1 **Title:** Evaluating the effect of forest loss and agricultural expansion on Sumatran tigers

2 from scat surveys.

3

4 **Abstract**

5 Sumatran tigers (*Panthera tigris sumatrae*) are a critically endangered carnivore

6 restricted to the island of Sumatra, and like many other large mammals on the

7 Indonesian archipelago, they are threatened by high levels of poaching and widespread

8 habitat degradation. Here, we conduct the first range-wide assessment of Sumatran tiger

9 genetics using scat surveys and show that the wild population retains levels of genetic

10 heterozygosity comparable to mainland tigers. However, the population also exhibits

11 signs of subdivision due to the unprecedented rates of deforestation and land conversion

12 in the last 30 – 40 years. The fact that this subspecies retains such levels of

13 heterozygosity despite high rates of habitat loss and increasing isolation suggests a form

14 of genetic extinction debt with an elevated risk of extinction if no action is taken within

15 the next 30 – 100 years (see Kenney et al., 2014). However, the inherent time delay in

16 extinction debt provides opportunities for conservation if habitat quality can be

17 improved and connections between existing population fragments can be made. Our

18 study highlights the importance of genetic studies for providing baseline information to

19 improve the population management of highly threatened carnivore species. Mitigating

20 further habitat degradation and expansion of oil palm and other cash crops in this region

21 would improve the viability not only of Sumatran tiger populations, but of other

22 threatened large mammal species as well.

23

24 **Keywords:**

1. Introduction

Sumatra supports a disproportionately high level of global biodiversity. There are 5 bioregions on the island (freshwater swamp, lowland rainforest, montane rainforest, peat swamp, and tropical pine forest), that support up to 200 species of mammals and 580 species of birds, including some that are extinct or virtually so elsewhere in Indonesia, such as the rhino, elephant, and tiger (Whitten et al., 2000; Wikramanayake et al., 2002). Much of this biodiversity is at risk due to vast areas of primary forest (up to 0.38 million hectares per year) being cleared for timber products or converted to other land uses such as agriculture (e.g. coffee, rubber), oil palm, and *Acacia mangium* tree plantations (Margono et al., 2012; Sodhi et al., 2004; Stibig et al., 2014).

Much of the land clearance began in southern Sumatra in the 1970s when the Indonesian government introduced a transmigration scheme to relocate people from other islands in the archipelago (Imbernon, 1999). It is now home to nearly 51 million people spread across 10 provinces (BPS-Statistics Indonesia, 2016), and it is estimated that between 1969 and 1993 up to 8 million people relocated and cleared 1.7 million hectares of lowland forest for settlements and agricultural smallholdings (Barber and Schweithelm, 2000; Gaveau et al., 2009a). Much of this degraded forest was converted to industrial timber estates and oil palm plantations in the early 2000s, and with little accessible low elevation forest remaining in south Sumatra, attention has now turned to the peat swamp forests of east Sumatra (Margono et al., 2014).

It is estimated that ~70% of Sumatra's primary lowland forest has already been lost and this trend is set to continue as Indonesia aims to meet much of the global demand for

50 palm oil, pulp, and timber products (Geist and Lambin, 2002; Kinnaird et al., 2003;

51 Suyadi, 2010). With net returns of up to $13 000 per hectare of tropical timber or oil

52 palm there are many commercial barriers to conserving the remaining primary habitat

53 (Wilcove et al., 2013).

54

55 Tiger conservation, like that of rhinos and elephants, poses a difficult challenge in this

56 context as they require a large amount of space, have a tendency towards conflict with

57 people in secondary forest or at protected area boundaries, and are under constant threat

58 from poaching due to their commercial value (Linkie et al., 2018). The main remaining

59 populations of these species are therefore located in a few large protected areas of

60 primary lowland or montane forest (Wibisono et al., 2011).

61

62 Current estimates put the global tiger population at 3000 – 4000 individuals. Sumatra is

63 one of three regions combined (including India and Russia) containing ~80% of

64 remaining tiger habitat with a Sumatran population of ~500 tigers (Tilson et al., 1993;

65 Linkie et al., 2008a; Goodrich et al., 2015). The Sumatran tiger (*Panthera tigris*

66 *sumatrae*) is recognized as a distinct subspecies due to its unique location, genetics, and

67 morphological differences (Cracraft et al., 1998; Kitchener, 1999; Hendrickson et al.,

68 2000; Luo et al., 2004; Kitchener and Yamaguchi, 2010; Wilting et al., 2015). It also

69 represents the last remaining population of Sunda tigers since the Java and Bali

70 subspecies are now extinct (Xue et al., 2015).

71

72 Continued land conversion across the tiger's range has created a patchwork of primary

73 forest (lowland, montane or peat swamp), secondary forest, and human disturbance that

74 prompted the creation of Tiger Conservation Landscapes (TCLs), and more recently

75 Source Sites, which overlap with the distribution of highly threatened species such as

76 the Sumatran rhino, Asian elephant, and Sumatran orangutan (Sanderson et al., 2006;

77 Walston et al., 2010; Wich et al., 2016). Although tigers can inhabit a broad range of

78 forest types, abundance or occupancy rates are highest in areas of low human presence

79 and infrastructure (Carroll and Miquelle, 2006; Johnson et al., 2006; Harihar and

80 Pandav, 2012; Sunarto et al., 2012; Hebblewhite et al., 2014). Previous studies have

81 shown that tigers mostly require a suitable prey base and good ground cover for hunting

82 to persist, even in degraded forest (Linkie et al., 2008b; Smith, 2009; Sunarto et al.,

83 2012). Designation of these large conservation areas was therefore intended to protect

84 sufficient habitat and prey, free from human threats, to maintain self-sustaining tiger

85 populations. Sumatra holds 12 TCLs and 4 Source Sites covering up to 88 000 km^2

86 (Wibisono and Pusparini, 2010), and these largely overlap with protected area

87 boundaries. Here we use genetic data obtained from an island-wide scat survey to

88 explore how disruption of the once contiguous forest on Sumatra has affected this last

89 Sunda tiger subspecies.

90

91

92   **2. Material and Methods**

93 2.1 Sample collection

94 Fecal samples (scats) were collected from nine different field sites across Sumatra (Fig.

95 1a, Table A1). Samples were collected during dedicated scat collection surveys or

96 opportunistically during population monitoring studies prior to this study. Fresh samples

97 were also obtained from a facility holding wild tigers captured following conflict with

98   rural communities. Scat surveys were conducted in a range of habitat types (montane,

99   lowland, and production forests), and sampling transects followed animal trails and

100   logging routes in high tiger density areas identified from camera trap survey data

101   (unpublished results). Field teams covered one transect per day and each route was

102   sampled just once with teams instructed to collect all fecal samples likely to have been

103   deposited by a tiger based on size and appearance. Each sampling period lasted for an

104   average of 2 weeks. We also tested the use of a detection dog in 3 sites (Way Kambas

105   NP, Kerinci Seblat NP, and Batang Hari protection forest) using a 2-year old, male,

106   Labrador Retriever from Bogor, West Java. The dog was trained over 3 weeks by an

107   experienced dog handler to recognize the scent of tiger scats using samples from captive

108   individuals. Dog surveys were conducted alongside the field teams with 20-minute work

109   periods alternating with 10-minute rest breaks.

110

111   <u>2.2 Laboratory methods</u>

112   Each sample was initially preserved with silica gel beads in the field then transferred to

113   $\geq$ 96% ethanol once received in the laboratory. Extractions were performed using 2 - 3

114   mm scrapings taken from the outer surface of each scat. The QIAamp DNA stool mini

115   kit (Qiagen) was used for all extractions with some modifications (Table A2). A

116   NanoDrop spectrophotometer (Thermo Scientific) was then used to quantify the DNA

117   concentration for each sample. A tiger-specific Cytochrome b primer (Wetton et al.,

118   2004) was used to identify positive tiger samples. Two PCRs were performed for each

119   sample to confirm a positive result, indicated by a single PCR product of ~165 bp.

120   PCRs were performed in 10 μl reaction volumes containing 5 μl Qiagen Multiplex PCR

121   mix, 0.3 μM forward and reverse primers, 0.2 μl (10 mg ml^{-1}) BSA, and 1.2 μl fecal

122 DNA. PCR cycling conditions were as described by Driscoll *et al.* (2009) and PCR

123 products were visualized on a 2% agarose gel with 1% ethidium bromide. Sex

124 identification was performed using a felid-specific zinc finger primer pair (Pilgrim et

125 al., 2005). Sex was determined by a single PCR product for females (~163 bp) and 2

126 products for males (~160 and 163 bp). PCR reactions were performed using a 10 µl

127 reaction volume containing 5 µl Qiagen Multiplex PCR mix, 0.3 µM fluorescent

128 labelled forward primer, 0.3 µM reverse primer, 0.5 µl (10 mg ml^{-1}) BSA, and 3 µl fecal

129 DNA. PCR cycling conditions were: 95 °C for 15 mins, 45 cycles of [94 °C for 30 s, 56

130 °C for 1 min, and 72 °C for 30 s], followed by 72 °C for 10 mins. Fragment sizes were

131 determined by capillary electrophoresis on an ABI 3130 genetic analyzer (Applied

132 Biosystems).

133

134 Genotyping was performed using 24 fluorescent labelled microsatellite loci (Luo et al.,

135 2004; Table A3). Loci were amplified in pairs in 10 µl reaction volumes containing 5 µl

136 Qiagen Multiplex PCR master mix, 0.2 µM forward and reverse primers, 0.5 µl (10 mg

137 ml^{-1}) BSA, and 2 µl fecal DNA. PCR conditions were 95 °C for 15 mins, 20 cycles of

138 [94 °C for 15 s, 55 °C for 15 s and 72 °C for 30 s], followed by 35 cycles of [89 °C for

139 15 s, 55 °C for 15 s and 72 °C for 30 s], then a final extension step of 60 °C for 90 mins.

140 Microsatellite allele sizes were determined with GeneMarker software (SoftGenetics

141 LLC) and allele bins for each locus were confirmed with Tandem v1.08 (Matschiner

142 and Salzburger, 2009). Consensus multilocus genotypes were generated using a multi-

143 tubes approach (Taberlet et al., 1996). An allele had to appear twice to be accepted as a

144 true allele; a heterozygote genotype was provisionally accepted after 3 positive PCRs

145 and a homozygote provisionally accepted after 7 positive PCRs. Shaza (Macbeth et al.,

146 2011) was then used to determine the number of unique genotypes, whilst genotyping

147 error rates and probability of identity (PI_{SIB}) were estimated with Gimlet v1.3.3, Micro-

148 checker v2.3.3, Pedant v1.0, and MicroDrop (Johnson and Haydon, 2007; Valière,

149 2002; van Oosterhout et al., 2004; Wang et al., 2012). SHAZA uses a likelihood test to

150 distinguish between 3 different types of genotype match: (i) false matches in which

151 different individuals have the same genotype (shadows), (ii) false non-matches that

152 represent the same individual with different genotypes due to genotyping error, and (iii)

153 phantoms that are true matches rejected because of insufficient power. However, Shaza

154 is not able to distinguish duplicated genotypes (i.e. potential recaptures of the same

155 individual) from related individuals, so we used Colony v2.0.1.1 (Jones and Wang,

156 2010) to estimate the pairwise probability of individuals being full- or half-sibs.

157

158 2.3 Population genetics

159 Genepop v4.0 (Raymond and Rousset, 1995) was used to test for Hardy-Weinberg

160 equilibrium. Observed and expected heterozygosity were estimated using GenAlEx v6.4

161 (Peakall and Smouse, 2006). Unbiased expected heterozygosity was also calculated to

162 account for small sample sizes at each locus. Rare alleles with a frequency < 0.05 were

163 also removed from the dataset to minimize the impact of genotyping errors and to obtain

164 a conservative measure of diversity. Effective population size was estimated with

165 NeEstimator v2 (Do et al., 2014) using a linkage disequilibrium method accounting for

166 sampling error and with minimum allele frequencies set to > 0.05. We tested for

167 isolation-by-distance using a regression between Rousset's genetic differentiation

168 measure *a(r)* and the logarithm of least cost distances *ln(r)* as implemented in SPAGeDi

169 v1.3 (Hardy and Vekemans, 2002). Least cost distances were estimated between

170 individual sample locations using human footprint data from the Last of the Wild v2

171 (Sanderson et al., 2002) as our landscape map. Distances were computed in ArcView

172 3.1 with the Pathmatrix v1.1 extension (Ray, 2005). The inverse of the regression slope

173 was then used to estimate neighborhood size, a measure of effective population size

174 based on the distribution of individuals within a given area (Wright, 1946; Rousset,

175 2000). We also used GenAlEx to test for spatial autocorrelation using 50 km distance

176 classes up to a total distance of 1550 km using 9999 random permutations and 10 000

177 bootstraps (Peakall et al., 2003).

178

179 2.4 Population structure

180 We defined four separate regions to coincide with the current designation of Tiger

181 Conservation Landscapes and associated protected areas: 1. North - Ulu Masen/Gunung

182 Leuser ecosystem, 2. West - Kerinci Seblat NP and Batang Hari protection forest, 3.

183 East - Tesso Nilo NP, Bukit Tigapuluh NP, Kerumutan wildlife reserve, and Berbak NP,

184 and 4. South - Way Kambas NP (Fig. 1b). Regional differentiation was tested using

185 pairwise values of θ_w (Weir and Cockerham, 1984) computed in Genepop and a locus-

186 by-locus AMOVA implemented in Arlequin v3.1 (Excoffier et al., 1992, 2005) using 19

187 microsatellite loci and 16 000 permutations. We then used BayesAss v1.2 (Wilson and

188 Rannala, 2003) to estimate recent rates of gene flow between the four defined regions

189 (North, East, West, and South).

190

191 Analysis of population structure with no *a priori* grouping was performed using

192 Structure v2.3.3 (Pritchard et al., 2000), Tess v2.3.1 (François et al., 2006), and

193 Geneland (Guillot et al., 2005) (Table A5). Structure is the most commonly used

194 method for population structure analysis but it can be affected by unequal sample sizes

195 between populations and the presence of related individuals in a dataset (Anderson and

196 Dunham, 2008; Kalinowski, 2011; Wang, 2017). Tess and Geneland are also affected

197 by isolation by distance but can better incorporate spatial information (Safner et al.,

198 2011). Clumpp v1.1.2 (Jakobsson and Rosenberg, 2007) was then used to confirm

199 individual membership assignments for each population cluster. Individuals with a

200 membership coefficient of $q \geq 0.7$ were assigned to a single cluster, and individuals with

201 membership coefficients of $0.25 \leq q \leq 0.7$ were considered to have shared membership

202 between clusters.

203

204

205   **3. Results**

206 A total of 148 scats were collected over 15 months of sampling, and scat contents

207 included hair, bone fragments, body parts (claws, quills), soil, and vegetation. Transect

208 length varied from ~2.5 – 10 km and the number of scats encountered at each site varied

209 due to differences in survey effort and terrain, with lowland sites yielding far more

210 samples than submontane regions. More scats were observed on open trails and logging

211 roads compared to forest animal trails, due to the presence of heavy leaf litter and

212 decomposition on the forest floor. Most scats were dried or partially decomposed on

213 collection and varied in age (judged subjectively) from > 7 days old to > 1 month old.

214 Preliminary analysis did not reveal any significant correlation between PCR success and

215 scat location (e.g. animal trail, road, etc) or scat contents (e.g. bones, hairs, etc), though

216 fresher samples (< 1 month old) stored in ethanol generally performed well (data not

217 shown). We had variable success with the detection dog, mostly due to the high

218 temperatures and humidity, and the logistical challenges of transporting the dog with

219 our field teams. This combined with the ongoing cost of the dog's husbandry meant that

220 we found it far more effective to rely on field teams searching visually alone.

221

222 DNA concentration per extract ranged from ~6 - 192 ng μl^{-1}, but this did not correlate

223 well with PCR success. Thirty-seven samples were positive for tiger DNA and variable

224 results were obtained with the sex and microsatellite primers. Ten samples with very

225 low PCR success rates across all loci (< 10%) were discarded immediately from the

226 dataset, and we were able to determine putative sex for 15 of the 27 remaining samples

227 (8 males and 7 females). The mean number of positive PCRs estimated with Gimlet was

228 0.54 (range 0.25 - 0.88) across loci and 0.54 (range 0.36 - 0.77) across samples, with the

229 proportion of missing data per locus ranging from 12 - 72%. The 24 microsatellite loci

230 gave a PI_{SIB} value of 1.57 x 10^{-8}. Locus Fca 161 was monomorphic, and the most

231 informative locus was Fca 94. Average allelic dropout and false allele rates were 0.39

232 and 0.10 as estimated by Pedant with 15 000 search steps. Microchecker identified two

233 loci with possible stuttering (Fca 201, Fca 220), and analysis with MicroDrop

234 highlighted two other samples with allelic dropout rates > 0.50. Dropout rates above

235 0.50 have been shown to bias estimates of genetic diversity and population structure

236 (Smith and Wang, 2014). These two individuals plus the three problematic loci (Fca

237 161, 201, and 220) were therefore also removed from the dataset before subsequent

238 analysis. Shaza suggested that all the remaining samples represented unique individuals

239 apart from a possible match between two pairs of samples. Analysis with Colony

240 suggested that these two pairs were most likely to be full-sibs so they were retained. The

241 final dataset thus contained 25 individuals genotyped at 21 loci.

242

243 Overall, mean observed heterozygosity was 0.52 ± 0.03 s.e. and unbiased expected

244 heterozygosity (UHe) was 0.66 ± 0.03 s.e. (Table 1; Table A4). The population sample

245 did not appear to be in Hardy-Weinberg equilibrium ($F_{IS} = 0.201$), which may be due to

246 non-random mating or population subdivision. NeEstimator v2 gave an estimate of

247 effective population size (Ne) = 22.2 (95% CI 14.9 - 37.5), comparable to that from the

248 sibship assignment method in Colony (Ne = 18 with 95% CI 9 - 40). We also found a

249 significant pattern of isolation by distance, which gave a neighborhood size estimate of

250 29 individuals (95% CI 16 - 115).

251

252 Overall differentiation between regions was low ($\theta_w = 0.08$), with a θ_w value of ≤ 0.15

253 (95% CI 0.05 - 0.18) between the southern group and the rest of the island. This agreed

254 with the AMOVA analysis, which suggested that most of the genetic variance could be

255 explained by grouping the regions into North-West-East and South (Table 2; Table A6).

256 Results from BayesAss suggested that there was little migration into or out of the south

257 region (mean migration rates ≤ 0.06). Most gene flow occurred from the west to the

258 north, and from the west to the east (mean migration rates $\cong 0.20$).

259

260 We found evidence of spatial autocorrelation with a significant relationship between

261 genetic and geographic distance up to 850 km (Fig. A1). This is roughly equivalent to

262 half the length of Sumatra. Analysis with Structure, Tess and Geneland suggested two

263 to four genetic clusters with inconsistent assignment of individuals to the clusters (Fig.

264 2; Table A7). Structure analysis inferred two main clusters – (i) Riau samples north of

265 Tesso Nilo NP and (ii) the rest of Sumatra, including Ulu Masen, Kerinci Seblat

266 NP/Batang Hari, and Way Kambas NP. Structure results may have been biased by the

267 unequal sample sizes between regions, as it has been shown to assign all the individuals

268 from the largest sample to the same cluster (in this case the Riau samples). The output

269 from TESS also suggested two main clusters: one large group encompassing the

270 majority of the island, and a southern subgroup containing the Way Kambas samples. In

271 contrast, Geneland suggested 4 clusters: (i) an admixed northern group encompassing

272 Ulu Masen, (ii) a separate eastern group in Riau, (ii) an admixed east-west grouping

273 including Kerinci Seblat NP/Batang Hari and Jambi province, and (iv) a southern Way

274 Kambas group. These Geneland results infer some influence of underlying clinal

275 variation within the Sumatran population. Thus, due to the unequal sampling and

276 presence of isolation by distance, it was not possible to combine results from these three

277 clustering methods to infer one pattern of population structure.

278

279   **4. Discussion**

280 This study represents the first genetic survey of the wild tiger population on Sumatra to

281 include all the Tiger Conservation Landscapes and protected areas with global or long-

282 term priority. Overall, estimates of heterozygosity were higher than expected for an

283 island subspecies, with some evidence of southern Sumatran tigers becoming

284 genetically differentiated from the rest of the island. This is most likely due to reduced

285 migration into and out of this region as a consequence of an expanding human

286 population and agricultural footprint. With ongoing deforestation and land conversion

287 also occurring in Riau province, it is likely that tigers in eastern Sumatra will eventually

288 suffer a similar fate.

289

290 Sample collection over a period of 15 months generated 148 scats, which yielded

291 useable DNA data from 25 different tiger individuals. The limited number of samples is

292 in part due to the vast sampling area considered ($> 140,000$ km^2 of occupied forest) and

293 the low average population density of tigers on Sumatra (~$1 - 2$ individuals/100 km^2)

294 (Wibisono and Pusparini, 2010). It also serves to highlight that whilst non-invasive

295 samples such as faeces and hair are valuable sources of DNA for threatened mammal

296 species in humid, tropical environments, the proportion of samples that can ultimately

297 be used for genetic analysis ranges from ~$25 - 75\%$, necessitating prolonged and

298 repeated surveys for sample collection (e.g. Bhagavatula and Singh, 2006; Ernest et al.,

299 2000; Janečka et al., 2008; Lucchini et al., 2002).

300

301 We also attempted to use a detection dog to increase sample detection during our

302 surveys. Despite cultural sensitivities to handling dogs, the field teams adjusted well to

303 working alongside the detection dog once introductory training had been completed.

304 However, the high heat and humidity, hilly terrain, and changing locations challenged

305 both the dog's stamina and concentration, resulting in short periods of work before his

306 motivation and focus tailed off. Therefore, for this study, we found that the field teams

307 were more effective with consistent survey effort rather than the alternating rest and

308 work periods required for the dog surveys.

309

310 Although DNA quality has been shown to deteriorate with increasing sample age

311 (Piggott et al., 2004; Santini et al., 2007; Panasci et al., 2011), we collected all scats

312 during our surveys due to the expected low encounter rate for intact scats in this tropical

313 environment. Fecal DNA is particularly prone to genotyping errors such as allelic

314 dropout and false alleles, but our results are similar to other non-invasive studies in

315 carnivores (Broquet and Petit, 2004). Many different methods such as pre-amplification

316 and sample dilution have been proposed to improve PCR success for non-invasive

317 samples, but they had little effect in this study (data not shown). An ongoing pilot study

318 in our research group suggests that combining an appropriate method of sample

319 preservation (e.g. DNA/RNA Shield; Zymo Research), a DNA extraction method

320 including homogenization (e.g. using FastPrep-24; MP Biomedicals), and amplification

321 with inhibitor-resistant polymerases (e.g. KAPA2G Robust; KAPA Biosystems) can

322 greatly improve data quality (data not shown). As it is difficult to obtain good quality

323 scats in humid, tropical environments, others have explored the use of alternative

324 sources of DNA, such as swabs taken from urine scent marks, which have much higher

325 detection rates than scats in some sites (Caragiulo et al., 2015). For example, scent mark

326 to scat detection ratios in Tambling Wildlife Nature Conservation, southern Sumatra,

327 are typically between 3:1 and 4:1 (unpublished results). Tigers preferentially spray scent

328 on overhanging trees or leaves along territory boundaries with up to 3.7 and 1.0 marks

329 per km for males and females, respectively (Smith et al., 1989; Protas et al., 2010).

330 Lipids contained within the urine sprays enable them to persist on the surfaces of

331 vegetation (Andersen and Vulpius, 1999; Burger et al., 2008), and their characteristic

332 scent is easily detected by people for up to 3 weeks after deposition.

333

334 In this study, we used a subset of the microsatellite loci used by Luo et al. (2004) to

335 show that wild Sumatran tigers retain levels of genetic variation comparable to

336 mainland subspecies. Low heterozygosity has been shown to correlate with a high risk

337 of extinction for many species, and threatened or island species are thought to have ~60

338 - 65% of the microsatellite heterozygosity of similar or related non-endangered species

339 (Frankham and Ralls, 1998; Brook et al., 2002). Therefore, the level of genetic variation

340 found bodes well for Sumatran tigers as it suggests that overall the population has not

341 experienced significant genetic drift. Given that heterozygosity is expected to be lost at

342 a rate of $1/2Ne$ per generation due to genetic drift alone (Hedrick, 2005; Hamilton,

343 2009), we would expect Sumatran tigers to lose 1 - 3% of their genetic variation every

344 generation ($\sim$ every 5 – 7 years). This is in the absence of other threats and assumes that

345 current estimates of effective population size ($Ne \cong 18 - 29$) and generation time remain

346 unchanged in the future. This rate could be higher for the smallest subpopulations of

347 tigers ($N < 30$ individuals), which would result in a faster rate of decline and increased

348 differentiation from other subpopulations. While genetic drift and loss of genetic

349 variation at the subpopulation level could be counterbalanced to some extent by

350 migration or gene flow (e.g. Vilà et al., 2003), those at the subspecies level cannot be

351 ameliorated by migration. Hence, while maintaining or increasing connectivity is an

352 important part of the management of low density, wide-ranging species, the

353 fundamental management strategy should be to increase the overall population size by

354 expanding tiger habitat and/or improving habitat quality which then may also lead to

355 increasing connectivity.

356

357 Our results may also represent a type of genetic extinction debt, in which population

358 changes resulting from increased forest loss and poaching are subject to a time delay

359 (Habel et al., 2015). The delay between the environmental change and a genetic effect is

360 likely to be greater for long-lived species with low rates of population turnover

361 (Kuussaari et al., 2009). Ultimately, if the pace of forest loss and human activity

362 continues at its current rate it is likely that we will start to see signs of reduced

363 heterozygosity and greater population isolation on Sumatra (Helm et al., 2009).

364 Increased homozygosity (and the resulting inbreeding depression) have been associated

365 with increased extinction risk due to factors such as reduced reproductive success, a

366 decrease in population fitness, and increased susceptibility to disease (Amos and

367 Balmford, 2001; Spielman et al., 2004). Although these changes have been noted in

368 some carnivore populations (e.g. Johnson et al., 2010; Fredrickson et al., 2007), for

369 tigers there is little empirical evidence to determine at what level these changes would

370 occur.

371

372 The presence of isolation by distance suggests that Sumatran tigers are partly structured

373 by a neighborhood mating system in which individuals are more likely to mate within a

374 given area governed by dispersal distance. The estimated values of effective population

375 size in this study (N_e = 18 – 29) give an $N_e : N_c$ ratio in the range of ~0.04 - 0.06,

376 where N_c represents the total estimated population of 500 tigers. This is in line with

377 previous studies in Bengal and Amur tigers (N_e = 27 - 35) using genetic data and

378 variance in reproduction (Henry et al., 2009; Smith and McDougal, 1991), and is close

379 to the average ratio of 0.1 - 0.11 for wildlife populations (Frankham, 1995). However, it

380 is lower than other cat species such as the leopard, cheetah, and puma in which ratios of

381 0.25 – 0.64 have been recorded (Nowell and Jackson, 1996; Spong et al., 2000; Kelly,

382 2001). Analysis with MRatio (Garza and Williamson, 2001) did not provide evidence

383 for a recent population bottleneck (Smith, 2012) and thus other factors such as a

384 polygynous mating system, in which dominant males mate with most available females,

385 or sampling scale, may account for the low effective population size (Kaeuffer et al.,

386 2004; Neel et al., 2013). However, restricting our analysis to the neighborhood size

387 suggested by spatial autocorrelation (< 850 km) did not result in a significant difference

388 in the estimates of Ne (data not shown).

389

390 In the absence of gene flow, populations lose alleles under the influence of genetic drift

391 and become increasingly differentiated (Falconer and MacKay, 1996). It was expected

392 that geographic features such as Lake Toba and the Bukit Barisan mountain range might

393 influence tiger population structure as they interrupt the distribution of other large

394 mammals on Sumatra such as the tapir, orangutan, and rhino (Wich et al., 2016;

395 Pusparini et al., 2015; Linkie et al., 2013). However, telemetry data shows that some

396 tigers are capable of using ridgelines to cross the Bukit Barisan mountain range (Priatna

397 et al., 2012), and our study did not find any obvious genetic discontinuity caused by

398 these features. This is likely due to the tiger's dispersal ability, which can reach up to 65

399 km for males and 33 km for females (Smith, 1993; Goodrich et al., 2010), and

400 highlights the importance of understanding differences in species' abilities to disperse

401 across natural and anthropogenic barriers.

402

403 The high concentration of roads, settlements and plantations across parts of central

404 Sumatra were also expected to act as dispersal barriers (Smith et al., 1998; Kerley et al.,

405 2002; Linkie et al., 2006), but again our results suggest that either tigers have been able

406 to maintain a fairly continuous distribution using patches of 'stepping stone' habitat, or

407 more likely that insufficient time has passed for measurable genetic drift to have

408 occurred in this region. Given the tiger's long generation time of 7 years (Seal et al.,

409 1994), it could take up to 105 years (15 generations) for a landscape barrier to produce a

410 detectable genetic signature (Holzhauer et al., 2006; Landguth et al., 2010). Therefore, it

411 appears that the current Sumatran tiger population still exhibits evidence of the

412 continuous distribution and genetic variation present within the ancestral Sunda

413 population (Bay et al., 2014). However, given the current rates of land conversion to

414 commercial crops such as oil palm and agroforestry, it is probable that much of the

415 primary forest at lower elevations outside of conservation areas will be lost in the next

416 30 - 50 years (Holmes, 2002). Repeating a genetic study such as this in the future is

417 therefore likely to show a more extensive pattern of population isolation and a more

418 profound loss of genetic variation (Wearn et al., 2012; With, 2004).

419

420 In contrast to central Sumatra, there appears to be very little gene flow into or out of

421 Way Kambas NP in the southern tip of Sumatra - this national park showed the highest

422 pairwise F_{ST} and the lowest migration rates. These high F_{ST} values represent a separation

423 from the sampled TCL populations in western and eastern Sumatra. While we

424 acknowledge that there may be some exchange of individuals with the nearest protected

425 areas in Berbak/Sembilang NP and Bukit Balai Ranjang NP, Way Kambas covers a

426 relatively small area of isolated habitat (~1300 km^2) and has a small population of ~30

427 tigers with low occupancy rates (Wibisono et al., 2011; Sanderson et al., 2006).

428 Maintaining gene flow or connectivity and the quality of the surrounding matrix is

429 thought to be crucial to the survival of tigers within smaller protected areas

430 (Ranganathan et al., 2008). However, the prospects for increasing connectivity in this

431 region are bleak.

432

433 Primary lowland forest has been replaced by a mosaic of agricultural crops and

434 plantations, (Miettinen et al., 2008; Miettinen and Liew, 2010), and a zone of

435 urbanization surrounds the park such that there are no significant buffer zones suitable

436 for wildlife (Nyhus and Tilson, 2004; Imbernon, 1999). Although the early stages of

437 forest conversion may be beneficial to tigers due to the creation of secondary forest and

438 edge habitats that support many prey species (Berry et al., 2010; Maddox et al., 2007;

439 Barlow et al., 2007; Sunquist, 1981; Santiapillai and Ramono, 1987), many degraded or

440 previously logged areas are quickly converted to oil palm or other agricultural

441 plantations which are not as beneficial to tigers (Barber and Schweithelm, 2000).

442 Frontier activities by local communities at the borders of national parks/wildlife

443 reserves and agricultural concessions also commonly progress to more wide-scale

444 operations or permanent rural settlements (Smith, 2009). And some habitat degradation,

445 encroachment and hunting also occurs within park borders such that these are not the

446 inviolate refugia their names suggest (e.g. Forrest et al., 2011; Gaveau et al., 2009b).

447

448 Lowland peat swamp forest in eastern Sumatra is suffering a similar fate with land

449 being cleared at a rate of up to 2.3% per year (Uryu et al., 2008; Hansen et al., 2009;

450 Broich et al., 2011; Koh et al., 2011; Miettinen et al., 2012). Riau lost more than 50% of

451 its primary lowland forest between 1990 and 2010, and focus has now shifted to

452 primary peat swamp forest (Margono et al., 2012, 2014). This rate of deforestation is

453 likely to continue as Indonesia plans to increase its land allocation to oil palm, paper

454 and pulp to just under 15 million hectares by 2030 (Wilcove et al., 2013). These land

455 use types support much lower species richness compared to primary forest (~38%), and

456 tigers are commonly extirpated from these areas (Maddox et al., 2007; Smith, 2009;

457 Danielsen et al., 2009; Fitzherbert et al., 2008). This combination of poaching pressure

458 and impoverished habitat is therefore likely to result in a population decline and

459 increased genetic differentiation between protected areas as the options for tiger

460 movement across the agricultural matrix are reduced (Kenney et al., 1995; Linkie et al.,

461 2006; Chapron et al., 2008).

462

463 Tiger populations are more likely to suffer extinction debt in areas where there is

464 overlap with agricultural or rural development, and these could serve as priority hot

465 spots where intervention is most likely to be effective (Helm et al., 2009; Wearn et al.,

466 2012). Despite a national government moratorium on conversion of peatland and

467 primary forest since 2011 (Austin et al., 2014), the Ministry of Forestry has also

468 pledged a commitment to expanding the oil palm and timber industries to support

469 national and international demand (Karyaatmadja et al., 2011; Brockhaus et al., 2012;

470 Harahap et al., 2017). Uncertainties around land classification and implementation of

471 the moratorium have resulted in continued loss of primary forest on Sumatra,

472 particularly in Riau province and around Tesso Nilo NP (Harris et al., 2017). Therefore,

473 there needs to be greater coordination across different government policies (biofuels,

474 climate, forestry and agriculture) to ensure adequate protection of the primary and

475 secondary forested lands which are key to supporting the remaining tiger populations.

476

477

478 **5. Conclusions**

479 We present the first assessment of the effects of landscape change on the tigers on

480 Sumatra. Our results show that the Sumatran tiger has retained levels of genetic

481 diversity comparable to mainland subspecies and that there is evidence to suggest

482 reduced gene flow for tigers in the extreme south of Sumatra. Whilst we acknowledge

483 the limited sample size, the distribution of sampling sites represents a good proportion

484 of the remaining tiger habitat on Sumatra. Precise estimates of genetic variation can be

485 made with as few as 10 individuals (Smith and Wang, 2014), and therefore, our results

486 provide a good overview of the genetic status of the wild Sumatran tiger population.

487 This study also demonstrates that the genetic data obtained from non-invasive samples

488 is critical to understanding the genetic diversity and population structure of large-

489 bodied, low-density mammals such as the tiger; individuals are not easily captured for

490 biological sampling, baited hair traps are not reliable, and dens or latrines are rarely

491 seen. Similar methods are being used to study the Sumatran elephant and Sumatran

492 rhino, which will provide more information on the effects of land conversion on other

493 threatened large mammal species.

494

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Conflict of Interest

The authors have no conflicts of interest to declare.

TABLES

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976 **Table 1.** Estimates of genetic diversity in subspecies of *Panthera tigris*. Microsatellite

977 loci were not identical between studies but showed some degree of overlap between the

978 loci used.

Tiger subspecies	No. of individuals	No. of loci	Observed heterozygosity	Expected heterozygosity	Reference
P.t. sumatrae	25	21	0.52 ± 0.03 s.e.	0.64 ± 0.03 s.e.	This study
P.t. sumatrae	16	30	0.47 ± 0.02	0.49 ± 0.04	Luo *et al*. 2004
P.t. altaica	34	30	0.47 ± 0.02	0.46 ± 0.04	Luo *et al*. 2004
P.t. altaica	95	8	0.26 ± 0.11	-	Henry *et al*. 2009
P.t. corbetti	33	30	0.64 ± 0.02	0.67 ± 0.03	Luo *et al*. 2004
P.t. jacksoni	22	30	0.56 ± 0.02	0.57 ± 0.03	Luo *et al*. 2004
P.t. tigris	6	30	0.52 ± 0.04	0.57 ± 0.04	Luo *et al*. 2004
P.t. tigris	73	5	0.70 ± 0.16 s.d.	-	Mondol *et al*. 2009

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982 **Table 2.** Pairwise differentiation (θ_w) for regional groups in the Sumatran tiger

983 population. Estimates were computed in Genepop and significant values ($p < 0.05$) are
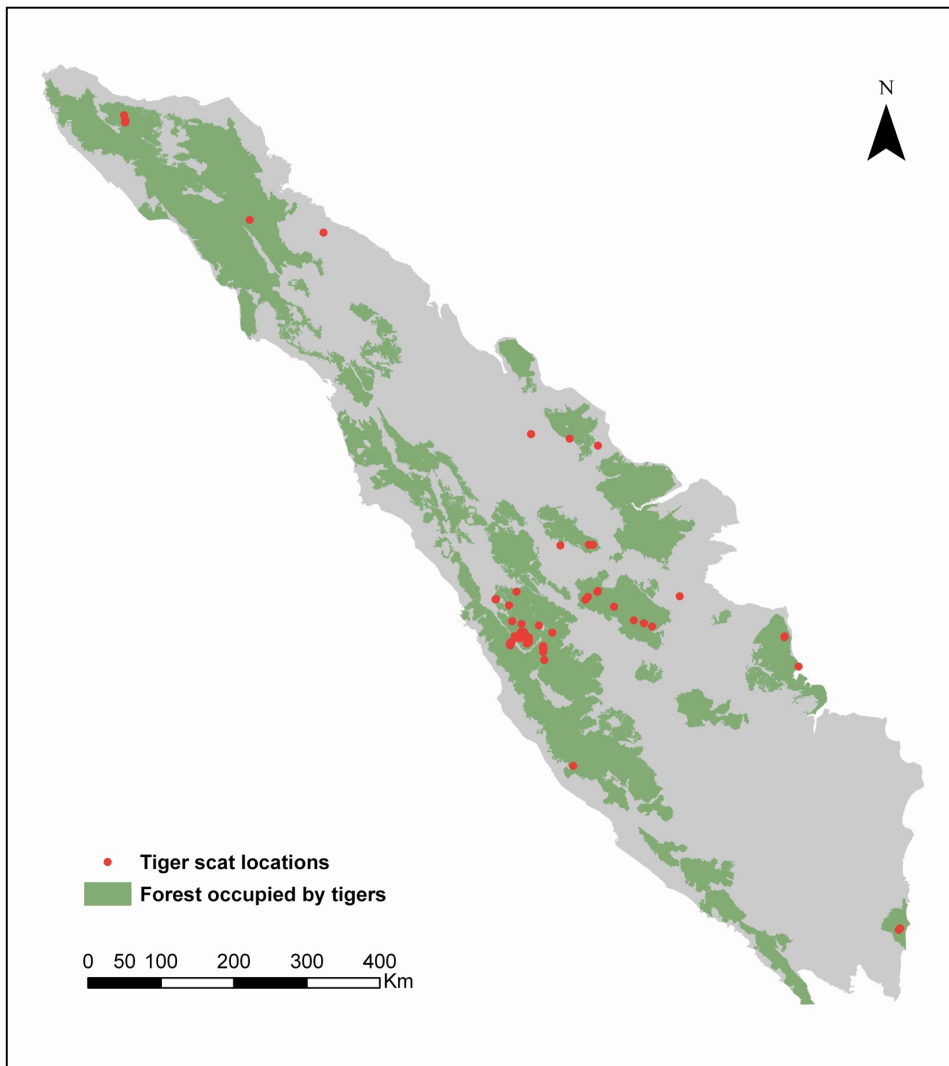
984 indicated with an asterisk.

	North [†]	East	West	South
North	-			
East	0.07[*]	-		
West	0.06	0.03	-	
South	0.15[*]	0.15[*]	0.13[*]	-

985 [†] *North* - Ulu Masen-Gunung Leuser ecosystem; *East* - Tesso Nilo NP, Kerumutan

986 Wildlife Reserve, Berbak NP; *West* - Kerinci Seblat NP, Batang Hari protection forest;

987 *South* - Way Kambas NP.
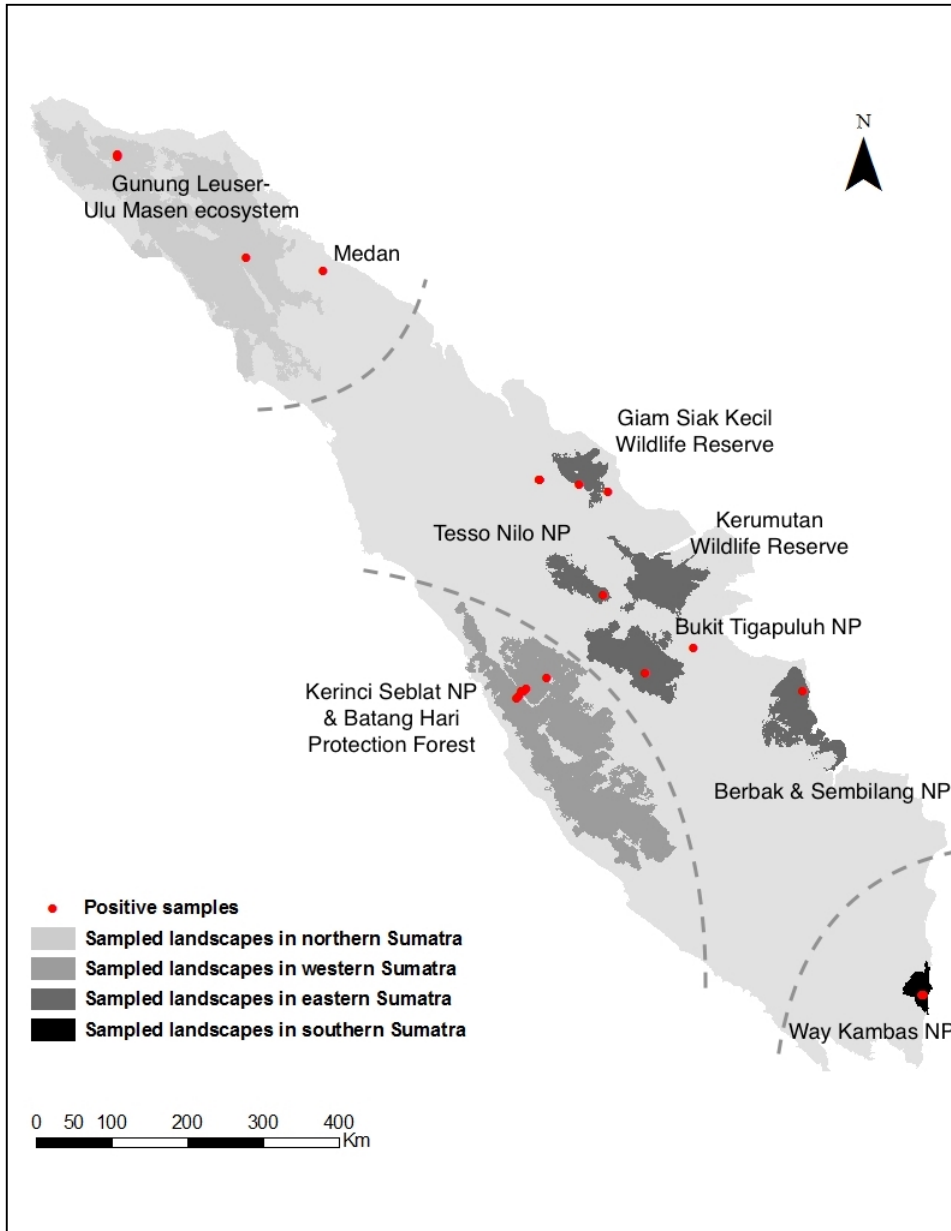
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FIGURES

Fig. 1a. Map showing the remaining Sumatran forest habitat that is occupied by tigers (data from Wibisono and Pusparini 2010). Locations where faecal samples were collected are indicated by the red points.

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**Fig. 1b.** Regional subdivision of the Tiger Conservation Landscapes and protected areas

sampled during this study. The Northern group includes the Ulu Masen ecosystem; the

Western group includes Kerinci Seblat NP and Batang Hari protection forest; the

Eastern group includes Tesso Nilo NP, Kerumutan wildlife reserve, Bukit Tigapuluh

NP, and Berbak NP; and the Southern group includes Way Kambas NP. Locations of

the tiger positive samples are represented by the red points

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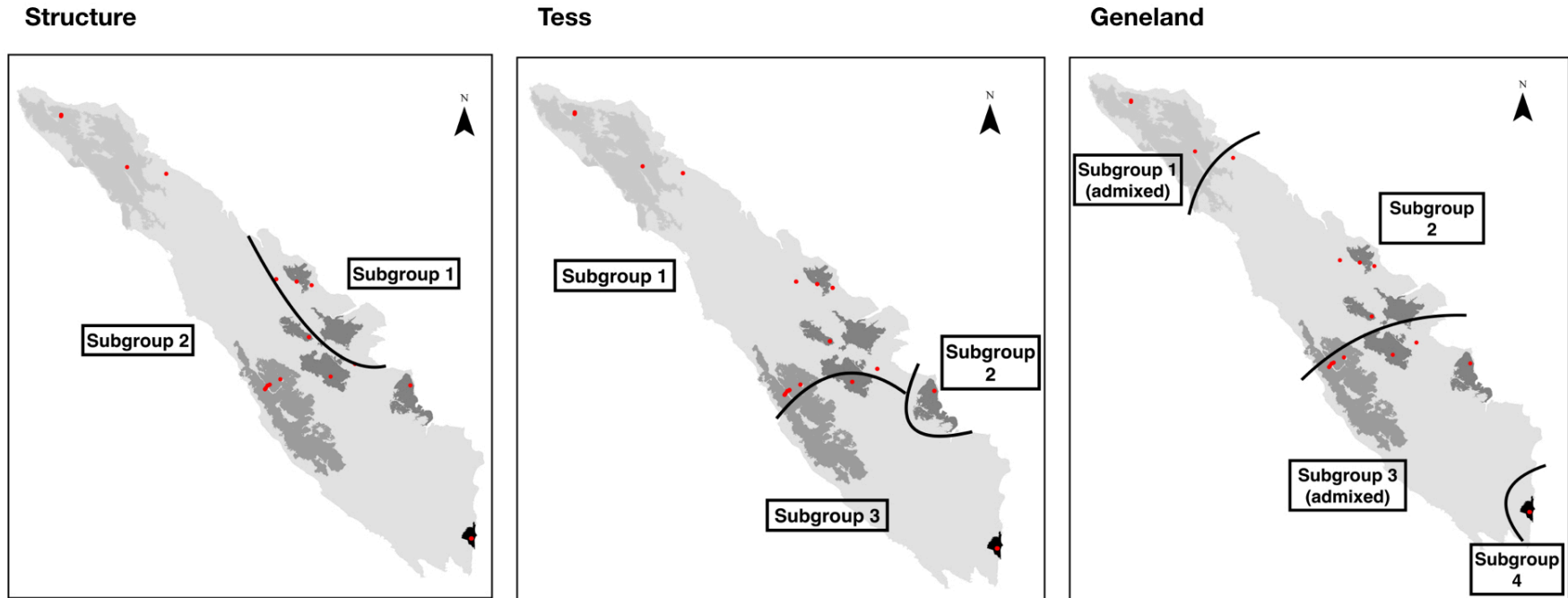
1015 **Fig. 2.** Maps showing the genetic subgrouping of positive tiger samples using 3 different algorithms in Structure, Tess, and Geneland.

1016 Stucture preferentially separated northern Riau samples from the rest of Sumatra. Tess placed southern Way Kambas samples into a

1017 separate group. Geneland suggested 4 subgroups, which could reflect underlying isolation by distance.