J Ornithol
DOI 10.1007/s10336-017-1507-y

ORIGINAL ARTICLE

Weak evidence for fine-scale genetic spatial structure in three sedentary Amazonian understorey birds

Juliana Menger[1,2,3] · Jasmin Unrein[2] · Maria Woitow[2] · Martin Schlegel[2,3] · Klaus Henle[1,3] · William E. Magnusson[4]

Received: 31 May 2017 / Revised: 25 August 2017 / Accepted: 19 October 2017

Abstract The ecological characteristics of a species, along with small-scale landscape features are known to affect the patterns of genetic structure within populations. Due to dispersal limitation, closely-related individuals tend to be closer spatially, leading to spatial genetic structure. Physical barriers also may prevent individuals from dispersing further, and lead individuals on one side of a barrier to be more related than individuals from different sides. We tested these hypotheses by examining patterns of fine-scale spatial genetic structure within populations of three relatively sedentary Amazonian-forest understorey birds that differ in their ecological requirements. We sampled birds in a 10,000 ha reserve, covered by largely undisturbed old-growth forests and traversed by a central ridge. We found positive spatial genetic structure at short distances only for *Percnostola rufifrons*, a treefall-gap specialist. Positive genetic structure occurred at 6 km for *Glyphorynchus spirurus*, a solitary bark-forager; no spatial genetic structure was found for *Gymnopithys rufigula*, an army-ant follower. Individuals of none of the three species were more related on a given side of the ridgeline than between different sides but, at greater distances, there was a tendency of individuals located on opposite sides of the ridgeline to be less related than individuals located on the same side, for all species analysed. Our study indicates that local topographic features do not prevent, but likely reduce, gene flow within populations in continuous forests, and that the development of fine-scale spatial genetic structure may depend on the dispersal propensity of a species. Thus, studies of species assemblages need to account for the different ecological characteristics of the constituent species.

Keywords *Gymnopithys rufigula* · *Glyphorynchus spirurus* · Microsatellites · Neotropical birds · *Percnostola rufifrons* · Spatial genetic structure

Zusammenfassung

Schwache Hinweise auf eine räumlich-genetische Feinstruktur bei drei sesshaften Vögeln aus dem Unterholz des Amazonas Waldes

Die ökologischen Eigenschaften einer Art beeinflussen zusammen mit kleinmaßstäbigen Landschaftsmerkmalen die Form der genetischen Struktur innerhalb von Populationen. Aufgrund einer begrenzten Ausbreitung befinden sich nahverwandte Individuen in räumlicher Nähe zueinander, was zu einer räumlich-genetischen Struktur führt. Physikalische Barrieren können ebenfalls die Individuen an einer weiteren Ausbreitung hindern. Das führt dazu, dass Individuen auf der einen Seite der Barriere näher miteinander verwandt sind als Individuen von unterschiedlichen Seiten. Wir haben diese Hypothesen durch die Untersuchung der räumlich-

Communicated by M. Wink.

✉ Juliana Menger
j.menger@ufz.de

[1] Department of Conservation Biology, UFZ-Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318 Leipzig, Germany

[2] Faculty of Biosciences, Pharmacy and Psychology, University of Leipzig, Talstr. 33, 04103 Leipzig, Germany

[3] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[4] Coordenação de Pesquisa em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Avenida André Araújo 2936, Manaus CEP 69067-375, Brazil

Published online: 03 November 2017

genetischen Feinstruktur innerhalb der Populationen von drei relativ sesshaften Vogelarten, die im Unterholz des Amazonas Regenwaldes leben und sich in ihren ökologischen Anforderungen unterscheiden, getestet. Die Proben wurden in einem 10.000 ha großen Reservat gesammelt, welches größtenteils mit unberührtem Primärwald bedeckt und von einer zentral liegenden Kammlinie durchzogen ist. Nur für *Percnostola rufifrons* haben wir eine positive räumlich-genetische Struktur auf kurzen Distanzen gefunden. Dieser ist ein Spezialist für kleine Lichtungen, sogenannte „treefall-gaps". Eine positive räumlich-genetische Struktur wurde für den solitär lebenden *Glyphorynchus spirurus* bei einer Distanz von 6 km festgestellt, welcher nach Insekten in der Rinde von Bäumen sucht. Für den Wanderameisen folgenden *Gymnopithys rufigula* wurde keine räumlich-genetische Struktur gefunden. Hinzu kommt, dass bei allen Arten die Individuen auf einer Seite der Kammlinie nicht näher verwandt waren als Individuen von unterschiedlichen Seiten. Auf größere Distanzen gesehen, konnte für alle drei Vogelarten eine Tendenz festgestellt werden, dass Individuen von unterschiedlichen Seiten der Kammlinie weniger miteinander verwandt waren als Individuen einer Seite. Unsere Studie zeigt, dass lokale topografische Gegebenheiten nicht den Genfluss in Populationen in zusammenhängenden Wäldern verhindern, aber möglicherweise reduzieren und dass die Entstehung einer räumlich-genetischen Feinstruktur vermutlich von der Ausbreitungsneigung der Art abhängt. Folglich müssen bei Untersuchungen zu Artenzusammensetzungen die verschiedenen ökologischen Besonderheiten der einzelnen Spezies berücksichtigten.

Introduction

Genetic structuring is inversely related to gene flow, which in turn depends highly on the dispersal ability of the organisms. As birds are considered to be good dispersers, genetic structuring is expected to be low in most populations (Crochet 2000). However, many species of birds do display dispersal restrictions, particularly Neotropical rainforest birds (Moore et al. 2008), leading to genetic differentiation even at local scales (Bates 2002; Brown et al. 2004; Woltmann et al. 2012). Moreover, levels of genetic differentiation among populations of many Neotropical rainforest birds have been shown to be explained by their ecological traits (Burney and Brumfield 2009; Khimoun et al. 2016).

Neotropical lowland *terra firme* forests hold a taxonomically and ecologically diverse group of understorey-dwelling birds (Powell et al. 2015a) that vary in their dispersal capabilities. For instance, insectivorous birds are considered to be more sedentary than frugivorous species (Karr 1976); birds that frequent edges or treefall gaps are more prone to crossing habitat gaps than birds restricted to the forest interior (Şekercioğlu et al. 2002); and flocking birds that rely on nomad army-ant raids to obtain their food typically range over larger areas than do solitary ones (Van Houtan et al. 2006). As such, diet, habitat specialization and foraging behaviour are all ecological traits that could affect the extent to which Neotropical understorey birds disperse, so that the development of fine genetic structure is expected to be species-specific. However, it may be difficult to predict which species will show the most structure because the majority of information on movement relates to adults, but vagrant juveniles may be responsible for most gene flow.

Not only ecological characteristics influence the dispersal of Neotropical understorey birds; physical and environmental barriers are also known to reduce gene flow, increase spatial genetic divergence among populations and, ultimately, may lead to speciation (Smith et al. 2014). Although the effects of human-induced barriers (Barnett et al. 2008; Bates 2002; Brown et al. 2004; Hermes et al. 2016; Woltmann et al. 2012) and large-scale landscape features (Fernandes et al. 2013; Gutiérrez-Pinto et al. 2012; Sandoval et al. 2016; Weir 2009) on the genetic differentiation among populations have been well assessed, the spatial genetic structuring within populations of Neotropical birds and possible effects of small-scale barriers have barely been studied (see a review in Fernandes 2013). Patterns of fine-scale spatial genetic structure within populations can provide important evidence about dispersal and other aspects of a species' biology (Peakall et al. 2003). For instance, small-scale dispersal barriers may affect the distribution of relatives, so that individuals on either side of a barrier are expected to be genetically more related than individuals from opposite sides. Additionally, populations under restricted dispersal are predicted to show spatial genetic structure, with relatedness between individuals decreasing with increasing geographic distance (Smouse and Peakall 1999). Local genetic structure may also be generated from sex-bias in dispersal, with stronger structuring displayed by the most philopatric sex (Banks and Peakall 2012). As male birds tend to remain in their natal territory and females to disperse further (Greenwood 1980), males will presumably display stronger genetic structuring than females.

In this study, we examined patterns of fine-scale spatial genetic structure within populations of three sedentary Amazonian forest-understorey birds that differ in their ecological requirements, and thus possibly, in their dispersal propensity: *Gymnopithys rufigula* (Thamnophilidae), *Percnostola rufifrons* (Thamnophilidae) and *Glyphorynchus spirurus* (Dendrocolaptidae). As an army-ant follower, *Gymnopithys rufigula* relies on the nomadic movements of army-ant swarms to obtain its food, thus it tends to move longer distances than the other species (Willis and Oniki 1978). *Percnostola rufifrons* is a treefall-gap specialist, whose adults defend small territories

(Johnson et al. 2011). *Glyphorynchus spirurus* is a solitary bark-forager that maintains small and stable territories over time (Blake and Loiselle 2012; Johnson et al. 2011). Therefore, we tested whether these species (1) display an overall positive spatial genetic structure, (2) males and females differ in their fine-scale structure, and (3) a small topographic ridge separating two watersheds acts as a barrier to gene flow.

Methods

Study area

This study was conducted in the Ducke Forest Reserve (DFR), a 10,000 ha old-growth *terra firme* forest located on the outskirts of Manaus city, in the Brazilian Amazon (Fig. 1a). The city of Manaus has been rapidly growing towards the western borders of DFR, but the reserve's eastern limits are still connected to large portions of forest. The DFR has complex topography, with a central ridge dividing the reserve into two watersheds; the eastern streams flow to tributaries of the Amazon River (white water), whereas the western streams flow to tributaries of the Negro River (black water) (Fig. 1b). Thus, the spatial configuration of DFR provides an excellent opportunity to test the questions presented in the introduction.

Study species

Gymnopithys rufigula is an obligate army-ant follower found exclusively in the Guiana Shield, northern Amazon (Zimmer and Isler 2003). Medium-sized (mean mass = 28.6 g; Menger et al. (2017b)), *Gymnopithys rufigula* maintains roosting and nesting territories, but lacks feeding territories because they rely on the nomadic and widely-spaced colonies of army ants to obtain their food (Brumfield et al. 2007; Chaves-Campos and DeWoody 2008; O'Donnell et al. 2012; Willson 2004). The species exhibits little sexual dimorphism, but males and females can be distinguished by their interscapular patch, which is white in males and tawny-orange in females. Menger et al. (2017b) assessed the overall local genetic structure, but did not investigate the effects of the ridgeline on the spatial genetic structure and relatedness of *Gymnopithys rufigula* within DFR.

Percnostola rufifrons is a non-migratory bird confined to northern Amazonian forests (Zimmer and Isler 2003). Similar to *Gymnopithys rufigula* in size (mean mass based on 85 individuals = 28.5 g; JM *personal observation*), *P.*

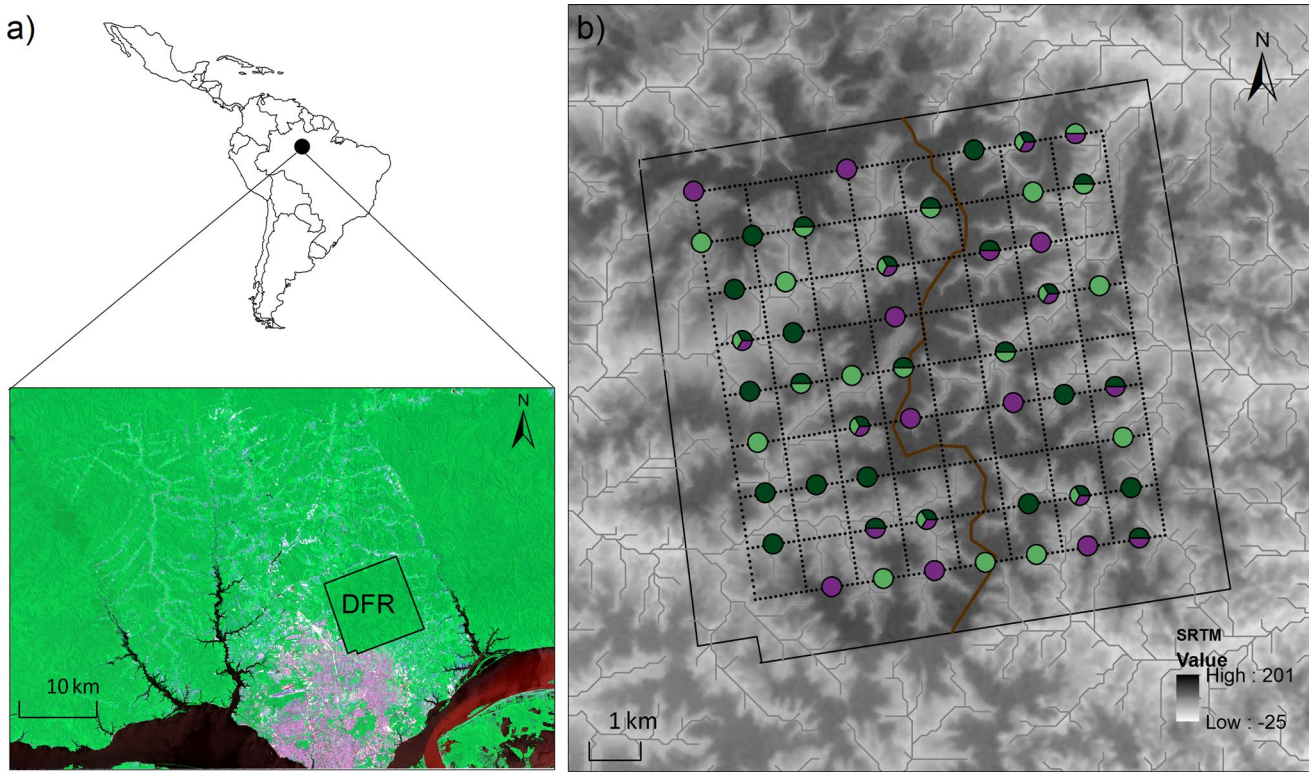

Fig. 1 Location of Ducke Forest Reserve (DFR), Manaus, Amazonas State, Brazil (**a**). Topography and streams in the study area, showing the 47 sampling plots (circles) where blood samples were taken (**b**). A brown line divides the reserve into eastern (n = 21) and western (n = 26) watersheds; colours indicate where each species was sampled (dark green: *Gymnopithys rufigula*; pale green: *Percnostola rufifrons*; purple: *Glyphorynchus spirurus*) (colour figure online)

rufifrons is a solitary sallier, specialized on treefall-gaps (Antongiovanni and Metzger 2005). Its territory size has been estimated to be relatively small (5.6 ha; Johnson et al. (2011)). Males of the species are greyish, with black crown and throat, while females are largely pale orange-rufous.

Glyphorynchus spirurus is the smallest woodcreeper species in DFR (mean mass based on 279 individuals = 13.2 g; JM *personal observation*). Common over most of its range from southern Mexico to eastern Brazil, this insectivorous bird occurs in the understorey of old-growth forests, but also in forest edges and secondary forests (Marantz et al. 2003). As a bark forager, it usually feeds alone or in pairs, and may join understorey mixed-species flocks passing through its territories (Powell et al. 2015b). *Glyphorynchus spirurus* maintains small (5.2 ha, Johnson et al. 2011) and stable territories over time (Blake and Loiselle 2012). Although males may be slightly larger than females, *Glyphorynchus spirurus* does not show sexual dimorphism in plumage (Marantz et al. 2003).

Sampling and DNA extraction

Blood samples of *Gymnopithys rufigula* ($n = 80$), *P. rufifrons* ($n = 39$) and *Glyphorynchus spirurus* ($n = 40$) were collected in the DFR during the dry season (July to October) of three consecutive years (2012–2014). Birds were captured with mist nets at 49 sampling points distributed throughout both watersheds (Fig. 1b). Resampling was avoided by tagging each individual with a single metal leg band issued by the Brazilian Centre for Bird Conservation—CEMAVE. Blood samples of approximately 50 µl were collected via venipuncture and stored in absolute ethanol or in Queen's lysis buffer (Seutin et al. 1991). Birds were then released unharmed. Blood samples were deposited in the Genetic Resource Collection of the Instituto Nacional de Pesquisas da Amazônia—GRC-INPA. DNA was extracted and purified from the whole blood using the Promega Wizard Genomic DNA Purification Kit, following the manufacturer's protocols.

Sex determination

As *Gymnopithys rufigula* and *P. rufifrons* exhibit sexual dimorphism in plumage, males ($n = 40$, $n = 20$; respectively) and females ($n = 40$, $n = 19$; respectively) were identified in the field. The sex of *Glyphorynchus spirurus* was identified by PCR amplification of NIPBL genes using primers NIPBL-i16F and NIPBL-i16R (Suh et al. 2011). PCR was carried out in a total volume of 12.5 µl containing 8.4 µl double-distilled water, 0.5 µl DNA (10–20 ng/µl), 0.1 µl Thermo Fisher DreamTaq Green DNA Polymerase (5 U/µl), 1.25 µl dNTPs (2 mM), 1.25 µl DreamTaq Green buffer (10×), 0.5 µl forward primer (10 Mm) and 0.5 µl reverse primer (10 Mm). Thermal cycling proceeded as follows: 95 °C for 3 min, followed by 35 cycles of 94 °C for 60 s, 52 °C for 60 s and 72 °C for 80 s, finishing with 72 °C for 5 min. Results were analysed by electrophoresis in 1% agarose gel. Our analyses of *Glyphorynchus spirurus* were based on 20 males and 20 females.

Microsatellite genotyping

Gymnopithys rufigula was genotyped at 13 microsatellite loci (Table 1) described in Menger et al. (2017a). All 13 loci met Hardy–Weinberg equilibrium (HWE), showed no evidence of linkage disequilibrium with other loci and exhibited no evidence for null alleles, as demonstrated in Menger et al. (2017b). *Percnostola rufifrons* was genotyped at nine cross-amplified loci developed for other avian species (Table 1), using protocols and PCR conditions as in Menger et al. (2017a). *Glyphorynchus spirurus* was genotyped at eight microsatellite loci described in Unrein et al. (2017). Additionally, three extra loci developed for other avian species (Table 1) were cross-amplified, using protocols and PCR conditions as in Unrein et al. (2017).

All loci of *P. rufifrons* and *Glyphorynchus spirurus* were checked for null alleles using the Micro-Checker v.2.2.3 (Van Oosterhout et al. 2004). Deviations from HWE and exact tests of linkage disequilibrium between pairs of loci were calculated in the Genepop web v.4.2 (Rousset 2008).

Genetic diversity

We assessed within-species genetic diversity by the observed (H_o) and expected (H_e) heterozygosity calculated in Cervus v.3.0.7 (Kalinowski et al. 2007) and by standardized allelic richness (AR) estimated using a rarefaction method implemented in SPAGeDi v.1.5 (Hardy and Vekemans 2002). To test whether those variables differ among species, we used analysis of variance for unbalanced sample size in R software (R Core Team 2016).

Population inference

We used Structure v.2.3.4 (Pritchard et al. 2000) assuming an admixture model with correlated allele frequencies to infer the number of genetically distinct clusters (K) within each species. We set a burn-in period of 100,000 followed by additional 1,000,000 iterations and 20 replicates were run at each K to identify the best estimate of K from 1 to 6. We determined K based on the log posterior probability of the data for a given K (Pritchard et al. 2000) and on the rate of change in the log probability of the data between successive clusters—the ΔK statistic (Evanno et al. 2005). We used the Structure Harvester v.0.6.94 to calculate K and ΔK (Earl and

Table 1 Allelic richness (AR), observed (H_o) and expected (H_e) heterozygosity of 23 microsatellite loci within populations of three forest-understorey birds in the Ducke Forest Reserve

Locus	*Gymnopithys rufigula*			*Percnostola rufifrons*			*Glyphorynchus spirurus*		
	AR	H_o	H_e	AR	H_o	H_e	AR	H_o	H_e
Glysp02[a]							8.9	0.500	0.543
Glysp03[a]				15.0	0.821	0.858	15.9	0.750	0.844
Glysp05[a]							9.0	0.650	0.754
Glysp06[a]							18.9	0.850	0.862
Glysp09[a]				4.0	0.385	0.441	18.8	0.850	0.911
Glysp14[a]							14.9	0.800	0.839
Glysp15[a]							5.0	0.475	0.470
Glysp16[a]							22.8	0.875	0.878
Gyru02[b]	19.8	0.875	0.921						
Gyru03[b]	20.1	0.925	0.913						
Gyru06[b]	13.0	0.763	0.774				5.9	0.400	0.487
Gyru07[b]	18.8	0.863	0.913	2.0	0.256	0.226			
Gyru10[b]	13.1	0.900	0.899	12.0	0.744	0.789			
Gyru11[b]	17.7	0.900	0.917	8.0	0.769	0.834			
Gyru12[b]	9.2	0.663	0.777						
MyEx26[c]	4.9	0.413	0.414						
CAM-06[d]				4.0	0.410	0.534			
CAM-17[d]	6.5	0.725	0.711	3.0	0.410	0.541			
CAM-18[d]	4.7	0.425	0.479	4.0	0.615	0.523	5.0	0.700	0.691
CAM-24[d]				3.0	0.154	0.169			
TG01-040[e]	2.9	0.138	0.153						
TG02-088[e]	15.3	0.975	0.919				8.0	0.600	0.667
TG12-015[e]	2.5	0.225	0.284						
All loci (mean)	11.4	0.676	0.698	6.1	0.480	0.517	12.1	0.567	0.615

[a]Primer sets developed by Unrein et al. (2017) and [b]Menger et al. (2017a)

[c]Primer developed by Barnett et al. (2007), but modified by Menger et al. (2017a)

[d]Primer sets described in Dawson et al. (2013) and [e]Dawson et al. (2010)

vonHoldt 2011) and Clumpp v.1.1.2 to calculate the average probability of individual membership to a specific cluster over the 20 replicates (Jakobsson and Rosenberg 2007).

Spatial genetic structure

To investigate fine-scale patterns of genetic structure within DFR, we used spatial autocorrelation analysis in the GenAlEx v.6.502 (Peakall et al. 2003; Peakall and Smouse 2012; Smouse and Peakall 1999). By correlating genotypes of mapped individuals, spatial autocorrelation analysis is able to identify the scale of genetic structure without prior knowledge of that scale (Heywood 1991). We used a pairwise geographic and a pairwise squared genetic distance matrix to calculate a spatial autocorrelation coefficient *r*, and obtained statistical significance by 9999 random permutations (Peakall et al. 2003; Smouse and Peakall 1999). We calculated *r* for distance classes of 1 km, i.e., the minimum distance between sampling points.

To test whether individuals located on a given watershed were more related than individuals from different watersheds, we calculated the autocorrelation coefficients separately for western–western (WW), eastern–eastern (EE), and opposite-watersheds (WE) pairs across distance classes of 1 km. We assessed the significance of the genetic patterns by determining the 95% bootstrap confidence interval about the autocorrelation *r* values for each group.

To test for differences in spatial genetic structure between sexes, we also performed spatial autocorrelation analysis separately for males and females, and compared the patterns of genetic structure between sexes by determining the 95% bootstrap confidence intervals (CI) for the autocorrelation *r* values for each sex (Banks and Peakall 2012). If female-biased dispersal is present, we expect CI's between sexes not to overlap, with *r* values significantly greater in males.

Patterns of genetic relatedness between watersheds

To visualize differences in patterns of genetic relatedness between watersheds, we performed a Principal Coordinate Analysis (PCoA) using the Lynch–Ritland pairwise genetic relatedness matrix (Lynch and Ritland 1999) in the GenAlEx

v.6.502 (Peakall and Smouse 2006, 2012). If individuals within a given watershed are more related than between watersheds, points separate into distinguishable clouds. Additionally, we tested for differences in mean pairwise relatedness between watersheds by using 9999 random permutations, as implemented in the GenAlEx v.6.502 (Peakall and Smouse 2006, 2012).

Gene flow

We used the BayesAss v.3.0 (Wilson and Rannala 2003) to estimate rates and direction of recent gene flow between eastern and western watersheds within DFR. The BayesAss relies on a Bayesian approach and MCMC sampling to estimate migration over the last few generations (Wilson and Rannala 2003). The BayesAss was run with 10 million iterations, a sampling frequency of 1000, a burn-in of 10% and otherwise default settings. We tested several mixing-parameter values to achieve acceptance rates of 20–60% for migration rates (m), allele frequency (a) and inbreeding coefficients (f). The final model parameter values for all species were set at $m = 0.4$, $a = 0.4$ and $f = 0.7$. We used the Tracer v.1.6 to assess convergence (Rambaut et al. 2014).

Results

Genetic diversity

All *P. rufifrons* and *Glyphorynchus spirurus* loci conformed to HWE expectations and no pair of loci was found to be in linkage disequilibrium. Allelic richness, observed (H_o) and expected heterozygosity (H_e) were similar among the three species (all P values > 0.09, Table 1).

Population inference

The highest log posterior probability of the data obtained via Structure analyses was $K = 1$ for all species (Fig. 2a–c). The highest value for ΔK suggested a $K = 2$ for *Gymnopithys rufigula* and *Glyphorynchus spirurus*, and a $K = 5$ was suggested for *P. rufifrons* (Fig. 2d–f). We, hence, assigned membership of each individual to the clusters with K set to 2 for all species. However, all individuals within species were assigned to each of the clusters with a probability of ~ 0.5. We additionally assigned membership of each *P. rufifrons* individual to the clusters with K set to 5, but the probability of individual membership in each cluster was 0.2. These

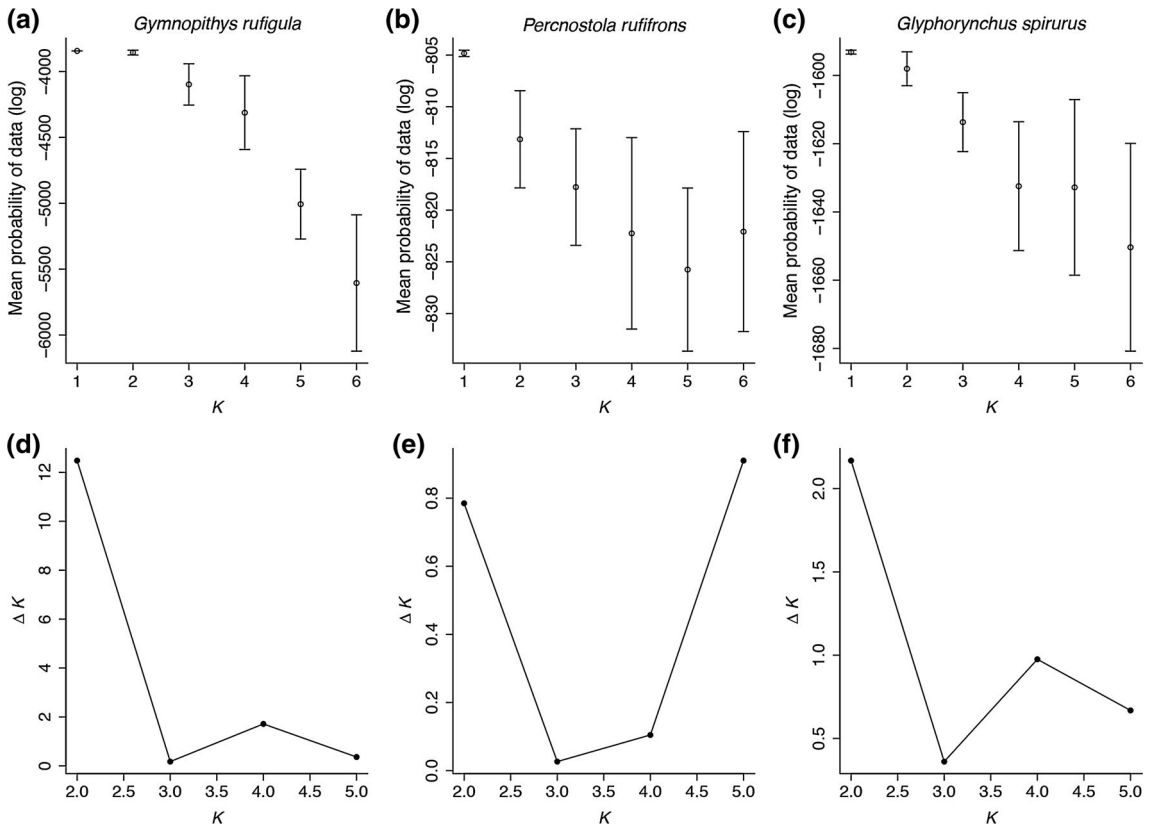

Fig. 2 Number of populations inferred by structure for *Gymnopithys rufigula*, *Percnostola rufifrons* and *Glyphorynchus spirurus*. Mean log likelihoods for each K (± SD; **a**–**c**) and the rate of change in the log probability of the data between successive clusters (ΔK; **d**–**f**)

results indicate that most likely all individuals within each species belong to the same population.

Spatial genetic structure

Gymnopithys rufigula did not display spatial genetic structure, indicating that genotypes were randomly distributed at the scale of the DFR, as already shown in Menger et al. (2017b) (Fig. 3a). *Percnostola rufifrons* was the only species to show positive genetic structure at short distances, with the *r* value crossing zero at 1 km, suggesting stronger dispersal limitation for this species (Fig. 3b). *Glyphorynchus spirurus* displayed positive genetic structure at a distance class of 6 km, with the *r* value crossing zero at 7 km, indicating that individuals separated by more than this distance are less genetically similar than expected for random mating independent of distance (Fig. 3c).

There was a tendency of WE-pairs to be less related than WW- and EE-pairs at greater distance classes, but 95% error bars overlapped at all distance classes and for all three species (Fig. 3d–f), indicating that the central ridgeline has little effect on gene flow within DFR. Males and females of all species showed similar patterns of genetic structure; there was thus no evidence for sex-biased dispersal (Fig. 3g–i).

Patterns of genetic relatedness between watersheds

The PCoA did not show any apparent structuring into eastern and western watersheds for any of the species (Fig. 4). That is, the individuals sampled within a given species had similar genetic relatedness in both watersheds. Mean pairwise relatedness was low for all species and similar in both watersheds (all $P > 0.1$).

Gene flow

Estimates of contemporary gene flow obtained from the BayesAss suggested high self-recruitment rates for all species in both watersheds (Fig. 5). Gene flow between watersheds was similar for the *Gymnopithys rufigula* (Fig. 5), while asymmetrical gene flow between eastern and western watersheds was detected for the other two species. Higher

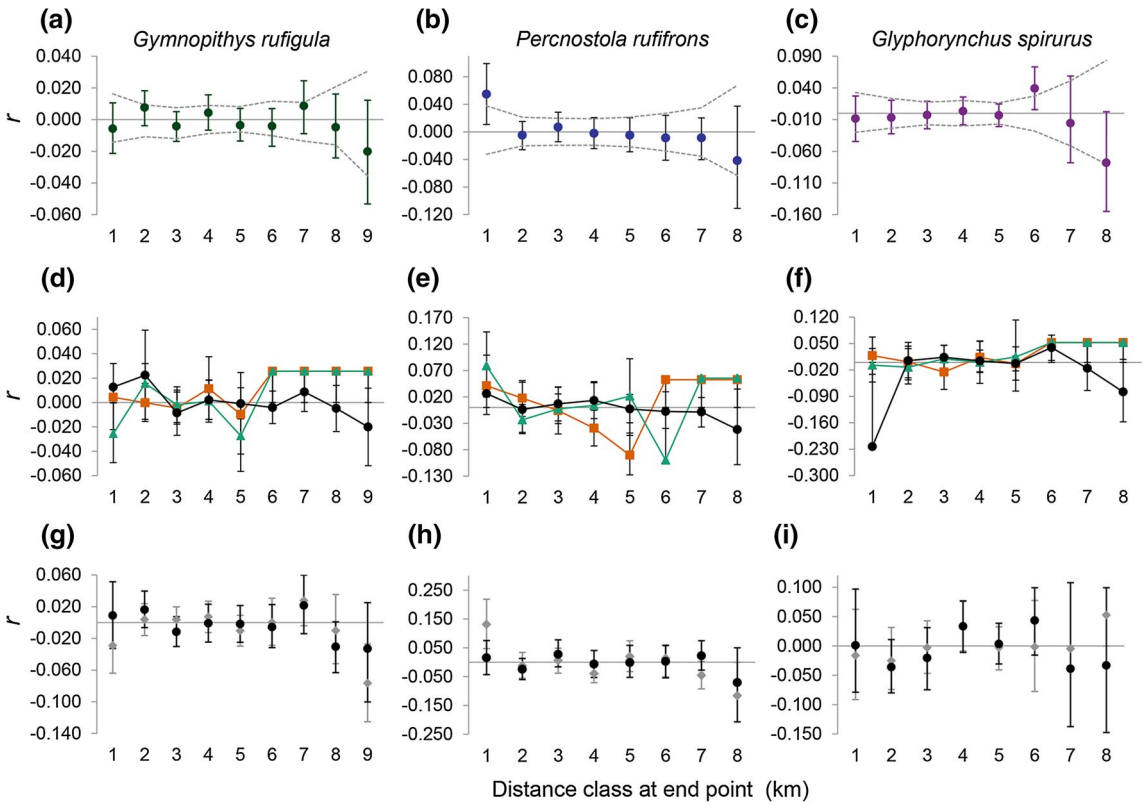

Fig. 3 Correlograms of the genetic autocorrelation coefficient *r* as a function of distance generated from 80 *Gymnopithys rufigula* individuals (**a***), 39 *Percnostola rufifrons* individuals (**b**) and 40 *Glyphorynchus spirurus* individuals (**c**) within DFR. Comparisons between western–western (green triangles), eastern–eastern (orange squares) and opposite-watershed (black circles) pairs are shown for the three species (**d**, **e** and **f**, respectively); as well as comparisons between males (black circles) and females (grey diamonds) of each species (**g***, **h** and **i**, respectively). The 95% bootstrapped (error bars) and permuted (dashed lines) confidence intervals are shown for distance classes of 1 km. Asterisk adapted from Menger et al. (2017b) (colour figure online)

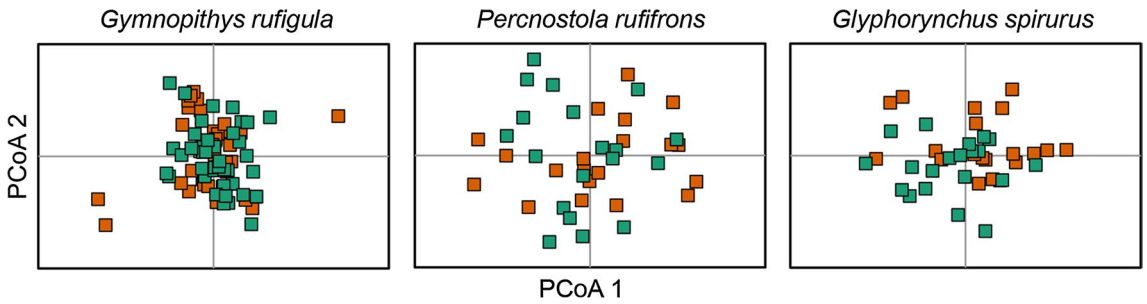

Fig. 4 Principal coordinate analysis (PCoA) based on Lynch–Ritland pairwise genetic relatedness for each study species. Orange squares represent individuals sampled in the eastern watershed and green squares represent individuals sampled in the western watershed of the DFR (colour figure online)

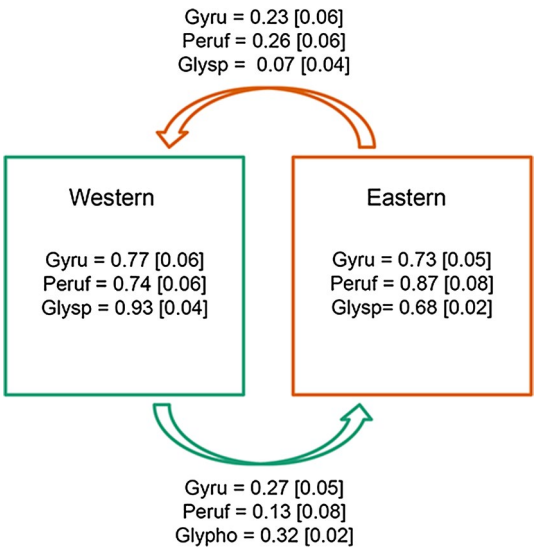

Fig. 5 Contemporary gene flow in DFR. Numbers within boxes denote the proportion of individuals expected to remain within a given watershed [± SD]; arrows indicate direction of gene flow, while numbers above/below arrows indicate the proportion of immigrants [± SD]. Gyru *Gymnopithys rufigula*, Peruf *Percnostola rufifrons*, Glysp *Glyphorynchus spirurus*

gene flow from the eastern to the western watershed was found for *P. rufifrons*, while *Glyphorynchus spirurus* displayed the opposite pattern (Fig. 5).

Discussion

In this study, we present new and additional information on the local, within-population genetic structure of three relatively sedentary Amazonian understorey birds: *Gymnopithys rufigula*, *P. rufifrons* and *Glyphorynchus spirurus*. None of the three species showed strong evidence for genetic structuring at the scale of this study, an indication that individuals are able to disperse occasionally distances as great as 10 km. We did not find differences in spatial genetic structure between sexes, suggesting that males and females of all three species disperse similarly. Individuals were not more related within a given watershed than between watersheds for any species, thus refuting the hypothesis of the ridgeline as a dispersal barrier within DFR. However, our analyses of contemporary gene flow showed individuals of all species tending to stay within their original watershed, rather than emigrating, with no consistency in the direction of gene flow among species. The number of species examined at this scale is still small, but our results agree with the general idea that ecological characteristics influence levels of genetic structuring in sedentary Neotropical birds (Burney and Brumfield 2009).

Spatial genetic structure and foraging behaviour

Foraging behaviour and sociability in insectivorous forest-understorey Neotropical birds are tightly linked. Species that mandatorily join interspecific flocks to forage tend to range more widely than do solitary species (Stouffer and Bierregaard 1995; Van Houtan et al. 2006). Obligate army-ant followers can move distances greater than 5 km (Van Houtan et al. 2007), while most solitary species do not move farther than 300 m from their territories (Laurance et al. 2004). Although obligate army-ant-following birds, such as the *Gymnopithys rufigula*, lack feeding territories and may range widely when tracking army-ant colonies, they maintain small roosting/nesting territories (Willis and Oniki 1978). In species with small well-defended territories, juveniles may have to disperse greater distances to find a breeding space. On the other hand, large foraging ranges give more chances for extra-pair copulations, and this would favour genetic dispersal. Although extra-pair copulations are likely to be much less important than dispersal of juveniles for genetic structuring, both mediate gene dispersal and, therefore, should reduce genetic structure at finer scales (Double et al. 2005).

Nevertheless, we might expect *Gymnopithys rufigula* to display some degree of genetic structuring in their roosting/nesting territories. Because we sampled birds systematically

throughout DFR, and caught individuals randomly, we cannot tell which activity they were engaged in—feeding, roosting or nesting—at the time of capture. As such, relatedness between nearest roosting/nesting neighbours might have been overlooked in our study. Chaves-Campos and DeWoody (2008) have found similar overall results for another army-ant-following bird, and demonstrated that even nearest roosting/nesting neighbours lack fine scale genetic structure. Therefore, we are confident that the absence of genetic structure within the *Gymnopithys rufigula* population is not an artifact created by our sampling design. As we did not detect any genetic structure at the scale of DFR, studies encompassing larger areas will be necessary to detect the scale at which genetic structuring occurs within populations of *Gymnopithys rufigula*.

Percnostola rufifrons was the only species to show a positive spatial genetic structure at short distances, indicating stronger dispersal limitation for this species. It is not surprising, considering that this is a solitary insectivorous bird that has very small territories (Zimmer and Isler 2003). Four subspecies of *P. rufifrons* are currently recognized, with their distributions assumed to be delimited by wide Amazonian rivers (Isler et al. 2001). At local scales, however, little is known about dispersal barriers for this species, as forest gaps and narrow roads through a forest do not prevent its movements, as they do for other solitary species (Laurance and Gomez 2005; Laurance et al. 2004). Our results also suggest that local-scale topographic features, such as the central ridgeline of the DFR, are not enough to impede, but possibly reduce, dispersal of *P. rufifrons*. In any case, our spatial autocorrelation analyses showed that individuals located within 1 km tend to be more related than at random, confirming that this solitary species is more dispersal-limited than the flocking species. While physical features do not seem to act as dispersal barriers for *P. rufifrons* at fine scales, other intrinsic dispersal limitations, such as habitat preferences, mate choice (Fletcher et al. 2015; Vasudev and Fletcher 2016) and juvenile dispersal behaviour are likely to explain patterns of dispersal and gene flow within its populations.

The smallest of the three species, *Glyphorynchus spirurus*, is a taxonomically polytypic species, with at least 13 subspecies recognized (Marantz et al. 2003). Similarly to *P. rufifrons*, major Amazonian rivers delimit the distribution of *Glyphorynchus spirurus* subspecies (Fernandes et al. 2013), as does the Andean cordillera (Milá et al. 2009). At local scales, previous field observations and recapture studies have indicated high site fidelity for adult *Glyphorynchus spirurus* (Blake and Loiselle 2012). Although we expected the development of fine-scale genetic structure in this species, it is not always safe to infer genetic dispersal from behavioural observations of adult individuals, as genetic dispersal generally occurs through juveniles, i.e., natal dispersal (Greenwood and Harvey 1982; Koenig et al. 1996). However, we did find *Glyphorynchus spirurus* at a distance class of 6 km to be more related than expected by chance. Thus, its genetic patch size, i.e., the distance over which individuals were not genetically independent (Sokal and Wartenberg 1983), appears to be about 7 km (when the autocorrelation coefficient r decreases to zero). This result is also in accordance with Van Houtan et al. (2007), who estimated, based on long-term capture-recapture data, a maximum dispersal distance of 8 km for *Glyphorynchus spirurus*, when moving within continuous forests.

Males and females disperse similarly

Although female-biased dispersal is prevalent in birds (Greenwood 1980), we found no evidence of this; spatial genetic structure was similar between sexes, and males of all three species did not display greater r values than females. We consider these results suggestive, but not fully conclusive, as detecting differences in spatial genetic autocorrelation between sexes requires large sample sizes and extreme divergence between male and female dispersal (Banks and Peakall 2012).

Patterns of genetic relatedness between watersheds

We failed to detect differences in relatedness between watersheds; we found rather a random distribution of genotypes within DFR for all species. This indicates that the central ridge is not a strong barrier to gene flow for any of the study species. Neotropical understorey insectivorous birds are highly sensitive to forest disturbance and their movements are often reduced in human-modified landscapes (Powell et al. 2015a), but in continuous old-growth forests, birds tend to move further (Powell et al. 2015b, 2016; Van Houtan et al. 2007). Our results are in agreement with these studies, suggesting, furthermore, that small topographic barriers are not enough to restrict gene flow in largely undisturbed old-growth forests, such as that encountered at DFR. Moreover, the overall low relatedness within DFR suggests that kin do not remain spatially clustered and that costs of longer distance dispersal may be less than the costs of mating with a spatially closer relative. Low relatedness could also indicate high rates of extra-pair fertilizations; all three species are socially monogamous, but the extent to which they are genetically monogamous is unknown. Nonetheless, refined biological and ecological data that could help us to comprehend how the genetic relatedness of birds is affected by dispersal and mating behaviour are still scarce. A better understanding of the evolutionary significance of dispersal for these and other Amazonian understorey birds will only be achieved when both ecological and genetic data are available and combined (Double et al. 2005).

Gene flow

Due to the connection of DFR to larger stretches of forest on its eastern and northern borders, and thus a larger source population, we expected higher gene flow from the eastern to the western watershed. We found higher gene flow from the eastern to the western watershed only for *P. rufifrons*. Estimates of gene flow were similar in both directions in *Gymnopithys rufigula*, the species in our sample that had the least genetic structuring. *Glyphorynchus spirurus* even showed the opposite pattern: a higher proportion of individuals migrated from the western to the eastern watershed. Asymmetrical dispersal towards the east could be explained by this bird's high territoriality and site-fidelity, associated with the proximity of Manaus on the western borders of DFR. We recaptured most *Glyphorynchus spirurus* in the same plot in which they were originally captured, with one individual being recaptured in the same plot 5 years after its first capture (JM, *unpublished data*). This indicates that territories are largely occupied and dispersing juveniles have to move far east, as outside the western limits of DFR the environment is unsuitable, and areas through which birds could safely disperse no longer exist.

Conclusions

Our study shows that local topographic features do not prevent gene flow within populations of sedentary Amazonian understorey birds in continuous forests. To understand if restricted movements translate into reduced effective dispersal (i.e., gene flow), more studies that combine capture–recapture data and molecular approaches are needed (Alcaide et al. 2009). The development of fine-scale spatial genetic structure may depend on the ecological traits of the species, such as foraging behaviour and territoriality, longevity and behaviour of dispersing juveniles, though there are insufficient data to make firm conclusions. This possibility should be taken into account in the design of experimental studies encompassing several species. This study also emphasizes the need for further investigations of sex-biased dispersal, as patterns of dispersal between sexes of socially monogamous Neotropical birds remain poorly understood. Finally, temporal genetic sampling (Husemann et al. 2015) is warranted to follow the state of these populations in years to come, as the isolation of DFR from other areas of continuous forest seems inevitable.

Acknowledgements The Brazilian Science Funding Agency CAPES awarded a stipend to JM (Process 12401-12-9). The Brazilian Program for Biodiversity Research PPBio (Grant 457544/2012-0), the National Institute for Amazonian Biodiversity INCT-CENBAM (Grant 573721/2008-4) and the Brazilian Long-Term Ecological Research Project PELD (Grant 403764/2012-2) through the Brazilian National Research Council CNPq supported this study. Fieldwork infrastructure, guidance and technical support was provided by INPA, PPBio, PELD and the program Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA). The German Centre for Integrative Biodiversity Research-iDiv provided additional support for consumables.

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All activities involving birds were conducted under approval of the Brazilian Centre for Bird Conservation-CEMAVE (Permit 3576) and the Brazilian Biodiversity Authorization and Information System-SISBIO (Permit 34850). All necessary steps to minimize animal suffering during handling were taken and birds were never kept in captivity or injured by any means. None of the three studied species is globally threatened (BirdLifeInternational 2016).

References

Alcaide M, Serrano D, Tella JL, Negro JJ (2009) Strong philopatry derived from capture–recapture records does not lead to fine-scale genetic differentiation in lesser kestrels. J Anim Ecol 78:468–475. doi:10.1111/j.1365-2656.2008.01493.x

Antongiovanni M, Metzger JP (2005) Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. Biol Conserv 122:441–451. doi:10.1016/j.biocon.2004.09.005

Banks SC, Peakall ROD (2012) Genetic spatial autocorrelation can readily detect sex-biased dispersal. Mol Ecol 21:2092–2105. doi:10.1111/j.1365-294X.2012.05485.x

Barnett JR, Woltmann S, Stenzler L, Bogdanowicz SM, Lovette IJ (2007) Isolation and characterization of microsatellite markers from the chestnut-backed antbird, Myrmeciza exsul. Mol Ecol Notes 7:1070–1072. doi:10.1111/j.1471-8286.2007.01780.x

Barnett JR, Ruiz-Gutierrez V, Coulon A, Lovette IJ (2008) Weak genetic structuring indicates ongoing gene flow across White-ruffed Manakin (Corapipo altera) populations in a highly fragmented Costa Rica landscape. Conserv Genet 9:1403–1412. doi:10.1007/s10592-007-9463-3

Bates JM (2002) The genetic effects of forest fragmentation on five species of Amazonian birds. J Avian Biol 33:276–294. doi:10.1034/j.1600-048X.2002.330310.x

BirdLifeInternational (2016) IUCN Red List for birds. http://www.birdlife.org on 05/12/2016

Blake JG, Loiselle BA (2012) Temporal and spatial patterns in abundance of the Wedge-billed Woodcreeper (Glyphorynchus spirurus) in lowland Ecuador. Wilson J Ornithol 124:436–445

Brown LM, Ramey RR, Tamburini B, Gavin TA (2004) Population structure and mitochondrial DNA variation in sedentary Neotropical birds isolated by forest fragmentation. Conserv Genet 5:743–757. doi:10.1007/s10592-004-1865-x

Brumfield RT, Tello JG, Cheviron ZA, Carling MD, Crochet N, Rosenberg KV (2007) Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). Mol Phylogenet Evol 45:1–13. doi:10.1016/j.ympev.2007.07.019

Burney CW, Brumfield RT (2009) Ecology predicts levels of genetic differentiation in Neotropical birds. Am Nat 174:358–368. doi:10.1086/603613

Chaves-Campos J, DeWoody JA (2008) The spatial distribution of avian relatives: do obligate army-ant-following birds roost

and feed near family members? Mol Ecol 17:2963–2974. doi:10.1111/j.1365-294X.2008.03811.x
Crochet PA (2000) Genetic structure of avian populations—allozymes revisited. Mol Ecol 9:1463–1469. doi:10.1046/j.1365-294x.2000.01026.x
Dawson DA et al (2010) New methods to identify conserved microsatellite loci and develop primer sets of high cross-species utility—as demonstrated for birds. Mol Ecol Resour 10:475–494. doi:10.1111/j.1755-0998.2009.02775.x
Dawson D et al (2013) High-utility conserved avian microsatellite markers enable parentage and population studies across a wide range of species. BMC Genomics 14:176. doi:10.1186/1471-2164-14-176
Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry, and infidelity: Dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). Evolution 59:625–635
Earl DA, vonHoldt BM (2011) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361. doi:10.1007/s12686-011-9548-7
Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol 14:2611–2620. doi:10.1111/j.1365-294X.2005.02553.x
Fernandes AM (2013) Fine-scale endemism of Amazonian birds in a threatened landscape. Biodivers Conserv 22:2683–2694. doi:10.1007/s10531-013-0546-9
Fernandes AM, 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. Mol Phylogenet Evol 66:270–282. doi:10.1016/j.ympev.2012.09.033
Fletcher RJ Jr, Robertson EP, Wilcox RC, Reichert BE, Austin JD, Kitchens WM (2015) Affinity for natal environments by dispersers impacts reproduction and explains geographical structure of a highly mobile bird. Proc R Soc B Biol Sci. doi:10.1098/rspb.2015.1545
Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162. doi:10.1016/S0003-3472(80)80103-5
Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. Annu Rev Ecol Syst 13:1–21. doi:10.1146/annurev.es.13.110182.000245
Gutiérrez-Pinto N, Cuervo AM, Miranda J, Pérez-Emán JL, Brumfield RT, Cadena CD (2012) Non-monophyly and deep genetic differentiation across low-elevation barriers in a Neotropical montane bird (Basileuterus tristriatus; Aves: Parulidae). Mol Phylogenet Evol 64:156–165. doi:10.1016/j.ympev.2012.03.011
Hardy OJ, Vekemans X (2002) Spagedi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol Ecol Notes 2:618–620. doi:10.1046/j.1471-8286.2002.00305.x
Hermes C, Döpper A, Schaefer HM, Segelbacher G (2016) Effects of forest fragmentation on the morphological and genetic structure of a dispersal-limited, endangered bird species. Nat Conserv 16:39–58. doi:10.3897/natureconservation.16.10905
Heywood JS (1991) Spatial analysis of genetic variation in plant populations. Annu Rev Ecol Syst 22:335–355. doi:10.1146/annurev.es.22.110191.002003
Husemann M, Cousseau L, Callens T, Matthysen E, Vangestel C, Hallmann C, Lens L (2015) Post-fragmentation population structure in a cooperative breeding Afrotropical cloud forest bird: emergence of a source-sink population network. Mol Ecol 24:1172–1187. doi:10.1111/mec.13105
Isler ML, Alonso JA, Isler PR, Whitney BM (2001) A new species of *Percnostola* antbirds (Passeriformes: Thamnophilidae) from Amazonian Peru, and an analysis of species limits within *Percnostola rufifrons*. Wilson Bull 113:164–176. doi:10.1676/0043-5643(2001)
Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806. doi:10.1093/bioinformatics/btm233
Johnson EI, Stouffer PC, Vargas CF (2011) Diversity, biomass, and trophic structure of a Central Amazonian Rainforest bird community. Braz J Ornithol 19:1–16
Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16:1099–1106. doi:10.1111/j.1365-294X.2007.03089.x
Karr JR (1976) Seasonality, resource availability, and community diversity in tropical bird communities. Am Nat 110:973–994
Khimoun A et al (2016) Habitat specialization predicts genetic response to fragmentation in tropical birds. Mol Ecol 25:3831–3844. doi:10.1111/mec.13733
Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517. doi:10.1016/S0169-5347(96)20074-6
Laurance SGW, Gomez MS (2005) Clearing width and movements of understory rainforest birds. Biotropica 37:149–152. doi:10.1111/j.1744-7429.2005.04099.x
Laurance SGW, Stouffer PC, Laurance WF (2004) Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia. Conserv Biol 18:1099–1109. doi:10.1111/j.1523-1739.2004.00268.x
Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. Genetics 152:1753–1766
Marantz CA, Aleixo A, Bevier LR, Patten MA (2003) Family Dendrocolaptidae (Woodcreepers). In: del Hoyo J, Elliott A, Sargatal J, Christie DA (eds) Handbook of the Birds of the World. Lynx Edicions Barcelona, pp 358–447
Menger J, Gerth M, Unrein J, Henle K, Schlegel M (2017a) Isolation and characterization of polymorphic microsatellite loci from the Rufous-throated Antbird Gymnopithys rufigula (Aves: Thamnophilidae). Wilson J Ornithol 129:407–411
Menger J, Henle K, Magnusson WE, Soro A, Husemann M, Schlegel M (2017b) Genetic diversity and spatial structure of the Rufous-throated Antbird (Gymnopithys rufigula), an Amazonian obligate army-ant follower. Ecol Evol 7:2671–2684. doi:10.1002/ece3.2880
Milá B, Wayne RK, Fitze P, Smith TB (2009) Divergence with gene flow and fine-scale phylogeographical structure in the wedge-billed woodcreeper, Glyphorynchus spirurus, a Neotropical rainforest bird. Mol Ecol 18:2979–2995. doi:10.1111/j.1365-294X.2009.04251.x
Moore RP, Robinson WD, Lovette IJ, Robinson TR (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecol Lett 11:960–968. doi:10.1111/j.1461-0248.2008.01196.x
O'Donnell S, Logan CJ, Clayton NS (2012) Specializations of birds that attend army ant raids: an ecological approach to cognitive and behavioral studies. Behav Proc 91:267–274. doi:10.1016/j.beproc.2012.09.007
Peakall ROD, Smouse PE (2006) Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295. doi:10.1111/j.1471-8286.2005.01155.x
Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update Bioinformatics 28:2537–2539. doi:10.1093/bioinformatics/bts460
Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, Rattus fuscipes. Evolution 57:1182–1195. doi:10.1111/j.0014-3820.2003.tb00327.x

Powell LL, Cordeiro NJ, Stratford JA (2015a) Ecology and conservation of avian insectivores of the rainforest understory: a pantropical perspective. Biol Conserv 188:1–10. doi:10.1016/j.biocon.2015.03.025

Powell LL, Wolfe JD, Johnson EI, Hines JE, Nichols JD, Stouffer PC (2015b) Heterogeneous movement of insectivorous Amazonian birds through primary and secondary forest: a case study using multistate models with radiotelemetry data. Biol Conserv 188:100–108. doi:10.1016/j.biocon.2015.01.028

Powell LL, Wolfe JD, Johnson EI, Stouffer PC (2016) Forest recovery in post-pasture Amazonia: testing a conceptual model of space use by insectivorous understory birds. Biol Cons 194:22–30. doi:10.1016/j.biocon.2015.11.025

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://beast.bio.ed.ac.uk/Tracer

Rousset F (2008) GENEPOP'007: a complete re-implementation of the genepop software for Windows and Linux. Mol Ecol Resour 8:103–106. doi:10.1111/j.1471-8286.2007.01931.x

Sandoval HJ, Gómez JP, Cadena CD (2016) Is the largest river valley west of the Andes a driver of diversification in Neotropical lowland birds? Auk. doi:10.1642/AUK-16-91.1

Şekercioğlu ÇH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sandí RF (2002) Disappearance of insectivorous birds from tropical forest fragments. Proc Natl Acad Sci 99:263–267. doi:10.1073/pnas.012616199

Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. Can J Zool 69:82–90. doi:10.1139/z91-013

Smith BT et al (2014) The drivers of tropical speciation. Nature 515:406–409. doi:10.1038/nature13687

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573. doi:10.1038/sj.hdy.6885180

Sokal RR, Wartenberg DE (1983) A test of spatial autocorrelation analysis using an isolation-by-distance model. Genetics 105:219–237

Stouffer PC, Bierregaard RO (1995) Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445. doi:10.2307/2265818

Suh A, Kriegs JO, Brosius J, Schmitz J (2011) Retroposon insertions and the chronology of avian sex chromosome evolution. Mol Biol Evol. doi:10.1093/molbev/msr147

Unrein J, Menger J, Weigert A, Henle K, Schlegel M (2017) Isolation and characterisation of novel polymorphic microsatellite markers for the Wedge-billed Woodcreeper Glyphorynchus spirurus. Avian Biol Res 10:24–26. doi:10.3184/175815617X14799886573066

Van Houtan KS, Pimm SL, Bierregaard ROJ, Lovejoy TE, Stouffer PC (2006) Local extinctions in flocking birds in Amazonian forest fragments. Evol Ecol Res 8:129–148

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecol Lett 10:219–229. doi:10.1111/j.1461-0248.2007.01004.x

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) Micro-checker: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538. doi:10.1111/j.1471-8286.2004.00684.x

Vasudev D, Fletcher RJ Jr (2016) Mate choice interacts with movement limitations to influence effective dispersal. Ecol Model 327:65–73. doi:10.1016/j.ecolmodel.2016.01.014

Weir JT (2009) Implications of genetic differentiation in Neotropical montane forest birds. Ann Mo Bot Gard 96:410–433. doi:10.3417/2008011

Willis EO, Oniki Y (1978) Birds and army ants. Annu Rev Ecol Syst 9:243–263

Willson SK (2004) Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. Ornithol Monogr. doi:10.2307/40166802

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Woltmann S, Kreiser BR, Sherry TW (2012) Fine-scale genetic population structure of an understory rainforest bird in Costa Rica. Conserv Genet 13:925–935. doi:10.1007/s10592-012-0341-2

Zimmer KJ, Isler ML (2003) Family Thamnophilidae (Typical antbirds). In: del Hoyo J, Elliot A, Christie DA (eds) Handbook of the birds of the world, vol 8. Broadbills to Tapaculos. Lynx Edicions, Barcelona, pp 448–681