



Messing about on the river: the role of geographic barriers in shaping the genetic structure of Bornean small mammals in a fragmented landscape

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Abstract

Landscape features may restricting dispersal and gene flow, and increase demographic isolation among sub-populations. In addition, landscape features may represent potential dispersal barriers depending on species vagility. To predict the persistence of populations and to formulate adequate conservation measures it is essential to understand the ability of species to transverse landscape barriers. Using population genetic techniques we assessed the importance of physical barriers along the Kinabatangan River for a suite of non-volant small mammals. *Cytochrome b* sequence variation was examined for each of the 19 species sampled across both riverbanks. Haplotype networks and molecular variance analyses indicated contrasting patterns of genetic isolation between riversides for different taxa. Genetic isolation between riversides ranged from moderate to complete in tree shrews and squirrels, whereas no isolating effect could be detected in murids and gymnures. Although genetic divergence between forest fragments on the same side of the river could only be studied in a subset of six species, the results suggest an additional dispersal barrier for two of these studied species. While barrier effects of a paved road and tributaries could not be verified, large oil palm plantations seem to have disrupted gene flow in these species. Furthermore, the findings suggest higher genetic connectivity on the more continuously forested compared to the more fragmented river-side, and underline the importance of forest corridors as essential conservation measures to maintain genetic diversity in a fragmented landscape such as that along the Kinabatangan River.

Keywords Small mammals · Geographic barriers · Dispersal · Landscape fragmentation · Gene flow · Borneo

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Introduction

Dispersal is the primary behavioural mechanism determining gene flow within and among populations and has substantial effects on the genetic structure. Its restriction leads to a reduction or interruption of gene flow, a decreased genetic diversity within and increased genetic differentiation among populations (Broquet and Petit 2009). Especially in populations with a low effective population size, increased inbreeding can easily occur and cause inbreeding depression, i.e. may decrease the fitness of individuals (Freeland 2008). In the long term, the evolutionary potential of the population may be lost, and the risk of extinction increases (Frankham 2005). As a consequence, the ability of species to cope with habitat changes and reduced landscape connectivity determines the distribution and viability of species (Garant et al. 2007).

The use of genetic data has suggested an important role of geographic landscape features such as rivers in shaping

the ecological and genetic variation of species (Geffen et al. 2004; Trizio et al. 2005; Coulon et al. 2006). Geographic features may compound the effect of fragmentation, restricting dispersal capabilities even further. Furthermore, in anthropogenically modified forest landscapes structural conditions often differ strongly from the original habitat and canopy gaps open up. Numerous species have limited tolerance to such structural variation and are unable to cross these barriers, resulting in dispersal limitations and genetic changes within and among populations (McDonald and St. Clair 2004; Heidinger et al. 2013; Edwards et al. 2014; Janecka et al. 2016; Fahrig 2017). Therefore, assessing the effects of geographic features on the distribution of species has become essential to inform conservation measures that typically aim to improve the genetic connectivity between subpopulations (Prevedello and Vieira 2010).

Tropical small mammals form highly diverse and structured ecological communities and differ greatly in their life history traits and ecological requirements (Wells et al. 2007), thus making a good model system to assess the importance of geographical barriers on patterns of genetic diversity for species with different ecological requirements.

The Kinabatangan River in north-eastern Borneo is the longest river in Sabah, Malaysia. Large-scale logging activities and habitat conversion in this highly productive floodplain has created a mosaic of fragmented forest and oil palm plantations. Embedded in this mosaic, forest connectivity has been disrupted by landscape features such as river tributaries, plantations and a paved road. Goossens et al. (2006) demonstrated that orang-utan dispersal is negatively affected by fragmentation in this landscape, leading to decreased gene flow and reduced genetic diversity. In addition, the Kinabatangan River itself represents a major barrier for dispersal and has an important role in shaping orang-utan genetic structure (Goossens et al. 2005; Jalil et al. 2008). However, such knowledge is still lacking for Bornean small mammal species.

Recent studies in other regions of the world have demonstrated the importance of rivers as barriers to gene flow (Oshida et al. 2011; Rocha et al. 2011; Ćosić et al. 2013), and verified the strong effect of anthropogenically modified landscapes on dispersal capabilities and genetic connectivity in small mammals (Gerlach and Musolf 2000; Trizio et al. 2005; Stephens et al. 2013; Bani et al. 2017). But most studies investigating the effect of geographic barriers on dispersal and genetic structure have mainly focused on a single species (Patton et al. 1994; Colombi et al. 2010; Nicolas et al. 2011; Ćosić et al. 2013; Russo et al. 2016), or few species from the same genus (Kennis et al. 2011; Oshida et al. 2011; Rocha et al. 2014). This study is to our knowledge the first investigating the influence of different landscape features on migration and population connectivity in a comprehensive community of Bornean small mammals.

Non-volant small mammals represent one of the largest and most diverse mammalian groups on Borneo and comprise various species of Rodentia, Scandentia, and Eulipotyphla (Payne and Francis 2007; Phillipps and Phillipps 2016). Due to the scarcity of available information on their dispersal (e.g. Emmons 2000; Wells et al. 2006a, 2008a, 2008b; Nakagawa et al. 2007; Shadbolt and Ragai 2010), nothing is known about the influence of geographic and man-made landscape features on their migration and genetic structuring. However, species affinities to water and swimming abilities should be crucial for maintaining gene flow across geographic features such as large rivers. Constraints on dispersal due to the presence of the Kinabatangan River are thus predicted to lead to a decrease in gene flow between populations from either side, and increased population genetic differentiation should exist between the two riversides. On the other hand, gene flow across the river can be expected in species which have an affinity to water and good swimming capabilities such as murid rodents (Evans et al. 1978; Cook et al. 2001; Nicolas and Colyn 2006; Santori et al. 2008). This has, for example, been confirmed in various Neotropical murid rodents (e.g. Patton et al. 1994; Colombi et al. 2010; Roratto et al. 2014). Furthermore, it can be expected that isolated or dissected forest fragments (e.g. by road or plantation) should show larger genetic discontinuities and a higher genetic differentiation than fragments connected by forest corridors. Moreover, invasive and generalist species (e.g. *Rattus* spp., plantain squirrels) are known to be more tolerant to anthropogenic habitat modifications (Nakagawa et al. 2006; Francis 2008; Phillipps and Phillipps 2016), and therefore predicted to be less strongly affected by forest fragmentation than strictly forest dependent rodents and tree shrews (Emmons 2000; Francis 2008; Phillipps and Phillipps 2016).

The aim of this study is to test the influence of the Kinabatangan River and its tributaries, and other fragmenting landscape features such as plantations, and a road on the genetic structure and gene flow of non-volant small mammals. In addition to these landscape features, life history and sex-specific reproductive strategies are important in shaping population structure (Chambers and Grant 2010). The spatio-temporal variability in resources, competition, and inbreeding avoidance are crucial drivers of dispersal (e.g. Greenwood 1980; Smale et al. 1997; Lawson Handley and Perrin 2007) and sex-specific differences in the benefits of philopatry often lead to a sex bias in dispersal (e.g. Greenwood 1980; Lawson Handley and Perrin 2007; Galliard et al. 2012; Mabry et al. 2013). Due to differences in the dispersal and reproductive behaviour of males and females, genetic structure may differ between sexes. We therefore also investigated the genetic variation in males and females separately to infer the dispersal regime for the study species.

The relatively rapid mutation rate of mitochondrial (mtDNA) compared to nuclear DNA, and the absence of recombination events, which result in an effectively clonal inheritance, make mtDNA an informative and well established marker for phylogeography studies (Freeland 2008). Due to the availability of universal primers, which allow data to be obtained from a suite of different species without any a priori knowledge, *cytochrome b* (*cyt b*) provided a well-suited marker for this study. To uncover the relative importance of landscape features in shaping population structure in species with different ecological requirements, mitochondrial *cyt b* sequences in a variety of small mammals were examined to investigate (I) the isolating effect of the Kinabatangan River, and to assess (II) restricted migratory capabilities caused by landscape barriers along the riverbanks of the Kinabatangan River. Furthermore, to investigate possible sex-biases in the dispersal of the study species, we inferred and compared (III) potential signals of dispersal by males and females.

Materials and methods

Study area and sampling

Small mammals were sampled along the Kinabatangan River in eastern Sabah (05°20′–05°45′N, 117°40′–118°30′E), Malaysian Borneo. Running over a length of 560 km, the Kinabatangan is the longest river in Sabah, with diverse habitats, consisting of mangroves, swamp forest, riverine forest, seasonally flooded forest, riparian and mixed dipterocarp forest (Azmi 1998). Large areas of forest have been cleared and converted to agricultural landscapes (i.e. oil palm plantations) along the Kinabatangan, and the remaining forest is isolated in patches. Today, 27,000 hectares of disturbed forest are gazetted as the Lower Kinabatangan Wildlife Sanctuary (LKWS) (Ancrenaz et al. 2004; Goossens et al. 2005; Fig. 1). Animals were sampled in 19 trapping sites [18 in forest, one in plantation (site SP in Fig. 1) from both sides of the river (north: 11, south: 8; Fig. 1)]. Sampling sites in close spatial proximity (≤ 7 km distance) and without separation by a geographic feature were considered as one site (differing in coloration in Fig. 1). Besides the Kinabatangan River, large tributaries (perennial, no overlapping of opposing branches), the main road (paved, two-lane, without game fences along its course through study area, in parts bordered by human settlements) and oil palm plantations were considered as geographic features potentially constraining landscape connectivity (Fig. 1). Based on this classification scheme, five sites (NA–ND, distances 4–23 km) were defined for the northern riverside and six (SE–SI, distances 3–31 km) for the south (Fig. 1). On the northern riverside the road acted as a potential barrier between site NA and

site NB. Site NB and site ND were connected by a forest corridor varying in width and containing two sites (site NC_a: width < 300 m, site NC_b: width > 300 ≤ 800 m). Such a corridor was absent south of the river, where larger tributaries were also more numerous (i.e. between site SE and site SP, site SF and site SG, and between site SG and site SH, Fig. 1). Oil palm plantations are located between site SE and site SF, site SF and site SG as well as between site SH and site SI, and the road dissects site SE and site SP.

During the dry seasons (June–November) of 2011–2013, animals were trapped in systematic capture-release sessions using a standardised trapping scheme. In each sampling site, traps were placed at 15 m intervals along transects of 135 m length. Per site 2–4 transects were established parallel at a distance of 25–75 m from each other, and parallel to the river, 20–400 m inland. On each transect 10 locally made wire mesh life traps (31 cm (length) × 21 cm (width) × 15 cm (height) or 28 cm × 18 cm × 12 cm), baited with oil palm fruits, were installed at different heights (ground, > 0–2 m) and on different substrates (litter, branches, vines or logs) targeting a variety of small mammals with different microhabitat preferences. In the seasons 2012 and 2013 an additional trap was placed in each transect in ≥ 4 m height above ground to target strictly arboreal species. All traps were checked twice within 24 h on six consecutive days. Traps were kept open overnight to capture nocturnal non-volant species. Traps were checked the following morning and immediately baited again to capture diurnal taxa. Each trapping station was labelled and the coordinates were taken with a GPS device (GPSMap60CSx, Garmin Deutschland GmbH, Gräfelting, Germany). In the three field seasons a total trapping effort of 9024 trap nights was achieved.

Trapped animals were transferred to a cloth bag, weighed, sexed, and standard morphometric measurements (Yasuma et al. 2003; Payne and Francis 2007) were taken. Photos were taken from the head, back, belly, tail and the complete animal (dorsal and lateral view) and fur, tail and foot colour were recorded qualitatively for later species characterisation. A tissue sample was taken from the ear and stored in 2 ml tubes with 1.5 ml *n*-Lauroyl-Sarcosine buffer (Seutin et al. 1991). For individual identification in case of a recapture, each animal was marked with a pattern cut in the fur of the animal's back before the animal was released at its point of capture.

Fieldwork was conducted under the permission of the Economic Planning Unit Malaysia (Permit No.: UPE: 40/200/19/2871) and the Sabah Biodiversity Centre. All samples were transported under the permit of CITES [Export-Permit No. JHL(PB)600-3/18/1/1Jld.10/(103), Certificate No. 0602 and Export-Permit No. JHL(PB)600-3/18/1/1Jld.10/(494), Certificate No. 0689 and 0690; Import-Certificate No. E-05027/12 and E-05957/13] and

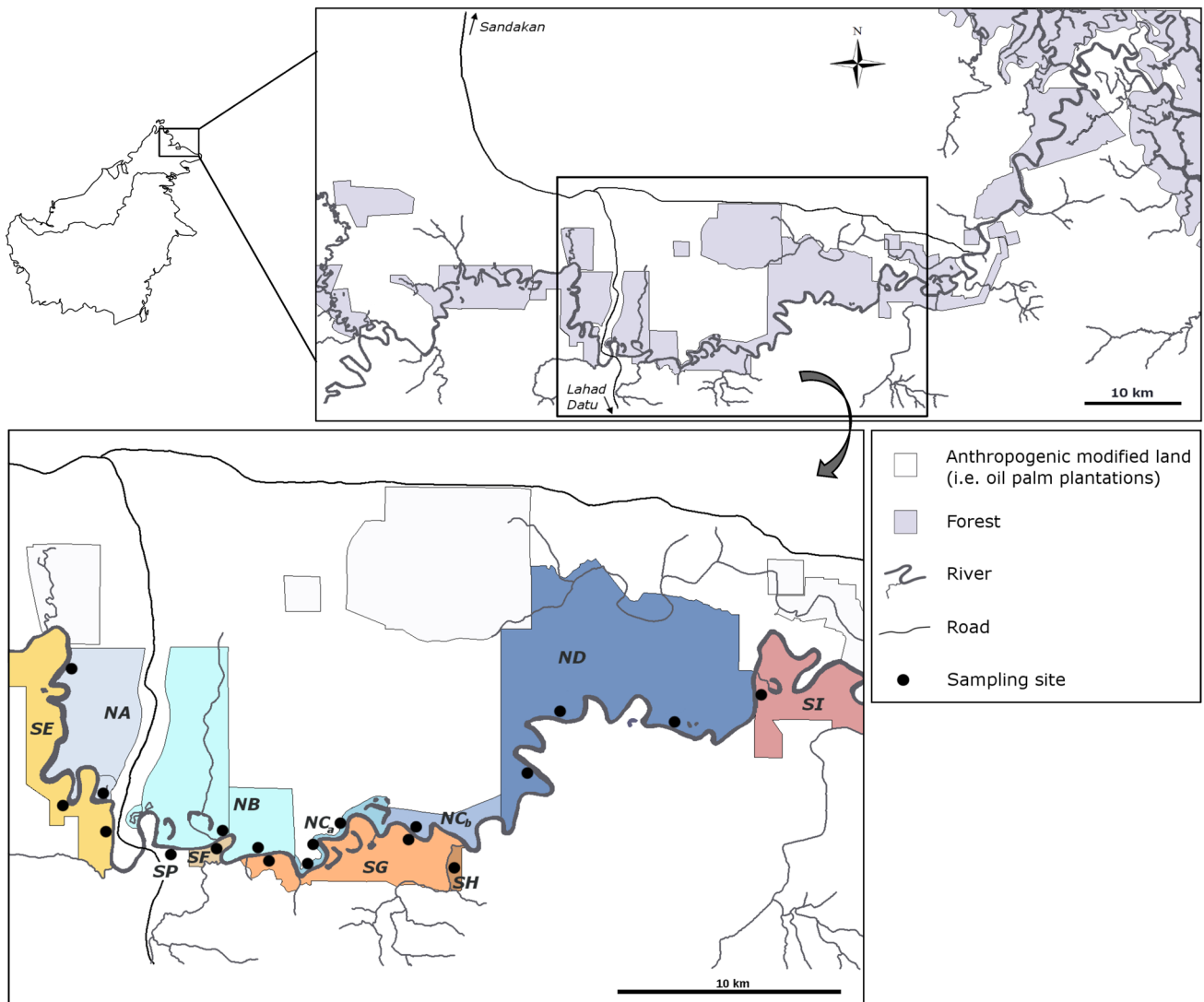


Fig. 1 Map of the LKWS, locations of sampling sites (circles), and sites grouped by the fragment of origin (coloration)

the Sabah Biodiversity Centre [Export-Licence No.: JKM/MBS.1000-2/3(38)].

DNA amplification and sequence analysis

DNA was extracted from a subset of tissues ($n = 511$) using a HotSHOT extraction protocol (Truett et al. 2000). Subsequent amplification of the mitochondrial *cytochrome b* (*cyt b*) gene was carried out using the universal primers L14727 5' TGAYATGAAAAAYCATCGTTG '3 (Pääbo et al. 1988) or L14841 5' AAAAAGCTTCCATCCAAC ATCTCAGCATGATGAAA '3 (Kocher et al. 1989) and the primer MVZ16 5' AAATAGGAARTATCAYTCTGG TTTRAT '3 (Smith and Patton 1993). The *cyt b* gene in tree shrews (i.e. *Tupaia longipes* and *Tupaia gracilis*) was

amplified using an optimised primer (L14841tupaia 5' CCAGCYCCATCAAAYATYTCMTCATGATGAAAC'3), which was designed based on previously generated *cyt b* sequences of *Tupaia tana* and *Tupaia minor*. The amplicons generated by the primer pairs L14727–MVZ16 and L14841/L14841tupaia–MVZ16 had a length of 875 bp and 755 bp, respectively. DNA amplification was performed in a 15 μ l reaction of 5 μ l Multiplex PCR Master Mix (Qiagen), 0.1 μ l Q-solution (Qiagen), 0.6 pmol of each primer, and 0.5–1 μ l template DNA. Reactions were amplified with an initial denaturation at 95 $^{\circ}$ C for 15 min, followed by 35 cycles of 45 s at 95 $^{\circ}$ C, 1:30 min at 47 $^{\circ}$ C and 1 min at 72 $^{\circ}$ C, and a final extension at 72 $^{\circ}$ C for 10 min.

PCR products were sent to Eurofins (Ebersberg, Germany) for sequencing. All samples were sequenced in forward direction. Subsequent sequence alignment and

editing was performed in Sequencher version 4.9 (GeneCodes) and BioEdit version 7.2.5 (Hall 1999).

Taxonomic classification

Unambiguous species assignment of captured animals on the basis of morphometric data alone was not always possible. Therefore, phylogenetic analysis based on *cyt b* and *16S rRNA* sequencing was conducted whenever necessary for taxonomic classification. Details on the methodological approach for the taxonomic clarification are in the Supplementary material.

All *cyt b* sequences generated for taxonomic clarification were used in later phylogeographic analyses (n=385). In addition, from tree shrews, squirrels and gymnures at least 20 samples (10 from each riverside, whenever possible) were sequenced at the *cyt b* locus (n=126) for subsequent phylogeographic analyses.

Analyses of genetic diversity and population structure

Mitochondrial haplotypes were identified and intraspecific haplotype (*h*) and nucleotide (π) diversity were estimated for each species using DnaSP version 5.10.1 (Librado and Rozas 2009). A Mann–Whitney U Test was conducted in Statistica version 6.1 (StatSoft Inc. 2004) to assess differences

in haplotype and nucleotide diversity between riversides, whenever possible ($\alpha=0.05$). Intraspecific haplotype sharing and genetic distances between species at sites on either side of the river were visualised using a minimum-spanning network computed in Arlequin version 3.5 (Excoffier and Lischer 2010). Based on AMOVA and ϕ_{ST} -statistics, implemented in Arlequin v. 3.5 (1000 permutations, $\alpha=0.05$), genetic variation between the two riversides was estimated for all species sampled in large numbers on both sides of the river ($n \geq 10$ per riverbank). In order to identify effects of the river, sites were assigned to their respective riverside for AMOVA (three hierarchical levels: riverside, site, individual) analysis. For the assessment of potential barriers within each riverside, an AMOVA (site, individual) was conducted for the northern and southern riverside separately, and significant pairwise ϕ_{ST} -signals between all sites with $n \geq 3$ individuals (Table 1) were explored. Because of its potential transitional position between site NC_a and site ND, site NC_b was not included in these analyses.

Sex-biased dispersal

We investigated sex as a determinant of gene flow in all species for which males and females could be sampled in sufficient numbers (at least eight individuals for each sex). Since mitochondrial markers are uniparentally inherited via the mother, maternally related males and females share

Table 1 Analysed *cyt b* sequences

Species	North						South						All	
	NA	NB	NC _a	NC _b	ND	Total	SE	SP	SF	SG	SH	SI		Total
<i>Chiropodomys</i> sp.					1	1							–	1
<i>Maxomys surifer</i>						–			2	14		8	24	24
<i>Maxomys whiteheadi</i>	10	14	12	21	32	89	19		21	41	5	7	93	182
<i>Niviventer cremoriventer</i>	2	6	12	1	3	24	5			3		3	11	35
<i>Rattus exulans</i>		1	2			3	2	1	1	1			5	8
<i>Rattus rattus</i>		2	2	1		5	3	2	1	1			7	12
<i>Rattus tanezumi</i>	1	3	1		2	7	2	10			1		13	20
<i>Rattus</i> sp.		5		1	13	19	3			2	23	1	29	48
<i>Sundamys muelleri</i>	6	3	9	4	7	29	10		1	4	8	3	26	55
<i>Callosciurus notatus</i>	2	3	2	1	3	11	5		2	2	2	2	13	24
<i>Callosciurus prevostii</i>		3			1	4	1		1				2	6
<i>Sundasciurus hippurus</i>			1		4	5							–	5
<i>Sundasciurus lowii</i>	3				7	10	2		2	4		2	10	20
<i>Ptilocercus lowii</i>						–			1	1			2	2
<i>Tupaia gracilis</i>					4	4	3						3	7
<i>Tupaia longipes</i>	4	3		1	3	11	3		2	5		2	12	23
<i>Tupaia minor</i>			3	1		4							–	4
<i>Tupaia tana</i>	3	2	1	1	3	10	3		2	3	1	1	10	20
<i>Echinosorex gymnura</i>		4			4	8	2			3		2	7	15

Given is the number of sequences per site, the total number of analysed sequences for each riverside and the overall number of analysed sequences for each species, respectively

the same haplotype. However, immigrants may carry a different, less frequent haplotype into a population. Consequently, haplotype diversity should be higher in the dispersing sex and unique haplotypes within sites can be assumed to be a signal of (recent) immigration. Furthermore, genetic differentiation between sites should be lower in the more dispersed sex.

In addition, haplotype diversity was compared between males and females in three ways: first, haplotype diversity was determined as the overall number of haplotypes in males and females. Second, the number of sex-specific haplotypes was compared between males and females. Third, the overall number of unique haplotypes (= only present in one animal per site) was determined for males and females separately. Only sites in which both sexes were sampled were included in this last analytical step. Genetic differentiation between sites was calculated for each sex separately (for all sites with $n \geq 3$) using pairwise ϕ_{ST} -statistics, and a Mann–Whitney U Test (Statistica version 6.1, StatSoft Inc. 2004) to detect significant signals between sexes ($\alpha=0.05$), whenever possible.

Results

Small mammal species richness along the Kinabatangan and their genetic diversity

A total of 1185 non-volant small mammals were sampled in the three field seasons between 2011 and 2013. Based on phenotypic characteristics and/or phylogenetic analysis (Supplementary material), animals could be taxonomically assigned to 19 different taxa of rodents (murids and squirrels), tree shrews, and gymnures. While rodents showed high species diversity with nine different murid and four squirrel species, only one gymnure was trapped. Tree shrews were represented by five different taxa (Table 1).

From the 14 species trapped on both sides of the river (Table 1) a 589–791 bp fragment of the *cyt b* gene was amplified and sequenced. Within this DNA fragment no insertions or deletions could be detected. The number of variable sites (*s*) varied from one in *Rattus exulans* to 48 in *Maxomys whiteheadi*. The highest number of haplotypes could be identified in *M. whiteheadi* (34), and only two haplotypes were identified in *R. exulans*, *Rattus rattus*, and *Rattus tanezumi* (Supplementary material, Table S2). Overall haplotype diversity ranged from $h=0.167$ (*R. rattus*) to $h=0.967$ (*Callosciurus notatus*), while nucleotide diversity varied from $\pi=0.0005$ (*R. exulans*) to $\pi=0.0178$ (*T. tana*). *R. exulans*, *R. rattus*, and *R. tanezumi* showed low haplotype and nucleotide diversity but most other species had high haplotype diversity (Supplementary material, Table S3). Comparing populations from the northern and the southern

riverbank, significant differences in haplotype and nucleotide diversity could not be detected in any of the analysed species (Supplementary material, Table S3).

Genetic differentiation across the Kinabatangan River

Interspecific differences in geographic haplotype distribution and the isolating effect of the river were examined by comparing the species-specific minimum-spanning networks (Fig. 2 and Supplementary material, Fig. S1). The haplotype network patterns can be broadly grouped into three categories. *Sundasciurus lowii*, *Tupaia tana*, and *Tupaia gracilis* formed distinct haplotype clusters on either side of the river. (Network type 1, Fig. 2a). No haplotype sharing was observed among groups between the two riversides in these three species. The haplotype networks of *Tupaia longipes*, *Callosciurus notatus*, and *Callosciurus prevostii* showed no such grouping of haplotypes into distinct clusters. However, haplotype sharing between different sides of the river was never observed in *C. prevostii* and occurred only once in *C. notatus* and *T. longipes* (Network type 2, Fig. 2b). The third type (Fig. 2c and Supplementary material, Fig. S1) of network was seen in the murid species *M. whiteheadi*, *Niviventer cremoriventer*, *Sundamys muelleri*, *Rattus* sp., and in *Echinosorex gymnura*. They showed no distinct haplotype clustering whether north or south of the river with frequent haplotype sharing between sites from both riversides. The rat species *R. exulans*, *R. rattus*, and *R. tanezumi* most likely also belong to this third type, but only two haplotypes could be identified in each species, one of which was shared between the two riversides, while the other was not (Fig. 2c).

Nine species were sampled in sufficient numbers (at least 10 individuals per riverside) to be included in the analysis of molecular variance between riversides (Table 2). Pairwise genetic differences between riversides were high and significant only in the squirrel *S. lowii* and the tree shrew *T. tana* (both Network type 1) and the highest percentages of molecular variance were also explained by the riversides in these two species (Table 2). In addition, in the whole dataset, the percentage of genetic variance partitioned within local groups was low and significant in these two species, allowing us to infer generally low gene-flow between sites for them. In all other species pairwise ϕ_{ST} -statistics and AMOVA analysis revealed no clear partitioning effect of the Kinabatangan River on molecular variance (Table 2).

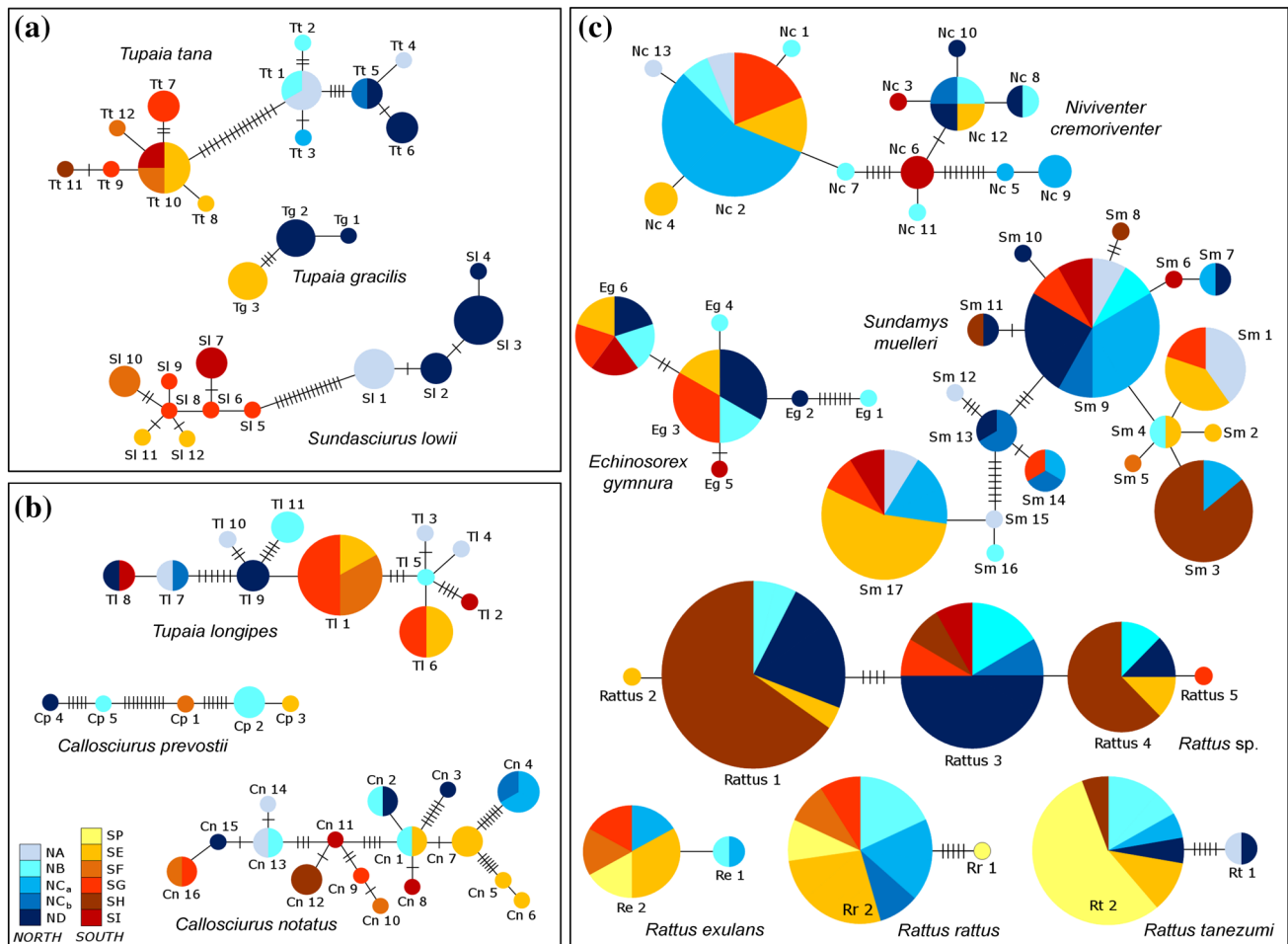


Fig. 2 Three broad categories of minimum-spanning network: Network type 1 (a), Network type 2 (b), Network type 3 (c). In each network, each haplotype is represented as a circle. The diameter of the

circle corresponds to haplotype frequency, with smallest circles representing singletons. Mutational steps between haplotypes are indicated as vertical bars

Genetic differentiation along the Kinabatangan River

Haplotypes were distributed widely along the river in *E. gymnura* and in most murid species except in *Maxomys surifer*, where the distribution of haplotypes was typically restricted to single locations, and only one haplotype was shared between sites on the southern riverside (Supplementary material, Fig. S1). Similarly, no haplotype sharing between sites was found in *S. lowii*, *C. prevostii*, and *T. gracilis* (Fig. 2). Analysing the two riversides separately, significant genetic variation among sites within riversides was found in six species, but only in *S. lowii* on both riversides (Table 2).

Based on significant pairwise genetic differences between sites, we could infer the impact of geographical features, other than the Kinabatangan River itself, on gene flow for six members of the resident small mammal community that could be sampled in large enough numbers.

Significant differences could be detected on the southern riverside between site SF and site SG, site SE and site SF, and between site SH and site SI. Interestingly, these sites are separated by an oil palm plantation (Table 3). No significant differences were found between sites separated by a large tributary (site SG and site SH). Likewise, between site NA and site NB, which are separated by a road, no significant genetic differentiation could be found. Furthermore, between sites without any putative geographic barrier no significant genetic differentiation existed, even if spatially distant from each other (e.g. site NB and site ND) (Table 3).

Signals of male- vs. female-biased dispersal

Based on haplotype analyses a signal of sex-biased dispersal could be detected in two species (Supplementary material, Table S4). In *M. surifer* and *M. whiteheadi* the overall number of haplotypes, the number of sex-specific haplotypes, and the number of unique haplotypes at a given

Table 2 Pairwise differences (ϕ_{ST}) between riversides and intraspecific percentage of genetic variance between riversides, within riversides, and within sites are given for the whole population, and for both riversides, respectively

Species	Pairwise ϕ_{ST} (between riversides)	Percentage of variance						
		All			North		South	
		Between riversides	Between sites, within riversides	Within sites	Between sites	Within sites	Between sites	Within sites
Network type 1								
<i>Sundasciurus lowii</i>	0.84396**	78.62 ⁺	15.75**	5.63**	75.23**	24.77	71.13**	28.87
<i>Tupaia tana</i>	0.82422**	80.85**	7.82*	11.33**	46.75*	53.25	33.23	66.77
Network type 2								
<i>Callosciurus notatus</i>	0.06036 ⁺	−2.09	34.81**	67.27**	43.84*	56.16	23.97 ⁺	76.03
<i>Tupaia longipes</i>	0.10149 ⁺	5.40	9.01	85.59 ⁺	4.91	95.09	16.63	83.37
Network type 3								
<i>Maxomys whiteheadi</i>	0.01050 ⁺	−0.59	3.82**	96.77**	1.28	98.72	5.55**	94.45
<i>Niviventer cremoriventer</i>	−0.03064	−15.34	38.73**	76.61**	27.76**	72.24	53.57 ⁺	46.43
<i>Rattus tanezumi</i>	0.28795 ⁺	1.46	65.22 ⁺	33.32	34.62	65.38	0.00	0.00
<i>Rattus sp.</i>	0.05740 ⁺	−3.04	11.36	91.68	−14.55	114.55	25.37 ⁺	74.63
<i>Sundamys muelleri</i>	0.01426	−3.01	11.76 ⁺	91.25 ⁺	−3.18	103.18	22.09*	77.91

Species are listed in order of their associated haplotype network category (Network type 1–3) as described in Fig. 2

⁺ ≤ 0.1 , * ≤ 0.05 , ** ≤ 0.01

Table 3 Pairwise genetic differences (ϕ_{ST}) between sites

Species	Road	Tributary	Tributary + Plantation	Road + Tributary + Plantation	Small distance	Large distance	Large distance + Plantation
	NA–NB (9.71 km)	SG–SH (3.11 km)	SF–SG (5.74 km)	SE–SF (5.92 km)	NB–NC _a (4.26 km)	NB–ND (15.51 km)	SH–SI (15.89 km)
<i>Maxomys whiteheadi</i>	0.03602	−0.03250	0.06687**	0.09985**	0.06790	0.04376	−0.08650
<i>Niviventer cremoriventer</i>	–	–	–	–	0.11749	0.22439	–
<i>Rattus sp.</i>	–	–	–	–	–	−0.14553	–
<i>Sundamys muelleri</i>	−0.24784	0.28973	–	–	−0.20732	0.06808	0.32948*
<i>Callosciurus notatus</i>	–	–	–	–	–	−0.22449	–
<i>Tupaia longipes</i>	0.01887	–	–	–	–	0.26316	–

Separating geographic features (road, plantation, tributary) and euclidean distances between sites are provided for all investigated pairings

* ≤ 0.05 , ** ≤ 0.01

site (“haplotype singletons”) was higher in males than in females (Supplementary material, Table S4), indicating a male-biased dispersal in these species. In contrast, haplotypes were rather evenly distributed between sexes in *N.*

cremoriventer, *Rattus sp.*, *S. muelleri*, *C. notatus*, *S. lowii*, *T. longipes*, and *T. tana* (Supplementary material, Table S4). Differences between the sexes can be most likely explained by the different sample sizes for both sexes in these species.

However, a sex-bias in dispersal could not be verified in any of the analysed species based on pairwise ϕ_{ST} -statistics (Supplementary material, Table S4).

Discussion

Small mammal diversity along the Kinabatangan River and their genetic diversity

The composition of Bornean small mammal communities has been described at several locations throughout Borneo (Nor 2001; Wells et al. 2007, 2014; Nakagawa et al. 2006; Bernard et al. 2009; Charles and Ang 2010) and often comprises between 12 (Bernard et al. 2009; Charles and Ang 2010) and 22 (Nakagawa et al. 2006) non-volant small mammals of the orders Rodentia (murids, squirrels and porcupines), Scandentia (tree shrews), and Eulipotyphla (gymnures and shrews). To our knowledge, the present study is the first verifying the presence of 19 different non-volant small mammal species in habitats along the Kinabatangan River. The composition of the small mammal communities along the Kinabatangan River is similar to that of other locations studied in Borneo, and indicates a rather high α -diversity with 19 different species, which includes both species native and potentially invasive to Borneo. Some species were only identified using molecular techniques which confirm the presence of cryptic species including *R. tanezumi*, in addition to *R. rattus*.

Despite the high levels of habitat fragmentation along the Kinabatangan, mtDNA diversity was relatively high in most species, except in the *Rattus* species *R. exulans*, *R. rattus*, and *R. tanezumi* (only two haplotypes) (Pagès et al. 2013; Thomson et al. 2014). High haplotype diversity coupled with low nucleotide diversity can indicate a population bottleneck followed by rapid growth and parallel accumulation of mutations (Grant and Bowen 1998). Such a scenario was previously invoked for orang-utans along the LKWS (Jalil et al. 2008). For the *Rattus* species *R. exulans*, *R. rattus* and *R. tanezumi*, however, low haplotype and low nucleotide diversity may rather indicate a recent founder event, and the presence of only two haplotypes, one of which being high in frequency, may even imply a very limited number of founders. The Pacific rat (*R. exulans*) as well as black rats (Oceanic form: *R. rattus*, Asian form: *R. tanezumi*) are known to be strongly associated with human settlements (Roberts 1991; Payne and Francis 2007; Aplin et al. 2011; Banks and Hughes 2012), and could very likely have invaded the landscape around LKWS more recently as a consequence of the forest loss starting in the 1950 and human habitation (Latip et al. 2013). The conversion of forest along the Lower Kinabatangan to agriculture has provided suitable habitats

for these species and their presence in the plantation sampling site supports their adaptation to anthropogenically altered environments.

Connectivity of Bornean small mammals across the Kinabatangan River

Haplotype networks and genetic variance analyses indicate contrasting levels of genetic isolation between riversides within species sampled on both sides of the Kinabatangan River. Clear genetic separation between riversides, indicating a strong influence of the Kinabatangan River as a barrier for dispersal, was found in *S. lowii*, *T. tana*, and *T. gracilis*, and was supported for those species trapped on one riverside only such as *M. surifer*, *S. hippurus*, and *T. minor*. Moderate genetic isolation was found between riversides in *C. notatus*, *C. prevostii*, and *T. longipes*, indicating a moderate barrier function of the Kinabatangan River. No genetic separation between riversides indicates an unimpeded dispersal across the Kinabatangan, and this was found in the remaining murid rodents and in the moonrat *E. gymnura*.

Consequently, the Kinabatangan River represents an important landscape feature for shaping the genetic structure and constraining dispersal for some species, notably in squirrels and tree shrews. Sporadic reports of squirrels crossing water bodies in North America and Asia (e.g. Applegate and McCord 1974; Pauli 2005; Brunke pers. obs.) show that certain squirrel species are able to swim. However, the presence of only one haplotype (out of 24 samples) shared between riversides in *C. notatus*, implies that this species crosses the river only rarely. The same may also be true for the tree shrew *T. longipes*, where only one haplotype (among 23 samples) was shared between riversides. Although no observations exist on the swimming capabilities of tree shrews, they generally prefer dense understorey and avoid open areas without cover that may expose them to predators (Emmons 2000).

In contrast, most murids are known to be good swimmers (e.g. Evans et al. 1978; Cook et al. 2001; Nicolas and Colyn 2006; Santori et al. 2008; Brunke pers. obs.), and migration across rivers have been confirmed in murid rodents elsewhere (e.g. Patton et al. 1994; Colombi et al. 2010; Roratto et al. 2014; Russo et al. 2016). Therefore, migration across the river in murids is not surprising. Interestingly, this study allowed us to infer swimming and river crossing in wild Bornean moonrats for the first time. Limited knowledge of *E. gymnura* ecology is mainly on captive individuals (Liat 1967; Gould 1978), but aquatic feeding activities have been observed, including swimming and diving, and morphological adaptations to this behavioural trait have been identified (Gould 1978). Additionally, stomach content analyses indicated a partially aquatic diet (fish and crabs, Liat 1967).

For species with an affinity to water such as murids and the moonrat, the Kinabatangan River may even facilitate dispersal. When species with swimming capabilities (murids and moonrat) use the river, they may eventually disperse over longer distances by passive drifting downriver than if they would only move by terrestrial locomotion. Future studies are needed to evaluate this possible enhancing effect of the river on dispersal distances in more detail.

The mixed effects of large rivers on dispersal were shown also in comprehensive studies on Neotropical bird communities (e.g. Capparella 1988, 1991; Burney and Brumfield 2009). Capparella (1988, 1991) suggested an important role of species-specific differences of ecological niches for migratory propensities across rivers. Here, understory species are the least likely to cross large light gaps such as rivers, compared to species inhabiting the forest canopy and open areas, which probably are more accustomed to light gaps. In our study, the river acted as a barrier mainly for the diurnal species, whereas all but one nocturnal species (all murids besides *M. surifer*) showed signals of dispersal across the river. It can be hypothesised that diurnal species such as squirrels and tree shrews, which move preferably in dense cover of the forest (Emmons 2000; Wells et al. 2006a), may also avoid open areas, such as larger rivers, as a predator avoidance strategy, while nocturnal rats may be safe to cross the river in the cover of the darkness.

Connectivity of Bornean small mammals along the Kinabatangan River

A variety of landscape features occur along the Kinabatangan River, including large tributaries, a road and oil palm plantations, which may potentially affect dispersal and genetic connectivity for small mammals. In general, low genetic differentiation coupled with a broad geographic distribution of haplotypes implies relative unrestricted migration among sites. This was typically found in the murid species. Furthermore, dispersal across the river may help to reduce the effect of terrestrial barriers and may help to explain the high genetic connectivity in murids. High genetic differentiation among sites along both riversides was only found unambiguously in *S. lowii*, indicating strong limitations in its terrestrial vagility, coupled with a low dispersal across the river. Both, low terrestrial and low aquatic dispersal, may lead to an especially accented genetic isolation of this species along the river.

No obvious effect of large tributaries on migration could be detected in any species. As the size and/or the width of rivers are likely to determine the extent to which such a barrier is permeable for small mammals (Russo et al. 2016), it is possible that the Kinabatangan River represents the only river barrier in the area. Furthermore, water levels fluctuate throughout the year and may allow occasional crossing of

tributaries by otherwise constrained species during the dry season, which may be sufficient to maintain detectable gene flow in such species.

Likewise, the one major road seems not have affected inferred dispersal in any of the small mammal species, although a barrier effect of major roads has been reported for other small mammals in other regions of the world (Gerlach and Muslof 2000; Goosem 2002; Rico et al. 2007). In particular, wide roads (> 30 m) represent an almost impermeable barrier for small mammals (Gerlach and Muslof 2000; Rico et al. 2007). It is possible that the width of the road (about 7 m road surface) is not enough to have resulted in genetic isolation or that the time span since the construction of the road (ca. 20 years before this study) may not have been long enough to result in genetic differentiation.

Although sample sizes were small in most species, in species with a high number of samples distinct levels of genetic differentiation existed between sites separated by plantations, while sites connected by forest corridors of the same distance showed no genetic differentiation. This indicates that landscape features (i.e. oil palm plantations) have an impact on the dispersal of non-volant small mammals along the Kinabatangan River, and emphasises the importance of forest corridors for population connectivity, which evidently increases animal movements and gene flow between patches (Bennett 1990; Haddad et al. 2003). Future studies, comprising larger sample sizes and/or employing genetic markers with higher resolving power (e.g. microsatellites or SNPs) would clearly be needed to clarify this question.

Evidence for sex-specific dispersal patterns in Bornean small mammals

Physical barriers restricting migration of individuals and shaping genetic structures should have a greater impact on the dispersing sex than on the philopatric sex. However, dispersal patterns have not been studied in most Bornean small mammal species until now. Wells et al. (2008a) detected differences in the movement patterns of Bornean small mammals based on mark-recapture analysis, and suggested an influence of sex for *M. surifer*, *M. whiteheadi*, *N. cremoriventer*, *S. muelleri*, and *T. longipes*. Additionally, Munshi-South (2008) described a female-biased dispersal in *T. tana* on the basis of microsatellite analysis.

Although male-biased dispersal is the dominant dispersal pattern in most mammals due to higher benefits of philopatry for females (Greenwood 1980), we found signals of male-biased dispersal only in the murids *M. surifer* and *M. whiteheadi*, but this was solely based on higher haplotype diversity in males than in females. These findings do not exclude the possibility that females might occasionally disperse too, but possibly less frequently and over shorter distances than males.

No clear signal of sex-biased dispersal could be detected in *N. cremoriventer*, *Rattus* sp., *S. muelleri*, *C. notatus*, *S. lowii*, *T. longipes*, and *T. tana*, because haplotypes were rather evenly distributed between sexes in these species. Nevertheless, findings for the squirrel species are congruent with other studies (Waser and Jones 1983; Wauters and Dhondt 1992; Smale et al. 1997), which suggested dispersal by both sexes, at least for *C. notatus* and *S. lowii*.

It needs to be acknowledged that the rather small sample sizes have limited the scope of the haplotype and ϕ_{ST} -analysis, and that larger sample sizes are needed to detect signals of sex-biases in dispersal, unambiguously. Furthermore, because of its uniparental inheritance through the maternal line, mtDNA has some limitations, and differences in dispersal rates among sexes may manifest differently in the genetic structure of males and females. Therefore, further studies encompassing a range of paternally and bi-parentally inherited markers, in addition to maternally inherited marker, are clearly necessary to complete the understanding of possible proximate and ultimate factors that determine and influence the dispersal of males and females in these rather cryptic animals. Especially, because large gaps still exist in the knowledge of the socioecology and behaviour of most Bornean small mammal species.

Conservation implications

A diverse small mammal community was confirmed in the present study. However, extensive land conversion to oil palm plantations, habitat fragmentation and the large Kinabatangan River create physical barriers which may constrain the connectivity of small mammal populations by restricting dispersal. The genetic analyses carried out here found some support for this effect in some but not all studied species. The Kinabatangan River acts as an important geographic feature shaping the genetic structure of Bornean small mammals in very different ways by either restricting (in squirrels and tree shrews) or potentially even promoting dispersal (in murids and gymnures). Species able to cross the river (i.e. murids) may genetically even benefit from its presence, since the use of the river for migration may mitigate the effects of other barriers along the river. On the other hand, species which seem not to cross the river (*S. lowii*, *T. tana*, *M. surifer*) are expected to suffer much more from forest fragmentation along both riversides. In particular, *S. lowii* showed very limited gene flow along the river, but the scarcity of information about its ecological requirements limits speculations about the restricting habitat factors.

Although findings were limited to a small number of species, this study revealed that plantations affected dispersal and gene flow in small mammals more than any other studied barrier beside the Kinabatangan River, such as its tributaries or a paved road. The higher genetic connectivity

along the northern compared to the southern riverside in most of the small mammals is most likely due to the presence of forest corridors along the northern border of the river. Given that not all small mammal species can cross the river, such corridors should also be established on the highly fragmented southern riverside to increase population connectivity. This would constitute an important conservation measure especially for those species the Kinabatangan represents a major barrier for dispersal (such as *S. lowii*, *T. tana*, and *M. surifer*).

Finally, many studies have shown that invasive species can have an impact on the persistence of the native fauna, and are even capable of replacing it (Banks and Hughes 2012; Wells et al. 2014). Moreover, invasive species have been identified as the second most important cause of biodiversity loss after habitat destruction (Abdelkrim et al. 2005), and as a major vector of diseases for humans and wildlife alike (Meerburg et al. 2009; Aplin et al. 2011). This study has confirmed the presence of three invasive rat species (*R. exulans*, *R. rattus*, and *R. tanezumii*) in both anthropogenic modified and forest habitats of the LKWS, and other studies confirmed these rat species in forest habitats elsewhere on Borneo (e.g. Nakagawa et al. 2006; Wells et al. 2006b, 2007, 2014), which emphasises their potential to invade into forest environments. It is difficult to predict which of the native small mammal species will persist or suffer from competition with these invasive species. However, previous studies demonstrated that larger species are often dominant over smaller ones (Banks and Hughes 2012) and this pattern of competitive dominance has been confirmed for black rats in other regions (e.g. Harris and Macdonald 2007; Harper and Cabrera 2010; Guo et al. 2017). Potential implications of these invasive rats for the native fauna need to be urgently assessed by establishing monitoring programmes across different sites and both riversides. Eventually, effective conservation measures need to be developed that include management decisions on the invasive species but also on those that may be negatively affected by them to ensure the long-term survival of the native species and to preserve the biodiversity within the forest along the Kinabatangan River.

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