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Genetic analysis suggests dispersal among chimpanzees in a fragmented forest landscape in Uganda

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Habitat fragmentation is a leading threat to global biodiversity. Dispersal plays a key role in gene flow and population viability, but the impact of fragmentation on dispersal patterns remains poorly understood. Among chimpanzees, males typically remain in their natal communities while females often disperse. However, habitat loss and fragmentation may cause severe ecological disruptions, potentially resulting in decreased fitness benefits of male philopatry and limited female dispersal ability. To investigate this issue, we genotyped nearly 900 non-invasively collected chimpanzee fecal samples across a fragmented forest habitat that may function as a corridor between two large continuous forests in Uganda, and used the spatial associations among co-sampled genotypes to attribute a total of 229 individuals to 10 distinct communities, including 9 communities in the corridor habitat and 1 in continuous forest. We then used parentage analyses to infer instances of between-community dispersal. Of the 115 parent–offspring dyads detected with confidence, members of 39% ($N = 26$) of mother–daughter dyads were found in different communities, while members of 10% ($N = 5$) of father–son dyads were found in different communities. We also found direct evidence for one dispersal event that occurred during the study period, as a female's sample found first in one community was found multiple times in another community 19 months later. These findings suggest that even in fragmented habitats, chimpanzee males remain in their natal communities while females tend to disperse. Corridor enhancement in unprotected forest fragments could help maintain gene flow in chimpanzees and other species amid anthropogenic pressures.

KEYWORDS
chimpanzee, dispersal, ecological corridor, genetic tracking, habitat fragmentation, *Pan troglodytes*

1 | INTRODUCTION

Habitat fragmentation, the process by which areas of habitat are subdivided into smaller and more isolated patches, poses a leading threat to global biodiversity (Haddad et al., 2015). Habitat fragmentation disturbs ecosystem stability and negatively impacts abundance in a variety of taxa (Haddad et al., 2015). Notably, habitat fragmentation has been shown to reduce the likelihood of dispersal in taxa including birds (Cooper & Walters, 2002), invertebrates (Baguette, Mennechez, Petit, & Schtickzelle, 2003), and mammals (Fietz, Tomiuk, Loeschcke, Weis-Dootz, & Segelbacher, 2014). Here, we define dispersal as the relocation of an organism from its birthplace to its breeding (or

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potential breeding) site (Howard, 1960). Limitations on dispersal can lead to inbreeding depression, thereby limiting population viability and heightening extinction risk (Dudash & Fenster, 2000).

By facilitating movement of individuals between habitat patches, habitat corridors may help buffer the deleterious effects of habitat fragmentation (Beier & Noss, 1998). Such corridors may be constructed or occur naturally. They can be defined structurally, for example, as a linear strip of habitat connecting two larger areas of similar habitat, or functionally, for example, forest fragments as 'stepping stones' that facilitate movement among larger forest patches (Bennett, 2003). Corridors have been shown to increase ranging ability and resource access (Haddad et al., 2003). They also maintain or increase dispersal ability, thereby potentially aiding gene flow and population viability (e.g., understory birds [Castellón & Sieving, 2006], tigers [Sharma et al., 2013], and gorillas [Bergl et al., 2012]). Forests harbor relatively high biodiversity but are highly impacted by ongoing fragmentation (Haddad et al., 2015), so understanding how structural and functional corridors help promote forest connectivity is increasingly important.

Great apes are highly dependent upon forest habitats; anthropogenic habitat loss and fragmentation, along with hunting and disease, are key threats to their survival (Junker et al., 2012; Walsh et al., 2003). In the past two decades, there has been a marked decline in remaining suitable habitat for African great apes (Junker et al., 2012). For example, up to 81% of chimpanzees (*Pan troglodytes*) in West Africa live outside protected areas, often in fragmented and degraded forests (Kormos, Boesch, Bakarr, & Butynski, 2003). Similarly, an estimated 78% of Bornean orangutans (*Pongo pygmaeus*) live outside protected areas, with large-scale commercial agriculture such as oil palm production posing a major threat to orangutan survival (Wich et al., 2012). Some studies have indicated that great apes display behavioral flexibility with regard to their diets (Ancrenaz et al., 2015; Hockings & McLennan, 2012), nesting patterns (Last & Muh, 2013; McCarthy, Lester, & Stanford, 2017), and activity budgets (Hockings, Anderson, & Matsuzawa, 2012; Krief et al., 2014) in heavily human-impacted environments. However, little research has focused on patterns of philopatry and dispersal under conditions of habitat fragmentation. Responses to fragmentation have critical implications for great ape conservation, particularly as habitat corridors are increasingly valued as a strategy to enhance gene flow in fragmented great ape habitats (Imong, Robbins, Mundry, Bergl, & Kühl, 2014; Nater et al., 2013).

Chimpanzees live in territorial communities characterized by sex-biased patterns of male philopatry and female dispersal (alternatively termed "transfer"), with flexible fission–fusion subgrouping patterns and a promiscuous mating system (Goodall, 1986). Sex-biased dispersal is thought to confer fitness benefits for both sexes, with female dispersal decreasing the risk of inbreeding (Pusey, 1980) and male philopatry underlying same-sex bonding patterns that enable coordinated hunting, territory defense, and coalitionary aggression (Langergraber, Mitani, & Vigilant, 2007; Muller & Mitani, 2005). Females typically disperse from the natal community upon reaching sexual maturity around 13 years of age (Boesch & Boesch-Achermann, 2000; Nishida, 1990; Reynolds, 2005), although there is considerable variability in the likelihood of female dispersal. Reported transfer rates vary from between half to nearly all females in most studied communities (Boesch & Boesch-Achermann, 2000; Nishida, 1990; Reynolds, 2005; Wroblewski et al., 2015). However, female transfer has not been confirmed in a single highly isolated community at Bossou, Guinea (Sugiyama, 1999). Because dispersal decisions can impact a female's reproductive success (Williams, Pusey, Carlis, Farm, & Goodall, 2002), transfer should be expected under suitable environmental and social conditions. Factors affecting female dispersal timing and likelihood include resource availability, social rank, within-group competition, and affiliative relationships (Stumpf, Emery Thompson, Muller, & Wrangham, 2009; Williams et al., 2002; Wroblewski et al., 2015).

With regard to male philopatry, the typically aggressive nature of interactions between males of different communities appears to preclude the possibility of adult male dispersal (Boesch et al., 2008; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Wilson, Wallauer, & Pusey, 2004), which has never been confirmed. The occurrence of infanticide also precludes the movement of males as dependent offspring (Langergraber, Rowney, Crockford, et al., 2014; Townsend, Slocombe, Thompson, & Zuberbuehler, 2007) and rates of extra-group paternity are expected to be quite low, particularly in eastern chimpanzees (<5%; Langergraber, Rowney, Schubert, et al., 2014; Langergraber, Siedel, et al., 2007; Wroblewski et al., 2009).

Habitat loss and fragmentation may influence patterns of philopatry and dispersal. Fragmentation may decrease chimpanzee density and community cohesion (Balcomb, Chapman, & Wrangham, 2000; Wrangham, Gittleman, & Chapman, 1993), resulting in weaker social bonds among isolated sub-groups as well as the potential for communities to fission into multiple smaller communities. Benefits of male philopatry, such as cooperative territory defense, may lessen as low resource density leads to large home ranges that are energetically costly or implausible to defend (Amsler, 2010; Mitani & Rodman, 1979). Simultaneously, the costs of female dispersal may increase in fragmented landscapes (Chaine & Clobert, 2012), as traveling outside the forest can involve road crossings, harassment from local people, or other threats leading to chimpanzee injuries or death (Hockings, Anderson, & Matsuzawa, 2006; McLennan, Hyeroba, Asiimwe, Reynolds, & Wallis, 2012). The increasing isolation of forest fragments may also make it more challenging for a female to locate habitat outside her natal community with remaining resident chimpanzee communities. Limited resource availability may lead to higher within-group competition, so immigrant females may be at increased risk of aggression from resident females and may obtain fewer resources, limiting reproductive success (Kahlenberg, Thompson, Muller, & Wrangham, 2008; Williams et al., 2002). Conversely, decreased chimpanzee density or lower community cohesion could reduce reproductive opportunities, potentially leading to subsequent dispersal following transfer from the natal community, termed "secondary dispersal" or "secondary transfer." Although secondary dispersal is common in some primate species (Harcourt, Stewart, & Fossey, 1976; Sterck, Willems, van Hooff, & Wich, 2005), it has been observed only rarely in chimpanzees and under conditions of severe demographic disturbance (Nishida, Hiraiwa-Hasegawa, Hasegawa, & Takahata, 1985; Rudicell et al., 2010). Delayed female dispersal following the onset of reproduction in the natal community has also rarely been reported (Langergraber, Rowney, Crockford, et al., 2014; Nishida et al., 1985; Rudicell et al., 2010; Williams et al., 2002). In sum, habitat loss and fragmentation may plausibly alter expected sex-biased differences in the general patterns of male philopatry and female dispersal in chimpanzees.

Chimpanzees inhabit a fragmented forest landscape between the Budongo and Bugoma Forests in western Uganda (Figure 1). The rate of habitat fragmentation in this region has been particularly steep in the past several decades, leading to the possibility of severe demographic shifts in the chimpanzee population. Because observation of elusive wild chimpanzees over a large landscape is untenable, we previously used genetic analysis of DNA from noninvasive samples to infer that this approximately 1,200-km^2 landscape is inhabited by an estimated 260–320 chimpanzees distributed in nine postulated communities (McCarthy et al., 2015). Although putative community memberships of male chimpanzees corresponded largely to the distribution of Y-chromosome haplotypes, 4 of 14 Y-chromosome haplotypes were shared among multiple putative communities. Partial dissolution of male philopatry via male dispersal or community fissions are among the possible explanations, but evaluating this possibility requires additional genetic data beyond Y-chromosome haplotypes.

Several other measures may potentially be used to infer the degree of sex-biased philopatry and dispersal in natural populations, for example by comparing average relatedness values or genetic differentiation between the sexes (e.g., Städele, Van Doren, Pines, Swedell, & Vigilant, 2015). These measures permit broad inferences regarding overall patterns but do not provide detail regarding the group dynamics driving those patterns nor the temporal scale over which sex-biased differences emerged. Further, such measures can display stochastic variation, particularly in small communities with the potential for incomplete sampling biased toward family groups, and therefore do not reliably indicate sex differences in philopatry and dispersal (Lukas, Reynolds, Boesch, & Vigilant, 2005). For example, in a population of chimpanzees known from long-term behavioral observations to have strict male philopatry and nearly complete female dispersal, average within-community relatedness was not consistently higher among males than females (Lukas et al., 2005).

Alternatively, genetic information from the Y-chromosome can be complemented by analysis of biparentally inherited markers to elucidate parent–offspring community membership patterns

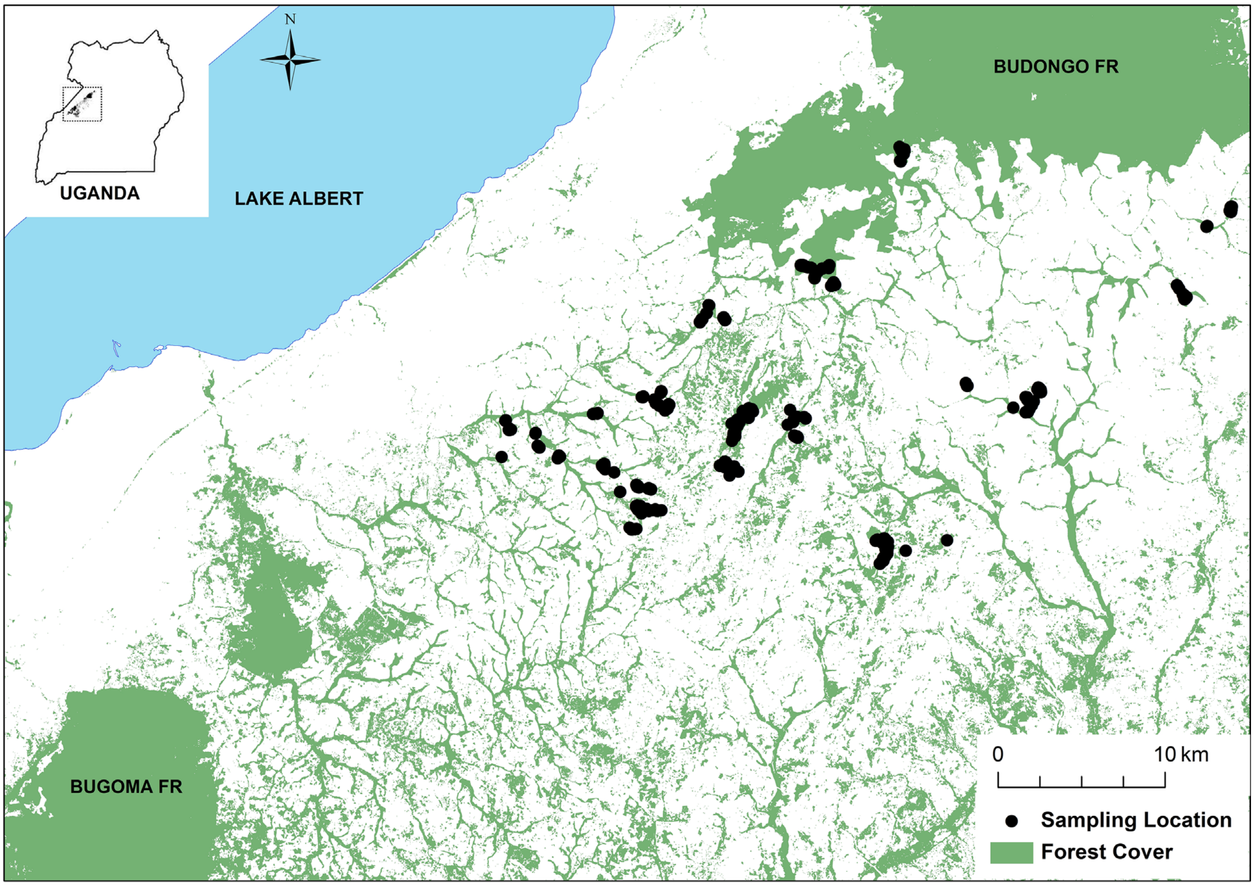

FIGURE 1 The study area in Uganda. The corridor habitat is located between the Budongo and Bugoma Forest Reserves (FR). The inset map displays the landscape's location in Uganda. Shading indicates forest cover during the study period (Hansen et al., 2013). Black circles indicate dung sample collection locations during this study

(Arandjelovic, Head, Boesch, Robbins, & Vigilant, 2014). This approach has the advantage of permitting inferences about recent patterns of philopatry and dispersal among genotyped individuals in the population undergoing habitat fragmentation. Under male philopatry and female dispersal, we expect father–son pairs to reside in the same community, and mother–daughter pairs to reside in different communities. Although such dyadic parentage analyses can reveal general sex biases in dispersal and philopatry, they cannot determine directionality of dispersal, as without information on the age of individuals, it is impossible to determine which member of the dyad is the parent and which is the offspring. Analyses of parentage trios (i.e., mother–father–offspring) can reveal the direction of dispersal, in that if a female is found in community A and both of her parents are found in community B, this indicates that this female dispersed from her natal community B to community A. Directionality of dispersal can also be inferred directly when an individual is found in one community then in another community at a later date.

Here we use these approaches to examine the dynamics of chimpanzee movement across the fragmented forest landscape connecting the Budongo and Bugoma Forests to assess the extent to which this landscape may function as a corridor for chimpanzee dispersal. We examine genetic evidence for male philopatry and female dispersal in chimpanzees to determine whether sex-biased patterns remain evident under the conditions of severe anthropogenic habitat alteration characterizing this landscape. Our results have implications for the conservation utility of this fragmented landscape, and in general illustrate the potential applicability of this genetic approach to infer population dynamics.

2 | METHODS

2.1 | Study area

The Budongo and Bugoma Forest Reserves are protected forests, each measuring >400 km^2 and harboring two of the largest chimpanzee populations in Uganda (Plumptre et al., 2010; Reynolds, 2005). The approximately 40 km long by 30 km wide region between these forests is a mosaic landscape comprising riparian forest fragments, grasslands, agricultural fields, and villages (1°37′–1°68′N and 31°1′–31°6′E; Figure 1). Climatic and pollen data indicate the Budongo Forest has been a standalone forest block for millenia, so this region to its south has likely existed as a riparian forest-grassland mosaic throughout that time (Paterson, 1991). However, this area has undergone substantial changes in recent decades as human populations have grown sharply, leading to the widespread conversion of unprotected riparian forests for agriculture (Mwavu & Witkowski, 2008). Between 1985 and 2014, an estimated 134 km^2 of forest was lost in this region, largely on privately owned land (Twongyirwe, Bithell, Richards, & Rees, 2015).

We collected data in this region from October through December 2011 and October 2012 through September 2013. Field data collection—described in detail in McCarthy et al. (2015)—was conducted with permission from the Uganda National council for Science and Technology, the Uganda Wildlife Authority, and the National Forestry Authority of Uganda. Institutional ethical consent was not necessary for this project since fecal sample collection was entirely noninvasive and required no contact with the chimpanzees. This research adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

2.2 | Genotype and community membership data used in parentage analyses

We collected 865 chimpanzee fecal samples noninvasively throughout this fragmented forest habitat, then extracted DNA and genotyped extracts using 14 autosomal microsatellite loci and the sex-determining amelogenin locus (McCarthy et al., 2015). From these genotypes, we identified 182 individuals, and obtained population size estimates of 256 (95% CI: 246–321) and 319 (288–357) using *capwire* two innate rates (TIRM) and spatially explicit capture–recapture (SECR) models, respectively.

With sufficient sampling, the spatial associations among genotypes can be used to infer patterns of group association (Arandjelovic et al., 2010, 2014; Jeffery, Abernethy, Tutin, Anthony, & Bruford, 2007). Over the 2-year period of data collection, we searched areas of riparian forest repeatedly, with up to 20 days of search effort per 1 × 1 km^2 grid cell of the study area. The genotypes from fecal samples collected across these searches indicated repeated sampling of many individuals (genotyped samples per individual chimpanzee: mean = 3.5, range: 1–12). When genotypes were found in association with other genotypes, for example, from samples collected under nests comprising a single group of similarly aged nests, they were assumed to belong to members of the same community (McCarthy et al., 2015). Using these repeatedly sampled genotypes and their associations, we constructed 100% minimum convex polygons (MCPs) using the Minimum Convex Polygon plugin for QGIS version 2.4.0 software (QGIS Development Team, 2018) to represent minimum community home ranges. Additional genotypes found within these polygons were also assumed to originate from members of the same community, since chimpanzees are territorial and a high degree of spatial overlap among communities, although possible, is generally not expected (Herbinger, Boesch, & Rothe, 2001; Nishida, 1979). In accordance with these expectations, all MCPs indicated entirely non-overlapping clusters (with the sole exception of one female genotype linking two MCPs; see section 3). These genotype clusters indicated the presence of at least nine putative chimpanzee communities, with each minimum home range typically encompassing numerous forest fragments (Figure 2; McCarthy et al., 2015). Available behavioral data from three chimpanzee communities under study in this region indicated similar abundances and distributions as these genetic data, further supporting the MCP community associations we assigned (McCarthy et al., 2015). For simplicity, hereafter we refer to the chimpanzees distributed among these putative communities in fragmented forest habitat "corridor chimpanzees" and the associated data as "corridor data."

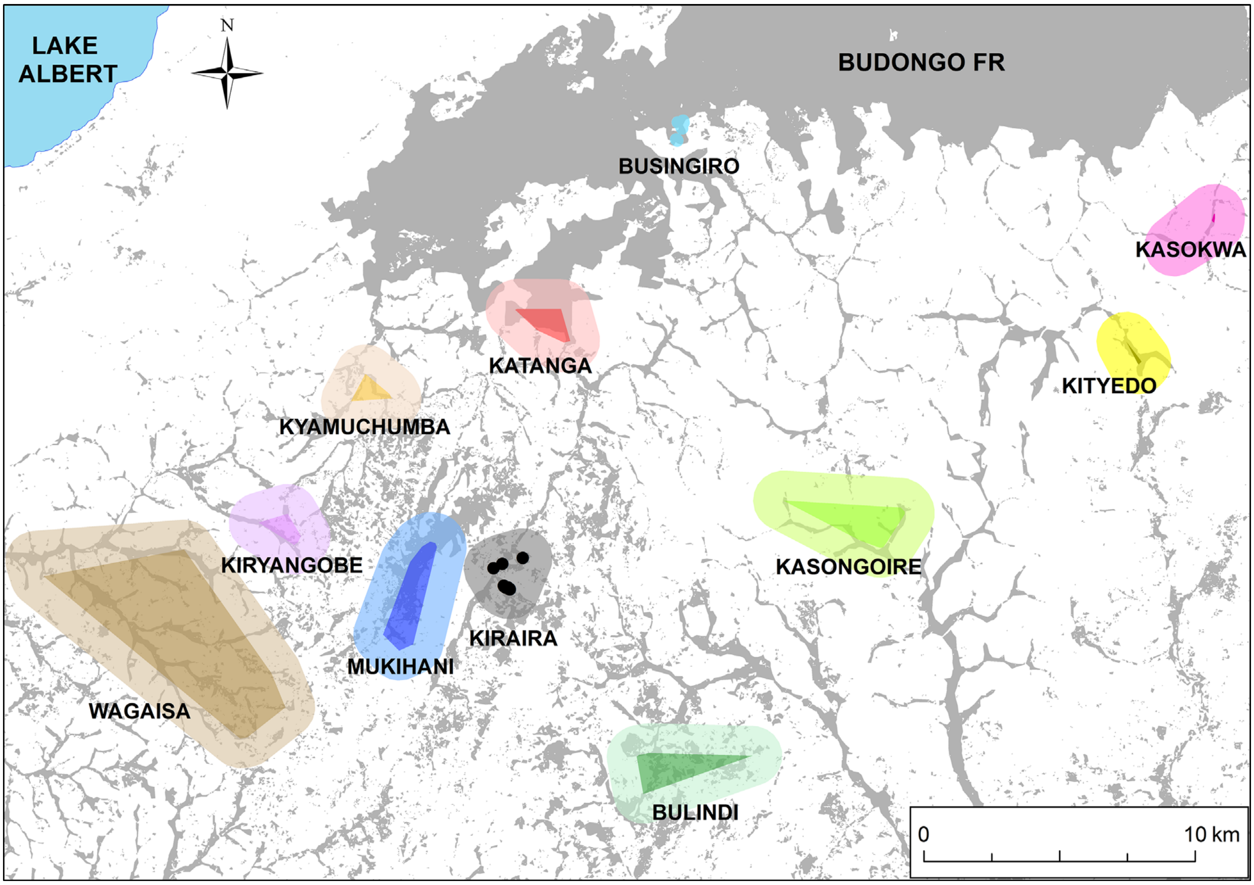

FIGURE 2 Minimum convex polygons (MCPs) for genotyped samples found in association. Each MCP is labeled with the name we assigned to the chimpanzee community, based on the name of a nearby village. MCPs for all communities include a lightly shaded 1-km buffer to indicate likely minimum home range sizes extending beyond sample collection locations, defined by the darker areas. Gray background shading indicates forest cover during the study period (Hansen et al., 2013). Kiraira comprised a small cluster of five genotypes found in repeatedly in association over the course of the study period and may indicate an additional community, though further data would be needed to clarify this (McCarthy et al., 2015). Busingiro, synonymously referred to as Siiba (McCarthy et al., 2015), refers to an area of continuous forest in the southern region of the Budongo Forest, and Busingiro locations indicated on the map are only those associated with samples collected for this study

2.3 | False positive error rate estimation in parentage assignments

We used likelihood-based methods to assign parentage with statistical confidence (Marshall, Slate, Kruuk, & Pemberton, 1998). Using this approach, erroneous parentage assignments are possible, including false positive assignments (Type I error), in which individuals are erroneously identified as a parent–offspring pair (Marshall et al., 1998). Incorrect parentage assignments are problematic when studying philopatry and dispersal patterns, as they can lead to erroneous conclusions regarding the occurrence of intrinsically rare dispersal events.

To estimate the potential for erroneous parentage assignments, we used 217 genotypes from the Ngogo and Kanyawara chimpanzee communities in Kibale National Park, Uganda, located approximately 130 km away from the Budongo-Bugoma landscape. Parent–offspring relationships in the Kibale communities are known with a high degree of certainty due to long-term study of habituated individuals and extensive genetics research (Langergraber et al., 2012). The Kibale and corridor data have comparable levels of completeness of genotypes, number of alleles per locus, and heterozygosity (Table S1), suggesting that the Kibale data may be used to estimate the rate of false positive assignment errors in the corridor data set.

Next we conducted parentage analyses with these Kibale data, using KinGroup v2 (Konovalov, Manning, & Henshaw, 2004) and CERVUS 3.0.7 software (Kalinowski, Taper, & Marshall, 2007) and microsatellite genotype data from the same 14 loci typed in the corridor chimpanzee population, as described in detail in the Supporting Information. When using the chimpanzee genotypes from Kibale for validation, we found that false positive rates were higher for father–son dyads and trios with male offspring than for mother–daughter dyads and trios with female offspring (Table S2), which is likely due to the higher frequency of closely related males than females in male philopatric chimpanzee communities. However, we reduced false positive error rates substantially overall by accepting only parentage assignments with a confidence level above 95%, by only accepting parent–offspring dyads and trios in which parents and offspring shared an allele at every locus, and by only accepting trios in which both parents were the highest likelihood matches with the offspring, given the genotype of the other candidate parent (Tables 1 and 2). In both the Kibale and corridor data sets respectively, KinGroup and CERVUS both classified the same parent–offspring dyads, but KinGroup also classified some additional dyads in both data sets with a high degree of confidence, so we present false positive assignment rates for both approaches (Tables 1 and 2) but emphasize the more extensive KinGroup parentage dyads in section 3.

2.4 | Parentage assignments in the corridor chimpanzees

We then applied these criteria to parentage analyses using 176 corridor chimpanzee genotypes (all those typed at ≥10 loci), as well as 53 genotypes from Busingiro in the southern region of the Budongo Forest (Figure 1). Of these 53 additional genotypes, 14 originated from samples collected during the current study while 39 were collected and genotyped previously (Langergraber et al., 2011). We included these Busingiro genotypes to look for evidence of gene flow between the putative corridor habitat and the continuous Budongo Forest. We assessed the relationship between parentage and community residence by detecting parent–offspring dyads and trios as detailed in the Supporting Information. To test whether the observed sex differences in the proportions of different community residence among KinGroup parent–offspring dyads were statistically significant, we conducted a permutation test programmed in R. We randomized the assignment of individuals to sex and restricted the permutations such that both members of any parent–offspring pair had the same sex throughout all permutations. We conducted 1,000 permutations of sex assignment and included the original data as one permutation. As a test statistic, we used the chi-square value obtained by comparing the sex of the parent–offspring dyad with whether the community residence of both members was the same or different. To assess whether the proportion of parent–offspring dyads with different community residence was significantly different than what would be expected due to false positive errors alone, we conducted a Fisher's Exact Test in R.

Next we analyzed the data in CERVUS to test for mother–father–offspring trios, which provide the highest likelihood mother and father combination for each potential offspring. We examined high-likelihood trios for instances of different community residence, which would indicate both dispersal and its likely directionality, given that daughters are expected to disperse from the natal community in which their parents reside.

TABLE 1 False positive error rates for parent–offspring assignments using KinGroup, based on 217 genotypes from Kibale National Park, Uganda

	Mother–daughter dyads		Father–son dyads	
p-value	*N*	%	*N*	%
<0.05	52	3.8	63	14.3–15.9
<0.01	52	3.8	63	14.3–15.9
<0.001	52	3.8	63	14.3–15.9
<0.0001	46	2.2	42	9.5

Where a range of values is presented, this indicates a dyad that could not be confirmed as true or false based on genetic or pedigree data, resulting in a lower and upper range for the false positive rates.

TABLE 2 False positive error rates for parent–offspring assignments using CERVUS, based on 217 genotypes from Kibale National Park, Uganda

	Mother–daughter dyads		Father–son dyads		Parent–daughter trios	
Confidence	*N*	%	*N*	%	*N*	%
>99%	32	0.0	26	7.7	30	0.0
>95%	43	2.3	29	6.9	30	0.0

Dyadic assignments were restricted to those in which parents and offspring shared an allele at every locus. Trio assignments were restricted to those in which daughters shared an allele at every locus with both parents, and to those in which both parents represented the highest probability match identified, given the genotype of the other parent.

The data used in dyadic parentage analyses did not include individual ages, so we were unable to infer which individual in a given dyad was the parent and which was the offspring. Further, we were unable to infer whether a dyad or trio contained an offspring too young to have dispersed yet from the natal community. Therefore, it should be noted that we inferred directionality of dispersal events only from trios and did not attempt to infer dispersal rates.

2.5 | Spatial analysis of repeatedly genotyped chimpanzees

In the corridor data, MCPs indicated a generally consistent pattern of non-overlapping clusters among more than 180 repeatedly sampled genotypes over the 2-year study period, suggesting the presence of distinct communities (McCarthy et al., 2015). If a genotype was found in association first with one MCP and then another across sampling occasions that were widely separated in time, this would represent a deviation from this pattern and could indicate a dispersal event. Therefore, we compared the MCP affiliations assigned to individual genotypes over the course of the study period to determine whether any changes occurred. Because chimpanzees are territorial and typically associate with members of just one community, they are not generally expected to be found within the MCP associated with another community unless due to dispersal (Goodall, 1986; Herbinger et al., 2001; Nishida, 1979).

3 | RESULTS

3.1 | Parentage assignments in the corridor chimpanzees

Father–son parentage analyses with >95% confidence yielded 5 of 48 (10%) father–son dyads with different community residence (Table S3). In contrast, of the 67 mother–daughter dyads, 26 (39%)

had different community residence, including 5 dyads between the corridor habitat and the Busingiro region of the Budongo Forest (Table S4). The observed proportions of dyads with different community residence among father–son and mother–daughter dyads differed significantly ($\chi^2 = 10.99$, $p_{\text{perm}} = 0.005$, Figure 3).

Among 12 CERVUS parent–daughter trios, 2 had different community residence. In one of these two trios, the daughter was attributed to a different community than that of her two parents, with a distance of 15 km between the mean sampling locations for these two communities. In the second trio with different community residence, however, the mother was attributed to a different community than the father and daughter, with a distance of 15 km again between the communities attributed to the mother and the daughter and father. The confidence associated with this trio was very high (trio log-likelihood ratio [LOD] score = 26.39, trio confidence score >99%). Additionally, when applying the restrictive criteria used here to trios in the Kibale data, we detected zero false positive assignments ($N = 30$; Table 2), so false positive trio assignments among the corridor chimpanzees are unlikely. If a true parent–offspring trio, this indicates the occurrence of a secondary or adult dispersal event in which the mother emigrated to a different community following reproduction in a prior community. In both of these cases, the putative transfers were directed toward communities of larger size inhabiting similarly degraded habitat (Kasokwa to Kasongoire and Bulindi to Wagaisa; see McCarthy et al., 2015). None of the 14 trios with male offspring had different community residence.

Because evidence of male dispersal is exceedingly sparse in chimpanzees, we aimed to rule out alternative explanations such as false positive father–son dyads prior to accepting these dyads with different community residence as evidence of male dispersal. We thus used a post hoc approach to examine the five father–son dyads with different community residence. First, we examined whether the distribution of members of these dyads, for example, into two distinct clusters, might suggest a recent community fissioning event. Members of these dyads were broadly distributed over numerous, mostly non-adjacent communities and sampled up to 20 km away from one another, suggesting that a single community fissioning event does not explain the pattern. Next, using data from Y-chromosome haplotypes available from previous work (Langergraber, Rowney, Crockford, et al., 2014; Langergraber, Rowney, Schubert, et al., 2014; McCarthy et al., 2015), we found that all five putative father–son dyads were composed of males with differing Y-chromosome haplotypes, and that these haplotypes differed by one to five loci (Table S3). Although in rare instances a mutation could lead to a father and son having two distinct Y-chromosome haplotypes, it would be highly unlikely that a father–son dyad differed at up to five loci, nor that all five father–son pairs associated with different communities shared this unusual feature in common. Instead, these dyads are most likely the result of false positive parentage assignments. Supporting this explanation, the proportion of father–son dyads with mixed community residence was lower than the expected false positive error rate and not statistically different from what would be expected due to false positive assignments (10.4% vs. 14.3–15.9% expected error; Fisher's Exact Test: $p = 0.58$). In contrast, the proportion of mother–daughter dyads with different community residence exceeded significantly the proportion of dyads that would be expected from false positive assignments ($p < 0.001$).

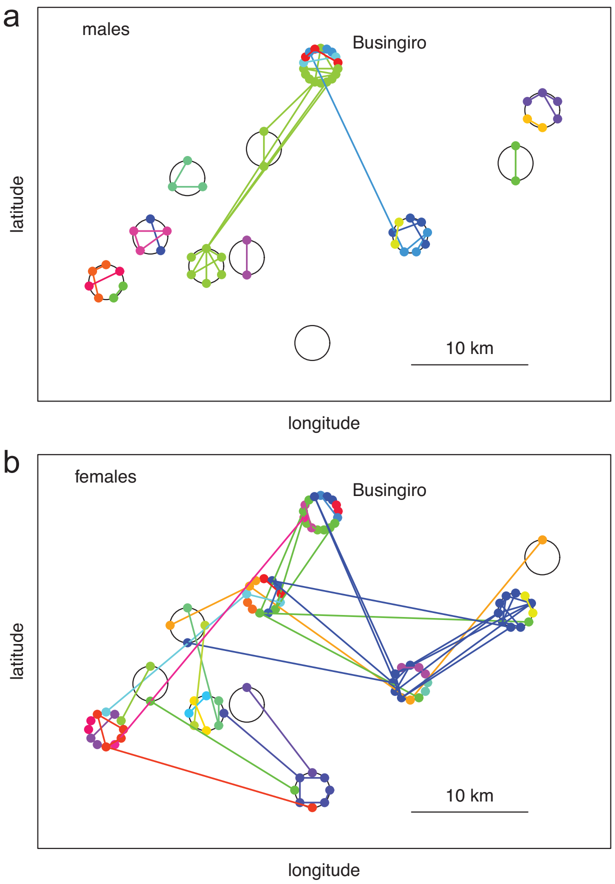

FIGURE 3 Parent–offspring dyads detected among the corridor and Busingiro chimpanzees using KinGroup. Black circles represent putative chimpanzee communities, arranged according to their relative spatial locations. All communities fall in the corridor with the exception of Busingiro, which is in the Budongo Forest and labeled for clarification. Dots indicate genotyped individuals, and lines connecting the dots indicate KinGroup parent–offspring assignments among dyads. The upper figure (a) indicates father–son dyads, while the lower figure (b) indicates mother–daughter dyads

3.2 | Spatial analysis of repeatedly genotyped chimpanzees

By examining the spatial locations of samples from individuals who were genotyped on multiple occasions, we identified the occurrence of one putative dispersal event during the study period. A female chimpanzee assigned the consensus ID "C73" was sampled in Katanga, a farm-forest mosaic near the southern border of the Budongo and Siiba Forest Reserves, in November 2011. The location of this sample fell within the MCP of the Katanga chimpanzee community. She was then sampled three times 19 months later during June 2013 at Kasongoire, an area with riparian forest fragments surrounded by sugar cane plantations located approximately 13 km from the sampling location at Katanga (Figure 4). These three samples were all located within the MCP associated with the Kasongoire chimpanzee community. In three of four total sampling occasions, her fecal sample was found in association with other nearby samples estimated to be of similar age based on their state of decay, indicating her likely affiliation with other chimpanzees in that community. On two of those three occasions, once in each community, the samples in association indicate C73's likely inclusion in a mixed sex party. On the third occasion, her sample was associated with one other female in Kasongoire. Dyadic parentage analyses further identified C73 as a member of a mother–daughter dyad. The second female in this dyad, presumably her mother, was affiliated with the Katanga chimpanzee community, providing further indication that C73 had emigrated from her natal community of Katanga.

4 | DISCUSSION

This study represents a broad-scale effort to examine patterns of philopatry and dispersal across multiple chimpanzee communities over more than 600 km^2 of fragmented forest habitat. Our findings support a pattern of male philopatry in a degraded habitat, with father–son dyads generally exhibiting matching community assignment and the exceptions to this pattern due to apparent false positive parentage assignments. Further, these results demonstrate that female dispersal has occurred in recent decades despite substantial habitat loss and fragmentation, with members of 39% of genetically attributed mother–daughter dyads associated with different communities. Five mother–daughter dyads with different community residence indicate potential gene flow between the putative corridor and nearby continuous forest, the Budongo Forest Reserve. We also found explicit genetic evidence of a female transfer event during the course of the study period, with a female detected first in one community and then on multiple occasions in a different community 19 months later.

Collectively, these findings, which indicate a pattern of sex-biased differentiation in philopatry and dispersal despite extensive forest loss and fragmentation, have implications for chimpanzee conservation. First, they demonstrate the conservation potential of unprotected forests. Though protected areas are typically given conservation priority, fragmented and unprotected habitats are highly common and may become increasingly valuable given their potential to act as both habitable areas and corridors for numerous species (Ancrenaz et al., 2015; McCarthy et al., 2015; McLennan & Plumptre, 2012; Turner &

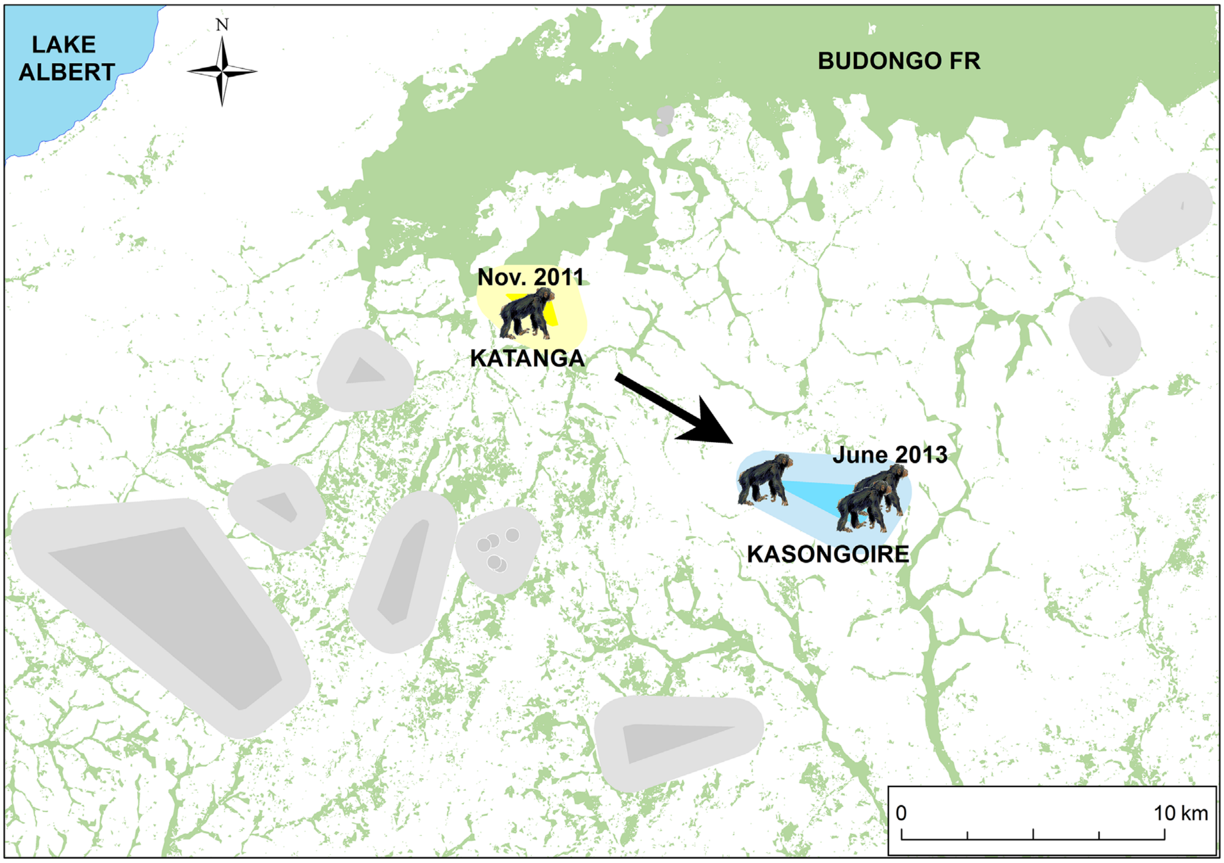

FIGURE 4 Locations of genotyped samples collected for female C73. A sample from this female was collected first in November 2011 in the boundaries of the Katanga MCP, then three times in June 2013 in the Kasongoire MCP. MCPs for all communities include a lightly shaded 1-km buffer to indicate likely minimum home range sizes extending beyond sample collection locations. Background shading indicates forest cover during the study period (Hansen et al., 2013). Chimpanzee illustration © Irene Goede Illustraties, used with permission

Corlett, 1996). Second, these findings suggest that translocation of individual chimpanzee communities, as has been suggested previously (McLennan & Hill, 2012; Reynolds, 2005), may be both unwarranted and detrimental to chimpanzees in this region and others like it, since it relies on the erroneous assumption that chimpanzees in this corridor are highly isolated within individual forest fragments. Indeed, translocation may actually disrupt gene flow since it would eliminate stepping stones among remaining chimpanzee communities by removing intermediary communities that may help maintain gene flow, thereby further isolating the remaining communities.

Even if female chimpanzee dispersal can still occur in highly fragmented habitats, other effects on its likelihood and timing are still possible. Though rarely reported, secondary transfer and the delayed transfer of adult parous females sometimes occur in chimpanzees and have been associated with severe disturbances in community structure and dynamics (Nishida et al., 1985; Rudicell et al., 2010). Strong ecological pressure from habitat loss could disrupt the structure of a community or constrain its size, thereby leading to unusual dispersal events in response. Our analyses identified one trio in which the mother was attributed to a different community than the father and daughter. Despite the high confidence score attributed to this trio, we must interpret this finding with caution given the possibility of a false positive parentage assignment. Nonetheless, this may indicate a secondary transfer event or the delayed transfer of a parous female who had reproduced in her natal community. Delayed or secondary transfer may be advantageous to females if resources or unrelated mates are particularly limited in the resident community, as may be the case under extreme situations of habitat alteration or social upheaval.

For dispersal to enhance gene flow it must lead to reproductive success in the female's new community. Due to a lack of data on chimpanzee ages or the directionality of dispersal events, it is not possible to infer the presence of offspring of dispersed females in this data set. Nonetheless, there is some evidence to indicate recent successful reproduction among the chimpanzees in this habitat. At Bulindi, a habituated chimpanzee community in this study area, infants and juveniles comprised 42% of the community during the study period (M. McLennan, pers. comm.). Further, infants and/or juveniles were observed visually in every chimpanzee community for which we had direct observations during the study period, which includes all but one putative community (M. McCarthy, unpublished data). While we cannot infer the proportion of these offspring born to immigrant versus natal females, the presence of immature chimpanzees indicates reproduction still occurred until the study period despite habitat fragmentation.

To better understand how habitat fragmentation affects dispersal rates in chimpanzees, one would need comparable data on dispersal patterns from chimpanzees in both fragmented and intact habitats. Unfortunately, such data have often been difficult to obtain, even among habituated chimpanzee communities in protected forests, since they typically rely on long-term observations to obtain adequate life history data and these are only just becoming available at some sites. Even where chimpanzees have been habituated, females can be more elusive than males, making inferences regarding putative transfers potentially erroneous (Langergraber, Rowney, Crockford, et al., 2014). Transfer rates can also vary substantially over time within communities and among nearby communities, given the influence of locally varying social and environmental factors that play a role in dispersal likelihood (Nishida et al., 1985; Rudicell et al., 2010).

It is important to note that the proportion of mother–daughter dyads with different community residence in this study does not directly indicate dispersal rates for communities in the corridor habitat. These rates cannot be inferred due to the lack of data on directionality of dispersal events and ages of females in each community. For example, many dyads with same community residence in our data set may comprise young daughters who were not yet old enough to disperse rather than adult daughters who remained in the natal community. Additionally, some female dispersal events may have occurred but gone undetected given our sampling limitations. Our stringent criteria to minimize false positive errors in parentage analyses also may have increased the potential for false negative errors. Therefore, caution is warranted to avoid erroneously interpreting these results as absolute rates of female dispersal. Nonetheless, this study presents dispersal patterns across a broad geographic scale in an increasingly common habitat type for chimpanzees and other great apes, thereby providing a starting point for future research in this region as well as for future comparative studies of philopatry and dispersal involving similar data.

Caution is also warranted when interpreting these results given that the timescale of dispersal events in relation to recent habitat degradation is unknown. Considering that maximum longevity for female chimpanzees is estimated at well over 60 years in the wild (Emery Thompson et al., 2007), and that mean dispersal age is approximately 13 (Stumpf et al., 2009), some dispersal events could have occurred over 40 years before the study period, when the forest was much less fragmented. However, given that females survive to a mean age of 30 (Hill et al., 2001), most dispersal events are likely to have occurred within the past two decades. In addition, we documented genetic evidence of a dispersal event during the study period, suggesting dispersal has not been entirely inhibited in recent years despite habitat changes.

Although these findings provide insight into the degree to which chimpanzees display sex-biased differences in philopatry and dispersal despite anthropogenic habitat disturbances, the likelihood of future dispersal events is difficult to predict. Considering ongoing habitat destruction and human–wildlife conflict in this region, a tipping point may soon be reached after which these relatively robust patterns can no longer be maintained. Therefore, given the conservation value of corridor habitats like this one, there is strong incentive to conserve remaining forests in this region to ensure the continued survival of endangered chimpanzees and other species that rely on this critically valuable habitat.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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