Evolutionary Journal of the Linnean Society, 2024, 3, kzae005
https://doi.org/10.1093/evolinnean/kzae005
Advance access publication 24 May 2024
Original Article

OXFORD

Original Article

Consistent accumulation of transposable elements in species of the Hawaiian Tetragnatha spiny-leg adaptive radiation across the archipelago chronosequence

Heidi Yang[1,2,*], Clément Goubert[3], Darko D. Cotoras[4,5], Dimitar Dimitrov[6], Natalie R. Graham[1,7], José Cerca[1,8,†], Rosemary G. Gillespie[1,†]

[1]Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA, United States
[2]Department of Ecology & Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, United States
[3]McGill Genome Centre, McGill University, Montreal H3A 0G1, QC, Canada
[4]Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany
[5]Department of Entomology, California Academy of Sciences, San Francisco, CA, United States
[6]Department of Natural History, University Museum of Bergen, University of Bergen, Bergen 7800, 5020, Norway
[7]Department of Biology, University of Hawaii at Hilo, Hilo, HI, United States
[8]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

[†]Equal contribution.

[*]Corresponding author. Department of Ecology & Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, United States. E-mail: hyangg@ucla.edu

ABSTRACT

The ecological and phenotypic diversity observed in oceanic island radiations presents an evolutionary paradox: a high level of genetic variation is typically required for diversification, but species colonizing a new island commonly suffer from founder effects. This reduction in population size leads to lower genetic diversity, which ultimately results in a reduction in the efficiency of natural selection. What then is the source of genetic variation which acts as the raw material for ecological and phenotypic diversification in oceanic archipelagos? Transposable elements (TEs) are mobile genetic elements that have been linked to the generation of genetic diversity, and evidence suggests that TE activity and accumulation along the genome can result from reductions in population size. Here, we use the Hawaiian spiny-leg spider radiation (*Tetragnatha*) to test whether TE accumulation increases due to demographic processes associated with island colonization. We sequenced and quantified TEs in 23 individuals representing 16 species from the spiny-leg radiation and four individuals from its sister radiation, the Hawaiian web-building *Tetragnatha*. Our results show that founder effects resulting from colonization of new islands have not resulted in TE accumulation over evolutionary time. Specifically, we found no evidence for an increase in abundance of specific TE superfamilies, nor an accumulation of 'young TEs' in lineages which have recently colonized a new island or are present in islands with active volcanoes. We also found that the DNA/hAT transposon superfamily is by far the most abundant TE superfamily in the *Tetragnatha* radiation. This work shows that there is no clear trend of increasing TE abundance for the spiny-leg radiation across the archipelago chronosequence, and TE accumulation is not affected by population oscillations associated with island colonization events. Therefore, despite their known role in the generation of genetic diversity, TE activity does not appear to be the mechanism explaining the evolutionary paradox of insular diversification in the *Tetragnatha* spiny-leg radiation.

Keywords: adaptive radiation; transposable elements; Tetragnatha; Hawaiian Islands; Araneae; founder effects; TE accumulation

INTRODUCTION

Adaptive radiation, the rapid diversification of a lineage into a wide range of ecological niches, provides a clear link between ecology and evolution (Schluter 2000, Gillespie *et al.* 2020). Many adaptive radiations are characterized by remarkable phenotypic and ecological variation, but the mechanisms initiating the process of diversification have proven to be difficult to study. A notable paradox is the high number of adaptive radiations observed on oceanic archipelagos, despite the fact that island colonization itself is associated with a drastic reduction of genetic diversity. The species' arrival to a remote oceanic island entails a strong founder event, which inevitably depletes genetic

Received December 14 2023; revised March 21 2024; accepted for publication May 3 2024

variation (Cerca *et al.* 2023b). Additionally, insular lineages are often subject to environmental disturbances and stochastic events that lead to local extinctions and population reductions (Frankham 1997). A reduction in effective population size (N_e) will lead to a reduction of its genetic diversity, and ultimately in a reduction of the efficiency of natural selection (Charlesworth 2009). Thus, identifying the source of genetic variation which acts as the raw material for ecological and phenotypic diversification in oceanic archipelagos remains an active question for evolutionary biologists.

Transposable elements (TEs) are mobile genetic sequences that can generate a variety of mutations, including changes in gene coding regions, *cis*-regulatory elements, and 3D chromatin structure, affecting gene regulation, and influencing overall genome sizes (Chénais *et al.* 2012, Belyayev 2014, Chuong *et al.* 2017, Fambrini *et al.* 2020, Choudhary *et al.* 2023). For example, a TE insertion has been implicated in the origin and evolution of the industrial melanism ecotype in the peppered moth, a textbook example of rapid adaptation (Hof *et al.* 2016). Accordingly, TE activity has been associated with the rise of novel traits, and diversification dynamics in the context of adaptive radiations (Kratochwil *et al.* 2022). In African cichlids, a TE insertion in the *cis*-regulatory region of a pigmentation gene led to the evolution of egg-spots (Santos *et al.* 2014) and accumulations of TEs in *Hox* genes have been documented in the *Anolis* lizard radiation (Feiner 2016). A high accumulation of TEs has been found in African cichlid fishes relative to outgroup taxa (Brawand *et al.* 2014), although recent evidence contradicts this (Ronco *et al.* 2021). Given the expected lack of genetic variation in populations present on recently colonized areas and that TEs are known facilitators of rapid adaptive evolution, TEs could be hypothesized as candidates in facilitating the generation of genetic variation required for the adaptive radiation to initiate and unfold in insular environments (Oliver and Greene 2012, Casacuberta and González 2013, Brawand *et al.* 2014, Ricci *et al.* 2018, Schrader and Schmitz 2019, Ronco *et al.* 2021).

While most TE insertions are thought to be deleterious and thus removed from the population (Kidwell and Lisch 1997), the genomic accumulation and subsequent contribution to genetic diversity of TEs has been linked to demographic oscillations. For example, reductions in N_e alter the efficiency of selection, thereby decreasing the efficiency of purifying selection to remove deleterious TE insertions (Blass *et al.* 2012, Tollis and Boissinot 2013, Xue *et al.* 2018, Bourgeois and Boissinot 2019). Indeed, differential fixation of TEs in *Drosophila subobscura* (García Guerreiro *et al.* 2008) and *Arabidopsis lyrata* (Lockton *et al.* 2008) suggest that oscillations in demography, such as bottlenecks, can increase TE accumulation patterns along genomes due to weak selection (Bourgeois and Boissinot 2019). However, there is nuance in demography's role; for example, purifying selection did not constrain the spread of L1 retrotransposons in *Anolis* lizards (Tollis and Boissinot 2013). Overall, demographic factors probably play a crucial role in determining the likelihood of TEs reaching fixation, with increased accumulation of TEs leading to novel mutations, which could underlie phenotypic and ecological diversity. In this regard, oceanic island radiations are perfect candidates to study the link between demography and TE accumulation patterns.

The Hawaiian island archipelago offers a unique opportunity to examine the dynamics of accumulation of TEs over the course of adaptive radiation, since the archipelago comprises a geological chronosequence of volcanic islands—resembling 'evolution on a conveyor belt' (Funk and Wagner 1995, Fleischer *et al.* 1998). Most lineages in the archipelago have colonized older islands, and progressed down the island chain as newer islands have formed (Shaw and Gillespie 2016). The *Tetragnatha* spiny-leg spider radiation follows this colonization pattern from older to younger islands, which consists of 17 species that divergently evolved into one of four ecomorphs: 'maroon', 'green', 'large brown', and 'small brown' (Gillespie 1991, 2004, Roderick and Gillespie 1998, Kennedy *et al.* 2022, Cerca *et al.* 2023a). Since the radiation unfolds from older to younger islands, one can test whether the more recent colonization events on the younger islands correspond to an increase in TE accumulation. During sequential island colonization, a reduction of population size, and associated reduction in N_e, occurs due to dispersal limitation across open water to newly forming volcanoes. Furthermore, the highly heterogeneous landscapes of Hawaiian Islands where lava flows frequently fragment the landscape and result in the formation of small, isolated, and transient pockets of forest (kīpuka), further alter patterns of demography and speciation. Indeed, habitat fragmentation has been proposed as a mechanism in driving diversification by creating a metapopulation dynamic with intermittent events of isolation and admixture (Carson and Templeton 1984, Vandergast *et al.* 2004, Roderick *et al.* 2012).

Using volcano age as a proxy for substrate age and colonization history, we test the hypothesis that population reductions associated with new island colonizations––and intra-island volcano colonizations––lead to an increase of TE accumulation in spiny-leg *Tetragnatha*. We then expect that species on the youngest volcanoes will have the highest overall abundance of TEs and highest proportion of young TEs, reflecting an increase in TE accumulation. To this end, we used whole-genome resequencing of 23 spiny-leg *Tetragnatha* individuals from the Hawaiian archipelago and characterized TE accumulation within the genomes, by estimating abundance of specific TE superfamilies, exploring the differential accumulation of young TEs, and correlating volcano age with TE accumulation.

METHODS

Data set

The collection and sequencing of the dataset has been described by Cerca *et al.* (2023*a*). Information on specimens used, sequencing depth, and identifiers for public databases is presented in Supporting Information Table S1. Briefly, they used Illumina paired-end sequencing to produce whole-genome resequencing data of 76 individuals across the *Tetragnatha* spiny-leg and web-building clades and aligned samples to the *T. kauaiensis* reference genome. Average depth of coverage ranges from 2× to 8× across individuals. We selected a total of 27 individuals, representing 16 species in the spiny-leg *Tetragnatha* radiation, and included 11 additional specimens of *T. anuenue*, *T. brevignatha*, *T. kamakou*, and *T. quasimodo* from different volcanic communities to account for volcano-specific differences in TE accumulation (Fig. 1A). The oldest volcano on which *Tetragnatha*

Figure 1. A, Hawaiian *Tetragnatha* species, including *Tetragnatha mohihi* (top left, small brown, spiny-leg clade), *T. tantalus* (top centre, green, spiny-leg clade), *T. filiciphilia* (top right, web-building clade), *T. pilosa* (bottom left, big brown, spiny-leg clade), *T. perreirai* (bottom centre, maroon, spiny-leg clade), and *T. stelarobusta* (bottom right, web-building clade). B, map of Hawaiian archipelago labelled with *Tetragnatha* spiny-leg species distribution. Islands are coloured as old (dark purple), middle-aged (medium purple), and young (light purple) with regard to their relative substrate age. Each island is in some cases the composite of multiple volcanoes, each indicated by coloured triangles in the key. Other species exist on multiple volcanoes, such as *Tetragnatha anuenue* (Kīlauea, Mauna Loa), *T. brevignatha* (Kohala, Kīlauea), and *T. quasimodo* (Waiʻanae, Molokaʻi, Haleakalā, Mauna Loa).

is present is the dormant shield volcano on Kauaʻi (ca. 5 Mya), and the youngest are the currently active volcanoes on Hawaiʻi: Mauna Loa (emergent lava flow to 700 000 years to 1 Mya) and Kīlauea (emergent lava flow to 210 000–280 000 years old) (Fig. 1B; Table 1). We complemented this dataset with four species of a sister lineage, the web-builder clade, including *T. maka* (Kauaʻi), *T. acuta* (Haleakalā), *T. filiciphilia* (Haleakalā), and *T. stelarobusta* (Haleakalā) (Table 1).

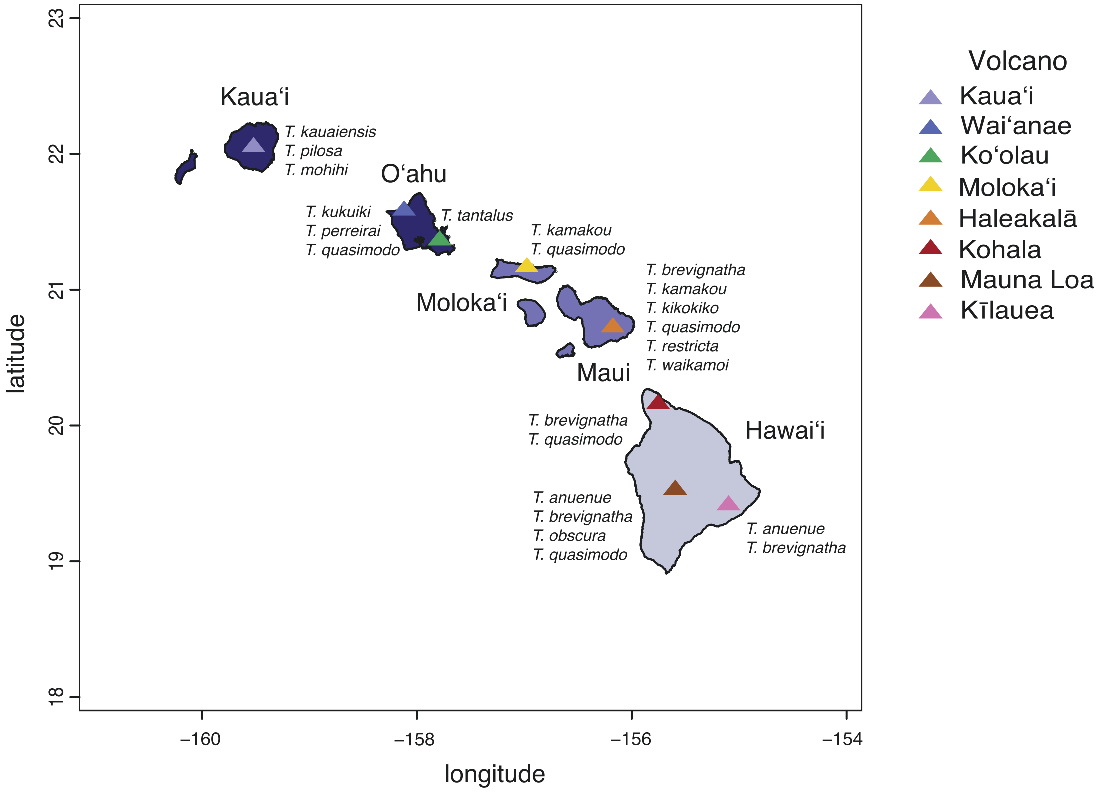

Figure 1. Continued

Table 1. Data set of *Tetragnatha* specimens.

Island		**Kaua'i**	**O'ahu**		**Moloka'i**	**Maui**	**Hawai'i**		
Volcano		**Kaua'i**	**Wai'anae**	**Ko'olau**		**Haleakalā**	**Kohala**	**Mauna Loa**	**Kīlauea**
Geological age (Myr)		5	2.5–3.9	1.7	1.3	0.75–1.1	1	0.7–1	0.21–0.28 (active)
Ecomorph	Species								
Spiny-leg small brown	*Tetragnatha anuenue*							x	x
	T. kikokiko		x			x			
	T. kukuiki								
	T. mohihi	x							
	T. obscura							x	
	T. restricta					x			
Spiny-leg large brown	*T. pilosa*	x							
	T. quasimodo		x		x	x	x	x	
Spiny-leg green	*T. brevignatha*					x	x	x	x
	T. kauaiensis	x							
	T. macracantha					x			
	T. tantalus			x					
	T. waikamoi					x			
Spiny-leg maroon	*T. kamakou*				x	x			
	T. perreirai		x						
Web-builder (outgroup)	*T. acuta*					x			
	T. filiciphilia					x			
	T. maka	x							
	T. stelarobusta					x			

The table shows which volcano and ecomorph type is associated with each specimen. There are 23 total spiny-leg specimens and four web-builders.

Phylogeny of the spiny-leg clade

To compare TEs across individuals in our sample and obtain comparative estimates, we started by constructing a molecular phylogeny of the species in our dataset. First, we cleaned the raw Illumina data by identifying and removing adapters using AdapterRemoval v.2.3.2 (Schubert *et al.* 2016), and used the Burrows–Wheeler Aligner v.0.7.17 (Li and Durbin 2009) to align these to the *T. kauaiensis* reference genome (Cerca *et al.* 2021). We excluded sequencing reads with mapping quality below 30, and estimated sequencing depth using samtools depth (Supporting Information Table S1). Using this alignment, we called variants using bcftools (Danecek *et al.* 2021). This involved using *bcftools mpileup* to generate genotype likelihoods for each alignment, and *bcftools call* to call variants. We then indexed these files using *bcftools index* and normalized indels using *bcftools norm*. We used *bcftools filter* specifying an indel gap size of 4 and including only sites where quality is above 20 and depth between 1× and 30×. Finally, we created a consensus fasta file for each individual using *bcftools consensus*. Finally, we used Phyluce to extract ultraconserved elements (UCEs) from the consensus genomes (Faircloth *et al.* 2012). This involved downloading the Arachnida UCE 1.1K v.1 set, and running Phyluce following its tutorial. Using this approach we obtained 29 UCEs, and aligned these using mafft v.7.130b (Katoh and Standley 2013). We concatenated the alignments using FASconCAT (Kück and Meusemann 2010) and ran a maximum likelihood (ML) phylogenetic tree using iqtree v.2.0.3, specifying 1000 ultrafast bootstraps (Hoang *et al.* 2018, Minh *et al.* 2020).

We noticed that the reconstructed ML phylogeny had low bootstrap support (Supporting Information Fig. S1), and was topologically incongruent with previous work (Kennedy *et al.* 2022, Cerca *et al.* 2023a). The lack of support probably stems from the low number of UCEs (29) recovered across the different genomes, which is likely to be due to the fragmented nature of the reference genome. As an alternative, we reconstructed a *kmer*-based neighbour joining (NJ) tree, which was topologically coherent with previous works (Kennedy *et al.* 2022, Cerca *et al.* 2023a) and which allowed us to obtain branch lengths. We used skmer v.3.2.1 (Marçais and Kingsford 2011, Ondov *et al.* 2016, Sarmashghi *et al.* 2019, Rachtman *et al.* 2022), a *k-mer* based method that estimates genetic distance between genome skims, or low-coverage sets of reads. Then, we estimated the pairwise evolutionary distances between the 27 individuals (Sarmashghi *et al.* 2019). This involved running '*skmer reference*', followed by '*skmer subsample*' to create 100 subsamples of the library as detailed in best practices. Finally, we used '*skmer correct*' to obtain corrected distance matrices of the subsample replicates. We then used fastme v.2.1.5 (Lefort *et al.* 2015) to obtain an NJ tree, and we rooted the tree with the sister taxa web-building clade (*T. acuta*, *T. filiciphilia*, *T. maka*, *T. stelarobusta*).

Classification and quantification of TEs

To classify and quantify TEs, we used dnaPipeTE, a pipeline designed for annotating, classifying, and quantifying TEs in low-coverage genome samples (<1× coverage) (Goubert *et al.* 2015). dnaPipeTE also identifies repeat elements such as low-complexity repeats and satellite repeats, which we included in our analyses. Before running dnaPipeTE, we generated a *de novo* library of repeats for the *T. kauaiensis* genome assembly produced by Cerca *et al.* (2021) using Repeat Modeler v.2.0.2 (Flynn *et al.* 2020). In addition, we obtained an arthropod-specific repeats consensus from RepBase (v.2014-01-31) (Jurka *et al.* 2005). We then concatenated the *de novo Tetragnatha*-based library and the RepBase-based database to obtain a final TE/repeat library. This library allows us to classify taxonomically relevant repeats within the low-coverage samples in our dataset.

We ran dnaPipeTE for each individual using the final TE/repeat library and specifying -genome_size 1.1 Gb -genome_coverage 0.25 -sample_number 2 for all individuals. We used the size of the *T. kauaiensis* reference genome across all specimens (1.1 Gb) assuming that genome size does not vary within the clade. We also ran dnaPipeTE three times for each of four different specimens to test robustness of the pipeline on our samples (Supporting Information Table S2). dnaPipeTE starts by assembling TE and repeat contigs, which are complete or partial assemblies of the averaged, or consensus, sequence of the recovered TE families and repeats. These contigs were then classified following the TE/repeat library we produced above. dnaPipeTE then calculated the blastn divergence between reads in each sample and consensus contigs, obtaining an approximate relative age of TE families and classifying TEs as young/old based on percentage divergence ('repeat landscapes'). We quantified repeat/TE abundance for each species by dividing the number of base pairs of TEs found from dnaPipeTE by the number of base pairs of all sequences considered by dnaPipeTE.

We used TE classification at the order, superfamily, and family level from dnaPipeTE outputs for all analyses. Specifically, TEs are classified hierarchically, similar to biological taxa. To aid interpretation, we include information on TE order (e.g. DNA transposon (DNA), long-terminal repeat (LTR), long interspersed nuclear element (LINE), short interspersed nuclear element (SINE)), and when referring to a specific superfamily, we denominate: order/superfamily (e.g. DNA/Academ, LTR/Copia, SINE/tRNA).

Comparative statistical analyses

We used the NJ and ML trees to infer the evolutionary patterns of TE accumulation for all TEs and for each TE group individually using a phylogenetic backbone. These analyses were done using the contMap function from the phytools v.2.0-3 R package (Revell *et al.* 2012). This function estimates ancestral states and maps continuous character evolution using a Brownian motion model. State change along branches is interpolated based on the estimates for each internal node following Felsenstein (1985).

We used Pearson's correlation test to determine relationships between volcano age and genome proportion as calculated by dnaPipeTE across the lineage. We ran additional statistical tests for each major TE or repeat element group (DNA, LINE, low-complexity repeat, LTR, simple repeat, satellite repeat, and SINE) to determine if there are element-specific trends in TE/repeat accumulation. Specifically, we grouped all the species present on the same volcano and averaged their TE abundances to perform Kruskal–Wallis tests, a nonparametric test for significant differences among groups for both genomic TE proportions of each repeat element and percentage of young TEs. We considered young TEs to be those <5% divergent from their consensus sequences, based on previous work that shows active or recently active TEs are within 0–5% divergence (Gardner *et al.* 2017, Lerat *et al.* 2019). We then calculated proportions of young TEs out of the total repetitive element content. If TEs are more active in more recently formed islands, we expected to see higher TE accumulation on individuals from younger volcanoes. As we found the DNA/hAT transposons to be the most abundant superfamily, we additionally tested if there are any significant differences between the TE accumulation present on the *Tetragnatha* communities from each volcano, by using a Kruskal–Wallis test for this subset of the data independently. We considered the same volcano-level groupings and as dependent variables the whole TE analysis.

RESULTS

TE abundance and diversity in Tetragnatha spiny-legs

Repetitive elements, which include TEs, satellite repeats, and low-complexity repeats, represent 16.15% of the genome on average across both the Hawaiian *Tetragnatha* spiny-leg clade (Fig. 2). From these, TEs alone make up on average 15.38% of the genome in the spiny legs. At the superfamily level, DNA/hAT transposons were the largest group, comprising on average 30.41% of classified TEs. The next most abundant TE superfamilies are LTR/Gypsy (6.71%), DNA/Academ (6.10%), RC/Helitron (4.95%), DNA/CMC (4.63%), and LINE/1 (4.63%) (Fig. 2).

In the whole dataset, *T. kukuiki* had the highest proportion of genomic repeat content (21.44%) and *T. brevignatha* (067; Big Island) the lowest (13.50%). At the intraspecific level, we found a variance of 5.08% in *T. quasimodo* (max. 20.7%, min. 15.62%), 0.56% in *T. anuenue* (max. 18.24%, min. 17.68%), 0.78% in *T. kamakou* (max. 16.83%, min. 16.05%), and 0.93 in *T. brevignatha* (max. 14.43%, min. 13.5%).

Ancestral state reconstructions of repeats are shown on Fig. 3 (analysis done on the retrieved NJ topology) and Supporting Information Fig. S2 (analysis done on the retrieved ML topology). We do not find a consistent pattern of increase in TE numbers in more species on younger islands (Fig. 3; Fig. S2).

We found little variation in the accumulation of TE superfamilies across individuals in the spiny-leg radiation and in the sister orb-weaver radiation (Fig. 4). Although DNA/hAT transposons are the most abundant of all TEs, we did not find significant differences in abundance between volcano communities (Kruskal–Wallis chi-squared, $P = .4335$; Supporting Information Fig. S4).

TE age distributions

The repeat landscape plot shows that most TEs display low divergence levels (Fig. 5). All individuals have two peaks of varying sizes: the largest peak is close to 0% divergence and a smaller peak is around 5% divergence (all individual repeat landscape plots are given in Supporting Information Fig. S5). *Tetragnatha restricta* from Haleakalā (Fig. S5) has a unique distribution pattern compared to the other spiny leg species, with a much higher representation of LINEs, LTRs, and SINEs in the first age peak.

The percentage of young TEs (i.e. TEs with an average of <5% divergence between reads and dnaPipeTE consensus) ranged between 40.85% and 50.82%, with an average of 45.63%. We found

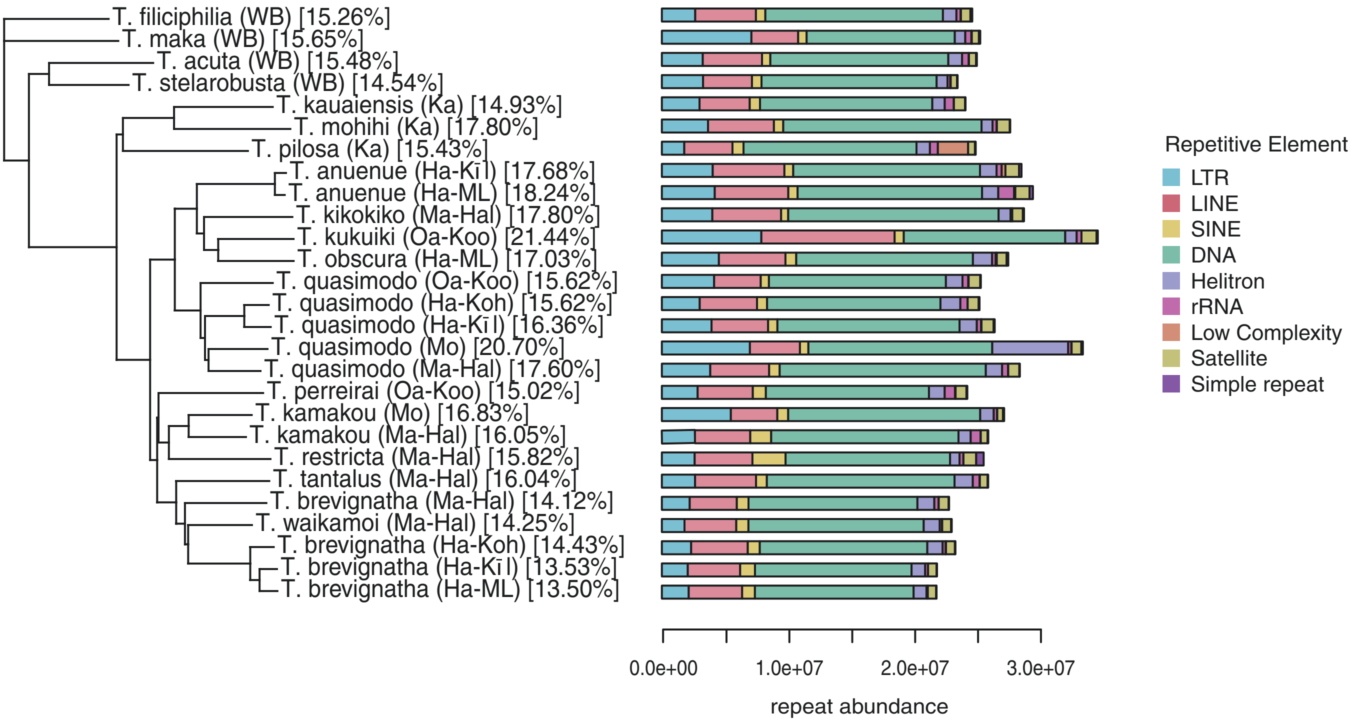

Figure 2. Abundance of repetitive elements across the Hawaiian *Tetragnatha* spiny-leg phylogeny. The phylogenetic tree was produced using an NJ algorithm (see Methods for an explanation). For each individual we provide the volcano where the population exists, repeat abundance (key to the right), and a percentage of genomic repeat content. DNA transposons comprise the majority of repetitive elements in all individuals. The units of repeat abundance are in base pairs, and unlabelled TEs (unknown) are not presented.

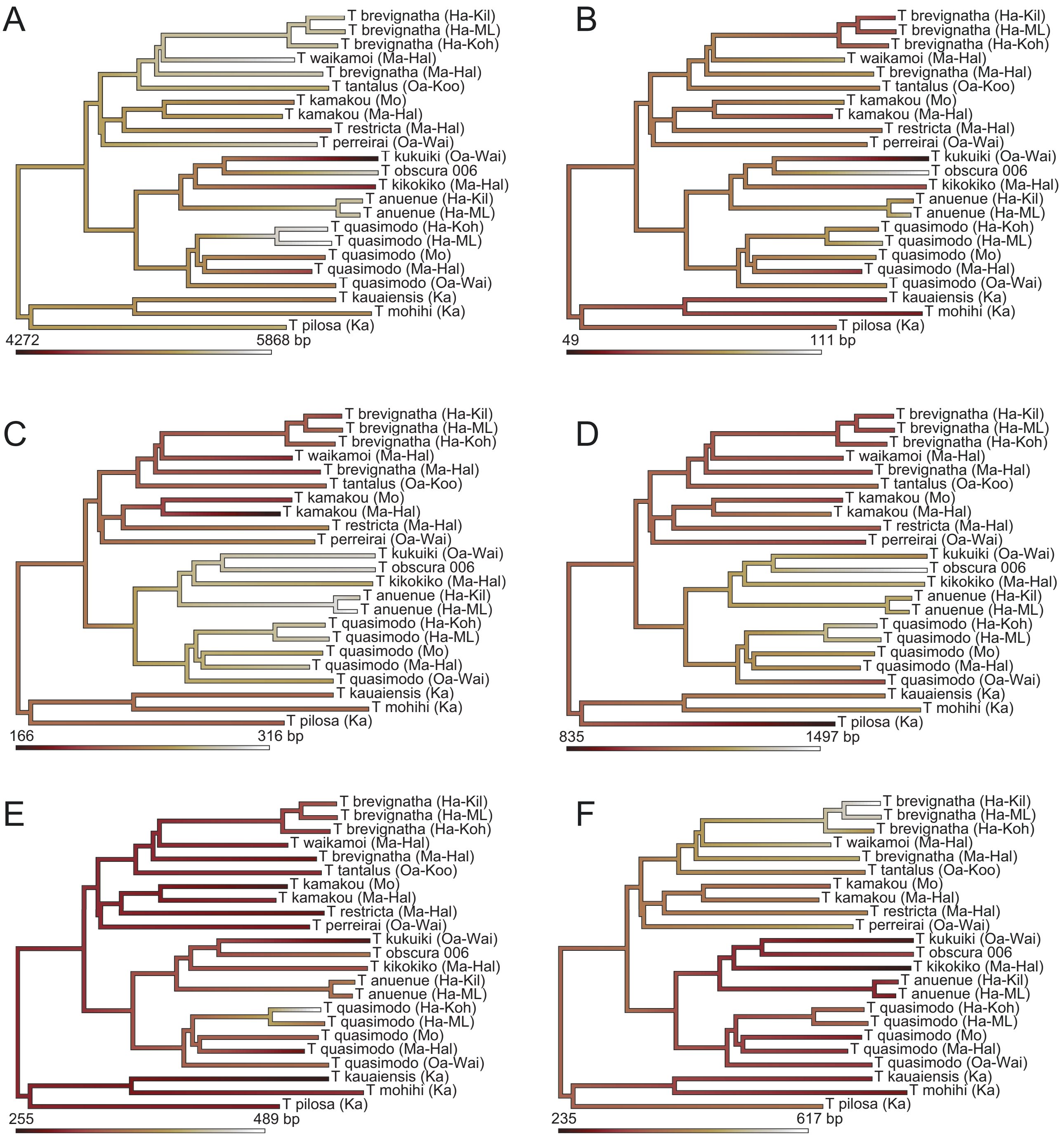

Figure 3. Evolutionary patterns of repeat amount based on the NJ tree topology. A—total number of TEs; B—simple repeats; C—satellite repeats; D—LTR TEs; E—Helitron TEs; F—SINEs.

no significant difference in young TE percentages across volcanoes (Kruskal–Wallis chi-squared, $P > .05$) (Fig. 5; Supporting Information Fig. S3).

Statistical analyses

The correlation between volcano age and total repeat abundance was not significant ($r = .002$, $P = .9928$; Supporting Information Fig. S6), indicating no linear relationship between the two variables (Fig. S7). Abundance of specific repeat elements did not differ significantly between volcanoes (Table 2a; Fig. S6), with the exception of satellite repeat abundance which differed significantly between the spiny leg and the web-building clade ($P = .037$; Table S2). Finally, the abundance of young TEs did not differ significantly between species from different volcanoes (Kruskal–Wallis chi-squared = 1.164, $P = .992$).

DISCUSSION

This study investigated the relationship between TE accumulation on the genome and species/population age in the *Tetragnatha* spiny-leg radiation, benefiting from the Hawaiian chronosequence. We hypothesized that the demographic

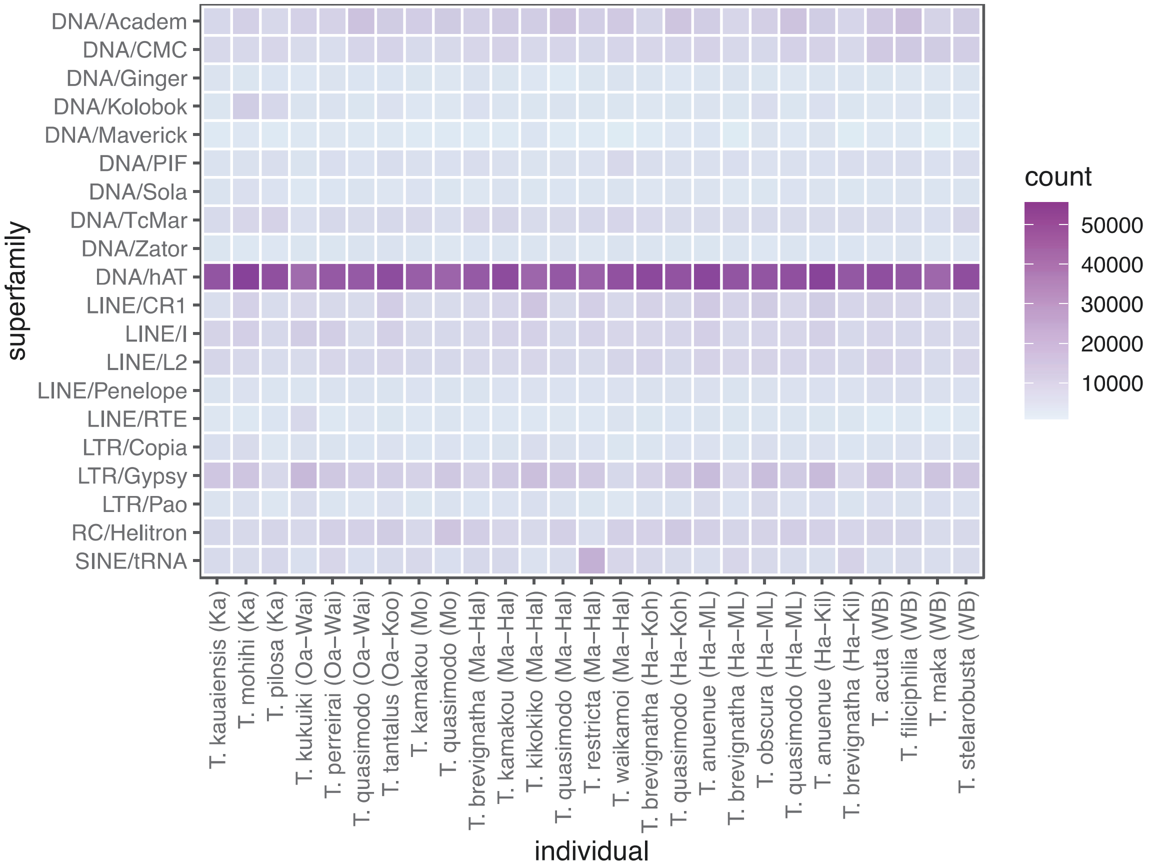

Figure 4. Accumulation of TE superfamilies in Hawaiian *Tetragnatha*. The *x*-axis shows different species, and the *y*-axis shows the accumulation of different TE superfamilies (count shows the number of base pairs). The 20 most abundant superfamilies are included. Individuals are ordered by volcano age from left to right (oldest to youngest), followed by the web builder individuals (WB).

oscillations associated with island colonization events trigger an increase of TE accumulation along the genome. We postulated that TE accumulation may explain the presumed increase in genetic variability despite the inevitable reduction of genetic variation resulting from founder effects. To test this hypothesis, we analysed the repeat abundance over a phylogenetic backbone (Figs 2, 3; Supporting Information Fig. S2) and accumulation of repeats at the superfamily level (Fig. 4), and unveiled the repeat accumulation of TEs through time (Figs 5, 6), with a specific focus on quantifying young TEs (Fig. 6). We formally tested the accumulation of repeat content in relation to volcano age, finding no statistically significant relationship, nor any correlation. If strong population oscillations would have led to an increase in TE activity, we would expect species from younger volcanoes to have the highest accumulation of TEs overall as well as young TEs. However, we observed no such trends and instead found a consistent accumulation of TEs in all populations and species, regardless of the age of the community present on each volcano.

No accumulation of overall TEs after early island colonization events

In the *Tetragnatha* spiny-leg adaptive radiation, the accumulation of TEs was not significantly affected by the island colonization event. The trajectory of island colonization can be analysed in a comparative phylogenetic setting (Figs 2, 3; Table 1), and this phylogeny is topologically consistent with previous *Tetragnatha* phylogenies (Gillespie 2004, Cerca *et al.* 2023a). Regardless of island age, genomic repeat content remained consistent across all spiny-leg individuals. For instance, lineages from the oldest island, Kaua'i, have an average of 15.82% of repeats, which is below the average of 16.15% of the entire spiny-leg dataset. Species on the volcanically active island of Hawai'i (Big Island) have an average of 15.8% genomic repeat content. Similarly, species that were sampled from multiple islands had no particular differences. Individuals from the same species occurring in different volcanoes had some variation in repeat content, but this was not correlated to the age of the island. The two individuals of *T. anuenue* from Hawai'i have 17.68–18.24% of their genome composed by repeats, the three *T. brevignatha* also from the island of Hawai'i ranged between 13.5 and 14.43%, and the two *T. kamakou* from Haleakalā and Moloka'i ranged between 16.05 and 16.83%. There was larger variation, from 15.62 to 20.7%, in *T. quasimodo* individuals sampled from four different islands. Unfortunately, we were not able to obtain data from continental species to establish a comparison with a mainland taxon. Regardless, our results suggest that the founder effects resulting from the colonization of a novel island do not impact the overall repeat content.

The lack of differences in overall accumulation of TEs as a result of population oscillations following a founder event suggests that demography does not greatly influence the overall TE

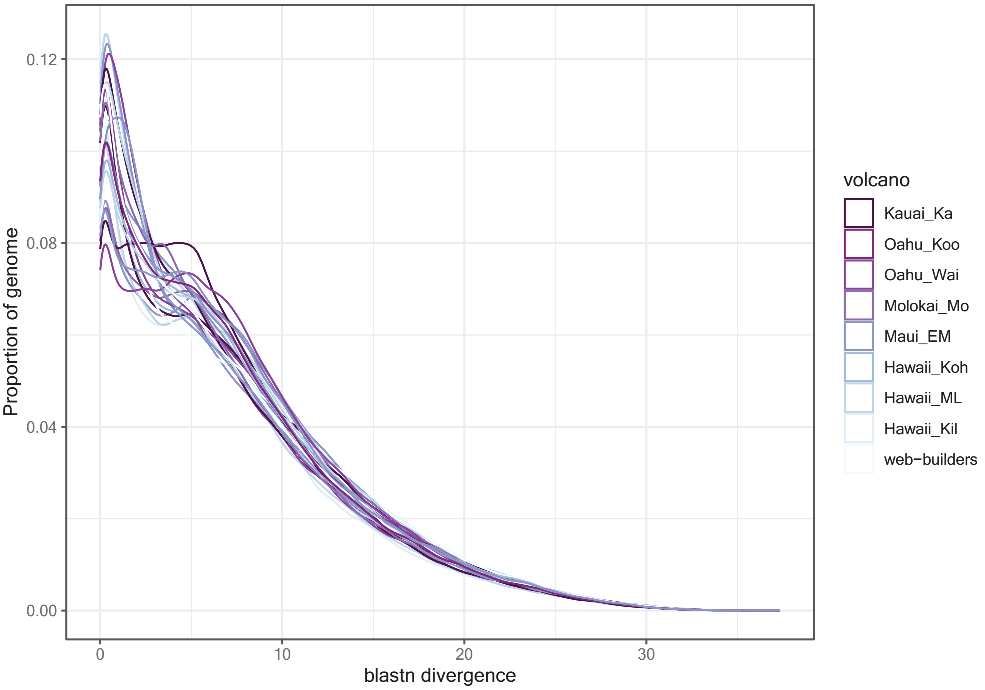

Figure 5. Repeat accumulation plot in *Tetragnatha* spiny-legs and sister web-builder clade. The y-axis shows the proportion of the genome, while the x-axis shows the blastn divergence, an indirect measure for TE age. Grouped by volcano, *Tetragnatha* individuals across the spiny-leg lineage and outgroup web-builder lineage exhibit similar patterns of TE age. All individuals exhibit similar patterns of a peak of TEs at <5% blastn divergence, a smaller peak of TEs at 5% divergence, and a steady decline of TEs at higher divergence levels.

Table 2. Outcomes of Kruskal–Wallis tests based on volcano for spiny-leg individuals for comparison of spiny-leg and web-builder individuals for each repetitive element type.

Element	Kruskal–Wallis chi-squared	*P*-value
DNA	7.149	.414
Helitron	7.842	.346
Low-complexity	2.853	.898
LINE	6.022	.537
LTR	9.188	.239
rRNA	5.465	.603
Satellite	6.219	.514
SINE	2.602	.919
Simple repeat	4.986	.662

content on *Tetragnatha* spiny-leg genomes. The evidence for the role of demography in promoting TE diversity along genomes has been mixed (reviewed in Bourgeois and Boissinot 2019), and it is possible that oscillations in demography related to early island colonization increase the expression of TEs, instead of increasing TE accumulation (García Guerreiro *et al.* 2008, Picot *et al.* 2008, Blass *et al.* 2012, Tollis and Boissinot 2013). Regardless, we expected that the founder events, together with the known small population sizes in insular species, would result in TE accumulation in *Tetragnatha*, as natural selection operates less efficiently in small populations and would ultimately increase overall TE content. Given our results, we reject the hypothesis that a reduction of population sizes is compromising the action of purifying selection in removing TEs along genomes (Blass *et al.* 2012, Tollis and Boissinot 2013, Xue *et al.* 2018, Bourgeois and Boissinot 2019). We recommend that future work focuses on quantifying both transcripts and genomic evolution of TEs at the family level, to obtain a full picture of repeat evolution. An improved assembled reference genome will also increase accuracy in calling TEs and other repetitive elements in the *Tetragnatha* radiation.

Volcanic activity across islands has been shown to be an important mechanism in driving population structuring of Hawaiian lineages (Wagner and Funk 1995, Roderick *et al.* 2012), which can create opportunities for geographical isolation and secondary contact, ultimately catalysing speciation and adaptation (Schluter 2000, Cotoras *et al.* 2018, Marques *et al.* 2019, Cerca *et al.* 2023a). Considering the oscillations resulting from the reduction of populations into isolated paths of forests (kīpuka), together with the stress imposed on populations and individuals following volcanic activities (Craddock 2016), we hypothesized that lineages inhabiting younger islands and volcanoes would have a higher accumulation of TEs. However, we reject these hypotheses, as we did not find significant correlations of age–TE accumulation, nor differences in genomic proportions of specific repeat elements (Table 2) and young TEs (Figs 5, 6).

No accumulation of specific TEs after early island colonization events

The analyses of TE order (e.g. LTRs, DNA; Fig. 2) and specific superfamilies (Fig. 4) show little TE diversity across individuals. In theory, one of the most common observations in TE accumulation is the release and accumulation of only a single TE family (Hawkins *et al.* 2006). For instance, genome deregulation as a result of stress, hybridization, or other evolutionary events could cause one or more TE repression mechanism [i.e. targeted TE

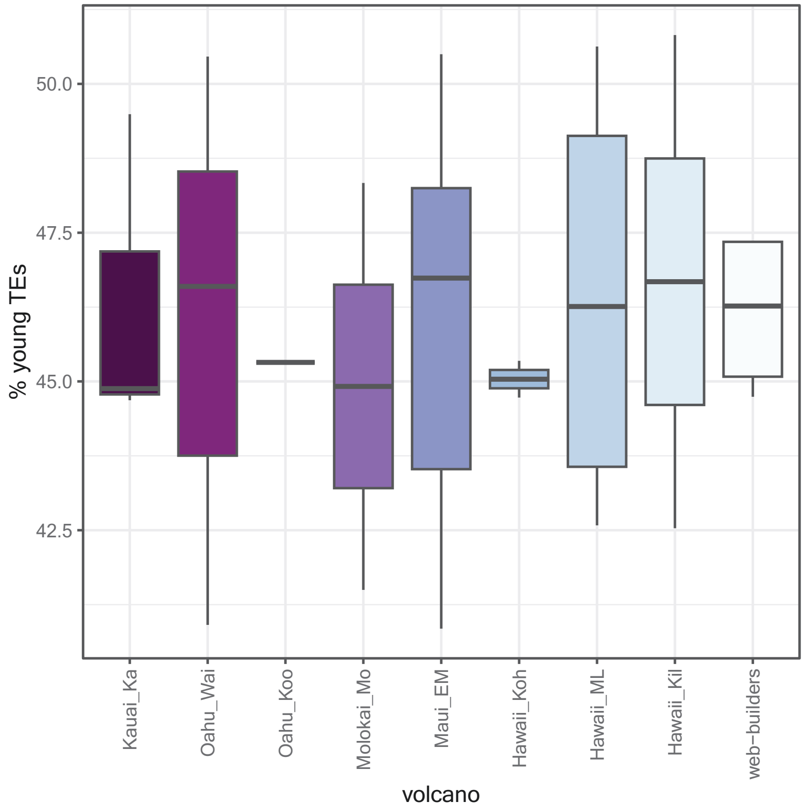

Figure 6. Percentage of young TEs across volcanoes. TEs were classified as young if they had <5% divergence from their consensus sequence. Oahu (Koo) has only one sample, so there is no variation across specimens.

methylation, small RNA, PIWI-interacting RNA (piRNA) in TEs, modification of histone marks] to be less efficient, typically leading to the release and expansion of a specific family (Slotkin and Martienssen 2007). If this was the case, we would not observe major differences in overall content, but we would observe expansions associated with a given TE group or even superfamily. However, this was not the case as we did not observe order-level expansions (Fig. 2) or superfamily expansions (Fig. 4). Despite the DNA/hAT superfamily being the most abundant superfamily across the radiation, there are no significant differences across species that would indicate a superfamily-specific burst following colonization to new volcanic communities. However, there are limitations to our low-coverage whole-genome sequencing data and analyses, as differential copy levels are not distinguishable at a finer scale with low-coverage approaches such as dnaPipeTE.

TE composition in Tetragnatha spiny-leg radiation

The classification of TEs in Arachnid genomes has been challenging, as a high proportion of unknown TEs and repeats are typically reported (e.g. Cerca *et al.* 2021, Wang *et al.* 2022). This is not surprising since there are no model organisms in Arachnids (Brewer *et al.* 2014). However, spider genomes are attractive targets for those interested in TE dynamics as there is a wide variation in TE content and genome size (Garb *et al.* 2018). We found that DNA/hAT transposons are the most common type of TEs detected in the analysed *Tetragnatha* genomes, followed by LTR/Gypsy transposons (Fig. 2). This is similar to the overall repeat content of other distantly related spider lineages (Cerca *et al.* 2021, Wang *et al.* 2022). DNA/hAT transposons were the most common TE superfamily, as reconstructed by dnaPipeTE, with 2668 contigs for the spiny-leg clade on average, compared to the next most abundant superfamily, LTR/Gypsy (average of 571 elements). In the *Tetragnatha* genomes, there were 11 different hAT families, the most common being hAT-Tip100, Blackjack, Charlie, and hATm. Furthermore, despite their low numbers over *Tetragnatha* genomes, we found significant differences in the number of satellite repeats between the spiny-leg lineage relative to the web-builder clade (Table 2). This is in agreement with previous investigations that suggested that satellites could be used as phylogenetic markers for closely related species, given their fast evolutionary rates (Pons and Gillespie 2004).

CONCLUSIONS

The fact that the most diverse and fascinating adaptive radiations on oceanic islands experience strong bottlenecks, which reduce their genetic diversity, presents a paradox. What is the source of genetic variation which acts as the raw material for ecological and phenotypic diversification in oceanic archipelagos? Here, we explored whether population oscillations associated with founder events could lead to a genome shock and bursts of TEs. We did not find an overall accumulation of TEs, no specific bursts of superfamilies, and no differences in the age of accumulation of TEs. While we conclude that strong population oscillation events did not act as a genome shock facilitating an increase in the overall genetic diversity of young populations/species on the spiny-leg clade, we cannot exclude the possibility that it has acted on specific genes or specific pathways which may be associated with phenotypic and environmental diversity.

SUPPORTING INFORMATION

Supporting Information data are available at *Linnean Society of Evolutionary Biology* online.

ACKNOWLEDGEMENTS

The authors would like to acknowledge a large number of people and institutions that collaborated at different stages of this research. The fieldwork in Hawaiʻi was supported by Laura Arnold, Timothy Bailey, David Benítez, Katie Champlin, James Friday, Jun Ying Lim, Emory Griffin-Noyes, Faith Inman-Narahari, Darcey Iwashita, Raina Kaholoaa, Jessie Knowlton, Rick Lapoint, Scott Laursen, Karl Magnacca, Elizabeth Morrill, Patrick O'Grady, Rita Pregana, Donald Price, David Rankin, William Roderick, Karen Uy, Erin Wilson-Rankin, and the Kīpuka team. The permit processing and access to different reserves and private land was possible thanks to Steve Bergfeld (DOFAW Big Island), Pat Bily (TNC Maui), Tabetha Block (HETF), Shalan Crysdale (TNC Big Island), Lance DaSilva (DOFAW Maui), Danae Dean (Kahoma Ranch), Charmian Dang (NAR), Melissa Dean (HETF), Betsy Gagne (NAR), Elizabeth Gordon (HALE), Lisa Hadway (DOFAW Big Island), Paula Hartzell (Lanaʻi Resorts, LLC), Greg Hendrickson (Kealakekua Ranch), Mel Johansen (TNC Big Island), Pomaikaʻi Kaniaupio-Crozier (Maui Land and Pineapple), Cynthia King (DLNR), Peter Landon (NAR Maui), Rhonda Loh (HAVO), Russell Kallstrom (TNC Molokaʻi), Joey Mello (DOFAW Big Island), Ed Misaki (TNC Molokaʻi), Elliot Parsons (Puʻu Waʻawaʻa HETF), Lani Petrie (Kapapala Ranch), Shawn Saito (Parker Ranch), Joe Ward (Maui Land and Pineapple), and Kawika Winter (Limahuli Botanical Garden). Publication of this article was made possible in part by support from the Berkeley Research Impact Initiative (BRII) sponsored by the UC Berkeley Library. We are grateful to two anonymous reviewers and an associate editor for offering constructing comments to this work.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

FUNDING

HHY was supported by the UC Berkeley Rose Hills Independent Summer Undergraduate Research Fellowship Program. DDC was supported by a Fulbright/CONICYT Doctoral Fellowship, Integrative Biology Department, and the Graduate Division of UC Berkeley, the Margaret C. Walker Fund (Essig Museum of Entomology), Sigma Xi, and an Alexander von Humboldt Postdoctoral Fellowship.

DATA AVAILABILITY

The data used in this article are available in the GenBank BioProject database at https://www.ncbi.nlm.nih.gov/bioproject/PRJEB64196/, and can be accessed with project accession number PRJEB64196.

REFERENCES

Belyayev A. Bursts of transposable elements as an evolutionary driving force. *Journal of Evolutionary Biology* 2014;**27**:2573–84. https://doi.org/10.1111/jeb.12513

Blass E, Bell M, Boissinot S. Accumulation and rapid decay of non-LTR retrotransposons in the genome of the three-spine stickleback. *Genome Biology and Evolution* 2012;**4**:687–702.

Bourgeois Y, Boissinot S. On the population dynamics of junk: a review on the population genomics of transposable elements. *Genes* 2019;**10**:419. https://doi.org/10.3390/genes10060419

Brawand D, Wagner CE, Li YI, *et al.* The genomic substrate for adaptive radiation in African cichlid fish. *Nature* 2014;**513**:375–81. https://doi.org/10.1038/nature13726

Brewer MS, Cotoras DD, Croucher PJP, *et al.* New sequencing technologies, the development of genomics tools, and their applications in evolutionary arachnology. *The Journal of Arachnology* 2014;**42**:1–15. https://doi.org/10.1636/m13-78.1

Carson HL, Templeton AR. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology and Systematics* 1984;**15**:97–131.

Casacuberta E, González J. The impact of transposable elements in environmental adaptation. *Molecular Ecology* 2013;**22**:1503–17. https://doi.org/10.1111/mec.12170

Cerca J, Armstrong EE, Vizueta J, *et al.* The *Tetragnatha kauaiensis* genome sheds light on the origins of genomic novelty in spiders. *Genome Biology and Evolution* 2021;**13**:evab262. https://doi.org/10.1093/gbe/evab262

Cerca J, Cotoras DD, Santander CG, *et al.* Multiple paths toward repeated phenotypic evolution in the spiny-leg adaptive radiation (*Tetragnatha*; Hawai'i). *Molecular Ecology* 2023a;**32**:4971–85. https://doi.org/10.1111/mec.17082

Cerca J, Cotoras DD, Bieker VC, *et al.* Evolutionary genomics of oceanic island radiations. *Trends in Ecology & Evolution* 2023b;**38**:631–42. https://doi.org/10.1016/j.tree.2023.02.003

Charlesworth B. Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics* 2009;**10**:195–205. https://doi.org/10.1038/nrg2526

Chénais B, Caruso A, Hiard S, *et al.* The impact of transposable elements on eukaryotic genomes: From genome size increase to genetic adaptation to stressful environments. *Gene* 2012;**509**:7–15. https://doi.org/10.1016/j.gene.2012.07.042

Choudhary MNK, Quaid K, Xing X, *et al.* Widespread contribution of transposable elements to the rewiring of mammalian 3D genomes. *Nature Communications* 2023;**14**:634. https://doi.org/10.1038/s41467-023-36364-9

Chuong EB, Elde NC, Feschotte C. Regulatory activities of transposable elements: from conflicts to benefits. *Nature Reviews Genetics* 2017;**18**:71–86. https://doi.org/10.1038/nrg.2016.139

Cotoras DD, Bi K, Brewer MS, *et al.* Co-occurrence of ecologically similar species of Hawaiian spiders reveals critical early phase of adaptive radiation. *BMC Evolutionary Biology* 2018;**18**:100. https://doi.org/10.1186/s12862-018-1209-y

Craddock EM. Profuse evolutionary diversification and speciation on volcanic islands: transposon instability and amplification bursts explain the genetic paradox. *Biology Direct* 2016;**11**:44. https://doi.org/10.1186/s13062-016-0146-1

Danecek P, Bonfield JK, Liddle J, *et al.* Twelve years of SAMtools and BCFtools. *GigaScience* 2021;**10**:giab008. https://doi.org/10.1093/gigascience/giab008

Faircloth BC, McCormack JE, Crawford NG, *et al.* Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology* 2012;**61**:717–26. https://doi.org/10.1093/sysbio/sys004

Fambrini M, Usai G, Vangelisti A, *et al.* The plastic genome: the impact of transposable elements on gene functionality and genomic structural variations. *Genesis* 2020;**58**:e23399. https://doi.org/10.1002/dvg.23399

Feiner N. Accumulation of transposable elements in *Hox* gene clusters during adaptive radiation of *Anolis* lizards. *Proceedings Biological Sciences* 2016;**283**:20161555. https://doi.org/10.1098/rspb.2016.1555

Felsenstein J. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 1985;**39**:783–91. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Fleischer RC, McIntosh CE, Tarr CL. Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K–Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* 1998;**7**:533–45. https://doi.org/10.1046/j.1365-294x.1998.00364.x

Flynn JM, Hubley R, Goubert C, *et al*. RepeatModeler2 for automated genomic discovery of transposable element families. *Proceedings of the National Academy of Sciences of the United States of America* 2020;**117**:9451–7. https://doi.org/10.1073/pnas.1921046117

Frankham R. Do island populations have less genetic variation than mainland populations? *Heredity* 1997;**78**:311–27. https://doi.org/10.1038/hdy.1997.46

Garb JE, Sharma PP, Ayoub NA. Recent progress and prospects for advancing arachnid genomics. *Current Opinion in Insect Science* 2018;**25**:51–7. https://doi.org/10.1016/j.cois.2017.11.005

García Guerreiro MP, Chávez-Sandoval BE, Balanyà J, *et al*. Distribution of the transposable elements bilbo and gypsy in original and colonizing populations of *Drosophila subobscura*. *BMC Evolutionary Biology* 2008;**8**:234. https://doi.org/10.1186/1471-2148-8-234

Gardner EJ, Lam VK, Harris DN, *et al*.; 1000 Genomes Project Consortium. The mobile element locator tool (MELT): population-scale mobile element discovery and biology. *Genome Research* 2017;**27**:1916–29. https://doi.org/10.1101/gr.218032.116

Gillespie RG. Hawaiian spiders of the genus *Tetragnatha*: I. Spiny leg clade. *The Journal of Arachnology* 1991;**30**:159–209. https://doi.org/10.1636/0161-8202(2002)030[0159:hsotgt]2.0.co;2

Gillespie R. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 2004;**303**:356–9. https://doi.org/10.1126/science.1091875

Gillespie RG, Bennett GM, De Meester L, *et al*. Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* 2020;**111**:1–20. https://doi.org/10.1093/jhered/esz064

Goubert C, Modolo L, Vieira C, *et al*. De novo assembly and annotation of the Asian tiger mosquito (*Aedes albopictus*) repeatome with dnaPipeTE from raw genomic reads and comparative analysis with the yellow fever mosquito (*Aedes aegypti*). *Genome Biology and Evolution* 2015;**7**:1192–205. https://doi.org/10.1093/gbe/evv050

Hawkins JS, Kim H, Nason JD, *et al*. Differential lineage-specific amplification of transposable elements is responsible for genome size variation in *Gossypium*. *Genome Research* 2006;**16**:1252–61. https://doi.org/10.1101/gr.5282906

Hoang DT, Chernomor O, von Haeseler A, *et al*. UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 2018;**35**:518–22. https://doi.org/10.1093/molbev/msx281

Hof AE't, Campagne P, Rigden DJ, *et al*. The industrial melanism mutation in British peppered moths is a transposable element. *Nature* 2016;**534**:102–5.

Jurka J, Kapitonov VV, Pavlicek A, *et al*. Repbase Update, a database of eukaryotic repetitive elements. *Cytogenetic and Genome Research* 2005;**110**:462–7. https://doi.org/10.1159/000084979

Katoh K, Standley DM. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 2013;**30**:772–80. https://doi.org/10.1093/molbev/mst010

Kennedy SR, Lim JY, Adams SA, *et al*. What is adaptive radiation? Many manifestations of the phenomenon in an iconic lineage of Hawaiian spiders. *Molecular Phylogenetics and Evolution* 2022;**175**:107564. https://doi.org/10.1016/j.ympev.2022.107564

Kidwell MG, Lisch D. Transposable elements as sources of variation in animals and plants. *Proceedings of the National Academy of Sciences of the United States of America* 1997;**94**:7704–11. https://doi.org/10.1073/pnas.94.15.7704

Kratochwil CF, Kautt AF, Nater A, *et al*. An intronic transposon insertion associates with a trans-species color polymorphism in *Midas* cichlid fishes. *Nature Communications* 2022;**13**:296.

Kück P, Meusemann K. FASconCAT: convenient handling of data matrices. *Molecular Phylogenetics and Evolution* 2010;**56**:1115–8. https://doi.org/10.1016/j.ympev.2010.04.024

Lefort V, Desper R, Gascuel O. FastME 2.0: A comprehensive, accurate, and fast distance-based phylogeny inference program: Table 1. *Molecular Biology and Evolution* 2015;**32**:2798–800. https://doi.org/10.1093/molbev/msv150

Lerat E, Goubert C, Guirao-Rico S, *et al*. Population-specific dynamics and selection patterns of transposable element insertions in European natural populations. *Molecular Ecology* 2019;**28**:1506–22. https://doi.org/10.1111/mec.14963

Li H, Durbin R. Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics* 2009;**25**:1754–60. https://doi.org/10.1093/bioinformatics/btp324

Lockton S, Ross-Ibarra J, Gaut BS. Demography and weak selection drive patterns of transposable element diversity in natural populations of *Arabidopsis lyrata*. *Proceedings of the National Academy of Sciences of the United States of America* 2008;**105**:13965–70. https://doi.org/10.1073/pnas.0804671105

Marçais G, Kingsford C. A fast, lock-free approach for efficient parallel counting of occurrences of k-mers. *Bioinformatics* 2011;**27**:764–70. https://doi.org/10.1093/bioinformatics/btr011

Marques DA, Meier JI, Seehausen O. A combinatorial view on speciation and adaptive radiation. *Trends in Ecology & Evolution* 2019;**34**:531–44. https://doi.org/10.1016/j.tree.2019.02.008

Minh BQ, Schmidt HA, Chernomor O, *et al*. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 2020;**37**:1530–4. https://doi.org/10.1093/molbev/msaa015

Oliver KR, Greene WK. Transposable elements and viruses as factors in adaptation and evolution: an expansion and strengthening of the TE-Thrust hypothesis. *Ecology and Evolution* 2012;**2**:2912–33. https://doi.org/10.1002/ece3.400

Ondov BD, Treangen TJ, Melsted P, *et al*. Mash: fast genome and metagenome distance estimation using MinHash. *Genome Biology* 2016;**17**. https://doi.org/10.1186/s13059-016-0997-x

Picot S, Wallau GL, Loreto ELS, *et al*. The mariner transposable element in natural populations of *Drosophila simulans*. *Heredity* 2008;**101**:53–9. https://doi.org/10.1038/hdy.2008.27

Pons J, Gillespie RG. Evolution of satellite DNAs in a radiation of endemic Hawaiian spiders: does concerted evolution of highly repetitive sequences reflect evolutionary history? *Journal of Molecular Evolution* 2004;**59**:632–41. https://doi.org/10.1007/s00239-004-2655-2

Rachtman E, Sarmashghi S, Bafna V, *et al*. Quantifying the uncertainty of assembly-free genome-wide distance estimates and phylogenetic relationships using subsampling. *Cell Systems* 2022;**13**:817–829.e3. https://doi.org/10.1016/j.cels.2022.06.007

Revell LJ, Mahler DL, Peres-Neto PR, *et al*. A new phylogenetic method for identifying exceptional phenotypic diversification. *Evolution* 2012;**66**:135–46. https://doi.org/10.1111/j.1558-5646.2011.01435.x

Ricci M, Peona V, Guichard E, *et al*. Transposable elements activity is positively related to rate of speciation in mammals. *Journal of Molecular Evolution* 2018;**86**:303–10. https://doi.org/10.1007/s00239-018-9847-7

Roderick GK, Gillespie RG. Speciation and phylogeography of Hawaiian terrestrial arthropods. *Molecular Ecology* 1998;**7**:519–31. https://doi.org/10.1046/j.1365-294x.1998.00309.x

Roderick GK, Croucher PJP, Vandergast AG, *et al*. Species differentiation on a dynamic landscape: shifts in metapopulation genetic structure using the chronology of the Hawaiian Archipelago. *Evolutionary Biology* 2012;**39**:192–206. https://doi.org/10.1007/s11692-012-9184-5

Ronco F, Matschiner M, Böhne A, *et al*. Drivers and dynamics of a massive adaptive radiation in cichlid fishes. *Nature* 2021;**589**:76–81. https://doi.org/10.1038/s41586-020-2930-4

Santos ME, Braasch I, Boileau N, *et al*. The evolution of cichlid fish egg-spots is linked with a cis-regulatory change. *Nature Communications* 2014;**5**:5149. https://doi.org/10.1038/ncomms6149

Sarmashghi S, Bohmann K, P. Gilbert MT, *et al*. Skmer: assembly-free and alignment-free sample identification using genome skims. *Genome Biology* 2019;**20**. https://doi.org/10.1186/s13059-019-1632-4

Schluter D. *The Ecology of Adaptive Radiation.* Oxford: Oxford University Press, 2000.

Schrader L, Schmitz J. The impact of transposable elements in adaptive evolution. *Molecular Ecology* 2019;**28**:1537–49. https://doi.org/10.1111/mec.14794

Schubert M, Lindgreen S, Orlando L. AdapterRemoval v2: rapid adapter trimming, identification, and read merging. *BMC Research Notes* 2016;**9**. https://doi.org/10.1186/s13104-016-1900-2

Shaw KL, Gillespie RG. Comparative phylogeography of oceanic archipelagos: hotspots for inferences of evolutionary process. *Proceedings of the National Academy of Sciences of the United States of America* 2016;**113**:7986–93. https://doi.org/10.1073/pnas.1601078113

Slotkin RK, Martienssen R. Transposable elements and the epigenetic regulation of the genome. *Nature Reviews Genetics* 2007;**8**:272–85. https://doi.org/10.1038/nrg2072

Tollis M, Boissinot S. Lizards and LINEs: selection and demography affect the fate of L1 retrotransposons in the genome of the green anole (*Anolis carolinensis*). *Genome Biology and Evolution* 2013;**5**:1754–68. https://doi.org/10.1093/gbe/evt133

Vandergast AG, Gillespie RG, Roderick GK. Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth and the potential for accelerated evolution. *Molecular Ecology* 2004;**13**:1729–43. https://doi.org/10.1111/j.1365-294X.2004.02179.x

Wagner WL, Funk VA. *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago.* Washington, DC: Smithsonian Institution Press, 1995.

Wang M, Yang Z, Wang C, *et al*. Exploration of the protein conformation and mechanical properties of different spider silks. *Journal of Molecular Structure* 2022;**1270**:133933. https://doi.org/10.1016/j.molstruc.2022.133933

Xue AT, Ruggiero RP, Hickerson MJ, *et al*. Differential effect of selection against LINE retrotransposons among vertebrates inferred from whole-genome data and demographic modeling. *Genome Biology and Evolution* 2018;**10**:1265–81. https://doi.org/10.1093/gbe/evy083