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1 **Trophic functioning of integrated rice-fish farming in Madagascar: insights from stable**
2 **isotopes ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$)**

3
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20 **Abstract**

21 Trophic dynamics of integrated rice and fish farming (IRF) systems were studied in irrigated
22 rice plots stocked with common carp in Madagascar. Fish feeding behavior was assessed by
23 analyzing stable carbon and nitrogen isotopes of fish and natural feed sources. Stable isotope
24 signatures of 45-day-old carp fry introduced into rice plots ($\delta^{13}\text{C} = -18.8\text{‰} \pm 0.5\text{‰}$,
25 $\delta^{15}\text{N} = 9.3\text{‰} \pm 0.6\text{‰}$) revealed that they had been fed chicken egg yolk and corn meal, in
26 accordance with local practices. However, after a 100-day growing period in experimental
27 rice plots, ^{13}C and ^{15}N depletion was observed for 145-day-old carp, indicating a change in
28 feeding sources. Under extensive conditions, common carp that fed on rice roots, sediments
29 and suspended particulate organic matter (i.e. plant debris and detritus) had a larger trophic
30 niche (3‰^2) than 45-day-old carp (1.2‰^2). Overall, common carp feeding behavior and the
31 trophic food web in the IRF system suggest that increasing natural productivity through
32 organic fertilization will enhance ecological intensification of both rice and fish production.

33

34 Keywords: Rice-fish farming, Common carp, Food web, Stable isotopes, Trophic niche
35 partitioning

36 **1. Introduction**

37 Integrated rice and fish farming (IRF) with aquatic animal aquaculture (i.e. rice-fish farming;
38 [Lu and Li, 2006](#)) is described as an ingenious agricultural system that produces fish and rice
39 within the same plot using the same amount of water, while benefitting from synergistic
40 effects. IRF systems decrease farmers' dependence on external inputs and increase the
41 efficiency of the entire system by optimizing the use of nutrients, energy and water. Fish such
42 as common carp (*Cyprinus carpio* L.) influence nutrient dynamics through consumption,
43 excretion and bioturbation ([Shin-ichiro et al., 2007](#)), which ultimately benefit the rice.
44 Conversely, rice provides a shelter and nursery for fish ([Little et al., 2001](#); [Noble, 2001](#)) and
45 is a source of food (invertebrates, and periphyton that develop on its stems; [Saikia and Das,](#)
46 [2009](#)). Overall, IRF with common carp can be considered as a symbiosis between rice and
47 fish whose mutual benefits provide ecosystem services ([Willot et al., 2019](#)).

48 From an economic viewpoint, IRF systems diversify farm production and generate a more
49 resilient source of income that depends less on market fluctuations than that of single-product
50 farms. In Madagascar, IRF has been promoted by the FAO since 1985 and by the non-
51 governmental organization APDRA since 2006 ([Dabbadie and Mikolasek, 2017](#)). Recent on-
52 farm experiments with local IRF in Madagascar indicated that their net rice yields were more
53 than 10% larger than traditional rice yields, in the absence of fertilizers or feed inputs
54 ([Mortillaro and Dabbadie, 2019](#)). Despite these obvious benefits, however, the potential of
55 IRF to address challenges related to food security and to alleviate poverty is constrained by
56 the small fish yields obtained in improved Madagascar systems (i.e. common carp + channel
57 and higher bunds; from 50 kg ha⁻¹ cycle⁻¹ to 350 kg ha⁻¹ year⁻¹, on average; [Mortillaro and](#)
58 [Dabbadie, 2019](#); [APDRA, 2018](#), respectively). However, the literature reports that fish yields
59 in IRF could reach 906-1 282 kg ha⁻¹ (i.e. fish and prawn) by increasing natural productivity
60 through application of 5 000 kg ha⁻¹ of cow dung ([Mohanty et al., 2004](#)). Similarly, when fish

61 are fed and/or rice fields fertilized, fish yields can reach up to 2.5 t ha⁻¹ in China, 2.0 t ha⁻¹ in
62 India, 805 kg ha⁻¹ in Indonesia, 980 kg ha⁻¹ in Bangladesh, 2.2 t ha⁻¹ in Vietnam and
63 900 kg ha⁻¹ in Thailand (Lu and Li, 2006).

64 Rice-based ecosystems are a large source of animal and plant diversity (Halwart, 2008).
65 Bambaradeniya et al. (2003) described the biodiversity associated with an irrigated rice
66 system in Sri Lanka; besides microbiobiodiversity, they found 494 species of invertebrates, 103
67 species of vertebrates and 89 species of macrophytes. Similarly, a total of 147 species were
68 reported from Cambodian rice field fisheries, comprised of 126 finfish species, 13 other
69 aquatic animal species (four species of snake; two species of frogs, snails, and bivalves; one
70 species of crab, prawn, and turtle), and eight aquatic plant species (Freed et al., 2020). These
71 species play a major role in feeding and providing nutrition to local communities, as a source
72 of self-recruiting species and in supporting the production of farmed fish in association with
73 rice (Halwart, 2006). However, the high biodiversity also suggests complex trophic
74 interactions. Characterizing the trophic food web in IRF systems may thus improve
75 knowledge about ecosystem functioning as well as ecological intensification of aquatic food
76 production. Indeed, ecosystem functioning provide information on the relationships among
77 organisms in order to guide the use of trophic resources and energy and maximize natural
78 processes to produce fish.

79 Stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are often used to characterize trophic
80 food webs. The basic principle is that the isotopic composition of a consumer's tissues reflects
81 that of its food (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984). Unlike
82 analysis of stomach contents, which provides information about the type of prey ingested, the
83 isotopic method provides an integrated measure of the food consumed over time, based on the
84 assimilation and metabolization of nutrients ingested (Hesslein et al., 1993; MacAvoy et al.,
85 2001). The stable nitrogen isotope ratio ($^{15}\text{N}:^{14}\text{N}$) estimates the trophic levels of species in an

86 ecosystem and characterizes predator-prey relationships. The stable carbon isotope ratio
87 ($^{13}\text{C}:^{12}\text{C}$) traces the origin of organic matter ingested by organisms, since each food source,
88 whether terrestrial or aquatic, has its own range of $\delta^{13}\text{C}$, which is strongly conserved along
89 trophic chains (Pinnegar and Polunin, 2000). Therefore, studying stable carbon and nitrogen
90 isotopes provides different but complementary types of information to characterize a food
91 web. In our study, we expected that stable carbon and nitrogen isotopes would characterize
92 the feeding behavior of common carp in a Madagascar IRF agriculture to aquaculture system.

93

94 **2. Materials and methods**

95 2.1. IRF system management

96 The experiment was conducted on-farm using experimental rice plots located near the village
97 of Tsiafahy (19°03'41.8"S, 47°36'36.3"E; 1 344 m.a.s.l.), Antananarivo Atsimondrano district
98 (Analamanga region, Madagascar). The experimental design and yields of the system were
99 previously described in Mortillaro and Dabbadie (2019) presenting the Malagasy rice-fish
100 farming study case. Briefly, three plots (P2: 863 m², P3: 713 m² and P5: 467 m²) with a total
101 area of 2 043 m² were selected. In accordance with traditional farming practices, rice was
102 sown on 1 October 2016 using a local rice strain (i.e. "Vary Botry"). Rice seedlings 61 days
103 old were transplanted on 1 December 2016. The experiment was then conducted for 100 days,
104 from 11 January to 24 April 2017, with the concurrent production of fish and rice starting 41
105 days after rice was transplanted. Fish were introduced somewhat later than usual due to low
106 rainfall in December 2016 and early January 2017. As recommended by the FAO and
107 APDRA (Dabbadie and Mikolasek, 2017), the traditional practices were improved: stocking
108 common carp, building larger and higher plot bunds, and increasing the water level in the rice
109 plots. Bunds improve and secure production by preventing fish from escaping during flood
110 events. Rice plots were completed by digging a channel through it (40-60 cm deep; 8.6% ±

111 1.5% of cultivated area), which served as a refuge for fish, especially during climatic hazards
112 (e.g. tropical cyclone Enawo, March 2017) or when the rice plots are drained during harvest
113 of the rice crop (Halwart and Gupta, 2004). The objective of these developments in
114 Madagascar was to guarantee an acceptable survival rate for the common carp and thus
115 increase fish production. The 45-day-old carp fry used in the experiment, with a mean weight
116 (\pm SD) of 2.5 g \pm 1 g and a mean length of 39 mm \pm 6 mm, were sourced from a fish farmer
117 near the experimental farm. The number of fry stocked in the three experimental rice plots
118 was 216 (P2), 178 (P3) and 116 (P5), which corresponded to a density of 0.25 fish m⁻².

119

120 2.2. Sampling procedures

121 2.2.1. Fish

122 Five 45-day-old carp were sampled at the beginning of the experiment prior to stocking. At
123 harvest, three 145-day-old carp from each rice plot were sampled (Table 1). All fish were
124 euthanized and dissected, and white muscle was sampled for stable isotope analysis.

125

126 2.2.2. Macroinvertebrates

127 Macroinvertebrates were monitored during the experiment prior to harvest. Despite frequent
128 sampling (every two weeks), only aquatic insects were found (i.e. adults or larvae; mainly
129 Hemiptera, Odonata and Diptera; Table 2). They were collected from the water column using
130 a 500 μ m mesh landing net (50 cm \times 30 cm) within rice straw, the refuge channel and along
131 the bunds. Three locations in the rice plots were sampled, which provided a composite sample
132 that was transferred into a labelled polypropylene tube and kept in a cooler until being taken

133 to the laboratory. Insect samples were then sorted and identified to the lowest taxonomic
134 level.

135

136 2.2.3. Zooplankton

137 Zooplankton were sampled at harvest using a plankton net (63 μm mesh, 40 cm diameter)
138 towed in the refuge channel before emptying the rice plot. Three plankton transects were
139 sampled in each plot (Table 1). For each sample, the plankton net was shaken to remove water
140 until the volume of the sample decreased below 40 mL. The collected material was then
141 transferred into polypropylene tubes (one per plankton transect and rice plot) and kept in a
142 cooler until being taken to the laboratory.

143

144 2.2.4. Suspended particulate organic matter

145 Suspended particulate organic matter (SPOM) was sampled at harvest using glass fiber filters
146 (Whatman GF/F, porosity 0.7 μm , 47 mm diam.) and a vacuum system under low pressure.
147 The filters were pre-combusted at 450°C for 12 h. Three water samples of 1.5 L each were
148 collected in bottles in the three rice plots (Table 1) and filtered until particulate material
149 saturated the filter (after 500 mL, on average). Each filter was then transferred into a labelled
150 polypropylene tube and kept in a cooler until being taken to the laboratory.

151

152 2.2.5. Sediments

153 Sediments were sampled at harvest at 15 locations in each rice plot, transferred into
154 polypropylene tubes and kept in a cooler until being taken to the laboratory. For each rice

155 plot, sediments from five locations were thoroughly mixed into a composite sample before
156 preparing the stable isotope sample (Table 1).

157

158 2.2.6. Weeds

159 Prior to harvest and during monitoring of the experiment, weeds were collected when
160 observed in rice plots (Table 2). Samples were transferred into single-use plastic storage bags
161 and kept in a cooler until being taken to the laboratory. Weed samples were then sorted and
162 identified to the lowest taxonomic level.

163

164 2.2.7. Rice

165 At harvest, three composite samples of rice compartments (i.e. leaves, roots and seeds) were
166 collected from each plot (Table 1). Quarter-meter squares (50 cm × 50 cm) made of
167 polypropylene tubes were thrown randomly into each rice plot three times. All rice plants
168 within the square were subsequently sampled, sorted by compartment (Table 1), transferred
169 into single-use plastic storage bags and kept in a cooler until being taken to the laboratory.

170

171 2.3. Sample preparation

172 Fish white muscle, aquatic insects, zooplankton, SPOM, sediments, weeds and rice were dried
173 at 45°C for 24-48 h, manually ground into a fine homogeneous powder and transferred into
174 Eppendorf Tubes®. Then, 1-50 mg of each dried sample was weighed and packed into a tin
175 capsule to analyze stable carbon and nitrogen isotopes simultaneously. Sample preparation
176 was realized in FOFIFA DRZVP laboratory in Antananarivo, Madagascar.

177

178 2.4. Stable isotopes

179 Stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analyzed by subcontracting to the
180 stable isotope laboratory of UMR B&PMP in Montpellier (France). For each compartment of
181 the rice plots, ^{13}C and ^{15}N in the same sample was analyzed using an automated on-line
182 system, including an Elementar Isoprime mass spectrometer coupled with a Eurovector
183 Euroflash 3000 elemental analyzer, thus characterizing the trophic functioning of the IRF via
184 isotope ratio mass spectrometry analysis. Results were expressed in δ unit notation as
185 deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$;
186 [Peterson and Fry, 1987](#)) following the formula:

187
$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \frac{R_{\text{sample}}}{R_{\text{standard}}} 10^3$$

188 where R is the ratio of heavy to light isotopes ($^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$).

189

190 2.5. Comparison of common carp isotopic niches

191 A standard ellipse area (SEA) was calculated for 45- and 145-day-old carp using the *Stable*
192 *Isotope Bayesian Ellipses in R* package (SIBER, version 2.1.4; [Jackson et al., 2011](#)). The SEA
193 Bayesian metric is a bivariate equivalent of the standard deviation that contains the mean core
194 population isotopic niche (ca. 40% of the data). SEA metrics were chosen prior to the convex
195 hull metric (TA: total area of the convex hull that encompasses the data points; [Layman et al.,](#)
196 [2007](#)), which includes outlier individuals. SEA metrics are more robust to differences in
197 sample size. The corrected version (SEAc) was then used to circumvent the bias caused by
198 small sample sizes. SEAc sizes were then compared using a Bayesian approach based on
199 Markov-chain Monte Carlo methods ([Jackson et al., 2011](#)). TA was compared to SEAc (Table
200 3), but data analysis focused on the latter.

201

202 2.6. Statistical analysis

203 One-way analysis of variance (ANOVA) was used to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among
204 145-day-old carp. Tukey's post-hoc tests were used to examine pairwise differences.
205 Assumptions of normality and homoscedasticity of residuals were tested using Shapiro-Wilk
206 and Bartlett tests, respectively. A two-sample Student's t-test was used to compare $\delta^{13}\text{C}$ and
207 $\delta^{15}\text{N}$ values between 45- and 145-day-old carp. Assumptions of normality and
208 homoscedasticity of residuals were tested using Shapiro-Wilk and Fisher tests, respectively.
209 Statistical analyses were performed using R software version 3.6.3, with a significance level α
210 of 0.05.

211

212 2.7. Data analysis

213 The theoretical sources of a trophic group were calculated using the graphic coordinates of the
214 consumer compartment's centroid as a reference point and adding a theoretical trophic
215 enrichment factor (TEF: 3.4‰ and 0.8‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively; [Zanden and](#)
216 [Rasmussen, 2001](#)) to it (Fig. 1). The closer a compartment lies to this point, the more it
217 contributes to feeding the consumer compartment. The theoretical signatures of fish meal
218 ($13.6\text{‰} \pm 0.1\text{‰}$ and $-19.9\text{‰} \pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively; [Kusche et al., 2018](#)),
219 chicken egg yolk ($6.3\text{‰} \pm 1.4\text{‰}$ and $-25.0\text{‰} \pm 3.4\text{‰}$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively; [Rogers,](#)
220 [2009](#)) and corn meal ($4.9\text{‰} \pm 0.6\text{‰}$ and $-12.7\text{‰} \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively;
221 [Yamada et al., 2003](#); [Enyidi et al., 2013](#)) were included in the analysis to consider 45-day-old
222 carp feed, which was not sampled in the current study. Mixing models (e.g. MixSIR, SIAR;
223 [Moore and Semmens, 2008](#); [Parnell et al., 2010](#)) were not used to estimate contributions of
224 sources to consumers' diets, because we assumed that (i) not all sources ingested could be

225 sampled and (ii) fish opportunism would create underdetermined systems (i.e. with more
226 sources than tracers), which increases the inaccuracy of models, even though they are
227 Bayesian (Brett, 2014; Stock et al., 2016). Thus, we focused on bulk data to avoid biased
228 estimates of source contributions.

229

230 **3. Results & discussion**

231 At the beginning of the experiment, the stable isotope signature of the 45-day-old carp
232 was $-18.8‰ \pm 0.5‰$ and $9.3‰ \pm 0.6‰$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Assuming a TEF of
233 $3.4‰$ and $0.8‰$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, between a prey and its predator (Zanden and
234 Rasmussen, 2001), the theoretical food source of 45-day-old carp had a mean signature
235 of $-19.6‰$ and $5.9‰$ (Fig. 1) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Fry of 10-20 days old can feed
236 on cladocerans, copepods and the small larvae and pupae of insects such as chironomids and
237 mosquitoes. Fry of 21-45 days old can also consume larger insect larvae, worms and small
238 shellfish (Colman et al., 1992). Although these sources were not sampled in the nursery
239 ponds, the stable isotope signatures of zooplankton and insects suggested that they
240 contributed little to young carp diets (Fig. 1, Table 3). On the contrary, the theoretical food
241 source signature of 45-day-old carp suggested that their food was composed mainly of animal
242 protein (chicken egg yolk; Fig. 1, Table 3) and carbohydrates from C₄ plants (corn meal; Fig.
243 1, Table 3). Local farmers have used both ingredients as the first artificial feed for common
244 carp since the FAO introduced them to Madagascar in the 1980s (Woynarovich, 1980, 1982;
245 Colman et al., 1992).

246 After 100 days of extensive farming in the rice plot, the signature of 145-day-old carp became
247 depleted compared to that of the 45-day-old carp, decreasing to $-24.9‰ \pm 1.0‰$ and
248 $5.7‰ \pm 0.9‰$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Fig. 1). They remained, however, in the range
249 of signatures found in rice plot ecosystems (Fig. 1, Table 3), which confirmed that feeding

250 had switched from external sources to natural resources. No differences among the three
251 experimental plots were measured at the end of the experiment (Table 3, ANOVA, $p > 0.05$).
252 The plots were thus considered to have similar signatures and availability of natural food
253 sources.

254 The theoretical food source of 145-day-old carp had a mean signature of -25.7‰ and
255 2.3‰ (Fig. 1) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The latter lay exactly in between the signatures
256 of rice roots, sediments and SPOM, which suggests that these three sources were consumed
257 (as plant debris and detritus). However, zooplankton, rice leaves and weeds had little to no
258 contribution to the carp diet (Fig. 1). Common carp has been described as consuming mainly
259 detritus and plants (more than 60%), followed by invertebrates associated with plant debris
260 (Fig. 3, [Matsuzaki et al., 2007](#); [Kanaya et al., 2009](#); [Ramírez-Herrejón et al., 2014](#)). Similarly,
261 gut contents analyses from common carp in rice-field of the Apatani plateau revealed a total
262 of 60 food items of which 22 belonged to the Chlorophyceae, 12 to the Cyanobacteria, 10 to
263 the Bacillariophyceae and 16 to several zooplankton taxa, while selectively feeding on
264 periphyton ([Saikia and Das, 2009](#)). It confirms that common carp can forage on a large
265 variety of food items, including invertebrates through bottom feeding (Fig. 3), although all of
266 them won't be assimilated in their tissues, as revealed by stable isotopes. However, C_4 weeds
267 (i.e. *Echinochloa colona*, *Fimbristylis ferruginea* and *Pycreus mundtii*; Table 2) displayed a
268 highly enriched carbon signature (Fig. 1; $\delta^{13}\text{C} = -11.3\text{‰} \pm 0.4\text{‰}$) suggesting no contribution
269 to the common carp diet. These weeds had either little to no contribution to the food web
270 unless through decomposition as suggested for other aquatic C_4 macrophytes in Amazon
271 floodplains ([Mortillaro et al., 2016](#)).

272 Although few insects had a signature similar to that of the theoretical food source, the mean
273 signature displayed a large heterogeneity ($-27.1\text{‰} \pm 2.6\text{‰}$ and $5.9\text{‰} \pm 2.9\text{‰}$ for $\delta^{13}\text{C}$ and
274 $\delta^{15}\text{N}$, respectively), which suggests the need for further investigation. For instance, Dadebo et

275 al. (2015) found 39.8% detritus and 26.7% Diptera (by volume) in common carp guts from
276 Lake Koka (Ethiopia). Frei et al. (2007) found that stocking common carp and tilapia in rice
277 fields had a significant influence on controlling weeds and dipterous insects. In our study, in
278 Madagascar, only Culicidae larvae (mosquitoes, Table 2; $\delta^{13}\text{C} = -24.1\text{‰}$ and $\delta^{15}\text{N} = 3.1\text{‰}$,
279 Fig. 1) belonged to Diptera, while the other insects collected belonged mainly to Hemiptera
280 and Odonata, which contribute less than 3% to the common carp diet according to the
281 literature (Dadebo et al., 2015). However, the insects sampling effort in this study was the
282 main limitation for a deeper assessment on their contribution to carp diet.

283 IRF is believed to provide ecosystem services, such as weed and pest control, via integrated
284 pest management (Frei et al., 2007; Kathiresan, 2007; Sinhababu et al., 2013). However,
285 although similar assumption was made in Madagascar by farmers and technicians, weeds and
286 insects did not contribute to the diet of 145-day-old carp. Common carp in our IRF system fed
287 mainly on detritus but also increased rice yields by more than 10% for improved IRF systems
288 (i.e. common carp + channel and higher bunds) as described in Mortillaro and Dabbadie
289 (2019), which is a major improvement considering the Madagascar needs for rice. Thus, while
290 feeding on natural resources, carp recycled organic matter as fertilizer for rice providing a
291 way for sustainable intensification of rice culture given the low incomes and available inputs
292 for farmers in Madagascar (Fig. 3). Fish excretion, which increases the nutrients available for
293 plants such as rice (Boyd et al., 2020), has been described as the main driver of larger rice
294 yields (Lu and Li, 2006; Shin-ichiro et al., 2007). Bioturbation caused by common carp may
295 also increase soil quality since oxygen supply (Ritvo et al., 2004) influences water
296 transparency and community composition, such as that of plankton and submerged
297 macrophytes (Shin-ichiro et al., 2007).

298 The SEAc based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the 45- and 145-day-old carp did not overlap and
299 were significantly smaller for the younger carp (Fig. 2, Table 3). In polyculture rice-fish

300 systems (i.e. *Barbonymus gonionotus*, *Oreochromis niloticus* and *Macrobrachium*
301 *rosenbergii*), similar results were found for common carp (1.36‰² to 2.04‰²; [Saowakoon et](#)
302 [al., 2021](#)). Thus, each group had different feeding habits, as the older carps appeared to have
303 more trophic plasticity (i.e. being able to forage on a large range of food items) than the
304 younger carps. The biodiversity available in Madagascar rice fields (Fig. 3) as food sources
305 for carp during the 100 days of the experiment was probably higher than that in nursery
306 ponds. The ability of older carp in using different resources was also confirmed by their
307 preferential consumption and retention of high-quality dietary sources such as formulated
308 feeds, which have been observed to contribute up to 76.5% of the carp diet ([Schultz et al.,](#)
309 [2012](#)). The small trophic niche of 45-day-old carp (Fig. 2, Table 3) was due to preferential
310 consumption of exogenous feeds (i.e. corn meal and chicken egg yolk), as observed in semi-
311 intensive in temperate fish polyculture, according to trophic niche partitioning ([Nahon et al.,](#)
312 [2020](#)). Indeed, after the onset of the juvenile period (20-25 mm; 20-30 days old) functional
313 morphology, feeding behavior and differential growth capacity of common carp change little
314 ([Vilizzi and Walker, 1999](#)).

315 In our study, sampling didn't permit to have a larger number of samples for sources during
316 the experiment. The experiment was done in farmers conditions where exhaustive sampling is
317 often an issue. However, as related to sources and as mixing models were not used, the
318 sample size was not a major issue for comparison with consumers (i.e. common carps).

319 **4. Conclusion**

320 Our study explains the trophic behavior of common carp in Madagascar IRF, which forage
321 mainly on detritus under extensive conditions. Preferential consumption of feeds was also
322 confirmed for fry, as previously observed for adults. Thus, although common carp are
323 opportunistic, when reared under extensive conditions, they are also ecosystem engineers that
324 influence ecosystem functioning and biodiversity through bioturbation, improving IRF

325 systems. This suggests that ecological intensification of Madagascar IRF using organic
326 fertilizers (e.g. rich in nitrogen, carbon and phosphorus), instead of synthetic fertilizers should
327 help increase natural productivity, particularly in a context of low incomes and available
328 inputs in Madagascar rural areas. Such ecological intensification through natural productivity
329 improvement and/or low feed inputs should be further assessed, as the integration with
330 lombricompost and earthworm culture to optimize the recycling of crop waste to feed the fish
331 and fertilize the rice. However, the little contribution of insects, weeds (e.g. C4) and
332 zooplankton to the common carp diet, suggest that further studies integrating species from
333 multiple trophic levels, including Madagascar native fish and freshwater prawn, can increase
334 overall productivity.

335

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504 **Figure captions**

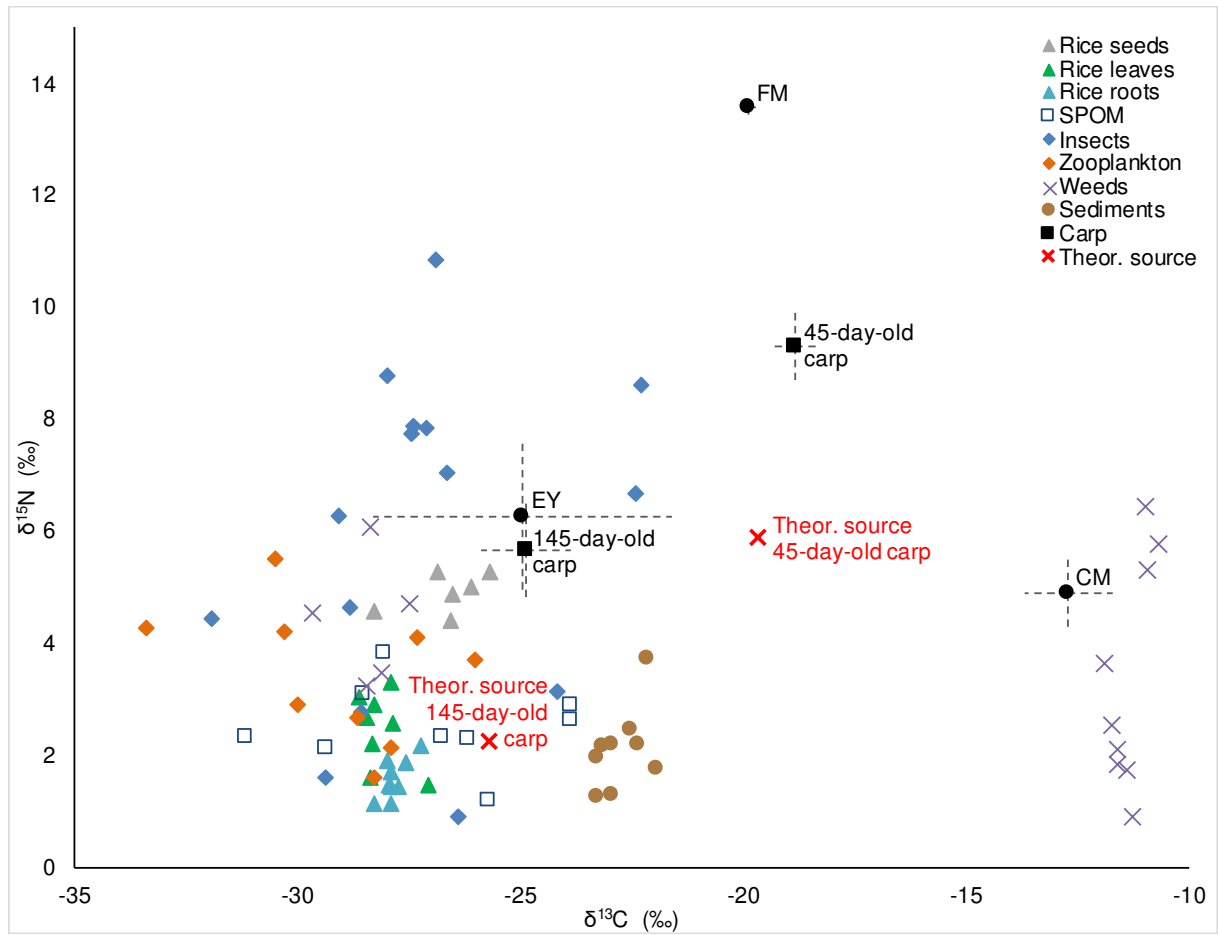
505 Figure 1. Dual stable isotope plot of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) showing the mean (\pm standard
506 deviation (SD)) isotopic signature of common carp, theoretical feed source and trophic
507 compartments collected from rice plots. The signatures of fish meal (FM), chicken egg yolk
508 (EY) and corn meal (CM) came from the literature. SPOM: suspended particulate organic
509 matter

510

511 Figure 2. a) Standard ellipse areas (SEAc) and b) density plots showing confidence intervals
512 of 45-day-old carp and 145-day-old carp in the rice-field experiment. Red crosses indicate
513 maximum-likelihood-estimated SEAc values obtained after 10 000 bootstrap iterations. Gray
514 shades from dark to light represent 50%, 75% and 95% credibility intervals.

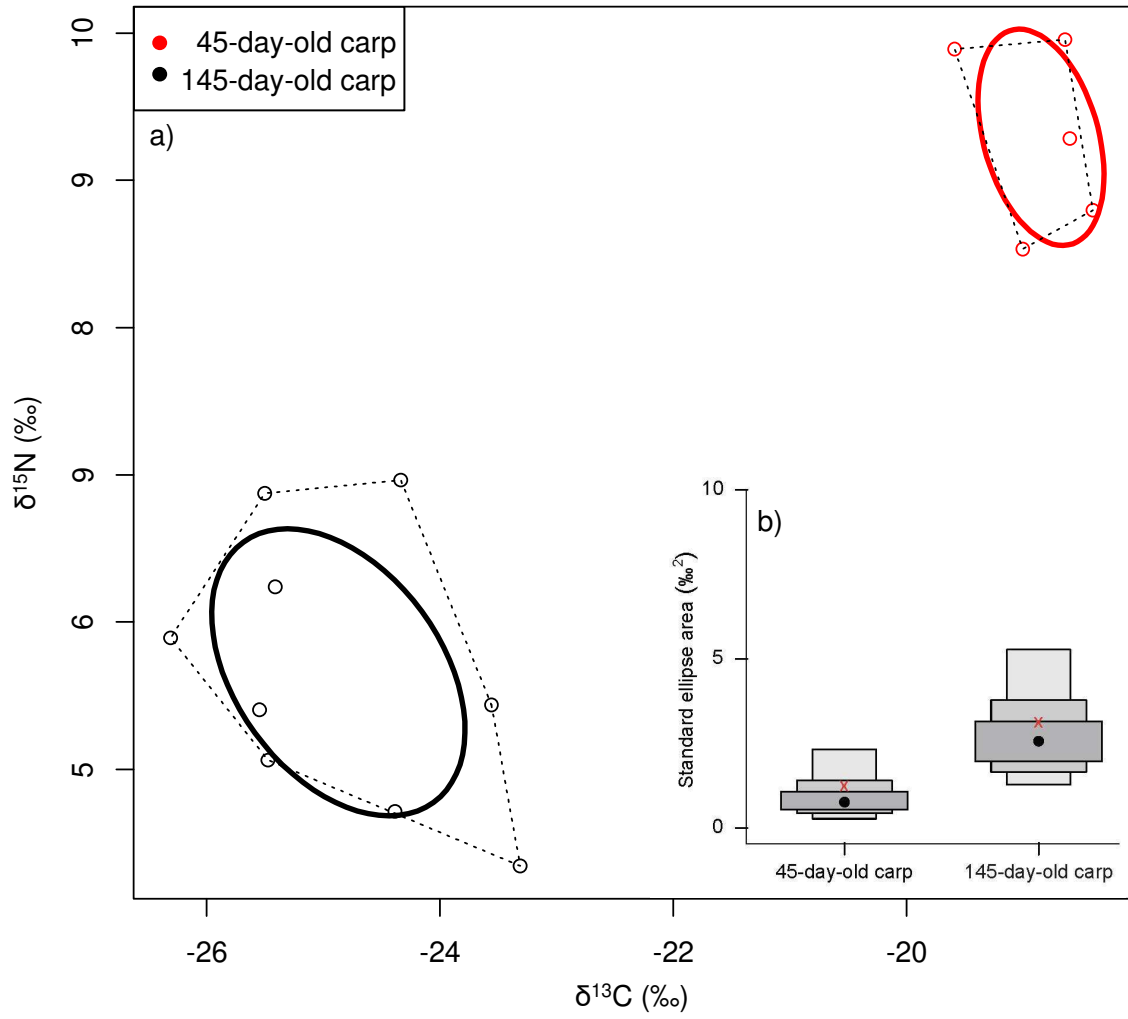
515

516 Figure 3. Illustration of the trophic functioning of the IRF system in Madagascar from
517 Mortillaro and Dabbadie (2019)

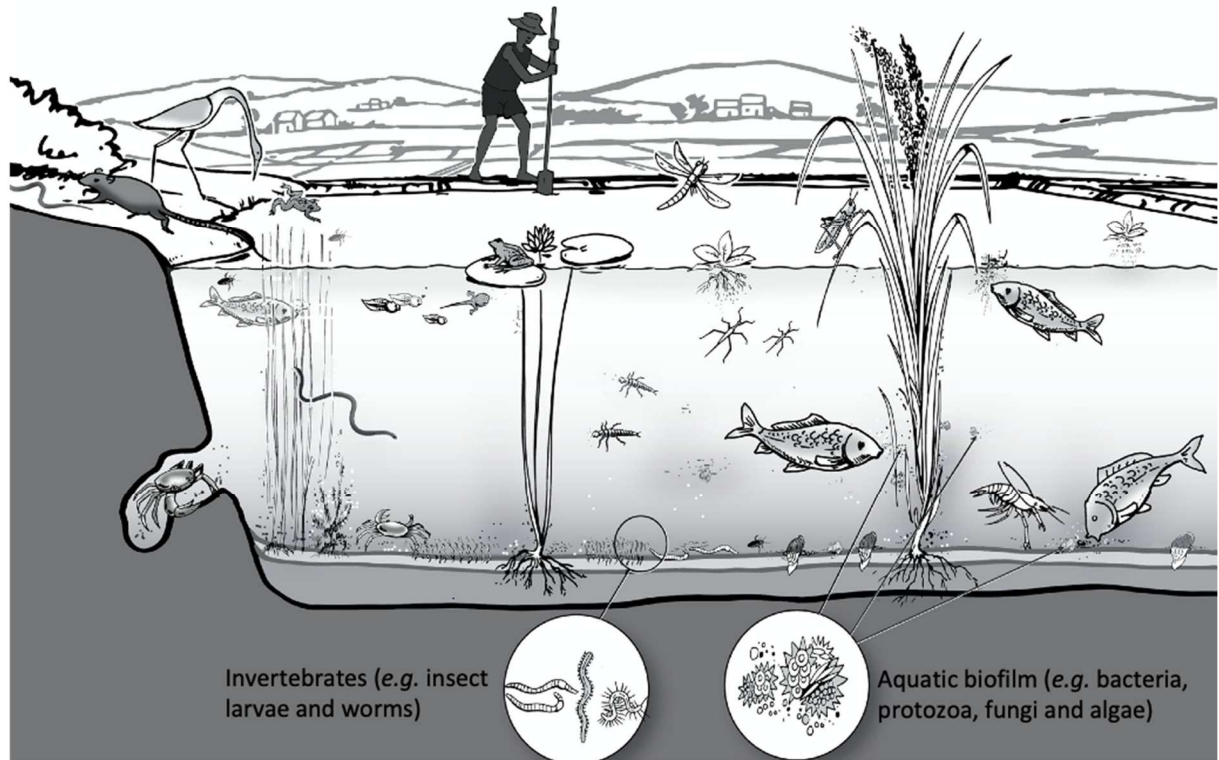


518

519 **Figure 1**



520
521 **Figure 2**



522
523

Figure 3

524 **Table 1.** Number of samples per compartment collected at harvest from the three
525 experimental rice plots (P2, P3 and P5). SPOM: suspended particulate organic matter

Compartment	P2	P3	P5	Weight (g)	Length (mm)
<i>Cyprinus carpio</i>	3	3	3	48 ± 22	142 ± 24
Rice leaves	3	3	3	-	-
Rice roots	3	3	3	-	-
Rice seeds	1	2	3	-	-
Zooplankton	3	3	3	-	-
SPOM	3	3	3	-	-
Sediments	3	3	3	-	-

526

527 **Table 2.** Insects and weed species (C₃ and C₄) collected in the experimental rice plots when
 528 observed. Insects were identified to the lowest taxonomic level (family, subfamily or
 529 infraorder).

Insect species	Order	n	Weed species	n	Type
Anisoptera larvae	Odonata	2	<i>Courtoisina cyperoides</i>	2	C ₃
Baetidae larvae	Ephemeroptera	2	<i>Schoenoplectus juncooides</i>	3	
Corixidae	Hemiptera	1	<i>Echinochloa colona</i>	3	C ₄
Culicidae larvae	Diptera	1	<i>Fimbristylis ferruginea</i>	3	
Dytiscidae larvae	Coleoptera	1	<i>Pycreus mundtii</i>	3	
Naucoridae	Hemiptera	2	-	-	
Notonectidae	Hemiptera	2	-	-	
Ranatrinae	Hemiptera	2	-	-	
Zygoptera larvae	Odonata	2	-	-	
Total		15		14	

530

531 **Table 3.** The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm standard deviation) of sampled compartments
 532 and, for common carp, corrected standard ellipse area (SEAc, ‰^2) and total area of the
 533 convex hull encompassing the data points (TA, ‰^2). Letters indicate significant differences in
 534 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between 45- and 145-day-old carp (Student's t-test, $p < 0.001$). No
 535 differences among 145-day-old carp in the three experimental rice plots were observed
 536 (ANOVA, $p > 0.05$).

Compartment	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	SEAc (‰^2)	TA (‰^2)
45-day-old carp	5	-18.8 ± 0.5^b	9.3 ± 0.6^b	1.2	1.0
145-day-old carp	9	-24.9 ± 1.0^a	5.7 ± 0.9^a	3.0	4.5
Plot P2	3	-24.4 ± 0.9	6.2 ± 0.8	-	-
Plot P3	3	-24.4 ± 1.1	4.7 ± 0.4	-	-
Plot P5	3	-25.8 ± 0.5	6.1 ± 0.7	-	-
Rice seeds	6	-26.6 ± 0.9	4.9 ± 0.4	-	-
Rice leaves	8	-28.1 ± 0.5	2.5 ± 0.7	-	-
Rice roots	9	-27.8 ± 0.3	1.6 ± 0.3	-	-
C ₃ weeds	5	-28.4 ± 0.8	4.4 ± 1.1	-	-
C ₄ weeds	9	-11.3 ± 0.4	3.4 ± 2.0	-	-
Sediments	9	-22.7 ± 0.5	2.1 ± 0.7	-	-
Zooplankton	9	-29.1 ± 2.2	3.5 ± 1.2	-	-
Insects	15	-27.1 ± 2.6	5.9 ± 2.9	-	-

537