Transposable elements are abundant, naturally occurring sources of genetic variation in populations, influencing genome evolution in diverse ways (Bennetzen, 2000; Biémont, Vieira, Borie, & Lepetit, 1999; Feschotte, 2008). Transposable elements can contribute to variation in quantitative traits, differences in fitness, and changes in gene expression (Mackay 1984; Mackay 1989; Shrimpton, Mackay, & Brown, 1990; Mackay, Lyman, Jackson, 1992; Long, Lyman, Morgan, Langley, & Mackay, 2000). Overall, due to the propensity of transposable elements to cause mutations, transposable elements are thought to be deleterious (Adrion, Song, Schrider, Hahn, & Schaack, 2017; Dimitri, 2003; Lee & Langley, 2012; Yang & Nuzhdin, 2003). However, transposable elements have also been associated with
increases in fitness due to changes in gene regulation, where they can act as enhancers, repressors, or other regulators of complex gene expression patterns (Mateo, Ullastres, & González, 2014). The number and location of transposable element insertions can vary substantially between species, populations, and individuals (Jakšić, Kofler, & Schlötterer, 2017; Kofler, Nolte, & Schlötterer, 2015b; Kofler & Schlötterer, 2015; Kofler, Senti, Nolte, Tobler, & Schlötterer, 2018; Vieira, 2008; Vieira & Biémont, 2004; Vieira, Lepetit, Dumont, & Biémont, 1999).

*Drosophila melanogaster* has the most well-annotated population of transposable elements. Transposable elements are active in *D. melanogaster*, with insertion rates between $10^{-3}$ and $10^{-5}$ elements per generation (Nuzhdin and Mackay 1994). Most transposable element insertions segregate at low population frequencies, due to either selection against insertions (transposition selection balance) or recent bursts of transposable element activity (Blumenstiel, Chen, He, & Genetics, 2014; Kofler, Nolte, et al., 2015). Newly invading transposable elements may initially have high transposition rates as the host machinery evolves new defenses (Johnson, 2010; Lee & Langley, 2012; Pasukyova, 2004; Romero-Soriano & Garcia Guerreiro, 2016; Slotkin & Martienssen, 2007; Yang & Nuzhdin, 2003).

*Drosophila melanogaster* recently evolved to be a human commensal and spread out of Africa to a worldwide distribution (around 10,000 years ago (Baudry, 2004; Kauer, Zangerl, Dieringer, & Schlötterer, 2002; Sprengelmeier et al., 2018; Wu et al., 1995; Yukilevich, Turner, Aoki, Nuzhdin, & True, 2010)). When organisms colonize new habitats, conditions may be stressful and they may encounter new congeners. Both of these conditions could potentially result in an increase in transposable element activity, through introgression and reduced efficacy of the organism's system for repressing transposable element activity, such as piRNA (Engels, 1992; Kofler, Nolte, et al., 2015). *D. melanogaster* from Africa have been observed to have a lower number of transposable element insertions than cosmopolitan *D. melanogaster*, which has been attributed to a “waking up” of transposable elements upon colonization of new habitats (Vieira et al., 1999). The sister species of *D. melanogaster*, *D. simulans*, also originated in Afrotropical climates and evolved into human commensals with cosmopolitan distributions throughout Europe and the Americas, albeit more recently (Sturtevant, 1920). Due to its more recent spread, and heterogeneity among populations in their transposable element content, it was previously proposed that the waking up of transposable elements in *D. simulans* is currently in progress (Vieira et al., 1999).

More recently, the most frequently used approach to studying transposable element abundance in *D. melanogaster* and *D. simulans* has been Pool-seq. Pool-seq has generated some interesting observations about transposable element dynamics; for example, in *D. melanogaster* it has confirmed that transposable elements are more abundant in cosmopolitan populations than in their ancestral African range (Kofler, Nolte, et al., 2015). Pool-seq documented the recent invasion of the P-element into *D. simulans* from *D. melanogaster*, highlighting the ever-changing transposable element landscape between species and populations (Kofler, Hill, Nolte, Betancourt, & Schlötterer, 2015a). While Pool-seq may be an effective tool for estimating population-level frequency, there is evidence that estimates of transposable element insertion dynamics can be confounded by differences in allele frequencies (Rahman et al. 2015). Furthermore, it is important to estimate the variance between genotypes in transposable element copy number, in addition to population-level variation. For example, how much of the observed population-level variation is due to individuals with high copy number rather than low population averages?

In *D. melanogaster*, the existence of multiple sequenced inbred panels lends themselves to estimating copy number and insertion site frequency between individual genotypes. Active families of transposable elements appear to be largely shared between populations, for example, in inbred strains of *D. melanogaster* from worldwide samples, the DGRP, and pooled noninbred flies from global samples; the majority of transposable element insertions are from the same six transposable element families (Rahman et al. 2015). However, these estimates of specific differences in transposable element load between genotypes were performed on a limited number of strains and have not been performed in other systems, including in *D. simulans*.

Here, I will specifically address three of these questions in *D. simulans*, to understand what observations from *D. melanogaster* are unique to the species and which are shared. First, how do transposon families differ between fly genotypes and which transposon families are most prevalent in these differences? Second, how do transposable elements differ between cosmopolitan and ancestral *D. simulans*? Third, how much difference do we see between *D. simulans* sequenced from inbred lines versus those sequenced directly from wild collections? I estimate variance in transposable element copy number between inbred genotypes, differences between wild and inbred lines, and differences between the populations in the mean and variance of transposable element copy number.

## Methods

### Fly lines

Twenty-one African *D. simulans* isofemale lines were collected by William Ballard in 2002 from Madagascar and Peter Andolfatto in 2006 from Kenya (Table 1, Jackson, Campos, Haddrill, Charlesworth, & Zeng, 2017). They were inbred in the laboratory for nine generations. During the process of inbreeding, five were lost and were sequenced from the original wild sample which had been preserved in ETOH (Table 1). These five lines will be used as an estimate of “wild” *Drosophila* transposable element load, compared to the inbred lines. The raw reads are 90-bp paired-end Illumina sequencing, and they were downloaded from SRA.
RESULTS AND DISCUSSION

3.1 Population-level variation

Of the 128 elements examined in the population, 85 have different mean numbers of insertions between the two populations (t-test, Bonferroni-corrected $p = .05/128$, Table 2, Table S1). Of those, only 17 are higher in the African populations, suggesting that overall the CA population has more transposable element insertion sites. Indeed, overall Californian D. simulans have an average of 1,797 insertions per genotype, while African D. simulans have 1,496 (Table 2). The five elements with the largest difference in copy number in Californian D. simulans compared to African are the INE-1, Tc1, transib2, 1,360, and Cr1a (Table 2). These are present on average in 37 more copies in Californian D. simulans compared to African (F test, Bonferroni-corrected $p = .05/128$). Twenty elements have different and larger variance in the Californian D. simulans compared to Californian D. simulans (F test, Bonferroni-corrected $p = .05/128$).

The most abundant transposable elements in each population tend to be abundant in both populations, namely INE-1, Cr1a, and G6. The D. melanogaster pogo and Helitron elements were not present in these populations, which has been previously noted, suggesting that these transposable elements are not present in D. simulans (Kofler, Nolte, et al., 2015). Previous work using Pool-seq in D. simulans identified INE-1, roo, Cr1a, Rt1c, and hobo as the most abundant transposable elements in D. simulans, and G6 was among the less abundant elements (Kofler, Nolte, et al., 2015).

Some elements are not present in full-length copies within either population. Six transposable elements (Stalker4, Stalker, Bari2, Tc3, G7, and Tart-C) were never present as more than a fraction of an element in any individual, and they are likely old and degraded. G3 and hoper2 are estimated as being present in ~1 copy per individual in both populations; however, that copy or copies has internal deletions. For the G-element, all but a small fraction of reads map to one 140 bp sequence. A full-length version of Quasimodo (two copies) and gypsy6 (one copy) were present in one genotype, while in other genotypes Quasimodo appears to be old and degraded. Stalker3 is also present in one genotype as a full-length copy; however, in this case, old or degraded copies are not present in the other genotypes. Reads which map equally well to more than one location were filtered out; thus, this does not represent nonspecific mapping to repetitive elements.

3.2 Site frequency spectrum

I examined the site frequency spectrum of each transposable element in African and Californian D. simulans (Table 3). In some cases, there are no polymorphisms (Dmau\maeriner, Dmel\p-element); therefore, this is uninformative. Genome-wide, the Californian population has more intermediate frequency polymorphisms (measured using Tajima’s D; Signor et al., 2017) compared to the African population.
This is consistent with other work on spectrum between populations (Figure S1; Signor et al., 2017).

number of transposable elements with low-frequency SNPs in African respectively transposing in the species (Kofler, Nolte, et al., 2015). The larger, both populations, estimating the site frequency spectrum

Juan

D. simulans

Quasimodo

of Drosophila simulans number of transposable elements in individual genotypes

FIGURE 1 An outline of the pipeline used for estimating copy number of transposable elements in Drosophila simulans, as well as estimating the site frequency spectrum

TABLE 1 A list of the strains used for this study, including their collection location and inbreeding status

| Collection           | African Drosophila | Cosmopolitan Drosophila |
|----------------------|--------------------|-------------------------|
| N. Strains           | Kenya              | Madagascar              | California |
| N. Inbred            | 11                 | 10                      | 169        |
|                     | 8                  | 8                       | 169        |

(Figure S1), which may be expected to affect the site frequency spectrum. The site frequency spectrum must be interpreted along with Table 2—for example, Quasimodo is really only present in two full-length copies in a single individual; thus, this estimation of the site frequency spectrum is not informative with regard to the spread of Quasimodo in the population.

Elements with site frequency spectrum heavily biased toward low-frequency SNPs in Californian D. simulans include G6, flea, and Juan (Figure 2, Table 3). In African D. simulans, this includes Tabor, Transpac, flea, Juan, Bari1, G6, and accord (Figure 2, Table 3). Thus in both populations, G6, flea, Bari1, and Juan likely have recent activity. This is consistent with other work on Juan, which suggests it is actively transposing in the species (Kofler, Nolte, et al., 2015). The larger number of transposable elements with low-frequency SNPs in African populations may be due to the overall difference in the site frequency spectrum between populations (Figure S1; Signor et al., 2017).

3.3 | The p-element

The p-element recently invaded D. simulans from D. melanogaster as described in Kofler, Hill, et al. (2015); however, Pool-seq cannot tie p-element insertions to specific individuals and only determine the average number of insertions. What was reported previously was 0.4 insertions in Florida populations and 29 in South Africa (Kofler, Hill, et al., 2015). What we see in the California population is an average of two insertions, however that is because the majority of individuals do not have any insertions (137 individuals have less than 0.3 estimated copies, Figure 2). The remaining individuals have between 0.5 and 39 copies. It is interesting that it is not invading genotypes in the population at the same rate, but rather reaching high copy number in some genotypes and not others (Nuzhdin, 2000). It is possible that p-elements are just proliferating in strains that contained an active copy prior to collection (Nuzhdin, Pasyukova, & Mackay, 1997). This was observed previously in laboratory strains of D. melanogaster, though contamination and introgression may also have played a role (Rahman et al. 2015).

3.4 | Transposable elements in individual genotypes

Some transposable elements have considerably higher copy number in particular genotypes compared to the population average. For example, in one genotype Dsim\ninja is present in 29 copies, compared to the population mean of three (Figure 3). Dsim\ninja has 10 fixed differences and 27 polymorphisms in this strain from the California population, and the population average is 7.5 fixed differences and 264 polymorphisms. This suggests that Dsim\ninja was recently active in this genotype. This is true of several transposable elements which have outliers in the population. Stalker2 has an outlier genotype with 17 fixed SNPs and eight polymorphisms, compared to a population average of 14 fixed SNPs and 43 polymorphisms. Other transposable elements with large outliers in the California population include gypsy10, opus, blood, GATE, diver, Tabor, INE-1, diver2, idefix, 1731, 412, and 297.

Sampling of the African populations was much more limited; thus, less genotype-specific variation is sampled, and indeed, only two transposable elements had large outliers, in both the same genotype from Madagascar: copia and diver. This genotype had 20 copies of copia, compared to a population frequency of 4–11, as well as 11 fixed differences and 20 polymorphisms (compared to a population average of 10 fixed differences and 78 polymorphisms). For diver, this genotype had 20 fixed differences and 84 polymorphisms, compared to a population average of 12 fixed differences and 215 polymorphisms (and 30 copies compared to 4–10 for the rest of the population).

3.5 | Wild versus inbred strains of D. simulans

The outlier genotype from Africa that has more copies of copia and diver is one that was inbred in the laboratory. In general, being inbred in the laboratory is not affecting overall transposable element copy number; however, as comparing between lines that were sequenced directly upon collection and those that there inbred, there is no significant difference between the mean number of transposable elements for any transposable element family. The activity of copia and diver is specific to a genotype, rather than to “wild” or “inbred” strains. Those that “wake up” in individual lines appears to be due to sampling of individuals that are permissive or contain active transposable elements, rather than an overall increase in transposable element activity in inbred lines.

3.6 | Comparison to other studies

Tirant has previously been reported as having higher copy number in African D. simulans, potentially due to a recent mobilization of the element (Fablet, McDonald, Biémont, & Vieira, 2006). We find
that pattern here, including a higher variance in the African populations where copy number ranges from 2 to 6.68, compared to 2–3.8 in California (Fablet et al., 2006). The Dmau\mariner element has a higher copy number in Africa than in the Californian D. simulans, from 0–5 with an average of 2.33, compared to 0–3 with an average of 1.22 (Figure 3). Dmau\mariner also contains no polymorphisms,
which is consistent with a recent spread of Dmau\mariner in D. simulans (Capy, Chakrani, Lemeunier, Hartl, & David, 1990; Capy, Koga, David, & Hartl, 1992). The G6 element has a large difference from previously reported values, with an average of 66 insertions in Californian D. simulans and 69 in African. However, only 37 insertions were reported total for a previously estimated population of
| TE family | CA average | AF average | TE family | CA average | AF average | TE family | CA average | AF average |
|-----------|------------|------------|-----------|------------|------------|-----------|------------|------------|
| 297       | 0.29       | 0.29       | GATE      | 0.28       | 0.53       | NOF       | 0.37       | 0.37       |
| 412       | 0.31       | 0.31       | gtwin     | 0.35       | 0.35       | opus      | 0.38       | 0.38       |
| 1,360     | 0.26       | 0.26       | gypsy     | 0.35       | 0.35       | Osvaldo   | 0.37       | 0.37       |
| 1731      | 0.23       | 0.23       | gypsy10   | 0.35       | 0.35       | P-element | -          | -          |
| 17.6.     | 0.44       | 0.44       | gypsy11   | 0.44       | 0.44       | pogo      | -          | -          |
| 3S18      | 0.16       | 0.16       | gypsy12   | 0.35       | 0.35       | Porto1    | 0.41       | 0.41       |
| accord    | 0.08       | 0.08       | gypsy2    | 0.42       | 0.42       | Q-element | 0.32       | 0.32       |
| accord2   | 0.36       | 0.36       | gypsy3    | 0.33       | 0.33       | Quasimodo | 0.05       | 0.05       |
| aurora-element | 0.31 | 0.31 | gypsy4 | 0.22 | 0.22 | R1-2 | 0.33 | 0.33 |
| baggins   | 0.29       | 0.29       | gypsy5    | 0.24       | 0.24       | R1A1-element | 0.32 | 0.32 |
| Bari1     | 0.05       | 0.05       | gypsy6    | 0.33       | 0.33       | R2-element | 0.35       | 0.35       |
| Bari2     | 0.40       | 0.40       | gypsy7    | 0.24       | 0.24       | roo       | 0.14       | 0.14       |
| blood     | 0.18       | 0.18       | gypsy8    | 0.36       | 0.36       | rooA      | 0.32       | 0.32       |
| BS        | 0.34       | 0.34       | gypsy9    | 0.41       | 0.41       | rover     | 0.42       | 0.42       |
| BS3       | 0.42       | 0.42       | HB        | 0.34       | 0.34       | R1a       | 0.39       | 0.39       |
| BS4       | 0.37       | 0.37       | Helena    | 0.19       | 0.19       | R1b       | 0.29       | 0.29       |
| Burdock   | 0.22       | 0.22       | Helitron  | -          | -          | R1c       | 0.35       | 0.35       |
| Circe     | 0.28       | 0.28       | HeT-A     | 0.43       | 0.43       | S-element | 0.42       | 0.43       |
| copia     | 0.11       | 0.11       | HMS-Beagle| 0.32       | 0.32       | S2        | 0.42       | 0.42       |
| Cr1a      | 0.24       | 0.24       | HMS-Beagle2| 0.42       | 0.42       | springer | 0.35       | 0.35       |
| diver     | 0.29       | 0.29       | hobo      | 0.23       | 0.23       | Stalker   | 0.28       | 0.28       |
| diver2    | 0.28       | 0.28       | hopper    | 0.33       | 0.33       | Stalker2  | 0.15       | 0.15       |
| Dm88      | 0.40       | 0.40       | hopper2   | 0.37       | 0.37       | Stalker3  | -          | -          |
| DmaH\mariner | -   | -          | l-element | 0.26       | 0.26       | Stalker4  | 0.25       | 0.25       |
| Doc       | 0.15       | 0.15       | Idefix    | 0.38       | 3.70       | Tabor     | 0.08       | 0.08       |
| Doc2-element | 0.20 | 0.20       | INE-1     | 0.31       | 0.31       | TAHRE     | 0.40       | 0.40       |
| Doc3-element | 0.35 | 0.35       | invader1  | 0.39       | 0.39       | TART-A    | 0.31       | 0.31       |
| Doc4-element | 0.37 | 0.37       | invader2  | 0.29       | 0.29       | TART-B    | 0.34       | 0.34       |
| Dsim\ninja | 0.30 | 0.30       | invader3  | 0.20       | 0.20       | TART-C    | 0.10       | 0.10       |
| F-element | 0.22       | 0.22       | invader4  | 0.40       | 0.40       | Tc1       | 0.34       | 0.34       |
| FB        | 0.37       | 0.37       | invader5  | 0.44       | 0.44       | Tc1-2     | 0.40       | 0.40       |
| flea      | 0.04       | 0.04       | invader6  | 0.14       | 0.14       | Tc3       | 0.08       | 0.08       |
| frogger   | 0.17       | 0.17       | lvk       | 0.34       | 0.34       | Tirant    | 0.35       | 0.35       |
| Fw2       | 0.44       | 0.44       | jockey    | 0.10       | 0.10       | Tom1      | 0.29       | 0.29       |
| Fw3       | 0.36       | 0.36       | jockey2   | 0.40       | 0.40       | transib1  | 0.30       | 0.30       |
| G-element | 0.53       | 0.53       | Juan      | 0.06       | 0.06       | transib2  | 0.34       | 0.34       |
| G2        | 0.35       | 0.35       | looper1   | 0.34       | 0.34       | transib3  | 0.37       | 0.37       |
| G3        | 0.50       | 0.50       | mariner2  | 0.42       | 0.42       | transib4  | 0.40       | 0.40       |

(Continues)
In addition, in the populations reported here the G6 element has primarily low-frequency polymorphisms (Table 3), suggesting that this is a recent expansion of copy number. Overall, our estimates are higher than the work of Kofler, Hill, et al., 2015, which focuses on euchromatic insertions and only estimates more than one insertion per line for four transposable elements (1,360, hobo, roo, and Tc-2).

### TABLE 3 (Continued)

| TE family | CA average | AF average | TE family | CA average | AF average | TE family | CA average | AF average |
|-----------|------------|------------|-----------|------------|------------|-----------|------------|------------|
| G4        | 0.33       | 0.33       | Max-element | 0.39       | 0.39       | Transpac  | 0.04       | 0.04       |
| G5        | 0.34       | 0.34       | McClintock  | 0.19       | 0.19       | X-element | 0.25       | 0.27       |
| G5A       | 0.37       | 0.37       | mdg1       | 0.40       | 0.40       | Xanthias  | 0.25       | 0.25       |
| G6        | 0.10       | 0.10       | mdg3       | 0.15       | 0.15       | ZAM       | 0.31       | 0.31       |
| G7        | 0.36       | 0.36       | micropia   | 0.24       | 0.24       |           |            |            |

Note: Dmau\mariner and the p-element are present in at least one population, but have no polymorphic SNPs. Other elements without an estimated site frequency spectrum are not present in the population.

### FIGURE 2

(a) Estimated copy number for the p-element in Californian and African Drosophila simulans. Each bar represents an individual from the population. As expected, the p-element was not found in the African population sampled in the early 2000s, but by 2012 when the Californian D. simulans was sampled, it had invaded. (b) Estimated copy number for G6 in Californian and African D. simulans. Each bar represents an individual from the population G6 has a high copy number in both populations of D. simulans, which was not recorded in previous studies on African D. simulans. (c) The site frequency spectrum in the last row also suggests recent spread of the G6 element in D. simulans, as there are primarily low-frequency SNPs. Note that while fixed SNPs are included in this graph to illustrate divergence from Drosophila melanogaster, they are not included in the estimation of average site frequency spectrum shown in Table 3.

#### 3.7 Comparison to D. melanogaster

INE-1, 1,360, jockey, hobo, roo, and p-element have been estimated as the most abundant transposable elements in D. melanogaster (Rahman et al., 2015; Kofler, Nolte, et al., 2015). The most abundant transposable elements in both populations of D. simulans in this study were G6, Cr1a, and INE-1. However, roo and hobo are...
both quite abundant in *D. simulans*, and 1,360 is abundant in cosmopolitan populations. In both *D. melanogaster* and *D. simulans*, transposable element copy number is lower in African populations, suggesting that colonization is associated with increased transposable element activity (Vieira et al., 1999). However, overall the lack of reporting of individual population values makes comparison difficult.

In *D. simulans*, there is some evidence, either genotypes with large increases in copy number or a site frequency spectrum biased toward low-frequency alleles, that *Dsim\ninja*, *Dmau\mariner*, *p-element*, *gypsy10*, *opus*, *blood*, *GATE*, *diver*, *Tabor*, *INE-1*, *diver2*, *Idefix*, 1731, 412, 297, G6, *flea*, *Bar1*, *Transpac*, *Tabor*, *accord*, and *Juan* are active. *gypsy10*, *blood*, *Juan*, G6, *Tabor*, *Transpac*, *accord*, and *diver* have been previously reported as undergoing a burst of activity in *D. simulans* and in *D. melanogaster*, likely due to recent invasion (Kofler, Nolte, et al., 2015). *Flea*, *Idefix*, 412, and 297 are also thought to be active, though due to an older invasion in the genome of *D. melanogaster* (Kofler, Nolte, et al., 2015). G6 has been reported as having low copy number in *D. melanogaster*; however, it was also potentially recently active.

Thus, *D. melanogaster* and *D. simulans* share many active families of transposable elements and appear to be experiencing an increase in transposable element copy number concurrent with worldwide expansion.

4 | CONCLUSIONS

*Drosophila simulans* is currently being invaded by transposable elements, and this spread is likely occurring concordant with the worldwide colonization of *D. simulans*, as has been posited by previous studies (Lachaise et al., 1988; Vieira et al., 1999; Biémont et al., 2003). African populations have their own transposable element dynamics, with some transposable elements seeming to share activity between populations (G6) and others being more active in African *D. simulans* (*baggins*, *Bar1*, etc.). It would be interesting to explore transposable element dynamics in other populations of *D. simulans* to understand the generality of the patterns seen here. Transposable element load is an attribute of species, populations, and individual
genotypes. In inbred laboratory genotypes, active transposable element copies may be inherited by some genotypes and not others, and active transposable elements can accumulate over time (Nuzhdin et al., 1997). This can cause differences over time in the number of insertions within a genotype and large differences between genotypes in transposable element copy number (Nuzhdin et al., 1997). This may also be reflective of natural patterns in which transposable elements proliferate in particular genotypes rather than at low levels in the population as a whole (Nuzhdin, 2000). Overall, looking at variance between individuals is an important part of understanding the ways in which transposable elements maintain themselves in populations.

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CONFLICT OF INTEREST
None declared.

AUTHOR CONTRIBUTIONS
S.S. conceived the study, performed the analysis, and wrote the paper.

DATA AVAILABILITY STATEMENT
All data are available at the Sequence Read Archive under SRP075682 and PRJEB7673.

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