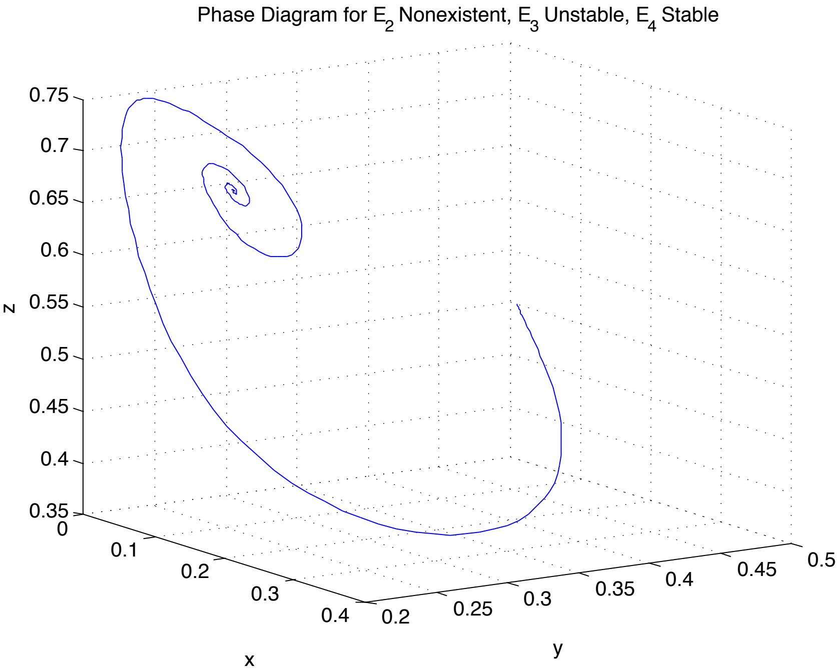

**Figure 5:** A solution spirals towards $E_4$ when stable. In this case, $E_1$ is unstable, $E_2$ is nonexistent, and $E_3$ is unstable. Parameters used: $A_1 = 1.0, A_2 = 5.0, A_3 = 0.1, A_4 = 2.0, A_5 = 0.2, A_6 = 1.5, A_7 = 2.0, A_8 = 0.1$.

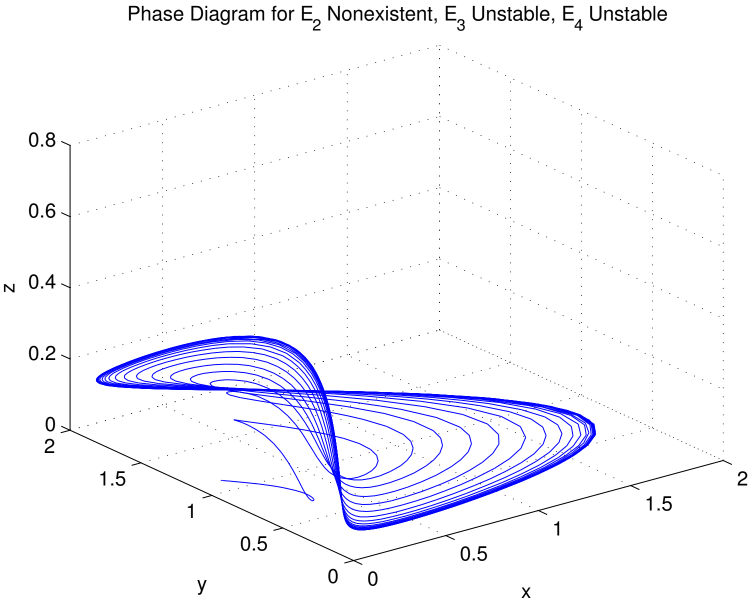

**Figure 6:** A stable limit cycle emerges when $E_4$ becomes unstable. As before, $E_1$ is unstable, $E_2$ is nonexistent, and $E_3$ is unstable. Parameters used: $A_1 = 1.0, A_2 = 5.0, A_3 = 0.1, A_4 = 3.0, A_5 = 2.0, A_6 = 1.0, A_7 = 3.0, A_8 = 0.1$.

# 4 Simulations

We use the `ode15s` ODE solver in MATLAB to simulate the model; the default `ode45` solver was not suitable for all cases due to stiffness of the system. To parametrize the model, we use the values in Table 1. Ranges are provided for parameters that we vary in our simulations. The key parameters of interest are $d_1$, $d_2$, and $b_2$, since our control methods are limited to increasing lionfish harvest, reducing grouper harvest, and increasing grouper predation on lionfish (e.g. by training them to consume lionfish as has been demonstrated in the Cayman Islands [2]). We also examine the case $b_1 = 0$ in order to examine the effects of discounting IGP from the system.

In our simulations, we consider three harvesting scenarios varying by region: the United States, the Bahamas, and the Exuma Cays Land and Sea Park (ECLSP) in the Bahamas. We assume Nassau grouper to be a representative serranid and extend their regional harvesting legislation to harvesting of the population $P_2$ in our model. In the USA, Nassau grouper fishing is prohibited at all times [29]. In most of the Bahamas, fishing is legal except during an annual closed season coinciding with the grouper's breeding period [3]. In the ECLSP, all fishing has been banned since 1986, resulting in a far more robust grouper population than in the rest of the Bahamas [3, 26]. We assume ECLSP grouper are at equilibrium with the prey population.

Our base simulation assumes no harvesting and median grouper predation on lionfish, with initial populations at the grouper and prey equilibrium, but with a founder population of two lionfish. As expected, the results show that lionfish are able to invade the system, with grouper and prey populations declining rapidly in the first years of the simulation.

We next consider more specific scenarios. Grouper predation on lionfish at our minimum calculated rate of $b_2 = 0.0026885$ with no harvesting on either species results in an unstable grouper population and stable lionfish population. Lionfish populations surpass grouper populations after 20.4 years. This may reflect the initial situation at ECLSP prior to the majority of grouper recognizing the lionfish as prey. Even assuming higher rates of grouper predation on lionfish, the minimum rate at which it would have to occur for coexistence (approximately $b_2 = 0.00387536$) is greater than the calculated maximum predation rate, $b_2 = 0.0037515$ (see Figure 7). For predation rates higher than an upper threshold of $b_2 = 0.00824755$, the lionfish population becomes unstable. A lower predation rate of $b_2 = 0.005168$. results in coexistence with equal-sized lionfish and grouper populations. Based on these simulations, we conclude that grouper can suppress or destroy lionfish populations if their IGP rate is sufficiently high.

Figure 8 illustrates the assumption of low predation ($b_2 = 0.0026885$) at the ECLSP, no grouper harvesting, but some lionfish harvesting (in the range $d_1 = 0.24167 - 0.2606$). Here, coexistence is possible. For higher levels of harvesting, the grouper–prey equilibrium becomes stable and the lionfish population becomes unstable.

In Figure 9, we consider the case without IGP and with no harvesting on either species. In this case, the lionfish population is stable while the grouper population dies out and becomes smaller than the lionfish population after 11 years. This suggests that groupers can suppress lionfish populations if both competitive and predatory effects are significant, but not if competition alone is the only interaction. If IGP is implemented in this scenario, then grouper decline is slowed, and increasing IGP rates on lionfish will eventually prevent invasion altogether.

In summary, for ECLSP, the model suggests that lionfish suppression is due to both predation and competition. Furthermore, provided that grouper predation on lionfish is increased beyond our estimated range, grouper will be an effective biocontrol of lionfish, able to minimize or eliminate their populations over time.

Finally, our simulations suggest that during the first years of a lionfish invasion, their populations may remain relatively stable. However, if interactions with lionfish case both grouper and prey populations to decline rapidly during this time, then lionfish populations will be able to rise.

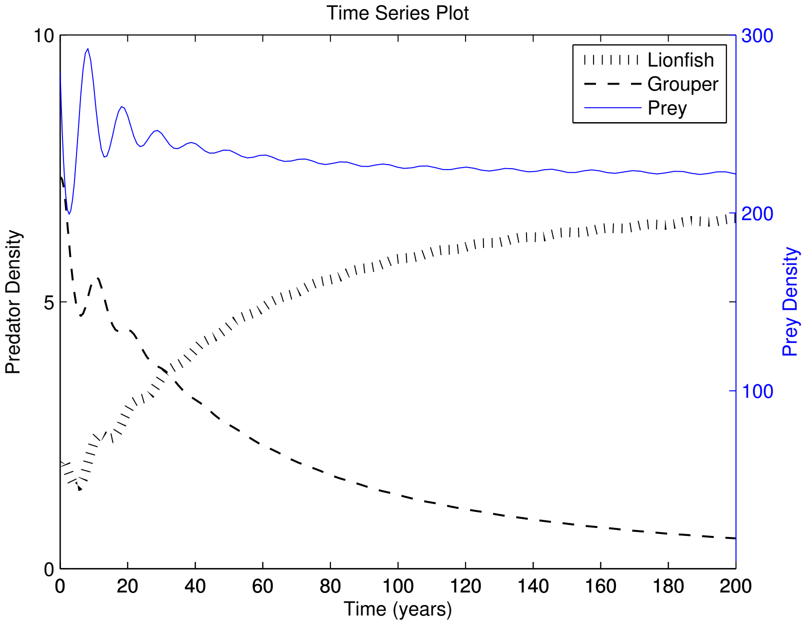

**Figure 7:** Low initial lionfish density with maximum estimated IGP ($b_2 = 0.0037515$) and no harvesting ($d_1 = d_2 = 0.22$). This may simulate ECLSP assuming grouper consistently predate on lionfish. IGP greatly slows the rate of lionfish takeover compared to Figure 9 but does not stop it.

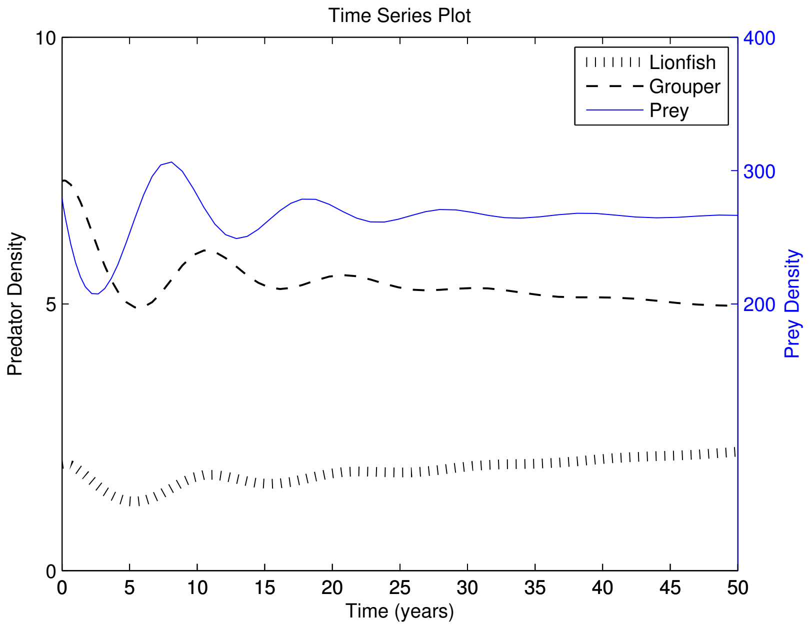

**Figure 8:** Low initial lionfish density with minimum calculated IGP ($b_2 = 0.0026885$), no harvesting on grouper ($d_2 = 0.22$), and slight harvesting on lionfish ($d_1 = 0.25$). This may simulate ECLSP if such harvesting is allowed.

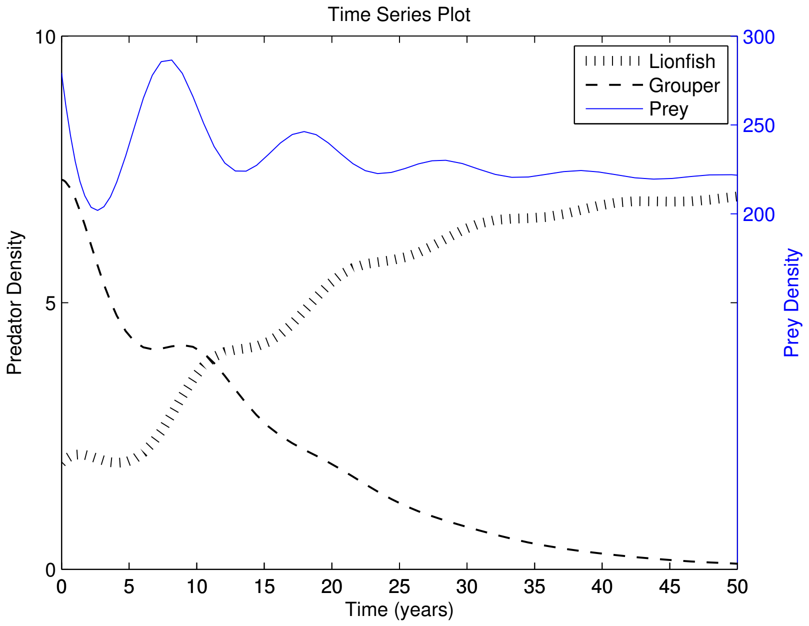

**Figure 9:** Low initial lionfish density with no IGP ($b_1 = b_2 = 0$) and no harvesting ($d_1 = d_2 = 0.22$). This may simulate ECLSP starting at the beginning of the lionfish invasion, assuming grouper never learn to consume lionfish and lionfish are negligible consumers of grouper.

We next suppose low grouper density at the beginning of the lionfish invasion. This may simulate areas in the western Atlantic where groupers have not yet recovered from past or current harvesting and so have not reached their equilibrium populations.

We assume our minimal calculated predation rate on lionfish ($b_2 = 0.0026885$) and examine two cases of grouper harvesting. First, we consider grouper overfishing ($d_2 = 0.6$) to be still occurring when the lionfish invade (as may be the case in the Bahamas [3]). Second, we examine the case where grouper harvesting is banned prior to the lionfish invasion (resulting in the natural mortality rate $d_2 = 0.22$). This case represents the east coast of the United States, where Nassau grouper fishing became illegal in 1992, but populations have not yet recovered [29].

The first case is illustrated in Figure 10, which shows an extremely rapid lionfish invasion, with groupers dying out after 5 years. The second case in Figure 14 demonstrates that lionfish are still able to surpass groupers, but do not replace them as coexistence will occur.

In these simulations, we assumed no lionfish harvesting, since the species was novel to the regions. This allowed lionfish to rapidly take over the groupers' niche. This supports the theory that grouper overfishing has allowed the lionfish invasion to be so successful.

Even with lionfish harvesting, their growth cannot be fully stopped. In Figure 11, we consider the extremely high lionfish removal rate of $d_1 = 0.72$ – which would require consistently thorough and effective harvesting – but even this is insufficient to stop lionfish population growth. However, reducing the grouper harvesting rate to $d_2 = 0.24167$, allows a threshold lionfish removal rate of $d_1 = 0.25$ which causes population coexistence, although grouper populations are extremely small (see Figure 12). Figure 13 demonstrates that elevating lionfish removal to $d_1 = 0.3$ is sufficient for eradication (albeit over a period of centuries), with both grouper and prey populations remaining stable (see 15). This decline would occur more rapidly for increased lionfish harvesting or decreased grouper harvesting.

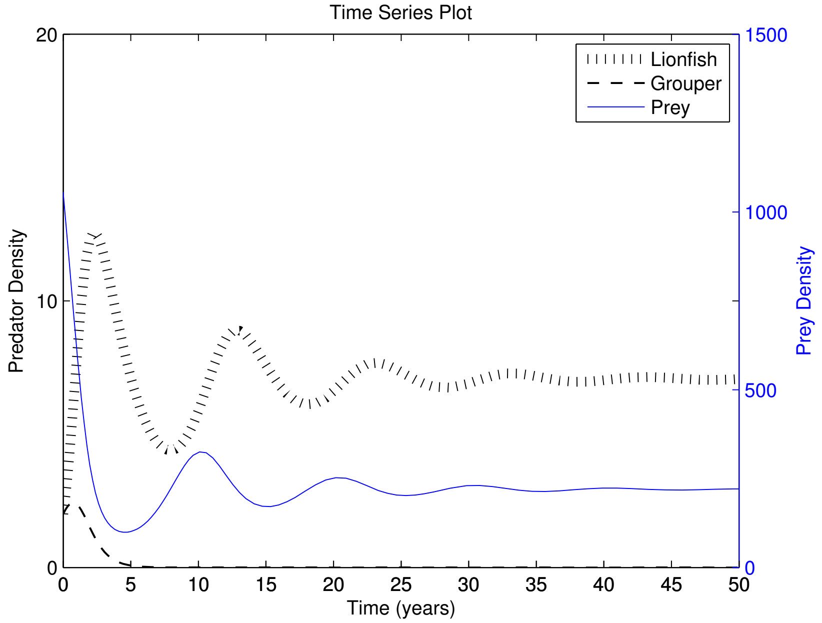

**Figure 10:** Low initial predator density with no harvesting and low predation on lionfish ($d_1 = 0.22$, $b_2 = .0026885$), and moderate fishing on grouper ($d_2 = 0.6$). This may reflect the Bahamas with grouper overfishing. Lionfish invasion and grouper extinction occur rapidly.

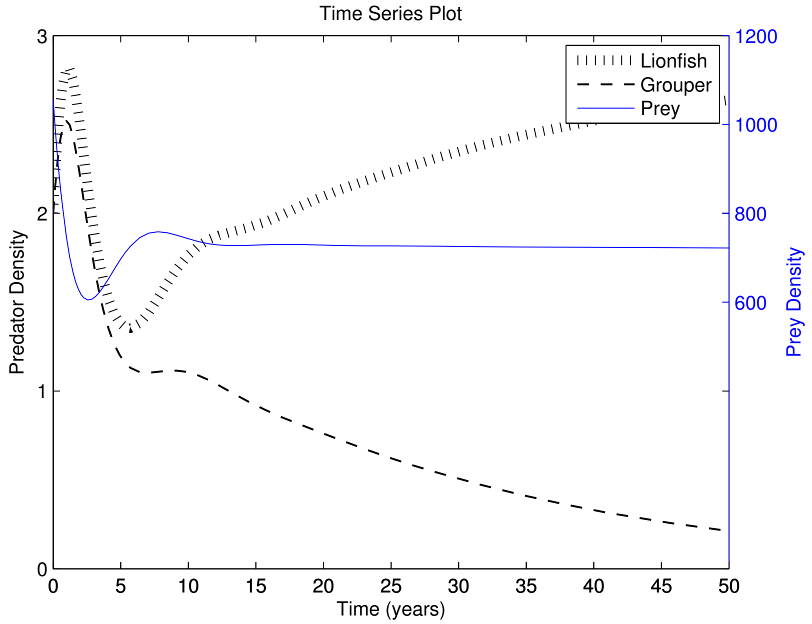

**Figure 11:** Low initial predator density with $b_2 = 0.0026885$. This may reflect the Bahamas, where despite high lionfish removal ($d_1 = 0.72$), continued grouper harvesting ($d_2 = 0.6$) allows lionfish to be successful. Notice that despite the initial decrease in lionfish population, they are still able to persist as the grouper population declines.

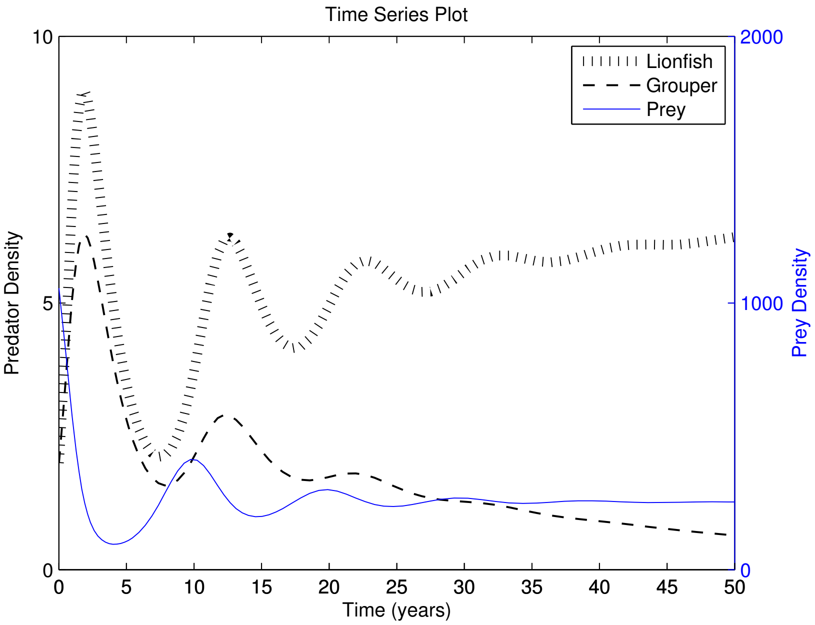

**Figure 12:** Low initial predator density with $b_2 = 0.0026885$, $d_1 = 0.25$, $d_2 = 0.2416$. This may reflect the Bahamas, where coexistence is possible with low harvesting of both species.

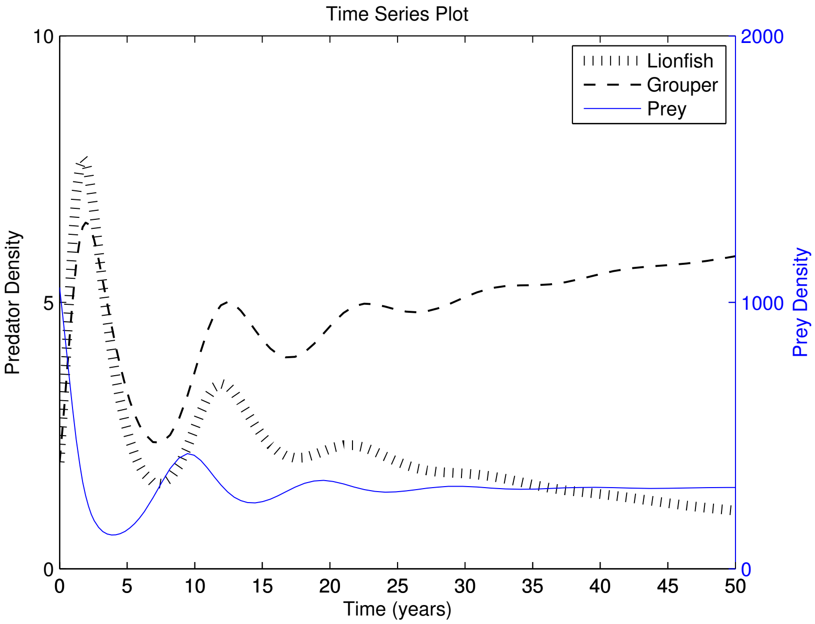

**Figure 13:** Low initial predator density with $b_2 = 0.0026885$, $d_1 = 0.3$, $d_2 = 0.22$. This may reflect the Bahamas, where lionfish may be able to be eradicated if they are harvested much faster than grouper.

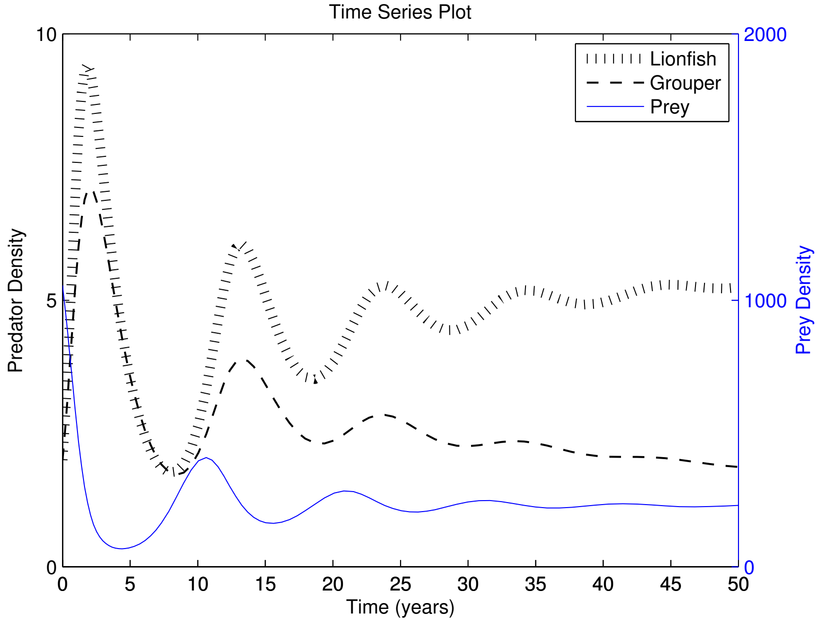

**Figure 14:** Low initial predator density with $b_2 = 0.0026885$, $d_1 = 0.22$, $d_2 = 0.22$. This may simulate the eastern coasts of the United States, where, at the initial stages of the invasion, harvesting of Nassau grouper was banned due to overfishing. With no harvesting on grouper, the lionfish can still invade, but coexistence is possible.

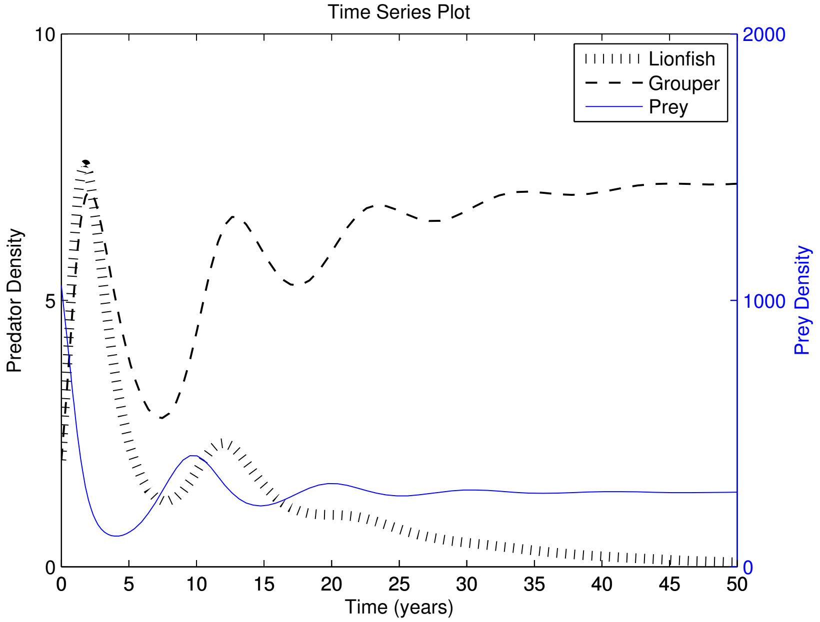

**Figure 15:** Low initial predator density with $d_1 = 0.22, b_2 = .0026885, d2 = 0.3$. This reflects the same scenario as in Figure 14 but with slight harvesting on lionfish. This is enough to drive the population to extinction over time.

# 5 Sensitivity Analysis

Sensitivity analysis is used to determine the parameters most influential on the outcome of a model. It is useful both to find the parameters that must be estimated most precisely and to determine which parameters should be altered to obtain a desired result.

In our case, we are interested in controlling lionfish populations. This could be accomplished by (1) preventing invasibility of the grouper-prey equilibrium $E_3$, (2) reducing the lionfish growth rate $P_1'$, or (3) ensuring the coexistence equilibrium $E_4$ exists and minimizing its $x$ component. As stated in Section 4, the parameters of interest are $d_1$, $d_2$, $b_1$, and $b_2$. The quantities of interest are the conditions $X, Y < 0$ that guarantee stability of the lionfish–prey and grouper-prey equilibria respectively (assuming their existence), the coexistence equilibrium values of $x$ and $y$, and the conditions $w_1$ and $w_4$ that guarantee stability of the coexistence equilibrium. These quantities

We determine the sensitivity $s_\rho$ of a quantity $Q$ to a parameter $\rho$ using the formula

$$s_\rho = \frac{\partial Q}{\partial \rho}.$$

This represents the reciprocal of the decrease in $\rho$ required to reduce $Q$ by 1, e.g. a sensitivity of $-30$ indicates that $\rho$ should be increased by $\frac{1}{30}$ to reduce $Q$ by 1. However, the importance of an additive change in a small parameter is very different than in a large parameter. Rather than comparing absolute changes, we convert the sensitivities to sensitivity indices or elasticities $e_\rho$, which compare percentage changes of parameters and values:

$$e_\rho = \left| \frac{\rho}{Q} \right| \frac{\partial Q}{\partial \rho}.$$

We use the absolute value of the scaling factor to maintain the original interpretation of positive and negative sensitivities. In our model, all parameters are positive; however, these parameters cause some quantities of interest to be negative, which would result in their elasticities having meaning opposite to that of the other elasticities. For consistency, we therefore use the magnitude of this factor rather than its signed value.

The resulting elasticities are displayed in Figure 16, with their computed values provided in Appendix B. Note that in all cases, $b_1$ and $d_2$ have the same sign, which is opposite to the sign shared by $b_2$ and $d_1$. These pairs of parameters are harmful to the grouper and lionfish populations respectively: increasing $b_1$ increases lionfish consumption of grouper (and thus grouper mortality) and increasing $d_2$ increases grouper natural mortality, while increasing $b_2$ increases lionfish consumption of grouper and increasing $d_1$ increases lionfish natural mortality.

Grouper conservation and lionfish suppression would imply $Y$ should be large (so $E_2$ is unstable and grouper are not ecologically replaced), $X$ should be small (so $E_3$ is stable and lionfish are unable to invade), $x^*$ representing lionfish coexistence density should be minimized, $y^*$ representing grouper coexistence density should be maximized, and both $w_1$ and $w_2$ should be large (to guarantee stability of the coexistence equilibrium). The analysis of $e_\rho$ suggests there is no simple way to adjust the parameters to meet these goals. Rather, conservation efforts may vary depending on the specific scenario.

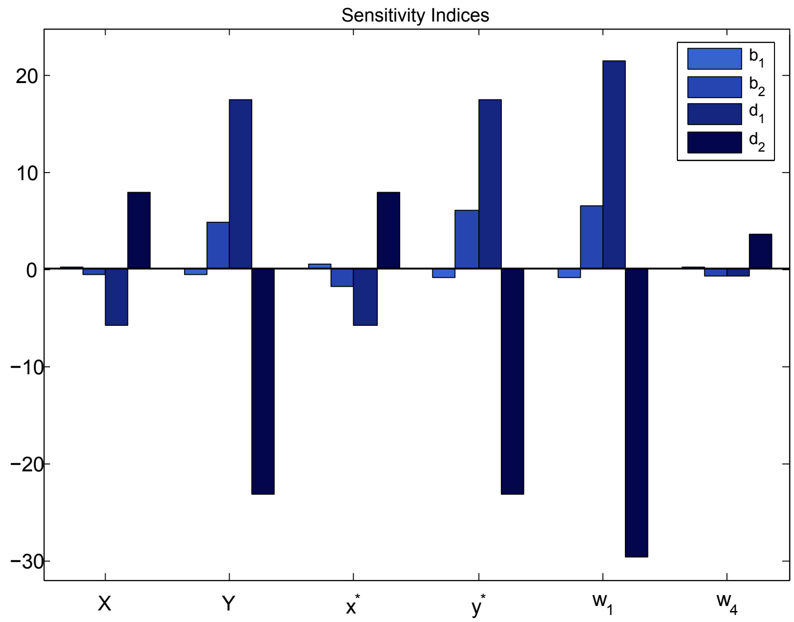

**Figure 16:** Sensitivity analysis of stability conditions for $E_2$ and $E_3$, the lionfish and grouper components of the coexistence equilibrium, and the stability condition for the coexistence equilibrium.

Our sensitivity analysis can be used to suggest methods for control in a specific region, depending on the current lionfish population. In regions currently without lionfish, our model suggests creating local stability of $E_3$ by reducing grouper mortality would be sufficient to prevent them from establishing. If lionfish are already established, then this would likely have no effect. Instead, the first objective should be to ensure instability of $E_2$, so lionfish do not completely replace grouper. Since complete eradication of lionfish is highly infeasible [4, 22], creating a stable coexistence equilibrium that sustains minimal populations of lionfish will ensure all populations coexist and grouper remain in relatively high density.

Finally, the elasticity analysis indicates that grouper mortality ($d_2$) is consistently the most influential parameter among those we examined. Based on this result, we conclude that lionfish suppression programs might better focus on grouper conservation than on lionfish harvest.

## 6 Discussion

The Indo-Pacific lionfish was introduced into the western Atlantic where it is devastating the native ecosystems. Lack of predation – due both to overfishing of native species and their unfamiliarity with lionfish – and abundance of prey – due to the prey's unfamiliarity with lionfish – have allowed the lionfish to flourish in its invaded habitat, to the detriment of native predators and prey.

Native grouper and lionfish likely compete for the same prey species and consume each other's young. This results in a symmetric IGP model of lionfish, grouper, and prey. We conducted a mathematical analysis of this model to show five biologically-possible equilibria: an unstable trivial equilibrium, a conditionally stable prey equilibrium, and three conditionally existent and conditionally stable equilibria: lionfish–prey, grouper–prey, and coexistence. We observed limit cycles formed from a Hopf bifurcation which implies that populations may never stabilize to fixed values. We explored the dynamics of this system numerically by varying parameters to simulate different existence and stability combinations. We proved some cases to be impossible and located a Hopf bifurcation.

Parameters were obtained from the literature and simulated a variety of cases of harvesting and IGP rates. This showed that grouper can serve as an effective lionfish biocontrol provided their predation rates on lionfish are sufficiently high and they are not subject to excessive harvesting. Our sensitivity analysis showed that grouper mortality is consistently more influential on key quantities in the model than is lionfish mortality.

Grouper conservation may be more effective than harvesting in terms of lionfish control. Their populations should be increased by ending grouper harvest in areas already invaded by lionfish and in areas at risk of invasion. If training grouper to consume lionfish is effective, we recommend doing this to improve the efficiency of grouper's lionfish control. Our model shows harvesting on lionfish can be effective, but since this is only effective as long as harvesting continues, natural biocontrol is a more ideal solution.

Our model does not account for egg and larval dispersal. Since both lionfish and grouper disperse during their egg and larval stages, fecundity of adults living in a small area does not significantly contribute to that area's future breeding population; this is also the lionfish's primary method of colonization [9, 15, 24]. Simulating the model over a network of spatial patches would permit the study of dispersal dynamics and could thus describe the species population dynamics more realistically. Implementation of varying control strategies in each patch would allow the level of regional coordination to be determined.

Future research on this model could also include a more detailed bifurcation analysis and optimal control to determine the most effective conservation strategies. The model could be improved by including age structure, as IGP generally occurs when adults of one species prey on juveniles of another [30]. Cannibalism on young lionfish by adults could be included in an age-structured model.

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# Appendices

## A Parameter Estimation

Many parameters depend implicitly on the sizes of the individuals in each class. It is therefore useful to calculate the median sizes of lionfish, grouper, and their prey.

Morris (2009) [20] determined the average (± SE) total length of lionfish to be 217 ± 7 mm. Using the total length-weight (mm-g) conversion formula provided by Cerino for 782 lionfish from North Carolina and the Bahamas [7] ($W = .000002285TL^{3.335}$), these lionfish are 126.9 to 157.4g (median 141.6g). At this size, all males and nearly all females are sexually mature [20].

Grouper size was obtained from the median reported length for Nassau grouper, i.e. 512mm standard length [33]. Using the SL-weight regression for the Bahamas ($W = 0.0000214SL^{3.03}$) yields a weight of 3463.4g [33].

Mean ± SE TL of prey in 2004 vs. 2006 was 44.2 ± 1.7 mm, (sample size = 122) vs. 43.9 ± 1.5 mm, (sample size = 94) [28]. Thus, the low TL is 42.4mm, the high TL is 45.9mm, and the weighted average is 44.1cm. Using the length-weight regression (g-cm) for prey ($W = 0.015L^{2.998}$) [8], the weights range from 1.15g to 1.4g, with a median of 1.28g. This is similar to average lionfish prey size estimates by Côté (2010) of 4cm and 1g [8].

### Predation rates on prey $(a_1, a_2)$

We estimate $a_2$ to be between the piscivore predation rate of 0.01 [5] and 0.045 (median 0.023), the grouper predation rate on non-snapper and non-parrotfish prey given by Kellner [17]. Since lionfish have 2.4 times the negative effect on reef fish as do native groupers [2], we assume their consumption to be higher than grouper consumption. Therefore, we estimate a range of 0.02 to 0.05 (median 0.035) for $a_1$.

For purposes of simulation, we fix both values at their maximum, since Kellner's estimate is specific to grouper and is therefore likely to be more accurate.

### Intraguild predation rates $(b_1, b_2)$

Assume that grouper consumption of lionfish compared to other prey (i.e. $b_2/a_2$) is proportional to their biomass density compared to that of other prey. We follow Cerino [7] and consider the estimated fish densities in the Bahamas of 742 kg/ha of prey fish and 393 lionfish/ha, which is 49.8717 kg/ha to 61.8582 kg/ha, with a median of 55.6488 kg/ha. Multiplying the resulting lionfish–prey ratio by our low, high, and median estimates for $a_2$, this gives a low estimate for $b_2$ of 0.0026885, a high of 0.0037515, and a median of 0.0031874.

Some data exists on lionfish consumption rates on grouper. Munoz examined 183 stomachs containing 826 prey fish and found Serranidae comprised 6.3% of total number of prey consumed [28]. Morris [20] examined 1069 stomachs containing 1,876 prey items; 15 stomachs contained serranids. They comprised 4.3% of lionfish diet by volume and 1.5% by percent number. We thus estimate that grouper constitute between 1.5% and 6.3% (mean 3.9%) of the consumption rate of lionfish on prey. This gives a low estimate for $b_1$ of 0.0003, a high estimate of 0.00315, and a median of 0.000897. For simulation, we assume the median, i.e. $b_1 = 0.000897$.

### Biomass conversion efficiency $(c_1, c_2)$

The grouper reproductive efficiency is assumed to be $c_2 = 0.0175$ [5,17]. Lionfish grow more rapidly than native grouper [2], so we assume them to be slightly more efficient consumers and fecundate more rapidly. Thus, we set $c_1 = 0.02$.

### Removal rate $(d_1, d_2)$

Assuming no harvesting, removal of grouper is due solely to natural mortality. We estimate $d_2 = 0.22$ [17]. If harvesting occurs, we consider additional mortality rates of up to 0.5 [17]. This yields a range of 0.22–0.72 for this parameter.

Barbour (2011) used a range of 0.2–0.5 for adult lionfish natural mortality [4]. However, since the low end of this range is very similar to the value used by Kellner, we assume lionfish and grouper have the same natural mortality, i.e. the low values for $d_1$ and $d_2$ are both 0.22.

### Mass scaling factor $(m_1, m_2)$

The mass scaling factors convert biomass of consumed lionfish and grouper into equivalent biomass of prey. We use our low, median, and high estimates for lionfish, grouper, and prey sizes in the following calculations. In simulation, we assume the median values.

Assuming lionfish consume grouper that are 1/4 to 1/2 of their size (median 3/8), then these prey have TL from 52.5 to 112 (median 81.375). Converting this into SL with the averaged TL–SL ratio formulas for Cuba, Jamaica, and the Bahamas ($TL = 2.68333 + 1.11SL$) yields values from 44.87988 to 98.4835 (median 70.8934). Converting this into grams yields 2.16836g to 23.45875g (median 8.66462g). Converting this into prey weights yields $m_2 = 1.55$–$20$ with a median of 6.77.

Since grouper can grow far larger than lionfish, we suppose that they may consume any size of lionfish. Therefore, we use our 126.9 to 157.4g (median 141.6g) estimates for their size. This gives $m_1 = 90.643$–$136.87$ with a median of 110.625.

### Prey growth parameters $(r, K)$

The prey's maximum per capita growth rate was assumed to be the herbivore growth rate 0.447 given by Baskett [5].

Prey carrying capacity was derived by assuming the grouper-prey equilibrium $E_3$ of 1240 prey in a 200 m$^2$ area, with a median of 1.805 grouper [17]. This yields the equality $R = 686.98P_2$. Using this and our other parameter estimates with high grouper harvesting, we can solve for $K$, which is

$$K = \frac{686.98rd_2}{a_2(686.98rc_2 - d_2)} \approx 1056.$$

## B Sensitivity Analysis

We use Maple to compute elasticities of the stability conditions for $E_2$ and $E_3$, the lionfish and grouper components ($x^*$ and $y^*$) of the coexistence equilibrium, and the stability conditions ($w_1$ and $w_2$) for the coexistence equilibrium. The values are given below.

| Value | $b_1$ | $b_2$ | $d_1$ | $d_2$ |
|---|---|---|---|---|
| $X$ | 0.0240 | −0.6299 | −5.9513 | 7.7751 |
| $Y$ | −0.6735 | 4.6332 | 17.3379 | −23.3396 |
| $x^*$ | 0.3239 | −1.9852 | −5.9513 | 7.7751 |
| $y^*$ | −0.9734 | 5.9885 | 17.3379 | −23.3396 |
| $w_1$ | −0.9449 | 6.3403 | 21.2586 | −29.8030 |
| $w_2$ | 0.1092 | −0.8146 | −0.7699 | 3.4029 |