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

Running Title: **Testing connectivity hypotheses**

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SIGNIFICANCE STATEMENT

We investigate how habitat heterogeneity affects divergence processes and compare these processes between sympatric rodent species across the vast geographic area of the Western Amazon. This study appeals to the broad readership given the themes of landscape genomics analyses in relation to habitat heterogeneity, as well as tests of how differences in habitat associations in little-studied area employing taxa of the Amazon's seasonal floodplain forests (*várzea*) and non-flooded forests (*terra-firme*).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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 analyze about 13,000 SNPs 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 (MLPE) 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 IBD 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 conclusions: 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 modeling 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 geographic 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 behavioral traits (e.g., mating patterns, migration capacity, habitat use), which may create resistance or facilitate organisms 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 (Salo et al., 1986; Matocq et al., 2000) 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 & 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 geographic 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 versus flooded). *P. simonsi* primarily inhabits upland and relatively stable non-flooded forest (*terra-firme*) environments surrounded by flooded areas (Patton et al. 2000; Patton & Leite, 2015), 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 geographic 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 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 versus seasonal floodplain forests or *várzea* forests) of Amazonian taxa, as well as potential linkages with the high biodiversity of the Western Amazon biome.

2. MATERIAL AND METHODS

2.1. Genomic data

Genomic data was 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 (Fig. 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 (Fig. 1), and we note that the small sample sizes are compensated to some extent by more than 10,000 SNPs sequenced with good coverage (> 30X) 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 et al., 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, Universidade de São Paulo, Piracicaba, São Paulo, Brazil (LMUSP). In addition, some samples were obtained from several scientific collections (see Appendix S1 in Supporting Information: Table S1.1). Specimens were identified using morphologic diagnostic traits (described in Patton & Leite, 2015). One double digest Restriction-site Associated DNA (ddRAD) 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 in Supporting Information.

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" v3.4.0 (Frichot & Francois, 2014), *ii*) Discriminant Analysis of Principal Component (DAPC) using "adegenet" v2.1.3 (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, as the most common method in population genomics that allows reduction of the complexity of genomic data while preserving its covariance, PCA were conducted. However, given PCA's sensitivity to sample size, missing data, number of loci, presence of clines, and isolation by distance (Puechmaille, 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 HWE, 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 (Frichot et al., 2014).

Ten replicates of each *K*-value, for *K* of 1 to 10 potential genetic clusters were run for the sNMF analyses with different regularization parameters values (α = 10, 100, 500, 1000, 2000, 4000) following Dalapicolla et al. (2021); the best *K* was estimated applying a minimum cross-entropy value (Frichot et al., 2014). For the DAPC, genetic clusters (*K*) between 1 and 10 were tested using all PCs (100% of the variance); the Bayesian Information Criterion (BIC) 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 genetic clusters (Miller et al., 2020).

The following genetic diversity metrics were calculated for each genetic cluster identified in each species: expected heterozygosity (HE_{EXP}), nucleotide diversity (π), and inbreeding coefficient (F_{IS}), using the *Query* function available in "r2vcftools" v0.0.0.9 (Pope, 2020). Tests of significant differences in diversity values (among species and among genetic clusters) 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 genetic clusters using the *gl.fst.pop* function in "dartR" v1.9.9.1 (Gruber & Georges, 2019) with 100 bootstraps. All analyses were performed in R 3.6.3 (R Core Team, 2020).

2.3. Isolation by distance (IBD)

The association between geographic and genetic distance was tested using Mantel tests (Mantel, 1967) based on *i*) a geographic (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" v1.7-16 (Dray & Dufour, 2007); details on environmental distances are given in Appendix 2.2. A genetic PCA-distance between individuals was calculated using *distance* function in "ecodist" v2.0.7 (Goslee & Urban, 2007) based on the Euclidean distance, retaining the number of PCs according to the Broke Stick Rule in *screenplot* function in "vegan" v2.5-7 (Oksanen et al., 2019); this metric was used because of its performance for IDB 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 genetic cluster (i.e., verifying whether the correlation and significance values were dependent on any specific genetic cluster). Procrustes analyses were also used to test the similarity between taxa in the structuring of genetic variation, under the expectations of isolation by distance (IBD) (Knowles et al., 2016). The associations tests between genetic variation and geography was 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 (IBR)

Isolation by Resistance (IBR) 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" v3.1-152 (Pinheiro et al., 2020) and the "corMLPE" v0.0.3 package (https://github.com/nspope/corMLPE). A random effect specifying pairwise distances of individuals from the same versus different genetic clusters 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 geographic (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)* topographic distance; *iii)* river network distance; *iv*) habitat productivity distance (a resistance layer created from species distribution models, SDM, in which temperature, precipitation, and potential evapotranspiration (PET) variables act as a habitat productivity proxy (Hawkins et al., 2003; Li et al., 2011, see Appendix S2.2 and see Appendix S3: Fig 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 (Gumbricht et al., 2017), which represent movements within a landscape based on habitat preferences. Resolution for all raster variables was 30 arc-sec (~1Km² per cell), except for the wetlands raster that was resampled from the original spatial resolution (231 m²) using *resample* function from "raster" v3.4-10 (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 4 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, topographic distance was included because we expect 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 topographic 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 and 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., $r^2 > 0.6$; Fig. S3.2; see also Castilla et al., 2020; Jaffé et al., 2019; Rutten et al., 2019) using the *dredge* function from "MuMIn" v1.43.17 (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 ($\Delta AIC < 2$) were identified (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" v3.6.3 (Castilla et al., 2020; Jaffé et al., 2019). Likelihood ratio tests (LRT) 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_{Σ}^2 that measures the proportion of variance explained by each predictor (Jaeger et al., 2017) were estimated with the *r2beta* function in the "r2glmm" v0.1.2 (Jaeger, 2017). The relative importance of each predictor in explaining functional connectivity was determined by summing AIC weights over all models with $\Delta AIC < 2$ using functions *get.models* and *importance* in R package "MuMIn". All analyses were performed in R 3.6.3.

277
278
279 **3. RESULTS**
280 After processing the raw sequence reads and applying stringent filtering criteria, 12,784 independent SNPs (i.e., one SNP
281 randomly selected per locus) in *P. simonsi* (n = 17) and 13,971 independent SNPs in *P. steerei* (n = 19) were retained (Table
282 S1.5). Note that fewer than the original 20 individuals per species were retained because of poor sequencing (i.e., sequences
283 for the individual did not pass quality control filters).
284
285 **3.1. Genetic structure and genetic diversity**
286 Geographic structuring of genetic variation differs between the sympatric species, with stronger genetic structure apparent
287 in *P. steerei* compared with *P. simonsi*. For example, *P. simonsi* individuals are scattered throughout the multivariate space
288 (the first two PC explained 24.89% of the variance; Fig. 2a); only samples from Lower Juruá River and Purus River are
289 relatively isolated. For *P. steerei,* three well-defined genetic clusters are clear in the multivariate space (the first two PCs
290 explaining 46.1% of variation; Fig. 2b). Only one significant PC in *P. simonsi*, versus three significant PCs in *P. steerei*,
291 was recognized by the Tracy-Widom tests of eigenvalues (Table S1.6). These results are consistent with sNMF (Fig. 2c) and
292 DAPC analyses (Fig. S3.3). Namely, there is not widespread mixed ancestry among individuals of *P. steerei*; only three
293 individuals have an ancestry with more than 20% of their genetic makeup tracing to a different cluster (Fig. 2c). This is
294 corroborated by fairly high F_{ST}-values among the genetic clusters of *P. steerei* that range from 0.27 to 0.56 (see Table S1.7).
295 Genetic diversity is fairly similar between the species, although *P. steerei* shows higher average F_{IS} (Table S1.8),
296 which is not surprising given the regional genetic clusters detected in *P. steerei* (Fig. 2b). In fact, there are greater
297 differences in genetic diversity among the genetic clusters within *P. steerei* than there are between the two species (Table
298 S1.9; Fig. S3.4).
299
300 **3.2. Isolation by Distance models**
301 Significant isolation by distance (IBD) was detected in both species using the Procrustes analyses and the Mantel tests with
302 geographic distance, and in *P. steerei* (the seasonal floodplain species) the Mantel test based on the river network distance
303 was also significant (Table S1.10). These results were generally robust to sequential exclusion of a genetic clusters (GCs)
304 (in fact, the correlation coefficient increased in most of these permutations); the exception was a marginal non-significant
305 Mantel tests based on the river network distance when GC3 in *P. steerei* was removed (Table S1.10). ANCOVA did not
306 show significant differences in the slope of genetic and geographic distances between the species (F = 2.179; p-value =
307 0.071) (Fig. S3.5a), indicating no significant differences between the species in attenuation of gene flow with geographic
308 distance. However, the ANCOVA indicated significant differences between the species (F = 9.2682; p-value < 0.001; Fig.
309 S3.5c) for Mantel tests based on river network distance along the rivers, although the slopes for the individual genetic
310 clusters in *P. steerei* did not differ significantly (Fig. S3.5b, d).
311 The strength of the association between genes and geography as measured by the Procrustes analyses is similar
312 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
313 that the Procrustes results are robust (i.e., they did not change significantly when a genetic cluster was excluded; Table
314 S1.11). However, despite similar degrees of association between genes and geography of the species, the deviations from
315 expectations under IDB in each species, and/or the degree of deviation (even for shared localities), are not the same (Fig. 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 (Fig. 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 (Fig. 3), irrespective of whether the Galvez individuals are included.

3.2. Isolation by Resistance models based on different environmental predictors

The best IBR models in *P. simonsi* and *P. steerei* differ (Table 1; Table S1.12-S1.13) and there is no strong spatial dependence of residuals in the models for either species (Fig. 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 (Fig. 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 (Fig. 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 is associated with lower relatedness of individuals, or conversely increasing the genetic distance; Fig. 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 (Fig. 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 (Fig. 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 is similar, with larger distances associated with greater genetic distances (i.e., lower values of relatedness; Fig. 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_{Σ}^2; Table S1.15), the effect is similar when summed across models in each species (see Fig. 4). Topographic and Euclidean (Geographic) distances are not identified as having an important effect on functional connectivity in either species (see Fig 4; Table 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 favor 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*

355 from the *terra-firme* forests (Fig. 2; Table S1.8). Model comparisons identifying landscape features that affect functional
356 connectivity (i.e., the dispersal capacity) in each species showed that different forest types can impose different constraints
357 on gene flow. We discuss evidence from our statistical modeling of genetic variation that points to factors contributing to
358 differences in the genetic structure of the ecologically divergent sympatric taxa. As with broad generalizations about
359 Amazonian rivers acting as barriers (see Pirani et al., 2019; Smith et al., 2014), our findings suggest that such broad
360 generalizations about gene flow in species based on their association with specific forest types may be limited as well.
361
362 **4.1. Gene flow across vast geographic areas**
363 For species with distributions that cover vast areas, such as the Western Amazon, the expansive distances
364 involved are themselves expected to influence gene flow. That is, populations separated by large geographic distances are
365 expected to experience little gene flow compared with geographic proximate ones. Unsurprisingly, this basic expectation of
366 isolation-by-distance (IBD) is met in both spiny rate species. Geographic distance also explains similar proportions of
367 genetic variation between the sympatric species (i.e., the strength of the relationship between geographic and genetic
368 distance is similar; see Fig. 3, Fig. S3.5, and Table S1.10), and there is no significant difference in the attenuation of gene
369 flow with Euclidean geographic distance between the species (Fig. S3.5). Note that the similar fits to IBD models are
370 unlikely to be an artifact of population size disparities (see Excoffier et al., 2009; but see He et al., 2013), suggesting that
371 connectivity does not differ between the species. However, this similarity in the fits of IBD models might reflect the
372 geographical scale of the study. At large spatial scales of broadly distributed species, the potential effects of habitat
373 association on connectivity may be masked by the predominant effects of geographic distance (Lanier et al., 2015; Massatti
374 & Knowles, 2014).
375 Despite their fit to IBD, the species show some pronounced differences in their respective deviations from IBD
376 and geographic structuring of genetic variation (Fig. 2). For example, the deviations from IBD evident in geo-genetic space
377 of the Procrustes analysis (Fig. 3) in the seasonal floodplain species, *P. steerei*, follow the river channel in the genetic
378 cluster (GC) 1 and GC3, while the deviations in GC2 is restricted to headwaters areas (Fig. 3b). This result is consistent
379 with the significant IBD Mantel tests based on river network distance (Table S1.10; Fig. S3.5c), as with tests in other
380 aquatic species (e.g., Murphy et al., 2018).
381 These results reinforce the impact of rivers on gene flow. However, in the Western Amazon (and at least for the
382 taxa studied here) an argument can be made for a more nuanced perspective, and one that recognizes that when rivers act as
383 conduits for gene flow, the lack of river connections can leave an indelible mark on genetic variation in floodplain *várzea*
384 forest inhabitants (Fig. 3). In our study, a factor limiting gene flow may be the restricted distribution of seasonal floodplain
385 forest at headwaters (Salo et al., 1986; Hess et al., 2015). Specifically, if the lack of rivers routes for dispersal in *P. steerei*
386 results in regional structuring of genetic variation (Fig. 3b), but only in this floodplain *várzea* forest taxon that utilizes rivers
387 for dispersal, then the absence of region genetic structuring in *P. simonsi* (Fig. 3a) is less surprising. However, if rivers were
388 acting as barriers (e.g., Ribas et al., 2012), the difference in regional structuring would remain an unresolved conundrum
389 because it seems very unlikely that *P. simonsi'*s association with non-flooded *terra-firme* forest would make it less prone to
390 be influenced by historical barriers associated with rivers.
391 On the surface, this perspective might seem to be contradictory with existing literature. For example, we note that
392 the pronounced regional structuring of genetic variation detected in *P. steerei* is similar to expectations based on the effects
393 of historical barriers in other Amazonian regions (e.g., Da Silva & Patton, 1998 Fernandes et al., 2013). The genetic clusters

394 detected in *P. steerei* (Fig. 2), and specifically the delineation of genetic cluster 2 and 3 (GC2 and GC3 in Fig. 3) indeed
395 coincide with the Iquitos structural arch, a geomorphological feature that demarcates geological units associated with the
396 origin of river basins and subbasins in the Amazon (Albert et al., 2018). However, this correspondence between genetic
397 divergence patterns with the formation of geographic barriers (e.g., the Iquitos Arch, which blocked the transport of
398 Andean-derived sediments from the Western Amazon during the Pliocene; van Soelen et al., 2017), which has been
399 identified in other phylogeographic studies of vertebrates in the region (e.g., Da Silva & Patton, 1998; Gascon et al., 2000;
400 Patton et al., 2000). Our work highlights that this correspondence should not be reflexively viewed as evidence of the river
401 barrier hypothesis, and that it is also entirely consistent with the hypothesis of a lack of river connections, especially in
402 species in which rivers serve as routes of dispersal (i.e., in floodplain *várzea* forest inhabitants, but not those from the *terra-*
403 *firme* forests).
404 As discussed below, with 46.7% in *P. simonsi* and 59.9% in *P. steerei* of genetic variance explained by the best
405 fit IBR models (i.e., upper bound for conditional R^2; Table 1), a considerable amount of variation remains unexplained by
406 the IBR models. This indicates that there are factors that were not explicitly tested in our study. It is possible that the
407 association between gene and geography on a regional scale relates to variation in the historical stability of the South
408 American wetlands (Prado et al., 2019). However, studies have shown little variation in precipitation (Cheng et al., 2013),
409 temperature (Colinvaux et al., 1996), and vegetation (Häggi et al., 2017) since the last glacial maximum (Pleistocene) in the
410 Western Amazon. Previous mtDNA genetic studies have also suggested stable population sizes in both *P. steerei* and *P.*
411 *simonsi* in the Western Amazon since the last glacial maximum (Lessa et al., 2003; Matocq et al., 2000). So, it seems
412 unlikely stability is responsible for the differences in regional structuring of genetic variation between the spiny rat species.
413 Dissecting the association between genes and geography further, shows that there are also some differences between the
414 species in the structure of genetic variation locally (for example, individuals from the Lower Juruá and Purus in both
415 species; Fig. 3). However, additional taxa are needed to evaluate the extent to which there might be a deterministic
416 explanation, and to rule out the possibility that some of the differences reflect historical contingency.
417
418 **4.2 Forest association and functional connectivity in spiny rats**
419 Tests of the suite of models for explaining functional connectivity in *P. steerei* and *P. simonsi* as a function of
420 various ecological and environmental predictor variables share some common features. All variables representing
421 differences between forest types (habitat resistance, habitat productivity, and river network distance) were detected as
422 important influence on functional connectivity in at least one of the species (Fig 4; for details see Table S1.15); the primary
423 exception is topographic distance, which may simply reflect the relative lack of variation in altitude in Western Amazon at
424 the scale of our study (Vormisto et al., 2004). Moreover, in neither species is the effect of geographic distance (while
425 significant in the Mantel tests) a component of the best fit IBR models that incorporate environmental variables (Table 1),
426 nor does it have a significant contribution when summing across IBR models (Fig. 4). This difference in the effect of
427 geographic distance is not unexpected because resistance variables that co-vary with geographic distance may led to
428 spurious inferences (Dormann et al., 2013; Fig. S3.2), and the MLPE mixed models account for the non-independence of
429 genetic pairwise distances variables, unlike Mantel tests, which can inflate r^2 values (Clark et al., 2002; Harrison et al. 2018;
430 Shirk et al., 2018; Silk et al. 2020).
431 With respect to the best fit or most probable models in predicting genetic variation, there was one key variable in
432 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_{Σ}^2 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 – Fig. 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 geographic scale of our study no doubt contributes 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 modeling 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 geographic 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 geographic 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 doesn't.

Tables

Table 1: The best fit models (ΔAIC < 2 with the best fit model in bold) for observed geographic distribution of relatedness coefficients in *P. simonsi* (the non-flooded forest/*terra-firme* species) and in *P. steerei*, (the seasonal floodplain forests/*várzea* species) using MLPE. The contribution of each predictor variable (and standard error, in parentheses) calculated with REML (see Material and Methods 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 (LRT) 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.

Models	Habitat	Productivity	River	logL	ρ	Conditional R^2 (C.I. 95%)	*p*-value
P. simonsi:							
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
P. steerei:							
Habitat + River****	**-0.032 (0.006)**	**.**	**-0.111 (0.008)**	**163.332**	**0.469**	**0.668 (0.732 – 0.599)**	**.**

FIGURE LEGENDS

Figure 1. Geographical sampling of individuals for the genomics 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 color-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.

Figure 2. Principal Components Analysis (PCA) of (a) *P. simonsi* (non-flooded forests/*terra-firme,* as represented by the icon) and (b) *P. steerei* (seasonal floodplain forests/*várzea*, as represented by the icon), with individuals color-coded by the different river regions (see Fig. 1 for distribution details). The three genetic clusters (GC) delineated in *P. steerei* were also identified by (c) the sNMF approach based on ancestry coefficients, whereas a single genetic cluster was identified for *P. simonsi* (see Fig. S3.3).

Figure 3. Procrustes analyses of (a) *P. simonsi* and (b) *P. steerei* with triangles representing the geographical sampling localities and circles the individuals in geo-genetic space (symbols are color-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 Fig. 2) are labeled 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.

Figure 4. Relative importance of each environmental predictor variable in explaining functional connectivity for the best fit models ($\Delta AIC < 2$) among the MLPE regression models for (a) *P. simonsi* and (d) *P. 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 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 (0.00) are considered significant for models similarly to LTR results. 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.

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

REFERENCES

Albert, J. S., Val, P., Hoorn, C., Albert, J. S., Val, P., & Hoorn, C. (2018). The changing course of the Amazon River in the Neogene: center stage for Neotropical diversification. *Neotropical Ichthyology*, *16*(3), e180033. https://doi.org/10.1590/1982-0224-20180033

Aleixo, A. (2006). Historical diversification of floodplain forest specialist species in the Amazon: a case study with two species of the avian genus *Xiphorhynchus* (Aves: Dendrocolaptidae). *Biological Journal of the Linnean Society*, *89*(2), 383–395. https://doi.org/10.1111/j.1095-8312.2006.00703.x

Balkenhol, N., Cushman, S., Storfer, A., & Waits, L. (2015). *Landscape genetics: concepts, methods, applications*. John Wiley & Sons.

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R., … Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*(7610), 144–147. https://doi.org/10.1038/nature18326

Bredin, Y. K., Hawes, J. E., Peres, C. A., & Haugaasen, T. (2020). Structure and composition of terra firme and seasonally flooded várzea forests in the western Brazilian Amazon. *Forests*, *11*(12), 1–20. https://doi.org/10.3390/f11121361

Cadena, C. D., Gutiérrez-Pinto, N., Dávila, N., & Terry Chesser, R. (2011). No population genetic structure in a widespread aquatic songbird from the Neotropics. *Molecular Phylogenetics and Evolution*, *58*(3), 540–545. https://doi.org/10.1016/j.ympev.2010.12.014

Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, *35*(7), 1187–1201. https://doi.org/10.1111/j.1365-2699.2007.01870.x

Carvalho, C. S., Lanes, É. C. M., Silva, A. R., Caldeira, C. F., Carvalho-Filho, N., Gastauer, M., Imperatriz-Fonseca, V. L., Nascimento Júnior, W., Oliveira, G., Siqueira, J. O., Viana, P. L., & Jaffé, R. (2019). Habitat loss does not always entail negative genetic consequences. *Frontiers in Genetics*, *10*, 1101. https://doi.org/10.3389/fgene.2019.01101

Castilla, A. R., Méndez-Vigo, B., Marcer, A., Martínez-Minaya, J., Conesa, D., Picó, F. X., & Alonso-Blanco, C. (2020). Ecological, genetic and evolutionary drivers of regional genetic differentiation in *Arabidopsis thaliana*. *BMC Evolutionary Biology*, *20*(1), 1–13. https://doi.org/https://doi.org/10.1186/s12862-020-01635-2

Cheng, H., Sinha, A., Cruz, F. W., Wang, X., Edwards, R. L., d'Horta, F. M., Ribas, C. C., Vuille, M., Stott, L. D., & Auler, A. S. (2013). Climate change patterns in Amazonia and biodiversity. *Nature Communications*, *4*(1), 1411. https://doi.org/10.1038/ncomms2415

Clarke, R. T., Rothery, P., & Raybould, A. F. (2002). Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. *Journal of Agricultural, Biological, and Environmental Statistics*, *7*(3), 361–372. https://doi.org/10.1198/108571102320

Colinvaux, P. A., De Oliveira, P. E., Moreno, J. E., Miller, M. C., & Bush, M. B. (1996). A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science*, *274*(5284), 85–88. https://doi.org/10.1126/science.274.5284.85

Constantine, J. A., Dunne, T., Ahmed, J., Legleiter, C., & Lazarus, E. D. (2014). Sediment supply as a driver of river meandering and floodplain evolution in the Amazon Basin. *Nature Geoscience*, *7*(12), 899–903. https://doi.org/10.1038/ngeo2282

Dalapicolla, J., Alves, R., Jaffé, R., Vasconcelos, S., Pires, E. S., Nunes, G. L., ... Oliveira, G. (2021). Conservation implications of genetic structure in the narrowest endemic quillwort from the Eastern Amazon. *Ecology and Evolution*, *11*(15), 10119–10132. https://doi.org/10.1002/ECE3.7812

Da Silva, M. N., & Patton, J. L. (1998). Molecular phylogeography and the evolution and conservation of amazonian mammals. *Molecular Ecology*, *7*, 475–486. https://doi.org/10.1046/j.1365-294x.1998.00276.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*(4), 1–20. https://doi.org/10.18637/jss.v022.i04

Emmons, L. H. (1982). Ecology of *Proechimys* (Rodentia, Echimyidae) in southeastern Peru. *Tropical Ecology*, *23*(2), 280–290.

Excoffier, L., Foll, M., & Petit, R. J. (2009). Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 481–501. https://doi.org/10.1146/annurev.ecolsys.39.110707.173414

Fabre, P. H., Patton, J. L., & Leite, Y. L. R. (2016). Family Echimyidae (hutias, South American spiny-rats and coypu). In D. E. Wilson, T. E. J. Lacher, & R. A. Mittermeier (Eds.), *Handbook of the Mammals of the World. Vol 6. Lagomorphs and Rodents I* (pp. 552–641). Lynx Edicions.

Fenderson, L. E., Kovach, A. I., & Llamas, B. (2020). Spatiotemporal landscape genetics: Investigating ecology and evolution through space and time. *Molecular Ecology*, *29*(2), 218–246. https://doi.org/10.1111/mec.15315

Fernandes, A. M., Gonzalez, J., Wink, M., & Aleixo, A. (2013). Multilocus phylogeography of the Wedge-billed Woodcreeper *Glyphorynchus spirurus* (Aves, Furnariidae) in lowland Amazonia: widespread cryptic diversity and paraphyly reveal a complex diversification pattern. *Molecular Phylogenetics and Evolution*, *66*(1), 270–282. https://doi.org/10.1016/j.ympev.2012.09.033

Frichot, E., & Francois, O. (2014). *LEA: an R package for landscape and ecological association studies*. http://membres-timc.imag.fr/Olivier.Francois/lea.html

581 Frichot, E., Mathieu, F., Trouillon, T., Bouchard, G., & François, O. (2014). Fast and efficient estimation of individual ancestry coefficients. *Genetics*,
582 *196*(4), 973–983. https://doi.org/10.1534/genetics.113.160572
583 Gascon, C., Malcolm, J. R., Patton, J. L., da Silva, M. N., Bogart, J. P., Lougheed, S. C., ... Boag, P. T. (2000). Riverine barriers and the geographic
584 distribution of Amazonian species. *Proceedings of the National Academy of Sciences*, *97*(25), 13672–13677.
585 https://doi.org/10.1073/pnas.230136397
586 Godoy, J. R., Petts, G., & Salo, J. (1999). Riparian flooded forests of the Orinoco and Amazon basins: A comparative review. *Biodiversity and*
587 *Conservation*, *8*(4), 551–586. https://doi.org/10.1023/A:1008846531941
588 Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, *22*(7), 1–19.
589 https://doi.org/10.18637/jss.v022.i07
590 Gruber, B., & Georges, A. (2019). *dartR: importing and analysing SNP and silicodart data generated by genome-wide restriction fragment analysis*.
591 https://cran.r-project.org/package=dartR
592 Gumbricht, T., Roman-Cuesta, R. M., Verchot, L., Herold, M., Wittmann, F., Householder, E., ... Murdiyarso, D. (2017). An expert system model for
593 mapping tropical wetlands and peatlands reveals South America as the largest contributor. *Global Change Biology*, *23*(9), 3581–3599.
594 https://doi.org/10.1111/gcb.13689
595 Häggi, C., Chiessi, C. M., Merkel, U., Mulitza, S., Prange, M., Schulz, M., & Schefuß, E. (2017). Response of the Amazon rainforest to late Pleistocene
596 climate variability. *Earth and Planetary Science Letters*, *479*, 50–59. https://doi.org/10.1016/J.EPSL.2017.09.013
597 Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A
598 brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *2018*(5), e4794. https://doi.org/10.7717/peerj.4794
599 Harvey, M. G., Aleixo, A., Ribas, C. C., & Brumfield, R. T. (2017). Habitat association predicts genetic diversity and population divergence in amazonian
600 birds. *American Naturalist*, *190*(5), 631–648. https://doi.org/10.1086/693856
601 Hawkins, B. A., Porter, E. E., & Diniz-Filho, J. A. F. (2003). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds.
602 *Ecology*, *84*(6), 1608–1623. https://doi.org/10.1890/0012-9658(2003)084[1608:PAHAPO]2.0.CO;2
603 He, Q., Edwards, D. L., & Knowles, L. L. (2013). Integrative testing of how environments from the past to the present shape genetic structure across
604 landscapes. *Evolution*, *67*(12), 3386–3402. https://doi.org/10.1111/evo.12159
605 Hess, L. L., Melack, J. M., Affonso, A. G., Barbosa, C., Gastil-Buhl, M., & Novo, E. M. L. M. (2015). Wetlands of the Lowland Amazon Basin: Extent,
606 Vegetative Cover, and Dual-season Inundated Area as Mapped with JERS-1 Synthetic Aperture Radar. *Wetlands*, *35*(4), 745–756.
607 https://doi.org/10.1007/s13157-015-0666-y
608 Hijmans, R., & van Etten, J. (2015). raster: Geographic Data Analysis and Modeling. In *R package version 3.4-10*.
609 Hoban, S., Bruford, M., D'Urban Jackson, J., Lopes-Fernandes, M., Heuertz, M., Hohenlohe, P. A., ... Laikre, L. (2020). Genetic diversity targets and
610 indicators in the CBD post-2020 Global Biodiversity Framework must be improved. *Biological Conservation*, *248*, 108654.
611 https://doi.org/10.1016/j.biocon.2020.108654
612 Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., ... Antonelli, A. (2010). Amazonia through time: Andean uplift,
613 climate change, landscape evolution, and biodiversity. *Science*, *330*(6006), 927–931. https://doi.org/10.1126/science.1194585
614 Jaeger, B. C. (2017). *r2glmm: computes R squared for mixed (multilevel) models*. https://cran.r-project.org/package=r2glmm
615 Jaeger, B. C., Edwards, L. J., Das, K., & Sen, P. K. (2017). An R2 statistic for fixed effects in the generalized linear mixed model. *Journal of Applied*
616 *Statistics*, *44*(6), 1086–1105. https://doi.org/10.1080/02664763.2016.1193725
617 Jaffé, R., Veiga, J. C., Pope, N. S., Lanes, É. C. M., Carvalho, C. S., Alves, R., ... Imperatriz-Fonseca, V. L. (2019). Landscape genomics to the rescue of a
618 tropical bee threatened by habitat loss and climate change. *Evolutionary Applications*, *12*(6), 1164–1177. https://doi.org/10.1111/eva.12794
619 Jombart, T., & Ahmed, I. (2011). adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics*, *27*(21), 3070–3071.
620 https://doi.org/10.1093/bioinformatics/btr521
621 Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured
622 populations. *BMC Genetics*, *11*(1), 1–15. https://doi.org/10.1186/1471-2156-11-94
623 Junk, W. J., & Piedade, M. T. (1993). Herbaceous plants of the Amazon floodplain near Manaus: Species diversity and adaptations to the flood pulse.
624 *Amazoniana: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas*, *12*(3/4), 467–484. http://hdl.handle.net/21.11116/0000-0004-
625 896E-7
626 Knowles, L. L., Massatti, R., He, Q., Olson, L. E., & Lanier, H. C. (2016). Quantifying the similarity between genes and geography across Alaska's alpine
627 small mammals. *Journal of Biogeography*, *43*(7), 1464–1476. https://doi.org/10.1111/jbi.12728
628 Lanier, H. C., Massatti, R., He, Q., Olson, L. E., & Knowles, L. L. (2015). Colonization from divergent ancestors: glaciation signatures on contemporary
629 patterns of genomic variation in Collared Pikas (*Ochotona collaris*). *Molecular Ecology*, *24*(14), 3688–3705. https://doi.org/10.1111/mec.13270

Lara, M., & Patton, J. L. (2000). Evolutionary diversification of spiny rats (genus *Trinomys*, Rodentia: Echimyidae) in the Atlantic Forest of Brazil. *Zoological Journal of the Linnean Society*, *130*(4), 661–686. https://doi.org/10.1006/zjls.2000.0240

Leite, R. N., & Rogers, D. S. (2013). Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives. *Organisms Diversity & Evolution*, *13*(4), 639–664. https://doi.org/10.1007/s13127-013-0140-8

Leite, Y. L. R. (2003). Evolution and systematics of the Atlantic Tree Rats, genus *Phyllomys* (Rodentia: Echimyidae) with description of two new species. *University of California Publications in Zoology*, *132*, 1–118.

Lessa, E. P., Cook, J. A., & Patton, J. L. (2003). Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(18), 10331–10334. https://doi.org/10.1073/pnas.1730921100

Li, H., Qu, W., Obrycki, J. J., Meng, L., Zhou, X., Chu, D., & Li, B. (2020). Optimizing sample size for population genomic study in a global invasive lady beetle, *Harmonia axyridis*. *Insects*, *11*(5), 290. https://doi.org/10.3390/insects11050290

Li, W., Zhang, P., Ye, J., Li, L., & Baker, P. A. (2011). Impact of two different types of El Niño events on the Amazon climate and ecosystem productivity. *Journal of Plant Ecology*, *4*(1–2), 91–99. https://doi.org/10.1093/jpe/rtq039

Manel, S., & Holderegger, R. (2013). Ten years of landscape genetics. *Trends in Ecology and Evolution*, *28*(10), 614–621. https://doi.org/10.1016/j.tree.2013.05.012

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology and Evolution, 18*(4), 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*(2), 209–220. http://www.ncbi.nlm.nih.gov/pubmed/6018555

Massatti, R., & Knowles, L. L. (2014). Microhabitat differences impact phylogeographic concordance of codistributed species: genomic evidence in montane sedges (*Carex* L.) from the Rocky Mountains. *Evolution*, *68*(10), 2833–2846. https://doi.org/10.1111/evo.12491

Massatti, R., & Knowles, L. L. (2016). Contrasting support for alternative models of genomic variation based on microhabitat preference: species-specific effects of climate change in alpine sedges. *Molecular Ecology*, *25*(16), 3974–3986. https://doi.org/10.1111/mec.13735

Matocq, M. D., Patton, J. L., & Da Silva, M. N. F. (2000). Population genetic structure of two ecologically distinct amazonian spiny rats: separating history and current ecology. *Evolution*, *54*(4), 1423–1432. https://doi.org/10.1111/j.0014-3820.2000.tb00574.x

McLaughlin, J. F., & Winker, K. (2020). An empirical examination of sample size effects on population demographic estimates in birds using single nucleotide polymorphism (SNP) data. *PeerJ*, *8*, e9939. https://doi.org/10.7717/peerj.9939

McRae, B. H. (2006). Isolation by resistance. *Evolution*, *60*(8), 1551–1561. https://doi.org/10.1111/j.0014-3820.2006.tb00500.x

McRae, B. H., & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proc Natl Acad Sci U S A*, *104*(50), 19885–19890. https://doi.org/10.1073/pnas.0706568104

Miller, J. M., Cullingham, C. I., & Peery, R. M. (2020). The influence of a priori grouping on inference of genetic clusters: simulation study and literature review of the DAPC method. *Heredity*, *125*(5), 269–280. https://doi.org/10.1038/s41437-020-0348-2

Murphy, M. O., Jones, K. S., Price, S. J., & Weisrock, D. W. (2018). A genomic assessment of population structure and gene flow in an aquatic salamander identifies the roles of spatial scale, barriers, and river architecture. *Freshwater Biology*, *63*(5), 407–419. https://doi.org/10.1111/fwb.13071

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nazareno, A. G., Bemmels, J. B., Dick, C. W., & Lohmann, L. G. (2017). Minimum sample sizes for population genomics: an empirical study from an Amazonian plant species. *Molecular Ecology Resources*, *17*(6), 1136–1147. https://doi.org/10.1111/1755-0998.12654

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: community ecology package*. http://cran.r-project.org/package=vegan

Papadopoulou, A., & Knowles, L. L. (2016). Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(29), 8018–8024. https://doi.org/10.1073/pnas.1601069113

Patterson, N., Price, A. L., & Reich, D. (2006). Population structure and eigenanalysis. *PLoS Genetics*, *2*(12), 2074–2093. https://doi.org/10.1371/journal.pgen.0020190

Patton, J. L., & Leite, R. N. (2015). Genus *Proechimys* J. A. Allen, 1889. In J. L. Patton, U. F. J. Pardiñas, & G. D'Elía (Eds.), *Mammals of South America, Volume 2: Rodents* (pp. 950–989). University Of Chicago Press.

Patton, J. L., Da Silva, M. N., & Malcolm, J. R. (2000). Mammals of the rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin American Museum of Natural History*, *244*, 1–306. https://doi.org/10.1206/0003-0090(2000)244%3C0001:MOTRJA%3E2.0.CO;2

Patton, J. L., Pardiñas, U. F. J., & D'Elía, G. (2015). *Mammals of South America, Volume 2, Rodents*. The University of Chicago Press.

679 Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: an inexpensive method for *de novo* SNP
680 discovery and genotyping in model and non-model species. *PLoS ONE*, *7*(5), e37135. https://doi.org/10.1371/journal.pone.0037135
681 Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2020). *nlme: linear and nonlinear mixed effects models*. https://cran.r-project.org/package=nlme
682 Pirani, R. M., Werneck, F. P., Thomaz, A. T., Kenney, M. L., Sturaro, M. J., Ávila-Pires, T. C. S., ... Knowles, L. L. (2019). Testing main Amazonian
683 rivers as barriers across time and space within widespread taxa. *Journal of Biogeography*, *46*(11), 2444–2456. https://doi.org/10.1111/jbi.13676
684 Pope, N. (2020). *r2vcftools: An R interface for vcftools. R package version 0.0.0.9000.*
685 Prado, J. R., Percequillo, A. R., Thomaz, A. T., & Knowles, L. L. (2019). Similar but different: Revealing the relative roles of species-traits versus biome
686 properties structuring genetic variation in South American marsh rats. *Journal of Biogeography*, *46*(4), 770–783. https://doi.org/10.1111/jbi.13529
687 Puechmaille, S. J. (2016). The program structure does not reliably recover the correct population structure when sampling is uneven: subsampling and new
688 estimators alleviate the problem. *Molecular Ecology Resources*, *16*(3), 608–627. https://doi.org/10.1111/1755-0998.12512
689 R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/
690 Ribas, C. C., Aleixo, A., Nogueira, A. C. R., Miyaki, C. Y., & Cracraft, J. (2012). A palaeobiogeographic model for biotic diversification within Amazonia
691 over the past three million years. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*(1729), 681–689,
692 https://doi.org/10.1098/rspb.2011.1120.
693 Rutten, A., Cox, K., Scheppers, T., Broecke, V., Leirs, H., Casaer, J., ... Leirs, H. (2019). Analysing the recolonisation of a highly fragmented landscape by
694 wild boar using a landscape genetic approach. *Wildlife Biology, 2019*(1), 1–11. https://doi.org/10.2981/wlb.00542
695 Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemelä, P., Puhakka, M., & Coley, P. D. (1986). River dynamics and the diversity of Amazon lowland
696 forest. *Nature*, *322*(6076), 254–258. https://doi.org/10.1038/322254a0
697 Shirk, A. J., Landguth, E. L., & Cushman, S. A. (2017). A comparison of individual-based genetic distance metrics for landscape genetics. *Molecular*
698 *Ecology Resources*, *17*(6), 1308–1317. https://doi.org/10.1111/1755-0998.12684
699 Shirk, A. J., Landguth, E. L., & Cushman, S. A. (2018). A comparison of regression methods for model selection in individual-based landscape genetic
700 analysis. *Molecular Ecology Resources*, *18*(1), 55–67. https://doi.org/10.1111/1755-0998.12709
701 Sikes, R. S. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of*
702 *Mammalogy*, *97*(3), 663–688. https://doi.org/10.1093/jmammal/gyw078
703 Silk, M. J., Harrison, X. A., & Hodgson, D. J. (2020). Perils and pitfalls of mixed-effects regression models in biology. *PeerJ*, *8*, e9522.
704 https://doi.org/10.7717/peerj.9522
705 Smith, B. T., McCormack, J. E., Cuervo, A. M., Hickerson, M. J., Aleixo, A., Cadena, C. D., ... Brumfield, R. T. (2014). The drivers of tropical speciation.
706 *Nature*, *515*(7527), 406–409. https://doi.org/10.1038/nature13687
707 Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, *68*(3), 571–573.
708 https://doi.org/10.2307/3544927
709 Thom, G., Xue, A. T., Sawakuchi, A. O., Ribas, C. C., Hickerson, M. J., Aleixo, A., & Miyaki, C. (2020). Quaternary climate changes as speciation drivers
710 in the Amazon floodplains. *Science Advances*, *6*(11), eaax4718. https://doi.org/10.1126/sciadv.aax4718
711 Tracy, C. A., & Widom, H. (1994). Level spacing distributions and the Bessel kernel. *Communications in Mathematical Physics*, *161*(2), 289–309.
712 https://doi.org/10.1007/BF02099779
713 van Soelen, E. E., Kim, J.-H., Santos, R. V., Dantas, E. L., Vasconcelos de Almeida, F., Pires, J. P., ... Sinninghe Damsté, J. S. (2017). A 30 Ma history of
714 the Amazon River inferred from terrigenous sediments and organic matter on the Ceará Rise. *Earth and Planetary Science Letters*, *474*, 40–48.
715 https://doi.org/10.1016/J.EPSL.2017.06.025
716 Vormisto, J., Tuomisto, H., & Oksanen, J. (2004). Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? *Journal*
717 *of Vegetation Science*, *15*(4), 485–494. https://doi.org/10.1111/j.1654-1103.2004.tb02287.x
718 Voss, R. S., & Emmons, L. H. (1996). Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American*
719 *Museum of Natural History*, *230*, 1–115.
720 Voss, R. S., Lunde, D. P., & Simmons, N. B. (2001). The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna part 2. Nonvolant
721 species. *Bulletin of the American Museum of Natural History*, *263*, 3–236. https://doi.org/10.1206/0003-
722 0090(2001)263<0003:TMOPFG>2.0.CO;2
723 Wittmann, F., Schöngart, J., & Junk, W. J. (2010). Phytogeography, species diversity, community structure and dynamics of Central Amazonian floodplain
724 forests. In Wolfgang J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, & P. Parolin (Eds.), *Amazonian floodplain forests: ecophysiology,*
725 *biodiversity and sustainable management* (pp. 61–102). Springer.
726 Woods, & Kilpatrick. (2005). Infraorder Hystricognathi Brandt, 1855. In D. E. Wilson & D. M. Reeder (Eds.), *Mammal Species of the World. A*
727 *Taxonomic and Geographic Reference* (Volume 2, pp. 1538–1600). Johns Hopkins University Press.

Wright, S. (1943). Isolation by Distance. *Genetics*, *28*(2), 114–138. http://www.ncbi.nlm.nih.gov/pubmed/17247074

Yang, J., Benyamin, B., McEvoy, B. P., Gordon, S., Henders, A. K., Nyholt, D. R., … Visscher, P. M. (2010). Common SNPs explain a large proportion of the heritability for human height. *Nature Genetics*, *42*(7), 565–569. https://doi.org/10.1038/ng.608

BIOSKETCH

The authors share an interest in the study of processes that structure the genetic variation among taxa and across geography. JD: designed and performed the experiments, gathered and analyzed the data, wrote the manuscript and made the figures and tables; JRP: designed the experiments, provided analysis tools, and contributed to writing of the manuscript; ARP: designed the experiments, provided reagents/materials/analysis tools, and contributed to writing the manuscript; LLK: designed the experiments, provided reagents/materials/analysis tools, and contributed to writing the manuscript.

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Tables

Table 1: The best fit models (ΔAIC < 2 with the best fit model in bold) for observed geographic distribution of relatedness coefficients in P. simonsi (the non-flooded forest/terra-firme species) and in P. steerei, (the seasonal floodplain forests/várzea species) using MLPE. The contribution of each predictor variable (and standard error, in parentheses) calculated with REML (see Material and Methods 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 (LRT) 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.

Models	Habitat	Productivity	River	logL	ρ	Conditional R^2 (C.I. 95%)	p-value
P. simonsi:							
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
P. steerei:							
Habitat + River****	**-0.032 (0.006)**	**.**	**-0.111 (0.008)**	**163.332**	**0.469**	**0.668 (0.732 – 0.599)**	**.**