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A Hanski core-satellite species system

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Research

Amphibian diversity in the Amazonian floating meadows: a Hanski core-satellite species system

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The Amazon catchment is the largest river basin on earth, and up to 30% of its waters flow across floodplains. In its open waters, floating plants known as floating meadows abound. They can act as vectors of dispersal for their associated fauna and, therefore, can be important for the spatial structure of communities. Here, we focus on amphibian diversity in the Amazonian floating meadows over large spatial scales. We recorded 50 amphibian species over 57 sites, covering around 7000 km along river courses. Using multi-site generalised dissimilarity modelling of zeta diversity, we tested Hanski's core-satellite hypothesis and identified the existence of two functional groups of species operating under different ecological processes in the floating meadows. 'Core' species are associated with floating meadows, while 'satellite' species are associated with adjacent environments, being only occasional or accidental occupants of the floating vegetation. At large scales, amphibian diversity in floating meadows is mostly determined by stochastic (i.e. random/neutral) processes, whereas at regional scales, climate and deterministic (i.e. niche-based) processes are central drivers. Compared with the turnover of 'core' species, the turnover of 'satellite' species increases much faster with distances and is also controlled by a wider range of climatic features. Distance is not a limiting factor for 'core' species, suggesting that they have a stronger dispersal ability even over large distances. This is probably related to the existence of passive long-distance dispersal of individuals along rivers via vegetation rafts. In this sense, Amazonian rivers can facilitate dispersal, and this effect should be stronger for species associated with riverine habitats such as floating meadows.

Keywords: ecological modelling, flood-pulse, long-distance dispersal, zeta diversity



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Introduction

Tropical rainforests and their associated river basins are among the most species-rich regions on earth. Mechanisms that have generated and regulate tropical biodiversity are far from being fully understood and hence remain subject of debate (Hill and Hill 2001, Rull 2011, Richardson and Pennington 2016, Rull and Carnaval 2020). This is particularly true for the Amazon region, with various hypotheses explaining the origin of its current biota (Haffer 1997, Antonelli et al. 2009, Leite and Rogers 2013, Cracraft et al. 2020). Although there is some consensus on the importance of dispersal limitation (Smith et al. 2014) and vicariance related to geological and climatic histories (Haffer 2008, Hoornt et al. 2010), many questions remain unanswered about the structure of biodiversity in different parts of the Amazon region. Given floating meadows can have an influence on the structure of Amazonian biodiversity, our study seeks to provide insights into the patterns and drivers of species diversity in this kind of habitat using amphibians as a study model.

The Amazon catchment is the largest river basin on earth and drains the most spacious extant rainforests in the world. Up to 30% of its waters flow across floodplains (Junk et al. 2011). These adjacent flat areas, also known as 'várzeas' in the whitewater rivers (cf. Junk et al. 2012), form a complex mosaic of continuous interconnected habitats such as open waters (e.g. lakes) and flooded forests (Junk et al. 2012). In the lowland Amazonia, the non-flooded vegetation is known as 'terra firme' forest. In the open waters, aquatic and semi-aquatic rooted or freely floating plants, also known as floating meadows, abound (Junk 1970). Besides their important role in the nutrient cycles, they also provide shelter, feeding, reproduction, spawning and nursery habitats for various organisms (Junk 1973, 1997). Especially in the wet season, when lakes and rivers become connected, vegetation fragments known as macrophyte rafts are carried downstream, acting as passive long-distance dispersal media for the floating meadow fauna (Schiesari et al. 2003).

Although annual precipitation in Amazonia is usually high, rainfall regimes have a remarkable temporal variation, with regionally pronounced dry and wet seasons in some regions (Villar et al. 2009). In consequence of the rainy season, floods invade the floodplains. The constant switch between periodic inundations and drought (i.e. flood pulse), rather than being catastrophic events, is the driving force in the Amazonian river–floodplain system (Junk et al. 1989). In regions where the flood pulse is predictable and prolonged, the floodplain's biota responds to the flooding by adaptations at different levels, and characteristic community structures are formed (Junk et al. 1989, Junk and Wantzen 2006).

Given the instability of floating meadows due to the flood pulse, only a small set of species are able to occupy these habitats. These species are expected to have adapted to life in this kind of habitat and, consequently, should be locally abundant and common across the large geographic space. Moreover, due to the lateral ingression of species in response to the

flood pulse, we also expect to find in the floating meadows species that are actually associated with adjacent ecosystems, such as low and high várzeas (cf. Wittmann et al. 2002). However, not being adapted to life in the floating vegetation, these occasional occupants are expected to be both locally rare and infrequent in the meadows across the geographic space. This might be especially true for amphibians. As demonstrated by Ramalho et al. (2018), habitats experiencing different levels of flooding are often associated with distinct sets of amphibian species. Besides being ecologically similar and phylogenetically closely-related, these species usually present fidelity to their preferred habitats fine-tuned by flood pulses and infrequently occupy adjacent environments as a bet-hedging insurance strategy (Ramalho et al. 2018).

This dichotomy between 'core' species, which are locally abundant and regionally common, and 'satellite' species, which are locally rare and patchily distributed over only a few sites, is known as Hanski's core-satellite (HCS) model (Hanski 1982, 1991, Hanski and Gyllenberg 1993). In the HCS model, the two functional groups of species are assumed to operate under different ecological rules. Even though the HCS is a key theoretical hypothesis in ecology, until now there was no proper methods to test it, with most cases only supported by the phenomenological pattern of a bimodal occupancy frequency distribution of species.

In this paper, we test the functional aspects of the HCS hypothesis by differentiating the ecological drivers behind 'core' and 'satellite' species. We do so by applying a new methodology that correlates zeta diversity, a set of multi-site similarity metrics that separate the contribution of rare to widespread species to compositional turnover (Hui and McGeoch 2014, Latombe et al. 2017, McGeoch et al. 2019), to environmental and geographic gradients. Specifically, we ask, using amphibians of Amazonian floating meadows as a model group: 1) are species distributions shaped at random in space, or do they show regional structured patterns? 2) If so, which are the main drivers of structuration? And 3) does the distribution of species fit the HCS model?

Material and methods

Study area

We compiled site-wise lists of amphibian species based on data that we collected in the field between 2001 and 2018 at 43 sites in Amazonia plus published data from 14 sites (adopted from Hödl 1977, Upton et al. 2014, Ramalho et al. 2016, 2018, Böning et al. 2017). Data compilation was opportunistic at a minimum effort of 5–8 hours/day by two workers over several consecutive days (more details in Böning et al. 2017). Given that all workers have a profound knowledge and have experience with collecting amphibian data in the field for many years, we expect that our local species lists are next to complete. The maximum straight-line distance spanned by our sampling is 2630 km from Yurimaguas in Peru to Almeirim in Brazil (Fig. 1). Actually,

along river courses, this sampling covers around 7000 km, i.e. 4243 km along the Solimões/Amazon river (39 sites), 2341 km along the Purus river (14 sites), 405 km along the Madeira river (three sites), and 35 km along the Oriximiná river (one site). The Negro, Tapajós and Xingu rivers were not included in our sampling, since they are clear- and blackwater rivers (i.e. rivers with transparent water, low amounts of sediments and low to intermediate nutrient status, cf. Junk et al. 2011). Under these conditions, considerably fewer floating meadows develop than in whitewater rivers (i.e. rivers with muddy waters, high amounts of sediments and rich in nutrients, cf. Junk et al. 2011, 2012, Junk and Piedade 1997). Maps were created using ESRI ArcGIS 10.2. For lists of sites, see Supporting Information.

Data handling

We identified species based on adult morphology and vocalizations (cf. Böning et al. 2017); taxonomy followed Frost (2020). Three species (*Dendropsophus leucophyllatus*, *D. reticulatus*, *D. triangulum*) of the *D. leucophyllatus* species complex (cf. Caminer et al. 2017, Pirani et al. 2020) were provisionally considered as one ‘supertaxon’, as species identifications remain difficult. Species life-history traits (predominant lifestyle and reproductive strategy) were obtained from a global database (Oliveira et al. 2017) and our unpublished

data. For the category ‘predominant lifestyle’, ‘terrestrial’ accounts for ground-dwelling species, ‘aquatic’ and ‘semi-aquatic’ for species that live mainly or partially in water, and ‘arboreal’ for species that occupy the vertical stratification of vegetation. Species primary habitat (i.e. floating meadows, várzea and terra firme forest) followed our unpublished data and Ramalho et al. (2018). Because of the low detectability of Gymnophiona given their strictly aquatic or fossorial habits, we only included species of the order Anura in the diversity analyses.

Diversity analyses

The spatial structure of biodiversity has traditionally been studied using the classical approaches of Whittaker (1960, 1972), i.e. alpha, beta and gamma diversities. Nevertheless, the best method to partition diversity is still debated (Chao et al. 2012). Zeta diversity (ζ), the number of species shared by multiple assemblages, is a novel concept and metric that unifies incidence-based diversity measures, patterns and relationships, turning into a propitious method for measuring biological diversity (Hui and McGeoch 2014, McGeoch et al. 2019). The number of assemblages (or sites) considered is the order of zeta, where ζ_1 is equivalent to alpha diversity, ζ_2 is equivalent to pairwise beta diversity, ζ_3 is the number of species shared by any three sites, and so on. Zeta

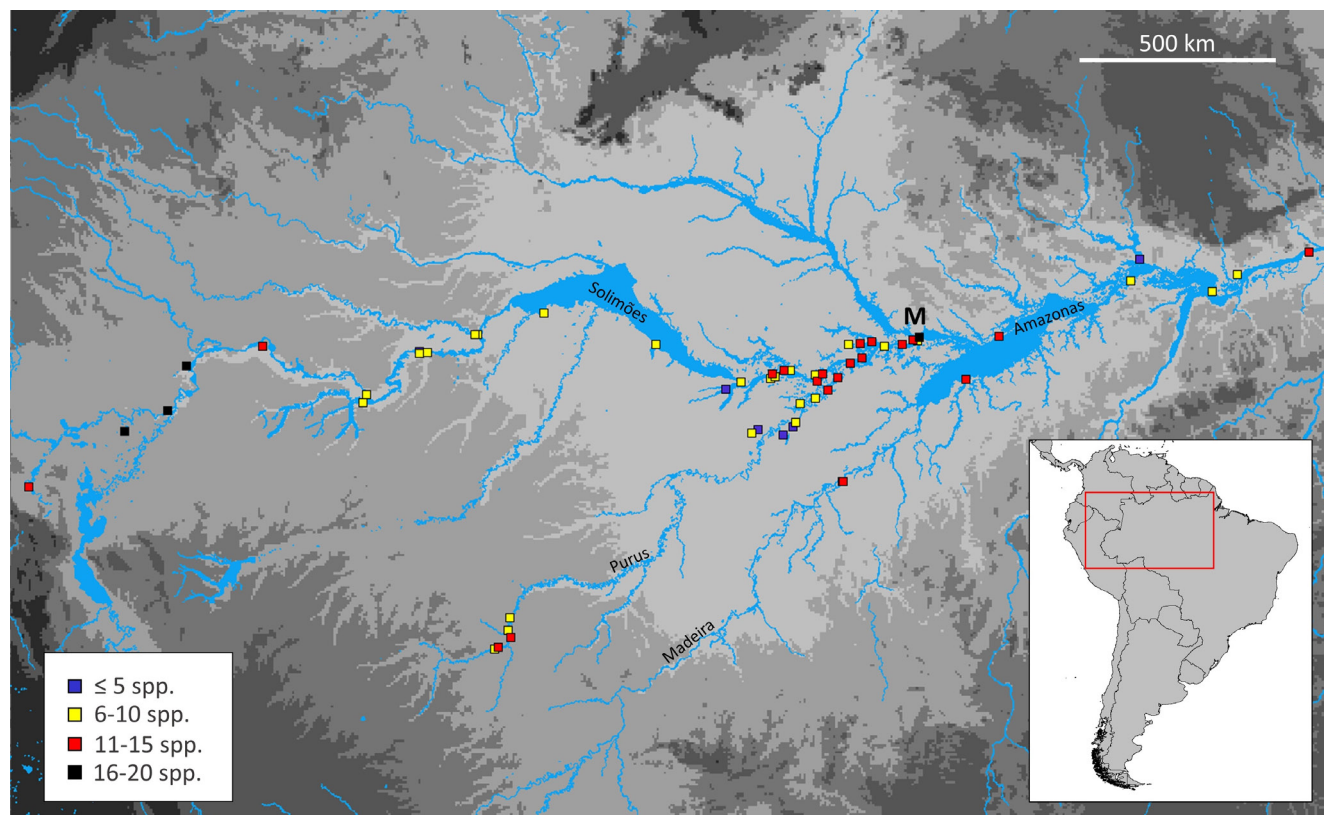


Figure 1. Map of amphibian species richness per floating meadow site in Amazonia (coloured squares), showing that most species-rich sites are situated in the upper basin and in the central basin, close to the Manaus region (M), where large rivers meet. Rivers in blue include inundation zones. Background grey shades refer to different altitudes (lighter shades indicate lower altitudes).

diversity considers the contribution of rare, intermediate and common species to compositional change, and allows to test hypotheses on the relative importance of deterministic (i.e. niche-based) versus stochastic (i.e. random/neutral) assembly processes in generating patterns of biodiversity (Latombe et al. 2018a).

Integrating zeta diversity into generalised dissimilarity modelling (multi-site generalised dissimilarity modelling, MS-GDM) allows to understand the importance of environmental gradients and spatial distance in explaining the compositional turnover of the whole spectrum of species, from rare to common (Latombe et al. 2017, 2018a). GDM is a versatile technique that uses a combination of generalised linear models and I-splines to assess the importance of different variables for explaining turnover. GDM generates a monotonic, non-linear spline for each environmental variable and distance, to explain their contribution to pairwise turnover, and MS-GDM generalises this for different orders of zeta diversity. The amplitude of a spline compared to those of other variables indicate the relative importance of a variable to explain species turnover. The non-linearities of a spline indicate if the impact of environmental differences in turnover varies along the environmental gradient (e.g. differences in precipitations are expected to matter more in areas with overall low amounts of precipitation, and the slope of the spline should therefore be steeper than for areas with high precipitation). Applying MS-GDM to different orders of zeta enables to assess how the relative impact of distance and environmental variables vary for different levels of species rarity (low orders of zeta) and commonness (high orders of zeta) (Latombe et al. 2017, 2018a).

In this regard, zeta diversity and MS-GDM become important tools to understand and describe the diversity patterns of amphibians in the Amazonian floodplains, allowing us to shed light on the processes and drivers of these patterns. Moreover, given its very characteristics, MS-GDM provides a means to test whether common species (higher orders of zeta; largely 'core' species) operate under different rules/processes/mechanisms from rare species (lower orders of zeta; largely 'satellite' species), thus becoming an excellent tool to test the HCS hypothesis.

Zeta diversity computations

Zeta diversity and MS-GDM analyses were computed in R (<www.r-project.org>) using the *zetadiv* package ver. 1.1.1 (Latombe et al. 2018b, c). All scripts, codes and data used to run analyses are available online on the Dryad repository <<https://doi.org/10.5061/dryad.pg4f4qrp3>>. To explore general patterns of diversity, we calculated the number of species shared by combinations of two to 30 sites (i.e. zeta values ζ_2 to ζ_{30}) along with the average richness per site (i.e. alpha diversity), corresponding to ζ_1 .

To identify potential differences in diversity patterns at large and regional scales, we used three sub-sampling schemes to compute zeta values and species retention rates (cf. Latombe et al. 2018a, b, c, McGeoch et al. 2019). When 'all

combinations' (ALL) were used, the spatial position of sites was not taken into account in the calculations. This scheme considers combinations of sites that may be far from each other and are therefore less likely to share species than closer sites. We used this scheme to identify the general pattern of diversity at large scales, i.e. the entire Amazon basin.

Contrary to ALL, when using the 'nearest neighbours' sub-sampling schemes we did take into account the spatial position of sites across a gradient. This kind of analysis allows to detect abrupt changes in species composition across spatial gradients, contrary to other indices of turnover (McGeoch et al. 2019). We used this approach to explore the possible existence of structured turnover at more regional scales, i.e. along different rivers. To compute ζ_i using the 'nearest neighbours non-directional' scheme (NON), each site was associated with its $i-1$ nearest neighbour using straight-line distances (SLD) between sites based on their geographic coordinates. Additionally, to compute ζ_i using the 'nearest neighbours-directional' scheme (DIR), each site was associated with its nearest downstream neighbour along the river. To do that, we used a modification of the original *zetadiv* function and an asymmetric distance matrix (Supporting information) with true distances in km along river courses (DRC) between sites. To impose constraints against unwanted associations (i.e. with upstream sites), in the distance matrix we used values 3 times higher than the maximum DRC between sites (= 4243 km) for sites located upstream in the same river, and values 100 times higher for sites located in different rivers (i.e. in upstream positions before rivers meet). DRC were calculated in ArcGIS using the Amazon GIS-Based River Basin Framework (Venticinque et al. 2016). Besides using raw zeta values (i.e. absolute number of species shared by sites), we also performed analyses using normalised versions of zeta to avoid the influence of large differences in richness among sites (McGeoch et al. 2019). We used the Simpson-equivalent versions of zeta (ζ_{ij}/S_j) (where S_j is the minimum number of species over the i assemblages in the specific combination j) and the Sørensen-equivalent version (ζ_{ik}/S_{0k}) (where S_{0k} is the average number of species per assemblage in the specific combination k , that is, the alpha diversity of the combination k). Computing these two versions of zeta diversity enabled us to assess the impact of nestedness on turnover (i.e. when the composition of a small site is a subset of the species present in a bigger or richer site), since nestedness is considered in the Sørensen but not in the Simpson version (Baselga 2010).

Distance decay

To assess the effect of distance on the number of species shared by multiple sites, we computed the distance-decay of zeta diversity for zeta orders 2 to 8. We used a general additive model under shape constraint (SCAM; Pya and Wood 2015), which imposes a monotonic decay on the relationship between distance and zeta values, as we assumed that distance must be mechanistically inversely proportional to species similarity. We ran analyses using raw and normalised versions of zeta (equivalent to Simpson and Sørensen) for two

different types of distance, to examine the patterns at large and regional scales. To explore the general pattern at the large scale, we performed tests using SLD between sites based on their geographic coordinates. To explore regional patterns, we ran analyses using DRC arranged in a symmetric distance matrix (Supporting information). In this analysis, to prevent associations between sites in different rivers, we used values 1.5 times higher than the maximum DRC (= 4243 km) for sites located in upstream positions when different rivers meet. These two kinds of analyses also allowed us to explore the effects of dispersal on the distance decay, with SLD disclosing the signal of active terrestrial dispersal between sites, and DRC underscoring the importance of passive long-distance dispersal promoted by floating meadows along rivers.

Environmental drivers of species turnover

To assess how distance and difference in environmental conditions explain species turnover, we performed MS-GDM analyses following Latombe et al. (2017, 2018a). We ran MS-GDM for zeta orders 2 to 8, based on 11 environmental variables (seven numerical, four categorical, Supporting information) and distance between sites. As for the distance decay calculations, we used SLD between sites based on their geographic coordinates and a symmetric distance matrix based on DRC with constraints to unwanted associations (Supporting information). We used bioclim variables derived from the gridded CHELSA global climate dataset at 30 arc sec resolution from CHELSA (Karger et al. 2017a, b). CHELSA is suggested to perform better than WorldClim (Bobrowski and Schickhoff 2017), especially in remote areas where climate stations are sparse (Karger et al. 2017a), as it is the case in Amazonia. These 19 bioclim variables were tested for multicollinearity following Dormann et al. (2013) and seven were selected (variance inflation factor, $VIF \leq 3.7$) based on their relevance for amphibian distribution in Amazonia (Wiens et al. 2006, Bonetti and Wiens 2014, Godinho and Silva 2018): Temperature seasonality (Bio4), Mean temperature of wettest quarter (Bio8), Mean temperature of driest quarter (Bio9), Annual precipitation (Bio12), Precipitation seasonality (Bio15), Precipitation of wettest quarter (Bio16), and Precipitation of driest quarter (Bio17). Body water type (lake/river), water colour (white/black/clear) and stream order data were obtained from the Amazon GIS-Based River Basin Framework (Ventocinque et al. 2016). Terrestrial ecoregions were obtained from the World Wildlife Fund (WWF, Olson et al. 2001).

Results

Species composition and distribution patterns

We identified 50 species (49 Anura, one Gymnophiona) over 57 sites (Fig. 1). The full species list per site is available in the Supporting information. At the family level, we recorded 35 species of Hylidae, seven of Leptodactylidae, and

three of Bufonidae, while Craugastoridae, Dendrobatidae, Microhylidae, Pipidae and Typhlonectidae were each represented by one species. Twenty-nine species have arboreal, 13 terrestrial, and eight aquatic/semi-aquatic predominant lifestyles as adults. With regard to reproductive strategies, one species is viviparous, two are endotrophic (i.e. no free larvae) and 47 have aquatic larvae.

Most species-rich sites (15–20 species) were situated in the upper basin and in the central basin, where large rivers meet (Fig. 1). Considering the dataset used for diversity analyses (i.e. only anurans, 49 species), 27 species were infrequent (≤ 5 sites), 15 intermediate (> 5 and < 28 sites), and seven frequent (found in more than half of sites; that is ≥ 28 sites) (occupancy frequency distributions available in the Supporting information). Out of the 27 infrequent species, 13 were recorded only in one site each, of which ten were represented by merely one individual. Thirteen species were considered to be primarily associated with floating meadows (of which seven were frequent across sites), 31 with várzeas (19 infrequent, 12 intermediate), and five with terra firme forests (four infrequent, one intermediate). All terrestrial species were either infrequent (nine species) or intermediate (four species) across sites. All frequent species were hylid tree-frogs with arboreal or semi-aquatic habits that were highly associated with floating meadows (Supporting information).

Zeta diversity

The declines of zeta diversity values with increasing zeta order were similar for the three different sub-sampling schemes (more details on results, including zeta values, in the Supporting information). In all scenarios explored, zeta diversity values rapidly declined to zero and retention rates rapidly increased. The decline was slightly shallower when using 'nearest neighbours' than ALL (Fig. 2A–B) as expected, since closer sites are more likely to share species. Furthermore, declines were similar for Sørensen (Supporting information) and for Simpson analyses (Fig. 2B, D), although slightly steeper for Sørensen for low orders of zeta, suggesting little to none effect of nestedness in the system. This is consistent with the lack of increase in species diversity along the river stream (Supporting information). In ALL, the species retention rate assumed a modal shape (Fig. 2C), starting to decline by zeta order 13. It means that, for higher orders of zeta, even the most common species are less likely to be retained when adding sites, and that the study extent (57 sites) encompasses the community structuration. For 'nearest neighbours', the species retention rates constantly alternated between peaks and slopes (Fig. 2C–D), indicating the existence of regional structured assemblages. For all analyses, zeta values basically coincided from zeta order 15 on (Supporting Information), indicating the scale of spatial aggregation of the species. These results indicate the existence of a small set of common species shared by several sites and a large number of rare species that are not shared when doing cross-region comparisons.

The exponential parametric form fitted the data better than the power law, as shown by lower AIC values (Supporting

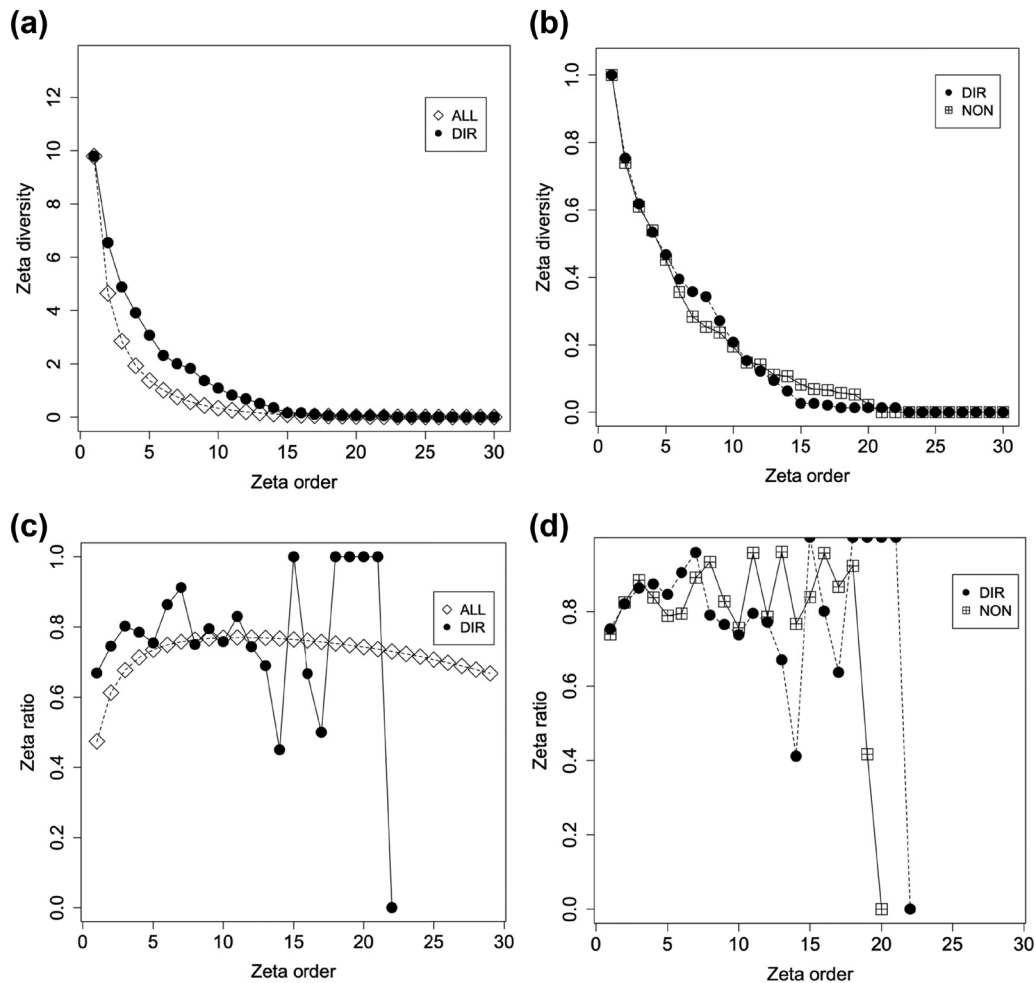


Figure 2. Zeta diversity decline (A, B) and retention rate (C, D) for the ALL, DIR and NON subsampling schemes using raw data (A, C) and Simpson equivalents (B, D), showing that zeta diversity values rapidly decline to zero and retention rates rapidly increase. More details on results are available in the Supporting information.

information). Usually, such an exponential decline means an equal probability of retaining a species as the number of sites increases (i.e. the presence of a species in a random site is independent of the species occupancy), and therefore indicates stochastic processes at play. Nevertheless, it is noteworthy that the differences between AIC values of both forms were larger for ALL (-100) than for DIR ($31-46$) and NON ($15-40$), indicating that deterministic processes gain importance at more regional scales and when taking into account the position of sites along rivers.

Distance decay

Distance decay results showed different patterns for SLD and DRC calculations (Fig. 3). In all analyses, decay was more pronounced for lower orders of zeta ($\zeta_{2,3}$), indicating a rapid loss of rare species, often narrow-ranged, with increasing distances. For rare species, decay stopped at shorter distances for DRC (~ 1500 km for ζ_2 ; ~ 1200 km for ζ_3) than for SLD

(~ 2000 km for ζ_2 ; ~ 1500 km for ζ_3). Note nonetheless that this was due to combinations of sites across different rivers, for which we used 3 times the maximum distance for the DRC. When pairs of sites on different rivers were excluded from DRC analyses (i.e. removing the points with the maximum distance from Fig. 3), the plateau disappeared, and the Pearson correlation became higher than for SLD (Supporting information). For more common species (ζ_{4-6}), distance decay was less pronounced: for SLD, there was a first decline with a threshold at ~ 400 km, then a plateau from ~ 400 to ~ 800 km, and another decline from ~ 800 to ~ 1100 km, yet less pronounced; for DRC, there was a constant decline of more common species until ~ 1100 km, when decay stopped (note that we could not run analyses when all sites are on the same river for zeta orders > 2 , as this was not feasible from the *zetadiv* package, and removing points with the maximum distance from Fig. 3 only eliminates combinations with all sites on different rivers). All things considered, overall patterns of distance decay showed the existence of three main

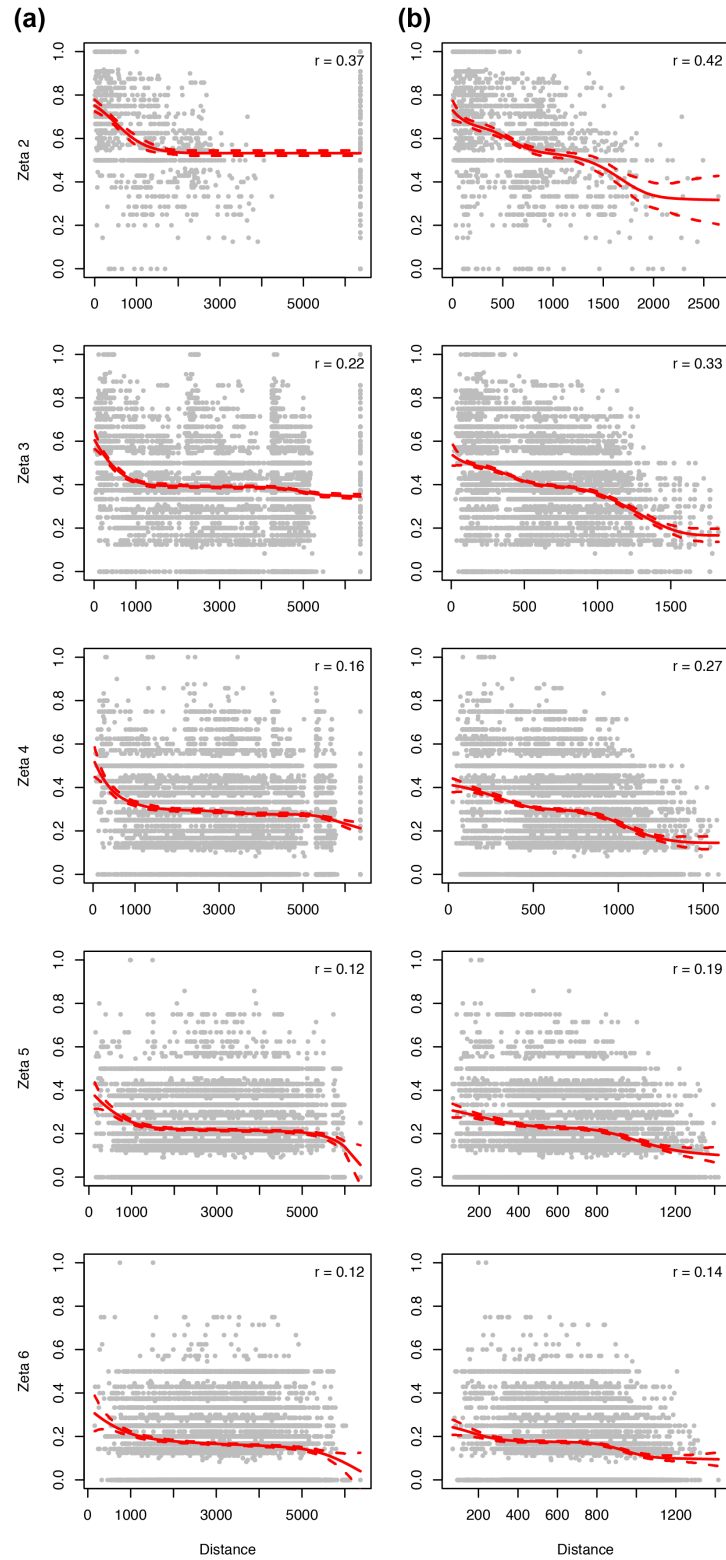


Figure 3. Distance decay of zeta diversity (Simpson equivalents) for zeta orders 2–6 using a) true distances along river courses (DRC) between sites; and b) straight-line distances (SLD) between sites based on their geographic coordinates, showing a rapid loss of rare species, often narrow-ranged, with increasing distances. SCAM fitting curves in red.

sections: a first rapid decay at short distances, a middle-range plateau, and a long-distance decay (Fig. 3). These patterns were stronger for common species and for DRC analyses.

Environmental drivers of turnover

When using SLD to perform analyses (Fig. 4), spatial distance between sites was the most important variable explaining turnover for rare species ($\zeta_{2,3}$), but not for more common species ($\zeta_{4,8}$). When using DRC (Fig. 5), the relative importance of distance between sites strongly decreased, with climatic variables becoming more important to explain turnover for both rare and common species. The turnover of rare species was controlled by a wider range of climatic features than the turnover of common species. For $\zeta_{2,3}$, using DRC, Temperature seasonality (Bio4), Precipitation of the wettest quarter (Bio16), Mean temperature of the driest quarter (Bio9) and Precipitation seasonality (Bio15) were central predictors of species distributions. In contrast, the turnover of common species ($\zeta_{4,8}$) was mainly influenced by Temperature seasonality (Bio4) and, to a lesser extent, by Precipitation of the wettest quarter (Bio16).

The shapes of the I-splines curves provide insights on the range of each variable over which the effect on species turnover is more important, with steeper slopes meaning greater importance. Distance, for instance, had a constantly increasing rate in all analyses, indicating that, as expected, the rate of compositional turnover is higher with increasing distances between sites. Moreover, the shapes of I-spline curves for Temperature seasonality (Bio4; standard deviation of the monthly mean temperatures $\times 100$) suggest that even small differences in seasonality greatly influence turnover when seasonality is low. On the other hand, where seasonality is higher than the ten percentile between the minimum and maximum values, differences have little influence on turnover. In this higher seasonality region, as the increasing slopes indicate, increasing values would nonetheless incur higher turnover. It is interesting to note that this region with low seasonality in temperatures and high turnover rates includes 22 sites (38% of total) along three different large rivers (Fig. 6). Further, when considering only DRC, the I-spline curves for Precipitation of the wettest quarter (Bio16) indicate that turnover is not sensitive to changes in precipitation in regions with intermediate values (0.3–0.6), but it is sensitive to changes in drier (<0.3) and wetter (>0.6) regions, especially for lower orders of zeta ($\zeta_{2,4}$) (Fig. 5). Finally, the compositional turnover of rare species ($\zeta_{2,3}$) was more sensitive to changes of temperature in cooler than in hotter regions, as the curves for the Mean temperature of the driest quarter (Bio9) indicate, and Precipitation seasonality (Bio15) was more important in areas where seasonality in rains are less pronounced.

Discussion

General patterns of diversity

Amazonia is home to more than 600 amphibian species, most of them in the order Anura (Godinho and Silva

2018, Mayer et al. 2019, Vacher et al. 2020). We found most species-rich floating meadow sites to be located in the upper Amazon basin (Fig. 1, Supporting information). This is well in accordance with the general diversity patterns reported for amphibians (Duellman 1988, 1999, Azevedo-Ramos and Gallati 2002, Godinho and Silva 2018). Aside from this western portion, general amphibian richness in Amazonia is equally lower across the central and lower basins (cf. Godinho and Silva 2018; Fig. 2A). Our study confirmed this pattern in floating meadows too, except for the central basin (i.e. the Manaus region close to the confluences of the Purus, Solimões/Amazon, Negro and Madeira rivers; Fig. 1), which was our second most species-rich region. This pattern is not exactly surprising, since confluences of large rivers in the Amazon basin have been demonstrated to affect general diversity patterns of both aquatic and terrestrial fauna (Fernandes et al. 2004, Laranjeiras et al. 2020).

River confluences are generally expected to enhance species richness since they promote habitat heterogeneity (Benda et al. 2004, Rice et al. 2008). Moreover, in the central Amazon basin, species diversity in the floodplains is expected to be high as a reflex of the high predictability, duration and amplitude of the flood pulse (Junk and Wantzen 2006, Junk et al. 2011) coupled with the great extension of inundation zones (Melack and Hess 2010) in this region. Besides directly influencing amphibian richness, these factors also increase herbaceous plant diversity in this region (Junk and Piedade 1993), indirectly increasing microhabitat diversity for amphibians that occupy floating meadows. Nevertheless, we cannot rule out that the greater amphibian richness that we found close to Manaus is an effect of the enormous sampling effort in this region (cf. Mayer et al. 2019), as the geographic distribution of our own sites reflect (Fig. 1).

Finally, one can argue that if macrophyte rafts really work as means of dispersal along rivers (cf. Schiesari et al. 2003), then the diversity patterns of species occupying floating meadows should be, at least to a certain extent, similar to those of aquatic organisms. In fact, stochastic metapopulation models of riparian vegetation communities suggest that, in river networks, increased directional dispersal promoted by rivers reduces local diversity, and that communities exhibit abrupt changes where large tributaries meet (Muneepeerakul et al. 2007), a pattern similar to what we observed. Moreover, Fernandes et al. (2004) reported that the local diversity of electric fishes along the Amazon river mainstream is enhanced by river confluences, although they did not find an accumulation of species into a downstream direction. These patterns are also similar to what we observed for amphibians in floating meadows (Fig. 1, Supporting information), suggesting that the diversity patterns of amphibian species occupying floating meadows are indeed similar to those of aquatic organisms.

The 'core' and 'satellite' species

By using MS-GDM as a new tool to test the HCS hypothesis, as captured by high and low orders of zeta diversity, we were able to clearly identify the existence of two functional groups of amphibian species that operate under different ecological

All species – Euclidean distance

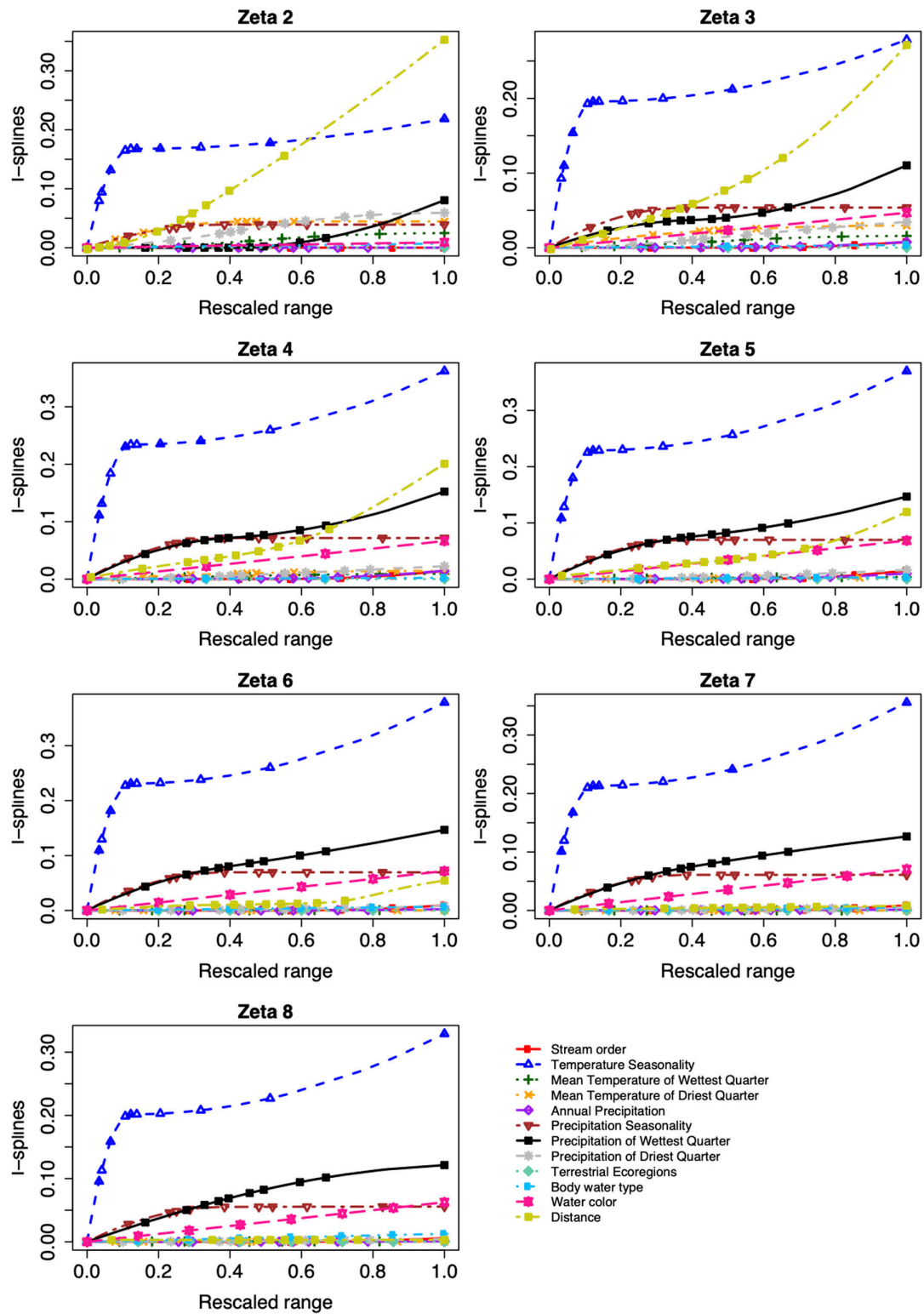


Figure 4. MS-GDM analyses for zeta orders 2-8 using environmental features and straight-line distances (SLD) between sites based on their geographic coordinates, showing that spatial distance between sites is the most important variable explaining turnover for 'satellite' but not for 'core' species, and that Temperature seasonality is an important predictor of distributions for both 'core' and 'satellite' species.

All species – river distance

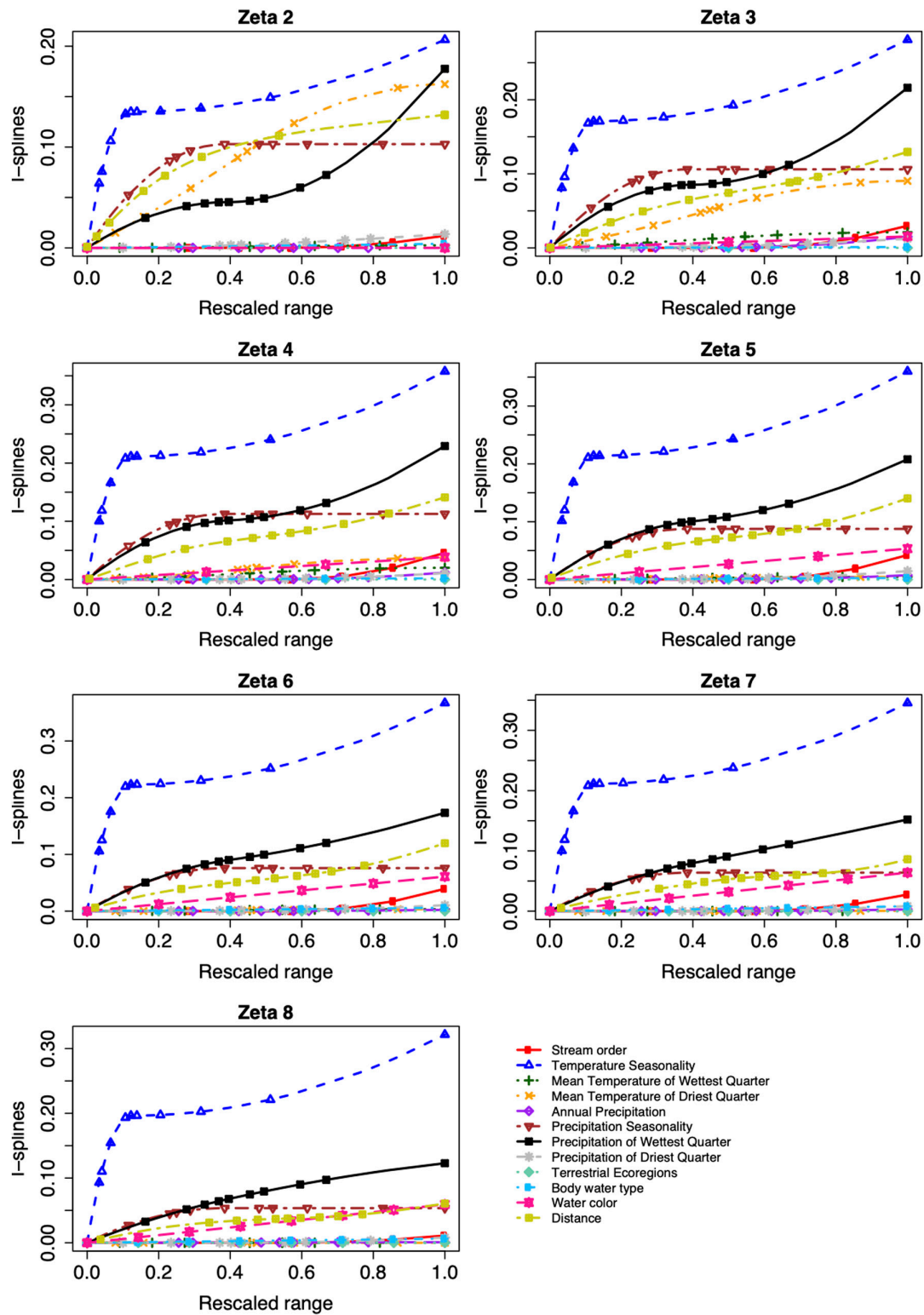


Figure 5. MS-GDM analyses for zeta orders 2-8 using environmental features and true distances along river courses (DRC) between sites, showing that the turnover of 'satellite' species is controlled by a wider range of climatic features than the turnover of 'core' species, and that Temperature seasonality is the principal predictor of distributions for both 'core' and 'satellite' species.

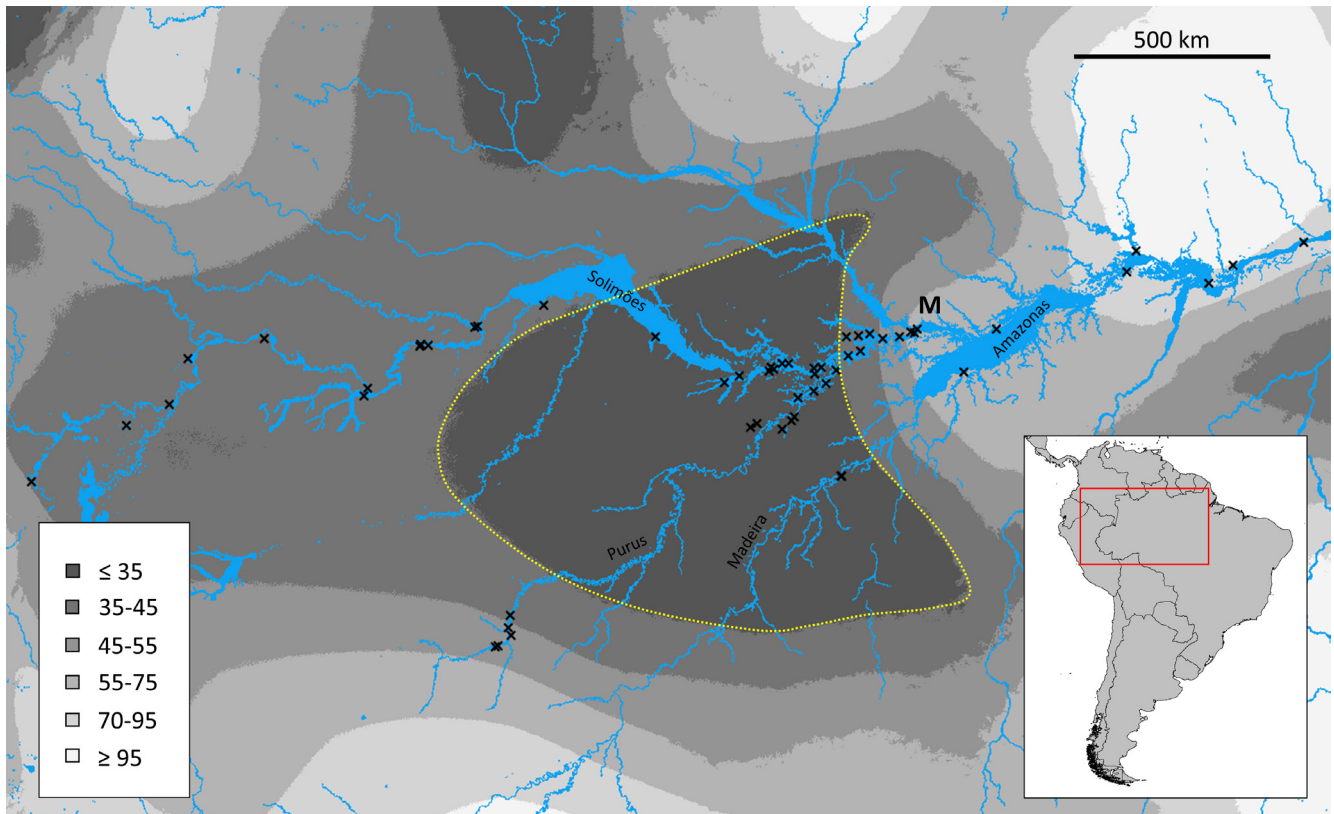


Figure 6. Map of sampling sites projected against different regimes of seasonality in temperature (Bio4, i.e. grey-scaled background) in Amazonia. The yellow line delimits the 10-percentile region with low seasonality in temperatures and high turnover rates.

processes in the Amazonian floating meadows. This division was not only based on their occupancy frequency distributions across the space, but also in their ecological and biological features. Not surprisingly, it also reflects their phylogenetic relationships. All this coupled together supports the HCS hypothesis.

The 'core' species in our system are those feasibly associated with floating meadows (Supporting information). They are well adapted to life in the floating vegetation, presenting either arboreal or aquatic/semi-aquatic lifestyles and reproductive modes associated with lentic waters. Except for the aquatic toad *Pipa pipa*, they are all small-bodied hylid treefrog species (except for the medium-sized *Boana raniiceps* and *B. punctata*) that occupy the meadows for breeding, sheltering, foraging and dispersal, and that are usually locally abundant (Upton et al. 2014, Böning et al. 2017, Ramalho et al. 2018, Ganança et al. 2021, Fonte et al. unpubl.). More than that, they are suggested to have fidelity to this environment, being usually rare in adjacent environments (cf. Ramalho et al. 2018, Ganança et al. 2021, Fonte et al. unpubl.). Around 25% of our species fit the 'core' role, of which 7 were frequent (≥ 28 sites) across our sampling. These were found in 28-48 sites, encompassing distances as large as 4200 km along true river courses (2630 km in straight line distance). On the other hand, roughly 75% of our species are primarily associated with low and high várzeas and terra firme forests (Supporting

information). Although they can be common and locally abundant in these habitats, they are considered only occasional or accidental occupants of the floating meadows. They are terrestrial (e.g. bufonids, craugastorids, leptodactylids, microhylids) or arboreal (hylid) species primarily associated with shrubs and large trees. Out of these, we considered as 'satellite' the 23 species that were infrequent across our sampling (≤ 5 sites). We considered the remaining 13 species as 'intermediate' (recorded in > 5 and < 28 sites).

It is important to note that the 'core' and 'satellite' roles are not merely occurrence-based, but that they are also strongly related to the ecological function of species in the system. In this regard, although the frequency distribution of 'core' and 'satellite' species is usually expected to be bimodal (Hanski 1982, 1991, Hanski and Gyllenberg 1993), unimodal patterns with a peak in the 'satellite' species (as it seems to be our case, Supporting information) can also be observed when the spatial scale of the region is increased (Collins and Glenn 1991). Moreover, as demonstrated for other taxonomic groups such as vascular plants, grasshoppers, birds and small mammals, the HCS model does not necessarily apply to all taxa within a single spatial scale, with functional 'core' and 'satellite' species occurring only at local scales for some taxa (Collins and Glenn 1991). In this sense, it is possible that some amphibian species that were infrequent and rare at large scales across our sampling still fit the functional 'core' role at local scales.

Drivers of species turnover

The relative importance of different ecological processes to explain species diversity is highly influenced by the spatial scale of the analyses (Chase 2014). In our case, if we consider the entire Amazon basin (as inferred from ALL and SLD analyses; Fig. 2, 3B, 4), random placement was the main driver of amphibian diversity in the floating meadows. At more regional scales, i.e. taking into account the position of sites along different rivers (as inferred from 'nearest neighbours' and DRC analyses; Fig. 2, 3A, 5), climate was more important than distance to explain species turnover, and deterministic processes gained relevance as drivers of species diversity. This is in accordance with the findings of Ganança et al. (2021), who showed that local amphibian diversity in floating meadows is not randomly determined and that local turnover is driven by deterministic (i.e. niche-based) processes.

As our MS-GDM analyses revealed, the turnover of 'satellite' species was higher with increasing distances between sites than the turnover of 'core' species (Fig. 4, 5). A possible explanation is that our 'core' species have larger geographic ranges across Amazonia (because of long-distance dispersal promoted by macrophyte rafts) while our 'satellite' species have smaller geographic ranges (because of limited active dispersal through forests). Yet, this hypothesis still remains to be tested. MS-GDM analyses also revealed that the turnover of 'satellite' species was controlled by a wider range of climatic features. A possible explanation is that 'satellite' species have stronger environmental restrictions and thus can only thrive in regions where their physiological requirements are met (i.e. environmental filtering, Keddy 1992). An alternative explanation is that, in response to the environment, in some regions 'satellite' species use floating meadows more often than in others. This could be related to a combination of factors such as biological interactions (competition, predation, etc.), resource availability (food, etc.), historical colonization, and local composition of herbaceous plants. In fact, Ganança et al. (2021) showed that local amphibian diversity in floating meadows is mediated by habitat conditions (e.g. water depth, macrophyte morphotype, etc.) selecting species ecomorphological traits (e.g. body size, toe pads, foot webbing, tadpole habit, etc.). In this sense, local turnover is driven by the ability of species to occupy locally available habitats. Since terrestrial and larger arboreal species (i.e. our 'satellite' species) are only able to occupy specific species of plants in the meadows (Upton et al. 2014, Ganança et al. 2021), their occurrence can be favoured or hampered depending on the local plant composition. In this sense, given that environmental conditions also influence plant diversity in the floating meadows (Junk 1970), local plant diversity in response to climatic features can therefore indirectly influence local amphibian diversity. As our results suggest, this effect should be stronger for 'satellite' species, given that they lack adaptations to life in the meadows, and weaker for 'core' species.

Finally, as inferred from MS-GDM results, Temperature seasonality (Bio4) was the principal predictor of distributions for both 'core' and 'satellite' species, with changes in

compositional turnover being especially higher in regions with lower temperature seasonality (Fig. 4, 5, 6). This can be a reflex of the narrow temperature niche breadth usually observed in tropical amphibians (Bonetti and Wiens 2014). In general, tropical species are suggested to have narrow climatic tolerances for temperature due to limited temperature seasonality in the tropics (Janzen 1967), and this pattern was demonstrated for amphibians (Quintero and Wiens 2013). Specifically, temperature seasonality shows significant phylogenetic conservatism in hyliid treefrogs, seemingly limiting the dispersal of tropical clades into temperate regions (Wiens et al. 2006). However, we must note that this specific region with higher turnover rates – presumably in response to temperature seasonality – encompasses sites along three different large rivers before they meet (Fig. 6). Therefore, we can speculate that the high turnover rates observed in this region can be also related to the existence of limited dispersal between rivers.

The role of rivers on amphibian dispersal

Since amphibians as a group are predominantly site-loyal and of low vagility (Vences and Wake 2007), large rivers are commonly considered important barriers to their dispersal, especially in the lowland Amazonia (i.e. riverine barrier hypothesis, Gascon et al. 1996, 1998, 2000; Loughheed et al. 1999; Dias-Terceiro et al. 2015; Fouquet et al. 2015; Moraes et al. 2016, but see Santorelli et al. 2018 and Ruokolainen et al. 2019). In fact, large whitewater rivers such as the Amazon, the Madeira and the Purus have been recently suggested to delimit amphibian biogeographic regions (Godinho and Silva 2018, Vacher et al. 2020). Even though there is no strong consensus about the riverine barrier effect upon amphibians as a group, it seems to be stronger for terra firme forest species with more specialised reproductive modes (e.g. direct development without aquatic larvae), and weaker for várzea species with more generalist reproductive modes (e.g. eggs and tadpoles in lentic water) (e.g. Gascon et al. 1998, Fouquet et al. 2015). Yet, most conjectures concerning the riverine barrier effect upon amphibians are based on their presumed weak ability to actively move across riverbanks, and little attention has been given to their potential ability to passively move across and along rivers. Since macrophyte rafts do represent an important medium of passive long-distance dispersal for amphibians (Schiesari et al. 2003, Fonte et al. 2019), in some cases rivers can in fact facilitate dispersal instead of hampering it. If this is true, this effect should be stronger for typical floating meadows species and, as a consequence, they can be expected to have large geographic ranges across Amazonia. Even though this still remains to be tested, our study can provide some clues. In fact, most of our 'core' species were frequent across the entire Amazon basin and some of them were registered across sites as far as 2,630 km in straight line distance. Furthermore, in accordance with this, Fouquet et al. (2007) demonstrated that true widespread Amazonian species are usually associated with rivers and adjacent open areas, strengthening the hypothesis that rivers can promote long-distance dispersal.

All things considered, our study helps to shed light on the dispersal dynamics of amphibians in the Amazonian river-floodplain system. As our distance decay and MS-GDM results showed (Fig. 3, 4, 5), distance was an important variable explaining species turnover for ‘satellite’ species but was clearly not a problem for ‘core’ species, indicating that the latter have a stronger dispersal ability even at large distances. In general, as inferred from our distance decay results (Fig. 3), there are seemingly three main processes at play: species do have low active dispersal abilities (i.e. rapid decay at short distances); macrophyte rafts facilitate passive dispersal along rivers (i.e. middle-range plateau); and there are indeed cross-river barriers to dispersal (i.e. long-distance decay). Specifically, the effects of dispersal limitation are stronger for ‘satellite’ species, whereas the effects of passive long-distance dispersal are stronger for ‘core’ species.

Caveats

Tropical wetlands are complex systems, and no single process alone can properly explain the origin, regulation and diversification of their biota. Also, current geographic and environmental conditions are only a snapshot in time and hence do not necessarily capture all the dynamic aspects of community assembly through time (Wiens and Donoghue 2004, Jenkins and Ricklefs 2011, Ricklefs and Jenkins 2011, Baselga et al. 2012, Silva et al. 2014). This might especially apply to the Amazonian floodplains (Irion et al. 1997) where river network (Ruokolainen et al. 2019) and wetland vegetation (Kirschner and Hoorn 2020) have changed over time. Moreover, insufficient taxonomic knowledge hampers the understanding of real distributional patterns of Amazonian amphibians. Species definitions are mainly based on morphology, although morphological evolution in this group is usually highly conserved and plagued with homoplasy (Fouquet et al. 2007, Vences and Wake 2007). Partly unsolved taxonomy is still a remaining problem in Amazonian anuran diversity, especially as cryptic species diversity is an important phenomenon (Funk et al. 2011, Gehara et al. 2014, Vacher et al. 2020). On the other hand, recent investigations also showed that geographically widespread anurans do exist in Amazonia (Fouquet et al. 2007, Gehara et al. 2014, Vacher et al. 2020). Even though this taxonomic unsureness might affect our analyses, the inherent uncertainty of evolutionary entities is a conventional scientific limitation that cannot be magically solved or simply stamped out (Hey et al. 2003). That said, even though ‘true’ species identifications remain difficult for some taxa that we recorded, we can ensure consistency in species identifications across sites. Furthermore, considering the huge extent of our dataset, we cannot rule out that discrepancies during data sampling (e.g. observer accuracy, sampling duration and time of the year) and bias in site selection (Mayer et al. 2019) eventually influenced our results. However, since we aim at the macroecological scale seeking for the more ‘general picture’, we expect that these caveats did not impair the conclusions derived from our analyses. Instead, we believe our results help

to shed light on the patterns and drivers of amphibian diversity in the Amazonian river–floodplain system.

Closing remarks

In conclusion, we found two functional groups of amphibians operating under different ecological processes in the floating meadows. ‘Satellite’ species are primarily associated with várzeas and terra firme forests, being only occasional or accidental occupants of the floating vegetation. Their turnover is controlled by a wider range of climatic features and increases much faster with distances. ‘Core’ species are associated with the floating meadows, and distance is not a limiting factor for them. This is probably related to the existence of passive dispersal of individuals along rivers. Since ‘core’ species are more common in the floating meadows, it is expected that they will be more frequently carried away by macrophyte rafts.

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.pg4f4qrp3>> (Fonte et al. 2021).

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