Evidence of seed dispersal of *Virola surinamensis* (Myristicaceae) by a catfish in Eastern Amazonia, Brazil

Evidência de dispersão de sementes de *Virola surinamensis* (Myristicaceae) por um bagre na Amazônia Oriental, Brasil

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Abstract: The aim of this study was to investigate the potential of the midnight catfish *Auchenipterichthys longimanus* (Siluriformes: Auchenipteridae) to disperse seeds of *Virola surinamensis* in the Caxiuanã National Forest, in the Eastern Amazon, Brazil. We conducted an experiment to compare germination rates and times of seeds from stomachs of fish with those collected from nutmeg trees (treatment I), with seeds with intact aril (treatment II), and with seeds without aril (treatment III). Treatment III exhibited the highest percentage of germination (90%), followed by treatments I (69%) and II (57%). Time of germination also varied among groups. Seeds with intact aril showed longer average germination times ($\approx$ 33 days to germinate) when comparing with seeds from the stomach of the fish ($\approx$ 28 days) and seeds without aril ($\approx$ 25 days). Our results showed that the frugivorous catfish did not damage the nutmeg seeds and support the conclusion that *A. longimanus* may be an effective disperser of *V. surinamensis* in riparian forests of the Caxiuanã region. These findings are consistent with other studies that have shown that many plant species to be dispersed by fishes.

Keywords: Amazon. Catfish. Ichthyochory. Seed germination.

Resumo: Neste trabalho, investigamos o potencial papel de dispersão de sementes de *Virola surinamensis* pelo bagre *Auchenipterichthys longimanus* (Siluriformes: Auchenipteridae) em rios da Floresta Nacional de Caxiuanã, na Amazônia Oriental, Brasil. Conduzimos um experimento para comparar as taxas de germinação e a velocidade de germinação das sementes encontradas em estômagos do peixe (tratamento I) com sementes coletadas diretamente de árvores: tratamento II (sementes com arilo intacto) e tratamento III (sementes com arilo removido). O tratamento III obteve a maior porcentagem de germinação (90%), seguido por sementes dos tratamentos I (69%) e II (57%). A velocidade de germinação também variou entre os grupos. Nossos resultados indicam que o hábito frugívoro de *A. longimanus* não inviabiliza as sementes e, desta forma, o bagre pode desempenhar importante papel na dispersão de *V. surinamensis* na região de Caxiuanã. Estes resultados são consistentes com estudos anteriores, que mostraram que algumas espécies de plantas podem ser efetivamente dispersadas por peixes.

Palavras-chave: Amazônia. Bagre. Ictiocoria. Germinação de semente.

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INTRODUCTION

Seed dispersal is the process in which seeds are carried away from the mother-plant to 'safe' distances, where predation and competition are expected to be lower (Schupp *et al*., 2010). Dispersal syndrome is one of the main factors in determining species composition and structure of ecosystems (Parolin *et al*., 2013), and is based on either abiotic or biotic agents or vectors of dispersal (van der Pijl, 1982; Levin *et al*., 2003), namely: anemochory (wind), hydrochory (water), zoochory (animals), and autochory (the plant itself). In common, all vectors affect the recruitment, genetic structure, spatial distribution, and diversity of plant species (Tiffney, 2004; Correa *et al*., 2015a).

Within zoochory, vertebrates are of paramount importance as seed dispersers (Almeida-Neto *et al*., 2008), with mammals and birds as the main agents of this complex ecological process (Correa *et al*., 2007). However, seed dispersal by fish (ichthyochory) may represent the oldest biological relationship between plants and vertebrates (Tiffney, 2004). Fishes are suggested as potential seed dispersers due to their consumption of large quantities and diversity of fruits, and consequently the presence of intact seeds in their digestive tracts (Lucas, 2008; Anderson *et al*., 2009; Reys *et al*., 2009). Despite ichthyochory having been described more than one hundred years ago (Huber, 1910), most of the available studies of fish-mediated seed dispersal were published over the past decades (Anderson *et al*., 2009, 2011; Galetti *et al*., 2008; Horn *et al*., 2011; Boedeltje *et al*., 2015; Correa *et al*., 2015a, 2015b), and ichthyochory has been appraised for only a few species (see literature in Horn *et al*., 2011).

Although knowledge of ichthyochory has recently increased, there is much to investigate considering the enormous diversity of fish and plants. In South American floodplain ecosystems, particularly in the Amazon Basin, more than 150 fish species of several orders (including Siluriformes, the catfishes) are reported consuming fruits and seeds of more than 500 plant species (Gottsberger, 1978; Goulding, 1980; Correa *et al*., 2015b); some plant species rely on catfishes for seed dispersal (Kubitzki & Ziburski, 1994; Barbosa & Montag, 2017).

In this context, the midnight catfish *Auchenipterichthys longimanus* (Günther, 1864), a species in the family Auchenipteridae, was reported as a fruit-eater in the Eastern Amazon (Freitas *et al*., 2011, 2017), mainly with the consumption of wild nutmeg trees *Virola surinamensis* (Rol.) Warb. Hence, the presence of intact seeds of *V. surinamensis* in the stomachs of *A. longimanus* led us to investigate the potential role of this fish in nutmeg seed dispersal. The aim of this study was to answer the following questions: (i) Are the seeds of *V. surinamensis* consumed by the midnight catfish destroyed during digestion?; and (ii) what are the effects of digestion on the germination rates and times of intact seeds consumed by *A. longimanus*? To answer these questions, an experiment was conducted to compare germination of seeds obtained from the stomach of the catfish with seeds collected directly from nutmeg trees. To consider *A. longimanus* as a potential disperser, we expect that seeds consumed by the fish present viable seed and high values of germination performance.

MATERIAL AND METHODS

The study site was conducted in the Caxiuanã National Forest (1º 45' 27.5" S, 51º 27' 33.2" W), located in the lower Amazon Basin between the Tocantins and Xingu rivers, State of Pará, Brazil. The region is described as having blackwater rivers and flooded forest within a matrix of lowland Amazon rainforest with a negligible floodplain due to the drowning of valleys of the Anapu River during the Holocene (Behling & Costa, 2000). Thus, the region is defined as a 'ria lake', showing little variation in fluviometry between hydrological periods (Costa *et al*., 2002).

Fish were captured with gillnets in March/2009 during the local flood season. After collection, each specimen was dissected for stomach removal, then fixed in 10% formalin solution for approximately 48 h and transferred to 70% ethanol. Voucher specimens were deposited in the ichthyological collection of the Museu Paraense Emílio Goeldi (MPEG) in Belém (Pará, Brazil) under the codes: 15257-15259, 15260-15264, 15432-15442, 15498-15507, 15544-15555, 15844-15860, and 16221-16231.

The germination experiment consisted of comparing germination rates and times of *V. surinamensis* seeds under different treatments. Seeds obtained from the stomachs were washed in running water and stored in paper bags with vermiculite for conservation purpose, and were designated 'treatment I'. Because of the large size of the seed (mean size 2.5 cm ± 0.1 cm; Gurgel *et al.*, 2006) when compared to the fish size (mean standard length 13.5 cm ± 0.2 cm; Freitas *et al.*, 2016), the fish strips off the fleshy aril and regurgitates the entire seed (T. Freitas, personal observation), instead of gut passage, as is common in many other fishes (Parolin *et al.*, 2013). Seeds collected directly from four random fruiting trees of *V. surinamensis* were subdivided in: seeds with preserved aril (treatment II), and seeds without aril (treatment III), that were removed manually to simulate a situation of which the fallen fruit attract an animal that fed on the aril, without swallowing the seeds.

All seeds were planted in black soil and exposed to the same environmental conditions in the nursery garden of the Botany Department of the MPEG. Every 24 h, seeds were checked and were considered as germinated after the appearance of the radicle (Cardoso *et al.*, 1994). The experiment ended when no further germination occurred for seven consecutive days (Maia *et al.*, 2007).

Treatments were evaluated for the germination rates (GR%) based on the formula *GR = (GS/SA) * 100*, modified from Labouriau & Valadares (1976), where: GS is the number of germinated seeds in a given group (treatment I, II or III) and SA is the total number of seeds in the same group. In order to assess possible differences in the GR% between groups a contingency table (χ^2) was used to confirm or refute the viability of seeds retrieved from the stomach of *A. longimanus*.

Time of germination was also measured for the treatments of seeds considering the time (in days) that seeds took to germinate. For each seed, the exact day of germination was determined, and an analysis of variance (ANOVA) was applied to verify differences in the germination timing within treatments. If significance value was obtained a pairwise test was posteriorly applied. All statistical analyses respected their assumptions and were performed with a significant level of 5% (Zar, 2009). The study design and statistical steps are summarized in Figure 1.

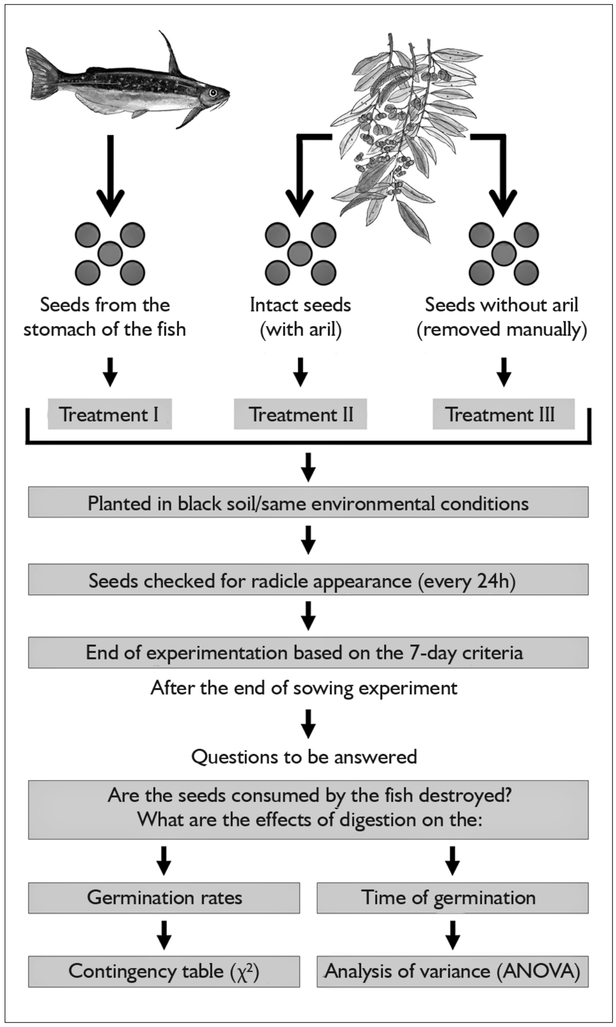

Figure 1. Schematic diagram showing study design and statistical analyses. Illustration from Freitas *et al.* (2010), with permission.

RESULTS

Sampling consisted of 71 seeds from 47 specimens of *A. longimanus* (1.5 seeds per fish) (treatment I), 58 seeds with intact aril (treatment II), and 48 seeds with the aril removed (treatment III). Seeds of treatment I and II began to germinate on the 20th day, and seeds of treatment III on the 24th day. Based on the 7-day criteria, the experimentation ended on the 49th day. Germination rates varied among the three groups ($\chi^2 = 13.673$, $p = 0.001$; Table 1). Treatment II obtained higher germination rates (GR% = 90%, n = 43), followed by treatment I (69%, n = 49) and treatment III (57%, n = 33).

Time to germination also varied among groups ($F = 20.861$, $p < 0.001$; Table 1), since seeds from treatment II germinated after 25.4 days of planting, following by seeds from treatment I (27.6 days) and treatment III (33.1 days). However, these differences were more noticable when comparing treatment I with treatment III (pairwise test $p < 0.001$), and treatment II with treatment III (pairwise test $p < 0.001$). No difference was shown between germination times of seeds from the stomach (treatment I) and seeds with aril (treatment III) (pairwise test $p = 0.102$).

DISCUSSION

We assessed the germination rates and times of nutmeg seeds (*Virola surinamensis*) removed from the stomach of the midnight catfish *Auchenipterichthys longimanus* and seeds collected directly from trees. Our results indicated that the frugivorous habit of *A. longimanus* did not damage the nutmeg seeds. Instead, the midnight catfish appears to enhance germination of *V. surinamensis*, since the presence of the aril on seeds (which is removed by the fish during digestion) led to lower rates of germination and longer times to germination. Under natural conditions, the removal of the aril by an animal may be necessary to guarantee or accelerate the germination of the seeds (Kays *et al*., 2011; Howe, 2016). Evidence of seed dispersal of *Virola* spp. has been commonly demonstrated by mammals (rodents and primates) and birds (toucans and curassows) (Howe, 1981, 1985; Howe *et al*., 1985) and is assessed for the first time by a fish.

The higher germination rate recorded for the treatment II may be related to the manual removal of the aril. In general, seeds ingested by animals go through chemical and mechanical processes in the digestive tract and may result in damage to some propagules (Traveset *et al*., 2008). Here, we observed a smoothly reduction in viability of seeds potential for germination. Additionally, time of germination recorded in the present study was consistent with the results of previous studies of *V. surinamensis*, in which the first radicles emerged between the 15th and 27th days after planting (Cardoso *et al*., 1994; Gurgel *et al*., 2006). Given that the germination rate of ingested seeds was higher than for seeds with aril, and that seed germination time of ingested seeds and seed without aril were similar, it seems likely that *A. longimanus* can contribute to the dispersal process of *V. surinamensis*.

The potential for seed dispersal by *A. longimanus* has been previously demonstrated by Mannheimer *et al*. (2003)

Table 1. Germination tests of the seeds retrieved from the stomach of *Auchenipterichthys longimanus* (treatment I), and seeds obtained from fruiting trees of *V. surinamensis*: seeds with aril (treatment II) and seeds without aril (treatment III), collected in the Caxiuanã National Forest, State of Pará, Brazil.

Treatments	Germination rate				Time of germination		
	Germinated seeds (%)	Not germinated seeds (%)	Chi-square (χ^2)	Chi-square p-value	Average time for germination (days)	F-value	ANOVA p-value
Treatment I	49 (69%)	22 (31%)	13.673	0.001	27.6	20.861	< 0.001
Treatment II	33 (57%)	25 (43%)			33.1		
Treatment III	43 (90%)	5 (10%)			25.4		

in Amazonian lakes (Trombetas River, central Amazon). These authors recorded high germination rates for seeds of *Cecropia* sp. (Urticaceae) ingested by the fish. They also recorded movements of *A. longimanus* in the flood period from non-silted to the shallow, heavily silted area, and they argued that the fish movements into the lake and inside the silted area potentially distribute seeds. Studies with Doradidae catfishes (a family related to Auchenipteridae) also revealed their potential role of seed dispersal by fish; Pilati *et al*. (1999) recorded a 95% germination rate for the seeds of *Cecropia pachystachya* Trec. retrieved from the digestive tract of *Pterodoras granulosus* (Valenciennes, 1833) in the Paraná River basin in southern Brazil; Barbosa & Montag (2017) recorded high germination rates of *Euterpe oleracea* Mart. consumed by *Lithodoras dorsalis* (Valenciennes, 1840) in the Eastern Amazon.

Fruits of *V. surinamensis* contributed as much as 80% (Alimentary Index; Kawakami & Vazzoler, 1980) of the diet of *A. longimanus* (Freitas *et al*., 2011), during the high water period, which coincides with the fruiting season of the wild nutmeg tree (Parolin *et al*., 2013). This emphasizes the importance of interactions between terrestrial ecosystems, in the form of fruits and seeds, and the aquatic fauna, as recognized in previous studies (Gottsberger, 1978; Goulding, 1980; Barbosa & Montag, 2017).

Finally, two main aspects further emphasize the potential role of the midnight catfish as a seed disperser of *V. surinamensis*: i) seeds present a thin, low-density, lipid-rich tissue that is associated with short-term flotation (i.e. < 10 days; Lopez, 2001), and ii) given the absence of a relevant local flood pulse and the reduced current in the rivers of Caxiuanã, the potential of hydrochory is considerably decreased. Although seed dispersal effectiveness increases with fish size (Galetti *et al*., 2008), *A. longimanus* may play an important role in the dispersal of *V. surinamensis* because of its abundance in the rivers of the Caxiuanã National Forest and the absence of overexploitation pressure on this fish species (Montag *et al*., 2013). Our study may be especially important because *V. surinamensis* is listed as an endangered species by the IUCN (1998), which reinforce that *A. longimanus* catfish are useful for the maintenance and conservation of this plant population in a protected area at the Eastern Amazon basin.

CONCLUSION

The results demonstrate that the ingestion of nutmeg *Virola surinamensis* seeds by the catfish *Auchenipterichthys longimanus* did not inhibit seed germination. Therefore, this auchenipterid catfish could plays a role in the dispersal of this endangered plant species of the region of the Caxiuanã National Forest.

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