


Exploring dispersal barriers using landscape genetic resistance modelling in scarlet macaws of the Peruvian Amazon

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Received: 18 July 2016 / Accepted: 20 October 2016 / Published online: 21 November 2016
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Abstract

Context Dispersal is essential for species persistence and landscape genetic studies are valuable tools for identifying potential barriers to dispersal. Macaws have been studied for decades in their natural habitat, but we still have no knowledge of how natural landscape features influence their dispersal.

Objectives We tested for correlations between landscape resistance models and the current population genetic structure of macaws in continuous rainforest to explore natural barriers to their dispersal.

Methods We studied scarlet macaws (*Ara macao*) over a 13,000 km² area of continuous primary Amazon rainforest in south-eastern Peru. Using remote sensing imagery from the Carnegie Airborne Observatory, we constructed landscape resistance surfaces

in CIRCUITSCAPE based on elevation, canopy height and above-ground carbon distribution. We then used individual- and population-level genetic analyses to examine which landscape features influenced gene flow (genetic distance between individuals and populations).

Results Across the lowland rainforest we found limited population genetic differentiation. However, a population from an intermountain valley of the Andes (Candamo) showed detectable genetic differentiation from two other populations (Tambopata) located 20–60 km away ($F_{ST} = 0.008$, $P = 0.001–0.003$). Landscape resistance models revealed that genetic distance between individuals was significantly positively related to elevation.

Conclusions Our landscape resistance analysis suggests that mountain ridges between Candamo and Tambopata may limit gene flow in scarlet macaws. These results serve as baseline data for continued

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-016-0457-8](https://doi.org/10.1007/s10980-016-0457-8)) contains supplementary material, which is available to authorized users.

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landscape studies of parrots, and will be useful for understanding the impacts of anthropogenic dispersal barriers in the future.

Keywords Population genetics · Dispersal · Movement ecology · Feathers · Microsatellites · Neotropics · Andes · Barriers · LiDAR

Introduction

Dispersal is an important ecological process as it allows individuals to locate new resources, avoid competition, and avoid inbreeding depression. On a larger scale, dispersal influences spatial population dynamics, maintains genetic diversity and enables adaptation (Clobert et al. 2012; McDougald et al. 2012; Szövényi et al. 2012; Orsini et al. 2013; Smith et al. 2016). Flight ability is assumed to be a good proxy for dispersal (Hanski et al. 2004; Kokko and López-Sepulcre 2006) as it often correlates with range size (Böhning-Gaese et al. 2006), but understanding what influences dispersal in flying species at a landscape scale is important. Both natural and man-made landscape features can impede gene flow, with roads, rivers, or mountain ridges being potentially impenetrable barriers for some species (Storfer et al. 2007). Direct tracking to infer dispersal across these structures is notoriously difficult (Schofield et al. 2013) but landscape genetics can help elucidate relationships between landscape features and gene flow (Manel et al. 2003; Storfer et al. 2007; Manel and Holderegger 2013), and identify potential dispersal barriers (Andrew et al. 2012).

The Amazon basin is a highly diverse and globally important ecosystem which is undergoing rapid changes such as continual development of highways and gold mining exploration at an enormous scale (Beheregaray and Caccone 2007; Asner et al. 2013; Baraloto et al. 2015; Keenan et al. 2015). To understand the effect of these changes on Amazonian fauna, we need baseline data about their biology and ecology in continuous, natural habitat. Macaws have been studied for decades in their natural habitat in south-eastern Peru, providing insights about their breeding biology (Brightsmith 2005; Vigo et al. 2011; Olah et al. 2014), foraging ecology (Brightsmith 2004), parasitology (Olah et al. 2013),

population dynamics (Lee and Marsden 2012), and conservation (Brightsmith et al. 2005). Nevertheless, knowledge about how natural landscape features affect their home-range and dispersal is still lacking.

Recent studies have shown contrasting results about genetic structure in macaws. For example, some studies found very low genetic differentiation among populations in continuous rainforest at scales of 100 km distance (Table 1), which might be expected given their large size and strong flying ability. Other studies, however, showed significant genetic differentiation between populations separated by only 80–170 km (Table 1). Unfortunately, these studies did not explicitly include spatial information in their genetic analyses and they had limited sample sizes mainly from nesting birds, limiting insights into the mechanisms behind these contrasting patterns. More progress can be made in understanding dispersal at landscape scales if spatial information about relevant habitat features is incorporated into landscape genetic analyses and more extensive, non-invasive samples are analyzed from a wide geographic scale (Andrew et al. 2013).

In the Peruvian Amazon, the preferred habitat of scarlet macaws (*Ara macao*) is considered to be lowland primary rainforest (Collar et al. 2016), consistent with the general pattern of macaw distribution noted by Forshaw (2011) to be up to 500 m above sea level (asl). Within our study site, the foothills of the Andes Mountains rise to over 1000 m asl and thus might act as natural barriers to their dispersal. Scarlet macaws also prefer riverside rainforest habitats with emergent trees so they can access the canopy from the side (Britt et al. 2014), and habitat suitability can influence gene flow (Wang et al. 2008). In this study we used population genetic structure analysis and landscape resistance modelling to test whether elevation, canopy height, river system and above-ground carbon distribution (biomass) might influence dispersal in macaws.

Methods

Study site and target species

This study was conducted in the Tambopata/Candamo region of the south-eastern Peruvian Amazon, including two large protected areas: (1) the Tambopata

Table 1 Previous population genetic studies of large macaws with varying scale and habitat among populations

Species	Countries	Comparison	Distance (km)	Habitat between populations	N	# Genetic markers	F_{ST}	P	References
Scarlet macaw (<i>Ara macao cyanoptera</i>)	Costa Rica	Two populations	80	Montane areas to the coast of the Pacific, roads	41; 55	7	0.048	<0.001	Monge et al. (2016)
	Guatemala and Belize	Two populations	170	Heavily degraded landscape (roads, agriculture)	13; 61	11	0.2	<0.001	Schmidt (2013)
	Guatemala	Among three focal breeding areas	<35	Primary rainforest	7; 8; 16	11	<0.009	>0.05	Schmidt (2013)
Hyacinth macaw (<i>Anodorhynchus hyacinthinus</i>)	Brazil	Two populations	100	Cerrado habitat	16; 16	4	0.05	0.12	Faria et al. (2008)
	Brazil	Two pairwise populations	1600	Heavily degraded landscape (roads, agriculture, cities)	6; 16; 16	4	>0.25	<0.001	Faria et al. (2008)

National Reserve (13°8'S, 69°37'W; 2747 km²) and (2) the Bahuaja-Sonene National Park (13°30'S, 69°47'W; 10,914 km²). The area is tropical moist forest receiving an average annual rainfall of 3236 mm (Brightsmith 2004). Elevation gradually increases from the Lower Tambopata (lowland rainforest with average elevation of 200 m), to Upper Tambopata (lowland rainforest closer to the foothills of the Andes Mountains, 260 m), and Candamo (intermountain valley, 350 m) surrounded by foothills of the Andes (up to 1300 m) that separate this region from Tambopata (Fig. 1).

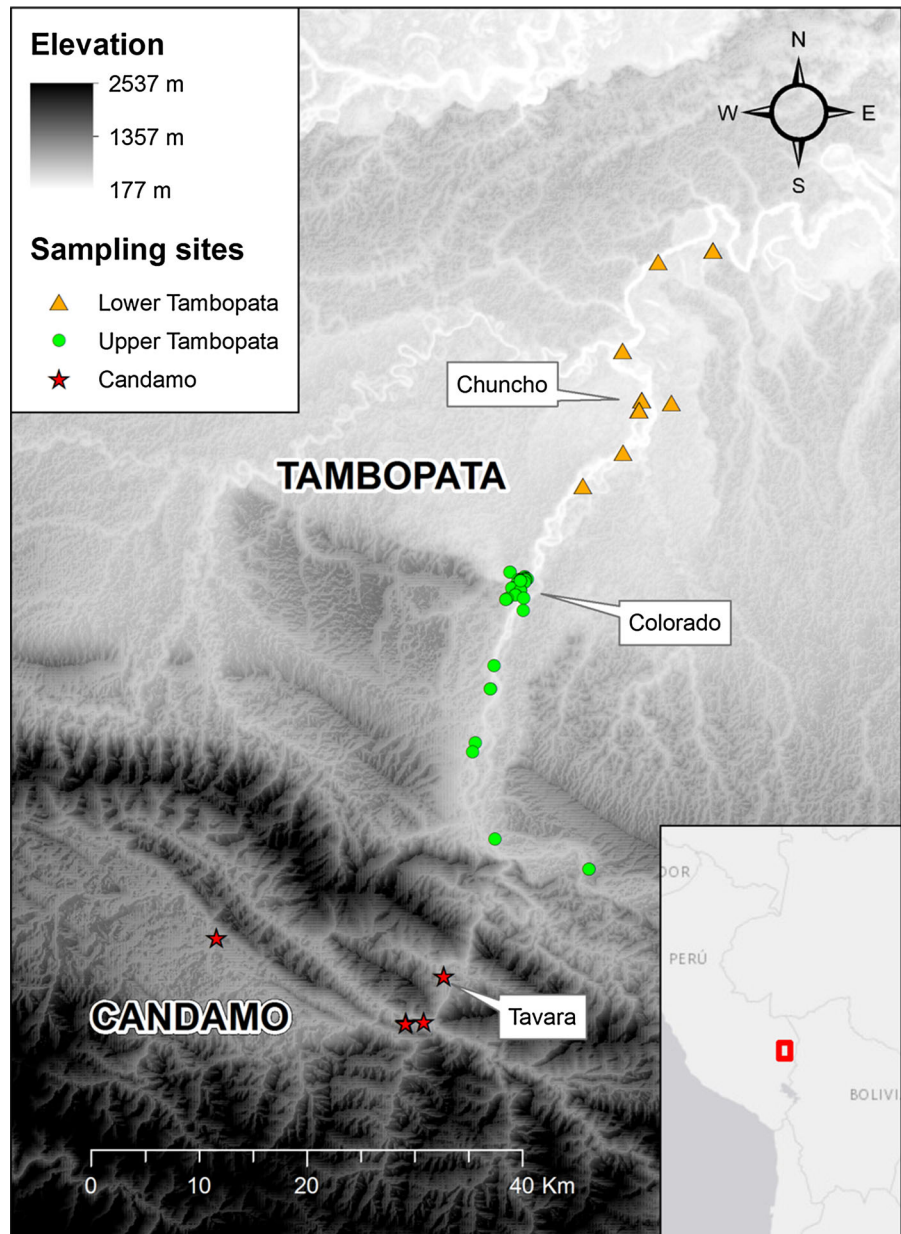
The distribution of the scarlet macaw extends from Mexico to Bolivia (BirdLife International and NatureServe 2014). Although population sizes are decreasing in some regions, they are presently listed as Least Concern with an estimated global population size between 20,000 and 50,000 individuals (IUCN 2014). They are secondary cavity nesters using hollows of emergent trees (Brightsmith 2005; Renton and Brightsmith 2009) and also occupy artificial nests in our study site (Olah et al. 2014).

Sample collection and genetic markers

A total of 166 DNA samples was collected during the breeding season (November–April) each year between 2009 and 2012. We collected 126 DNA samples non-invasively by sampling naturally shed feathers from nests, around nesting and roosting sites, and from clay licks (Fig. 1). We collected about 100 µL of blood from the jugular vein of 22 macaw nestlings and 18 adults in natural and artificial nests, accessed by using single-rope ascending techniques (Olah et al. 2014). Blood samples were stored in 70 % ethanol or on FTA paper (Whatman). When blood samples from known family units were identified, siblings or parent/offspring samples were excluded from the analyses (keeping samples of one parent whenever possible), so that only non-related individuals were included in the data set.

DNA was amplified at nine species-specific, polymorphic microsatellite markers: SCMA 09, SCMA 14, SCMA 22, SCMA 26, SCMA 30, SCMA 31, SCMA 32, SCMA 33, SCMA 34 (Olah et al. 2015). Genotyping errors were calculated from randomly selected samples that yielded full genotype data, and the markers selected in this study showed low or no error and low amplification failure (Olah et al. 2016).

Fig. 1 Locations of scarlet macaw (*Ara macao*) DNA samples in the foothills of the Andes, south-eastern Peru. Sampling sites were located around three major clay licks: Chuncho (N = 26), Colorado (N = 35), and Tavera (N = 19)



Molecular sexing of individuals was performed using the P8_SCMA_F/P2_SCMA_R primers (Olah et al. 2016).

Population-level genetic differentiation

We divided the study area into three sampling sites based on geographic location: Lower Tambopata (N = 54), Upper Tambopata (N = 82), and Candamo (N = 30), which were mainly aggregated around large

clay licks (Fig. 1). We used analysis of molecular variance (AMOVA) in GenAlEx 6.5 (Peakall and Smouse 2006, 2012) to partition genetic variation within and among these sampling sites and to estimate overall and pairwise population genetic differentiation (F_{ST}) (Wright 1965; Excoffier et al. 1992; Peakall et al. 1995). Tests for genetic differentiation were performed by 1000 random permutations. In order to assess if there was any bias in F_{ST} estimation given the uneven sample size, we performed AMOVA on

randomly subsampled sets of 30 samples from each site using the ‘shuffle’ function of GenAIEx. The means and standard errors were calculated across 10 replicates.

Individual-level population structure analysis

We used two different Markov chain Monte Carlo (MCMC) Bayesian clustering models to identify potential population genetic structure. The first was STRUCTURE 2.3.4 (Pritchard et al. 2000) for which we used the admixture model, correlated allele frequencies, and no location priors (Falush et al. 2003). Burn-in was set to 50,000 iterations, followed by 50,000 MCMC iterations and replicated 10 times for each value of the number of genetic clusters (K) from 1 to 5. We used STRUCTURE Harvester (Earl and vonHoldt 2012) to determine K (Evanno et al. 2005). The second analysis was conducted in GENELAND 4.0.0 (Guillot et al. 2005) which includes geographical coordinates for each individual. This inclusion makes it more sensitive to weak genetic structure than the STRUCTURE analysis because spatially adjacent individuals are more likely to be in the same cluster (Guillot et al. 2012). We used the uncorrelated allele frequency model (Guillot et al. 2005) with 500,000 MCMC repetitions (saving every 100th iteration), and allowed K to vary between 1 and 5, with 5 independent runs. We set spatial uncertainty of coordinates to 10 km based on estimated daily movements (Munn 1992). We also used individual multilocus spatial autocorrelation analysis for each sex separately (Smouse and Peakall 1999; Peakall et al. 2003) to investigate potential sex-biased dispersal.

Individual-level landscape resistance analysis

We conducted landscape resistance analyses at two scales: (1) across the whole study area including all individuals ($N = 166$) and (2) across a subset of the data ($N = 112$) focusing on Upper Tambopata and Candamo. The latter, finer-scale analysis allowed us to specifically examine if gene flow was restricted by the foothills of the Andes and this is the main geographic barrier separating these two areas.

We developed five landscape resistance models to examine whether topography and vegetation affected macaw gene flow. The models were based on maps

derived from the Carnegie Airborne Observatory (<http://cao.carnegiescience.edu>) using high-resolution radar and LiDAR (light detection and ranging) mapping technologies (Asner et al. 2012, 2014). Each was compiled on a separate raster grid with a 100 m (1 ha) resolution in ARCMAP 10.2 (ESRI). (1) The isolation-by-distance model (IBD) was a null model where each cell was given a value of one to investigate the effect of distance alone (Cushman et al. 2006). (2) The elevation model (Elev), based on a digital elevation model (meters above sea level), investigated the effect of topography on gene flow. (3) The tree canopy height (TCH) model considered the distribution of emergent canopy trees which are used by macaws as nests. This landscape feature might influence gene flow through an effect of habitat suitability [e.g., lower or higher gene flow in areas of preferred habitat (Smith et al. 2016)]. (4) The above-ground carbon distribution (ACD) model, representing biomass (Girardin et al. 2010) was used as a proxy for habitat complexity. Scarlet macaws in tropical rainforest prefer riverside habitats with gaps in the canopy that contain lower biomass (Britt et al. 2014). (5) The river distance model (Rio) was used to determine if the preferred riverside habitat of scarlet macaws acted as a dispersal corridor. This model was developed with a 500 m buffer zone at each side along the river system, with values of ‘1’ given to the cells of the grid within this buffer zone and ‘100’ outside of this zone, representing floodplain versus *terra firme* areas.

We used CIRCUITSCAPE 4.0.3 to generate landscape resistance values between each pair of individuals, taking into account all possible pathways (McRae and Beier 2007). To test the effect of the landscape on genetic distance, we used two different methods: Mantel and partial Mantel tests in a causal modelling framework (Cushman et al. 2006), and multiple regression of distance matrices (MRDM; Legendre et al. 1994). These methods were implemented in the ‘ecodist’ library (Goslee and Urban 2007) for R (R Core Team 2013) with P values based on 5000 permutations.

Causal modelling began with simple Mantel tests of IBD and all other resistance models. We then conducted partial Mantel tests to assess the significance of relationships between genetic distance and landscape resistance, given the spatial distance between samples (Partial 1). We assessed significance using one-tailed P -values for simple Mantel tests

($\alpha = 0.05$) and two-tailed P values for partial Mantel tests (Goslee and Urban 2007). Elevation was an exception to this, as we predicted resistance would increase with elevation and thus report a one-tailed P value for that model. When there was a significant correlation in the first partial Mantel test, we calculated the effect of the IBD model on genetic distance while controlling for the landscape resistance model (Partial 2). Where Partial 1 was significant and Partial 2 was nonsignificant, we inferred significant effects of the landscape resistance model on genetic distance, beyond the effects of geographic distance (Cushman et al. 2006; Smith et al. 2014). For MRDM, we analysed the IBD model separately and then together with each other resistance model. Thus, these models included one predictor for IBD and a maximum of two predictor variables for all other models (Smith et al. 2016).

We generated cumulative current maps for every pair of samples with CIRCUITSCAPE to identify areas which contribute most to connectivity between sample sites (McRae et al. 2013). Maps were visualized in QGIS 2.14 (<http://www.qgis.org>).

Results

Population genetic analyses

Among the 166 scarlet macaws in our data set, the mean allele number was 15.7 and mean expected heterozygosity was 0.884 (Table S1). We identified 74 males and 69 females (23 unknown) using the sexing markers. STRUCTURE and GENELAND indicated a single genetic cluster and lack of population boundaries among all individuals at both a large- and small scale. Results from STRUCTURE Harvester and GENELAND are given in Fig. S1 of the supplementary material. The AMOVA analysis revealed a low but significant level of genetic differentiation among the three populations ($F_{ST} = 0.005$, $P = 0.001$). The Candamo population was significantly different from the other two populations (Lower Tambopata $F_{ST} = 0.008$, $P = 0.003$; Upper Tambopata $F_{ST} = 0.008$, $P = 0.001$), driving the overall significant differentiation. Upper and Lower Tambopata populations were not significantly different ($F_{ST} = 0.001$, $P = 0.199$).

The replicated AMOVA analysis at equal sample sizes ($N = 30$) across the three populations showed very similar results (mean $F_{ST} = 0.005$, $SE = 0.0005$, 10 replicates) indicating little or no bias in estimation due to the sample size variation. The replicated pairwise population comparisons also showed similar results to the full analysis for Candamo versus Lower Tambopata (mean $F_{ST} = 0.007$, $SE = 0.0007$, 10 replicates), Candamo versus Upper Tambopata (mean $F_{ST} = 0.008$, $SE = 0.001$, 10 replicates), and Upper-versus Lower Tambopata (mean $F_{ST} = 0.002$, $SE = 0.0004$, 10 replicates).

No significant patterns of spatial genetic structure were detected by spatial autocorrelation analysis of individual-by-individual genetic distance when females and males were analyzed separately (Fig. S2), thus there was no evidence of sex-biased dispersal.

Landscape resistance models

There were no significant effects of the landscape resistance models at the large scale (whole study area). However, at the small scale, we found a significant effect of elevation on genetic distance between Candamo and Upper Tambopata ($r_M = 0.128$, $P = 0.02$; Table 2; Fig. 2). Both isolation-by-distance and elevation (max. 1200 m) were significant explanations of the genetic distance in a simple Mantel test and in the MRDM analysis (Mantel $P_{IBD} = 0.021$, $P_{Elev} = 0.01$; MRDM $P_{IBD} = 0.031$, $P_{Elev} = 0.021$; Table 2; Fig. 2). Isolation-by-distance was not significant when controlling for elevation in the partial Mantel test ($r_M = -0.104$, $P = 0.98$; Table 2), indicating that elevation, not geographic distance on its own, influences genetic distance between individuals.

Discussion

To our knowledge, this is the first study to combine population genetic analysis with spatially-explicit habitat information in a landscape genetic study of parrots. Our study in the Amazon rainforest habitat of scarlet macaws, where no high mountain ranges exist, suggested extensive gene flow and high dispersal ability. Nevertheless, we found evidence for some restriction of their gene flow in the foothills of the Andes Mountains indicating that high mountain

Table 2 The effect of geographic distance (IBD) and landscape resistances (ACD, Elev, TCH, Rio) on genetic distance in scarlet macaw (*Ara macao*) using causal modelling and multiple regression of distance matrices (MRDM)

Scale of analysis	Mantel test type	Predictor	Mantel test		MRDM	
			r_M	P	R^2	P
Large scale (N = 166) three populations	Simple	IBD	0.023	0.201	0.001	0.385
	Simple	ACD	0.022	0.548	0.001	0.833
	Simple	Elev	0.054	0.088	0.007	0.148
	Simple	TCH	0.024	0.474	0.001	0.826
	Simple	Rio	−0.023	0.713	0.001	0.667
	Partial 1	ACD IBD	0.004	0.944		
	Partial 1	Elev IBD	0.080	0.063		
	Partial 1	TCH IBD	0.006	0.914		
	Partial 1	Rio IBD	−0.029	0.632		
	Partial 2	IBD Elev	−0.063	0.914		
Small scale (N = 112) two populations	Simple	IBD	0.080	0.021	0.006	0.031
	Simple	ACD	0.064	0.144	0.007	0.280
	Simple	Elev	0.110	0.010	0.023	0.021
	Simple	TCH	0.071	0.080	0.007	0.276
	Simple	Rio	−0.009	0.889	0.007	0.263
	Partial 1	ACD IBD	−0.031	0.640		
	Partial 1	Elev IBD	0.128	0.020		
	Partial 1	TCH IBD	−0.027	0.681		
	Partial 1	Rio IBD	−0.033	0.632		
	Partial 2	IBD Elev	−0.104	0.980		

For partial Mantel tests, genetic distance (y) was modeled as a function of x given z ($y \sim x|z$). Significant effects are shown in bold. All regression analyses included IBD either alone or with one other spatial predictor variable

IBD isolation by distance, ACD aboveground carbon distribution, Elev elevation above sea level, TCH tree canopy height, Rio river distance

ranges can impose dispersal limitations to macaws. Given the large and rapid changes occurring in the Amazon, our results provide a valuable baseline from which to compare future studies of global change in this region.

Isolation-by-elevation at the Andean foothills

Both of our landscape genetics analysis methods (causal modelling and MDRM) indicated significant isolation-by-elevation between two populations of macaws separated by only 20 km of mountain ridges over 1000 m in the Andean foothills. This suggests that elevation can form a natural dispersal barrier, influencing gene flow even in large, strong flying species.

Our results about the genetic differentiation in Candamo (Table 2) might point towards more restricted gene flow between the birds in this valley and the two lowland populations separated by high (about 1000 m) foothills of the Andes (Fig. 1). A recent satellite telemetry study in Upper Tambopata (ten tagged scarlet macaws) estimated their 9-month home range to be 1730 km² (J. Boyd and D. J. Brightsmith, unpublished data). In that study, movements always occurred to the north-east (away from the foothills) up to 150 km but they always returned to the same area or even the same nest hollow to breed. They flew much further than the distance between Candamo and Tambopata but none of the tagged macaws were detected in Candamo, or even flew near to the foothills.

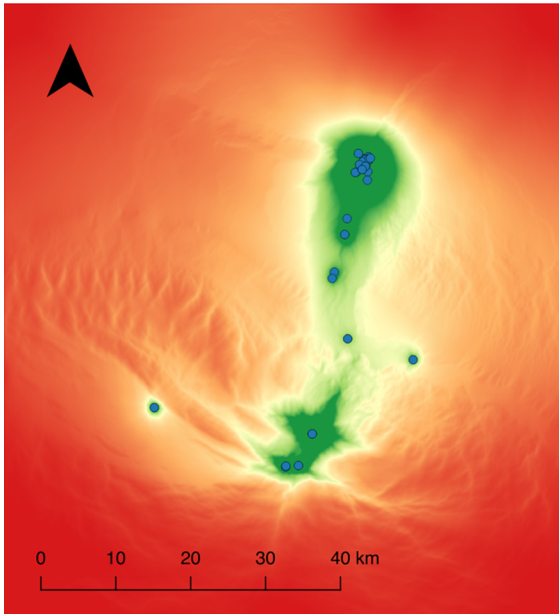
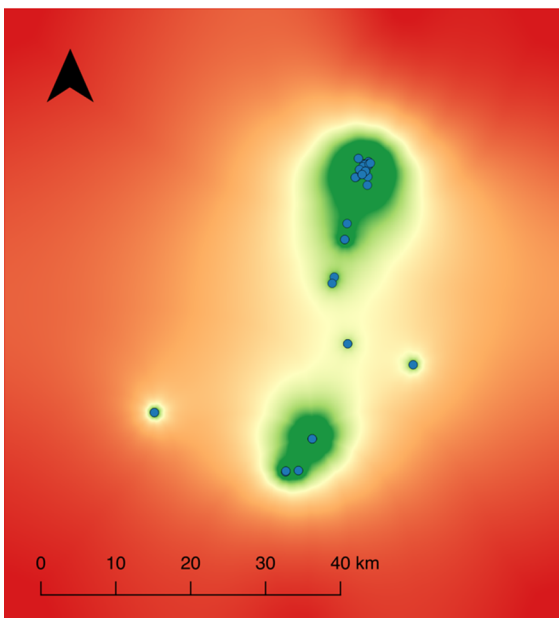
(A) Elevation model (Elev)**(B) Isolation-by-distance (IBD) model**

Fig. 2 Cumulative resistance maps of CIRCUITSCAPE models for scarlet macaws (*Ara macao*) in the Peruvian Amazon. Colors indicate the predicted areas of conductance (*green*) and resistance (*red*) among the samples (*blue circles*). The analysis was based on samples from Candamo and Upper Tambopata sites. (Color figure online)

Although they fly long distances, the philopatry and nest fidelity of these macaws suggest that dispersal rarely occurs over large scales. Furthermore, our results suggest that movements of birds between the valley of Candamo and the lowland might be limited by the high elevation. Despite the significant genetic differentiation between Candamo and Tambopata, the low magnitude of F_{ST} indicates that dispersal does occur between these areas. The only obvious connection between Candamo and the lowland Tambopata is a small river which cuts through multiple parallel mountain ridges (Fig. 1). The cumulative current maps highlight this river as a conductance funnel (Fig. 2) potentially providing the corridor for gene flow. Although our river model showed no significant correlation itself with the genetic structure, its effect was incorporated into the elevation model as rivers also represent the lowest elevation in the landscape.

Dispersal models show that birds may evolve to avoid risky movements even if they are capable of doing so (Shaw et al. 2014). The dispersal of scarlet macaws from Candamo might be explained by a combination of habitats, river system, and elevation gradients. Other factors like unsuitable habitat, temperature or humidity might also influence gene flow but data were not available for analysis in the current study. In future, these data and more detailed LiDAR maps could be used to explore spatial patterns of gene flow in finer detail.

Despite parrots and macaws being noted for their capability of flying long distances over large landscapes (Faria et al. 2008), our landscape resistance models indicate that high elevation might create barriers for these species. Landscape resistance has also been implied by the work of Monge et al. (2016) who attributed the observed genetic differentiation between two large scarlet macaw populations of Costa Rica (Table 1) to montane barriers rather than recent habitat fragmentation. The central cordilleras of Costa Rica and Panama ranging in elevation from 500 to 3800 m are recognized to separate the two subspecies of scarlet macaw (Schmidt 2013), further suggesting that mountains can act as geographic barriers for macaws.

Recent studies have raised concerns about using partial Mantel tests in landscape genetics because they

assume linearity between distance matrices (Legendre and Fortin 2010) and disregard information about other factors (e.g., mating and dispersal) influencing gene flow (Graves et al. 2013). Despite problems with partial Mantel tests, simple Mantel tests are appropriate for testing isolation by distance (Guillot and Rousset 2013), so our results of IBD in scarlet macaws are unlikely to be biased. Furthermore, both causal modelling and MRDM analyses indicated similar effects of elevation on gene flow in macaws, giving us greater confidence in our findings.

Population structure of scarlet macaws in Tambopata

Previous studies on macaws (Table 1) suggested low genetic differentiation among populations living in undisturbed habitat. Our study site consists of two adjacent protected areas with a total area of more than 13,000 km² of primary rainforest. The Bayesian approaches could not detect any population structure in our samples from Tambopata. We identified 74 males and 69 females (23 unknown) among our samples, but we did not detect any sex-biased dispersal. In monogamous species like macaws, competition for both mates and resources is likely to affect both sexes equally, leading to predictions of equal rates of dispersal (Dobson 1982).

Implications for conservation

Understanding landscape effects on gene flow is important for conservation management (Segelbacher et al. 2010; Keller et al. 2015), but these patterns are still unknown for most species. Macaws still inhabit a large nationally-protected lowland rainforest in Tambopata, but the rapidly growing human population along the recently built inter-oceanic highway is a serious conservation issue in the region (Tickell 1993; Conover 2003; Baraloto et al. 2015). The apparently natural population of macaws within this area has allowed us to obtain baseline data that may become useful for future conservation genetic studies, for example evaluating macaw response to human induced habitat fragmentation. The Candamo valley and its vicinity, which is also a biological hotspot, is of commercial interest for oil extraction and gold mining

activities (Finer et al. 2008; Asner et al. 2013). Repeated DNA sampling over the same area could also be compared to our results in the future, to see if accelerated habitat degradation could push the species to cross previously avoided natural barriers like high mountain ridges.

Conclusion

In our study of scarlet macaws, we found no evidence for strong population genetic structure across the lowland of Tambopata (over 80 km). These results indicate that gene flow is extensive and correlates with the large home range of these birds. We found evidence of a single population of scarlet macaws in Tambopata, over a large protected area. However, our study also suggests that high elevation might act as a natural barrier to gene flow, as the Candamo population situated behind mountain ridges was genetically differentiated from the other lowland populations. Intermountain rainforest valleys similar to Candamo can host other populations of scarlet macaws over their distribution range. The Candamo valley also hosts a large diversity of other species, some with much more restricted dispersal movements than large macaws. Our findings provide baseline information about natural dispersal barriers in parrots that can assist in understanding the influence of rapid anthropogenic change on their genetic population structure in the Amazon Basin.

Acknowledgments This research was funded by the Loro Parque Foundation, Rufford Small Grant Foundation, Idea Wild, and The Australian National University. Thanks for technical laboratory support to Christine Hayes and Cintia Garai. We thank for the laboratory space provided by the Unidad de Biotecnología Molecular, Laboratorio de Investigación y Desarrollo, Universidad Peruana Cayetano Heredia in Lima, Peru. We thank to Janice Boyd, Texas A&M University to provide us preliminary results from the satellite telemetry analysis on scarlet macaws in Tambopata. Samples were collected under research permits from the Servicio Nacional de Areas Naturales Protegidas (SERNANP) in Peru. CITES permits were provided by the Peruvian and Australian authorities. Genetic access to the samples was granted by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) in Peru. The Animal Experimentation Ethics Committee of the Texas A&M University approved all methods. The Carnegie Airborne Observatory portion of this study was supported by a grant to G.P.A. from the John D. and Catherine T. MacArthur Foundation. Two anonymous referees provided helpful comments that improved the manuscript.

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