

Amphibian diversity and its turnover in floating meadows along the Amazon river

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Manuscript received: 20 September 2016

Accepted: 10 November 2016 by JÖRN KÖHLER

Abstract. Anuran amphibians are a key group when assessing diversity patterns in Amazonia. Of the many different habitat types in this region exploited by anurans, floating meadows have received little attention. These are semi-anchored, thick plant mats on the surface of water bodies. We characterize the diversity of anuran communities encountered in this habitat and explore the Amazon River species turnover. Thirty-five species were recorded at seven floating meadow sites. Species richness varied among them but similarity was commonly high between neighbouring floating meadows. Upper Amazon basin sites were more similar to each other than to central Amazonian sites. Central Amazonian sites had limited similarity to each other. High densities in certain anuran species suggest that floating meadows provide highly beneficial habitats, while the presence of other, less common species may result from ‘accidental’ drift. Yet anuran beta-diversity is relatively similar. We suggest that this is likely due to the fluid nature of floating meadows, which have the ability to disperse anurans.

Key words. Amphibia, Anura, Hylidae, Leptodactylidae, Pipidae, Amazonia, Brazil, Peru, alpha-diversity, beta-diversity.

Introduction

Anurans are a remarkably species-rich group; ca. 6,500 species are globally known (www.amphibiaweb.org, accessed 1 October 2016). Among the most species-rich regions is the Amazon basin (DUELLMAN 1999). About one tenth of all known frog species occurs in this region (BOLAÑOS et al. 2008, FROST 2017), and they constitute a key group when assessing general diversity patterns in this mega-diversity region (LYNCH 1979, ANTONELLI et al. 2010, JENKINS et al. 2013). Recent studies have contributed to a more comprehensive understanding of anuran diversification in Amazonia (e.g., FOUQUET et al. 2007, SANTOS et al. 2009, WIENS et al. 2011, GEHARA et al. 2014). Of the many different ecoregions and habitat types encountered in Amazonia (cf. OLSON et al. 2001, GOULDING et al. 2003), many have been considered by the ongoing investigation process. However, floating meadows have received little attention.

Floating meadows, locally known as flotantes, gramalotes or capim flutuante, describe semi-anchored, thick plant mats found on the surface of water bodies (mainly of white water) across the entire Amazon catchment, such as rivers, streams, lagoons and lakes. The dominant floristic elements can be characterized as macrophytes, and main species involve grasses (*Paspalum repens*, *Echinochloa polystachya*), water hyacinths (*Echhornia crassipes*), water lettuce (*Pistia stratiotes*) and water ferns. These formations are fast-growing and can double their area size in about two weeks’ time. Floating meadows undergo high spatial and seasonal dynamics, structured by seasonal flooding pulses (JUNK et al. 1989). This includes drift of meadow pieces of variable size. Moreover, floating meadows in most parts of Amazonia do occur for four to five months during the seasonal floods only. They disappear when the temporarily flooded shore area – the várzea – dries with diminished precipitation. Then the otherwise floating plants be-

come terrestrial until the water level rises again (JUNK 1970, 1973, 1997, JUNK et al. 1989, GOULDING et al. 2003, KRICHER 2011). However, floating meadows can be locally present for 9–12 months, as for instance observed by UPTON (2015) in the Pacaya-Samiria Reserve, Peru. This seemed to be dependent on the yearly flood pulse and how severe flood levels were.

Numerous anuran species have been reported from floating meadows, sometimes in remarkable densities. Several of them exploit these plant formations for reproduction, as calling activity, egg clutches and tadpoles (in the submerged root systems) have been frequently found (HÖDL 1977, SCHIESARI et al. 2003, UPTON 2015). Other species are rare, show no reproductive activity and sometimes their occurrence is apparently due to ‘accidental’ dispersal (HÖDL 1977, HOOGMOED 1993, UPTON et al. 2014). Besides amphibians, various other vertebrate and invertebrate groups inhabit floating meadows (JUNK 1970, SCHIESARI et al. 2003). As a consequence, the spatial and seasonal dynamics of this habitat raise intriguing questions in ecology, biogeography, evolution and conservation biology. However, our knowledge on floating meadow fauna is extremely sparse. Taking anurans, the best studied group, merely a hand full of publications are available. HÖDL (1977) studied spatial and acoustic partitioning, and SCHIESARI et al. (2003) examined the potential impact of meadow drift. Both studies took place in the mid-course of the Amazon River in Brazil. HOOGMOED (1993) provided lists of species found in floating meadows in Suriname, Bolivia and on the lower Amazon River in Brazil. Investigating floating meadow amphibians of the Upper Amazon River in Peru, UPTON et al. (2011, 2014) and UPTON (2015)

described community structure, seasonal change and other life-history aspects.

Over the last few years we have studied anuran diversity of floating meadows between Yurimaguas in Peru and Manaus in Brazil, in total encompassing a distance of ca. 2,500 km along the Amazon (or Solimões) River and its tributary, the Huallaga River. The aim of this paper is, by combining our own with published data, to characterize the species diversity of anuran communities encountered in this habitat and to compare them in the light of the Amazon River species turnover.

Methods

Field studies

Floating meadows across six sites (Fig. 1) were examined during different seasons, excluding the dry season, in different years (Table 1). Five were in the Upper Amazon basin, of which one was in the Pacaya-Samiria Reserve surveying lakes, channels and rivers (cf. UPTON et al. 2014, UPTON 2015), while the others were on the Huallaga and Amazon Rivers (non-protected areas). The sixth site was the central Amazonian Catalão Lake in the vicinity of Manaus. In addition, information provided by HÖDL (1977) for the nearby Janauari Lake was considered in this paper (data adapted to current taxonomy). The two central Amazonian sites were in non-protected areas.

Nocturnal canoe surveys were undertaken to find adults amphibians using opportunistic visual surveys, and at Yurimaguas, Nauta, Iquitos and Pevas also acoustic surveys. At Catalão tadpoles were collected using a wired



Figure 1. Map of the Amazon basin showing sites at which floating meadow anuran communities were studied in this paper. From left to right Yurimaguas, Pacaya-Samiria, Nauta, Iquitos, Pevas, Janauari and Catalão (for details see Table 1).

Table 1. Key information related to field studies.

Study site	Latitude, longitude (decimal degrees)	Observation period(s)	Sampling effort
Yurimaguas (Loreto, Peru)	-5.89, -76.11	March 2012 (peak of rainy season)	5–8 hours/day by 2–3 workers on 4 days
Pacaya-Samiria (Loreto, Peru)	-4.89, -74.36	May-June 2009; April-September 2012 + 2013 (transition from rainy to dry season, decreasing water level)	2–3 hours/day by 3–4 workers on 210 days
Nauta (Loreto, Peru)	-4.53, -73.55	March 2012; March 2013 (peak of rainy season)	5–8 hours/day by 2 workers on 24 days
Iquitos (Loreto, Peru)	-3.76, -73.25	April 2012; March-April 2013 (slightly beyond peak of rainy season)	5–8 hours/day by 2 workers on 22 days
Pevas (Loreto, Peru)	-3.32, -71.86	April 2013 (peak of rainy season)	5–8 hours/day by 2 workers on 5 days
Januari (Amazonas, Brazil)	-3.22, -60.03	November 1974-January 1975 (almost at peak of rainy season, increasing water level)	unknown
Catalão (Amazonas, Brazil)	-3.17, -59.91	August-September 2011 (onset of the rainy season); January-July 2013 (rainy season and transition from rainy to dry season)	5–6 hours/day by 2 workers on 30 days

net with a 30 cm diameter and mesh-size of 3 mm². Species were identified based on our experience in Neotropical anuran taxonomy and by using published references (adults: RODRÍGUEZ & DUELLMAN 1994, DUELLMAN 2005, GAGLIARDI-URRUTIA 2010, LIMA et al. 2012; tadpoles: HERO 1990, LYNCH & SUÁREZ MAYORGA 2011). Vouchers were collected and deposited at CORBIDI (Centro de Ornitología y Biodiversidad, Lima), PAULO BÜHRNHEIM Zoological Collection at the Universidade Federal do Amazonas, Manaus, Brazil (CZPB-AA). Taxonomy and nomenclature follows FROST (2017).

Sampling effort with regard to year, collection period, man-hours or observer bias (by implication) varied among the entire data set and is not further considered in our analyses. However, we expect that in general our sampling effort was sufficient, allowing for conclusions on species diversity and turnover: Based on the sampling efforts at Yurimaguas, Nauta, Iquitos and Pevas, we computed species saturation estimates (Appendix 1); these suggest that the majority of taxa was discovered. Following COLWELL et al. (2012), abundance- (ACE, Chao1) and incidence-based estimators (ICE, Chao2) were calculated with EstimateS 9.1.0 (<http://viceroy.eeb.uconn.edu/estimates/>).

Diversity measures

In order to determine alpha-diversity, non-parametric standard measures were applied: Simpson index, Shannon index and Shannon evenness (MAGURRAN 1988, 2004). They were computed using PAST 3.10 (<http://nhm2.uio.no/norlex/past/download.html>). Via bootstrapping (9,999 random samples), we calculated 95% confidence intervals and provide means in the manner of HARPER (1999).

To examine beta-diversity, we calculated pairwise diversity t-tests with PAST, based on Simpson (cf. BROWER et al.

1998) and Shannon indices (cf. MAGURRAN 1988), respectively. In this measure, high similarity between two sites is suggested to occur at P-values < 0.05. The species turnover was further assessed with CAP (Community Analysis Package; www.pisces-conservation.com) by means of standard measures for beta-diversity, i.e., SØRENSEN index and JACCARD similarity coefficient. Additionally, we computed the coefficient of biogeographic resemblance (CBR) of DUELLMAN (1990). According to this author, the CBR is similar to the JACCARD similarity coefficient but more robust. Specimen count data were not available for the sites Januari and Catalão, so that they could only be considered in the last three mentioned measures.

Results

Anuran communities

Our analysis revealed that at least 35 anuran species in twelve genera and four families are associated with floating meadows of the Amazon River system. Only nine (i.e., about one fourth) of the recorded species were not members of the family Hylidae, a group of otherwise predominantly arboreal frogs. A list of all taxa encountered and their quantities at the various study sites is provided in Table 2.

Four species were present at all seven sites (*Dendropsophus haraldschultzi*, *Sphaenorhynchus carneus*, *S. dorisae*, *S. lacteus*) and another two at six sites (*Boana lanciformis*, *Leptodactylus leptodactyloides*). However, these species were not always the most common ones. Remarkably high abundances were encountered in *Boana punctata*, *Dendropsophus leali*, *D. triangulum* (the first and last at most study sites each the most common species), *Scinax garbei*, *Sphaenorhynchus carneus*, *Trachycephalus typhonius* and *Leptodactylus leptodactyloides*. Locally, hundreds of individuals of these species were found, but

Table 2. List of anuran taxa encountered and their quantities at seven study sites (Table 1); for two sites only presence (p) and absence (0) data are available. Abbreviations: A – arboreal; Q – aquatic; SA – semiaquatic; T – terrestrial (RODRÍGUEZ & DUELLMAN 1994, DUELLMAN 2005, LIMA et al. 2012).

Taxon	Life style	Yurimaguas	Pacaya-Samiria	Nauta	Iquitos	Pevas	Janauari	Catalão
Bufonidae								
<i>Rhinella marina</i>	T	1	10	23	7	0	0	0
Hylidae								
<i>Dendropsophus bifurcus</i>	A	0	43	1	2	0	0	0
<i>Dendropsophus haraldschultzi</i>	A	4	70	11	5	7	p	p
<i>Dendropsophus leali</i>	A	0	7	219	47	0	0	0
<i>Dendropsophus leucophyllatus</i>	A	10	0	32	20	0	0	p
<i>Dendropsophus rossalleni</i>	A	3	27	0	0	0	p	0
<i>Dendropsophus triangulum</i>	A	10	416	315	13	0	p	0
<i>Dendropsophus walfordi</i>	A	0	0	0	0	0	p	p
<i>Boana boans</i>	A	0	1	0	0	0	p	0
<i>Boana cinerascens</i>	A	0	0	0	1	0	0	0
<i>Boana lanciformis</i>	A	9	31	16	1	10	p	0
<i>Boana multifasciata</i>	A	0	0	0	0	0	0	p
<i>Boana punctata</i>	A	37	615	258	186	0	p	p
<i>Boana raniceps</i>	A	0	0	0	0	0	p	p
<i>Lysapsus bolivianus</i>	SA	0	0	0	0	0	p	p
<i>Osteocephalus taurinus</i>	A	0	1	0	0	0	0	0
<i>Scarthyla goinorum</i>	A	0	3	7	0	21	0	p
<i>Scinax boesemani</i>	A	0	0	0	0	0	p	0
<i>Scinax garbei</i>	A	0	42	337	1	20	0	p
<i>Scinax iquitorum</i>	A	0	0	0	1	0	0	0
<i>Scinax nebulosus</i>	A	0	0	0	0	0	p	p
<i>Scinax ruber</i>	A	0	4	0	20	0	0	p
<i>Scinax pedromedinae</i>	A	0	2	13	0	0	0	0
<i>Sphaenorhynchus carneus</i>	SA	3	116	411	34	37	p	p
<i>Sphaenorhynchus dorisae</i>	SA	20	64	58	1	17	p	p
<i>Sphaenorhynchus lacteus</i>	SA	3	85	77	23	37	p	p
<i>Trachycephalus typhonius</i>	A	0	0	354	6	2	0	p
Leptodactylidae								
<i>Adenomera hylaedactyla</i>	T	0	0	2	0	0	0	0
<i>Leptodactylus bolivianus</i>	T	0	0	16	1	0	0	0
<i>Leptodactylus leptodactyloides</i>	T	11	25	190	10	2	0	p
<i>Leptodactylus macrosternum</i>	T	0	0	0	0	0	0	p
<i>Leptodactylus petersii</i>	T	0	21	0	0	0	0	p
<i>Leptodactylus podicipinus</i>	T	0	0	0	0	0	0	p
<i>Leptodactylus wagneri</i>	T	0	0	3	0	0	p	0
Pipidae								
<i>Pipa pipa</i>	Q	0	1	0	0	0	0	0
Total number of individuals		111	1,586	2,343	379	116	no data	no data
Total number of species	33	11	20	19	18	9	15	19

not at all study sites where they were present. About half of all recorded species (19 in total) were observed at only one or two of the studied sites and in comparatively low abundances (Table 2).

Alpha-diversity

The number of species (and genera) encountered varied among study sites with Pevas ranking the lowest and

Pacaya-Samiria the highest (Fig. 2A, Table 2). Despite this, Simpson and Shannon index analyses (only carried out for the five Upper Amazon basin sites; for index values see Appendix 2) revealed similar entropy for all study sites, with Nauta (19 species) having the highest and Iquitos (18 species) the lowest value. In both the Simpson and Shannon index, the 95% confidence intervals occasionally overlapped among study sites (Figs 2B, C). Shannon evenness was less similar over them (Fig. 2D). It was highest in Yurimaguas and Pevas, which had the fewest species. Evenness was comparatively low in the other three, relatively species-rich Upper Amazon basin sites. That is, the discrepancy in the number of individuals per species (and site) showed more variation in Pacaya-Samiria, Nauta and Iquitos.

Beta-diversity

Table 3 provides the results of the diversity t-tests (for the Upper Amazon basin sites only). Significantly high similarity, based on both Simpson and Shannon index data, between two study sites was found four times (Yurimaguas/Nauta, Pacaya-Samiria/Nauta, Nauta/Iquitos, Iquitos/Pevas), and when based on Shannon index data only, another four times (Yurimaguas/Pacaya-Samiria, Yurimaguas/Iquitos, Pacaya-Samiria/Pevas, Nauta/Pevas). That is, when two sites were direct neighbours they often revealed highly significant values. If not, this was the case at least in next-nearest neighbours. Some of the more distant sites also showed high similarities to each other (e.g., Pacaya-Samiria with Pevas), but the geographically most distant ones, Yurimaguas and Pevas, were not significantly similar.

THE SØRENSEN index and the JACCARD similarity coefficient (Table 4), likewise the CBR (Appendix 3), corroborated these findings (taking 0.5 as a threshold for discriminating 'low' and 'high' similarity). But there was in general a high similarity among the sites Yurimaguas, Pacaya-Samiria, Nauta and Iquitos. Values of the SØRENSEN index varied little, while in the JACCARD similarity coefficient and the CBR, similarity was clearly highest for Nauta/Iquitos. It was lowest for Yurimaguas/Pacaya-Samiria and Yurimaguas/Nauta (the latter not in the CBR, however). Pevas revealed notable similarity with some sites of afore described 'cluster' under the SØRENSEN index and the CBR.

There was overall little similarity of the upper basin sites with the two central Amazonian sites (Table 3, Appendix 3). As an exception, when applying the SØRENSEN index and the CBR, Januairi was somewhat similar to Yurimaguas. Also both Januairi and Catalão were relatively similar in the CBR, but otherwise both had little in common.

Discussion

Anuran communities and diversity

We identified 35 anuran species to occur in floating meadows of the Amazon River, ranging 9–20 per study site.

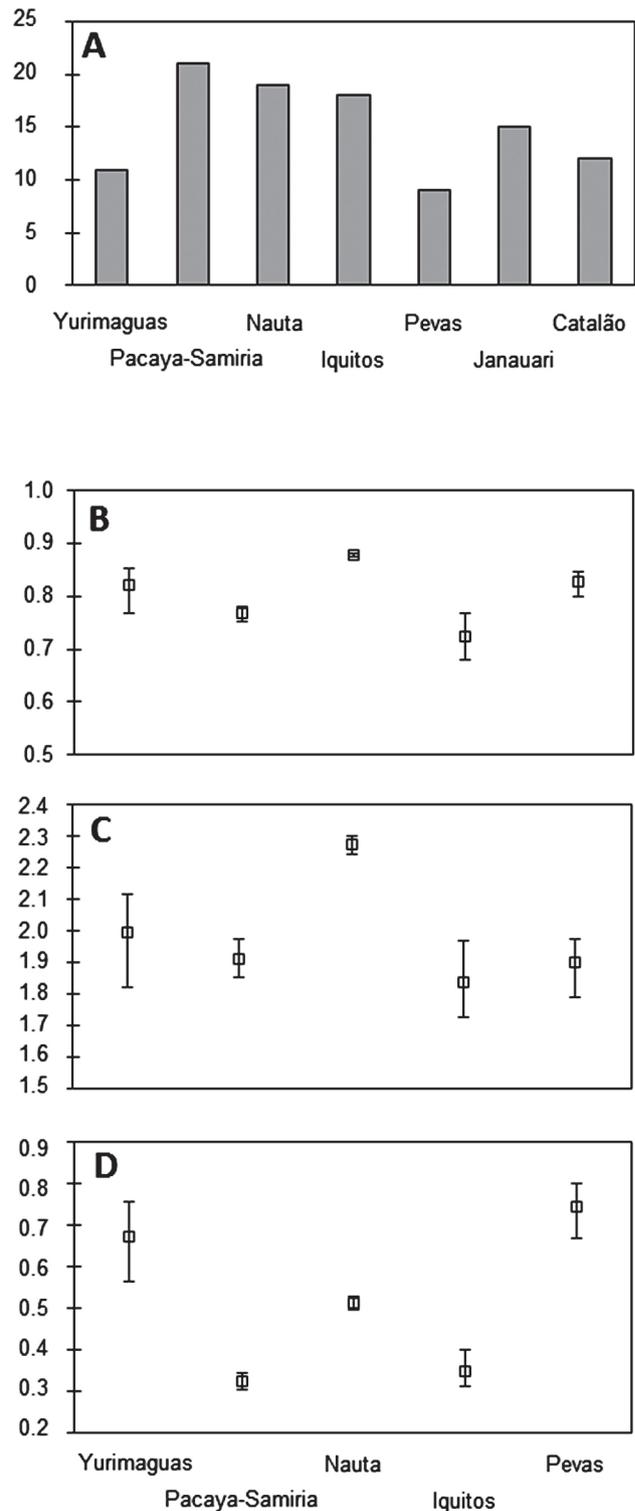


Figure 2. For the various floating meadow anuran communities ordered from upriver to downriver (cf. Fig. 1), (A) the number of species encountered, (B) the Simpson index [1-D], (C) the Shannon index [H], and the (D) Shannon evenness. In (B–D) the mean (square) out of 9,999 randomizations with the upper and lower 95% confidence intervals are given (values are provided in Appendix 3).

Table 3. Results of pairwise diversity t-tests (P-values) for five floating meadow anuran communities in terms of Simpson and (in italics) Shannon indices. Values in bold indicate significant P-values at < 0.05 (i.e. high similarity of two sites).

	Yurimaguas	Pacaya-Samiria	Nauta	Iquitos	Pevas
Yurimaguas		<i>0.321</i>	0.001	<i>0.122</i>	<i>0.329</i>
Pacaya-Samiria	0.026		> 0.001	<i>0.294</i>	<i>0.892</i>
Nauta	0.012	> 0.001		> 0.001	> 0.001
Iquitos	0.002	0.066	> 0.001		0.420
Pevas	0.761	> 0.001	> 0.001	> 0.001	

Table 4. Beta-diversity for seven floating meadow anuran communities by means of the SØRENSEN index (in italics) and the JACCARD similarity coefficient, each ranging 0–1. High similarity is defined by ≥ 0.5 , such values are indicated in bold.

	Yurimaguas	Pacaya-Samiria	Nauta	Iquitos	Pevas	Januari	Catalão
Yurimaguas		0.65	0.65	0.69	0.60	0.62	<i>0.46</i>
Pacaya-Samiria	0.48		0.70	0.68	0.55	0.51	<i>0.46</i>
Nauta	0.48	0.54		0.79	0.62	<i>0.46</i>	0.51
Iquitos	0.53	0.52	0.65		0.59	<i>0.42</i>	0.54
Pevas	0.43	0.38	0.45	0.42		<i>0.42</i>	0.57
Januari	0.44	0.35	0.30	0.27	0.26		0.53
Catalão	0.30	0.34	0.34	0.37	0.40	0.36	

Based on our observations and confirmed by the pertinent literature (HÖDL 1977, HOOGMOED 1993, SCHIESARI et al. 2003, UPTON et al. 2014, UPTON 2015), several of these taxa might be considered as typically associated with this habitat, since they were found at most or all study sites along a ca. 2,500-km river stretch (e.g., *Boana punctata*, *Dendropsophus haraldschultzi*, *D. triangulum*, *Sphaenorhynchus* spp.; cf. Table 2). Nineteen species, despite them encompassing relatively large geographical ranges of Amazonia (FROST 2017), were recorded at only one or two study sites. Some certainly might not be considered typical, but yet for the majority of taxa this kind of allocation is premature.

None of the species recorded by us exclusively lives in floating meadows, as all also occur in other habitats (e.g., DUELLMAN 2005, LIMA et al. 2012, UPTON 2015). It is noteworthy that most of them (i.e., hylids) elsewhere are arboreal and live in bushes and trees up to several metres above ground. Accompanied by the high density of individuals, we conclude that floating meadows are highly beneficial habitats, at least to some of these taxa (e.g., *Dendropsophus triangulum*, *Hypsiboas punctatus*, *Scinax garbei*). The availability of shelter to tadpoles in the complex root zone of floating meadows and the high nutritional quality of detritus resulting from the decomposition of plants make floating meadows advantageous reproductive sites. Many anurans are frequently observed to reproduce in this habitat (HÖDL 1977, UPTON et al. 2014, UPTON 2015, authors' unpubl. observ.). In addition, the prolonged (partly permanent) availability of water, even early and late in the rainy season (JUNK 1997), and the increased dispersal abilities (SCHIESARI et al. 2003, UPTON 2015) may be among the advantages of floating meadows to anurans.

Although Simpson and Shannon indices (calculated for Upper Amazon basin study sites) were largely similar, the studied floating meadows showed some variation in alpha-diversity. In Yurimaguas and Pevas, relatively few species in low densities were found. In contrast, Pacaya-Samiria and Nauta had more species, several of them in quantities of hundreds of individuals (Table 2). We have not investigated meadow size or geographic proximity to larger river tributaries or forests (as potential source habitats), but these could have effects on the alpha-diversity of floating meadows. At Nauta for instance, the Marañón and the Ucayali Rivers confluent, and at Catalão, two major tributaries to the Amazon River confluent (Rio Solimões and Rio Negro). Likewise, sampling effort, in particular the collection period, may explain the observed variation (cf. Table 1).

Relatively low Shannon evenness was identified for Pacaya-Samiria, Nauta and Iquitos. Among the many species encountered here, several were comparatively rare (Table 2). In part, these may be species with relatively limited or patchy (cf. DAHL et al. 2009) distributions, like *Scinax iquitorum* (COUTINHO MACHADO et al. 2015), or those that are hard to find, like the aquatic *Pipa pipa*. Some caution is needed, however, when assessing anuran diversity of floating meadows. Interestingly, certain species were sparse in our sampling, although in general these are common generalists in other habitats, like *Boana boans*, *H. cinerascens*, *Adenomera hylaedactyla* or *Osteocephalus taurinus* (DUELLMAN 2005, LIMA et al. 2012). Apparently, these anurans are more associated with 'terra firme' areas (i.e., non-flooded) and do not reproduce in floating meadows (authors' unpubl. observ.). We rather expect that in these species occasionally single individuals become 'stranded' in floating meadows when drifted away from their habitats.

Species turnover

An intriguing aspect in floating meadow biology is the effect of high temporal and spatial dynamics to the species turnover (JUNK et al. 1989). Various observations can be made on the data studied in this paper. One is that signals of nearest-neighbour effects are visible, obviously due to frequent drift and perhaps even via intrinsic terrestrial dispersal. At the same time, similarity of species compositions in floating meadows might underlay a non-gradual turnover. That is, drift may not always result in contact of a moving piece with just the proximate floating meadow. Instead, by means of jump dispersal, such pieces may collide only with a floating meadows much further downstream (cf. SCHIE-SARI et al. 2003). As a result, non-neighbouring sites could show more similar species communities than neighbouring sites. Combining both effects would, in the long term, result in a homogenization of species communities among sites.

However, homogenization might not be observed over the entire Amazon River. With increasing distance, species compositions should become more dissimilar again because of other reasons. In the upper basin, one reason is that drift is unidirectional only. Hence, species can disperse into the central and lower basin, but taxa that are absent from the upper basin (e.g., *Dendropsophus walfordi*, *Lysapsus bolivianus*, *Scinax nebulosus*; FROST 2017) cannot raft via floating meadows into it. The situation may be different in the lower basin, as with tidal change, floating meadows can even be transported upstream (cf. GOULDING et al. 2003), but we currently lack data on lower basin floating meadow amphibian communities. Another reason is that under the concept of ecological niche potency it is expectable that drift may slide species out of the area where they can potentially survive. For instance, in some anurans, which are known from the upper basin (e.g., *Dendropsophus bifurcus*, *Scinax pedromedinae*; FROST 2017), we found no evidence that they have managed to expand their distributions downstream into the central basin, although technically possible via floating meadow drift.

It is premature to entirely confirm or reject the hypothetical scenarios mentioned. However, trends of homogenization as well as of inter-regional dissimilarity with long distance can be found in our results. The Upper Amazon basin sites exhibit an overall high similarity in species compositions. Both nearest neighbour and regional jump dispersal may be corroborated by our findings. In particular, the dissimilarity of the two central Amazonian sites, where the water volume is much more immense than in the upper stream (GOULDING et al. 2003), implies that jump dispersal is important. Moreover, the species found at these sites compared to those from the upper basin suggest that homogenization decreases with larger distance.

Methodical aspects

Seasonal climate regimes influence the catchability of frogs and toads, which is also the case in floating meadows (au-

thors' unpubl. observ.). We have incorporated data from different seasons here. But we believe to have solved the potential problem by excluding data purely collected during dry seasons. For this reason, we did not use information provided by HOOGMOED (1993) from Caxiuanã on the Curuá River of the lower basin, near the mouth of the Amazon River site.

Although we can show species saturation curves for study sites (Appendix 1), it might be worth addressing sampling efforts in future research. This does not only refer to key aspects such as duration of sampling and man-hours (which we expect to be sufficient in this study). Also effects of anthropogenic disturbance, area size of meadows, weather etc. might be considered when recording anurans in floating meadows.

At Catalão, species records partly relied on tadpole sampling only (e.g., *Dendropsophus haraldschultzi*, *Scarthyla goinorum*, *Scinax garbei*, *Sphaenorhynchus dorisae*). This implies that this is a potent method to detect amphibians in floating meadows, notwithstanding that larval descriptions are only available for a limited number of taxa (PROVETE et al. 2012) and species identifications in part remain difficult.

Methodological improvement in recent years has brought to light that nominal frog species can comprise complexes of distinct taxa, including Amazonian taxa (e.g., FOUQUET et al. 2007, FUNK et al. 2012, GEHARA et al. 2014). Sorting species is a challenge to future research. In this paper, we follow a taxonomically more conservative approach. We will not rule out that anurans from different study sites treated as conspecifics by us will have to be allocated to distinct taxa, e.g., in the frame of pan-Amazonian amphibian DNA barcoding studies.

Conclusions

Floating meadows are an important habitat for anuran species. Several of them can be considered typically associated with floating meadows due to their repeated presence in this habitat over a large geographic area and their occurrence in high abundances. Yet anuran beta-diversity across the Amazonian sites surveyed is relatively similar, at least within the upper basin versus central Amazonia. This is likely due to the fluid nature of floating meadows, which are washed downstream and have the ability to disperse anurans and apparently other life forms. Floating meadows may play a so far unnoticed key role in understanding the observed Amazonian diversity of certain animal and plant taxa associated with flowing water.

Acknowledgements

We are very grateful to Brazilian and Peruvian authorities for providing permits to perform field studies: Brazil – Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio (29197); Peru – Resolución Jefatural No 005-2013-SENANP-JEF, 0256-2104-MI-NAGRI-DGFFS/DGEFFS). Part of our research was conducted under a formal agreement between Trier University and Centro de Or-

nitología y Biodiversidad (CORBIDI). The work of BÖNING, LÖTTERS and WOLF benefitted from a grant by the 'Stiftung Artenschutz'. MENIN received financial support of the SISBIOTA Program 'Girinos do Brasil' – Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #563075/2010-4), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP #10/52321-7), and a Research Productivity grant from CNPq. UPTON's work was supported by the University of Kent alumni scholarship, The Durrell Institute of Conservation and Ecology, Fund Amazonia, Wildlife Conservation Society, Earthwatch Institute, Operation Wallacea and Operation Earth. JIŘÍ MORAVEC and an anonymous reviewer kindly commented on a manuscript version of this paper.

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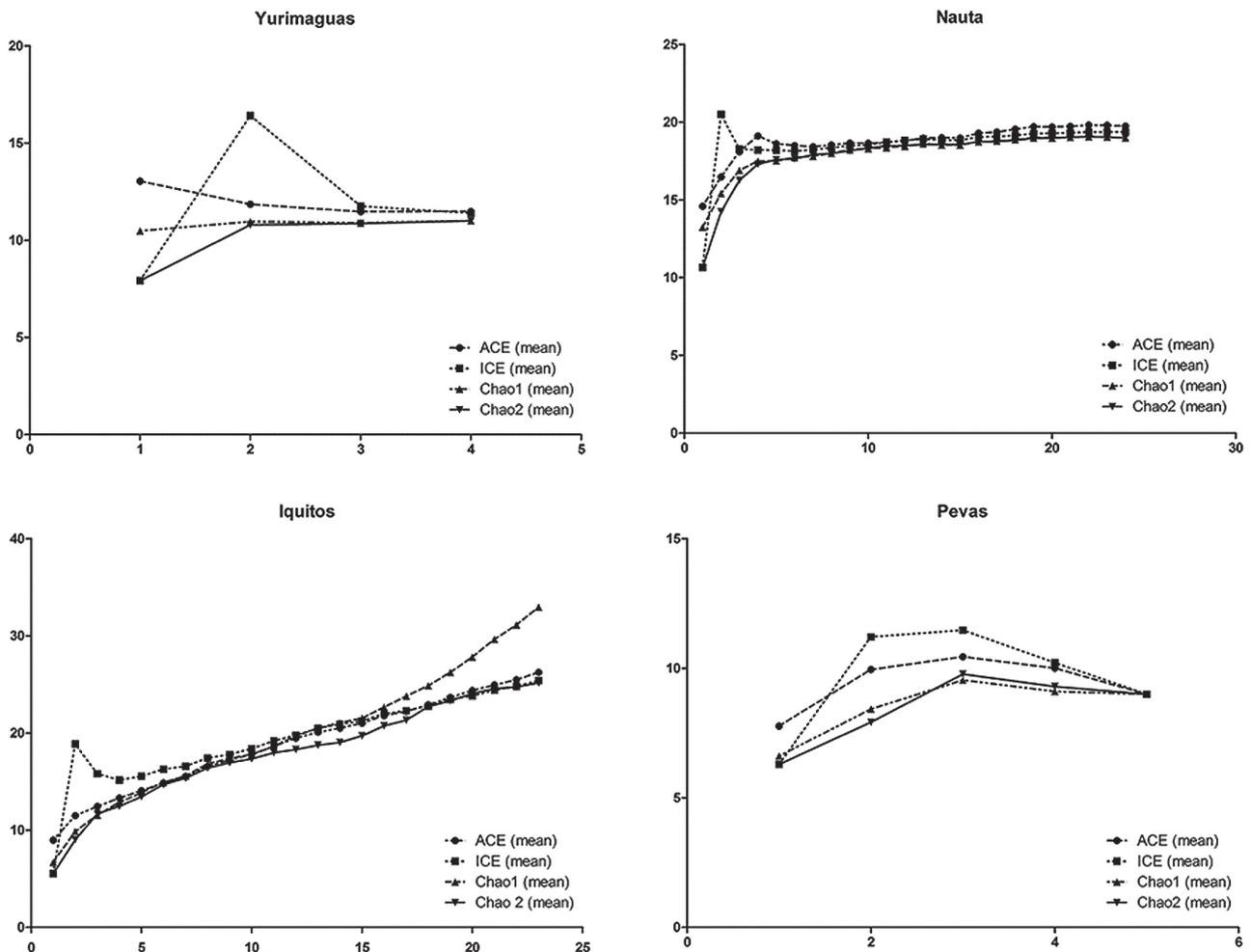
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Amphibian diversity and its turnover in floating meadows along the Amazon river

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Appendix 1

Species saturation curves of four estimators (abundance-based: ACE, Chao1; incidence-based: ICE, Chao2) for four floating meadow sites in Peru conducted with EstimateS 9.1.0. Calculations were each performed with 100 runs, using the bias-corrected formula for Chao1 and Chao2, and the upper abundance limit for rare or infrequent species set as 10 for ACE and ICE. In each graph, the x-axis shows the number of observations (number of days) and the y-axis shows the number of estimated species.



Appendix 2

Mean values and 95% confidence intervals (in parentheses) for alpha-diversity measures illustrated in Figure 2.

	Yurimaguas	Pacaya-Samiria	Nauta	Iquitos	Pevas
Simpson index [1-D]	0.820 (0.768, 0.853)	0.766 (0.751, 0.780)	0.879 (0.874, 0.882)	0.725 (0.700, 0.7663)	0.828 (0.798, 0.844)
Shannon index [H]	1.996 (1.821, 2.115)	1.910 (1.854, 1.971)	2.273 (2.241, 2.303)	1.835 (1.700, 1.969)	1.902 (1.790, 1.976)
Shannon evenness [E]	0.669 (0.561, 0.753)	0.322 (0.304, 0.342)	0.511 (0.495, 0.526)	0.348 (0.300, 0.398)	0.744 (0.666, 0.801)

Appendix 3

Beta-diversity for seven floating meadow anuran communities by means of the coefficient of biogeographic resemblance (CBR, DUELLMAN 1990) in bold. Integral numbers indicate how many species two sites have in common.

	Yurimaguas	Pacaya-Samiria	Nauta	Iquitos	Pevas	Januari	Catalão
Yurimaguas	11	9	10	9	6	8	5
Pacaya-Samiria	0.56	21	14	14	9	9	6
Nauta	0.67	0.70	19	15	9	8	8
Iquitos	0.62	0.72	0.81	18	8	7	7
Pevas	0.60	0.60	0.64	0.57	9	7	7
Januari	0.62	0.50	0.47	0.42	0.58	15	7
Catalão	0.38	0.33	0.47	0.42	0.58	0.47	15