

# Defaunation shadow on mutualistic interactions

Raul Costa-Pereira<sup>a,1</sup>, Christine Lucas<sup>b</sup>, Marcelo Crossa<sup>c</sup>, Jill T. Anderson<sup>d</sup>, Bianca Weiss Albuquerque<sup>e</sup>, Eurizângela P. Dary<sup>e</sup>, Maria T. F. Piedade<sup>e</sup>, Layon O. Demarchi<sup>e</sup>, Elizabeth R. Rebouças<sup>e</sup>, Gilvan da S. Costa<sup>e</sup>, Mauro Galetti<sup>a</sup>, and Sandra Bibiana Correa<sup>f</sup>

Tregidgo et al. (1) show that size-selective overfishing has drastically depleted and downsized populations of tambaqui (*Colossoma macropomum*) along the Purus River, Amazonia. Because fishers have historically targeted the largest individuals, tambaqui ~1,000 km upriver are twofold larger than those near the Manaus rainforest metropolis (1). Here, we demonstrate that this overfishing shadow has cascading consequences, reaching beyond the sustainability of this fishery. By effectively dispersing seeds of >100 species, tambaqui plays a major role in the natural regeneration of Amazonian floodplain forests (2–5). However, due to gape limitation, only large-bodied tambaqui can disperse large-seeded fruits (3). Thus, we hypothesize that the tambaqui's key ecological function as a seed disperser is diminished by the striking fisheries-induced downsize.

We constructed a niche model of food web structure (6), using the statistical relationship between tambaqui body size and fruit size, to infer losses in seed dispersal potential. First, we measured the fruit or seed (for dehiscent species) size of 264 species from Purus floodplain forests (7). We then used fish and fruit size data from 629 individual-level feeding records to model the upper boundary of the tambaqui's feeding range, using a 95% quantile regression (6). A decrease of 1 kg in body weight leads to a reduction of 3 mm in the maximum size of a fruit that a tambaqui can ingest ( $\log_{10}$ -transformed; intercept = 0.39,  $\beta$  = 0.29; Fig. 1). Finally, we used this relationship to calibrate our niche model and predict which plant species from the Purus regional pool could be dispersed by tambaqui near Manaus versus ~1,000 km upriver.

The downsizing of tambaqui near Manaus leads to a substantial reduction in its seed dispersal potential (Fig. 2). The largest tambaqui caught upriver in the fisher's lifetime (1) can consume fruits (while ingesting seeds intact) up to ~6 cm long, which is ~90% of the

Purus River floodplain species pool. In contrast, the largest tambaqui near Manaus are biomechanically unable to consume fruits >4.4 cm in length (Fig. 2A). However, given the mean fish size caught recently (1), tambaqui near Manaus can only consume fruits <2.8 cm in length. Our model indicates that tambaqui reaching the maximum body size for the species (2) would even be able to disperse megafauna fruits (~7 cm) (8).

Our results illustrate that the defaunation shadow around Manaus, driven by the urban demand for food, may collapse not only the harvested species but also its ecological function. Historical overfishing of tambaqui has already removed the largest seed dispersers, indirectly affecting mutualistic interactions with plants. Large-seeded floodplain taxa (e.g., *Areaceae*, *Sapotaceae*) are usually disperser-limited and do not float, relying on large-sized fish to disperse their seeds (5). Moreover, these taxa significantly contribute to carbon stocks in Neotropical rainforests (9). Because body size is also positively associated with long-distance seed dispersal (10), the downsizing of tambaqui can also reduce the genetic diversity of floodplain plant populations (1). Our results add an additional level of complexity to Tregidgo et al.'s (1) conclusions, highlighting that the legacy of overharvesting can scale-up to ecosystem-level impacts, potentially affecting the structure and function of floodplain forests.

## Acknowledgments

We thank José Ramos for technical assistance at the Instituto Nacional de Pesquisas da Amazônia herbarium. R.C.-P. was supported by Grant 2014/20924-5, São Paulo Research Foundation (FAPESP), and E.P.D. was supported by Fundação de Amparo a Pesquisa do Estado do Amazonas (FAPEAM). M.G. is the recipient of a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellowship.

<sup>a</sup>Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, São Paulo, Brazil; <sup>b</sup>Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Iguá 4225, CP 11400, Montevideo, Uruguay; <sup>c</sup>Acqua Consultoria Ambiental, Montevideo, 11.500, Uruguay; <sup>d</sup>Department of Genetics and Odum School of Ecology, University of Georgia, Athens, GA 30602; <sup>e</sup>Instituto Nacional de Pesquisas da Amazônia, 69067-375, Manaus, AM, Brazil; and <sup>f</sup>Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762

Author contributions: R.C.-P., M.G., and S.B.C. designed research; R.C.-P. and S.B.C. performed the research; R.C.-P. analyzed data; R.C.-P. wrote the paper with substantial contribution from S.B.C.; C.L., M.C., J.T.A., B.W.A., E.P.D., and M.T.F.P. provided data on tambaqui feeding records; L.O.D., E.R.R., and G.S.C. measured fruit and seed sizes; and C.L., J.T.A., M.T.F.P., and M.G. edited the manuscript.

The authors declare no conflict of interest.

Published under the [PNAS license](#).

<sup>1</sup>To whom correspondence should be addressed. Email: raulcpereira@gmail.com.

Published online March 7, 2018.



- 1 Tregidgo DJ, Barlow J, Pompeu PS, de Almeida Rocha M, Parry L (2017) Rainforest metropolis casts 1,000-km defaunation shadow. *Proc Natl Acad Sci USA* 114:8655–8659.
- 2 Araújo-Lima C, Goulding M (1997) *So Fruitful a Fish: Ecology, Conservation, and Aquaculture of the Amazon's Tambaqui* (Columbia Univ Press, New York).
- 3 Anderson JT, Saldaña Rojas J, Flecker AS (2009) High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia* 161:279–290.
- 4 Lucas CM (2008) Within flood season variation in fruit consumption and seed dispersal by two characin fishes of the Amazon. *Biotropica* 40:581–589.
- 5 Correa SB, Costa-Pereira R, Fleming T, Goulding M, Anderson JT (2015) Neotropical fish-fruit interactions: Eco-evolutionary dynamics and conservation. *Biol Rev Camb Philos Soc* 90:1263–1278.
- 6 Gravel D, Poisot T, Albouy C, Velez L, Mouillot D (2013) Inferring food web structure from predator–prey body size relationships. *Methods Ecol Evol* 4:1083–1090.
- 7 Luize BG, Silva TSF, Wittmann F, Assis RL, Venticinque EM (2015) Effects of the flooding gradient on tree community diversity in Várzea forests of the Purus River, Central Amazon, Brazil. *Biotropica* 47:137–142.
- 8 Guimarães PR, Jr, Galetti M, Jordano P (2008) Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLoS One* 3:e1745.
- 9 Fauset S, et al. (2015) Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* 6:6857.
- 10 Anderson JT, Nuttle T, Saldaña Rojas JS, Pendergast TH, Flecker AS (2011) Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proc Biol Sci* 278:3329–3335.