



RESEARCH ARTICLE

Functional connectivity in sympatric spiny rats reflects different dimensions of Amazonian forest-association

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Abstract

Aim: Understanding how the landscape influences gene flow is important in explaining biodiversity, especially when co-distributed taxa across heterogeneous landscapes exhibit species-specific habitat associations. Here, we test predictions about the effects of forest-type on population connectivity in two sympatric species of spiny rats that differ in their forest associations. Specifically, we evaluate the hypothesis that seasonal floodplain forests (*várzea*) provide linear connectivity, facilitating gene flow among individuals, while non-flooded forests (*terra-firme*) may diminish the functional connectivity.

Location: Western Amazon, South America.

Taxon: *Proechimys simonsi* (non-flooded forests, *terra-firme*) and *Proechimys steerei* (seasonal floodplain forests, *várzea*).

Methods: We analyse about 13,000 single nucleotide polymorphisms along with characterizations of landscape heterogeneity for two forest types to test for differences in the functional connectivity. Influence of the landscape and environmental variables are quantified using maximum-likelihood population effect models to identify the relative importance of variables in explaining the gene flow.

Results: There are significant differences in functional connectivity between species. However, the genomic data does not support the conventional hypotheses of higher connectivity for inhabitants of *várzea* than those of *terra-firme*. Stronger genetic structure in *P. steerei* than *P. simonsi* based on isolation by distance models suggests reduced gene flow in species associated with *várzea* forests. Isolation by resistance reinforces that wetland habitats inhibit and promote the functional connectivity in *P. simonsi* and *P. steerei*, respectively, although large distances along the rivers can prevent gene flow in *P. steerei*.

Main conclusion: Interpreting differences between connectivity in taxa apparent from genetic analyses through the lens of a single dimension of Amazonian heterogeneity—that is, forest type—may be an oversimplification. Our statistical modelling and fit of the data to different models points to specific environmental and habitat differences between the ecological divergent spiny rat species that may contribute to differences in the genetic structure of these sympatric taxa.

KEYWORDS

isolation by resistance, landscape genetics, MLPE mixed models, phylogeography, RADseq, *terra-firme*, *várzea*



1 | INTRODUCTION

Landscape configuration and composition can influence gene flow among populations (Manel et al., 2003) such that organisms with different ecologies can show different connectivity patterns in the same landscape (Balkenhol et al., 2015). The effects of the landscape on the dispersal of organisms are understood as functional connectivity, given that it's not geographical distance alone that determines gene flow, but also how organisms perceive and respond to landscape structure (Manel & Holderegger, 2013). As such, the divergence process may differ among sympatric taxa when the species' ecologies affect connectivity among populations because of differences in how they perceive and respond to the landscape (Pirani et al., 2019), in addition to differences in the landscape structure of different habitat types (Massatti & Knowles, 2016; Prado et al., 2019).

Restrictive factors in a landscape may prevent movement and connection of the organisms (Taylor et al., 1993) through (i) isolation by resistance (IBR), where restrictions are based on landscape structure and configuration (McRae, 2006), or (ii) isolation by distance (IBD), where geographical distance determines the amount of dispersal (Wright, 1943). Connections (or conversely isolation) between populations can relate to historical processes, such as vicariance and dispersion events (Carnaval & Moritz, 2008; Ribas et al., 2012), or reflect ecological and behavioural traits (e.g., mating patterns, migration capacity, habitat use), which may create resistance or facilitate organism's movements across heterogeneous landscapes and environments and generate different patterns of local adaptation, genetic diversity and population structure (McRae & Beier, 2007).

Studies focusing on functional connectivity, gene flow and genetic diversity are important to explain biodiversity patterns, as well as to provide important information for conservation biology (Hoban et al., 2020), especially in poorly known environments, such as the Western Amazon (Barlow et al., 2016). Bordered by the Andean slopes to the west and the Negro River and Madeira River to the east (Leite & Rogers, 2013), the Western Amazon has a dynamic geological history unlike the rest of the Amazon and a unique river dynamic of meandering white-water rivers and seasonal floods (Hoorn et al., 2010; Matocq et al., 2000). Western Amazonian landscape is predominated by two dominant forest types: non-flooded or *terra-firme* forests, and seasonal floodplain forests or *várzea* forests. The non-flooded forests are above the maximum flood level of rivers and perennial streams, and it abuts the seasonally inundated floodplains forests (Bredin et al., 2020). As non-flooded systems, except for the occasional minor inundation of flood water (Hess et al., 2015), inhabitants of the *terra-firme* forests are hypothesized to experience greater stability, and hence are expected to be characterized by higher genetic diversity, compared with inhabitants of the floodplain forests (Harvey et al., 2017). On the other hand, seasonal flooding of *várzea* forests produce a dynamic of meandering river channels (Constantine et al., 2014) in which sections of land frequently move from one river side to the other, and as such, are hypothesized to facilitate gene flow among the populations of the inhabitants of this

forest (Matocq et al., 2000; Salo et al., 1986) via connectivity along the floodplains bordering rivers, as well as by temporary dispersal corridors between river basins during seasonal flooding of the *várzea* forests. This general framework has been supported by genetic studies of different members of the communities that inhabit the *várzea* forests, including species of birds (Aleixo, 2006; Cadena et al., 2011; Harvey et al., 2017), plants (Godoy et al., 1999) and mammals (Matocq et al., 2000). However, questions remain about the extent to which this hypothesis can be generalized, especially in organisms with different dispersal characteristics (see Thom et al., 2020).

Among the species-rich fauna that inhabits the non-flooded and seasonal floodplain forests of the Western Amazon (Voss & Emmons, 1996), the diversity of rodents stands out among mammals, especially the genus *Proechimys* J. A. Allen, a terrestrial spiny rat of the family Echimyidae (Fabre et al., 2016). With a wide Neotropical distribution that extends from Central America to the Brazilian Cerrado, covering the entire Amazon region (Patton & Leite, 2015; Woods and Kilpatrick, 2005), nine of the 22 species in the genus are found in the Western Amazon (Fabre et al., 2016; Patton & Leite, 2015). Within Western Amazon, records of sympatry (i.e., overlapping geographical distributions) and syntopy (i.e., overlapping collection sites) have also been documented for up to five species of *Proechimys* (Patton et al., 2000). Thus, sympatry among species of *Proechimys* is both more common and occurs across more species compared with other mammal taxa that occur sympatrically (Patton & Leite, 2015), as in the Atlantic Forest echimyid genera *Phyllomys* (Leite, 2003) and *Trinomys* (Lara & Patton, 2000). This is an unusual pattern, as most co-generic Neotropical rodent species are predominantly allopatric and/or parapatric (Patton et al., 2015). Differences in their ecology, including different habitat preferences are factors frequently invoked to explain the overlapping distributional patterns of *Proechimys* species (Emmons, 1982; Matocq et al., 2000; Patton et al., 2000; Voss et al., 2001). However, the potential explanations for the disproportionate occurrence of sympatry (i.e., divergent ecologies) have yet to be examined with regards to their consequences for the divergence process among sympatric taxa.

Here, we address this knowledge gap by testing how the pattern of connectivity within two sympatric species, *P. simonsi* and *P. steerei*, may differ in relation to the type of forest each inhabits (non-flooded vs. flooded). *P. simonsi* primarily inhabits upland and relatively stable non-flooded forest (*terra-firme*) environments surrounded by flooded areas (Patton & Leite, 2015; Patton et al. 2000), whereas *P. steerei* occurs in the seasonal floodplain (*várzea*) and in higher areas within *várzeas* called *restingas* during seasonal floods or secondarily in disturbed *terra-firme* forests adjoining flooded areas (Matocq et al., 2000; Patton & Leite, 2015). Analyses of mitochondrial DNA (mtDNA) of individuals along the Juruá River suggested that gene flow differs between the species and is consistent with general expectations based on their forest type association (i.e. *P. simonsi* presented lower levels of gene flow than *P. steerei*; Matocq et al., 2000). However, there were some notable peculiarities. Specifically, mtDNA genetic structure is stronger among headwaters areas than lower river areas and is more pronounced in *P. steerei* than

P. simonsi (Matocq et al., 2000), leading the authors to speculate that landscape features of the Juruá River, and possibly aspects of the species natural history traits, contributed to the counter-intuitive differences in the geographical structure of mtDNA between these species.

In this study, we overcome the limitations of single locus analyses by collecting genomic data from individuals sampled from multiple rivers across western Amazon to avoid site (or river) specific affects. As such, our study applies a comparative framework to address the generality of predictions about the effects of forest-type on population connectivity using analytical techniques to test if gene flow corresponds to expectations about functional connectivity. Specifically, and taking into account the mtDNA findings (Matocq et al., 2000), we evaluate the support for the hypothesis that seasonal floodplain forests provide linear connectivity, facilitating gene flow among *P. steerei* individuals. However, considering the unexpectedly strong genetic structure of mtDNA in *P. steerei*, relative to *P. simonsi* (Matocq et al., 2000), we also test a suite of models that differ in the landscape features they contain to explore how particular factors may potentially restrict gene flow in each spiny rat taxa. As such, our study moves beyond relying solely on concordance, or the lack-there-of, among taxa as a typical means for evaluating hypotheses about the effects of species-specific traits on gene flow (see Papadopoulou & Knowles, 2016). We discuss the implications of our results for understanding how the divergence process may differ because of species-specific ecologies (i.e., inhabiting non-flooded or *terra-firme* forests vs. seasonal floodplain forests or *várzea* forests) of Amazonian taxa, as well as potential linkages with the high biodiversity of the Western Amazon biome.

2 | MATERIALS AND METHODS

2.1 | Genomic data

Genomic data were collected from 41 individuals of two co-distributed species of spiny rats: *P. simonsi* ($n = 21$), which inhabits non-flooded forests (*terra-firme*), and *P. steerei* ($n = 20$), which occupies seasonal floodplain forests (*várzea*) from the Western Amazon (Figure 1). Note that sampling in the Western Amazon, as well as from different countries, is inherently difficult, and even more so for focused collections of co-distributed species, which limits the attainable sample sizes. Nevertheless, our sampling covers most of the distribution of each species, including areas of sympatry (Figure 1), and we note that the small sample sizes are compensated to some extent by more than 10,000 single nucleotide polymorphisms (SNPs) sequenced with good coverage ($>30\times$) for each species (see Li et al., 2020; McLaughlin & Winker, 2020; Nazareno et al., 2017).

Individuals were collected by the Laboratório de Mamíferos (Universidade de São Paulo) following the American Society of Mammalogists guidelines (Sikes, 2016) and the Brazilian legislation (permission SISBIO n. 14419-3) and are housed at the Coleção de Mamíferos da Escola Superior de Agricultura "Luiz de Queiroz,

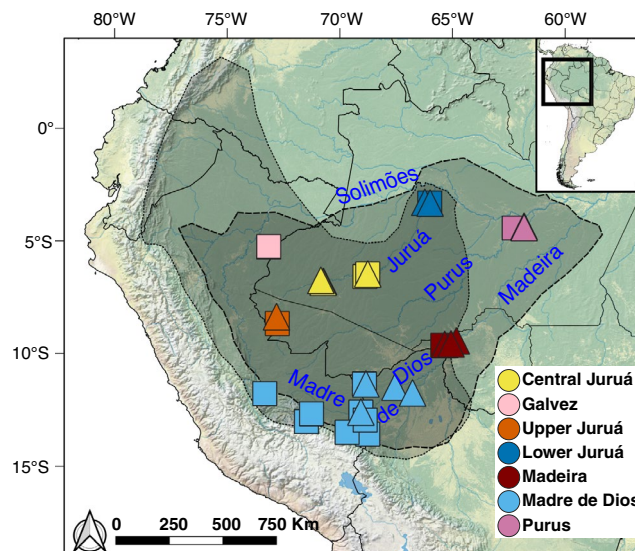


FIGURE 1 Geographical sampling of individuals for the genomic analyses of two sympatric *Proechimys* species from the Western Amazon, which differ in their habitat associations, with *P. simonsi* (shown in squares) in the non-flooded forests (*terra-firme*) and *P. steerei* (shown in triangles) in the seasonal floodplain forests (*várzea*). Each sample locality is colour-coded according to regional Amazonian rivers (see labels); gray areas represent known distribution range for these species, according to IUCN (www.iucnredlist.org) with pointed line for *P. simonsi* and dashed line for *P. steerei*; forested areas are shown in green and open areas in beige; map inset shows area of study.

Universidade de São Paulo, Piracicaba, São Paulo, Brazil (LMUSP). In addition, some samples were obtained from several scientific collections (see Table S1.1). Specimens were identified using morphological diagnostic traits (described in Patton & Leite, 2015). One double digest Restriction-site Associated DNA library was constructed following Peterson et al. (2012) protocol, generating 150 bp reads where one SNP was randomly selected per locus. More details about DNA extraction and library preparation, SNPs calling and filtering steps, see Appendix S2.1.

2.2 | Genetic structure and genetic diversity

Genetic structure in both species was evaluated using three different model-free approaches: (i) sparse non-Negative Matrix Factorization algorithms (sNMF) using "LEA" 3.4.0 (Frichot & Francois, 2014), (ii) Discriminant Analysis of Principal Component (DAPC) using "adegenet" 2.1.3 (Jombart & Ahmed, 2011), and (iii) Principal Component Analysis (PCA) using *dudi.pca* function in "adegenet" followed by Tracy-Widom tests for eigenvalues to select significant PCs (Patterson et al., 2006; Tracy & Widom, 1994). This set of analyses was chosen because of their complementarity. Specifically, PCA was conducted because it is the most common method in population genomics that allows reduction in the complexity of genomic data while preserving its covariance. However, given PCA's sensitivity



to sample size, missing data, number of loci, presence of clines and IBD (Puechmaile, 2016), we used more than one method to estimate genetic structure. In particular, as model-free approaches, DAPC and sNMF do not require population genetics assumptions (such as Hardy–Weinberg equilibrium, linkage disequilibrium and others), are computationally fast for genome-scale data, and do not require a priori definition of genetic groups. DAPC has proven effective even in complex population structures such as clines and hierarchical groups (Fenderson et al., 2020; Jombart et al., 2010). sNMF is similar to, but much faster than, STRUCTURE and ADMIXTURE for calculating ancestry coefficients (which DAPC and PCA do not) when estimating genetic clusters (GCs; Frichot et al., 2014).

Ten replicates of each K -value, for K of 1 to 10 potential GCs were run for the sNMF analyses with different regularization parameters values ($\alpha = 10, 100, 500, 1000, 2000, 4000$) following Dalapicola et al. (2021); the best K was estimated applying a minimum cross-entropy value (Frichot et al., 2014). For the DAPC, GCs (K) between 1 and 10 were tested using all PCs (100% of the variance); the Bayesian information criterion with the function *find.clusters* (Jombart et al., 2010; Miller et al., 2020) in “adegenet” was used to identify the best K (i.e., the one with the lowest value, as with the cross-entropy evaluation). The *xvalDapc* function in “adegenet” was used to select the best number of PCs to recover GCs (Miller et al., 2020).

The following genetic diversity metrics were calculated for each GC identified in each species: expected heterozygosity ($H_{E_{EXP}}$), nucleotide diversity (π), and inbreeding coefficient (F_{IS}), using the *Query* function available in “r2vcftools” 0.0.0.9 (Pope, 2020). Tests of significant differences in diversity values (among species and among GCs) were assessed with Tukey's test using *Query* function as well (see Prado et al., 2019). In addition, F_{ST} (SNP-based F -statistics) was used to measure genetic differentiation between GCs using the *gl.fst.pop* function in “dartR” 1.9.9.1 (Gruber & Georges, 2019) with 100 bootstraps. All analyses were performed in R 3.6.3 (R Core Team, 2020).

2.3 | Isolation by distance

The association between geographical and genetic distance was tested using Mantel tests (Mantel, 1967) based on (i) a geographical (Euclidean) distance matrix and (ii) a river network distance along the main river channels, using the *mantel.rtest* function with 10,000 permutations in “ade4” 1.7-16 (Dray & Dufour, 2007); details on environmental distances are given in Appendix S2.2. A genetic PCA-distance between individuals was calculated using *distance* function in “ecodist” 2.0.7 (Goslee & Urban, 2007) based on the Euclidean distance, retaining the number of PCs according to the Broke Stick Rule in *screenplot* function in “vegan” 2.5-7 (Oksanen et al., 2019); this metric was used because of its performance for IBD tests when sample sizes differ (Shirk et al., 2017) and it can be interpreted similarly to F_{ST} used in classical population-based Mantel tests. An analysis of covariance (ANCOVA) was performed to test if the slopes of the

Mantel tests differed between species. Robustness was examined by sequential elimination and replacement of each GC (i.e., verifying whether the correlation and significance values were dependent on any specific GC). Procrustes analyses were also used to test the similarity between taxa in the structuring of genetic variation, under the expectations of IBD; Knowles et al., 2016). The association tests between genetic variation and geography were quantified using the *protest* function in “vegan” package, see details for this methodology in Appendix S2.2. All analyses were performed in R 3.6.3.

2.4 | Isolation by resistance

Isolation by resistance analyses were conducted using maximum likelihood population effects (MLPE) mixed models (Clarke et al., 2002), and are more accurate for individual-based evaluation of functional connectivity on landscape (Shirk et al., 2018). Yang's relatedness coefficient (Yang et al., 2010), estimated in “r2vcftools” using the *Relatedness* function, was used as the response variable in the MLPE models because relatedness coefficients are more likely to represent recent gene flow (Balkenhol et al., 2015; Carvalho et al., 2019) and it is commonly applied for IBR tests based on individual-based genetic distances (Jaffé et al., 2019; Shirk et al., 2017). Mixed-effects regression models and least squares penalization with correlation structure were applied to account for the non-independence of genetic pairwise distances (Clarke et al., 2002), using the function *lme* in “nlme” 3.1-152 (Pinheiro et al., 2020) and the “corMLPE” 0.0.3 package (<https://github.com/nspop/corMLPE>). A random effect specifying pairwise distances of individuals from the same versus different GCs was used to control for population structure (Carvalho et al., 2019). Specifically, a full model containing all possible combinations among the predictors was fit to the genetic distances, considering five different resistance matrices as predictors: (i) the null model based on geographical (Euclidean) distance (which we expect will not be significant predictor/component for any IBR models if landscape features are important to functional connectivity), and four matrices representing environmental differences between non-flooded (*terra-firme*) forests and seasonal floodplain forests (*várzea*; Table S1.2): (ii) topographical distance; (iii) river network distance; (iv) habitat productivity distance: a resistance layer created from Species Distribution Models, in which temperature, precipitation, and potential evapotranspiration variables act as a habitat productivity proxy (Hawkins et al., 2003; Li et al., 2011, see Appendix S2.2; Figure S3.1), using presence-only data for both species (Table S1.3), and (v) habitat resistance based on a wetlands map for the Western Amazon (Gumbrecht et al., 2017), which represent movements within a landscape based on habitat preferences. Resolution for all raster variables was 30 arc-sec (~1 km² per cell), except for the wetlands raster that was resampled from the original spatial resolution (231 m²) using *resample* function from “raster” 3.4-10 (Hijmans & van Etten, 2015). All values in the resistance matrices were set to greater than zero to avoid errors in the model analyses (i.e., 0 values were replaced with 0.001). The

set of four variables incorporated into the competing models were chosen to capture aspects of the non-flooded (*terra-firme*) and seasonal floodplain (*várzea*) forests that differ, and hence, may result in dispersal differences in their respective inhabitants. For example, topographical distance was included because we expect that species will avoid movements between different forest types, and hence altitudes. Likewise, river network distance might be a critical predictor for the seasonal floodplain inhabitants (i.e., *P. steerei*), with *várzea* forests acting as a dispersal corridor along rivers. As with topographical distance, habitat productivity distance was included as a potential significant predictor of gene flow in both species because individuals are expected to disperse more commonly between areas with similar habitat productivity, given that productivity of seasonal floodplain forests (*várzea*) and non-flooded forest (*terra-firme*) are distinct (Junk & Piedade, 1993; Wittmann et al., 2010). Lastly, habitat resistance represents differential movements of the species based on habitat preferences and direct measures of habitat type. Specifically, the *P. steerei* the resistance matrix was built such that wetlands facilitated dispersal, whereas for *P. simonsi* the resistance matrix was built with wetlands posing greater resistance to gene flow (see Appendix 2.2; Table S1.4). If forest-types are important to functional connectivity in both species, this predictor will be significant in both species as well. Methodological details on the methodologies for calculating all resistance matrices are given in Appendix S2.2.

To avoid models containing highly correlated predictors, we eliminated models with highly correlated predictors (i.e., $r^2 > 0.6$; Figure S3.2; see also Castilla et al., 2020; Jaffé et al., 2019; Rutten et al., 2019) using the *dredge* function from “MuMIn” 1.43.17 (https://github.com/rojaff/dredge_mc). The retained models generated in this approach therefore contain all potential predictors, as opposed to an approach of a priori removal of correlated predictors with the highest variance inflation factor for identifying models without highly correlated predictors.

The best IBR models were identified by Akaike information criterion ($\Delta\text{AIC} < 2$; Harrison et al., 2018), with confidence intervals for coefficients of association estimated using restricted maximum likelihood (REML method; Silk et al., 2020). Spatial dependence of residuals from these models was evaluated by *acf* function in “stats” 3.6.3 (Castilla et al., 2020; Jaffé et al., 2019). Likelihood ratio tests were used to identify the best model among the nested models using the *anova.lme* function in the “nlme”, and the significance of predictors were estimated by chi-squared contingency table tests, using *drop1* function in “stats”. Conditional coefficients of determination (conditional R^2) for quantifying the variation explained by the model was calculated in “MuMIn” (Nakagawa & Schielzeth, 2013), and the semi partial R^2 that measures the proportion of variance explained by each predictor (Jaeger et al., 2017) were estimated with the *r2beta* function in the “r2glmm” 0.1.2 (Jaeger, 2017). The relative importance of each predictor in explaining functional connectivity was determined by summing AIC weights over all models with $\Delta\text{AIC} < 2$ using functions *get.models* and *importance* in R package “MuMIn”. All analyses were performed in R 3.6.3.

3 | RESULTS

After processing the raw sequence reads and applying stringent filtering criteria, 12,784 independent SNPs (i.e., one SNP randomly selected per locus) in *P. simonsi* ($n = 17$) and 13,971 independent SNPs in *P. steerei* ($n = 19$) were retained (Table S1.5). Note that fewer than the original 20 individuals per species were retained because of poor sequencing (i.e., sequences for the individual did not pass the quality control filters).

3.1 | Genetic structure and genetic diversity

Geographical structuring of genetic variation differs between the sympatric species, with stronger genetic structure apparent in *P. steerei* compared with *P. simonsi*. For example, *P. simonsi* individuals are scattered throughout the multivariate space (the first two PC explained 24.89% of the variance; Figure 2a); only samples from Lower Juruá River and Purus River are relatively isolated. For *P. steerei*, three well-defined GCs are clear in the multivariate space (the first two PCs explaining 46.1% of variation; Figure 2b). Only one significant PC in *P. simonsi*, versus three significant PCs in *P. steerei*, was recognized by the Tracy-Widom tests of eigenvalues (Table S1.6). These results are consistent with sNMF (Figure 2c) and DAPC analyses (Figure S3.3). Namely, there is not widespread mixed ancestry among individuals of *P. steerei*; only three individuals have an ancestry with more than 20% of their genetic makeup tracing to a different cluster (Figure 2c). This is corroborated by fairly high F_{ST} values among the GCs of *P. steerei* that range from 0.27 to 0.56 (see Table S1.7).

Genetic diversity is fairly similar between the species, although *P. steerei* shows higher average F_{IS} (Table S1.8), which is not surprising given the regional GCs detected in *P. steerei* (Figure 2b). In fact, there are greater differences in genetic diversity among the GCs within *P. steerei* than there are between the two species (Table S1.9; Figure S3.4).

3.2 | IBD models

Significant IBD was detected in both species using the Procrustes analyses and the Mantel tests with geographical distance, and in *P. steerei* (the seasonal floodplain species) the Mantel test based on the river network distance was also significant (Table S1.10). These results were generally robust to sequential exclusion of a GCs; in fact, the correlation coefficient increased in most of these permutations; the exception was a marginal non-significant Mantel test based on the river network distance when GC3 in *P. steerei* was removed (Table S1.10). ANCOVA did not show significant differences in the slope of genetic and geographical distances between the species ($F = 2.179$; $p = 0.071$; Figure S3.5a), indicating no significant differences between the species in attenuation of gene flow with geographical distance. However, the ANCOVA indicated significant

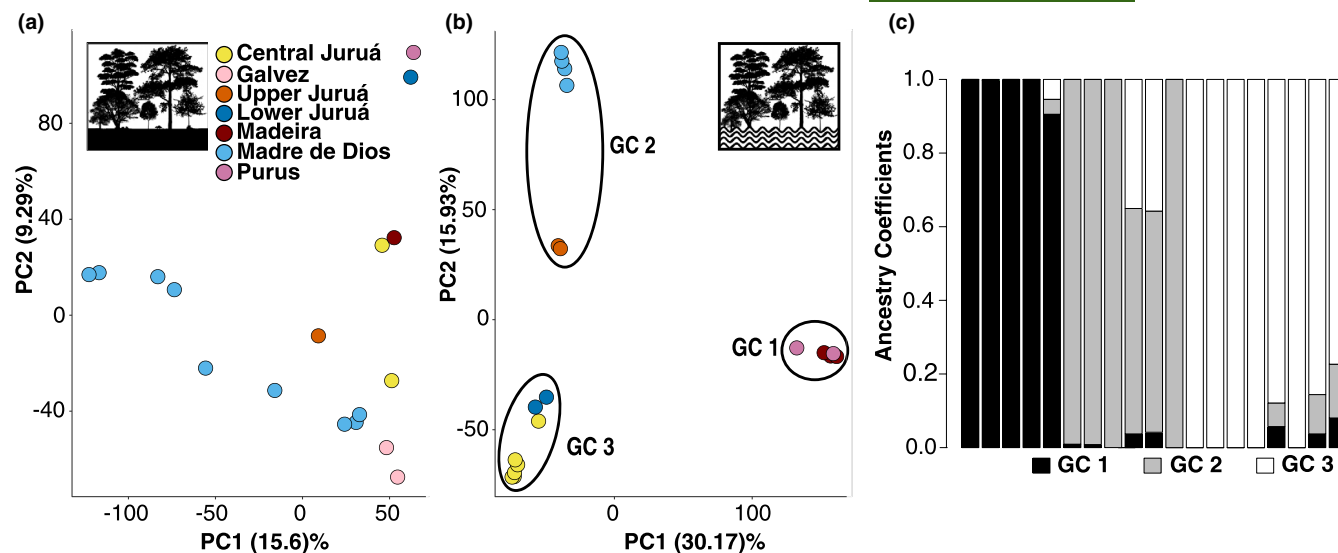


FIGURE 2 Principal components analysis of (a) *Proechimys simonsi* (non-flooded forests/terra-firme, as represented by the icon) and (b) *Proechimys steerei* (seasonal floodplain forests/várzea, as represented by the icon), with individuals colour-coded by the different river regions (see Figure 1 for distribution details). The three genetic clusters (GC) delineated in *P. steerei* were also identified by (c) the sparse non-Negative Matrix Factorization algorithms approach based on ancestry coefficients, whereas a single genetic cluster was identified for *P. simonsi* (see Figure S3.3)

differences between the species ($F = 9.2682$; $p < 0.001$; Figure S3.5c) for Mantel tests based on river network distance along the rivers, although the slopes for the individual GCs in *P. steerei* did not differ significantly (Figure S3.5b,d).

The strength of the association between genes and geography as measured by the Procrustes analyses is similar between the species ($t_0 = 0.799$ for *P. simonsi* and $t_0 = 0.765$ for *P. steerei*, $p < 0.001$; Table S1.10); permutation tests show that the Procrustes results are robust (i.e., they did not change significantly when a GC was excluded; Table S1.11). However, despite similar degrees of association between genes and geography of the species, the deviations from expectations under IDB in each species, and/or the degree of deviation (even for shared localities), are not the same (Figure 3). For example, individuals from the Lower Juruá are displaced in the geo-genetic map in both species, but individuals of *P. simonsi* are genetically more similar to those from the Purus River region to the east, whereas the individuals of *P. steerei* are genetically more similar to those from the more southern and western Central Juruá (Figure 3). Likewise, *P. simonsi* individuals from the Madeira are genetically more similar to those from the Central Juruá, rather than the Purus River region as in *P. steerei*. In general, individuals from the Upper Juruá and Madre de Dios in both species are positioned more similarly (Figure 3), irrespective of whether the Galvez individuals are included.

3.3 | IRB models based on different environmental predictors

The best IBR models in *P. simonsi* and *P. steerei* differ (Table 1; Tables S1.12–S1.13) and there is no strong spatial dependence of

residuals in the models for either species (Figure S3.6). In *P. simonsi*, four best fit models with $\Delta AIC < 2$ recover three important predictor variables for gene flow: habitat resistance, habitat productivity and river network distances (Figure 4a; Table 1; Table S1.14). With a lack of significant differences among the four models (based on likelihood-ratio tests), the simplest and best fit IBR model (i.e., the one with the fewest variables) is the one with habitat resistance distance (Figure 4b; Table S1.14), explaining around 34.9% of genetic variance (Conditional R^2 ; Table 1). Furthermore, the significance of predictors estimated by chi-squared also recovers only the habitat resistance distance as significant in each of the four models with $\Delta AIC < 2$ (Table 1), corroborating that among the five resistance predictors, habitat resistance is the only one significantly affecting functional connectivity in *P. simonsi* (i.e., higher habitat resistance distances are associated with lower relatedness of individuals, or conversely increasing the genetic distance; Figure 4c). In *P. steerei* the IBR analyses recover one best fit model (with $\Delta AIC < 2$) with two important predictors: habitat resistance and the river network distance (Figure 4d; Table 1; Table S1.14). For *P. steerei* only one model has a $\Delta AIC < 2$ and it contains two predictors that the chi-squared tests identify as significant: habitat resistance and river network distances (Figure 4e; Table S1.14), explaining 66.8% of the genetic variance (Conditional R^2 ; Table 1). The effects of the predictor variables on functional connectivity are similar, with larger distances associated with greater genetic distances (i.e., lower values of relatedness; Figure 4f,g).

For both species habitat resistance distance has a significant effect on connectivity. Although the relative importance of this variable differs between the best fit models for each species, where it is more relevant for *P. simonsi* than *P. steerei* (i.e., R^2_2 ; Table S1.15), the effect is similar when summed across models in each species (see

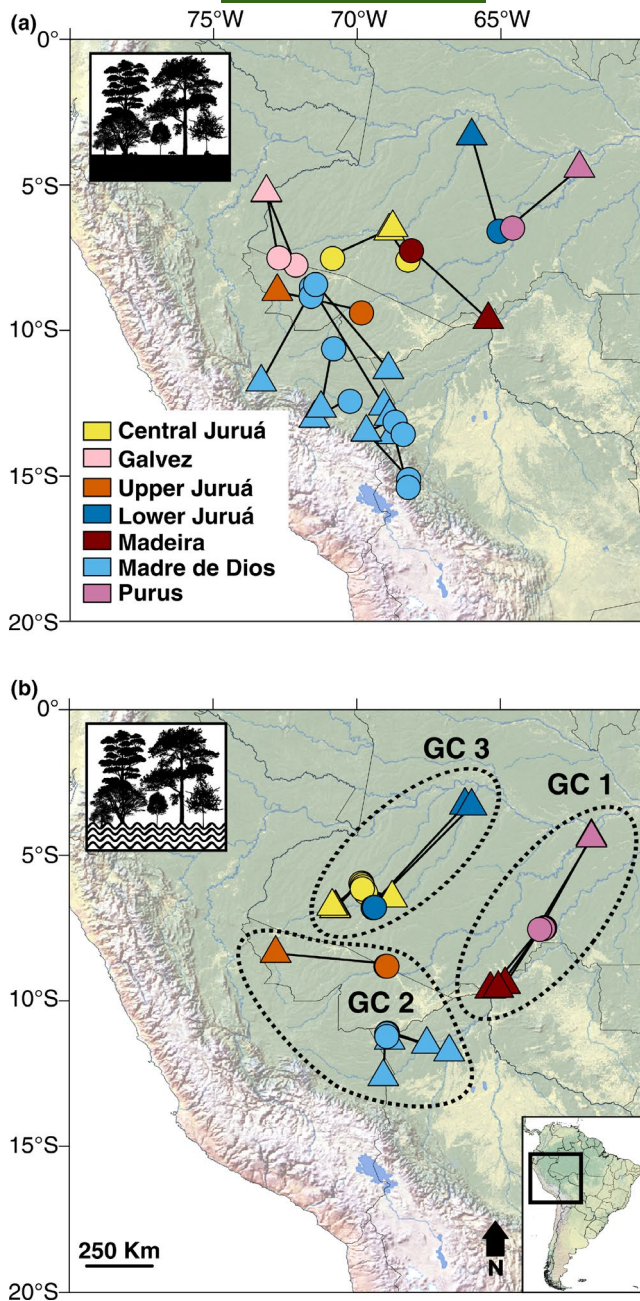


FIGURE 3 Procrustes analyses of (a) *Proechimys simonsi* and (b) *Proechimys steerei* with triangles representing the geographical sampling localities and circles the individuals in geo-genetic space (symbols are colour-coded by the different river regions). The length of the lines connecting the individuals to their respective sample localities (i.e., circles to the triangles) represent the degree of the deviation from the expectation in geo-genetic space under an isolation by distance model, with longer lines representing greater deviations. The three genetic clusters in *P. steerei* (see also Figure 2) are labelled and demarcated by dotted lines. Forested areas are shown in green on the map and open areas in beige; map inset shows area of study. Icons for the non-flooded forests/*terra-firme* in plot a, and the seasonal floodplain forests/*várzea* in plot b are shown. GC, genetic clusters

Figure 4). Topographical and Euclidean (Geographic) distances are not identified as having an important effect on functional connectivity in either species (see Figure 4; Tables S1.14–S1.15).

4 | DISCUSSION

The vast Amazon is well-recognized for its incredible species richness—what is less clear is the extent to which species divergence processes follow similar routes or not. For example, not only does the heterogeneity of a landscape differ depending on the specific forest type, but differences in ecological specialization of constituent taxa are also likely to impose different constraints on gene flow. Indeed, our findings suggest that population connectivity differs between two co-distributed spiny rat species. Moreover, genetic analyses do not support the hypothesis that the seasonal floodplain *várzea* forests favour higher connectivity among populations compared to the non-flooded *terra-firme* forests. Specifically, *P. steerei* from the *várzea* forests shows stronger genetic structure, higher heterozygosity and lower inbreeding than *P. simonsi* from the *terra-firme* forests (Figure 2; Table S1.8). Model comparisons identifying landscape features that affect functional connectivity (i.e., the dispersal capacity) in each species showed that different forest types can impose different constraints on gene flow. We discuss evidence from our statistical modelling of genetic variation that points to factors contributing to differences in the genetic structure of the ecologically divergent sympatric taxa. As with broad generalizations about Amazonian rivers acting as barriers (see Pirani et al., 2019; Smith et al., 2014), our findings suggest that such broad generalizations about gene flow in species based on their association with specific forest types may be limited as well.

4.1 | Gene flow across vast geographical areas

For species with distributions that cover vast areas, such as the Western Amazon, the expansive distances involved are themselves expected to influence gene flow. That is, populations separated by large geographical distances are expected to experience little gene flow compared with geographical proximate ones. Unsurprisingly, this basic expectation of IBD is met in both spiny rat species. Geographical distance also explains similar proportions of genetic variation between the sympatric species (i.e., the strength of the relationship between geographical and genetic distance is similar; see Figure 3; Figure S3.5; Table S1.10), and there is no significant difference in the attenuation of gene flow with Euclidean geographical distance between the species (Figure S3.5). Note that the similar fits to IBD models are unlikely to be an artefact of population size disparities (see Excoffier et al., 2009; but see He et al., 2013), suggesting that connectivity does not differ between the species. However, this similarity in the fits of IBD models might reflect the geographical scale of the study. At large spatial scales of broadly distributed species, the potential effects of habitat association on connectivity may be masked by the predominant effects of geographical distance (Lanier et al., 2015; Massatti & Knowles, 2014).

Despite their fit to IBD, the species show some pronounced differences in their respective deviations from IBD and geographical structuring of genetic variation (Figure 2). For example, the



TABLE 1 The best fit models ($\Delta AIC < 2$ with the best fit model in bold) for observed geographical distribution of relatedness coefficients in *Proechimys simonsi* (the non-flooded forest/terra-firme species) and in *Proechimys steerei*, (the seasonal floodplain forests/várzea species) using maximum-likelihood population effect

Models	Habitat	Productivity	River	logL	ρ	Conditional R^2 (CI 95%)	p-value
<i>P. simonsi</i>							
Habitat** + Productivity ^{ns}	-0.091 (0.015)	-0.020 (0.017)	—	58.698	0.048		0.149
Habitat**	-0.098 (0.013)	—	—	60.767	0.028	0.349 (0.233–0.467)	—
Habitat** + River ^{ns}	-0.095 (0.015)	—	-0.008 (0.015)	57.568	0.026		0.597
Habitat** + Productivity ^{ns} + River ^{ns}	-0.092 (0.016)	-0.021 (0.019)	0.003 (0.016)	55.577	0.050		0.345
<i>P. steerei</i>							
Habitat** + River**	-0.032 (0.006)	—	-0.111 (0.008)	163.332	0.469	0.668 (0.599–0.732)	—

Note: The contribution of each predictor variable (and standard error, in parentheses) calculated with restricted maximum likelihood (see Section 2.4 for details) are shown, as the significance of chi-squared contingency table tests each predictor in the models, with * for $p < 0.05$, ** for $p < 0.01$, ^{ns} if not significant. There was no statistically significant difference in the fit of the best models (in bold) for *P. simonsi* species and the other models using the likelihood-ratio tests in p-value column. Log-likelihoods (logL), and correlation coefficient, ρ , between relatedness coefficients and distances specified by each model. The conditional R^2 and its confidence intervals in parenthesis (a measure of variance explained by the entire model, including fixed and random effects) are also shown for the best fit models. Results for all models taking into account the correlations among the predictors variables (i.e., the uncorrelated models) are presented in Tables S1.12–S1.13.

deviations from IBD evident in geo-genetic space of the Procrustes analysis (Figure 3) in the seasonal floodplain species, *P. steerei*, follow the river channel in the GC 1 and GC3, while the deviations in GC2 is restricted to headwaters areas (Figure 3b). This result is consistent with the significant IBD Mantel tests based on river network distance (Table S1.10; Figure S3.5c), as with tests in other aquatic species (e.g., Murphy et al., 2018).

These results reinforce the impact of rivers on gene flow. However, in the Western Amazon (and at least for the taxa studied here) an argument can be made for a more nuanced perspective, and one that recognizes that when rivers act as conduits for gene flow, the lack of river connections can leave an indelible mark on genetic variation in floodplain várzea forest inhabitants (Figure 3). In our study, a factor limiting gene flow may be the restricted distribution of seasonal floodplain forest at headwaters (Hess et al., 2015; Salo et al., 1986). Specifically, if the lack of rivers routes for dispersal in *P. steerei* results in regional structuring of genetic variation (Figure 3b), but only in this floodplain várzea forest taxon that utilizes rivers for dispersal, then the absence of region genetic structuring in *P. simonsi* (Figure 3a) is less surprising. However, if rivers were acting as barriers (e.g., Ribas et al., 2012), the difference in regional structuring would remain an unresolved conundrum because it seems very unlikely that *P. simonsi*'s association with non-flooded terra-firme forest would make it less prone to be influenced by historical barriers associated with rivers.

On the surface, this perspective might seem to be contradictory to existing literature. For example, we note that the pronounced regional structuring of genetic variation detected in *P. steerei* is similar to expectations based on the effects of historical barriers in other Amazonian regions (e.g., Da Silva & Patton, 1998; Fernandes et al., 2013). The GCs detected in *P. steerei* (Figure 2), and specifically the delineation of GC 2 and 3 (GC2 and GC3 in Figure 3) indeed coincide with the Iquitos structural arch, a geomorphological feature that demarcates geological units associated with the origin of river basins and subbasins in the Amazon (Albert et al., 2018). However, this correspondence between genetic divergence patterns with the formation of geographical barriers (e.g., the Iquitos Arch, which blocked the transport of Andean-derived sediments from the Western Amazon during the Pliocene; van Soelen et al., 2017), which has been identified in other phylogeographical studies of vertebrates in the region (e.g., Da Silva & Patton, 1998; Gascon et al., 2000; Patton et al., 2000). Our work highlights that this correspondence should not be reflexively viewed as evidence of the river barrier hypothesis, and that it is also entirely consistent with the hypothesis of a lack of river connections, especially in species in which rivers serve as routes of dispersal (i.e., in floodplain várzea forest inhabitants, but not those from the terra-firme forests).

As discussed below, with 46.7% in *P. simonsi* and 73.2% in *P. steerei* of genetic variance explained by the best fit IBR models (i.e., upper bound for conditional R^2 ; Table 1), a considerable amount of variation remains unexplained by the IBR models. This indicates that there are factors that were not explicitly tested in our study. It is possible that the association between gene and geography on a regional scale relates to variation in the historical stability of the

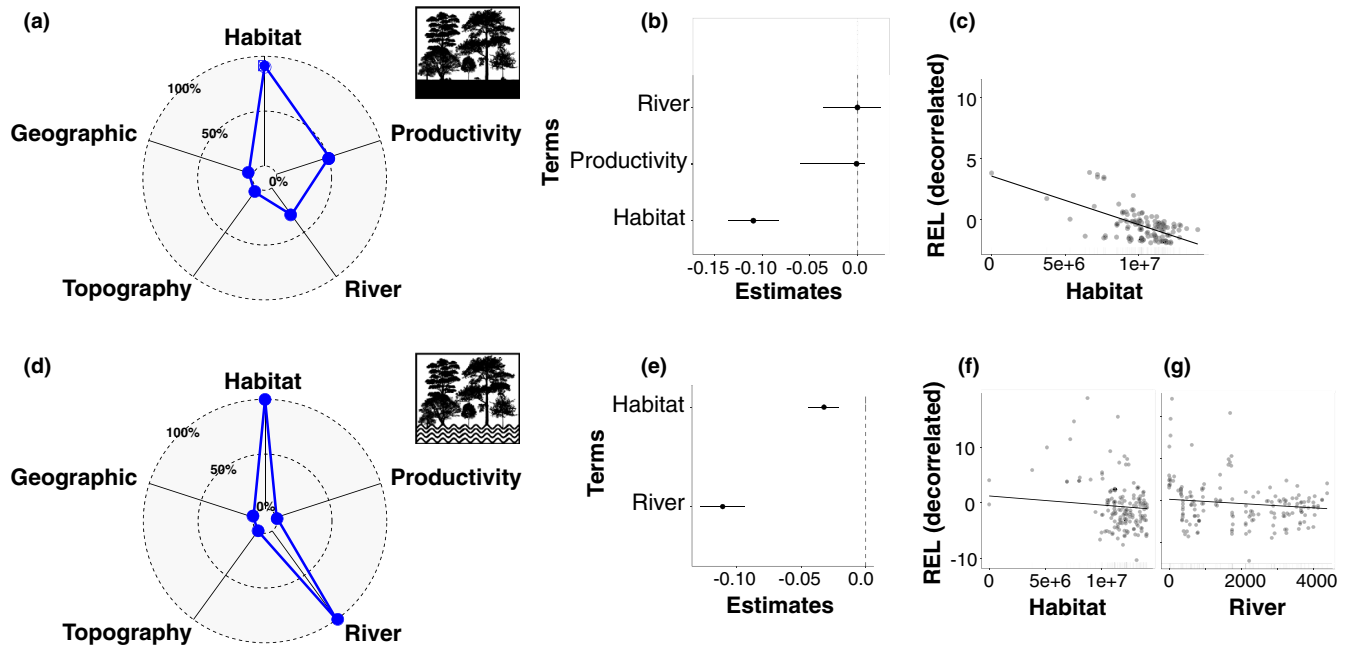


FIGURE 4 Relative importance of each environmental predictor variable in explaining functional connectivity for the best fit models ($\Delta AIC < 2$) among the maximum-likelihood population effect (MLPE) regression models for (a) *Proechimys simonsi* and (d) *Proechimys steerei* are shown in blue, where the relative importance of a variable increases towards the outer edge of the circle (circular dashed lines represent 0%, 50% and 100% of importance from the innermost to the outermost line, respectively). Importance of values are based on the sum of AIC weights over all models that include the predictor variable (for details see Table S1.15). Also shown are the icons for the non-flooded forests/*terra-firme* in plot a, and the seasonal floodplain forests/*várzea* in plot d. Coefficient plots for best-fitting models ($\Delta AIC \leq 2$) for (b) *P. simonsi* and (e) *P. steerei* (see Table S1.14 for details). Points represent model-averaged regression coefficients and horizontal lines the 95% confidence intervals. Variables that do not touch the vertical dashed line (0.0) are considered significant for models similar to likelihood ratio tests. Isolation-by-resistance effects of significant variables in (c) *P. simonsi* and (f–g) *P. steerei*. Plots indicate relationship between the relatedness coefficient (REL) and habitat resistance in (c) *P. simonsi* and in (f) *P. steerei* and river distance in (g) *P. steerei*. Relatedness values are decorrelated for the MLPE correlation structure

South American wetlands (Prado et al., 2019). However, studies have shown little variation in precipitation (Cheng et al., 2013), temperature (Colinvaux et al., 1996) and vegetation (Häggi et al., 2017) since the last glacial maximum (Pleistocene) in the Western Amazon. Previous mtDNA genetic studies have also suggested stable population sizes in both *P. steerei* and *P. simonsi* in the Western Amazon since the last glacial maximum (Lessa et al., 2003; Matocq et al., 2000). So, it seems unlikely stability is responsible for the differences in regional structuring of genetic variation between the spiny rat species. Dissecting the association between genes and geography further, shows that there are also some differences between the species in the structure of genetic variation locally (for example, individuals from the Lower Juruá and Purus in both species; Figure 3). However, additional taxa are needed to evaluate the extent to which there might be a deterministic explanation, and to rule out the possibility that some of the differences reflect historical contingency.

4.2 | Forest association and functional connectivity in spiny rats

Tests of the suite of models for explaining functional connectivity in *P. steerei* and *P. simonsi* as a function of various ecological and

environmental predictor variables share some common features. All variables representing differences between forest types (habitat resistance, habitat productivity and river network distance) were detected as important influences on functional connectivity in at least one of the species (Figure 4; for details see Table S1.15); the primary exception is topographical distance, which may simply reflect the relative lack of variation in altitude in Western Amazon at the scale of our study (Vormisto et al., 2004). Moreover, in neither species is the effect of geographical distance (while significant in the Mantel tests) a component of the best fit IBR models that incorporate environmental variables (Table 1), nor does it have a significant contribution when summing across IBR models (Figure 4). This difference in the effect of geographical distance is not unexpected because resistance variables that co-vary with geographical distance may lead to spurious inferences (Dormann et al., 2013; Figure S3.2), and the MLPE mixed models account for the non-independence of genetic pairwise distances variables, unlike Mantel tests, which can inflate r^2 values (Clarke et al., 2002; Harrison et al. 2018; Shirk et al., 2018; Silk et al. 2020).

With respect to the best fit or most probable models in predicting genetic variation, there was one key variable in common to both species: habitat resistance (river network distances were present only in *P. steerei*; Table 1). This variable corroborates the



potential links to mechanistic or functional predictors of gene flow for taxa with different forest associations; the variable habitat resistance also explains more than three times the genetic variance in *P. simonsi* species, the non-flooded (*terra-firme*) species, than in *P. steerei* (R^2_{E} in Table S1.15). Habitat resistance and river network capture different aspects of the ease of dispersal (i.e., resistance), across the landscape (see Appendix S2.2 for details on quantifying resistance for these two variables), and thus presumably gene flow across the landscape. Specifically, habitat resistance distance captures the relative likelihood of gene flow between sampled sites as a function of the distribution of wetland versus non-wetland habitats between those sites (i.e., traversing wetlands will not impose much resistance to gene flow for *P. steerei*, which inhabits the seasonal floodplain *várzea* forests, but wetlands would impose high resistance to gene flow in *P. simonsi*, which inhabits non-flooded *terra-firme* forest). In a similar fashion, connectivity via rivers is expected for *P. steerei*, which inhabits the seasonal floodplain forests distributed along rivers. If gene flow among sampled sites of *P. steerei* is primarily via river routes (as supported by Mantel tests—Table S1.10 and IBR models—Figure 4), this could explain the small but significant contribution of the habitat resistance distance variable to functional connectivity in the species (Table S1.15). Furthermore, during the annual inundations, the seasonal floodplain species *P. steerei* can occupy higher areas in the *várzea* forests or can move to adjacent non-flooded *terra-firme* areas, while *P. simonsi* the *terra-firme* species remains in its habitat given lack of evidence for movement across different forest types (see Matocq et al., 2000; Patton & Leite, 2015). As such, the relative importance of different environmental variables, especially habitat resistance, in predicting function connectivity in *P. steerei* versus *P. simonsi* also suggests that species-specific traits, in this case specific forest associations, can determine functional connectivity across populations. That is, dispersal in spiny rat taxa, and specifically those associated with floodplain *várzea* forest (but not *terra-firme* forests) maybe facilitated by rivers.

Studies of additional taxa, especially other mammal species, will provide the context to discern whether the spiny rat taxa studied here are atypical, or that differences in the traits of mammals compared with birds and plants underlie differing support for hypothesized connectivity based on forest-type (Papadopoulou & Knowles, 2016). We also recognize that our results are in contrast with some aspects of mtDNA study of *P. steerei* and *P. simonsi* from the Juruá River (see Matocq et al., 2000). Differences in the geographical scale of our study, without doubt, contribute to the differences observed between genomic variation and mtDNA variation (i.e., our results are based on analyses of individuals across the species' ranges, which span multiple rivers).

Our statistical modelling and fit of the data to different models points to specific environmental and habitat differences between the ecological divergent spiny rat species that may contribute to differences in the genetic structure of these sympatric taxa. Specifically, wetland habitats inhibit and promote the functional connectivity in *P. simonsi* and *P. steerei*, respectively, although large distances along

the rivers can prevent gene flow in both taxa (i.e., gene flow attenuates with geographical distance). Despite the significance of environmental and habitat variables associated with floodplain *várzea* forests versus non-flooded *terra-firme* forest that explain the genetic variation in the two taxa, it is notable that connectivity is not higher in the floodplain *várzea* forest species *P. steerei* as posited by traditional hypotheses and supported in bird species (Aleixo, 2006; Cadena et al., 2011; Harvey et al., 2017; but see Thom et al., 2020) and in some plants (Godoy et al., 1999). Furthermore, a significant proportion of unexplained genetic variance in the spiny rats indicates that differences in connectivity between the taxa cannot be understood through the lens of a single dimension of Amazonian heterogeneity—that is, forest type. In fact, we develop the argument that the presence of regional geographical structuring in *P. steerei* that is absent in *P. simonsi*, suggests that the lack of river connections, as well as other unidentified factors, play an important role in restricting gene flow.

Irrespective of the combination of factors that best explains genetic variation in the spiny rats, *P. steerei* or *P. simonsi*, our study does raise questions about the spectre of generalizable predictions about connectivity in species associated with seasonal floodplain *várzea* forests versus non-flooded *terra-firme* forest. As with other generalities that have been put forth for processes of divergence in the Amazon (e.g., the proposition that the major Amazon rivers act as barriers; see Pirani et al., 2019), generalized expectations for the divergence process in species that inhabit different forest types may similarly be limited in their explanatory power. Given the incredible biodiversity that characterizes the Amazon, perhaps it should not be expected that this diversity will follow a common set of predictions for genetic structure, or conversely connectivity, or surprising when it does not.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Genetic data and Supporting Information are available in Dryad: <https://doi.org/10.5061/dryad.4qrfj6qbf>. All R scripts are available at: https://github.com/jdalapicolla/LanGen_pipeline_version2; https://github.com/jdalapicolla/IBD_models.R; <https://github.com/jdalapicolla/MLPE.R>.

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BIOSKETCH

The authors share an interest in the study of processes that structure the genetic variation among taxa and across geography.

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SUPPORTING INFORMATION

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