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Panmixia in spiders (*Mecaphesa celer*, Thomisidae) despite fragmented habitat at Craters of the Moon in Idaho

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Abstract

1. A fragmented landscape, which contains a patchwork of vegetated hospitable areas and a barren intervening matrix, may reduce gene flow in a population and over time result in an increase in population structure.
2. We tested this prediction in crab spiders (*Mecaphesa celer* (Hentz, 1847)) inhabiting isolated habitat patches in the lava matrix of Craters of the Moon National Monument and Preserve, Idaho, USA.
3. Using reduced-representation genomic sequencing, we did not find evidence of population structure due to a reduction in gene flow among habitat patches.
4. Instead, our results show strong evidence of panmixia likely due to abundant juvenile dispersal and possible connectivity to outer regions surrounding the lava flows despite the species' habitat specificity.

KEYWORDS
gene flow, habitat fragmentation, kipukas, population genomics, RAD sequencing

INTRODUCTION

The natural world is becoming more fragmented, isolated, and altered. The many ecological processes of fragmented populations are complex (Young & Clarke, 2000). In some cases, detrimental effects may arise as isolation of populations and landscape fragmentation increases due to an intervening matrix that may be inhospitable and/or limit dispersal. The reduced dispersal ability of organisms, and ultimately decreased gene flow between fragmented populations, can result in increased population structure and decreases in the effective population size (Hedrick & Gilpin, 1997; Whitlock & Barton, 1997). The decreases in gene flow and effective population size can lead to genetic drift in the population and an overall decrease in genetic diversity at the subpopulation level (Frankham, 2015). Additionally, these populations may be unable to then purge detrimental alleles and others may become fixed. These impacts make it difficult for such a population to respond to environmental changes. Observing patterns of gene flow after natural landscape fragmentation, such as that occurring with lava flows can help identify potential parallel threats associated with anthropogenic fragmentation of landscapes (e.g., urbanisation, asphalt). However, much remains to be known about how the process of fragmentation in a mosaic landscape, in combination with both passive dispersal and a high chance of landing in a less hospitable or inhospitable habitat, may impact the diversity and evolutionary trajectory of arthropod species on a fine, genetic scale.

At the Biological Dynamics of Forest Fragments Project in Brazil, for over 40 years, large-scale ecological studies have occurred focused on the impacts of fragmentation on rainforest habitats. Almost every arthropod group studied exhibited a response to changes in the area, such as changes in abundances and overall species richness (Vasconcelos & Bruna, 2012). The impacts of changes in abundance can thereby influence population structure. In Hawaii, patchwork landscapes of lava and vegetation have been shown to drive population structure, particularly in *Drosophila* (Carson et al., 1990; Carson & Templeton, 1984; Craddock & Johnson, 1979).

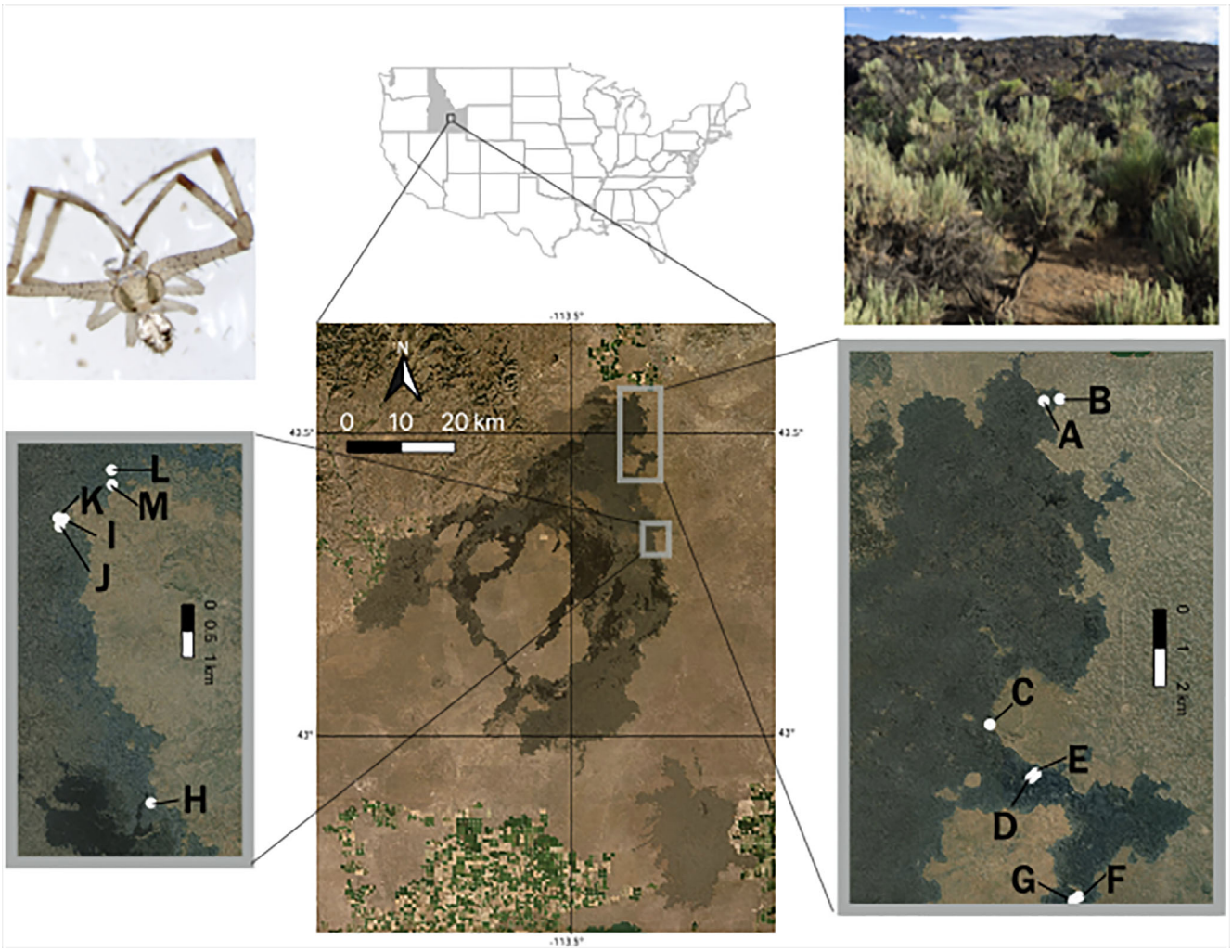

FIGURE 1 Map of Craters of the Moon National Monument and Preserve, Idaho, USA. Map inlays showing 13 kipuka locations where *Mecaphesa celer* spider collections occurred, each population denoted with a letter. Photo of *M. celer* individual (top left). View from in a kipuka and the surrounding lava flow (top right)

For arthropod populations that exist in a patchwork landscape where there is periodic surface turnover, such as by the eruption of lava flows, recolonization must occur from nearby areas. This in turn creates a metapopulation with shifting population structure as the mosaic changes through time with new eruptions continually modifying the landscape (Carson et al., 1990). Other work on arthropods in naturally fragmented areas, and particularly those separated by lava flows, have found population structure at small scales, both temporal and spatial (Roesch Goodman et al., 2012; Vandergast et al., 2004). For example, the long-jawed-orb-weavers, *Tetragnatha* spp., in Hawaii, which disperse by passive ballooning, show geographic population structure in a fragmented landscape of lava and forest fragments (Vandergast et al., 2004). The evolutionary impacts of forest fragmentation measured in the genetic analysis of the spiders occurred within approximately the last 150 years. In a Hawaiian planthopper (*Nesosydne chambersi*), a sap-feeding specialist, the genetic structure was found to be strongly associated with geographical location across lava substrates that ranged from 200 to 3000 years in age (Roesch Goodman et al., 2012). While the genetic structure has been observed in populations of arthropods within the geologically fragmented landscape of Hawaii and elsewhere, it has yet to be studied whether similar patterns are observed in arthropods in an analogous lava-fragmented system in the continental United States such as Craters of the Moon National Monument and Preserve (CRMO).

CRMO, located in south-central Idaho, USA (Figure 1), is an ideal system to explore patterns of gene flow in fragmented landscapes because, like with the Hawaii forest fragments, naturally produced islands of vegetation have been created between the sequential, inhospitable surrounding lava flows. There are over 500 of these lava-flow islands at CRMO, thus offering many replicates to detect the impacts of natural fragmentation on population structure. Between 15,000 years ago (kya) and as recently as 2 kya, the eruptive periods at CRMO have resulted in 60 overlapping flows that encompass nearly 1900 km^2 (Kuntz et al., 1982; National Park Service, 2011). After each eruption, these islands of vegetation surrounded by lava flows were formed. Vegetation-filled lava-flow islands are known as

kipukas, a derived term from the Hawaiian word kīpuka that is used to describe an area of older land that is completely surrounded by an area of younger lava flows (Vandergast & Gillespie, 2004). The kipukas at CRMO create a vegetated archipelago within an 'ocean' of basaltic lava. The size of the kipukas ranges from substantially less than 1 km^2 up to over 341 km^2 (National Park Service, 2018). This patchwork landscape is home to a diverse community of plants and animals, some of which are endemic to lava fields, the sagebrush steppe habitat, or the region (Idaho Conservation Data Center, 2008; Popovich, 2006).

Although the geology, flora, and some of the 2000 documented species of wildlife including charismatic megafauna such as pika and pronghorn within CRMO have been surveyed, invertebrates overall remain poorly studied (Camp et al., 2020; Cohn, 2010; Kuntz et al., 1982, 1986; Popovich, 2006). To date, one insect survey has occurred at CRMO and a later survey focused only on rare invertebrates, for example, in caves (Horning & Barr, 1970; Idaho Conservation Data Center, 2008). Therefore, abundance estimates and distributions of arthropods, including the crab spider *Mecaphesa celer*, at the regional scale of CRMO are unclear.

While dispersal distances in spiders can vary widely depending on species, habitat, and climatic variables, some spiders can travel great distances. Darwin noted small spiders descending from the air aboard the Beagle when it was at least 95 km away from land (Darwin, 1860). Crab spiders (Araneae: Thomisidae) aerially disperse relying on their fine fibres to catch air currents in a passive behaviour known as ballooning (Homann, 1934). Ballooning can be reinitiated in young individuals if cues used to determine resource and foraging suitability are not observed. For example, *Mecaphesa asperata* have been shown to primarily use indirect cues when choosing foraging sites such as a preference for blooming inflorescences and sites with lower abundances of conspecifics, as opposed to directly assessing prey density (Hanna & Eason, 2013). Further, this ballooning behaviour can be triggered by favourable environmental conditions like wind, or when conditions have become unfavourable due to changes in conspecifics or resource availability (Cordellier et al., 2020). Dispersal differs individually for some species that have been studied and may even differ between males and females, as females often defend their territory (Cordellier et al., 2020; Johnson et al., 2015; Wilcox, 2017).

These ambush predators, in particular those within the Genus *Mecaphesa*, exploit vegetation as a hunting habitat to prey on pollinators (Nentwig, 1986). Some species use camouflage to match the inflorescence(s), change colour, and/or can interfere with insect visual signals thereby increasing pollinator visits to the inflorescence(s) they occupy (Heiling et al., 2003). In this present study, the species *M. celer* was most often observed and collected on the inflorescences of Arrowleaf Balsamroot (*Balsamorhiza sagitatta*) and foliage of the shrub Big Sagebrush (*Artemisia tridentata*) within the sampled kipukas as these are some of the most predominant vegetation in kipukas at CRMO. The intervening less hospitable matrix of lava flows was not sampled in the present study. Given that *M. celer* is more restricted to vegetative hunting areas and exhibits passive dispersal, fragmentation by a low-quality intervening matrix may exacerbate this restriction of movement resulting in decreased dispersal and, over time, an increase in observed population structure.

Here, we present the first assessment of genome-wide patterns of the population structure of *M. celer* at CRMO. We predict that the geologically recent lava flows separating the kipukas sampled at CRMO might hinder the movement of *M. celer* between kipukas over various distances. Alternatively, given that most spider species balloon at some stage in their lifecycle, there is likely enough gene flow to lead to panmixia at the majority of loci in a genome. To test these hypotheses, we used Restriction-site-Associated DNA sequencing (RADseq; Andrews et al., 2016) to identify and genotype a large number of polymorphic nuclear loci at 13 localities in CRMO. The results of this study are critical for understanding the dispersal patterns that affect ecological processes, such as the maintenance of genetic diversity, as habitat is altered and fragmented over time by the lower quality and/or inhospitable matrix.

METHODS

Field collection, library preparation, and sequencing

To measure the population structure of *M. celer* at CRMO we collected spiders using beating sheets in 13 kipukas (denoted 'a'–'m' in Figure 1, Tables 1, and 2). Collection occurred in May 2017 and specimens were placed in 95% ethanol in the field and then stored at the University of Idaho, Moscow, ID, USA at −80°C until DNA extraction.

We extracted DNA for genetic sequencing from spider legs (2–6 per individual) using an OmniPrep Genomic DNA Extraction Kits (G-Biosciences, St. Louis, MO, USA) (refer to Table S1). DNA quality and quantity were assessed by agarose gel electrophoresis and with a Qubit fluorometer (Thermo Fisher Scientific, Waltham, USA).

We constructed a library for single-digest RADseq library for 84 individuals (2–13 individuals per kipuka), following the protocol of Ali et al. (2016), but without the final target capture step. We used the restriction enzyme PstI, which recognises a 6 base pair (bp) cut site, and individually barcoded each sample. Then, we pooled all samples into one library and performed size selection to select fragments from 300 to 700 bp. We amplified the library using 12 PCR cycles and sequenced in one lane of paired-end 150 bp reads using an Illumina Hi-Seq4000.

Sequence processing and genotyping

We removed PCR duplicates using STACKS v.2.2 (Rochette et al., 2019) with the 'clone_filter' unit. We filtered reads with the 'process_radtags' unit from Stacks using the default setting options of −q and −r, respectively, these options filter by reading quality using a sliding window and rescue barcodes with up to two errors. Based on the recommendations of (Rochette & Catchen, 2017) for parameter optimization in de novo analysis, we tested a range of M and n values from 1 to 9 (fixing $M = n$) and $m = 3$. For each parameter combination, we filtered the raw results keeping only loci shared by at least 80% of samples (−r 0.80) using the 'populations' unit from Stacks and plotted the number of loci and number of polymorphic sites. We chose $M = n = 3$ and $m = 3$ based on the

TABLE 1 The statistical values of genetic diversity per population from variant and all positions data (H_O, observed heterozygosity; H_E expected heterozygosity; π, nucleotide diversity; F_{IS}, inbreeding coefficient)

					H_O		H_E		π		F_{IS}	
Population	Latitude	Longitude	Number of individuals	Polymorphic loci (%)	Variant positions	All positions	Variant positions	All positions	Variant positions	All positions	Variant positions	All positions
a	43.55636	−113.35151	6	12.2145	0.2625	0.0321	0.2207	0.0270	0.2452	0.0300	−0.0345	−0.0042
b	43.5566	−113.34678	6	13.1579	0.2360	0.0311	0.2027	0.0267	0.2248	0.0296	−0.0237	−0.0031
c	43.49886	−113.36283	8	17.2294	0.1849	0.0319	0.1643	0.0283	0.1771	0.0305	−0.0224	−0.0039
d	43.46912	−113.35586	2	4.2628	0.5588	0.0238	0.3927	0.0167	0.5471	0.0233	−0.0177	−0.0008
e	43.4699	−113.35419	6	14.2503	0.2278	0.0325	0.1961	0.0279	0.2169	0.0309	−0.0245	−0.0035
f	43.44107	−113.34049	6	10.3277	0.2393	0.0247	0.2096	0.0217	0.2329	0.0241	−0.0131	−0.0014
g	43.43863	−113.34184	6	12.0655	0.2432	0.0293	0.2110	0.0255	0.2324	0.0280	−0.0234	−0.0028
h	43.28466	−113.29964	13	26.5144	0.1256	0.0333	0.1144	0.0303	0.1198	0.0318	−0.0142	−0.0038
i	43.33333	−113.32037	4	8.2920	0.3264	0.0271	0.2737	0.0227	0.3190	0.0265	−0.0175	−0.0015
j	43.3317	−113.32077	10	18.0238	0.1637	0.0295	0.1437	0.0259	0.1524	0.0275	−0.0303	−0.0055
k	43.33321	−113.32108	2	3.9480	0.6076	0.0240	0.4019	0.0159	0.5485	0.0217	−0.0886	−0.0035
l	43.43129	−113.30869	9	18.8183	0.1865	0.0351	0.1649	0.0310	0.1778	0.0335	−0.0206	−0.0039
m	43.3388	−113.3086	6	14.3496	0.2242	0.0322	0.1970	0.0283	0.2177	0.0312	−0.0128	−0.0018

TABLE 2 Pairwise F_{ST} values, above diagonal is Weir and Cockerham weighted F_{ST} estimate and below diagonal is Weir and Cockerham mean F_{ST} estimate (Weir & Cockerham, 1984)

	a	b	c	d	e	f	g	h	i	j	k	l	m
a	-	0.010901	−0.0016182	−0.0024845	0.017059	0.028782	0.0067101	−0.01635	−0.013372	0.0028037	−0.022422	−0.0024009	0.019504
b	0.001976	-	−0.0039227	−0.038199	−0.004336	−0.0047574	−0.0082659	0.00099454	−0.018282	−0.0059172	−0.072086	−0.018708	−0.0099502
c	−0.0030597	0.00089337	-	−0.03005	0.0066027	−0.0098087	−0.0042609	−0.0067154	−0.0090427	−0.002595	−0.044429	−0.0055936	−0.012417
d	−0.030193	−0.054415	−0.067911	-	−0.057858	0.031964	0.0025208	−0.026807	0.0034431	−0.036199	0	−0.068869	−0.056869
e	0.0062548	−0.0022416	0.002866	−0.071178	-	−0.011662	−0.0014984	0.005198	−0.016272	0.0076395	−0.016435	0.015806	0.0047035
f	0.0076116	0.00035046	−0.0098882	0.01825	−0.0047927	-	−0.0035471	0.0042487	0.010334	−0.0050923	0.0052541	−0.017902	−0.0063636
g	0.0019588	−0.0036809	−0.0034524	−0.024391	4.23E-05	−0.0018043	-	−0.0073897	0.0062318	0.012692	−0.0089912	−0.012578	0.013917
h	−0.01966	−0.0017846	−0.0047064	−0.076986	0.0030598	−0.013206	−0.0082133	-	−0.019777	0.0024563	−0.083346	0.011879	0.0080894
i	−0.0090462	−0.015562	−0.011029	−0.014106	−0.017705	0.0083618	−0.0037285	−0.022423	-	−0.022649	0.0078713	−0.011987	0.00098692
j	−0.0034148	−0.0018504	−0.0003195	−0.072265	0.0083207	−0.0069134	−0.0015165	−8.83E-05	−0.01879	-	−0.060172	0.019102	−0.0007342
k	−0.051277	−0.084047	−0.07099	−0.0055096	−0.048728	−0.013906	−0.044116	−0.10759	−0.0059684	−0.09904	-	−0.047745	−0.051763
l	−0.0069506	−0.010984	−0.0010192	−0.086576	0.003738	−0.016374	−0.0078944	0.0088539	−0.024182	0.0081005	−0.089633	-	−0.0097992
m	0.0028481	−0.0042811	−0.0058537	−0.072572	0.0022654	−0.0026175	0.0047316	0.0011696	−0.0090063	0.0017137	−0.075371	−0.0063976	-

plateau in a number of loci and stabilisation of the distribution of polymorphic sites (Rochette & Catchen, 2017). We removed loci genotyped in less than 50% and less than 90% of all samples to produce two datasets for subsequent analyses.

Population structure

To assess genetic clustering, we applied three methods to the filtered dataset. First, we performed principal components analysis (PCA) using PLINK v1.9 (Purcell et al., 2007). We plotted individuals on PC1 versus PC2 and PC2 versus PC3 for the two datasets. Using the dataset with loci genotyped in 90% of individuals, we removed the two most divergent specimens with high proportions of missing data (S53 from population 'h' and S67 from population 'l') and ran another PCA. Second, we tested for fine-scale population structure using FINERADSTRUCTURE v. 0.3.2 (Malinsky et al., 2018). This haplotype-based analysis provides greater power to detect subtle levels of genetic structuring through differences shared by co-ancestry (Lawson et al., 2012). Given that this analysis has been shown to be highly sensitive to missing data, we only used the dataset that retained SNPs genotyped in more than 90% of all individuals. We ordered the RAD loci according to linkage disequilibrium using the sampleLD.R script provided in FINERADSTRUCTURE in order to reduce the likelihood of overconfident clustering. Using the reordered loci, a co-ancestry matrix was inferred by FINERADSTRUCTURE and used as input for the Markov Chain Monte Carlo (MCMC) clustering algorithm. The MCMC chain ran for 100,000 iterations with a burn-in of 100,000 and a thinning interval of 1000 (Malinsky, n.d.). Third, we used TESS3 (Caye et al., 2016), which is useful in determining genetic barriers or genetic discontinuities in continuous populations, to incorporate spatial information to inform individual ancestry estimates. For each value of K, 100 independent runs were performed with a tolerance of 10^{-6} and 20 iterations per run. The most likely value of K corresponded to the minimum of the cross-entropy criterion, across the range $K = 1$–15. Additionally, we calculated F_{ST} (Weir & Cockerham, 1984) between kipukas with vcftools (Danecek et al., 2011).

Genetic diversity

We calculated the percent polymorphic sites as well as genetic diversity (observed heterozygosity [H_O], expected heterozygosity [H_E], nucleotide diversity [π] and F_{IS}) per population from variant and all positions using STACKS v2.2 (Rochette et al., 2019).

RESULTS

Quality of RAD genotyping

A total of 537,724,472 (268,862,236 PE) reads were obtained following the sequencing of 84 individuals (Table S1). After using the

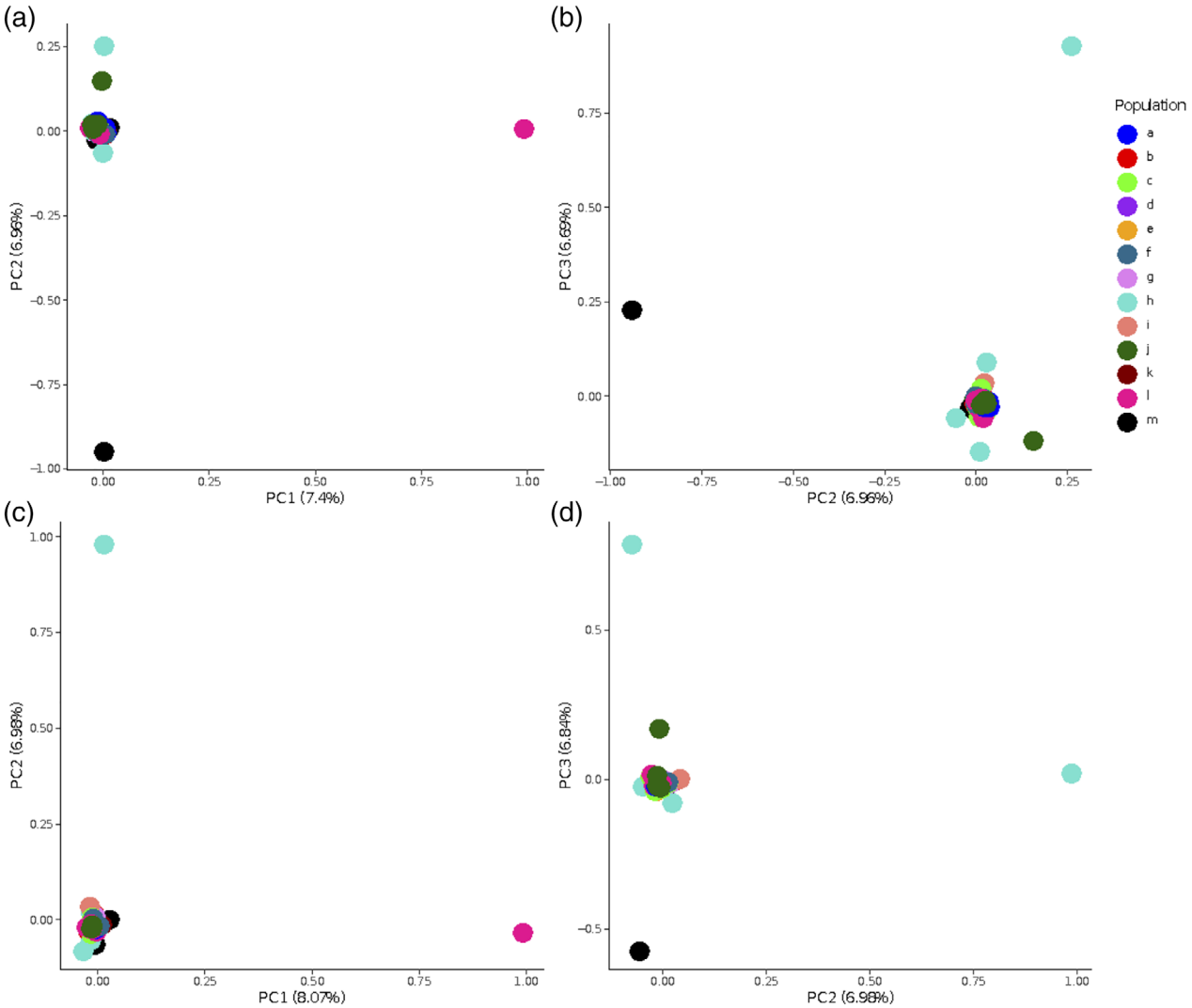

FIGURE 2 Principal components analysis (PCA) between populations for data with loci genotyped in 50% of all individuals (a,b) and genotyped in 90% of all individuals (c,d). (a,c) Principal components analysis with the first two axes plotted; (b) and (d) PCA of axis 2 and 3

Stacks 'clone_filter' unit to remove low-quality reads, ambiguous barcodes, and overrepresented sequences, 405,957,342 reads remained.

A catalogue containing 7,341,938 pre-filtered loci was created for all individuals.

For each individual, an average number of 112,256.2 ± 64,544.8 unfiltered loci were assembled with an average read depth of 7.4 ± 0.3 per stack. Due to a low read count, one individual was discarded. This resulted in 83 retained individuals, an average of 6.38 individuals per locality, with the number of reads per individual ranging from 127,600 to 3,773,676 (average per individual = 1,258,772.9).

Filtering at 50% and 90% missing genotypes produced a final dataset containing 11,206 SNPs and 2115 SNPs, respectively, distributed across the 83 individuals. This resulted in a mean depth per individual of 24.7 and 54.7 respectively and a mean missing per individual of 40.9% and 10.5%.

Population structure

The PCA did not reveal clustering based on the geographic location of the samples (Figure 2). One individual from kipuka 'l' (S67) was separated on PC1 (7.40% explained variation) from a large cluster of individuals and an individual from kipuka 'm' was separated from that larger cluster on PC2 (6.97% explained variation). Another individual from kipuka 'h' was separated on PC3 (6.69% explained variation). After removing individuals with high missingness (S53 from population 'h' and S67 from population 'l'), the resulting PCA was not more informative nor did the main result change (Figure S1). Using FINERADSTRUCTURE, we visualised the patterns of haplotype similarity (Figure 3). The structure provided by the FINERADSTRUCTURE analysis mostly corroborated the results of the PCA analysis in that there is little clustering based on geographic location. Individual S67, from kipuka 'l', has very low relatedness to all other individuals, which is also reflected in the PCA. In order to

determine genetic barriers or genetic discontinuities in continuous populations TESS3 was used (Figure 4) and the cross-validation criterion did not exhibit a clear plateau or a change in curvature without a wide variance in error. This indicates that there is no support for a best value of *K* from the TESS3 analysis (Caye et al., 2016; François & Durand, 2017). Considering all *K* values with a biologically meaningful interpretation is recommended (Meirmans, 2015) due to the large degree of uncertainty in determining the optimal value of *K* (Evanno et al., 2005; Pritchard et al., 2000) and different values of *K* may reflect different demographic processes. Up to seven clusters would be biologically plausible. Pairwise F_{ST} values range from −0.108 to 0.018 (Table 2).

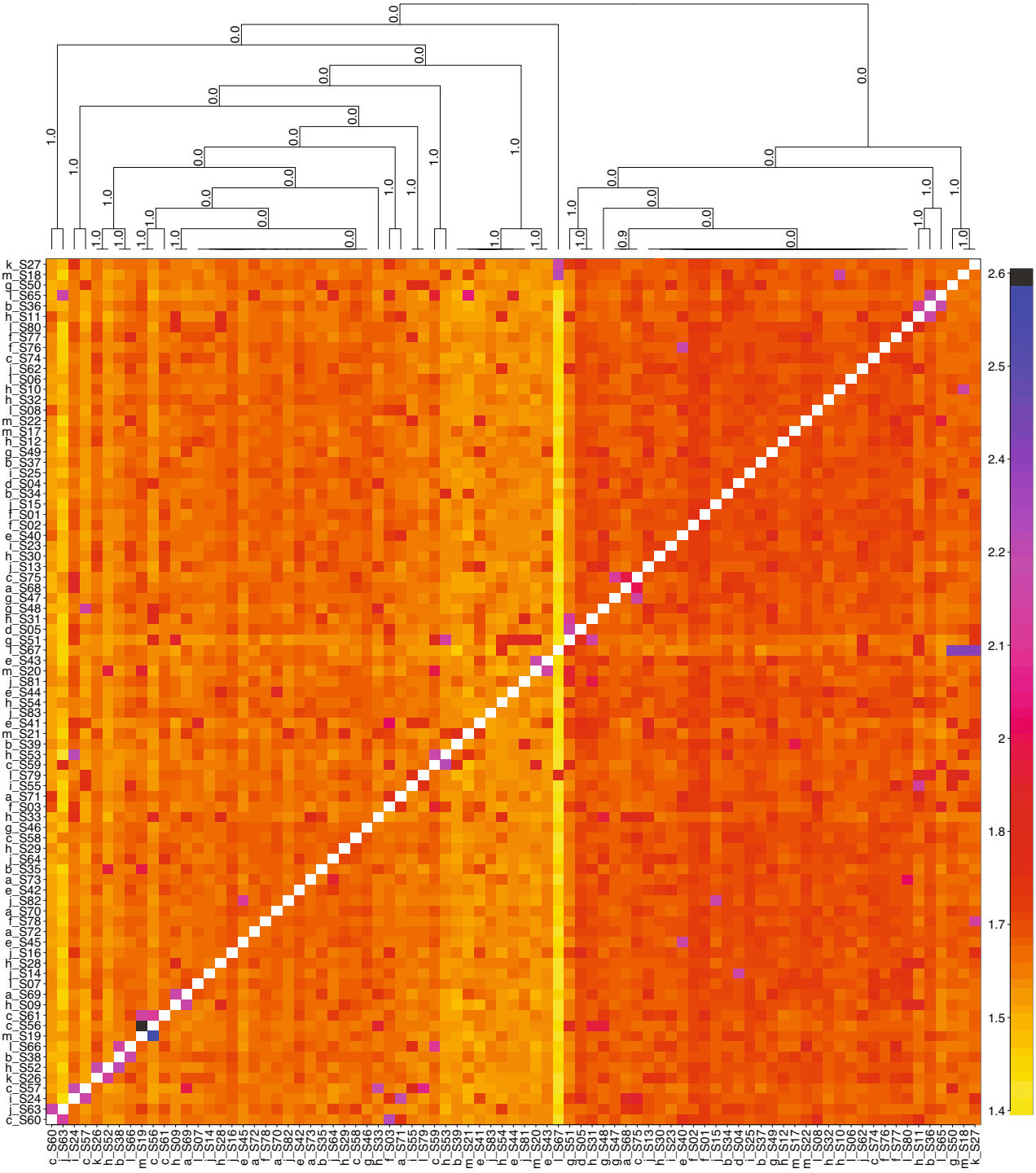

FIGURE 3 The co-ancestry matrix from the FINERADSTRUCTURE analysis based on the dataset of 2115 SNPs shows the patterns of haplotype similarity. Colours indicate the degree of relatedness between individuals, with yellow being low relatedness and black indicating high relatedness. Sampling sites do not show visible structuring

Genetic diversity

No evidence of inbreeding in *M. celer* at CRMO was found and all of the genetic diversity metrics were generally similar across all sampled kipukas. Even the most geographically distant populations within the lava flow matrix ('b' and 'h'), which are nearly 30 km apart, had an F_{ST} value of −0.0017846 (See Figure 1 and Table 2). The population pairs with the highest differences were between d and f (0.031964). The lowest differences were between population pairs 'k' and 'h' (−0.10759), however, many of the population pairs have negative F_{ST} values, which indicate that there is no detectable genetic variation between the populations and could be due to uneven sample sizes between kipukas (Weir & Cockerham, 1984).

As seen in Table 1, the percent of polymorphic sites per population ranged from 3.948 (kipuka 'k') to 26.5144 (kipuka 'h') with an average of 13.3426. With all positions, the observed heterozygosity at the population level ranged from 0.1256 (kipuka 'h') to 0.6076 (kipuka 'k') with an average of 0.2759; the expected heterozygosity for each population

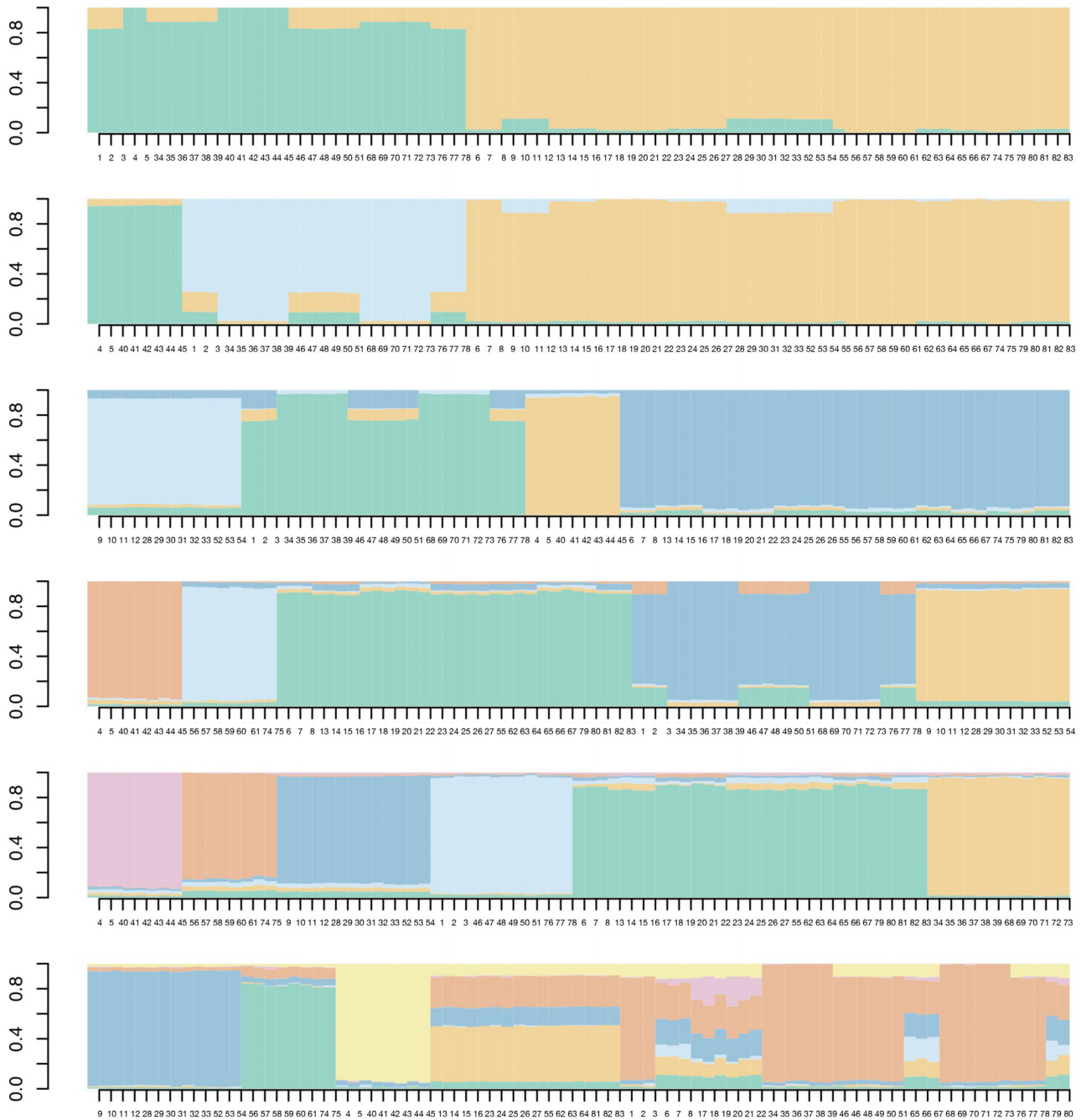

FIGURE 4 Individual ancestry at $K = 2$ through $K = 7$ as determined from TESS3 analysis. Each bar plot represents a unique individual and the *y*-axis represents the proportional membership of each individual to a given cluster. Due to the panmictic nature of the data, individuals change positions on each value of *K*

ranged from 0.1144 (kipuka 'h') to 0.4019 (kipuka 'k') with an average of 0.2225; the nucleotide diversity for each population ranged from 0.1198 (kipuka 'h') to 0.5485 (kipuka 'k') with an average of 0.2624; and the inbreeding coefficient in each population ranged from −0.0886 (kipuka 'k') to −0.0128 (kipuka 'm') with an average of −0.0264. When considering all nucleotide positions, the observed heterozygosity dropped to 0.0238 (kipuka 'd') and to 0.0351 (kipuka 'l'); the expected heterozygosity decreased to 0.0159 (kipuka 'k') and to 0.031 (kipuka 'l'); the nucleotide diversity ranged from 0.0217 (kipuka 'k') to 0.0335 (kipuka 'l'); and the inbreeding coefficient within each population ranged from −0.0055 (kipuka 'j') to 0.0008 (kipuka 'd').

Overall, when looking at variant sites only, kipuka 'h' had the lowest diversity (H_O: 0.1256; H_E: 0.1144; π: 0.1198) and kipuka 'k' had the highest diversity (H_O: 0.6076; H_E: 0.4019; π: 0.5485) (see Figure 1 and Table 1). However, sampling bias may have skewed these statistics given that these two populations had the minimum and the maximum number of individuals (and percent polymorphic sites) per population with kipuka 'k' having 2 individuals and kipuka 'h' having 13 individuals.

DISCUSSION

Contrary to what we expected, we find panmixia in this species of crab spider at CRMO. Three independent tests; PCA, FINERADSTRUCTURE, and TESS3, all with differing assumptions, indicate little genetic structure in the population based on geographic location. Of the pairwise F_{ST} indices for *M. celer*, which represent each kipuka we sampled, all were <0.02, further suggesting panmixia. This suggests that despite the geographic distance between distant sampling sites separated by lava flows, gene flow is occurring between populations within the lava field or there is connectivity to outer regions surrounding the lava flows. Therefore, the dispersal of these crab spiders is not currently negatively impacted by the fragmented structure of the landscape at CRMO by the most recent lava flows from approximately 2000 years ago. Thus, compared to a similar study on the population structure of Hawaiian spiders in a lava fragmented forest system, the genetic structure of *M. celer* is more similar to a generalist species (like *T. quasimodo*) than to a specialist species despite the habitat preferences of *M. celer* (Vandergast & Gillespie, 2004). Additionally, although not tested here, the landscape at CRMO could allow for movement of *M. celer* from the area surrounding the monument into the kipuka and lava matrix as well as movement within the monument between the kipukas and lava flows.

The finding of panmixia in *M. celer* could reflect the annual occurrence of long dispersal distances in juvenile stages (spiderlings) that occur immediately following emergence (Gertsch, 1939; Schmalhofer, 2011). After emergence from their egg sacs, spiderlings engage in passive dispersal and use of draglines, sometimes using multiple ballooning events and/or draglines (Homann, 1934). Each spiderling releases a silk thread until the wind picks up the spider and carries it away (Edwards, 1986). This ability to disperse by ballooning allows spiders to travel by wind to different habitats. Additionally, spiders have the ability to reinitiate ballooning if a habitat is encountered that does not have a suitable 'microhabitat' (Riechert & Gillespie, 1986). However, ballooning at CRMO could be costly as the chance of landing in unsuitable habitat is large compared to the relative size of the more suitable habitat within the kipukas. Further, as the prevailing wind at CRMO is primarily from the southwest and long-range dispersal would be unidirectional, our finding of little to no population structure between even the furthest kipukas in the north–south spatial arrangement may suggest that movement between kipukas is a rarer event than expected. The data suggest that movement between the kipukas seems to be occurring in a bidirectional manner, where short-range dispersal events occur in northern and southern directions. The spiders in the kipukas may instead be dispersing via very localised air movements when microclimatic factors are right (e.g., in times of low to no wind), rather than during sustained high wind. Arthropods, including spiders, use various cues to initiate dispersals such as wind, humidity, and light conditions (Richardson & Johnston, 1975; Suter, 2018). Previous work that quantified dispersal for 20 thomisid spiderlings found ballooning distances to be 2.7 m ± 2.3 m, highlighting that ballooning may function at a small local scale, as well as regional (Morse, 1993). This type of dispersal on a more localised scale due to microclimatic factors may better explain the low genetic structure observed, as *M. celer* moves north or south between nearby kipukas instead of being blown in a northeasterly direction.

M. celer females reach sexual maturity between June and August and after copulation lay 145 eggs on average that hatch approximately 3 weeks later (Fritz et al., 1985; Muniappan & Chada, 1970). Therefore, the overall dispersal cost could be offset as there is a likelihood that some spiderlings would end up in a favourable habitat by dispersing, have increased access to new resources, and reduced competition from conspecifics (Dean & Sterling, 1985; Simonneau et al., 2016). Furthermore, ballooning also reduces the chance of cannibalism between brood mates (Sheldon et al., 2017; Weyman, 1993) and the dispersal of individuals away from related offspring reduces the negative genetic consequences of inbreeding. Given that these spiders have the ability to use ballooning to disperse long distances and high fecundity to offset any loss due to ballooning into an unfavourable habitat, the observed panmixia could be explained by high rates of gene flow observed across the sampled locations that are separated by 2000-year-old lava flows.

High rates of gene flow have been observed in other arthropods. For example, a study of five Andean dung beetle species found panmixia (Linck et al., 2020), which may be in part due to the use of a common resource of dung that becomes a point of gene flow between different populations of each species when the dung is visited at the same point in time. At CRMO, the kipukas may be acting as a common resource for *M. celer* as they contain abundant vegetation and common habitat for copulation. This facilitates gene flow between the kipukas leading to panmixia of the population as there is also a selection on dispersal post-hatching to avoid cannibalism. This movement of individuals would increase gene flow. However, the use of a common resource does not necessarily lead to the panmixia of a species. In a study of two pine-feeding butterflies (Halbritter

et al., 2019), although both species rely on pine species for larval feeding, one species was found to be panmictic while the other showed strong evidence for population structure. The availability of certain vegetation may restrict movement in the adults of these species more so in one species, thereby showing population structure (*Neophasia terlooii*), than another panmictic species (*Neophasia menapia*) (Halbritter et al., 2019). In both examples mentioned, the dung beetles and butterflies are actively searching for a shared resource, unlike the crab spiders which participate in passive ballooning. However, in all cases a common resource is utilised in the habitat and dispersal limitations exist, leading to at times different observed patterns of population structure. The restriction of movement of a species is dependent on a combination of dispersal ability, resource use, and the characteristic(s) of their habitat matrix.

Reduced movement in fragmented habitats could lead to decreases in the effective population size within each fragment and ultimately impact the stability of each population in the future (Dixo et al., 2009). Although it is unknown whether the kipukas at CRMO were continuously occupied or re-colonised, or if a mixture of both occurred after an eruptive period, it is likely that kipukas remained continuously occupied as seen in kipukas in Hawaii and on Barro Colorado Island (Carson et al., 1990; Curtis et al., 2021). In that case, if populations were sampled after several generations following an eruptive period, we might expect to observe population structure due to a bottleneck as movement is restricted and rare alleles are removed due to drift. Over time, those populations may remain small if dispersal remains restricted or, as in the case of *M. celer*, gene flow in subsequent generations occurred possibly through ballooning and reduced genetic structure. Therefore, not all fragmentation, natural or anthropogenic, may cause a reduction in gene flow and an increase in population structure; however, this may be dependent upon a combination of a species' ability to disperse at different life stages, changes in resource availability, hospitability of the matrix, and/or length of time since fragmentation.

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CONFLICT OF INTEREST

All authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Figure S1. Principal Components Analysis (PCA) between populations for data with loci genotyped in 90% of individuals excluding two individuals (S53 from population 'h' and S67 from population 'l'), A) PCA with the first two axes plotted; B) PCA of axis 2 and 3.

Table S1. Data per specimen including the population, sample name, number of legs removed for DNA extraction, and total yield of DNA collected (μg).

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