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3   Pool choice in a vertical landscape: tadpole rearing site flexibility in

4   phytotelm-breeding frogs

5   Chloe A. Fouilloux[1], Shirley Jennifer Serrano-Rojas[2], Juan David Carvajal-Castro[3,4], Janne K.

6   Valkonen[1], Philippe Gaucher[5], Marie-Therese Fischer[2], Andrius Pašukonis[2,6†*], Bibiana

7   Rojas[1†*]

8   *[1]Department of Biology and Environmental Sciences, University of Jyväskylä, PO Box 35, FI

9   40001, Finland; chloe.a.fouilloux@jyu.fi, bibiana.rojas@jyu.fi; janne.valkonen@jyu.fi*

10   *[2]Department of Biology, Stanford University, 371 Jane Stanford Way, Stanford, CA 94305,*

11   *USA; shirley.serrano25@gmail.com; apasukonis@stanford.edu; fi5cher@stanford.edu*

12   *[3]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá DC,*

13   *Colombia; carvajaljcastro@gmail.com*

14   *[4]Department of Biological Sciences, St. John's University, Queens, NY, USA;*

15   *[5]USR LEEISA - Laboratoire Ecologie, Evolution, Interactions des Systèmes amazoniens,*

16   *CNRS-Guyane, Cayenne, French Guiana; philippe.gaucher@cnrs.fr*

17   *[6]Centre d'Ecologie Fonctionelle et Evolutive, CNRS, 1919 Route de Mende, 34293*

18   *Montpellier Cedex 5, France*

19   *[†]Authors to whom correspondence should be addressed*

20   **Equal senior author contribution*

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24   **Abstract**

25   Many species of Neotropical frogs have evolved to deposit their tadpoles in small water

26   bodies inside plant structures called phytotelmata. These pools are small enough to exclude

27   large predators but have limited nutrients and high desiccation risk. Here, we explore

28   phytotelm use by three common Neotropical species: *Osteocephalus oophagus,* an arboreal

29   frog that periodically feeds eggs to its tadpoles; *Dendrobates tinctorius,* a tadpole-

30   transporting poison frog with cannibalistic tadpoles; and *Allobates femoralis,* a terrestrial

31   tadpole-transporting poison frog with omnivorous tadpoles. We found that *D. tinctorius*

32   occupies pools across the chemical and vertical gradient, whereas *A. femoralis* and *O.*

33   *oophagus* appear to have narrower niches that are restricted primarily by pool height, water

34   capacity, alkalinity, and salinity. *Dendrobates tinctorius* tadpoles are particularly flexible,

35   and can survive in a wide range of chemical, physical, and biological conditions, whereas *O.*

36   *oophagus* seems to prefer small, clear pools and *A. femoralis* occupies medium-sized pools

37   with abundant leaf litter and low salinity. Together, these results show the possible niche

38   partitioning of phytotelmata among frogs, and provide insight into stressors and resilience of

39   phytotelm breeders.

40

41   **Keywords:** parental care; poison frogs; phytotelmata; niche partitioning, competition;

42   tadpoles

43   **Short title**: Pool choice in a vertical landscape

44

Introduction

The survival of young often hinges on the quality of the rearing environments created or chosen by their parents. Whether it is by building nests (birds: (Brown and Brown 1991); mice: (Bult and Lynch 1997, Zhao et al. 2016), digging burrows (rodents: (Svendsen 1976, Ebensperger et al. 2014), or depositing clutches/larvae (e.g., salamanders: (Ruano-Fajardo et al. 2014), frogs: (Pettitt et al. 2018)), the ecology of rearing sites is fundamental in shaping offspring success. For animals with external fertilization, breeding-site choice can be especially important, as optimal conditions for egg clutches may differ from the optimal environment for hatchlings and adults (fish: (Ottesen and Bolla 1998, Mikheev et al. 2001); salamanders: (Nussbaum 1987, Sih and Moore 1993); frogs: (Vági et al. 2019)). Many of these animals assess and prefer biotic and abiotic properties of breeding sites that can enhance offspring survival (Marsh and Borrell 2001, Mokany and Shine 2003, Brown and Shine 2005, Touchon and Worley 2015). Thus, characterizing the nurseries where offspring occur can provide information on the qualities parents assess when making these critical reproductive decisions.

The challenge of finding an optimal rearing site becomes especially apparent in terrestrial or arboreal breeding animals, whose larval forms are aquatic. For example, some treefrogs lay clutches overhanging water bodies. The placement of clutches is essential, as tadpoles from poorly placed clutches risk hatching and falling onto the ground (Wells 2007, Warkentin 2011). One remarkable amphibian strategy adapted to changing habitats between egg and larval stages involves parents that physically transport recently hatched tadpoles from terrestrial oviposition sites to small water-holding plant structures (phytotelmata), ponds, or

68   streams (Summers and Tumulty 2014, Schulte et al. 2020). Unlike other terrestrial breeding

69   amphibians, the physical transport of young allows parents to select the ideal environment for

70   their offspring to develop. Although it is difficult to extensively characterize streams and

71   ponds, microhabitats like phytotelmata provide a unique opportunity to fully measure the

72   biological, chemical, and physical aspects of a nursery, creating an opportunity to interpret

73   deposition choices with a depth of ecological information that is rarely available for other

74   rearing sites. Here, we investigate the chemical and physical properties of aquatic nurseries

75   that predict the presence of Neotropical tadpoles in phytotelm-breeding frogs.

76

77   The use of phytotelmata as tadpole nurseries can seem counterintuitive, as their small volume

78   makes them prone to desiccation and limited in food (Summers and McKeon 2004, Summers

79   and Tumulty 2014). However, their small size provides protection from large predators, and

80   various species have evolved different strategies for their offspring to succeed in these pools

81   (substrate specialisation: (von May et al. 2009, Pettitt et al. 2018); trophic egg-feeding:

82   (Weygoldt 1980, Brown et al. 2010); larval aggression/cannibalism: (Poelman and Dicke

83   2007, Gray et al. 2009, Rojas 2014); pool choice based on specific physical or chemical cues:

84   (Lin et al. 2008, Schulte et al. 2011). Despite the widespread use of phytotelmata, and the

85   non-random site selection shown by many frog parents, few studies go beyond quantifying

86   basic pool dimensions and pool occupation to understand tadpole deposition decisions.

87   Further, the bulk of phytotelm studies are focused only on bromeliads, while work exploring

88   potential trade-offs associated with different phytotelmata (i.e., physical and chemical

89   properties as well as food- and predator-related pressures), and how these change across a

90   vertical gradient, has gone largely overlooked.

4

91

92   To understand what variables drive phytotelm selection, we compared pool occupation by

93   three Neotropical frogs (*Dendrobates tinctorius*, *Allobates femoralis*, and *Osteocephalus*

94   *oophagus*) that were most frequently detected in phytotelmata throughout field surveys at our

95   study site in French Guiana. *Osteocephalus oophagus* is a hylid treefrog with bi-parental care

96   and obligately oophagous tadpoles (Jungfer and Weygoldt 1999, Almendáriz et al. 2000). As

97   in our field site, adults have been found to call and breed in bromeliads, tree-holes, and palm

98   axils close to the forest floor (Jungfer and Weygoldt 1999). Tadpoles of this species develop

99   in the same pool in which the eggs are deposited. *Allobates femoralis* is a terrestrial frog

100   closely related to dendrobatids. Adult males aggressively defend territories during the rainy

101   season (Roithmair 1992, Narins et al. 2003), from which they carry recently hatched tadpoles

102   to a variety of terrestrial pools including phytotelmata close to the ground (Ringler et al.

103   2009, 2013). Tadpoles of this species are omnivorous (McKeon and Summers 2013), but not

104   cannibalistic (Summers and McKeon 2004).

105

106   Following broad species-wide comparisons, we focus on a more detailed analysis of pool

107   choice in *D. tinctorius*, a phytotelm specialist with predatory and cannibalistic tadpoles

108   which are deposited in a range of phytotelm types (e.g., palm bracts, tree-holes, fallen trees;

109   Fig. 1 and Fig. 2) that occur from the forest floor to more than 20 m in vertical height

110   (Gaucher 2002, Rojas 2014, 2015). The use of the high canopy pools is perplexing because

111   *D. tinctorius* is commonly successful in terrestrial pools (Rojas 2014). It is known that pool

112   chemistry can change drastically depending on substrate ('dead' or 'live'; see Fig. 1), height,

113   and community composition (Ruano-Fajardo et al. 2014, Pettitt et al. 2018). Thus, better

114   understanding the ecology of high arboreal pools and characterizing phytotelmata across the

115   vertical gradient could help explain both the apparent success of *D. tinctorius* in a wide range

116   of pools, and why parents sometimes carry their offspring such heights. Further, *D. tinctorius*

117   tadpoles predate on other species of phytotelm-breeders, making it a key amphibian species

118   for understanding the niche partitioning amongst communities of phytotelm breeders. To our

119   knowledge, this is the first study providing detailed biotic, physical, and chemical

120   comparisons of phytotelm choice between Neotropical species.

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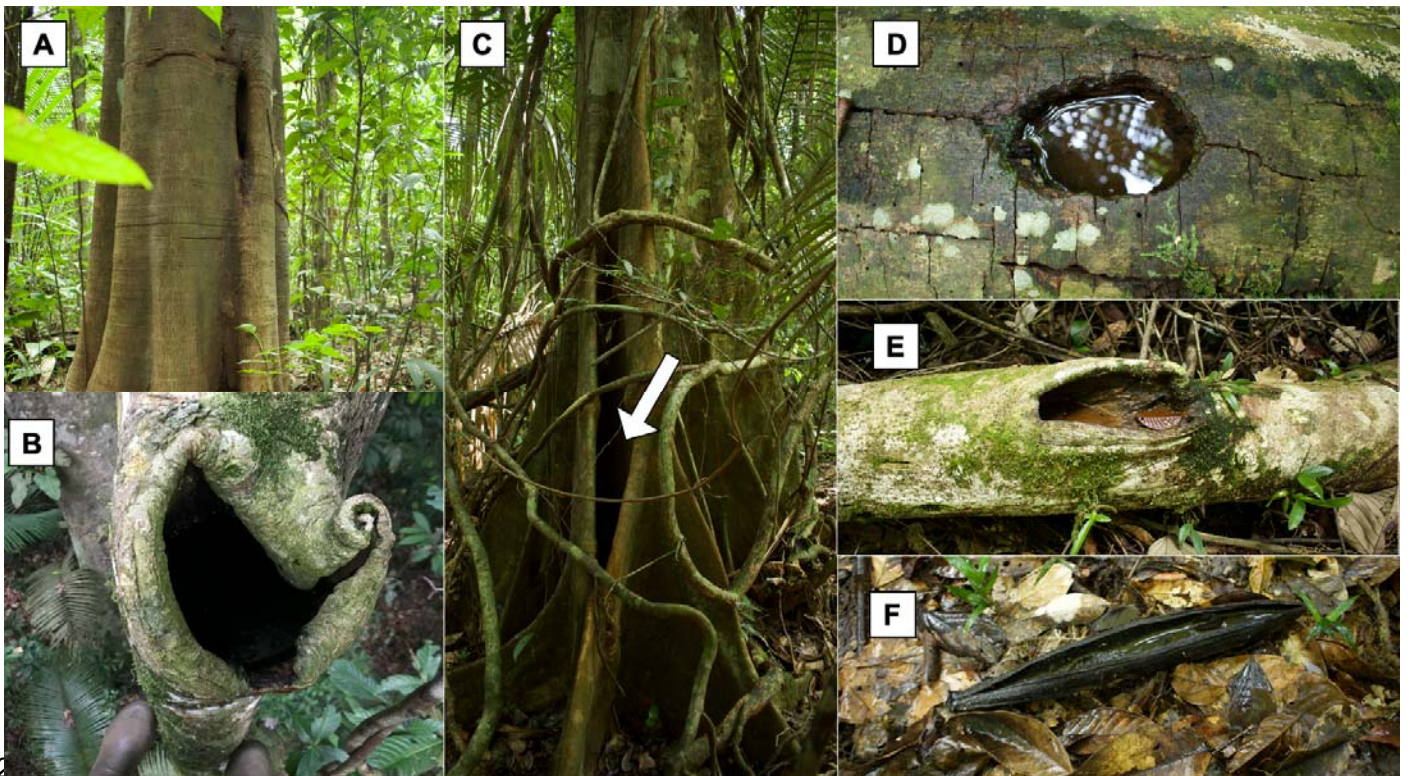
123   **Figure 1.** *Visual overview of sampled pool diversity. Photos show the diversity of pools*

124   *across the vertical gradient. Phytotelmata used by frogs include "live" substrate pools such*

125   *as tree holes (**A**), high arboreal pools (**B**), and buttresses (**C**). There were also commonly*

126   *occupied "dead" substrate pools such as fallen trees (**D, E**) and palm bracts (**F**).*

127

128

Material and methods

130 The study was carried out in the primary lowland terra-firme forest near the Camp Pararé at

131 the CNRS Nouragues Ecological Research Station in the Nature Reserve Les Nouragues,

132 French Guiana (4°02'N, 52°41'W) over two field seasons: 1st February to 20th March 2019,

133 and 30th January to 26th February 2020. The study area was chosen specifically because of

134 the high abundance of *D. tinctorius (Rojas and Pašukonis 2019)*. Pools were found with a

135 combination of field methods. We opportunistically searched for pools targeting suitable

136 microhabitats such as fallen trees, trees with buttresses and palm trees. In addition, pools

137 were discovered by using tracking to follow *D. tinctorius* during previous studies (Pašukonis

138 et al. 2019). We also used experimentally-induced tadpole transport in combination with

139 tracking (Pašukonis et al. 2017) to find additional pools used by *A. femoralis*. Trees with high

140 arboreal pools were discovered by locating calls produced by the treehole-breeding frogs

141 *Trachycephalus resinifictrix* and *T. hadroceps* during night surveys.

142

Sampled pools

144 We exclusively considered phytotelmata throughout this study. Pools could be classified into

145 two categories: dead substrates, which included holes in dead branches, fallen trees, and

146 fallen *Oenocarpus* palm bracts; or live substrates which included live tree trunks, branches,

147 roots, and buttresses. We did not sample bromeliads and non-phytotelm pools as these pools

148 are not used by *D. tinctorius.* Based on the pools' height and accessibility to different frog

149 species, we termed the pools as "ground access", "low arboreal" or "high arboreal" (Fig. 1,

150 2). Ground-access pools did not require vertical climbing ability to reach and included dead

151   fallen structures as well as pools in live roots or low buttresses. Low arboreal pools were

152   inside vertical structures low on the trunk or on high buttresses. High arboreal pools were

153   high on the trunk or in canopy branches and were accessed for sampling using rope-based

154   canopy access methods. There was a clear vertical separation between ground-access and

155   low-arboreal pools, which were all under 212 cm in height and between those and high

156   arboreal pools, which were all above seven meters in height. In total, we sampled 84 unique

157   pools across the 2019 and 2020 field seasons.

158

159   Several unique pools were sometimes found and sampled in the same tree. For all pools, we

160   recorded the pool type, location (latitude/longitude), height from the ground to the pool edge,

161   largest width and length parallel to the water surface, and the pool depth from the solid

162   sediment bottom to the maximum water level line. Based on these measurements, we

163   estimated the maximum water-holding capacity of each pool using the volume formula of a

164   semi-ellipsoid as in Rojas (2014). Other sampling methods differed between the two field

165   seasons.

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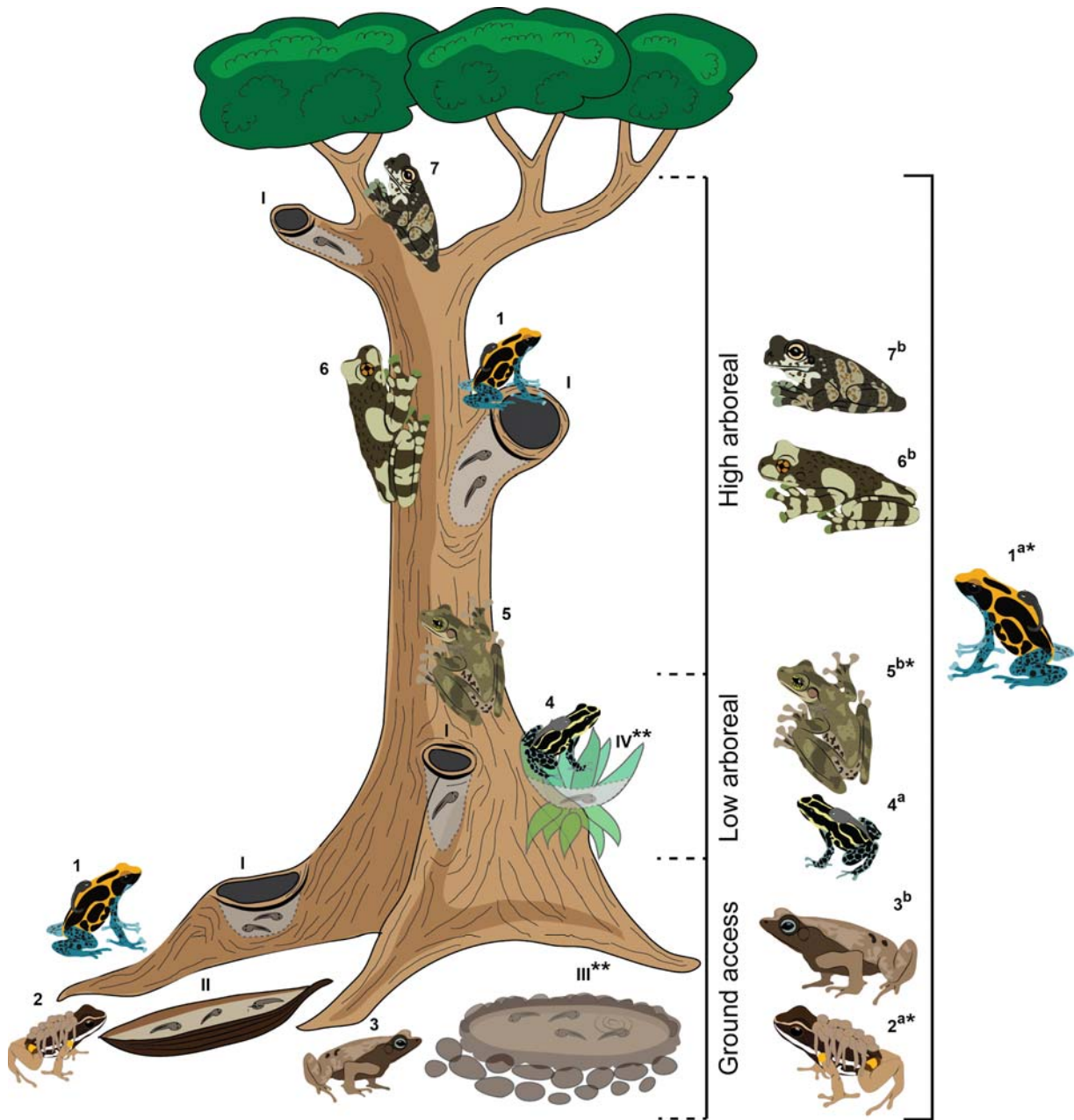
Figure 2. Vertical partitioning of the phytotelm-breeding anuran community in the Nouragues Nature Reserve, French Guiana. *Numbers indicate seven species detected during this study: 1. Dendrobates tinctorius, 2. Allobates femoralis 3. Rhinella castaneotica, 4. Ranitomeya amazonica, 5. Osteocephalus oophagus, 6. Trachycephalus resinifictrix, 7. T. hadroceps. Letters indicate species with a) terrestrial or b) aquatic eggs. Latin numerals indicate commonly used pool types: I. tree holes at various heights, II. fallen palm bracts, III.*

174   *ground puddles, IV. bromeliads. *Most commonly encountered species included in the*

175   *analysis; ** Pool types not sampled in this study (see methods).*

176

177   **2019 field season sampling**

178   In 2019, we quantified physical measures (height, pool dimensions, leaf-litter volume), biotic

179   measures (amphibian and invertebrate counts and diversity), as well as chemical

180   measurements (see Supp. Table 1 for description of all variables measured). For pools

181   accessible from the ground and smaller arboreal pools, we attempted to sample all tadpoles

182   and Odonata larvae (primary tadpole predators) in each pool. Initially, we carefully observed

183   the undisturbed pool and attempted to catch all tadpoles and Odonata larvae using a variety

184   of tools. We then syphoned the entire volume of the water and sediment from the pool,

185   emptied the leaf litter and searched for tadpoles and Odonata larvae. The volumes of water,

186   sediment, and leaf litter were measured. For deep arboreal pools, we repeatedly netted and

187   observed the pool until no more tadpoles were caught during five minutes of continuous

188   netting. We carefully scraped the inner walls of the pools and caught as many Odonata larvae

189   as possible. The leaf-litter volume could not be accurately measured for some deep arboreal

190   pools, but they typically were protected from falling leaves and had little leaf litter in them.

191

192   We used visually apparent morphological traits to identify tadpoles, except for *Allobates*

193   *femoralis, A. granti, and Ameerega hahneli*, which we could not reliably differentiate in the

194   field. Because *Allobates femoralis* was more common in our study area than *A. granti* and

195   *Am. hahneli* and we never observed *A. granti* and *Am. hahneli* directly at the pools we

196   classified all *A. femoralis*-like tadpoles as such. Is it important to note that some *A. granti*

10

197   and *Am. hahneli* tadpoles may have been misclassified as *A. femoralis*. However, this does

198   not affect the interpretation of our results as all three species are cryptic terrestrial poison

199   frogs similar in appearance, ecology and behavior. We also opportunistically recorded all

200   species of adult frogs heard or seen at each pool throughout the sampling period. This was

201   used as an amphibian diversity index between 0 and 8 species observed at each pool.

202   Tadpoles of only three out of seven recorded species, namely *D. tinctorius*, *O. oophagus* and

203   *A. femoralis*, were detected in pools with sufficient frequency for further analysis (N = 34

204   (2019), N = 7 and N = 10 pools, respectively).

205

206   Sampled invertebrates were counted, photographed, and classified only to a group level

207   (usually order or class) apparent in the field. To estimate the predation pressure on tadpoles

208   we used the total count and average size of all Odonata larvae detected in the procedure

209   described above. To estimate density and diversity of aquatic invertebrates, we carefully

210   searched and counted invertebrates in a sample of up to 10 liters of water and up to one liter

211   of sediment in proportion to the total estimated pool volume. For each liter of the water

212   volume sampled, we sampled ~ 100 mL of sediment from the bottom of the pool. When the

213   water volume was less than one liter or the amount of sediment was less than 100 mL, we

214   sampled the entire pool and recorded the exact volumes. In the final analysis, we used the

215   invertebrate density (count divided by the volume sampled) and the diversity index

216   corresponding to our classification (between 0 and 12). The following 12 categories were

217   used to quantify invertebrate diversity: Odonata Zygoptera larvae, Odonata Anisoptera

218   larvae, surface Coleoptera adults, diving Coleoptera adults, Coleoptera Scirtidae larvae,

219   Trichoptera larvae, Diptera Culicidae larvae, Diptera Chironomidae larvae, Diptera Tipulidae

220   larvae, other Diptera larvae, small red Annelida, other unidentified larvae. All water,

221   sediment, tadpoles and invertebrates were released back into the pool after sampling.

222

223   We measured water conductivity, salinity and total dissolved solids (TDS), dissolved oxygen

224   and temperature with electronic sensors (EZDO 7200 and pHenomenal OX4110H). Water

225   chemistry (KH (also known as alkalinity), hardness and NO_3) was recorded using aquarium

226   water testing strips (JBL EasyTest). All measures were taken from the undisturbed surface

227   water of the pool.

228

229   **2020 field season sampling**

230   The 2020 dataset focused solely on *D. tinctorius* tadpole counts and pH measurements of

231   weekly resampled ground access phytotelmata (N = 26) over the time period of a month

232   (February 2020). Rainfall data were provided by the Nouragues Ecological Research Station

233   from an above-canopy weather station in the study area. High arboreal pools (N = 8 (2020))

234   were only measured once. pH was recorded using a pH meter (AMTAST Waterproof pH

235   Meter). The pH meter was calibrated once per day, prior to pool sampling, using both acidic

236   (pH = 4) and neutral (pH = 7) calibration solutions. The pH of ground access pools was taken

237   directly by submerging the pH probe into the pool, and the measurement was recorded once

238   read-out stabilized. For arboreal pools, a sample of water was collected using a syringe,

239   which was then sealed at both ends. Once on the ground, one end of the syringe was opened,

240   and the pH was measured by submerging the pH probe into the syringe. Syringes were never

241   reused. Between pool sampling, the pH probe was wiped with a clean cloth and rinsed with

242   aquifer water.

243

244 **Statistical Analyses**

245 The presence of *D. tinctorius* in pools was analyzed using 2019 field data. As a result of the

246 high collinearity between variables in the 2019 dataset (see Supp Fig 1), we used a principal

247 components regression to analyze phytotelm ecology data. We first checked data for a non-

248 random structure following Björklund (Björklund 2019); then, we established that the

249 correlation matrices were significantly different from random (ψ = 10.22, p = 0; ϕ = 0.238, p

250 < 0.001) to ensure they were suitable for a PCA. Based on each PCs difference from random

251 matrices, we selected the first three principal components as predictors of probability for *D.*

252 *tinctorius* tadpole presence as a binomial response in the principal component regression

253 (PC1-3 explained about 53% of the variation proportion of variance explained $\pm$ SE : PC1 =

254 0.24 $\pm$ 0.48, PC2 = 0.17 $\pm$ 0.40, PC3 = 0.11 $\pm$ 0.33). We evaluated the fit of negative

255 binomial GLM models based on AIC ranks ((Akaike 1974); see Supp. Table 2). Models

256 within two AIC scores of each other were further evaluated by assessing the significance of

257 interactions between model terms.

258

259 To better understand which variables contributed significantly to each principal component,

260 we calculated which variables had index loadings larger than random data. Following the

261 methods outlined by Björklund (2019) and Vieira (2012), we randomized the data and

262 calculated new correlation matrices which we permuted 1,000 times. We then compared the

263 index of loadings ($IL_{ij} = u_{ij}^2 \times \lambda_i^2$, see Vieira (2012) for details) between each observed PC

264 and the randomly generated data to see which variables contributed significantly to each

265 principal component.

266

267 The 2020 dataset consisted of weekly resampled pools throughout February 2020. Models

268 took repeated measures of pool ID into account as a random effect. Both the presence of *D.*

269 *tinctorius* tadpoles (count; negative binomial family) and pH (Gaussian family) from

270 resampled pools were modeled using a mixed effects generalized linear model in the package

271 "glmmTMB" (Magnusson et al. 2020). Predictor structure for both pH and *D. tinctorius*

272 models were built based on biologically relevant variables (pool substrate, time, *D. tinctorius*

273 tadpole count (for pH model), water capacity, surface area:depth ratio). Using these

274 variables, models were first fit with relevant interactions (see Supp. Table 3, 4), which were

275 then removed if they did not contribute significantly to the model using single term deletions

276 (drop1). Residuals were diagnosed using the package "DHARMa" (Hartig 2020); final

277 models were then checked for overdispersion and zero-inflation and corrected as necessary.

278 All code was done in R (Core 2015).

279

280 **Results**

281 **Species-wide trends**

282 We detected tadpoles or adults of 7 species from 4 families using surveyed phytotelmata for

283 breeding (Fig. 2). Dendrobatidae: *Dendrobates tinctorius*, *Ranitomeya amazonica*,

284 Aromobatidae: *Allobates femoralis*; Hylidae: *Osteocephalus oophagus*, *Trachycephalus*

285 *resinifictrix*, *T. hardroceps*; Bufonidae: *Rhinella castaneotica*. The tadpoles of only three

286 species (*D. tinctorius*, *O. oophagus* and *A. femoralis*, present in N = 34, N = 7 and N= 10

287 pools, respectively) were detected frequently enough for further analysis. Although the data

288 on *D. tinctorius* are more robust, trends for *O. oophagus* (N = 125 tadpoles) and *A. femoralis*

14

289   (N = 117 tadpoles) emerge despite a smaller dataset. The species-wide dataset is based on the

290   sampling of 70 unique pools in 2019.
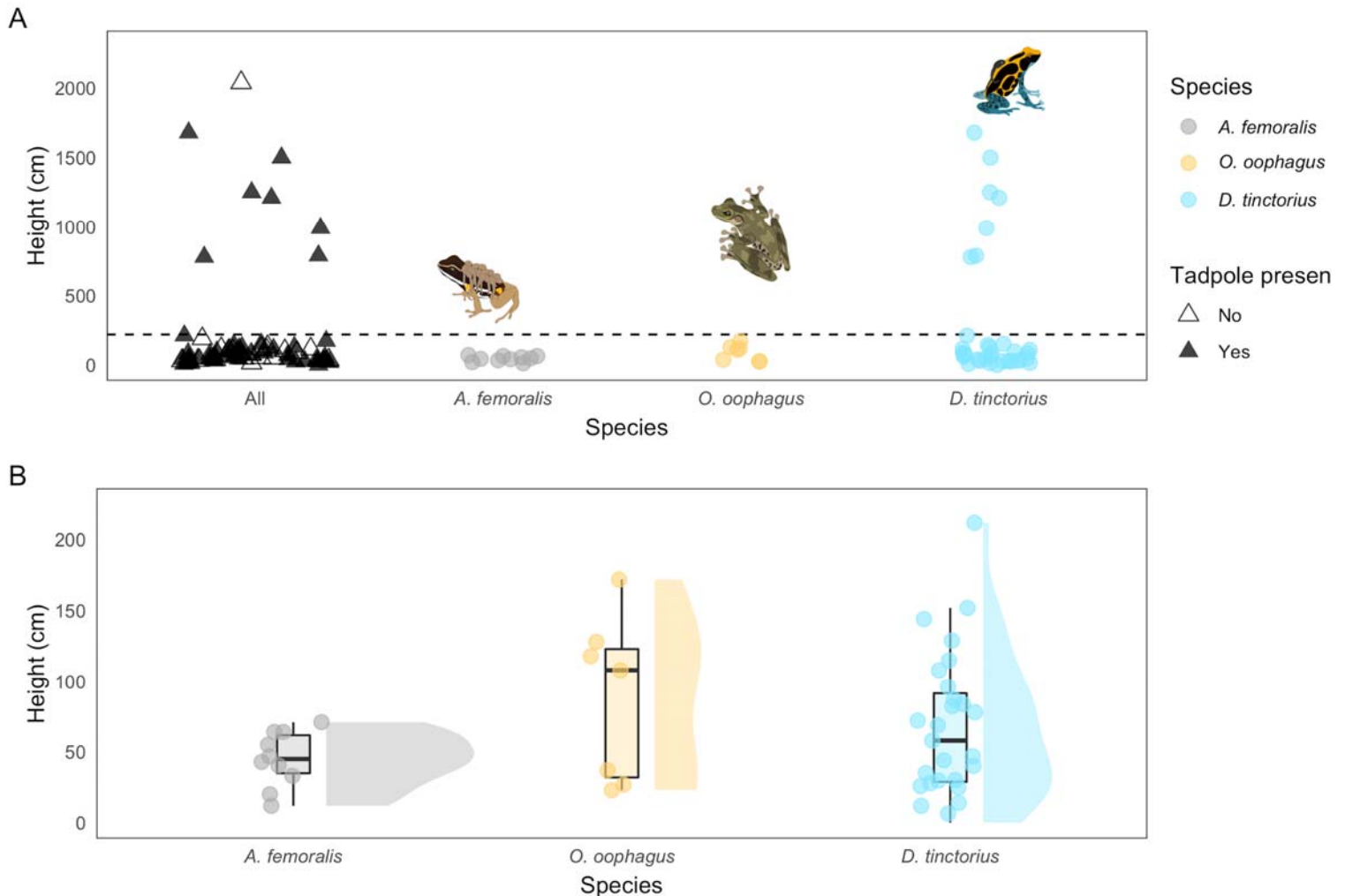
292   **Figure 3. Tadpole presence across the vertical landscape.** *Panel (**A**) shows all sampled*

293   *pools. For the "All" category, colored/empty triangles represent presence/absence data of all*

294   *three species. Dashed line is drawn at 220cm; pools above this limit are classified as high*

295   *arboreal pools. Panel (**B**) highlights occupied pools below 220 cm. Dendrobates tinctorius (N*

296   *= 34) tadpoles occur in pools across the vertical landscape. Distribution of O. oophagus (N =*

297   *7) and A. femoralis (N = 10) tadpoles shows possible vertical niche partitioning. Boxplot*

298   *whiskers extend 1.5 * interquartile range. Violin plots represent density distribution for*

299   *species occurrence. Data is from the 2019 field season.*

300

301   Differences in pool accessibility are highlighted by Fig. 3. Compared to *A. femoralis* and *O.*

302   *oophagus,* one of the most striking aspects of *D. tinctorius* ecology is its flexibility with

303   respect to site choice on a vertical axis. *Dendrobates tinctorius* tadpoles were found in pools

304   from the forest floor to more than 15 meters in the canopy. For *O. oophagus,* a strictly

305   arboreal frog in its adult stage, tadpoles were detected only in low arboreal pools, ranging

306   from 20 cm to 1.7 m in height. In *A. femoralis,* tadpoles were only found in ground-access

307   pools, and occurred at a maximum height of 71 cm.

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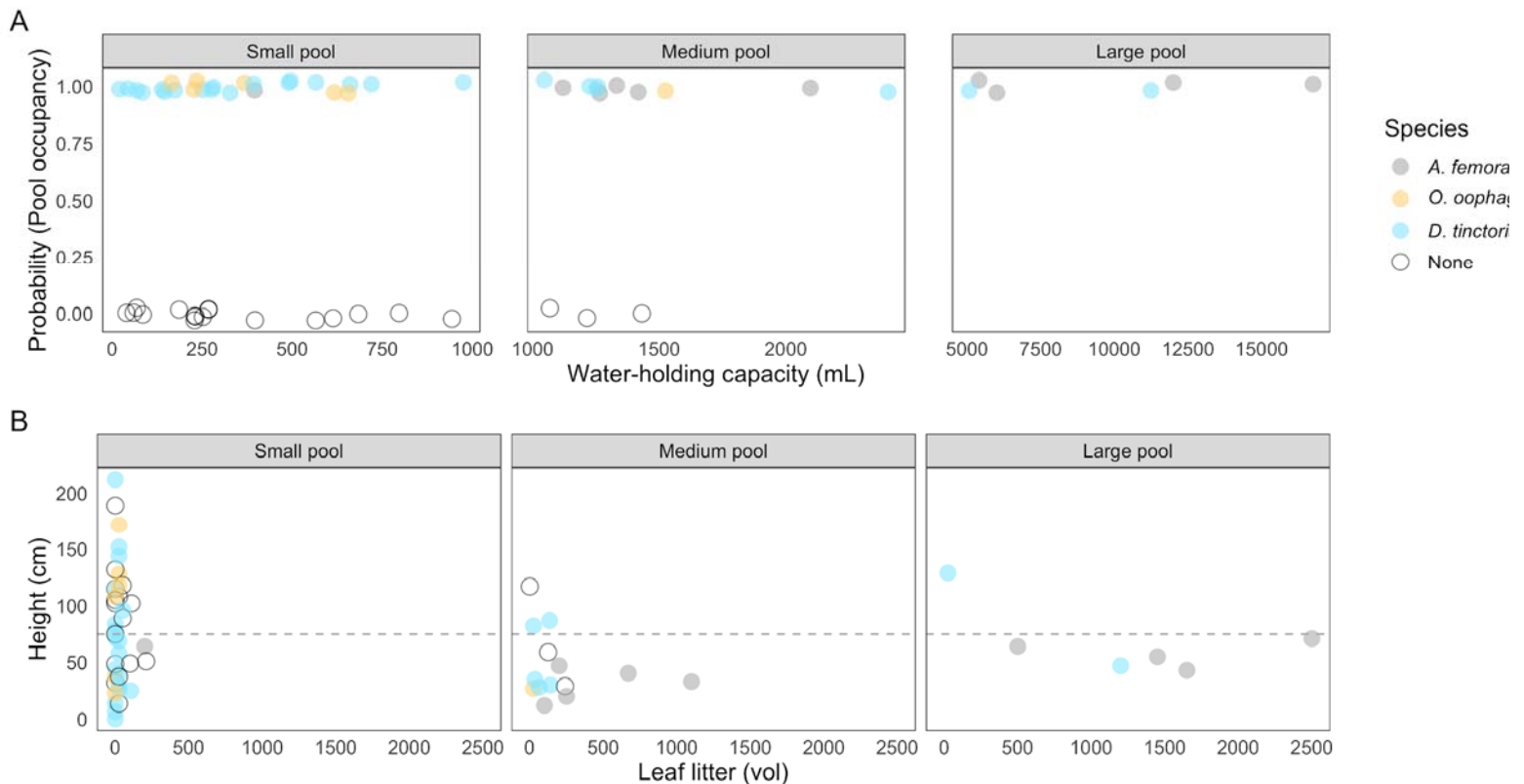
310 ***Figure 4. Pool occupancy based on water capacity and leaf-litter volume of phytotelmata.***

311 *All data are subsetted for low arboreal and ground-access pools (< 220 cm). Panel (**A**) is the*

312 *probability of pool occupancy (binomial, 0/1) based on water capacity; data are faceted*

313 *based on relative pool size (Small = < 1000 mL, Medium = < 5000 mL, and Large = > 5000*

314 *mL). Points are plotted with a small amount of random noise on the y-axis to facilitate*

315 *visualization of overlapping data. Panel (**B**) illustrates the correlation between leaf litter and*

316 *height, faceted by the same pool categories as Panel A. Points are colored by species*

317 *presence. Dashed line indicates the vertical limit of A. femoralis (< 75 cm). Out of the 62*

318 *ground-access and low arboreal pools observed, D. tinctorius co-occurred once with A.*

319 *femoralis and once with O. oophagus; O. oophagus and A. femoralis tadpoles were never*

320 *found in the same pool.*

321

322 Despite small sample sizes we found clear trends: *O. oophagus* tadpoles are heavily biased

323 towards small, clear pools and *A. femoralis* is present in medium and large pools with large

324 amounts of leaf litter, whereas *D. tinctorius* occurs throughout the sampled range (Fig. 4).

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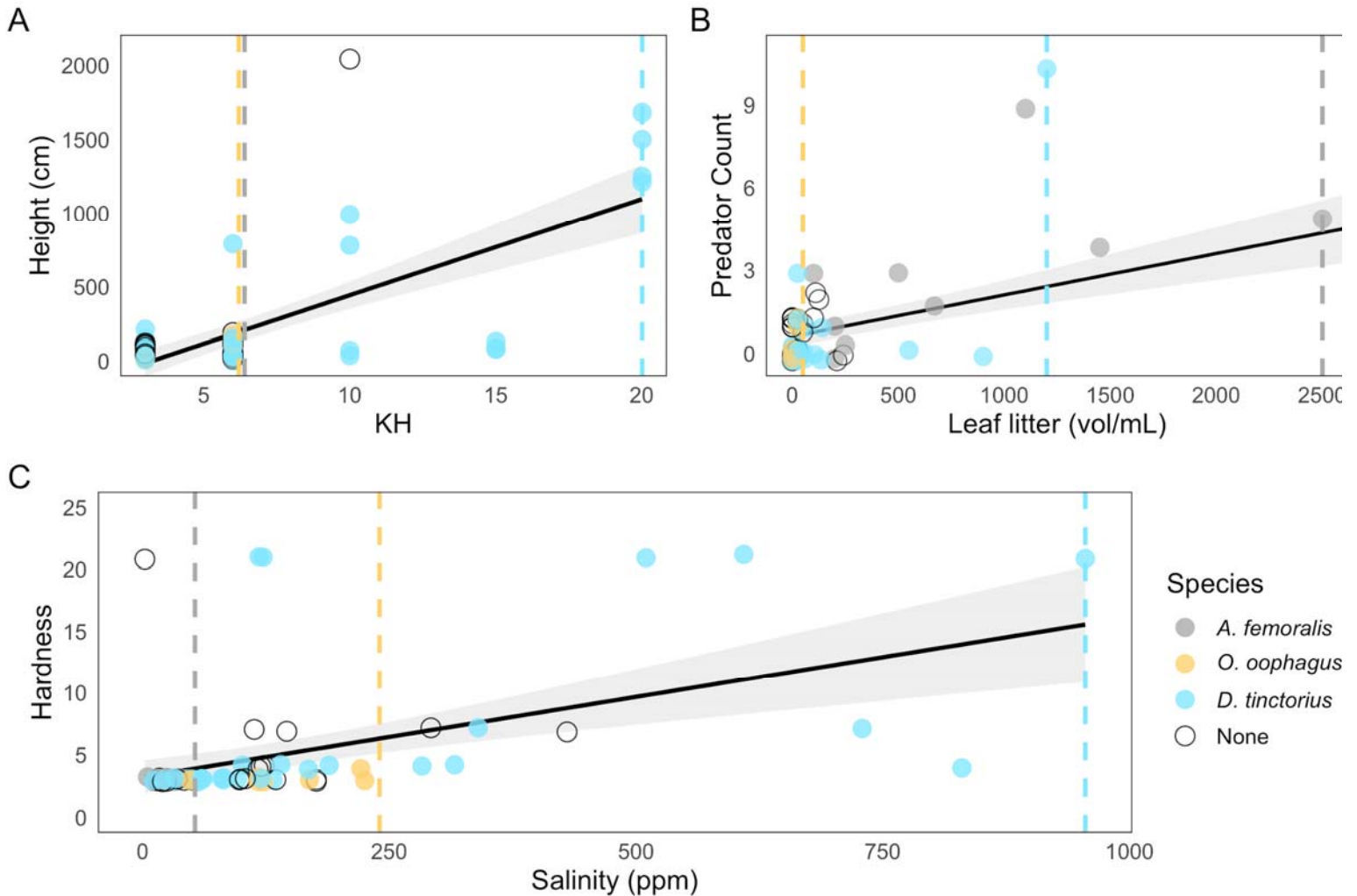
Figure 5. Chemical and physical predictors of tadpole presence in Neotropical tadpoles.
We find that D. tinctorius tadpoles are tolerant to a wide range of KH, hardness, height, and salinity values, but appear to be limited with respect to high leaf litter volumes. Plots are based on variables with varied species limits (dashed lines). Colored points represent species presence. Black lines are fit with a GLM smoother, with 95% CI highlighted in light grey.

As opposed to *A. femoralis* and *O. oophagus*, *D. tinctorius* can occupy chemically diverse pools, showing remarkable flexibility with respect to KH, salinity, and hardness that clearly limits the other species. *Allobates femoralis* and *O. oophagus* appear to exist in similar KH

18

336   ranges (KH = 3-6), while *D. tinctorius* appears more tolerant of extreme values (KH = 3-20).

337   *Allobates femoralis* tadpoles occurred in pools with a salinity range from 5 to 37 ppm, while

338   *O. oophagus* tadpoles occupied pools with a range from 48 to 225 ppm (Fig. 5, Panel C).

339   *Dendrobates tinctorius* again appears to have no functional limitation, occupying pools with

340   salinity from 11 ppm up to 955 ppm.

341

342   **Deposition site decisions: *Dendrobates tinctorius***

343   Because we detected *D. tinctorius* tadpoles much more frequently, we were able to conduct a

344   more thorough analysis of the variables predicting tadpole presence in this species (see Supp.

345   Table 1). We used principal components as predictors for *D. tinctorius* presence. Based on an

346   AIC model comparison, we did not detect any significant interactions between components

347   (Supp. Table 2). A negative binomial GLM only detected PC1 to play a significant role in

348   predicting tadpole presence (Table 1, CI: 0.08-0.42, p = 0.003), where an increase in

349   component value increased the probability of detecting tadpoles.

350

| Predictors	Estimates	Tadpole presence (Y/N) CI	p
(Intercept)	-0.85	-1.27 – -0.49	**<0.001**
PC1	0.25	0.08 – 0.42	**0.003**
PC2	0.09	-0.16 – 0.40	0.528
PC3	0.21	-0.07 – 0.48	0.144

351

352 *Table 1. Principal component regression of tadpole presence in phytotelm pools. Using a*

353 *negative binomial GLM, we found that only the first principal component is significant in*

354 *predicting tadpole presence.*

355

356 Following Björklund (2019), we found that, when compared to randomly generated matrices,

357 five out of the original 14 traits (see Supp. Table 1 for trait definitions) contributed

358 significantly to the first principal component. The significant traits can be broadly

359 categorized using three descriptors: (1) chemical (KH, $p < 0.001$; IL = 1.50, hardness, $p =$

360 0.001, IL = 1.30; salinity, $p < 0.001$, IL = 1.62); (2) physical (height, $p = 0.013$, IL = 1.06);

361 and (3) biological (invertebrate diversity, $p < 0.001$, IL = 1.20) (see Fig. 6). Altogether, these

362 results show that *D. tinctorius* tadpoles were found significantly more frequently in pools

363 with higher levels of hardness, KH, and salinity; higher in the vertical gradient; and with

364 more diverse invertebrate communities (Fig. 6).

365

366
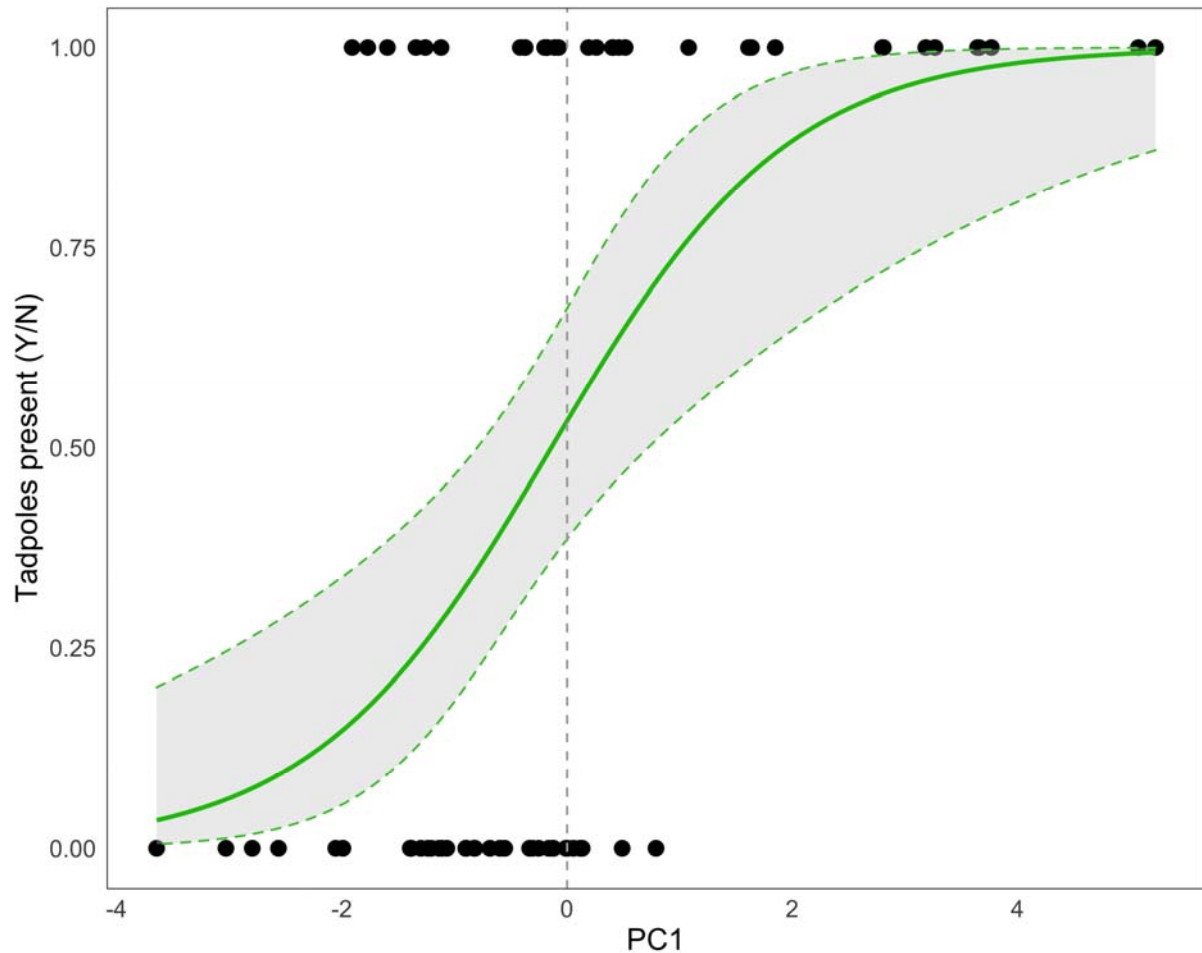
Figure 6. **Binomial response of *Dendrobates tinctorius* presence to the first principal component.** *Dashed lines represent the 95% confidence interval. Significant variables within this component are detailed in Supp. Table 1.*

Dendrobates tinctorius across temporal scales

Using both 2019 and 2020 datasets, we were able to follow phytotelmata across multiple timescales: 13 weekly resampled ground-access and low arboreal pools, 13 annually resampled ground-access and low arboreal pools, and 7 annually resampled high arboreal pools. Overall, we found that pools can persist over multiple sampling seasons. High arboreal pools appear to be the most stable with respect to both tadpole count and tadpole density

21

378   compared to low arboreal and ground-access pools sampled both years ($\bar{x}_{High}$ (2019) = 13.14

379   tadpoles, $\bar{x}_{High}$ (2020) = 10 tadpoles versus $\bar{x}_{Low}$ (2019) = 0.92 tadpoles, $\bar{x}_{Low}$(2020) = 1.31

380   tadpoles). High arboreal pools also had the highest average pH and KH (pH$_{High}$ = 6.73,

381   KH$_{High}$ = 15.14) compared to averages of other pool substrates (pH$_{(Low)Live}$= 4.35, pH$_{(Low)Dead}$

382   = 5.68; KH$_{(Low)Live}$ = 5.69, KH$_{(Low)Dead}$ = 5.88). Due to difficult accessibility, high arboreal

383   pools were sampled only once per year, and thus were excluded from further analysis

384   involving repeated sampling.

385

386   When considering pools resampled weekly over the course of a month, two trends emerge:

387   (1) pH is consistently higher in pools contained in 'dead' substrates than in 'live' substrates

388   *(Odds Ratio= 1.47, Table 2).* For all substrate types, however, pH values decreased over the

389   one-month sampling period (Fig. 7A; *Odds Ratio = -0.11, Table 2,* which may be related to

390   rainfall levels throughout the month); and (2) the number of *D. tinctorius* tadpoles can be

391   predicted, in part, by the interaction between pool substrate and pH (Fig.7B). Dead pools

392   have higher numbers of *D. tinctorius* tadpoles ($\bar{x}_{Live}$ = 0.72, $\bar{x}_{Dead}$ = 4.03, 2020 data). This

393   pH/substrate relationship is clearly important, as tadpoles occur in higher numbers in high pH

394   pools. Time (in weeks) was not detected as an important variable in determining *D. tinctorius*

395   tadpole numbers throughout the month.
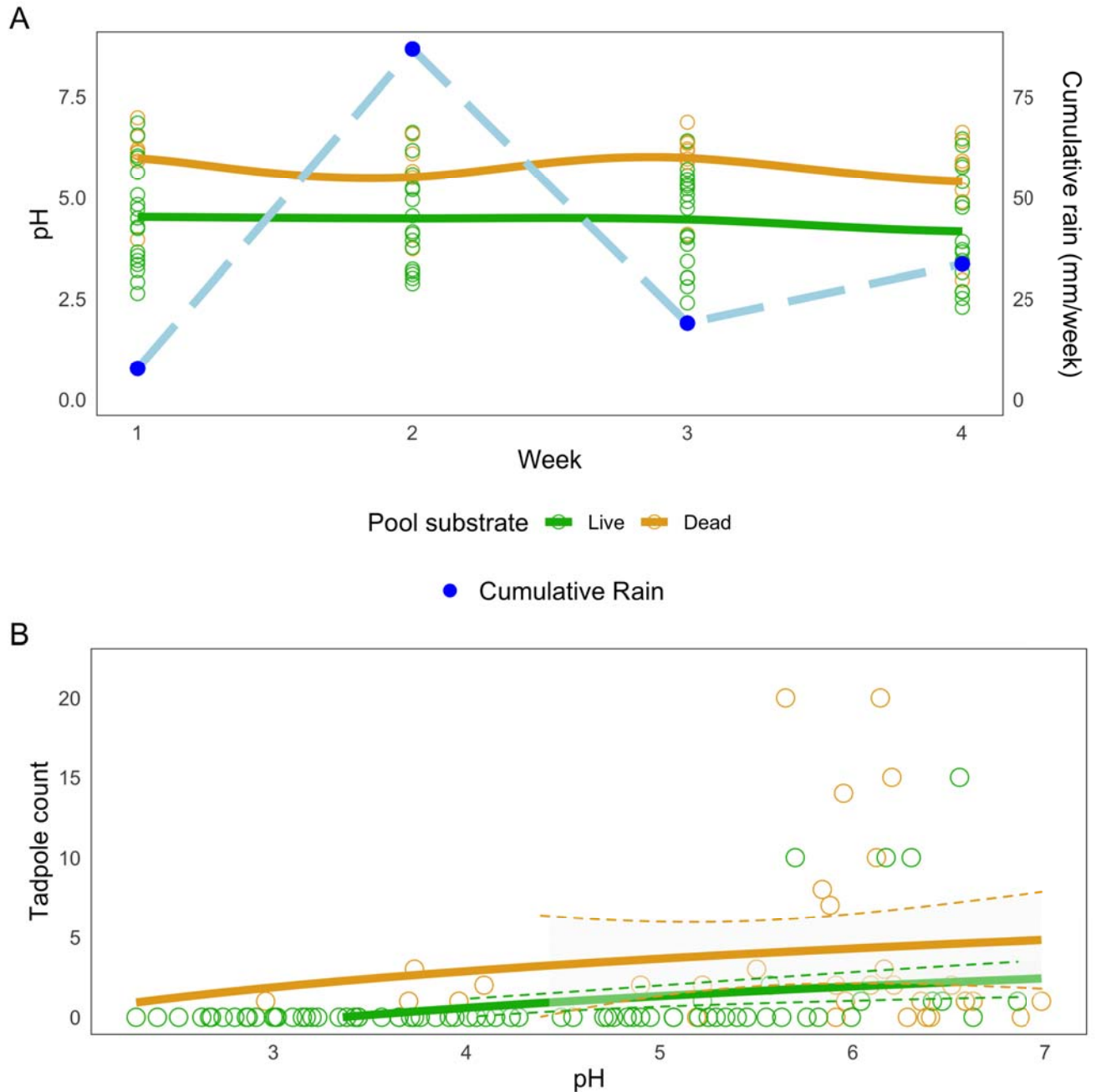
Figure 7. Phytotelm stability and tadpole presence across a month. *Panels (**A, B**) are subsetted to exclude high arboreal pools, and emphasize how pH is related to (**A**) pool substrate and (**B**) predicting D. tinctorius tadpole presence in resampled pools. Phytotelmata made of dead substrate have higher pH values than live substrate ($N_{Dead} = 8$, $N_{Live} = 18$; each resampled four times) (Table 2); more tadpoles are found in pools with a higher pH*

402 *(Table 3). Dashed lines represent 95% CI. Blue points in (A) indicate the weekly*

403 *accumulation of rainfall (February 2020). Tan lines are dead substrates and light green lines*

404 *are live substrates; lines in A are plotted with a "LOESS" fit and B with a "GLM" fit.*

405

Predictors	Estimates	CI	z	p
		pH		
(Intercept)	4.66	4.13 – 5.20	17.09	**<0.001**
Pool type [Dead]	1.47	0.56 – 2.37	3.17	**0.002**
Week	-0.11	-0.18 – -0.04	-2.93	**0.003**
Random Effects				
σ^2	0.20			
$\tau_{00\ pool\_id}$	1.13			

406

407 *Table 2. Negative binomial generalized mixed model predicting pH over time based on pool*

408 *substrate. Data include low arboreal and ground access pools. Pool type is a 2-level*

409 *categorical variable ("Dead", "Live"). Where pH is significantly higher in dead pool types*

410 *versus live pools type, and decreases over time.*

411

24

Predictors	*D. tinctorius* tadpoles (count)			
	Estimate	CI	z	p
(Intercept)	-10.35	-16.65 – -4.05	-3.22	**0.001**
Pool type [Dead]	11.08	2.96 – 19.21	2.67	**0.008**
pH	1.59	0.48 – 2.71	2.80	**0.005**
Week	-0.16	-0.39 – 0.06	-1.40	0.160
Pool type [Dead]: pH	-1.50	-2.93 – -0.07	-2.05	**0.040**

Random Effects

σ^2	2.62			
$\tau_{00 \text{ pool\_id}}$	1.87			

412

413 *Table 3. Negative binomial generalized mixed model predicting D. tinctorius tadpoles in*

414 *resampled pools in February 2020.*

415

416 Several pools (N = 5, 2020) dried out completely during the month-long observation period,

417 three of which were fallen palm bracts. Thus, although dead phytotelmata tend to have higher

418 pH values, and have a remarkable buffering capacity when filled, they also appear to dry out

419 more easily during dry periods.

420

421 **Discussion**

422 Juvenile stages of development are particularly deadly for animals with external fertilization.

423 Thus, the decision of where to breed and raise young is vital to offspring survival. In this

424 study, we investigated the tadpole rearing-site ecology of Neotropical phytotelm-breeding

425 frogs. Out of seven detected species, five showed some form of parental care, three out of

426   which were sufficiently common to infer patterns of pool choice. Broadly, we found that the

427   deposition choices of two of the three species are characterized by height and pool size, such

428   that *O. oophagus* tadpoles occur in small, low arboreal pools below ~ 2 m and *A. femoralis*

429   tadpoles occur in medium and large pools below ~ 1 m and with access only from the

430   ground, which is not surprising considering that adults are poor climbers (Roithmair 1992).

431   *Dendrobates tinctorius* tadpoles, in contrast, occur in pools from the ground to the canopy,

432   and of sizes ranging from 19.6 mL to 270L. When focusing on *D. tinctorius* pool choice, we

433   found that despite being able to tolerate an impressive range of physical/chemical factors,

434   tadpoles are more likely to be found in higher pools with greater levels of KH, salinity, and

435   hardness, and higher invertebrate diversity.

436

437   **Inter-specific comparison of rearing-site choices**

438   In line with previous research, we found that the preference for water capacity varies among

439   species, and that some of this variation is explained by parental behavior (Lin et al. 2008,

440   McKeon and Summers 2013, Summers and Tumulty 2014). For example, *O. oophagus*

441   provisions their tadpoles with trophic eggs (Jungfer and Weygoldt 1999), which allows

442   parents to choose very small arboreal phytotelmata with rather clear water and little food

443   (Brown et al. 2008a, b, 2010, Summers and Tumulty 2014). Despite the desiccation risk

444   associated with the notably small pools chosen by *O. oophagus*, their nurseries are predator-

445   free, which is often suggested as the primary factor driving the invasion of phytotelmata

446   (Crump 1974, Magnusson and Hero 1991, Gomez-Mestre et al. 2012, Summers and Tumulty

447   2014).

448

449   In contrast, *Allobates femoralis* does not provision tadpoles and preferably transports them to

450   medium-to-large ground access pools. These pools tend to have both high leaf-litter

451   concentrations and a high number of predators (Fig. 5B; concurrent with McKeon and

452   Summers (2013)). The effect of leaf litter on Neotropical tadpoles is unclear, but large

453   amounts have been found to have both positive effects (increased growth rate in African

454   tadpoles; (Lehtinen 2004)) and negative effects (decreased growth rate and development in

455   temperate-region tadpoles; (Williams et al. 2008)). Because *A. femoralis* are confined to

456   ground access phytotelmata due to their inability to climb, choosing to deposit their tadpoles

457   in pools containing high amounts of leaf litter may be their best option: despite the higher

458   predation risk (which *A. femoralis* fathers try to minimize (Ringler et al. 2018)), leaf litter

459   provides a source of food and shelter/predator protection to tadpoles that do not exist in clear

460   pools. Interestingly, the turbid leaf litter pools occupied by *A. femoralis* were functionally

461   available to *D. tinctorius*, who do not appear to use them. As *D. tinctorius* tadpoles are

462   predatory, clear pools may be better suited for visual foraging.

463

464   Contrary to our expectations, the water capacity of pools was not a key variable in predicting

465   *D. tinctorius* tadpole presence, corroborating Rojas' (2014) findings. While a higher water-

466   holding capacity is expected to decrease desiccation risk, pool volume and depth are not

467   always reliable measures for water-holding persistence in phytotelmata (Rudolf and Rödel

468   2005), making frogs adjust their preference based on other pool traits (see below). The

469   presence of large conspecifics, for instance, may be used as a cue of pool stability and thus

470   influence pool choice by males (Rojas 2014).

471

472   An unexpected variable that segregated all three frog species was pool salinity, which tends to

473   increase with height. Some high arboreal pools were particularly deep and a low turnover of

474   stagnant water could explain high salinity levels, where ions (and similarly, salts) concentrate

475   in pools over a long period of time (Sawidis et al. 2011). These pools were mostly occupied

476   by *D. tinctorius* tadpoles, which appear to withstand salinity conditions of up to 1,000 ppm.

477   *Allobates femoralis* tadpoles, in contrast, were only found in low-salt environments. Low

478   salinity is likely a byproduct of the high amount of leaf litter, which appears to buffer salt

479   concentrations (Roache et al., 2006; see Supp. Fig 3). As microbial activity is limited by high

480   salinities, low-salt pools are ideal for the production of detritus (Roache et al. 2006), the main

481   food source of *A. femoralis* tadpoles. *Osteocephalus oophagus* tadpoles were found in salinity

482   ranges from 48 to 225 ppm (Fig. 5C), and the relatively saline pools (> 700 ppm) that occur

483   within *O. oophagus* vertical ranges were only occupied by *D. tinctorius*. Adult *O. oophagus*

484   deposit their egg clutches in the water as opposed to the other two species, which only use

485   phytotelmata as tadpole-rearing sites. The saltier conditions of pools higher in the canopy may

486   not be suitable for eggs (Christy and Dickman 2002, Albecker and McCoy 2017), which may

487   limit the suitable conditions for oviposition in *O. oophagus*. Poison frogs, in contrast, can

488   escape these limitations because their clutches are terrestrial. Although the small sample size

489   does not allow any stronger interpretation, it appears that both chemical and physical variables

490   are important in shaping ideal pool conditions in *A. femoralis* and *O. oophagus*.

491

492   **Pool choice and flexibility in *Dendrobates tinctorius***

493   Over the two sampling seasons, the bulk of our study focused on the factors that shaped *D.*

494   *tinctorius* presence and persistence. Despite having sampled over 80 unique pools and found

495 350 *D. tinctorius* tadpoles (N = 208, 2019; N = 142, 2020), understanding the critical

496 variables that drive *D. tinctorius* pool choice is difficult because of the wide range of

497 physical and chemical properties in which these tadpoles occur. Further, the interactions

498 between physical, chemical, and biological characteristics in phytotelmata are complex and

499 collinear. Based on both our principal component regression and analysis, we found that the

500 probability of detecting *D. tinctorius* tadpoles increases positively with specific physical

501 (height), chemical (KH, salinity, and hardness), and biological (invertebrate diversity)

502 properties. Interestingly, we found that salinity, hardness, and KH also tend to increase with

503 increasing height (Supp. Fig 4). Overall, these chemical components tend to vary in the same

504 direction when moving up the vertical axis, suggesting a positive relationship between these

505 chemical and physical traits. Invertebrate diversity of occupied pools, in contrast, tends to

506 stay relatively constant across heights and might serve as an important food source for

507 predatory *D. tinctorius* tadpoles.

508

509 In this study, we found that KH increases with height, and pools with high KH are more

510 likely to have tadpoles in them. KH is a measure of a solution's buffering capacity or, in other

511 words, a solution's resistance to pH changes (Yang et al. 2008). KH values in low arboreal

512 and ground-access pools usually ranged from 3 to 6 KH, while average KH in high canopy

513 pools was 15. Interestingly, two of the five lower pools with a KH above 8 had *D. tinctorius*

514 counts of over 10 tadpoles, demonstrating that, when these conditions are available

515 terrestrially, *D. tinctorius* fathers take advantage of them. The apparent preference for high

516 alkalinity environments is interesting, as work studying the formation of fungal granules has

517 established that high-alkalinity conditions inhibit fungal growth (Yang et al. 2008). The

518   potential relationship of KH limiting the growth of fungi in phytotelm conditions is

519   noteworthy as amphibian fungal pathogens such as *Batrachochytrium dendrobatidis (Bd)*

520   spread aquatically (Rosenblum et al. 2010), and *Bd* presence (prevalence of ~5%) has been

521   reported for *D. tinctorius* in our study area (Courtois et al. 2015). Thus, the consistent

522   detection of *D. tinctorius* tadpoles in high KH pools could indicate that fathers are selecting

523   environments less prone to fungal contamination. Although we are unsure of the proximate

524   mechanisms driving the fathers' choice of particular chemical conditions in phytotelmata, we

525   establish here that KH, hardness, and salinity play an important role in shaping *D. tinctorius*

526   pool choice, and suspect that these chemical conditions may be linked to the long turn-over

527   time of high arboreal pools.

528

529   **The stability of ephemeral pools**

530   In 2020, we were able to follow a subset of low arboreal and ground access pools over a

531   month, recording the pH and *D. tinctorius* tadpole presence on a weekly basis. We found that

532   pools made of dead substrate (fallen palm bracts, dead trees) had a higher pH than live

533   substrates (tree holes). The gross average pH of dead phytotelmata across our sample was

534   5.68, which is almost exactly the value of unpolluted rainwater (pH = 5.65 when saturated

535   with atmospheric CO_2; (Koshy et al. 1997)). In contrast to most live substrates (average pH =

536   4.35), dead phytotelmata are usually in canopy gaps, where rain falls directly into the pools.

537   When reported, the pH of most phytotelmata is acidic (Kitching 2001, von May et al. 2009,

538   Poelman et al. 2013, Ramos et al. 2017); but see Lehtinen 2004, which shows that *Pandus*

539   bromeliads were close to neutral pH). However, most studies on phytotelmata are biased

540   towards living plants and trees, and assess chemical/biological variables of pools at a single

541   time point.

542

543   Throughout the month, all pool types decreased in pH (Table 2); a similar trend was also

544   found in bamboo phytotelmata in Peru (von May et al. 2009), suggesting a time-dependent

545   process causing pools to become increasingly acidic over time. Remarkably, some pools

546   dried out multiple times during our sampling period, and when refilled by rain were

547   approximately at the same pH as before the drying event (ex. palm bract originally pH 6.98

548   (Week 1), dried out (Week 2), refilled pH 6.87 (Week 3); live tree hole pH 2.91 (Week 1),

549   dried out (Week 2), pH 3.02 (Week 3)). This indicates that pool substrate may play an

550   important role in establishing pool pH. Three out of the five pools that dried out were dead

551   palm bracts, suggesting that this pool type, despite having favourable chemical conditions

552   when filled, may also be at a higher risk for desiccation and decomposition.

553

554   Surprisingly, pools in dead substrates, such as palm bracts and fallen trees, contained more

555   tadpoles than other pool types despite drying out more regularly across our month survey

556   (Table 3). Such pools tend to occur in forest gaps, which makes them more prone to

557   dessication. However, pools in these lit areas may also have more microbial activity and less

558   food limitation (Kitching 2001, Rudolf and Rödel 2005), making them attractive deposition

559   sites for tadpoles. Suitable pools are a limiting resource for frogs and other animals

560   (Donnelly 1989a, b, Fincke 1992, Poelman and Dicke 2007, Ringler et al. 2015) and new

561   pools for *D. tinctorius*, such as those in tree-fall gaps, appear unpredictably and are rapidly

562   occupied despite the high rates of competition and cannibalism (Rojas 2015). This strategy

31

563   can be particularly beneficial when parents arrive early to new pools, as it allows their

564   offspring to be predators rather than prey. Thus, the competition to be the first to deposit

565   tadpoles might make pools in dead substrates that occasionally dry out additionally attractive.

566

567   Interestingly, the size range of tadpoles in dead substrates is much more variable than in low

568   and high arboreal pools (CF, BR, AP pers. observ.), suggesting that the pools remain

569   attractive even when already occupied by larger cannibals. This pattern corroborates the

570   experimental evidence that *D. tinctorius* preferably deposit newly-hatched tadpoles in pools

571   already occupied by conspecifics (Rojas 2014, 2015); possibly, tadpole presence serves as an

572   indicator of pool stability, which might be more valuable to a father's deposition choice than

573   the risk of having his offspring cannibalized by conspecifics.

574

575   **High arboreal pools**

576   While most of our work focused on low arboreal and ground access pools, this study

577   provides one of the first thorough characterisations of high arboreal phytotelmata in the

578   Amazon. Gaucher (2002) unexpectedly found *D. tinctorius* tadpoles in canopy pools up to

579   25 meters high while studying the treefrog *Trachycephalus hadroceps*. Other poison frogs,

580   such as *D. auratus* have been reported to use arboreal tree holes as well (Summers 1990). We

581   found large numbers of tadpoles in arboreal pools up to 20 m in height, which suggests some

582   benefit of these pools given the presumed high energetic expense that fathers invest in

583   transporting their tadpoles from terrestrial oviposition sites.

584

585   One key advantage of high arboreal phytotelmata may be a regular food source provided by

586   *Trachycephalus* treefrogs that specialize in these pools. During this study, all of the suitable

587   high arboreal pools were found by locating nocturnal calls of *T. resinifictrix and T.*

588   *hadroceps*, indicating that these habitats were potentially used as breeding sites. Although the

589   breeding frequency of these treefrog species is sporadic (Gaucher 2002), successful breeding

590   events result in clutches that consist of hundreds to thousands of eggs and tadpoles, which *D.*

591   *tinctorius* tadpoles readily consume ((Gaucher 2002), personal obs. AP and BR). As

592   proposed by Gaucher (2002), it could be that *D. tinctorius* fathers cue on *Trachycephalus*

593   calls for locating high arboreal pools, but this warrants further investigation.

594

595   Unexpectedly, we also found that dead substrate pools share some characteristics with high

596   arboreal pools, particularly with respect to chemical qualities (a more basic pH), tadpole

597   abundance, and being a limited or hard-to-access resource. As such, both pool types offer

598   benefits that fathers may value: despite having a shorter life, novel pools (such as fallen palm

599   bracts and holes in fallen trees) are worth invading as deposition sites because they are easy

600   to access and have a high probability of having food, and a suitable chemical profile; high

601   arboreal pools, on the other hand, may have sporadic food and are hard to access, but they are

602   stable and less prone to chemical fluctuations. Together, these different pools are both

603   worthy deposition sites, as they provide different stable environments which create a range of

604   possible offspring success.

605

606   **Conclusions**

607   When comparing the occurrence of tadpole species in pools, one of the first trends that

608   emerges is the presence/absence on the basis of specific phytotelm characteristics. For

609   example, *A. femoralis* and *O. oophagus* vertical ranges technically overlap, yet tadpoles

610   never co-occur. In species that demonstrate a distinct morphological limitation or vertical

611   preference, it may be that tadpoles occur in pools because that is what is available to their

612   parents. These constraints play a role in the environment tadpoles are exposed to, and should

613   affect their physiology and behavior. But what about when parents are completely

614   unconstrained? *Dendrobates tinctorius* occur across the vertical gradient and occupy pools

615   that range from acidic (pH = 2.96) to neutral pH, with volumes from 19 mL to over 270L and

616   in pools that range from fresh to slightly saline (~1000 ppm), which hints at a remarkable

617   physiological flexibility that has been overlooked thus far. Therefore, physiological studies

618   comparing phytotelm-breeding tadpoles would be especially interesting to better understand

619   parental decisions. It is also warranted to measure *D. tinctorius* growth in pools with different

620   chemical compositions to see if (despite surviving) these tadpoles are paying a cost for the

621   deposition choices by their fathers.

622

623   In sum, natural history studies allow us to grasp species' flexibility; this is becoming

624   increasingly relevant when we consider the effects of climate change in the Amazon.

625   Forecasted changes in precipitation (Cochrane and Barber 2009, Silvestrini et al. 2011) will

626   have direct effects on animals dependent on plant-based water bodies, and surely the

627   chemical composition of the water bodies themselves. Further studies examining larval

628   anuran responses to challenging environmental conditions (especially KH and pH) are

34

629   necessary to better understand the potential resistance and adaptability of phytotelm-

630   dependent frogs and how this may shape species resilience in the future.

631

Significance statement

632

633   This two-year field project is a reflection of over a decade of natural history observation and

634   experiments in the Neotropics. In this study, we expand our knowledge of the ecology of

635   phytotelm-dependent frogs, this time focusing on a comparative overview between larval

636   species and the precise ecological factors that shape the microhabitats in which eggs and

637   larvae are deposited. The breadth of this work will surely engage a wide variety of readers

638   who are interested in ecological dynamics in the tropics.

639   Here, we synthesize the occurrence and interactions between three different amphibian

640   species, which contributes to understanding the dynamics of each species independently, but

641   this work is also a perspective into the interactions between larvae and parents within the

642   context of an ecological study. Species in this study are specifically plant-dependent as

643   tadpoles, which provides a unique opportunity to thoroughly survey and measure the

644   microhabitats in which they occur. Together, our findings show how biological, physical, and

645   chemical components interact in predicting larval presence in species with parental care,

646   which is a strategy present in ten percent of amphibians. We also provide the first detailed

647   account of the ecology of high arboreal breeding pools. Accessing trees more than 20 meters

648   in height is challenging, and conducting a thorough survey of these environments framed in

649   comparison to microhabitats across the vertical gradient is a testament to the scope of this

35

650   work. While our study is based on amphibians, it more broadly focuses on the ecology that

651   shapes larval deposition sites and the wide array of species' flexibility we observe in the

652   Neotropics.

653   Hopefully, a wide variety of researchers will be excited to learn more about the diversity of

654   microhabitats in the Amazon and a cross-species comparison of the amphibians that depend

655   on them.

656   **Data availability statement** All data will be archived in the data repository of the University

657   of Jyväskylä.

670 (7) different countries, backgrounds and career stages, as it significantly contributed to the

671 fulfilment and quality of the present study.

680   *Conflict of interest statement —* The authors declare no conflict of interest.

681 *Ethics statement* — The study was approved by the scientific committee of the Nouragues

682 Ecological Research Station and covered under a partnership agreement between BR, AP and

683 the Nouragues Nature Reserve (No 01-2019) . We strictly adhered to the current French and

684 European Union law, and followed the Association for the Study of Animal Behaviour's

685 (ASAB) Guidelines for the use of live animals in teaching and research (ASAB, 2017).

686

687 **Author contributions**

688 **Chloe Fouilloux:** Writing – original draft (lead); Investigation (equal); Data curation (equal);

689 Formal analysis (lead); **Shirley Jennifer Serrano-Rojas:** Investigation (equal); Data curation

690 (equal); Formal analysis (supporting); Writing - review and editing (supporting); **Juan David**

691 **Carvajal-Castro:** Investigation (equal); Writing - review and editing (supporting); **Marie-**

692 **Therese Fischer:** Investigation (supporting); Writing - review and editing (supporting);

693 **Janne Valkonen:** Methodology (supporting); Investigation (supporting); Writing - review

694 and editing (supporting); **Philippe Gaucher:** Investigation (supporting); **Andrius Pašukonis:**

695 Conceptualization (equal); Methodology (equal); Investigation (equal); Writing – review and

696 editing (equal); Supervision (equal); Funding acquisition (equal); **Bibiana Rojas:**

697 Conceptualization (equal); Methodology (equal); Investigation (supporting); Writing – review

698 and editing (equal); Supervision (equal); Funding acquisition (equal).

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856

857 **Speculations and alternative viewpoints**

858 *Dendrobates tinctorius* males typically father egg clutches of 2-5 tadpoles pers clutch and

859 breed year-round (Rojas and Pašukonis 2019). As a result of the presumed high energetic

860 expense from carrying each tadpole from each clutch singly, we hypothesize that tadpoles

861 transported later may be subject to bet-hedging by fathers.
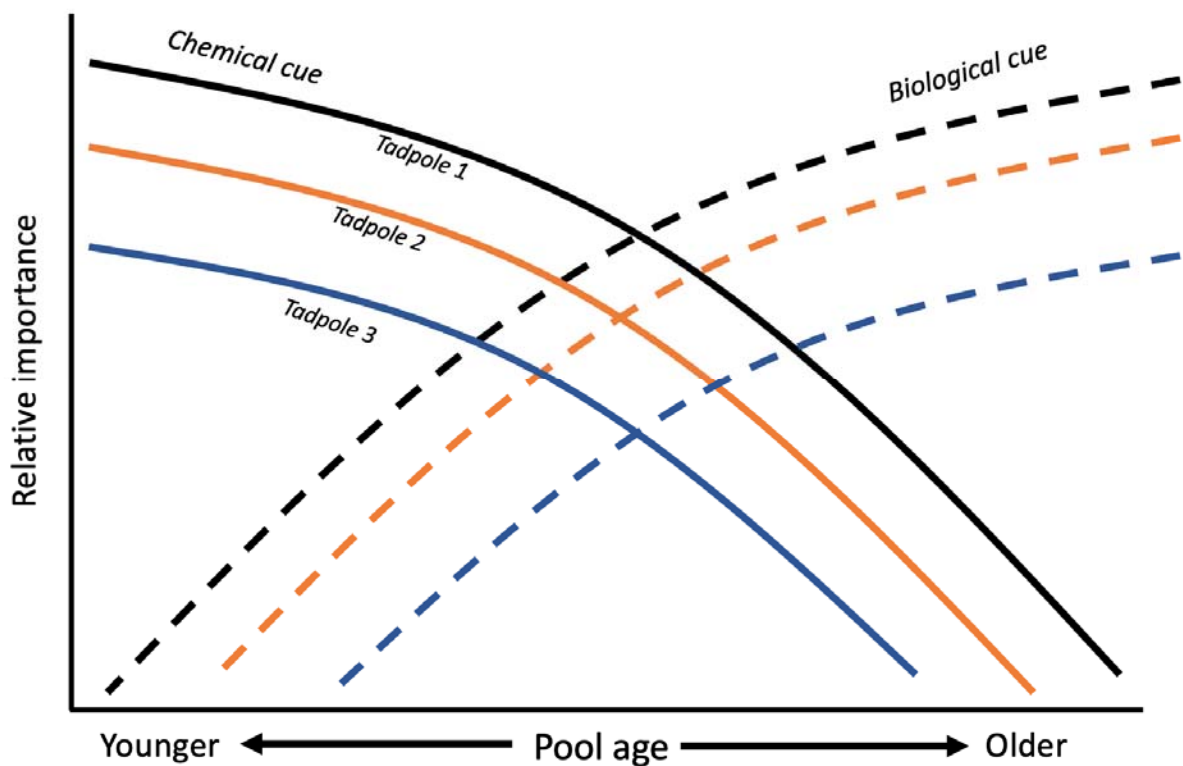
862

863 *Fig xx. Hypothetical succession of relative cue importance in phytotelmata across time.*

864

865   Combined with the important chemical aspects of pools shown from 2019 data, it seems that

866   fathers can cue on either chemical (KH, salinity, hardness) or biological components (the

867   presence of conspecifics) as information about pool stability. We speculate that the

868   importance of chemical and physical cues changes with respect to pool age. For example, in

869   new uninvaded pools, chemical cues of the pool may be more important (left-side of figure),

870   while in older, established pools that are more densely occupied, density serves as a main cue

871   for transporting fathers (right-side of figure). Finally, the value of these cues may vary with

872   the amount of offspring fathers are caring for. Hypothetically, fathers who must transport

873   more offspring are less discerning of where they transport latter tadpoles because they can

874   afford to make less "ideal" deposition decisions because of their large reproductive output.