

1 **How effective are frogs in regulating crop pest population in a natural**
2 **multi-trophic system??**

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32 **Abstract**

33 Abstract:

34 Potential of frogs as important natural pest control agents has been highlighted earlier. But
35 the effectiveness of frogs in regulating the pest load in intensive agricultural landscape in a
36 multi-trophic system is not clear. We performed controlled field experiment in paddy field
37 with a varying density (observed in high and low agricultural intensity (AI) areas) of a
38 commonly found frog species and compared the pest and pest predator build-up. The
39 consumption rate of the model amphibian was studied using enclosure experiment. The
40 consequent trophic cascade effect of frogs on both crop pest and other arthropod pest
41 predator was analyzed using mathematical population growth models. Although frogs
42 consumed pests, they could not reduce crop pest abundance. although a lesser frog density
43 found in high AI areas significantly affected the pest predator abundance. Based on the
44 functional response result, mathematical growth models demonstrated that with a constant
45 harvesting factor (Holling's Type II) frogs will always have a negative impact on the beneficial
46 natural enemy population due to intraguild predation thereby limiting its potential as a pest
47 regulator. Our study challenges the notion of frogs as an effective pest control agent and
48 argues that increasing habitat diversity might improve overall biological pest suppression.

49 Keywords: Frogs, Biological Pest regulation, Functional response, Intraguild predation, Trophic
50 cascade effect

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62 1. INTRODUCTION

63 Extensive use of agro-chemicals and habitat loss associated with agricultural intensification
64 has been identified as a major driver of biodiversity loss in agricultural landscape (Dudley
65 and Alexander, 2017; Balmford et al., 2012; Newbold et al., 2015; IUCN, 2014; Lajmanovich
66 et al., 2003). The negative impact of biodiversity loss on Ecosystem Service (ES) delivery in
67 agriculture has also been recognized widely (Brook et al., 2008; Tscharntke et al., 2005).
68 Ecological Intensification (EI) of agriculture on the other hand has been suggested as a
69 sustainable solution to conventional high external agro-chemical input-driven intensive
70 agriculture (Tittonell, 2014). EI involves restoration or improvement of the ES provisions in
71 agriculture e.g., crop pollination, biological control of crop pests, or soil biological activities.
72 However, there exists a serious gap in our scientific understanding about the underlying
73 ecological processes that generate ES (Firbank et al., 2013; Birkhofer et al., 2015; Naeem et
74 al., 2015; Bengtsson, 2015).

75

76 Biological control of crop pests is a key ES (Bengtsson, 2015; Ives et al., 2000; Wilby and
77 Thomas, 2002; Gurr et al., 2003). However, despite years of research, our understanding of
78 the underlying ecological processes that govern biological control, particularly, the complex
79 food web interactions that regulate the process, is still incomplete (Thies et al., 2005;
80 Bengtsson, 2015). Contrary to the benefits obtained from natural enemy population, several
81 studies have highlighted the detrimental effects it may have on the non-target population
82 (Clarke et al., 1984; Howarth, 1983, 1991). Hence any biological pest control strategy
83 warrants thorough scrutiny of the trophic cascade in a multi-species system.

84

85 Amphibians have long been recognized as potential natural predators for crop pests (Hamer
86 et al., 2004; Knutson et al., 2004; Gibbs et al., 2005; Loman and Lardner, 2006) being both
87 generalist and opportunist predator (Kathiwada, 2016; Schaefer et al., 2006; Mahan and
88 Johnson, 2007). The importance of amphibians in biological control, particularly in rice
89 cultivation has been particularly recognized (Li et al., 2008; Zhang et al., 2010; An et al.,
90 2012; Zhang, 2013). A sizeable abundance of amphibians is suggested to be efficient in
91 bringing down the rice pest population (Teng, et al, 2016; Fang et al., 2019). Kathiwada
92 (2016) reported a high proportion of rice pests in frogs' diet and recommended the
93 introduction of frogs as biological pest control in rice fields. Intensive agriculture has been
94 found to negatively impact frog population (Arntzen et al. 2017; Davies et al. 2018). Ghosh
95 and Basu (2020) reported reduced density of amphibian fauna in areas of high agricultural
96 intensification compared to low agricultural intensity areas. A decline in frog population in an
97 intensive agricultural landscape is therefore expected to impact ES delivery in rice fields.

98

99 However, most studies that reported the potential of frogs as pest regulators have not looked
100 at the effect frogs may have on non-target species especially beneficial natural arthropod pest
101 predators. These studies also have not investigated if frog predation of rice pests could
102 effectively bring down pest population through controlled multi-trophic field experiments.

103

104 The extent to which predation can regulate the prey population is influenced by the functional
105 response of the predator to changing prey density (Leeuwen et al., 2007; Williams and
106 Martinez, 2004; Wollrab and Diehl, 2015). It is therefore important to gain insights into the
107 functional response of frogs to changing density of rice pests before coming to a conclusion
108 about their effectiveness as rice pest regulator. However, none of the studies that prescribed
109 frogs as potential regulators of crop pests has considered this.

110 The present study attempts to bridge these gaps by testing the efficiency of frogs in regulating
111 crop pest population through a multi-trophic controlled field experiment conducted at the
112 Agricultural Experimental Farm, University of Calcutta, West Bengal, India using a focal
113 frog species available commonly in the agricultural fields across India. The experiment was
114 designed with field-realistic densities of frogs found in the high and low agricultural intensity
115 areas in the study region reported earlier by Ghosh and Basu (2020). Therefore, apart from
116 answering if frogs are efficient regulators of rice pests, the study also explores the impact of
117 agricultural intensification on ES delivery by frogs. We also assess the functional response of
118 the focal frog species to varying densities of a common rice pest in the study region. We also
119 predict if the focal frog species can be an efficient pest regulator in a multi-trophic system
120 using a mathematical model based on our results.

121

122 **2. Materials and Methods**

123 **2.1 Experiment Site**

124 The experiment was performed in the Agricultural Experimental Farm, University of
125 Calcutta, Baruipur Campus in West Bengal in 2018 (22.3787°N, 88.4361°E). The farm is
126 spread across an area of 210 acres with paddy being the major crop grown during the
127 monsoon. Total experimental area was 7,500 square meter. The follow-up mesocosm
128 experiment to study the nature of feeding response in amphibians was performed in the
129 University campus.

130 **2.2 Experimental design**

131 Three blocks of 50 X 50 meters area were selected to carry out the study. Each of the blocks
132 was divided into 6 experimental plots of 10 X 10 meters where we installed our experimental
133 units using drift fence of length 10m and height 3ft. Thus we installed a total of 18
134 experimental plots across an area of 7500 m². We left a buffer of 5m between each

135 experimental plot. We randomly assorted the plots to three different frog treatments which
136 were - one control without frogs, one with a treatment density of 10 frogs / 100 m² as
137 observed in low agricultural intensification and third with a treatment of 5 frogs / 100 m²
138 representing the density observed in high agricultural intensification zones (density data
139 obtained from a study conducted in Odisha along an agricultural intensification gradient,
140 Ghosh and Basu, 2020).

141 **2.3 Experimental model**

142 We used adult (5-6 cm) paddy field frogs or *Fejervarya limnocharis* as our model organism
143 as they are the most dominant in paddy fields of India (Dash and Mahanta, 1993). They are
144 prevalent in South Asia (Sumida et al., 2007). This species is also a generalist and feeds
145 mainly on insects (Chuang and Borzee, 2019) hence makes it a potential bioresource to test
146 their pest controlling efficiency. Apart from these, the species is categorized as least concern
147 by IUCN (IUCN, Conservation International and NatureServe, 2006), hence our study did not
148 put any undue extinction pressure. We collected amphibians by active search in August 2018
149 from within the campus area for release in experimental plots.

150 **2.4 Experimental plot preparation**

151 We selected paddy fields for its economic demand and the huge swathe of land under paddy
152 cultivation and used a local rice cultivar named “Patnai”.

153 We prepared the seedbed on 30th June at a density of 1916 seeds/ m² for a total seedbed area
154 of 210 m². Paddy saplings were transplanted around 30 days after preparing seedbed from 27
155 to 29 July 2018 at an average density of 762 plants/100 m². Before releasing the frogs, all
156 pots were covered with a mesh net of 48mm gap size to exclude predation risk on both the
157 pests and experimental frogs by birds as well as to prevent the escape of any frogs from the
158 experimental enclosures. Plots were left undisturbed for 15 days before the release of frogs.
159 Frogs were released on August 15th, 2018, after sunset when the temperature was low to

160 prevent desiccation. After leaving the system undisturbed in order to allow the animals to
161 overcome any stress during their release process, we started sampling from August 20th,
162 2018. No pesticides, herbicides, or any fertilizers were applied in the plots to eliminate any
163 detrimental effects on animals. The study continued throughout the vegetative phase until the
164 flower stage and crops were harvested at end of November 2018.

165

166 **2.5 Arthropod sampling**

167 All active and passive sampling was conducted from 6.00 hr to 13.00 hr of a day. For insect
168 sampling, we used the sweep netting method (Fatahuddin et al., 2020) with a standard-sized
169 sweep net of 24 inches length and an opening diameter of 12 inches. Sweep netting was done
170 10 times along each of the four sides of the experimental plots making a total of 40 sweeps
171 per plot. All specimens collected were wet preserved in 70% alcohol for later identification
172 and categorization.

173

174 **Passive sampling: Pest Infestation study**

175 We used a 1 X 1 meter wooden frame and placed it randomly within an experimental plot.
176 For each sampling, data on the total number of plants and total number of leaves were
177 collected. We selected 3 random plants within each such quadrat and inspected proportion of
178 infestation (Teng et al., 2016) by rice hispa (*Dicladispa sp.*), leaf folder (*Cnaphalocrocis*
179 *sp.*), defoliation, tungro, rice whorl maggot (*Hydrellia sp.*). For leaves where we could not
180 identify the infestation, were collected and preserved for later identification under expert
181 supervision. At each quadrat, we also searched for the presence of any pest or predator and
182 wet preserved the specimen in 70% alcohol for later identification. This method was
183 replicated 5 times for each plot per sampling.

184 We maintained the same sequence of sampling for the different treatments (6 plots for each
185 treatment) and pooled observations from 6 plots per treatment in each complete sampling
186 session. We averaged data for further statistical analysis and data representation. All the
187 samplings were repeated four times for each plot throughout the paddy growing season. This
188 covered all the successive stages of rice cultivation following transplantation to flowering
189 stage.

190 **2.6 Estimating the frog survival**

191 From 17.00 hr to 21.00 hr every day we counted the frogs and checked for any dead or
192 desiccated frog inside the experimental plot to ensure that the number of frogs remained
193 constant.

194

195 **2.7 Arthropod Identification**

196 We identified all arthropods obtained in active sampling up to genus level and broadly
197 grouped them into orders to categorize them as pests and non-pest natural predators (Khan
198 and Pathak, 1994; NICRA, 2011) for the purpose of this present study.

199

200 **2.8 Experiment to study the feeding potential in this species**

201 We performed a mesocosm experiment with one size class of frogs (5-6cm, adult) and three
202 prey densities of 8, 33, and 43. We used grasshoppers in this experiment as they are one of
203 the major paddy defoliators. Our field observation also showed the model amphibian feeding
204 on the grasshopper. The densities of grasshopper used were replicates from control treatments
205 of the field experiment (observed grasshopper densities were 8, 33, 43 and 44). The entire
206 experiment was replicated four times through the months of September till November 2019.
207 On the day of the experiment, one predator was transferred to the experimental mesocosm of
208 1x1 meter that was designed to mimic the natural environment of these predators. Health of

209 the mesocosm was maintained regularly. Total experimental time was set for 17 hr. At the
210 end of the experiment, we removed the predator and counted the remaining prey. All
211 predators had the same starvation period before they performed in an experiment. Since they
212 feed on live prey we also maintained a separate terrarium for the prey at varying densities to
213 check the mortality rate in 24 hr and found no death over the period.

214 To collect data on the handling time and attack rate of frogs, we replicated the experiment
215 with varying prey densities and recorded the feeding rates for 30min with a video camera
216 (Nikon 5200D) fitted outside the terrarium.

217

218 **2.9 Statistical analysis**

219 We performed a Kruskal-Wallis test to compare the difference in the number of transplanted
220 seedlings.

221 Proportion of pest infestation by 5 major paddy pests was checked using nested ANOVA
222 with a mixed-effects model where sampling phases and frog treatments were the fixed effects
223 and treatment within blocks was included as random effects. Comparison of means was
224 performed for both the fixed effects. We checked the significance of the random effects by
225 comparing the above described model with a second model containing only the fixed effects.

226 For total pest and pest predator count, a Generalized Linear Mixed Model (GLMM) with
227 negative binomial error distribution was applied to check their abundance with varying
228 phases of the paddy growth and frog treatments (Alexander et al., 2000; Linden and
229 Mantyniemi, 2011; Ghosh and Basu, 2020). The model structure was the same as that of the
230 nested ANOVA.

231 We performed a diagnostic test for the functional response (Pritchard et al., 2017) with prey
232 eaten as a function of prey provided. Based on the result we created a final model with attack
233 rate and handling time.

234 We used R software (version 3.5.2) (R Core Team, 2018) to perform all the analyses using
 235 packages- nlme, Mass, lmtest, multcomp, lme4, frair.

236 **2.10 Mathematical Growth Model:**

237 In the presence of n number of frogs, the pest and pest predator dynamics will vary
 238 depending on the consumption rate of these frogs (provided the resource available to the crop
 239 pests is constant across the three treatments) and also by their mutual birth and death
 240 processes in which the predator-prey interaction plays an important role.

241 We designate, x_1 = number of pests and x_2 = number of pest predators while “ n ” number of
 242 frogs act as predators for both the crop pests and the crop pest predators.

243 Since this frog species is a generalist, it does not have any preference for crop pests or
 244 predators, and its feeding process is assumed to be a random one, with a total mass “ m ” being
 245 consumed in “ T ” time, from a “meal” that consists of prey and predator, for which the model
 246 is assumed to be as follows.

247

248 **Model of frog predation on crop pest and predator:** It is clear from the above that if frogs
 249 were to feed exclusively on pests, it would need to eat $n_1 = (m/m_1)$ pests while if it were to
 250 feed exclusively on the predator, it would consume $n_2 = (m/m_2)$ predators where m_1 and m_2
 251 are the mass of pest and pest predator respectively. These can be satisfied with “success
 252 rates” that are proportional to $N_1 = (x_1/n_1)$ and $N_2 = (x_2/n_2)$ respectively and would occur with
 253 relative chances P_1 and P_2 given by,

254
$$P_1 = N_1 / (N_1 + N_2) = \frac{x_1/n_1}{x_1/n_1 + x_2/n_2} = \frac{\frac{m_1 x_1}{m}}{\frac{m_1 x_1}{m} + \frac{m_2 x_2}{m}} = \frac{m_1 x_1}{m_1 x_1 + m_2 x_2} \quad \dots\dots\dots 1$$

255
$$P_2 = 1 - P_1 = \frac{m_2 x_2}{m_1 x_1 + m_2 x_2} \quad \dots\dots\dots 1.1$$

256 Thus with n number of frogs present, the consumption rate of pests is :

257
$$(n n_1 P_1) / T = \frac{nm/T}{m_1} \cdot \frac{m_1 x_1}{m_1 x_1 + m_2 x_2} \quad \dots\dots\dots (2.1)$$

258 and the consumption rate for predators is

259
$$(nn_2P_2)/T = \frac{nm/T}{m_2} \cdot \frac{m_2x_2}{m_1x_1+m_2x_2} \dots\dots\dots(2.2)$$

260 The evolution equations of the pest and predator are then,

261
$$\frac{dx_1}{dt} = a_1x_1 - b_1x_1x_2 - \frac{(\frac{nm}{T})x_1}{m_1x_1+m_2x_2} \dots\dots\dots(3)$$

262
$$\frac{dx_2}{dt} = - a_2x_2 + b_2x_1x_2 - \frac{(\frac{nm}{T})x_2}{m_1x_1+m_2x_2} \dots\dots\dots(4)$$

263 For Eq (3), the first term is the natural birth rate of the pest while the second term is their
264 death rate due to feeding by the predator and the third term that follows from Eq (3) is the
265 death rate of the pest due to consumption by frogs. Similarly, for Eq(4), the first term is the
266 death rate of a predator in absence of prey while the second term is the predator's growth rate
267 as they feed on the prey, and the last term is the death rate of the predator due to consumption
268 by frogs.

269

270 **3. Results**

271 **3.1 Statistical Analysis**

272 **Control experiment**

273 The mixed effect models showed no significance in frog treatments for any of the five major
274 paddy pest infestation types. However their abundance varied with the growth phases of
275 paddy crop. Table 1 provides fixed effects in models for these 5 pest infestation types.

276 Pest abundance similarly showed a significant difference in the 2nd (p < 0.000), 3rd
277 (p<0.000), and 4th phase (p<0.000) of sampling but none of the frog treatments had any
278 significant effect (5 frog treatment p=.077; 10 frog treatment p=0.369).

279 Pest predator abundance appeared to be significantly affected by different phases of paddy
280 growth i,e the 2nd (p< 0.000), 3rd (p< 0.000), and 4th (p=0.006) sampling phases. But, the

281 abundance of these pest predators was also significantly affected by the lower density of
 282 frogs (5 frog treatment $p=0.016$; 10 frog treatment $p= 0.159$) (Table 2).
 283 Figure 1 shows a prominent difference in the pest predator dynamics compared to the
 284 respective abundance in the control plot. Since the resource available for the crop pests across
 285 the treatment is the same (Kruskal Wallis chi-squared = 2.9454, $df = 2$, p -value = 0.229), and
 286 other external factors remaining similar, such difference in pest and predator build-up can
 287 only occur due to the harvesting factor from frogs. However, this harvesting factor is proved
 288 to be limited in the Functional Response analysis presented in the following section.

289 3.2 Functional response from a mesocosm experiment

290 Diagnostic tests indicated the feeding response pattern in our focal frog species to be
 291 Holling’s Type II. We further built a model with attack rate and handling time, keeping
 292 exponential co-efficient “ q ” fixed at 0. The results showed a significant effect of handling
 293 time ($p = 0.000$) that validates our initial finding that the functional response is of Hollings’s
 294 Type II (Fig. 2). Therefore, our results show, that frogs, as predators don’t have an insatiable
 295 hunger but have a constant rate of feeding that is independent of prey density.

296 3.3 Assessment of trophic cascade through Mathematical growth model

297 For equations, 3 and 4 to be a non-trivial solution, $x_1 \neq 0$ and $x_2 \neq 0$,

$$298 \quad a_1 - b_1 x_2 - \frac{\left(\frac{nm}{T}\right)}{m_1 x_1 + m_2 x_2} = 0 \quad \dots\dots\dots(3.1)$$

$$299 \quad - a_2 + b_2 x_1 - \frac{\left(\frac{nm}{T}\right)}{m_1 x_1 + m_2 x_2} = 0 \quad \dots\dots\dots (4.1)$$

300 which describe the final steady-state, i.e. $dx_1/dt = 0 = dx_2/dt$. Thus on solving Eqs.(3.1,4.1)
 301 for the two unknowns, x_1 and x_2 , we get uniquely,

$$302 \quad x_2 = \frac{a_1}{b_1} - \frac{\left(\frac{nm}{T}\right)}{b_1[m_1 x_1 + m_2 x_2]} \leq \frac{a_1}{b_1} \quad \dots\dots\dots (5.1)$$

$$303 \quad x_1 = \frac{a_2}{b_2} + \frac{\left(\frac{nm}{T}\right)}{b_2[m_1 x_1 + m_2 x_2]} \geq \frac{a_2}{b_2} \quad \dots\dots\dots (5.2)$$

304 In absence of frogs, the solutions would be,

305 $x_2 = \frac{a_1}{b_1}$ and $x_1 = \frac{a_2}{b_2}$

306 which, as expected, are also the average values

307 $\langle x_1 \rangle = \left(\frac{1}{T}\right) \int x_1(t) dt = \left(\frac{a_2}{b_2}\right)$, $\langle x_2 \rangle = \left(\frac{1}{T}\right) \int x_2(t) dt = \left(\frac{a_1}{b_1}\right)$ for the usual Lotka-

308 Volterra case, around which $x_1(t)$ and $x_2(t)$ evolve in their limit cycle, where the integrals are

309 over $0 \leq t < T$ and T is sufficiently large. Our mathematical model, as of now, does not

310 explore the possibilities of limit cycles but shows that in presence of a frog as a tertiary

311 consumer, the trophic cascade effect would be negative for beneficial pest predators and

312 would have positive feedback on crop pest population.

313

314

315 **4. Discussion**

316 As our study reveals, although frogs consumed pests, the existing field densities of frogs in

317 our study region (Ghosh and Basu, 2020) are insufficient for significant pest regulation in the

318 natural environment. This holds true for both the high and low agricultural intensification

319 areas. Even at the highest field-realistic density of frogs as found in the low agricultural

320 intensity areas, pest population was not affected.

321 That the frogs do consume insect pests have been reported earlier (Hirai and Matsui, 2002;

322 Chen et al., 2005; Attademo et al., 2005; Yousaf et al., 2010). Teng et al. (2016) also showed

323 that a density of 100 frogs/67sq. m and 150 frogs/ 100sq. m could effectively control pests.

324 The ineffectiveness of frogs in controlling the insect population in our case could be due to

325 the inadequate abundance of frogs i.e., below the threshold density for effective regulation, in

326 the study sites.

327 Like any pest control strategy, the goal of a biological control strategy is to keep the pest

328 population below an economic threshold level (ETL). Though stomach content analysis gives

329 evidence towards amphibians contributing to pest consumption, drawing a conclusion about
330 their ability to reduce pest load below ETL based on such information will be presumptuous.
331 Although studies have reported a reduction in pest load in presence of frogs in a controlled
332 setup (Teng et al., 2016; Fang et al., 2019) these studies overlooked the impact on other
333 arthropod natural predators as found in natural settings.
334 We argue that frogs negatively impact the arthropod natural predators of crop pests in
335 multiple species systems and that makes them ineffective as a biological pest regulator.

336 **Antagonistic interaction with other natural enemies**

337 We observed crop pests belonging to orders Orthoptera, Coleoptera, Lepidoptera,
338 Hymenoptera, Diptera, Hemiptera, and arthropod predators belonged to orders Odonata,
339 Coleoptera, and Aranea. Such rice fields provide a potential ecosystem with huge prey
340 diversity (Fernando, 1995; Guerra and Araoz, 2015).

341 Our study shows that, in a multiple species system amphibians exhibited a preference for
342 pest predators rather than crop pests. Brown (1974) has reported the diet of amphibians in
343 croplands to be dominated by non-pests (94% of diet). Similar study by Khatiwada et al.
344 (2016) also shows amphibian diet is significantly composed of natural pest predators.
345 Generalist predators have an antagonistic effect in biological control especially (Perez-
346 Alvarez, Nault, & Pavedo, 2019) where the predation pressure is equal on all the prey species
347 (Wells, 2007). The effect and strength of intraguild predation with respect to frogs have not
348 been reported prior to this study. However, our study is the first to experimentally
349 demonstrate the effect and strength of intraguild predation with respect to frogs.

350 Our mathematical growth model corroborates our result and shows that with a limited feeding
351 rate the presence of frogs will always have a negative effect on the insect predator population
352 when they behave as a tertiary consumer in a system with both crop pests and arthropod
353 predators. If frogs feed on insect pests only, according to the growth equation for natural pest

354 predators (Eq. 4) their growth rate would decrease as they are robbed off their resource, and
355 eventually, there would be an increase in crop pest abundance. However, if the harvesting
356 factor is shifted completely towards the crop pest predator (Eq. 3) (if they were not
357 generalists but specialists instead, or if their feeding is influenced by the more active
358 predators (Ahmed et al., 2016)) there still would be an increase in crop pest abundance due to
359 release of interspecific interaction from pest predator population. Therefore the presence of
360 frogs will cause negative feedback on the crop pest predator population consequently
361 resulting in an increase in crop pest abundance. In intensive agricultural lands where the
362 arthropod pest predator population is disproportionately affected (Zhao et al, 2015) or is low
363 (Perez-Alvarez et al., 2019) amphibians could be a promising biological control agent.
364 Martin et al. (2013) estimated a decrease in natural pest control by 46% in landscapes that are
365 dominated by cultivatable arable lands. In such landscapes with impaired natural pest control
366 by insect predators, the harvesting factor of frogs will be shifted maximally to the crop pest
367 population.

368 **Feeding constraints of amphibians**

369 As our experimental result about the functional response shows, the feeding rate of *F.*
370 *limnocharis* is independent of prey density and the response is significantly affected by
371 handling time. Handling time (T_h) is associated with every prey item consumed and is
372 indifferent to the prey density. But even when the frog was presented with a higher density of
373 grasshoppers, the maximum number of prey consumed was determined by the time spent in
374 prey handling (T/T_h). This means that the rate of prey consumption by a predator declines at
375 higher prey densities due to handling constraints (Thorp et al., 2018). Therefore, this feeding
376 constraint of the frog will act as a limiting factor in controlling the pest population at a higher
377 density which will continue to grow in a single trophic interaction between crop pest and

378 frog. For effective biological control, a considerable abundance of the amphibian species
379 needs to be conserved in intensive agricultural lands.

380

381 Scientific management of beneficial landscape structures like semi-natural habitats,
382 hedgerows, ephemeral water bodies, degree of connectivity with adjoining remnant natural
383 vegetation, and habitat heterogeneity (Ghosh and Basu, 2020) enhances amphibian thriving.
384 Complex landscapes could weaken the strength of the intraguild predatory effects by
385 reducing niche overlap through spatial separation or even alternate resource availability
386 (Perez-Alvarez et al., 2019). Restoring the habitat diversity can therefore be expected to
387 promote service provisioning.

388

389 Our research significantly adds to the existing body of work exploring the potential of frogs
390 in biological control, particularly in tropical agroecological landscapes that are heavily
391 dependent on intensification of paddy cultivation to sustain their burgeoning populations
392 (Aditya et al. 2020). Our study highlights the importance of studying intraguild predation
393 effect as an important factor that determines the effectiveness of frogs as biological control
394 agents and highlights the importance of increasing the habitat diversity in the agricultural
395 landscape to weigh down the impacts of intraguild predation and to improve the overall ES
396 potential of natural predators, that has implications for food and livelihood security of
397 communities dependent on agriculture.

398

399 **Authors' Contribution**

400 PB and DG have conceived the idea and methodology; DG collected and analyzed data; SC
401 and DG developed the mathematical models: PB, DG and SC contributed to writing the

402 manuscript. All authors have made significant contributions to preparing the manuscript and
403 give approval for publication.

404

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415

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Pest/Disease	Fixed Effects	F value	p value ⁵⁹⁶
Tungro	Paddy growth phase	4.92 (3,20)	0.010* ⁵⁹⁷
	Frog treatment	1.09 (2,4)	0.41 ⁵⁹⁸
Defoliation	Paddy growth phase	6.21 (3,20)	0.003** ⁵⁹⁹
	Frog treatment	1.21 (2,4)	0.38 ⁶⁰⁰
Rice whorl	Paddy growth phase	2.08 (3,20)	0.13 ⁶⁰¹
	Frog treatment	1.93 (2,4)	0.25 ⁶⁰²
Leaf folder	Paddy growth phase	3.88 (3,22)	0.022* ⁶⁰³
	Frog treatment	0.73 (2,4)	0.53 ⁶⁰⁴
Rice hispa	Paddy growth phase	70.17 (3,20)	<.0001*** ⁶⁰⁵
	Frog treatment	2.32 (2,4)	0.21 ⁶⁰⁶

Table 1: Fixed effects (Paddy growth phase and Frog treatment) in Nested ANOVA models for the five

608 pest infestation types

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Response	Treatment		Paddy growth phase				
Response	Control	10 frogs	5 frogs	1 ST	2 ND	3 RD	4 TH
Pest abundance			0.09	0.000	0.000	0.006	
Predator abundance			0.01	0.000	0.000	0.000	

621 Table 2: Summary of results from GLMM for pest and insect predator build-up in response to

622 frog treatments and paddy growth phase

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639 Fig. 1.

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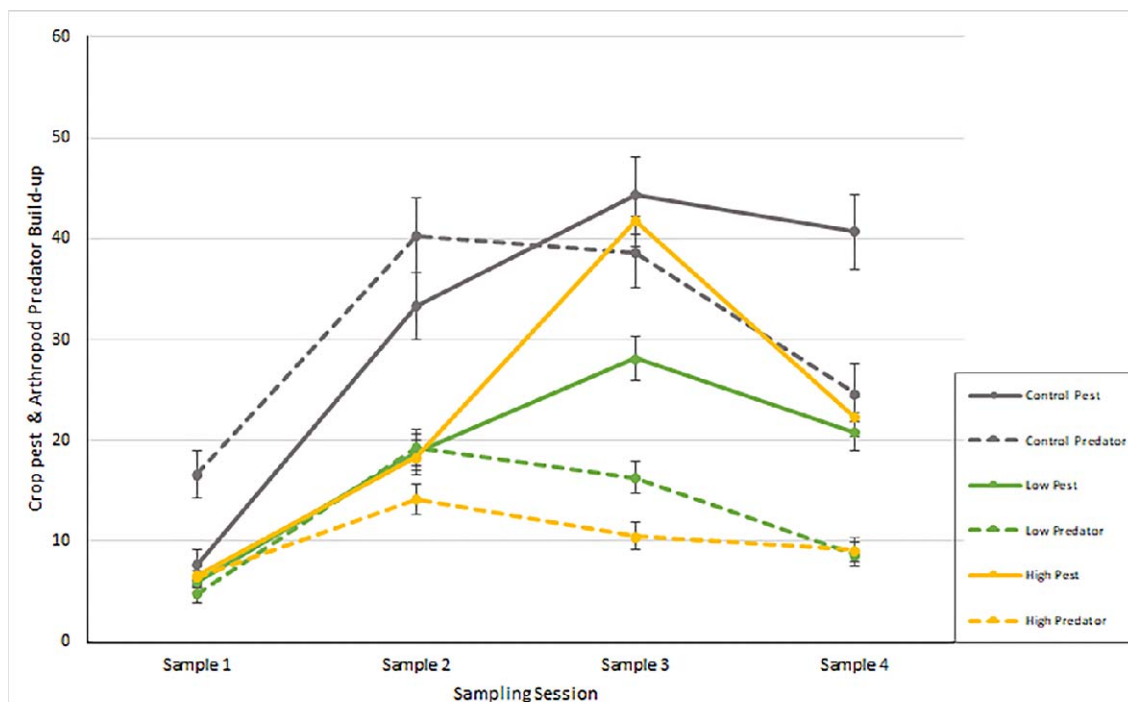
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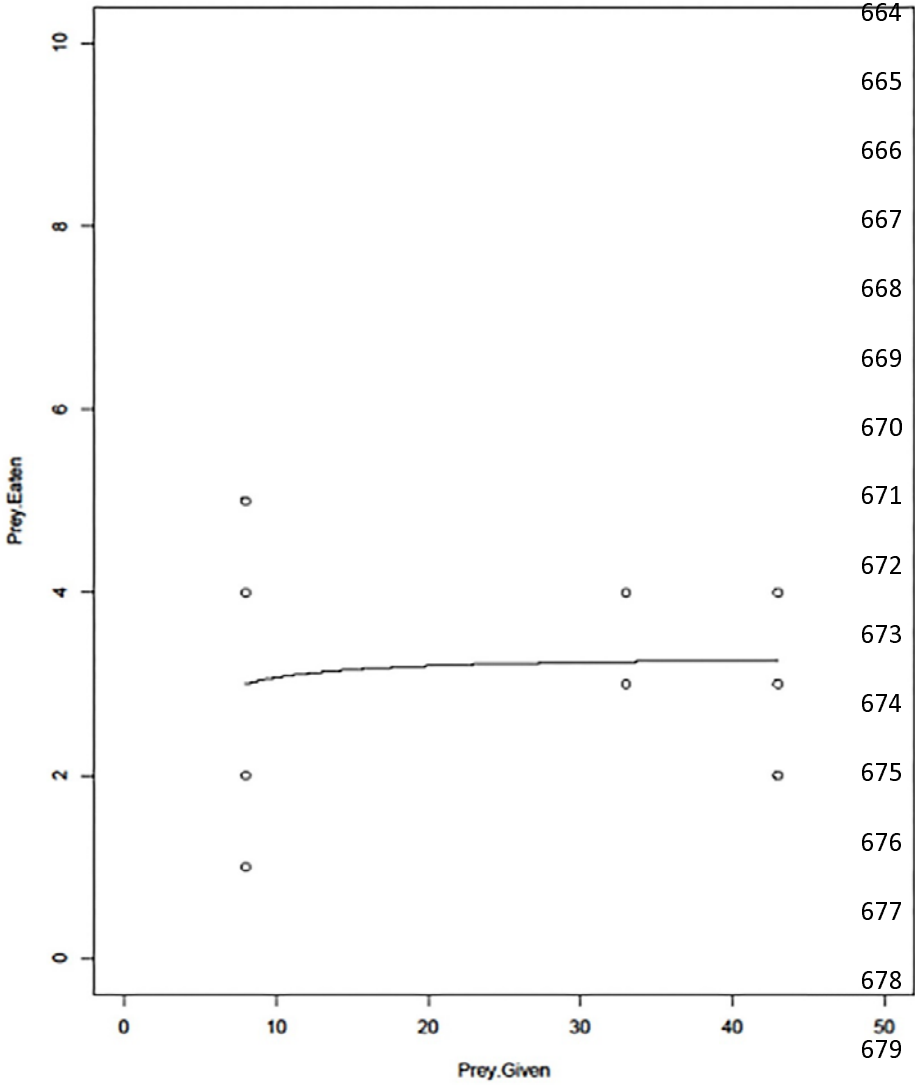
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660 Fig 2.

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687 Figures:

688 Fig. 1. Crop pest and insect predator build-up in control, at frog densities found in High
689 (10frogs/100 sq.m) and Low (5 frogs/100 sq.m) agricultural intensity areas at different
690 sampling intervals.

691 Fig 2. Functional response output showing Holling's Type II feeding nature in focal frog
692 species.

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