
Rosenzweig-MacArthur simulations on community ecology of Nagcarlan Kingfishers: Niche displacement and coexistence of upland Alcedinidae in Santa Barbara River, Laguna, Philippines

Jericho A. Trio

School of Environmental Science and Management,
University of the Philippines Los Baños, Philippines

Abstract — This study is anchored on Rosenzweig-MacArthur equations to explore trophic behavior between Alcedinidae kingfishers (*Halcyon gularis*, *Todiramphus chloris*, *Actenoides lindsayi*, *Alcedo atthis*) and ichthyofaunal prey (*Glossogobius aureus*, *Nomorhamphus pectoralis*, *Poecilia reticulata*, *Giuris margaritacea*, *Glossogobius illimis*) in the lotic habitats of the Santa Barbara River, Nagcarlan, Laguna. Two scenarios were considered, namely, (i) unbounded growth under free-lunch hypothesis and (ii) resource partitioning to assess population trajectories, displacement risks, and coexistence potential. Under the first scenario arrangements of a free-lunch hypothesis, exponential prey saturation triggers Type II functional responses, yielding maximal per-capita growth rates (λ): *H. gularis* (1.1875), *T. chloris* (3.375), *A. lindsayi* (1.1429), *A. atthis* (6.2857). The second scenario anchors on resource partitioning, where predation dampens prey to ~9,500-9,800 individuals with low oscillations: *H. gularis* stabilizes *N. pectoralis*, *T. chloris* curbs *P. reticulata*, *A. lindsayi* tempers *G. margaritacea*, and polyphagous *A. atthis* mitigates *G. aureus* and *G. illimis* surges. Specialists (*H. gularis*, *A. lindsayi*; Type II=0.38) coexist at ~2,000-3,000 individuals. These models underscore growth asymmetries favoring high-r species (generalists) informing interventions such as habitat conservation, niche enhancement, and resource augmentation amid uncertainties of tropical upstream ecology.

Keywords: *niche displacement, population ecology, Alcedinidae, resource partitioning, competitive exclusion, Philippine kingfishers*

I. INTRODUCTION

The competitive exclusion principle (CEP) derived from the works of Russian ecologist Georgy Gause, anchors on the premise how two species cannot coexist under the condition of competing for identical resources within a similar ecological niche. Rooted from Gause's laboratory experiments of *Paramecium* species, CEP asserts how differences in fitness and competitive ability may lead to the relative odds of displacement and eventual extinction of the inferior competitor (Hardin, 1960). In understanding the conception of niche displacement, mathematical modelling provides an avenue for projecting population trajectories under such contested domains. Anchored on ecological realism, the Rosenzweig-MacArthur (RM) predator-prey model recognizes how prey items have a tendency for self-limitation while predators exhibit functional responses and associated adaptations to efficiently capture prey (Mittelbach and McGill, 2019).

In permutations where multiple predators and an array of prey items exist within an ecosystem, the RM model frames competitive exclusion as the phenomenon where a predator species becomes dominant leading to exclusion and eventual extinction of less competitive predators. This ecological occurrence has ramifications on predator community behavior particularly those belonging within the same family, as in the case of the Alcedinidae avifauna of Nagcarlan, Laguna. It is critical to acknowledge how upland and upstream environments are characterized by headwaters in high-elevation terrains which often have steep gradients, and permeable bedrock which triggers rapid hydrological responses to precipitation (Gabrielli et al., 2012). These systems serve as critical sources for downstream ecosystems but exhibit profound uncertainty and volatility, driven by natural variability and anthropogenic influences.

Revolving on this premise of uncertain environments, the following study aims to: (i) identify Alcedinidae and ichthyofaunal species richness throughout the Santa Barbara River continuum, (ii) model scenarios of niche displacement and population trajectory of Alcedinidae relative to their ichthyofaunal prey items, and (iii) conceptualize interventions on possible niche displacement. As such two scenarios were simulated, (i) a free-lunch hypothesis for ichthyofaunal prey items of the Alcedinidae guild, and (ii) a resource partitioning scenario for upland Alcedinidae in Nagcarlan.

II. METHODOLOGY

Map of Life Engine

Shapefiles of barangays along the Santa Barbara River continuum (Sulsugin, Alumbrado, Talahib, and Sabang) were integrated to the Map of Life Engine. The Map of Life Engine is a platform developed by Yale University's Center for Biodiversity and Global Change. Launched around 2012 and continuously updated, it serves as a comprehensive global database and visualization tool for biodiversity data. Utilizing the Regions Feature tool, shapefiles of the riparian barangays were implemented, yielding an Excel file of species present (in terms of point observation and expert range) within the area. Point observations span from the 1700s (historical specimens) to the present day (2025), with the bulk from 1946–2014 in core integrated datasets, though real-time updates from citizen science platforms extend this to ongoing collections. Expert range maps from International Union for Conservation of Nature (IUCN), represent distributions circa 1980–2010, based on expert assessments at the time of compilation, but are periodically refined.

Study Site

Spanning 2.5 km, the Santa Barbara River is fed by headwaters in Entablado, Rizal. The river runs through Barangay Sulsugin before reaching its mouth at Barangay Sabang, where it joins the Lapad River in the vicinity of Santa Lucia, Nagcarlan. Under Philippine arrangements, an area is considered as upland if its slope is within 18° or exceeds such threshold (Suh, 2012). The Municipality of Nagcarlan, classifies Barangay Talahib and Barangay Sulsugin as upland barangays. Each has a slope of 19.2° (for Talahib) and 18.6° (for Sulsugin). The areas of Alumbrado and Sabang are still flagged as lowland areas each having a slope of 10.20° (for Sabang) and 11.9° (for Alumbrado).

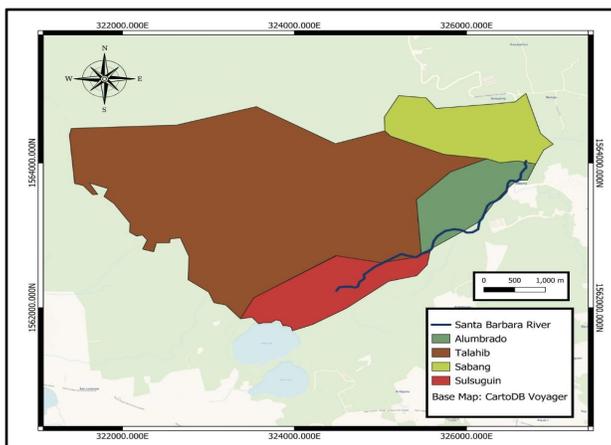


FIGURE 1. STUDY SITE FOR REMOTE SENSING (MAPPED USING QGIS 3.44.2)

III. RESULTS AND DISCUSSION

Santa Barbara River Community Ecology - Results from Remote Sensing

TABLE 1. REMOTELY SENSED ICHTHYOFAUNAL SPECIES OF THE SANTA BARBARA RIVER CONTINUUM

| Species | Common Name | Family | IUCN Status | Endemicity | Santa Barbara River Continuum | | |
|--------------------------------|-----------------------|-------------------|-------------|-------------------------|-------------------------------|-----------|------------|
| | | | | | Upstream | Midstream | Downstream |
| <i>Glossogobius aureus</i> | Golden goby | Gobiidae | Endemic | Endemic | | Present | Present |
| <i>Glossogobius illimis</i> | Celebes flathead goby | Gobiidae | Endemic | Endemic | Present | | Present |
| <i>Nomorhamphus pectoralis</i> | Common half-beak | Zenarchopt eridae | Endemic | Endemic | | Present | Present |
| <i>Poecilia reticulata</i> | Guppy | Poeciliidae | Endemic | Endemic | | Present | Present |
| <i>Giuris margaritacea</i> | Snakehead gudgeon | Eleotridae | Endemic | Endemic | | | Present |
| | | | | Species Richness | 1 | 3 | 5 |

* Map of Life Engine (Point observations and expert range)

Legend:

Presence of species: Cosmopolitan Native Invasive Alien Relict Endemic

Extinct Extinct in the Wild Critically Endangered Endangered Not Evaluated Least Concerned

Near Threatened Vulnerable Data Deficient

Referencing on remotely sensed ichthyofaunal species of the Santa Barbara River continuum, the downstream segment in Barangay Sabang recorded a high species count characterized by the presence of gobbies, half-beaks, gudgeons, and poecilids. Relative to Figure 1, it can be observed how the downstream segment of the Santa Barbara River exists as a confluence of three tributaries draining towards Lapad River. In terms of Alcedinidae sightings and Map of Life point observations, four kingfishers were identified— (i) *Halcyon gularis*, (ii) *Todiramphus chloris*, (iii) *Actenoides lindsayi*, and *Alcedo atthis* are persistent within the four barangays — Sulsugin, Alumbrado, Talahib, and Sabang in Nagcarlan.

Scenario building

Scenario 1 - Niche displacement under the free lunch hypothesis

The first simulation scenario utilizes a simplified Rosenzweig-MacArthur (RM) model under the premise of a free lunch hypothesis. Within these arrangements the prey guild is understood to expand exponentially in the absence of both intraspecific (and) interspecific competition. Recognizing density-independence, carrying capacity is non-existent in this set-up. Prey is to be construed as an unlimited resource. The predatory guild is constructed to behave under a multi-prey Holling Type II functional response. In community ecology, the multi-prey Holling Type II assumes that a predator cannot handle multiple items at once, thus time spent on one prey reduces time available for others (Holling, 1959). The predatory coven in this simulation is framed to upland Alcedinidae of Nagcarlan, Laguna, namely, *Halcyon gularis* (Brown-breasted Kingfisher), *Todiramphus chloris* (Collared Kingfisher), *Actenoides lindsayi* (Spotted Wood Kingfisher), and *Alcedo atthis* (Common Kingfisher). In terms of prey items, identified ichthyofauna included, *Nomorhamphus pectoralis* (Common Half-beak), *Glossogobius aureus* (Golden Tank Goby), *Poecilia reticulata* (Guppy), *Giuris margaritacea* (Snakehead Gudgeon), and *Glossogobius illimis* (False Celebes Goby).

Within these settings, the model assumes the absence of prey depletion by predation as predators as both predator and prey start a baseline population of 500 individuals per species. 50%

of individuals are females in both predator and prey. The behavior for prey-and-predator population is anchored on two ordinary differential equations relative to the Rosenzweig-MacArthur (RM) framework,

For prey population growth,

$$\frac{dN_j}{dt} = r_j N_j - \frac{P_i N_j}{1 + N_j}$$

Where,

- N_j : prey item density
- P_i : predatory guild density
- r_j : intrinsic growth rate

For predator population growth,

$$\frac{dP_i}{dt} = \frac{P_i N_j}{1 + N_j} - d_i$$

Where,

- N_j : prey item density
- P_i : predatory guild density
- d_i : death rate

The probability that niche partitioning occurs is excluded in this scenario as all Alcedinidae in the predator guild share ichthyofaunal prey equally, leading to relative displacement through varied intrinsic growth rates (where predator growth rate is represented as λ_i). The model limits niche displacement as “*relative exclusion*” of one predator species from a shared resource base over time, driven by differences in intrinsic growth rates under conditions of resource abundance (free-lunch). In contrast to competitive exclusion (as expressed in a Lotka-Volterra model on which shared resources result in absolute extinction), the discourse on niche displacement departs from the classic Paramecium experiment of Gause and is contextualized on exponential Alcedinidae growth relative to prey abundance. Displacement is realized when the proportion of a subordinate species in the predator guild declines to near-zero (Mittelbach & McGill, 2019). The simulation runs on a fifty-year projection where a log-scale was implemented to manage overflow. The following auxiliary variables were considered for parameter estimation, attack rate (a) and conversion efficiency (e). Predatory attack rate (a) on efficiently searching prey items is assumed to be constant among members of the Alcedinidae guild ($a = \sim 10^{-4}$); conversion efficiency (e) is construed as the predator biomass conversion intake, assumed in a 1:1 constant ratio.

Scenario 2 - Resource Partitioning

Under pragmatic ecological arrangements, the discussed phenomenon of niche displacement (simulated in the first scenario) may not be realized in conception, as avifaunal species spatially partition and coexist in their access to resource items. In community ecology, resource partitioning refers to the pathway where the division of scarce resources such as prey items, habitat, and foraging areas among similar species through varied resource utility facilitates coexistence by minimizing the odds of interspecific competition (Griffin & Silliman, 2011). For instance, in the context of the lentic environs of the South Llano River in Texas, USA, three sympatric Alcedinidae— the Green Kingfisher (*Chloroceryle americana*), Belted Kingfisher (*Megaceryle alcyon*), and Ringed Kingfisher (*Megaceryle torquata*), appear to coexist along the segments of the river continuum. *C. americana*, the most abundant Alcedinidae (0.48 individuals per river km), was resident year-round and predominantly used low perches (mean height 142.3

cm \pm 126.6 SD), often situated near shallow riffles (<0.5 m deep) ideal for capturing diminutive fish and crustaceans. On the other hand, *M. alcyon* (0.22 per km) and *M. torquata* (0.09 per km) Kingfishers, which migrate seasonally and are absent from mid-spring to mid-summer, favored elevated perches (means of 550.8 cm and 551.1 cm, respectively), enabling dives for larger prey like minnows up to 15 cm long (Chodacki and Skipper, 2019).

The third simulation scenario assumes conversion efficiency ($e = 0.05$), where consumed prey biomass is transformed to predator growth. 50% of females are assumed to exist in both predator and prey populations; a baseline population of 500 individuals per species was implemented for predator and prey guilds. Intraspecific predator competition is assumed to be absent beyond bottom-up limits; at stable proportions > 0.01 , niche partitioning is constructed to promote coexistence. In running the model, log-scale plots were introduced to avoid incremental deviations at $\log(0)$.

The following differential equations were considered to model resource partitioning of upland Alcedinidae:

(i) for prey behavior,

$$\frac{dN_j}{dt} = r_j N_j - \sum_{k=1}^4 \frac{a_{kj} N_j P_k}{1 + h_k \sum_{m=1}^5 a_{km} N_m}$$

(ii) for predator behavior,

$$\frac{dP_k}{dt} = e \left(\frac{\sum_{j=1}^5 a_{kj} N_j}{1 + h_k \sum_{m=1}^5 a_{km} N_m} \right) P_k - d_k P_k$$

Where,

- N_j represents prey population density
- N_k represents predator population density
- r_j represents intrinsic per capita growth rate of prey
- a_{kj} represents attack rate coefficient for predator k on prey j
- h_k represents handling time for predator k
- e represents attack efficiency fixed at 0.05
- d_k represents per capita death rate

It is critical to recognize that the denominator, $1 + h_k \sum_j a_{kj} N_j$, normalizes the Holling Type II functional response in the system of equations implemented. This results to a total consumption rate for predator k as $\frac{\sum_j a_{kj} N_j}{1 + h_k \sum_m a_{km} N_m} P_k$, construed as a weighted average over prey.

In terms of proportionality in prey loss allocation, $\frac{a_{kj} N_j}{1 + h_k \sum_m a_{km} N_m}$, is the specific removal rate for prey j by predator k . This system of equations secure the “no free-lunch” condition, whereby total predation depletes shared resources unless partition occurs.

Population trajectory and interventions

Scenario 1

Under a free-lunch hypothesis, prey guild members explode exponentially resulting in saturation to Alcedinidae Type II functional responses. Predator growth trajectory at max per-capita rates yields the following λ values — *H. gularis* (1.1875), *T. chloris* (3.375), *A. lindsayi* (1.1429), *A. atthis* (6.2857). With a baseline population of 500 individuals per species, Alcedinidae populations follow $P(t) = 500 \times \exp(\lambda t)$, derived from $\frac{dP}{dt} = \lambda P$. Absolute predator populations amplify with *A. atthis* expressing the steepest growth (10^{137}). Relative proportions reveal an episode of displacement, at year 50, *A. atthis* emerges as the dominant Alcedinidae, $\log_{10} P_{atthis}(50) = 139.7$; this manifests extreme growth when compared to, *T. chloris* (76.3), *H. gularis* (28.6), and *A. lindsayi* (27.6). Under an unbounded growth regime, it can be said that the maximal λ_i of *A. atthis* is an emergent property which eclipses its Alcedinidae relatives in

exploiting the ichthyofaunal communities of Santa Barbara River. *A. lindsayi* appears the Alcedinidae to be displaced as evident on having the lowest $\lambda = 1.1429$. Although absolute population increases 10^{25} , its predator guild members outpace it exponentially by year fifty. This implies apparent competition as unlimited prey triggers growth asymmetries particularly to low-fecundity species.

Three interventions assess conservation strategies to support the ecologically displaced *A. lindsayi*. The first intervention boosts reproductive output by 20%, raising the maximum birth rate to 1.5429. This prevents a population crash and increases absolute abundance to 1.2×10^{-5} individuals, though competition with *A. atthis* remains high. The second intervention focuses on mortality reduction by extending life expectancy to 8.4 years, which delays total competitive exclusion from 10 to 15 years and yields a final population of 9.8×10^{-4} . The third intervention implements top-down regulation by harvesting the dominant *A. atthis*, reducing its offspring by 20%. This strategy yields the most significant benefit for the subordinate species, cutting the dominant competitor's growth rate by 18.2% and allowing *A. lindsayi*'s population proportion to surge to 0.0076 by year 50. Collectively, these demographic shifts—whether through supplemental breeding, habitat-driven lifespan extension, or selective harvesting—demonstrate how targeted management can mitigate the competitive exclusion principle and promote long-term multispecies persistence within the predator guild.

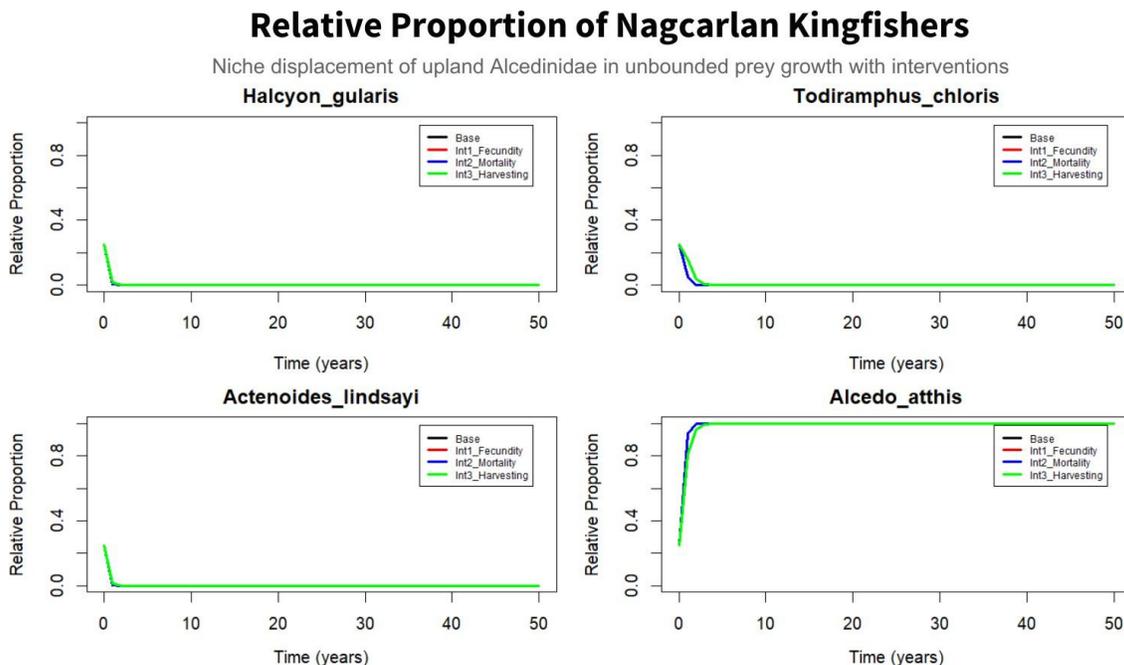


FIGURE 2. HYPOTHETICAL PREFERRED ICHTHYOFAUNAL PREY OF UPLAND ALCEDINIDAE

Scenario 2

The model implements the hypothetical correspondence between predator and prey populations of Santa Barbara River in Nagcarlan, Laguna under the arrangements of resource partitioning. Ichthyofaunal communities are dampened by Alcedinidae which prefers each species respectively. Under baseline conditions, *N. pectoralis*, expresses an intrinsic growth rate (71.5) mirrored by its reproductive output of 12 clutches/year and a life expectancy of two years; a gradual sigmoid growth over 10 - 20 years is expressed with predation from *H. gularis* dampening the population to ~9500-9900 individuals. In the case of Santa Barbaran gobies, dominance from scenario two is being mitigated by polyphagous *A. Atthis* of whom feasts on *G. aureus* and *G. illimis*. For instance, *G. aureus* and *G. illimis* follows a near-instantaneous growth to ~10,000 individuals at year one manifesting a mild damp due to predation resulting with a population of ~9800 and low-amplitude oscillations. Guppies such as *P. reticulata* experiences moderate growth over ~10 years, the population trajectory as it approaches carrying capacity behaves sigmoidally;

T. chloris predation stabilizes guppy population at ~9500 individuals as it reduces intrinsic growth rate by ~0.25-0.5. Gudgeon population (as in the case of *G. margaritacea*) experiences explosive early growth to ~10,000 by the first year of the 50-year projection; stronger damping and oscillations towards equilibrium, resulting to a population of ~9500 dampened by *A. lindsayi* predation.

Alcedinidae population behavior within a resource partitioning arrangement is not to be understood as isolated from prey guild members. It can be observed how for polyphagous Alcedinidae such as *A. atthis*, experienced an increase from 2000-3000 during initial years noting a slight proportion boost (0.28); the Holling Functional Type II response value for *A. atthis* of 0.0125 is flagged as unfavorable as it may cause decline of relative Alcedinidae (Dunn & Hovel, 2020). This behavior is seen on arrangements where niche partition is absent (scenario 1), on which *A. atthis* becomes the dominant species. Preferred specialists appear in two upland Alcedinidae, namely, *H. gularis* and *A. lindsayi*, where both share a Functional Type II response value of 0.38, indicating episodes of coexistence; in the context of such species, net per capita growth rate of 0.065 leads to exponential rise and eventual stabilization at ~2000-3000 individuals by year 50. Slight proportional advantages (~0.25-0.28) are expressed in *T. chloris*, contributing to total biomass ~8000; its trajectory mirrors preferred growth but with minor elevation.

In order to sustain resource partitioning among the Alcedinidae guild of Santa Barbara River, the following measures were pursued as forms of interventions in the baseline model— niche enhancement, handling reduction, and pulsating prey— pitied against a scenario of uniformity which diminishes partition. The interventions were limited to the displaced *A. lindsayi*'s in the previous model scenarios of this study. Life history statistics and attack efficiency of *A. lindsayi* (relative to its hypothetical preferred prey item, *G. margaritacea*) were considered to comprehend population trajectories in a fifty-year scenario.

Resource Partitioning Prey and Predator Population Trajectory

Baseline Conditions | Alcedinidae and ichthyofaunal communities of Santa Barbara River

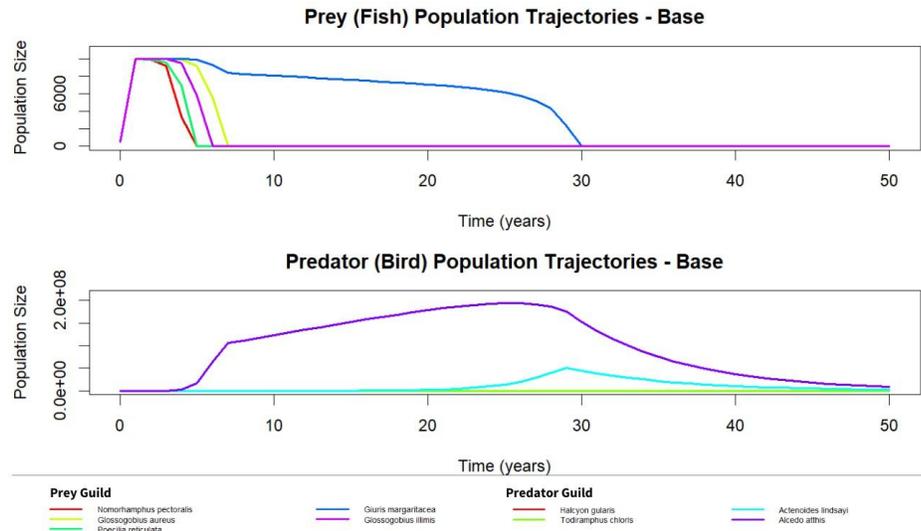


FIGURE 3. BASELINE CONDITIONS OF ALCEDINIDAE AND PREY GUILD MEMBERS OF SANTA BARBARA RIVER UNDER A RESOURCE PARTITIONING SET-UP

In the first intervention, increasing *A. lindsayi*'s attack rate by 7.5×10^{-4} reduces niche overlap with competitors, allowing the species to reach a 0.35 population proportion and stabilize at 4000 individuals while prey populations drop to 9000 with 8-year oscillations. The second intervention reduces handling time to 0.47 to enhance the Holling Type II functional response, which imposes stronger top-down regulation that drives prey equilibrium down to 8500 with shorter 6-year cycles, while *A. lindsayi* peaks at 5000 individuals and stabilizes at 4500. Under the third intervention, periodic supplementation of 1000 prey individuals creates transient spikes and a higher mean prey density of 9600, leading to a 20% increase in the *A. lindsayi* population and a 0.32 final proportion. These specialist gains are contingent upon resource partitioning; in a "Uniformity Scenario" where partitioning is removed, symmetric competition favors the generalist *A. atthis* (0.28 proportion), causing specialist populations to collapse to near-zero levels.

Resource Partitioning Prey and Predator Population Trajectory

Interventions | Upland Alcedinidae and ichthyofaunal communities of Santa Barbara River

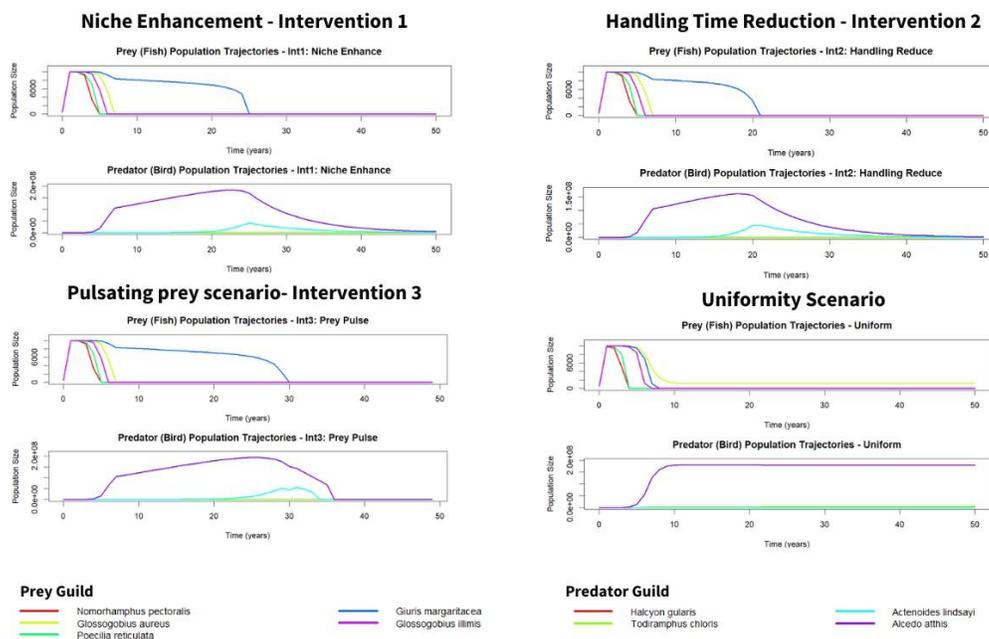


FIGURE 4. INTERVENTION SCENARIOS OF ALCEDINIDAE AND PREY GUILD MEMBERS OF SANTA BARBARA RIVER UNDER A RESOURCE PARTITIONING SET-UP

IV. CONCLUSION

As emphasized in the introductory segment of this study, upstream ecology is uncertain and volatile. Rivers on which upland Alcedinidae depend upon may vanish brought by droughts or sudden tectonic shifts, placing the predator guild in precarious settings. The RM model seeks to population behavior of upland Alcedinidae relative to their ichthyofaunal prey. The three scenarios affirm how the tendency of the environment to favor generalists (high-r species) rather than specialists. It is critical to recognize that these simulations are hypothetical; on-the ground observations are necessary to validate remotely sensed data as well as the trajectory generated by each scenario. As upland forests face the dire threats of unregulated deforestation, illegal mining, and urban sprawl both Alcedinidae and upstream ichthyofauna face uncertain futures. This places the necessity to consider crafted model interventions in the conception of municipal ordinances and policy grounded on science. In the absence of anthropogenic intervention, the odds of niche displacement is a surety. The last hymn of *A. lindsayi* and its brethren may be its finale within the forests of Nagcarlan.

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