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Competition Modeling of the Combined Impact of *Pterygoplichthys* spp. and Invasive *Trichogaster* spp. on Native Freshwater Fish: Stability, Sensitivity, and Management Scenarios

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ABSTRACT

Invasive fish threaten native freshwater fish communities, yet mathematical studies have mostly examined a single invader, leaving the combined effects of co-occurring invaders and their underlying mechanisms unquantified. This study develops a three-species ordinary differential equation model of janitor fish (*Pterygoplichthys* spp.), an invasive gourami population (*Trichogaster* spp.), and a native fish, in which the invaders affect the native fish through resource competition and an additional stress-induced mortality term. Equilibria and their local stability were analyzed by Jacobian linearization, the system was solved with the fourth-order Runge–Kutta method over 15 years, and normalized sensitivity indices and management scenarios were evaluated. All parameters and initial densities are hypothetical but literature-informed. The two invaders coexist at a locally asymptotically stable equilibrium (10,177 and 7,420 ind/km), whereas no positive three-species equilibrium exists and native exclusion is the only stable outcome. Without intervention, the native population declines by about 99% within 10 years. Competition accounts for more than 96% of the pressure on native fish, with janitor fish contributing about 61%, and native density is most sensitive to the janitor fish carrying capacity and the invasive-to-native competition coefficients. Harvesting janitor fish, even to complete removal or combined with habitat restoration, cannot keep native density above 50% of its carrying capacity, because gourami is released from competition. Effective management therefore requires the joint control of both invaders. These theoretical projections require field calibration before site-specific application.

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1. INTRODUCTION

The invasion of foreign species into aquatic ecosystems is one of the greatest threats to aquatic biodiversity worldwide [1]–[3], with substantial ecological and economic costs [4]. In Indonesia, this phenomenon has become an increasingly worrying ecological problem, especially with the entry and development of janitor fish (*Pterygoplichthys* spp.; locally known as ikan sapu-sapu) and gourami (*Trichogaster* spp.; locally known as ikan sepat) into various river and lake ecosystems. Both taxa were spread through the aquarium and aquaculture trades, and established populations now occur in many freshwaters, especially on Java and Borneo [5].

Janitor fish (*Pterygoplichthys* spp.) is native to South America and has become established in Indonesian freshwater systems, where it is fully non-native [5], [6]; it is known for its high adaptability, tolerance to poor water quality, and prolific reproduction [6], [7]. The second target taxon, gourami (*Trichogaster* spp.), is different in status: the genus itself is native to Southeast Asia, including parts of the Indonesian archipelago, so it is not treated here as non-native in the broad biogeographic sense. However, field surveys and distribution records report established, expanding populations of *Trichogaster* outside their historically native river systems, including in West Java waters where they co-occur with janitor fish and compete with local native fish assemblages [5], [8]. It is this ecologically invasive, translocated population, rather than the species as a whole, that is represented by N_2 in the present model; where the manuscript refers to *Trichogaster* spp. as an "invasive species," this specifically denotes populations established outside their native range and displaying the expansive, competitively dominant dynamics described in Section 1.1, not the taxon in its indigenous range.

Mathematical approaches in population ecology have proven to be a very effective tool in understanding and predicting the dynamics of invasive species [2], [9]. Mathematical models based on Ordinary Differential Equations (ODEs) allow us to: (a) quantify population growth rates, (b) analyze competitive balances between species, (c) predict long-term impacts on ecosystems, and (d) evaluate the effectiveness of various control strategies.

Existing mathematical work on invasive fish has largely followed two lines: single-species logistic or exponential growth models used to characterize the expansion of one invader [2], [9], and two-species Lotka–Volterra competition models used to analyze interference or competitive-exclusion dynamics between an invader and a resident species. Indonesian studies have analyzed related two-species models, such as a modified Lotka–Volterra competition model [10] and a harvested predator–prey model [11]. Three-species competition frameworks that combine two co-occurring invasive fish with a shared native competitor are comparatively rare, and where multi-species ODE models exist in the broader invasion-ecology literature, they seldom couple analytical Jacobian stability analysis with numerical (RK4) simulation, parameter sensitivity ranking, and quantitative evaluation of management interventions within a single framework. Two further mechanistic questions are typically left unresolved in this literature: how the impact of two simultaneous invaders on a native population should be decomposed into resource-competition and indirect, non-predatory mortality effects (e.g., habitat disturbance), and which parameters most strongly determine the trajectory of native-population decline. This study addresses both gaps.

This study aims to: (1) build a mathematical model that represents the population dynamics of the janitor fish and the invasive *Trichogaster* population in aquatic ecosystems, (2) analyze the equilibrium point stability of the system, (3) simulate invasive impact scenarios on native fish species, and (4) provide recommendations for control strategies based on quantitative analysis.

The novelty of this study is not the individual analytical tools, which are established (Lotka–Volterra competition, Jacobian linearization, RK4 integration, normalized sensitivity analysis), but their combination into a specific three-species model structure (equations (5)–(7)) that explicitly separates two distinct impact mechanisms acting on the native population: a resource-competition term ($\gamma_1 N_1 + \gamma_2 N_2$) representing direct overlap in food, space, and dissolved-oxygen use, and an additive mortality term (δP) representing indirect, non-predatory stress such as habitat disturbance and spawning-site loss. This mechanistic decomposition, combined with parameter sensitivity ranking and quantitative comparison of harvesting versus habitat-restoration interventions within one framework, is what distinguishes this study from prior work that examined a single invasive species, or a single impact mechanism, in isolation.

1.1. Biological Characteristics of Target Species

Janitor fish (*Pterygoplichthys* spp.) is an armored catfish of the Loricariidae family that has several prominent biological characteristics that support its invasive capabilities. A body covered with bone plates serves as protection from natural predators [6]. More importantly, it can breathe atmospheric air through a highly vascularized stomach [6], which allows it to survive in conditions of very low dissolved oxygen — a condition that is deadly for most native fish. Reproductively, janitor fish exhibit a particularly advantageous strategy in the context of invasion: they are highly fecund multiple spawners, with absolute fecundities of 923 to 14,777 eggs per female reported for *Pterygoplichthys pardalis* [12], and males guard the eggs and young in excavated burrows until hatching [12], [13].

Gourami (*Trichogaster* spp.), meanwhile, also show strong adaptations: tolerance of large temperature and pH fluctuations and of low dissolved oxygen, owing to a suprabranchial labyrinth organ that enables air breathing; the ability to live in slow-flowing streams, shallow lakes, and swamps with dense vegetation; and an opportunistic omnivorous diet in adults, as reported for the three spot gourami *Trichogaster trichopterus* [14].

1.2. Differential Equations in Population Ecology

Mathematical models based on differential equations have long been the foundation of theoretical ecology. Exponential population growth was first formulated by Malthus [15], which was later refined through a logistic model that took into account environmental capacity limitations [16]. A system of differential equations describing predator–prey interactions was developed independently [17], [18] and came to be known as the Lotka–Volterra model; its competition form underlies the principle of competitive exclusion [19]. A two-species competition model also developed from the Lotka–Volterra framework has been widely applied to study the dynamics of invasive species, including the invasion analysis of competing species in advective patchy (river-like) environments [20].

Modern concepts of species coexistence suggest that invasion is successful when a foreign species is able to grow positively when it is rare while the resident species is at its equilibrium density [21], a condition that can be mathematically analyzed through stability analysis. In the Indonesian context, the modified two-species competition model [10] as well as the predator–prey model modified by harvesting [11] are relevant methodological foundations. Current frameworks on threats and management of invasive species [1], [22] reinforce the urgency of quantitative modelling in invasive species management, while distribution records [5] and [6] confirm the existence of established janitor fish populations in various Indonesian waters.

Two clarifications on scope follow from the above. First, this study is primarily a theoretical and numerical modeling exercise rather than a field-calibrated case study of a specific river: the West Java references describe the setting that motivates the model, whereas all parameter values and initial densities are hypothetical rather than a site-validated dataset, and the results are accordingly framed as illustrative projections of interaction dynamics rather than site-specific forecasts. Second, regarding the mechanism of impact, the interaction between the two invasive species and the native population modeled in equations (5)–(7) is not literal predation; janitor fish and gourami do not prey on native fish. The dominant mechanisms are (i) direct exploitative competition for food, space, and dissolved oxygen, captured by the competition coefficients γ_1 and γ_2, and (ii) indirect, non-consumptive mortality arising from habitat modification (e.g., sediment disturbance from janitor fish burrowing) and disruption of spawning sites, captured by the additional mortality term δP. These two mechanisms, rather than direct predation, are what determine the structure of the impact model presented in Section 2.4.

2. METHODS

2.1. Research Design and Model Assumptions

This study is a quantitative, deterministic mathematical-modeling study. Its object of analysis is a system of ordinary differential equations (ODEs) describing three fish populations; therefore, no respondent sampling or research instruments were involved. The study proceeded in five stages: (1) formulation of the single-species, two-species, and three-species models under the assumptions listed below (Sections 2.2–2.4); (2) determination of the equilibrium points and their local stability by Jacobian linearization; (3) numerical solution of the models with the fourth-order Runge–Kutta method (Section 2.5) using the parameter values and initial conditions in Section 2.6; (4) local sensitivity analysis of the native population; and (5) simulation of management intervention scenarios (stages 2, 4, and 5 are described in Section 2.7). The model was verified internally by comparing the analytical equilibria with the equilibria reached numerically and by cross-checking the RK4 implementation against an independent adaptive solver (Section 2.5). Because long-term field time series for the study system are not available, external validation was not possible, and the model outputs are interpreted as theoretical projections rather than site-specific forecasts.

The models are based on the following assumptions, which simplify the real ecosystem while retaining the processes of interest:

1. The populations are spatially homogeneous and well mixed within a single river reach (one patch). Population sizes are expressed as densities, in individuals per kilometre of river (ind/km), and time is measured in years.
2. Food and space are limited, and the resulting intraspecific density dependence is represented by a carrying capacity (K) for each species.
3. Population change is deterministic and continuous in time; age, size, and sex structure are not considered.
4. All parameters (intrinsic growth rates, carrying capacities, interaction coefficients, and the additional mortality rate) are constant over the simulation period, so seasonal and interannual variation is ignored.
5. The populations are closed: there is no immigration, emigration, or restocking during the modeling period.
6. The invasive species affect native fish only through resource competition and indirect, non-consumptive mortality; predation is not included (Section 1.2).
7. No harvesting or other control is applied in the baseline model; interventions are introduced only in the scenarios described in Section 2.7.

2.2. Single Growth Model (Verhulst Logistic Model)

In the absence of interspecific interactions, the growth of each population is described by the Verhulst logistic equation [16], a first-order nonlinear autonomous ordinary differential equation [9], [23]:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad (1)$$

where:

N(t) = population density at time t (ind/km);

r = intrinsic growth rate (year^{-1});

K = carrying capacity of the environment (ind/km).

The analytical solution of equation (1) with the initial condition $N(0) = N_0$ is:

$$N(t) = \frac{K}{1+\left(\frac{K-N_0}{N_0}\right)e^{-rt}} \quad (2)$$

where N_0 is the initial population density. The solution is a sigmoid (S-shaped) curve: the population grows almost exponentially when $N \ll K$ and slows down as it approaches K, which is a globally asymptotically stable equilibrium for any $N_0 > 0$. Equation (2) is used directly for the single-species simulations (Scenario 1, Section 2.7).

2.3. Two-Species Competition Model (Lotka–Volterra)

The interaction between janitor fish (N_1) and gourami (N_2), which compete for the same food and space, is described by the Lotka–Volterra competition system [17], [18]:

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1+\alpha_{12}N_2}{K_1}\right) \quad (3)$$

$$\frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2+\alpha_{21}N_1}{K_2}\right) \quad (4)$$

where:

N_1, N_2 = population densities of janitor fish and gourami (ind/km);

r_1, r_2 = intrinsic growth rates (year^{-1});

K_1, K_2 = carrying capacities (ind/km);

α_{12} = per capita competitive effect of gourami (N_2) on janitor fish (N_1), relative to the intraspecific effect (dimensionless);

α_{21} = per capita competitive effect of janitor fish (N_1) on gourami (N_2), relative to the intraspecific effect (dimensionless).

System (3)–(4) is the special case of the three-species model (5)–(7) without native fish (P = 0) and is used to analyze the coexistence of the two invaders (Scenario 2, Section 2.7).

2.4. Impact Model on Native Species

As explained in Section 1.2, the two invasive species do not prey on native fish; their impact combines direct resource competition with indirect, non-consumptive mortality stress (e.g., habitat disturbance and loss of spawning sites). To represent this combined impact on the native fish population (P), the Lotka–Volterra competition model is extended to three species by (i) adding the competitive effects of the invaders, $\gamma_1 N_1 + \gamma_2 N_2$, to the density-dependent term of the native fish's logistic equation, and the reciprocal effects of native fish, $\beta_1 P$ and $\beta_2 P$, to those of the invaders, and (ii) adding a linear mortality term δP to the native fish equation to represent the non-competitive stress component. Unlike a consumer functional response [24], these terms do not imply any consumption of native fish:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2 + \beta_1 P}{K_1}\right) \quad (5)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1 + \beta_2 P}{K_2}\right) \quad (6)$$

$$\frac{dP}{dt} = r_p P \left(1 - \frac{P + \gamma_1 N_1 + \gamma_2 N_2}{K_p}\right) - \delta P \quad (7)$$

where P is the native fish density (ind/km); r_p (year^{-1}) and K_p (ind/km) are the intrinsic growth rate and carrying capacity of the native fish; β_1 and β_2 are the per capita competitive effects of native fish on janitor fish and gourami; γ_1 and γ_2 are the per capita competitive effects of janitor fish and gourami on native fish (all dimensionless); and δ (year^{-1}) is the additional mortality rate caused by indirect, non-predatory stress (habitat disturbance and spawning-site loss). The system is solved with the initial conditions $N_1(0)$, $N_2(0)$, and P(0) given in Table 1.

2.5. Fourth-Order Runge–Kutta Numerical Method (RK4)

Because no closed-form solution of the three-species system (5)–(7) is known, the system is solved numerically with the classical fourth-order Runge–Kutta method (RK4) [25]. RK4 was chosen because it is an explicit single-step method with fourth-order global accuracy, $O(h^4)$, at a modest computational cost, which is adequate for a smooth, non-stiff system such as (5)–(7). Writing the system in vector form dy/dt = f(t, y), where $y = (N_1, N_2, P)^T$ and f contains the right-hand sides of (5)–(7), one RK4 step from t_n to $t_{n+1} = t_n + h$ is:

$$k_1 = f(t_n, y_n)$$

$$k_2 = f\left(t_n + \frac{h}{2}, y_n + (\frac{h}{2})k_1\right)$$

$$k_3 = f\left(t_n + \frac{h}{2}, y_n + (\frac{h}{2})k_2\right)$$

$$k_4 = f(t_n + h,\ y_n + h\,k_3)$$
$$y_{n+1} = y_n + \left(\frac{h}{6}\right)(k_1 + 2k_2 + 2k_3 + k_4) \quad (8)$$

where h = Δt = 0.01 year is the time step. All simulations covered 15 years (1,500 steps) and were implemented in Python 3.13 with NumPy 2.5 and SciPy 1.18, and the figures were produced with Matplotlib 3.11. The numerical solution was verified in two ways: (i) repeating the simulation with h = 0.005 year changed the solution by less than 10^{-5} ind/km, and (ii) the manual RK4 implementation was cross-checked against scipy.integrate.solve_ivp with its adaptive explicit Runge–Kutta method (RK45, relative tolerance 10^{-10}), giving a maximum absolute difference below 10^{-5} ind/km over the 15-year horizon. The complete simulation code, which reproduces all results, tables, and figures reported in this article, is provided as Supplementary File S1.

2.6. Parameter Values and Initial Conditions

Because field measurements of growth and interaction rates for these populations are not available, the parameter values in Table 1 are hypothetical values chosen to be consistent with the biological characteristics described in Section 1.1, rather than statistically estimated quantities. The intrinsic growth rates were ordered $r_1 > r_2 > r_p$ to reflect the high fecundity and paternal egg protection of janitor fish and the broad environmental tolerance of gourami relative to native fish. The competitive effect of janitor fish on native fish was set larger than that of gourami ($\gamma_1 > \gamma_2$), reflecting its stronger habitat modification and benthic resource overlap, whereas the effects of native fish on the invaders were assumed to be weak ($\beta_1 = \beta_2 = 0.10$). The initial densities are likewise assumed: the native fish starts at 6,000 ind/km (75% of K_p), representing a population that is still close to its carrying capacity before invasion, and the invaders start at 500 and 800 ind/km, representing an early stage of invasion. The parameter values and initial conditions are presented in Table 1.

Table 1. Model parameter values and initial conditions

Parameter	Janitor fish (N_1)	Gourami (N_2)	Native fish (P)	Source
Intrinsic growth rate (r)	$r_1 = 1.80$ year^{-1}	$r_2 = 1.35$ year^{-1}	$r_p = 0.85$ year^{-1}	Hypothetical (literature-informed)
Carrying capacity (K)	K_1 = 15,000 ind/km	K_2 = 12,000 ind/km	K_p = 8,000 ind/km	Hypothetical
Competition between invaders (α)	$\alpha_{12} = 0.65$ (effect of N_2 on N_1)	$\alpha_{21} = 0.45$ (effect of N_1 on N_2)	–	Hypothetical
Competition of invader on native fish (γ)	$\gamma_1 = 0.78$	$\gamma_2 = 0.62$	–	Hypothetical
Competition of native fish on invader (β)	$\beta_1 = 0.10$	$\beta_2 = 0.10$	–	Hypothetical (assumed)
Initial density	$N_1(0)$ = 500 ind/km	$N_2(0)$ = 800 ind/km	P(0) = 6,000 ind/km	Hypothetical (assumed)
Additional mortality rate (δ)	–	–	$\delta = 0.05$ year^{-1}	Hypothetical

2.7. Equilibrium, Simulation, Sensitivity, and Intervention Analyses

Equilibrium points were obtained by setting the right-hand sides of (3)–(4) and (5)–(7) to zero. Their local stability was determined by linearization: an equilibrium is locally asymptotically stable if all eigenvalues of the Jacobian matrix evaluated at that point have negative real parts [23]. For the two-species system, this condition was expressed analytically through the trace and determinant of the Jacobian; for the three-species system, the eigenvalues were derived analytically where the Jacobian is block-triangular and computed numerically otherwise.

Three simulation scenarios were run. Scenario 1 describes the single-species growth of janitor fish and gourami using equation (2) with $N_1(0) = 500$ and $N_2(0) = 800$ ind/km. Scenario 2 describes competition between the two invaders using equations (3)–(4) with the same initial densities. Scenario 3 uses the full three-species system (5)–(7) with $N_1(0) = 500$, $N_2(0) = 800$, and $P(0) = 6{,}000$ ind/km. A reference run of the native population without invaders ($N_1 = N_2 = 0$) was also computed for comparison. Because the initial native density is assumed, Scenario 3 was repeated with $P(0) = 2{,}000$, 4,000, and 8,000 ind/km to test its influence on the results.

The influence of each parameter x on the native fish density in year 10, P(10), was quantified with the normalized sensitivity index [26], [27]:

$$S_x = \left(\frac{\partial P}{\partial x}\right) \times \left(\frac{x}{P}\right) \tag{9}$$

where the derivative was approximated by central finite differences with a ±1% perturbation of x. In addition, the simulation was repeated with each parameter decreased and increased by 20% to measure the resulting change in P(10). The parameters examined were r_1, r_2, K_1, γ_1, γ_2, and δ.

Management interventions were represented as modifications of the three-species model. In Strategy A (intensive harvesting), a constant-effort harvest of janitor fish at rate h_1 (year^{-1}) is added to equation (5):

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2 + \beta_1 P}{K_1}\right) - h_1 N_1 \tag{10}$$

In Strategy B (selective habitat restoration), the native carrying capacity is increased to $1.3K_p$ and combined with $h_1 = 0.25$ year^{-1}; Strategy C (integrated approach) combines $h_1 = 0.30$ year^{-1} with a 20% increase in K_p. Each strategy was evaluated against the conservation target of keeping the native population at or above 4,000 ind/km (50% of K_p) throughout the 15-year horizon, and its long-term outcome was assessed from the equilibrium of the modified system.

3. RESULTS AND DISCUSSION

3.1. Equilibrium Points

Equilibrium points (steady states) are obtained by setting all time derivatives equal to zero. For the two-species competition model (3)–(4), there are four equilibrium points: $E_0 = (0, 0)$, in which both species are absent; $E_1 = (K_1, 0)$ and $E_2 = (0, K_2)$, in which only janitor fish or only gourami persists at its carrying capacity; and the coexistence equilibrium $E^* = (N_1^*, N_2^*)$.

The coordinates of the coexistence equilibrium E* are:

$$N_1^* = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}} \quad (11)$$

$$N_2^* = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}} \quad (12)$$

When $\alpha_{12}\alpha_{21} < 1$, the denominators in (11)–(12) are positive, so E* is biologically feasible ($N_1^*, N_2^* > 0$) if and only if $K_1 > \alpha_{12}K_2$ and $K_2 > \alpha_{21}K_1$, that is, if each species limits its own growth more strongly than it limits the growth of its competitor [9], [19]. (If $\alpha_{12}\alpha_{21} > 1$, a positive E* exists only when both inequalities are reversed, and it is then a saddle point.) With the parameter values in Table 1, $K_1 - \alpha_{12}K_2 = 7{,}200 > 0$, $K_2 - \alpha_{21}K_1 = 5{,}250 > 0$, and $\alpha_{12}\alpha_{21} = 0.65 \times 0.45 = 0.2925 < 1$, so equations (11)–(12) give E* = (10,177; 7,420) ind/km.

For the three-species system (5)–(7), the equilibria are the trivial equilibrium $E_0 = (0, 0, 0)$; the single-species equilibria $E_1 = (K_1, 0, 0)$, $E_2 = (0, K_2, 0)$, and $E_p = (0, 0, K_p(1 - \delta/r_p))$, the last of which exists only if $r_p > \delta$; the two-species equilibria $E_{12} = (N_1^*, N_2^*, 0)$, E_{1p} (without gourami), and E_{2p} (without janitor fish); and a possible interior equilibrium $E_3 = (N_1, N_2, P)$ that satisfies the linear system $N_1 + \alpha_{12}N_2 + \beta_1 P = K_1$, $\alpha_{21}N_1 + N_2 + \beta_2 P = K_2$, and $\gamma_1 N_1 + \gamma_2 N_2 + P = K_p(1 - \delta/r_p)$. For the parameters in Table 1, $K_p(1 - \delta/r_p) = 7{,}529$ ind/km; the interior solution is (10,448; 7,847; −5,485) and E_{1p} = (15,452; 0; −4,523), so neither is biologically feasible, whereas E_{2p} = (0; 11,990; 95) ind/km is feasible. All feasible equilibria of both systems and their stability are summarized in Table 2.

Table 2. Equilibrium points of the two-species and three-species systems and their local stability (two-species system: equations (3)–(4); three-species system: equations (5)–(7); parameters in Table 1)

System	Equilibrium	Coordinates (ind/km)	Eigenvalues of the Jacobian	Stability
Two-species	E_0	(0; 0)	1.800, 1.350	Unstable (node)
	E_1	(15,000; 0)	−1.800, 0.591	Unstable (saddle)
	E_2	(0; 12,000)	−1.350, 0.864	Unstable (saddle)
	E*	(10,177; 7,420)	−1.607, −0.449	Stable (node)
Three-species	E_0	(0; 0; 0)	1.800, 1.350, 0.800	Unstable (node)
	E_1	(15,000; 0; 0)	−1.800, −0.443, 0.591	Unstable (saddle)
	E_2	(0; 12,000; 0)	−1.350, 0.864, 0.010	Unstable (saddle)
	E_p	(0; 0; 7,529)	−0.800, 1.710, 1.265	Unstable (saddle)
	E_{12}	(10,177; 7,420; 0)	−1.607, −0.532, −0.449	Stable (node)
	E_{2p}	(0; 11,990; 95)	−1.350, −0.009, 0.864	Unstable (saddle)
	E_{1p}, E_3	Not feasible (negative component)	–	–

3.2. Stability Analysis with the Jacobian Matrix

Following the procedure described in Section 2.7, the local stability of each equilibrium is determined from the Jacobian matrix of system (3)–(4) [23]:

$$J = \begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{pmatrix} \quad (13)$$

where f_1 and f_2 denote the right-hand sides of equations (3) and (4). At the trivial equilibrium E_0 the eigenvalues are $r_1 > 0$ and $r_2 > 0$, so E_0 is an unstable node. At E_1 the eigenvalues are $-r_1$ and $r_2(1 - \alpha_{21}K_1/K_2) = 0.591 > 0$, and at E_2 they are $-r_2$ and $r_1(1 -$

$\alpha_{12}K_2/K_1) = 0.864 > 0$; both are saddle points, which means that each invader can increase when rare in a habitat dominated by the other. At the coexistence equilibrium $E^* = (N_1^*, N_2^*)$, the elements of the Jacobian matrix are:

$$J_{11} = r_1\left(1 - \frac{2N_1^*}{K_1} - \frac{\alpha_{12}N_2^*}{K_1}\right) = -\frac{r_1N_1^*}{K_1} \quad (14)$$

$$J_{12} = -\frac{r_1\alpha_{12}N_1^*}{K_1} \quad (15)$$

$$J_{21} = -\frac{r_2\alpha_{21}N_2^*}{K_2} \quad (16)$$

$$J_{22} = r_2\left(1 - \frac{2N_2^*}{K_2} - \frac{\alpha_{21}N_1^*}{K_2}\right) = -\frac{r_2N_2^*}{K_2} \quad (17)$$

E^* is locally asymptotically stable if and only if both eigenvalues of $J(E^*)$ have negative real parts, which for a 2×2 matrix is equivalent to:

$$\mathrm{tr}(J) = J_{11} + J_{22} < 0 \quad \text{and} \quad \det(J) = J_{11}J_{22} - J_{12}J_{21} > 0 \quad (18)$$

Because $J_{11} = -r_1N_1^*/K_1 < 0$ and $J_{22} = -r_2N_2^*/K_2 < 0$, the trace is always negative, and $\det(J) = r_1r_2N_1^*N_2^*(1 - \alpha_{12}\alpha_{21})/(K_1K_2) > 0$ whenever $\alpha_{12}\alpha_{21} < 1$; hence E^* is locally asymptotically stable whenever it is feasible. For the parameters in Table 1, $\mathrm{tr}(J) = -2.056 < 0$ and $\det(J) = 0.721 > 0$, with real eigenvalues $\lambda_1 = -1.607$ and $\lambda_2 = -0.449$, so E^* is a stable node. All four equilibria are hyperbolic (no eigenvalue has zero real part), so their linearization determines the local behavior. Moreover, because E_0, E_1, and E_2 are unstable and the planar Lotka–Volterra competition system has no periodic orbits, every solution with positive initial densities converges to E^* [9], in agreement with the numerical results of Scenario 2 (Section 3.3).

For the three-species system, the Jacobian of (5)–(7) was evaluated at each feasible equilibrium (Table 2). At E_{12} the Jacobian is block-triangular because $P = 0$, so its eigenvalues are the two eigenvalues of $J(E^*)$ together with

$$\lambda_3 = r_p\left(1 - \frac{\gamma_1N_1^* + \gamma_2N_2^*}{K_p}\right) - \delta \quad (19)$$

Therefore, E_{12} is locally asymptotically stable if and only if E^* is stable and

$$\gamma_1N_1^* + \gamma_2N_2^* > K_p\left(1 - \frac{\delta}{r_p}\right) \quad (20)$$

that is, if the native fish cannot increase when rare in the presence of the invader community. For the parameters in Table 1, $\gamma_1N_1^* + \gamma_2N_2^* = 12{,}539$ ind/km exceeds $K_p(1 - \delta/r_p) = 7{,}529$ ind/km, so $\lambda_3 = -0.532$ and the eigenvalues of E_{12} are -1.607, -0.449, and -0.532. All other feasible equilibria have at least one positive eigenvalue (Table 2). At E_p, the eigenvalues in the N_1 and N_2 directions, $r_1(1 - \beta_1P/K_1) = 1.710$ and $r_2(1 - \beta_2P/K_2) = 1.265$ (with $P = 7{,}529$ ind/km), are positive, so both invaders can establish when rare, in line with the invasion criterion of [21]; at E_{2p}, janitor fish can invade at rate $r_1(1 - (\alpha_{12}N_2 + \beta_1P)/K_1) = 0.864$. At E_2, the eigenvalue in the P direction, $r_p(1 - \gamma_2K_2/K_p) - \delta = 0.010$, is only slightly positive, which shows that gourami alone almost excludes native fish. Under the baseline parameters, E_{12} is therefore the only locally asymptotically stable equilibrium, and the model predicts competitive exclusion of the native fish rather than three-species coexistence; the simulation in Section 3.3 confirms that the trajectory starting from the initial conditions in Table 1 converges to E_{12}.

3.3. Numerical Simulation Results

This section presents the RK4 simulation results for the three scenarios defined in Section 2.7: single-species growth (Scenario 1), competition between the two invasive species (Scenario 2), and their combined impact on the native fish population (Scenario 3). The corresponding trajectories are shown in Figures 1–3.

Scenario 1: Single Population Growth. Without interspecific competition, both janitor fish and gourami follow the sigmoid logistic pattern of equation (2) (Figure 1); the RK4 solution reproduces this analytical solution with a maximum absolute error below 10^{-5} ind/km. From equation (2), the time required to reach half of the carrying capacity is $t_{1/2} = \ln((K - N_0)/N_0)/r$. Janitor fish reach 50% of their carrying capacity (7,500 ind/km) at $t \approx 1.87$ years and gourami reach 50% of theirs (6,000 ind/km) at $t \approx 1.95$ years, while the times needed to reach 99% of the carrying capacity are about 4.4 and 5.4 years, respectively. The small difference in $t_{1/2}$ reflects two opposing effects: janitor fish has the higher intrinsic growth rate, whereas gourami starts from a higher initial density (800 versus 500 ind/km). These results describe the growth potential of each species in isolation; competitive superiority is examined in Scenario 2.

Scenario 2: Competition of two invasive species. When the two invasive species interact in the absence of native fish (Figure 2), gourami is initially more abundant because of its higher initial density, but janitor fish overtakes it at $t \approx 1.2$ years. The system then converges to the coexistence equilibrium $E^* = (10{,}177; 7{,}420)$ ind/km, coming within 1% of both equilibrium values after about 6 years, with a slight transient overshoot of janitor fish (maximum 10,237 ind/km at $t \approx 5.5$ years). This numerical behavior agrees with the analytical result that E^* is a stable node (Section 3.2 and Table 2).

Scenario 3: Impacts on native species. This is the most critical scenario from a conservation perspective (Figure 3). The native fish population, initially 6,000 ind/km (75% of its carrying capacity), declines sharply under the combined effects of competition and additional mortality. It falls below 3,000 ind/km at $t \approx 2.7$ years and below 1,000 ind/km at $t \approx 4.5$ years; at $t = 10$ years it is about 45 ind/km, a decrease of 99.3% from the initial value, and it continues to decline towards zero, in agreement with the stability of the native-exclusion equilibrium E_{12} (Section 3.2). The result does not depend on the assumed initial native density: for $P(0) = 2{,}000$–$8{,}000$ ind/km, the decline by year 10 ranges from 98.3% to 99.4%, and the native population falls below 1,000 ind/km within 3.9–4.6 years. Table 3 summarizes the numerical projections over 15 years.

Table 3. Population densities from the RK4 simulation of Scenario 3 (h = 0.01 year); percentages give the change in native fish density relative to t = 0

Year	Janitor fish N_1 (ind/km)	Gourami N_2 (ind/km)	Native fish P (ind/km)	Notes
0	500	800	6,000	Initial conditions
2	5,904	4,658	4,297	Rapid invasive expansion (−28.4%)
5	10,207	7,154	719	Invaders near equilibrium (−88.0%)
8	10,218	7,354	132	Native fish near collapse (−97.8%)
10	10,197	7,392	45	Native fish near extinction (−99.3%)
15	10,179	7,417	3	Approaching native exclusion E_{12} (−99.9%)

The pattern in Table 3 shows that the decline in native fish populations occurs progressively and nonlinearly. After a brief initial increase (to about 6,080 ind/km at t ≈ 0.4 years, while the invaders are still rare), the fastest decline (about 1,970 ind/km per year) occurs at t ≈ 2.2 years, and most of the loss takes place between the 1st and 5th years (from 5,812 to 719 ind/km), coinciding with the expansionary growth phases of both invasive species.

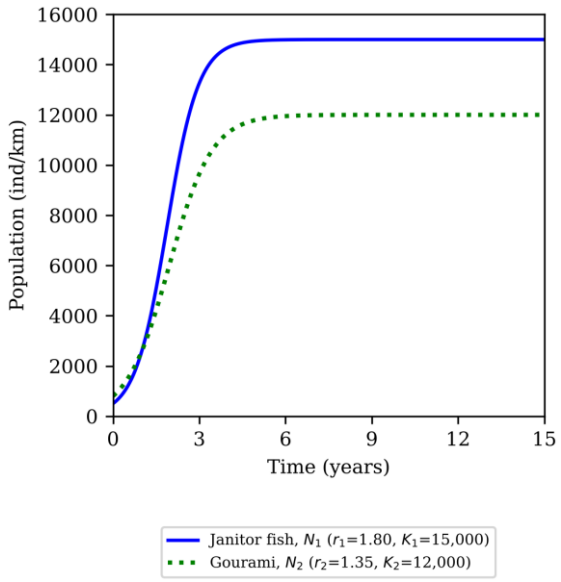


Figure 1. Logistic growth of janitor fish and gourami separately (Scenario 1): typical sigmoid curves, with janitor fish approaching its carrying capacity faster.

Figure 1 shows that both species follow the characteristic sigmoid curve of the Verhulst logistic model: growth is initially rapid and slows down as the carrying capacity is approached. Janitor fish approaches its carrying capacity more quickly than gourami (99% of K after about 4.4 versus 5.4 years) because of its higher intrinsic growth rate (r_1 = 1.80 year^{-1} versus r_2 = 1.35 year^{-1}), and it also attains a higher plateau (K_1 = 15,000 versus K_2 = 12,000 ind/km). Even in the absence of interspecific interactions, janitor fish therefore has a greater capacity for rapid population expansion, suggesting a stronger invasive potential.

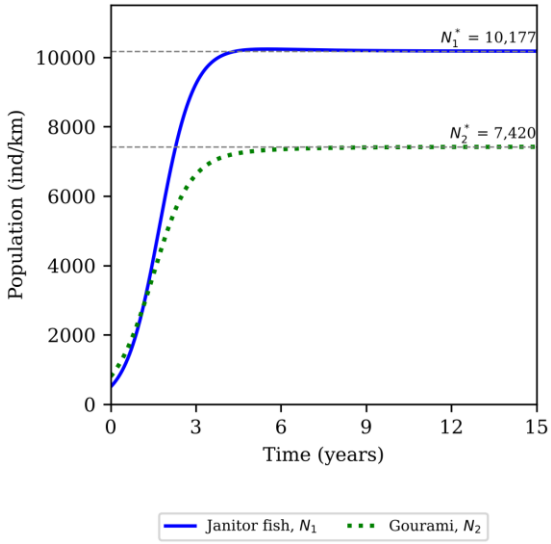


Figure 2. Competition dynamics of the two invasive species (Scenario 2), converging towards the coexistence point E* = (10,177; 7,420) ind/km within about 6 years.

Figure 2 shows the competitive dynamics between janitor fish and gourami based on the Lotka–Volterra competition model. Both populations persist, and after the first year janitor fish maintains a larger population than gourami. Apart from the small overshoot noted above, the trajectories approach the coexistence equilibrium monotonically, confirming the analytical stability result of Section 3.2. Interspecific competition alone therefore does not eliminate either invader but allows both to coexist, with janitor fish ecologically dominant.

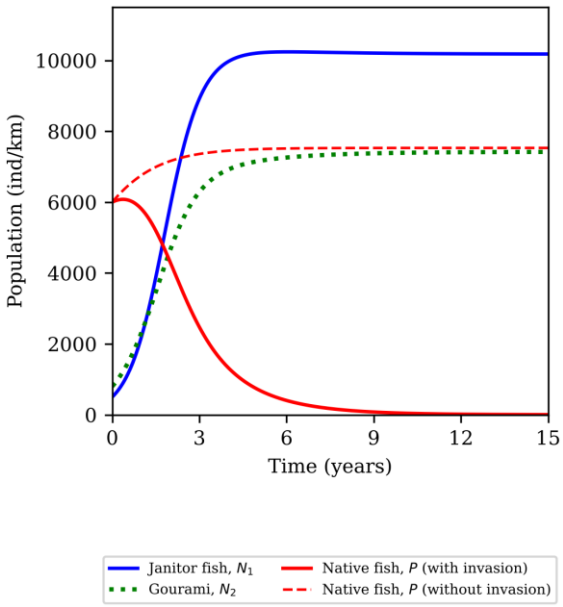


Figure 3. Combined impact on the native fish population (Scenario 3): a 99% decline by year 10 and convergence towards native exclusion; the dashed curve shows the native population without invasion.

Figure 3 shows the consequences of the simultaneous expansion of both invasive species for the native fish population. After a brief initial increase while the invaders are still rare, the native population declines continuously as janitor fish and gourami increase in

abundance, owing to cumulative competitive pressure and the additional mortality term. By year 10 it has fallen from 6,000 to about 45 ind/km (a reduction of about 99%), whereas in the reference run without invasion (dashed curve) it increases towards $K_p(1 - \delta/r_p) = 7{,}529$ ind/km. The gap between the two native-fish curves isolates the impact of invasion and highlights the importance of implementing management strategies before invasive populations become fully established.

3.4. Competition Dynamics and Ecological Dominance

Section 3.2 showed that, without external interference, the two invaders converge to a stable coexistence equilibrium E* at densities below their carrying capacities ($N_1^* \approx 0.68K_1$ and $N_2^* \approx 0.62K_2$). From the perspective of native species, however, this outcome is highly unfavorable. By inequality (20), the native fish can persist only if the weighted invader density satisfies $\gamma_1 N_1 + \gamma_2 N_2 < K_p(1 - \delta/r_p) = 7{,}529$ ind/km. At the invader coexistence point this quantity is 12,539 ind/km, about 1.7 times the threshold, so the invaders' equilibrium lies well outside the region in which native fish can grow: the invasive species persist at resource levels that are already too low for native fish.

The mechanism of the impact can be identified through the decomposition of equation (7): the decline of the native population is driven by two main components, namely (i) reduction of the effective capacity of the environment through the term $\gamma_1 N_1 + \gamma_2 N_2$, and (ii) additional δP mortality representing indirect impacts such as habitat destruction (sediment bioturbation by janitor fish) and spawning nest disturbances. At E*, the competition term removes $\gamma_1 N_1^* = 7{,}938$ ind/km (janitor fish) and $\gamma_2 N_2^* = 4{,}601$ ind/km (gourami) of effective capacity, while the mortality term reduces it by $K_p\delta/r_p = 471$ ind/km. Of the total reduction (13,010 ind/km), janitor fish therefore accounts for about 61%, gourami for about 35%, and indirect mortality for less than 4%. Competition alone would exclude the native population (with $\delta = 0$, $P(10) \approx 66$ ind/km instead of 45 ind/km), and the additional mortality mainly accelerates the decline.

These results are consistent with, and extend, earlier studies. The stable coexistence of the two invaders agrees with the classical coexistence condition of two-species Lotka–Volterra competition models [9]: each species limits its own growth more strongly than that of its competitor. By contrast, [10] showed that when one competitor grows exponentially, without intraspecific density dependence, coexistence becomes unstable, which underlines the role of the carrying capacities assumed here. For the native fish, the model reproduces the competitive exclusion principle [19]: when the combined competitive pressure of the invaders exceeds the native fish's effective carrying capacity, the native population cannot persist. Qualitatively, the predicted decline agrees with evidence that *Pterygoplichthys* reduces the survival and growth of native fishes [13] and with reviews and field reports of the impacts of established invasive fish, globally [7] and in Indonesian inland waters [5], which identify competition for food and space and habitat modification as major mechanisms. The present model adds a quantitative decomposition of these mechanisms: the sensitivity of $P(10)$ to δ is small ($S = -0.38$, Table 4) relative to K_1 ($S = -7.38$) and γ_1 ($S = -5.94$), indicating that, under the baseline parameters, the decline is driven primarily by resource competition, with indirect, non-predatory stress acting as a secondary, accelerating

component. Moreover, unlike harvesting studies of a single exploited population, such as the harvested predator–prey model of [11], the multi-invader structure shows that removing one invader can be offset by the competitive release of the other (Section 3.6).

3.5. Parameter Sensitivity Analysis

Table 4 presents the normalized sensitivity indices (equation (9)) of the native fish density in year 10, P(10), together with the changes in P(10) caused by ±20% changes in each parameter (Section 2.7). The influence of each parameter is classified as very high ($|S| \geq 5$), high ($2 \leq |S| < 5$), medium ($1 \leq |S| < 2$), low ($0.2 \leq |S| < 1$), or very low ($|S| < 0.2$).

Table 4. Sensitivity of the native fish density in year 10, P(10), to selected model parameters

Parameter	Sensitivity Index (S)	Change in P(t=10) for −20% / +20%	Interpretation
K_1 (janitor fish carrying capacity)	−7.38	+308.8% / −78.1%	Very high
γ_1 (janitor fish → native competition)	−5.94	+215.0% / −70.4%	Very high
γ_2 (gourami → native competition)	−3.39	+94.5% / −49.8%	High
r_1 (janitor fish growth rate)	−1.13	+34.0% / −16.6%	Medium
δ (additional mortality)	−0.38	+7.9% / −7.4%	Low
r_2 (gourami growth rate)	−0.11	+3.9% / −1.3%	Very low

The janitor fish carrying capacity (K_1, $S = -7.38$) and the competition coefficients γ_1 ($S = -5.94$) and γ_2 ($S = -3.39$) are the most influential parameters, whereas the intrinsic growth rate of janitor fish (r_1, $S = -1.13$) ranks fourth and δ and r_2 have little influence; negative indices indicate that increasing the parameter lowers P(10). The dominance of K_1 and γ_1 follows from the structure of the model: K_1 determines the equilibrium density N_1^* (equation (11)), and the product $\gamma_1 N_1^*$ is the largest component of the competitive pressure on native fish (Section 3.4). The growth rates r_1 and r_2, by contrast, mainly affect how fast the invaders approach equilibrium rather than the equilibrium itself, and therefore have a smaller effect on P(10). Because $P(10) \approx 45$ ind/km lies close to extinction, the responses to ±20% changes are large and asymmetric, so the local indices should be read as a ranking rather than as precise elasticities. For management, these results imply that measures which durably lower the equilibrium density or habitat suitability of the invaders (K_1) or their resource overlap with native fish (γ_1, γ_2) are more effective than measures that only slow invader growth.

3.6. Management Intervention Scenarios

Strategy A: Intensive Harvesting. Simulations of the harvested model (10) show that no janitor fish harvest rate keeps the native population above 4,000 ind/km (50% of K_p) within 15 years (Table 5). With $h_1 = 0.45$ year^{-1} the native population at year 15 is about 79 ind/km, and with $h_1 = 0.90$ year^{-1} about 581 ind/km. For $h_1 > 0.864$ year^{-1} (the growth rate of janitor fish when rare at E_{2p}; Section 3.2) janitor fish is eventually eliminated, but even its complete removal leaves only about 778 ind/km of native fish at year 15, and the system converges to E_{2p} = (0; 11,990; 95). The reason is competitive release: as janitor fish is removed, gourami increases from 7,417 to 11,918 ind/km at year 15, and gourami alone

nearly exhausts the native fish's effective carrying capacity ($\gamma_2 K_2 = 7{,}440$ ind/km versus $K_p(1 - \delta/r_p) = 7{,}529$ ind/km).

Strategy B: Selective Habitat Restoration. Restoring riparian vegetation and reducing sedimentation, represented by increasing the native carrying capacity to $1.3K_p$ (Section 2.7), together with $h_1 = 0.25$ year^{-1}, gives a native population of about 412 ind/km at year 15, which still tends to zero in the long run. The weighted invader density at the new equilibrium ($\gamma_1 N_1 + \gamma_2 N_2 \approx 11{,}063$ ind/km) exceeds the enlarged effective capacity ($1.3K_p(1 - \delta/r_p) \approx 9{,}788$ ind/km).

Strategy C: Integrated Approach. The combination of a moderate harvest $h_1 = 0.30$ year^{-1} and a 20% increase in habitat capacity gives a native population of about 245 ind/km at year 15, again declining towards zero in the long run (Table 5). Hence, within this model, interventions that target only janitor fish, even when combined with habitat restoration of the magnitude considered here, are insufficient: persistence of the native fish requires reversing inequality (20), i.e., reducing $\gamma_1 N_1 + \gamma_2 N_2$ below $K_p(1 - \delta/r_p)$, which in turn requires reducing both invasive populations, or their competitive overlap with native fish, simultaneously.

Table 5. Population densities (ind/km) under the management scenarios at year 15 and in the long term (equilibrium of the modified system)

Scenario	h_1 (year^{-1})	Native capacity	N_1 (year 15)	N_2 (year 15)	P (year 15)	P (long term)
Baseline (no intervention)	0	K_p	10,179	7,417	3	0
A: harvesting	0.45	K_p	4,880	9,793	79	0
A: harvesting	0.90	K_p	481	11,708	581	95
A: complete removal	≥ 1.80	K_p	0	11,918	778	95
B: restoration + harvesting	0.25	$1.3K_p$	7,215	8,705	412	0
C: integrated approach	0.30	$1.2K_p$	6,634	8,985	245	0

These findings carry three main limitations that should be weighed when interpreting the results. First, all parameters and initial densities in Table 1 are hypothetical, literature-informed values rather than direct measurements in the study system, so the projected decline of about 99% and the intervention outcomes reported above are best read as scenario-based, order-of-magnitude estimates rather than site-specific predictions. Second, the model assumes a single, spatially homogeneous patch with constant parameters and no migration (Section 2.1); it therefore does not capture spatial heterogeneity along a river course, seasonal parameter variation, or demographic and environmental stochasticity, all of which could alter the timing and magnitude of native-population decline in practice. Third, the sensitivity analysis is local and varies one parameter at a time, so it does not capture parameter interactions, and the costs and practical feasibility of the interventions were not modeled. Addressing these limitations, for example by incorporating reaction–diffusion spatial structure, time-series field calibration, stochastic perturbations, and global sensitivity methods, is identified as a priority for future research in Section 4.

4. CONCLUSION

This study developed a three-species ordinary differential equation model to quantify the combined impact of janitor fish and an invasive *Trichogaster* population on a native freshwater fish. The two invaders coexist at a stable equilibrium, but their combined competitive pressure exceeds the effective carrying capacity of the native fish; consequently, no positive three-species equilibrium exists, and native exclusion is the only locally asymptotically stable outcome. Without intervention, the native population is projected to decline by about 99% within 10 years. Resource competition, mainly from janitor fish, is the dominant impact mechanism, and the outcome is most sensitive to the janitor fish carrying capacity and the invasive-to-native competition coefficients rather than to invader growth rates. Harvesting janitor fish alone, even when combined with habitat restoration, cannot prevent the decline, because its removal releases gourami from competition.

These results indicate that management should control both invaders simultaneously, supported by measures that reduce invader habitat suitability and restore native habitat. Because the parameters are hypothetical and the model assumes a single homogeneous patch, the findings should be regarded as theoretical projections. Future work should calibrate the model with field data, evaluate joint control strategies and their costs, and incorporate spatial structure, stochasticity, and global sensitivity analysis.

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