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A story of vicariance? how the geology of oceanic archipelagos influenced the evolutionary history of endemic damselflies

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ABSTRACT

South Pacific islands provide an ideal study system to explore patterns of speciation, specifically examining the role of dispersal versus vicariance. Dispersal is often the suggested mechanism of diversification in the South Pacific, specifically among remote island chains. Here, we provide a phylogeny of several related genera of Coenagrionidae (Odonata: Zygoptera) from the South Pacific, based on five molecular loci, in order to examine patterns of speciation in the region. We used the endemic damselfly genera *Nesobasis, Nikoulabasis,* and *Vanuatubasis* found across both Fiji and Vanuatu. Knowledge of the geologic history of the region was used to inform our understanding of the evolution of these genera. Both archipelagos used to be part of the Vitiaz arc which spanned from the Solomon Islands to Tonga and began to break apart 10–12 Ma. Results of our divergence-time estimations and biogeographic reconstructions support that the breakup of this arc acted as a significant vicariance event in the evolution of these taxa. Specifically, it led to the extant generic diversity seen in these damselflies. We find that within the archipelago of Vanuatu, that Espiritu Santo served as an important source for dispersal to other islands with Malekula acting as a stepping stone to Efate.

1. Introduction

1.1. Island biogeography

Despite numerous studies examining biogeographical patterns, there remains great debate on which mechanisms of speciation (e.g., dispersal or vicariance) play a more prominent role in extant species distributions (Zink et al., 2000; Yoder and Nowak, 2006; Waters et al., 2013). Historically, the South Pacific has played an important role in this debate (MacArthur and Wilson, 1967). The South Pacific is an ideal region to test hypotheses of dispersal and vicariance due to its array of isolated island systems, proximity to both Australian and Asian fauna, and complex geologic histories (Keppel et al., 2009).

Long-distance dispersal is a commonly proposed mechanism for fauna on isolated islands in the South Pacific (Swenson et al. 2019; Tsang et al., 2020). Under this hypothesis, a larger land mass (i.e., Australia or Southeast Asia) acts as a source population with oceanic islands having lessening diversity the further away from the faunal source they are (MacArthur and Wilson, 1967; Whittaker et al., 2008; Valente et al., 2020). Mechanisms of long-distance dispersal include island-hopping (Toussaint and Balke, 2016), rafting (Vidal et al., 2008), birds (Harbaugh and Baldwin, 2007), and wind (Gillespie et al., 2012). An alternative hypothesis proposed for the faunal origin on these oceanic islands is metapopulation vicariance (Heads, 2014; 2018). This hypothesis suggests that organisms have persisted in distinct sub-populations separated by small, but passable barriers (e.g., islands in archipelagos) (Heads, 2014). In metapopulation vicariance, older fauna can persist on younger islands as the land masses go through periods of submergence and re-emergence (Heads, 2018). Notably, lineages that underwent metapopulation vicariance may have inaccurate ages reported if landmass ages are used as calibration points in divergence time estimation (see Heads, 2011). These lineages are also expected not to follow the progression rule in which the order of colonization coincides with island age (Swenson et al., 2019).

1.2. Challenges with divergence time estimation in island systems

The ages of faunal clades can provide critical insight into this debate between dispersal and vicariance. However, determining ages of clades in the South Pacific can be challenging due to the lack of proper

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calibration points (Seidel et al., 2021), a challenge exacerbated in small-range endemics. Previous studies using island systems have attempted to circumvent the lack of fossil calibration points by using geologic calibration points such as the age of island re-emergence (Jordan et al., 2003; Beatty et al., 2017). However, caution must be taken when using this approach as the age of some lineages predates that of the land mass they are found on (Heads, 2011). This is especially true on oceanic ridges or arcs whose islands have gone through multiple periods of submersion and re-emersion. One approach to overcoming this problem is to employ multiple dating strategies using a combination of fossils, molecular clocks, and landmass ages to calibrate the phylogeny (Seidel et al., 2021). In addition, treating the ages of landmasses as normal distributions rather than hard minimums can lessen the potential of underestimating clade ages (Forest, 2009; Beatty et al., 2017). Using these approaches, one can minimize and assess how the age of the island may be impacting the resulting clade ages.

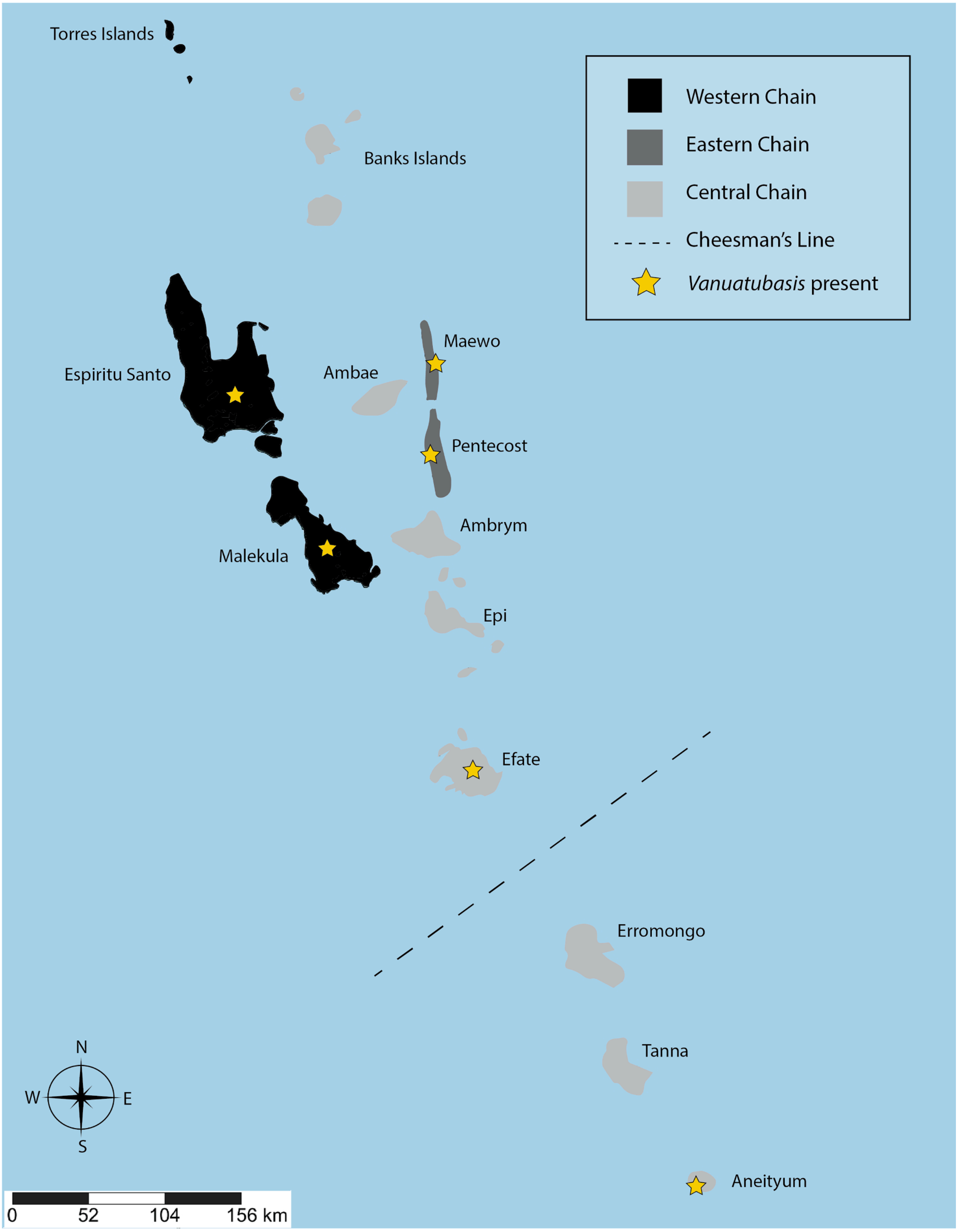

Fig. 1. Map of Vanuatu showing geologic island chains which correspond to island age. Map modified from SimpleMappr (Shorthouse, 2010). Western chain, ~ 33 mya; Eastern chain, ~ 11 mya; Central chain, ~ 5 mya.

1.3. *Vanuatu and the Vitiaz arc*

Island systems that were once part of oceanic arcs provide an intriguing situation for potential vicariance events in the South Pacific. One such arc is the Vitiaz arc which once spanned from the Solomon Islands to Tonga encompassing parts of both Fiji and Vanuatu (Crawford et al., 2003). Heads (2014) suggested that the breakup of this arc into its respective island systems could have led to important vicariance events for the region. Alternatively, the fauna of this archipelago could have originated from more recent dispersal events after the breakup of this arc. Due to Vanuatu's position in the middle of this oceanic arc, fauna on this archipelago may provide a critical piece in our understanding of the impact the Vitiaz arc breakup had on current faunal distributions.

Vanuatu remains a less studied group of islands and is often poorly represented in biogeographical analyses (Lucky and Sarnat, 2010; Bank et al., 2021). The country is made up of islands formed by oceanic volcanoes along the subduction zone where the Australian plate meets the Pacific plate (Mallick, 1975; Meffre and Crawford, 2001). The archipelago of Vanuatu has existed in some form since the mid to late Eocene (Carney et al. 1985; Crawford et al., 2003), and currently exposed islands are estimated to have formed in three periods corresponding to three major island groups (Fig. 1) (Greene et al. 1994). The western chain is the oldest set of islands composed of Espiritu Santo and Malekula. This chain was formed in the late Oligocene to middle Miocene (~11–33 mya) and has the largest island area in comparison to the more recently formed island groups (Greene et al. 1994). North of Espiritu Santo lies the Torres Islands, considered part of the western chain, that have recovered a slightly older age of 39 mya (Mitchell and Warden, 1971). The eastern chain was formed in the late Miocene to lower Pliocene (~4–11 mya) (Greene et al. 1994), around the same time Vanuatu likely separated from Fiji, and comprises Maewo and Pentecost. Vanuatu broke from Fiji around 10–12 mya, drifting southwest from its original, forming what is now the North Fiji basin (Meffre and Crawford, 2001; Martin, 2013). Finally, the central chain was formed as early as the late Pliocene (~5 mya) composing the central island of Banks Is., Epi, Ambae, Efate, Erromongo, Tanna and Aneityum (Greene et al. 1994). Active aerial volcanoes are restricted to this central chain (Carney et al. 1985).

Due to Vanuatu's former position, it is not surprising that faunistically it shares close affinities with Fiji and the Solomon Islands (Gibbons, 1985; Ingleby and Colgan 2003; Murienne et al., 2011). There are, however, hypotheses of recent dispersal events such as those from New Caledonia (Hamilton et al. 2010; Toussaint et al. 2015; Toussaint and Balke, 2016). Individual islands have also undergone periods of submersion and re-emergence throughout the region's history (Macfarlane et al. 1988). Interestingly, Hamilton et al. (2010) proposed a faunal and floral break termed "Cheesman's line", located just south of Efate splitting the northern islands from the southern islands (Fig. 1). Data supporting this break is found among reptiles, insects, birds, and many plants (Cheesman, 1957; Ackery et al. 1989; Goldberg et al. 2014). However, as sampling has been limited in this region (particularly for insects) with most of the sampling occurring on the Northern islands, more work is needed to evaluate the validity of this faunal break.

1.4. *South Pacific damselflies*

In order to investigate biogeographical patterns of colonization within Vanuatu, and the broader role of Vanuatu in South Pacific biogeography, we use an endemic group of damselflies found across this island chain. *Vanuatubasis* Ober and Staniczek, 2009 is composed of ten species (Ober and Staniczek, 2009; Saxton et al. 2022) and displays high levels of endemism (Saxton et al. 2020). Endemism is a pattern that appears across both Vanuatu and Fiji (Liebherr, 2005; Beatty et al. 2007). Members of this genus appear to inhabit a very narrow ecological niche and is almost exclusively found on alkaline streams (Saxton et al. 2021). Previous work found that *Vanuatubasis* rendered the endemic Fijian *Nesobasis* Selys, 1891 damselflies paraphyletic leading to the introduction of *Nikoulabasis* (Ferguson et al.2023). *Nesobasis* and the *Nikoulabasis* Ferguson et al. 2023 are damselfly genera only found on the Fijian islands, and work exploring their biogeography was completed in Beatty et al. (2017).

Here, we reconstruct a phylogeny for the genus *Vanuatubasis* in the context of its two sister genera and subsequently perform divergence-time estimation using this topology in order to examine the role of dispersal and vicariance in the evolutionary history of this genus.

Specifically, we examine ***1)*** *the effect the breakup of the Vitiaz arc had on both species and genus-level divergence,* ***2)*** *whether vicarnce or dispersal resulted in the biogeographical origin of Vanuatubasis* and ***3)*** *the order and direction in which Vanuatubasis colonized the islands of Vanuatu.*

2. Material and methods

2.1. *Taxon sampling*

Specimens of *Nesobasis* and *Nikoulabasis,* as well as several outgroups were gathered from previous studies (Beatty et al., 2017; Lorenzo-Carballa et al., 2019; Rivas-Torres et al., 2021; Ferguson et al. 2023). *Vanuatubasis* sequences were generated from 25 specimens, representing nine of the ten known species (missing *V. rhomboides* Saxton et al. 2022 which is only known from the type and one paratype specimen). Additional sequences for outgroups were generated from *Megalagrion* McLachlan, 1883 and *Pseudagrion* Selys, 1876 specimens in the BYU cryo-collection (Supp. File 1).

2.2. *Molecular methods*

Thoracic muscle tissue was removed from the specimens and DNA extractions were completed using Qaigen's DNeasy blood and tissue kit following the standard protocol with the exception of the last elution step being repeated twice with only half the suggested volume. We amplified five genes using polymerase chain reactions (PCR) with the primers and conditions listed in Beatty et al. (2017) and Lorenzo-Carballa et al. (2019). Three mitochondrial regions were amplified including two regions of cytochrome *c* oxidase I (COI/LCO) and one region of the small rRNA subunit (12S). In addition to two nuclear regions including arginine menthyltransferase (PRMT) and internal transcribed spacer I (ITS1) were included. Successful PCR products were sequenced at Brigham Young University's DNA Sequencing Center. Resulting sequences were examined for quality, trimmed, and aligned in Geneious (Biomatters, https://www.geneious.com) using MAFFT (Katoh & Standley, 2013) before being concatenated for subsequent analyses.

2.3. *Phylogenetic analyses and divergence time estimation*

We used Modelfinder (Kalyaanamoorthy et al., 2017), as implemented in IQ-Tree v.1.6.12 (Nguyen et al., 2015), to identify a best-fit model of molecular evolution. Tree reconstructions were done in IQ-Tree with 1000 ultrafast bootstraps (Hoang et al., 2018). The resulting maximum likelihood tree was adjusted in the R package *ape* using the command "chronopl" (Paradis and Schliep, 2019) such that the heights of the nodes were within the distributions we specified in our divergence time estimation (see below). In order to do this, we specified that node 154 (base of the *Ischnura* clade) was between 13.8 and 30 mya relative to the 15 mya fossil prior. Node 84 (the in-group) was set to be between 9 and 15 mya relative to the age of Viti Levu (12 mya). Lastly, node 150 (*Nikoulabasis,* in part) was set to be between 4 and 10 mya relative to the age of Vanua Levu (7 mya). The resulting tree was used as a fixed topology in our divergence time estimations.

Three different dating strategies were employed using a combination of three different priors (Supp File 1). Model 1 (M1) consisted of using a uniform outgroup fossil calibration (15 Ma hard minimum, 150 Ma hard maximum) in conjunction with soft, normal priors for age of Fijian islands used by Beatty et al. (2017) and a strict clock rate for insect mtDNA (0.0115 substitution per site) (Brower, 1994) was applied only to the mtDNA regions (i.e., COI, LCO 12S) of our alignment. Model 2 (M2) was estimated using a divergence rate for insect mtDNA in conjunction with a uniform fossil calibration (15 Ma hard minimum, 150 Ma soft maximum). Lastly, model 3 (M3) was estimated using only a uniform outgroup fossil calibration with the soft, normal priors for the Fijian islands. Age constraints for fossil priors are based on *Ischnura velenti* (15 Ma) (Bechly, 2000), the oldest known representative of this extant genus, and the crown Zygoptera group Hemiphlebiidae (150 Ma) (Vasilenko, 2005). Characters supporting the placement of *I. velenti* within *Ischnura* include its small size, strongly petiolated wings, the anal vein separating from the wing margin before the CuP-crossing, and the short and few tibial spurs (Bechly, 2000).

Divergence time estimation was completed in BEAST v2.6.6 via the CIPRES Gateway v.3.3 (Miller et al., 2010). Each model was run four times using a combination of clock models on both partitioned datasets and non-partitioned datasets (Relaxed Clock Exponential and Relaxed Clock Log Normal) and tree models (Birth-Death and Yule). All analyses except M3.1 were run with a chain length of 3000000. M3.1 was run with a chain length of 9,000,000 in order for the analysis to converge. Resulting log files were examined in Tracer v.1.7.2 (Rambaut et al., 2018) to ensure convergence (i.e., ESS values > 200). A consensus tree was generated for each analysis with a 10% burn-in.

2.4. Lineage-through-time plot

The resulting dated topology from M3.2 was trimmed using *ape* (Paradis and Schliep 2019) such that each species clade was represented by a single node, and so that only include in-group taxa (i.e., *Nesobasis, Nikoulabasis,* and *Vanuatubasis*) were included. We then generated a lineage-through-time plot based on the phylogeny using the “ltt.plot” function in *phytools* (Revell, 2012).

2.5. Ancestral range reconstructions

Ancestral range reconstructions were performed using the package *BioGeoBEARS* (Matzke, 2013) on the trimmed, dated topology from M3.2. We compared six models (i.e., DEC, DIVAlike, BAYAREAlike) with and without founder event speciation (+j). Models were compared using Akaike Information Criterion (AIC). There has been controversy that models with and without founder speciation cannot be directly compared (Ree and Sanmartin, 2018), but see Matzke (2022) for a rebuttal.

In order to best examine the biogeography of these genera, we ran analyses using two different methods of coding areas. First, to explore the biogeographical origins of *Vanuatubasis,* we coded extant ranges as one of two areas; Vanuatu and Fiji. The maximum extant distribution was set to two based on the number of areas available. Second, to explore the biogeographic patterns within Vanuatu, each species range was coded using distributional data compiled from Beatty et al. (2017), Lorenzo-Carballa et al. (2019), Rivas-Torres et al. (2021) and Saxton et al. (2022). Individual islands were all treated as discrete geographic areas with the exception of Viti Levu and Ovalau being considered one area due to all species on Ovalau also being present on Viti Levu (Lorenzo-Carballa et al., 2019). The maximum number of areas was set to three based on the maximum extant distribution. In order to account for younger islands being unavailable for colonization prior to their origin, we performed an additional set of analyses that were area-restricted with certain islands only being allowed to be occupied after specific periods of time (see Supp. File 2).

3. Results

3.1. Topology

We recovered TIM2 + F + I + G4 as the best fit model of molecular evolution according to the Bayesian Information Criterion. *Vanuatubasis* was recovered as monophyletic with high support (100% bootstrap). Consistent with previous studies (Ferguson et al. 2023), *Nesobasis* was found to be sister to *Vanuatubasis* (85% BS). The clade including *Nesobasis* + *Nikoulabasis* + *Vanuatubasis* was recovered with 100% BS. All of the seven species of *Vanuatubasis* tested for monophyly, the remaining two species were only represented by single specimens. *Vanuatubasis bidens* Kimmins, 1958 is recovered as sister to the rest of the *Vanuatubasis* clade (100% BS), followed by *V. evelynae* Saxton et al. 2022 being sister to the remaining *Vanuatubasis* (100% BS). Two major clades of *Vanuatubasis* were recovered; a clade from Malekula and Efate (100% BS), as well as a clade from Espiritu Santo, Pentecost, and Maewo (97% BS) (Supp File 3).

3.2. Divergence time estimation and lineage-through-time plot

All models recovered similar ages which can be found in Table 1. Model 3 consistently recovered the broadest 95% HPD while Model 1 recovered the narrowest 95% HPD. The median age of the most recent common ancestor of *Nesobasis* + *Nikoulabasis* + *Vanautubasis* was recovered to be 18.04–23.64 Ma depending on the model used. The median age for the MRCA of *Nesobasis* was recovered to be 14.23–19.63 Ma, while *Nikoulabasis* was recovered at 13.05–19.49 Ma. Finally, divergence time estimates found the MCRA of *Vanuatubasis* to be 7.25–10.47 Ma (Fig. 2). The resulting lineage-through-time plot based on the phylogeny recovered in M3.2 can be seen in Fig. 2B. Visual inspection of the graph shows a rapid accumulation of lineages after ~ 9 Ma followed by a plateau at ~ 5 Ma. The resulting slope of this line is 0.17 representing the average rate of accumulation of new lineages over ~ 24 Ma.

3.3. Ancestral range estimation

Results of all biogeographic analyses can be found in Supplementary File 4. Biogeographical analyses using only two areas recovered the DEC model as the best-fit model based on the AIC criteria (Table 2). Coded areas were as follows; (A) Fiji and (B) Vanuatu. The DEC model suggested a vicariance scenario where the crown of *Nesobasis* + *Nikoulabasis* + *Vanautubasis* (node 42) was recovered as (AB) with a 99% probability. The ancestral area of *Nesobasis* (node 73) was recovered as (A) with 100% probability. *Nikoulabasis* (node 44) was also recovered as (A) with 99% probability. Finally, *Vanuatubasis* (node 65) was recovered as (B) with 99% probability. All other analyses using a two area coding method recovered the ancestral area of all three genera as Fiji (A) being most probable, suggesting a dispersal scenario. However, notably DIVALIKE (LnL −6.28) recovered Fiji as the ancestral area for all three genera with a range expansion to Vanuatu (B) that led to subsequent vicariance when *Nikoulabasis* split from *Vanuatubasis* (Node 43) (Fig. 3).

Using the eleven-area coding method, the null model without any area restrictions was a better fit in all cases (Table 3). Coded areas were as follows; (A) Viti Levu / Ovalau, (B) Vanua Levu, (C) Koro, (D) Kadavu, (E) Taveuni, (F) Espiritu Santo, (G) Malekula, (H) Maewo, (I) Pentecost, (J) Efate, and (K) Aneityum. Using the null model, BAYAREALIKE + J was recovered as the best fit (LnL −104.9). In this model, the crown of *Nesobasis* + *Nikoulabasis* + *Vanautubasis* (node 42) was recovered as (BE) with a probability of 76.67%. Similarly, the ancestral area for *Nikoulabasis* (node 44) was recovered as (BE) with a 93.93% probability. The crown of *Nesobasis* (node 73) was reconstructed as 59.83% (B) Vanua Levu. The ancestral area for *Vanutubasis* (node 65) was 45.22% (F) Espiritu Santo and 48.33% (K) Aneityum followed by dispersal events to (G) Malekula, (H) Maewo, and (I) Pentecost. From (G) Malekula island a

Table 1
Results of divergence time estimation of models for each tree and clock combination. Median ages are given above the bracketed 95% HPD.

Model	Tree	Clock	MRCA (*Nesobasis* + *Nikoulabasis* + *Vanuatubasis*)	MRCA *Nesobasis*	MRCA *Nikoulabasis*	MRCA *Vanuatubasis*
Model 1. Fossil calibration with island-age priors						
M1.1	BD	RCE	18.60	15.57	13.05	7.33
			[15.31–22.93]	[12.87–19.49]	[10.65–19.49]	[5.70–9.31]
M1.2	BD	RCLN	18.71	15.66	13.10	7.31
			[15.20–23.03]	[12.48–19.25]	[12.48–19.25]	[5.63–9.28]
M1.3	YU	RCE	18.76	15.73	13.16	7.44
			[15.61–23.26]	[14.45–21.66]	[10.74–16.39]	[7.88–9.50]
M1.4	YU	RCLN	18.75	15.73	13.16	7.44
			[15.61–23.26]	[14.45–21.66]	[10.74–16.39]	[5.88–9.50]
Model 2. Fossil calibration with clock rate for mtDNA						
M2.1	BD	RCE	23.50	19.63	16.49	9.19
			[15.60–53.94]	[12.85–44.96]	[10.88–37.81]	[5.63–21.33]
M2.2	BD	RCLN	22.64	18.89	15.79	8.83
			[15.32–46.52]	[12.71–34.87]	[10.35–32.40]	[5.53–18.08]
M2.3	YU	RCE	23.34	16.35	19.49	9.25
			[15.59–44.65]	[12.92–37.38]	[11.02–31.56]	[5.96–17.83]
M2.4	YU	RCLN	22.81	18.99	15.95	8.97
			[15.57–42.63]	[12.79–35.64]	[10.74–30.02]	[5.81–17.08]
Model 3. Fossil calibration, clock rate for mtDNA, and island-age priors						
M3.1	BD	RCE	19.24	15.02	12.57	10.37
			[12.63–26.46]	[9.47–20.95]	[6.85–19.37]	[5.37–15.62]
M3.2	BD	RCLN	18.04	14.26	12.11	7.25
			[12.79–24.60]	[9.90–19.63]	[7.92–17.41]	[4.04–11.12]
M3.3	YU	RCE	19.15	14.97	12.89	10.47
			[12.78–26.99]	[9.66–21.55]	[7.52–19.87]	[5.44–16.54]
M3.4	YU	RCLN	19.19	15.43	12.77	8.24
			[14.08–25.54]	[12.61–23.27]	[8.65–17.90]	[5.10–12.42]

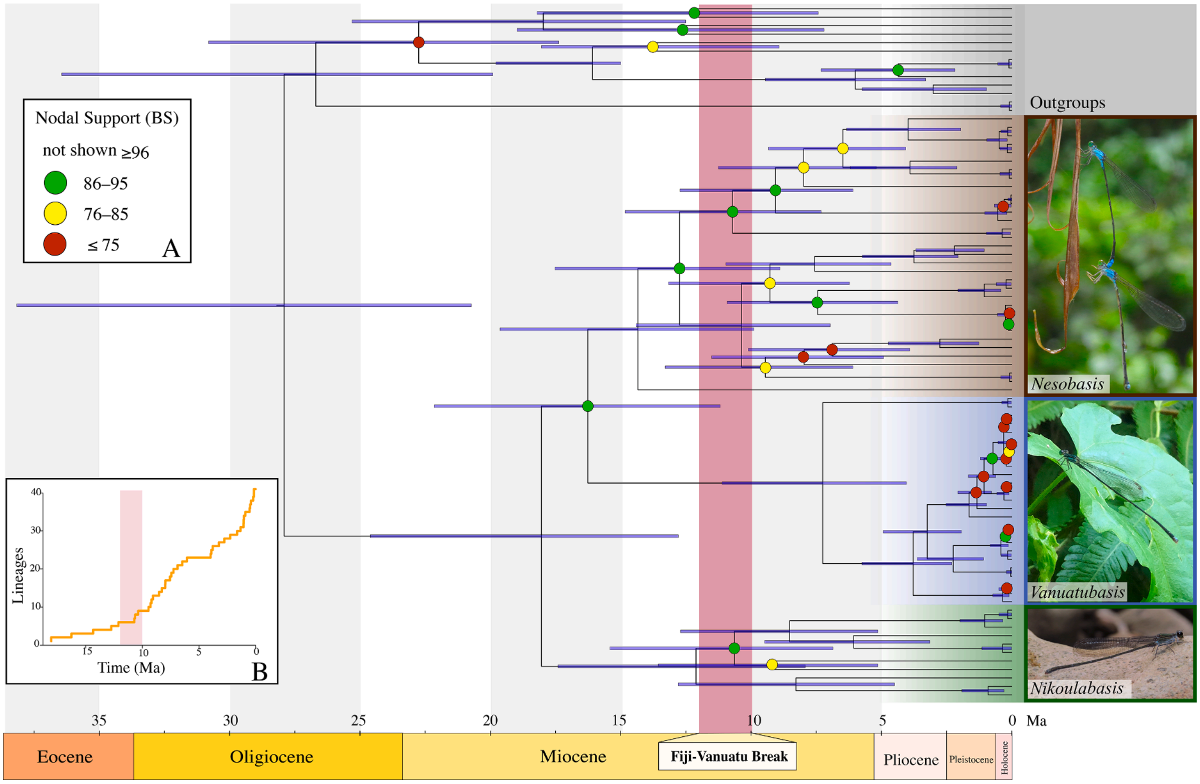

Fig. 2. Results of divergence time estimation based on M3.2; A) Nodal support < 95% BS are shown at nodes; B) lineage-through-time plot of in-group taxa based on ages obtained in M3.2.

subsequent dispersal to (J) Efate was reconstructed.

When area-restrictions based on island age were applied (see Suppl File 2), BAYAREALIKE + J was recovered as the best-fit model (Table 3). In this scenario the the crown of *Nesobasis* + *Nikoulabasis* + *Vanuatubasis* (node 42) was recovered as 62.20% (A) and 24.04% (AF) favoring a dispersal scenario from Fiji's Viti Levu / Ovalau to Vanuatu's Espiritu Santo. The ancestral area of *Nesobasis* (node 73) was recovered as (A) with 89.27% probability. *Nikoulabasis* (node 44) was recovered as (A) with 80.61% probability and (AF) as 12.11% probable. Finally, *Vanuatubasis* (node 65) was recovered as (F) with 56.54% probability and (A) 20.08% probable. Within Vanuatu, (F) Espiritu Santo served as the main island for subsequent dispersals to (G) Malekula, (H) Maewo, (I)

Table 2
BioGeoBEARS analysis results for all models tested using only two areas.

Model	# areas	n	d	e	j	LnL	AIC
DEC	2	2	1.00e-12	1.00e-12	0	−3.58	11.17
DEC + J	2	3	1.00e-12	1.00e-12	1.00e-5	−3.58	13.17
DIVAlike	2	2	3.81e-03	1.00e-12	0	−6.28	16.56
DIVAlike + J	2	3	1.00e-12	1.00e-12	0.013	−4.94	15.88
Bayarealike	2	2	3.85e-03	3.97e-03	0	−9.40	22.8
Bayarealike + J	2	3	1.00e-12	1.00e-07	0.013	−5.34	16.69

Pentecost, and (K) Aneityum. From (G) Malekula island, subsequent dispersal to (J) Efate occurred (Fig. 4).

4. Discussion

The South Pacific islands are produced from continental remnants, coral uplifts, volcanoes, etc. (Neall et al., 2008), making them one of the most interesting and complex biogeographic systems on our planet. Biodiversity on these islands is often both largely endemic and relatively low compared to other tropical regions of the world. This combination provides a tractability and makes South Pacific islands ideal laboratories for biogeography. Yet, relatively little has been done outside of a few island chains (e.g., Jordan et al., 2003), and even less for insects. Additionally, the role of Vanuatu and the Vitiaz arc in current generic and species diversity in the South Pacific has not been deeply examined. Here, we provide the first in-depth look at the colonization patterns within the archipelago of Vanuatu.

4.1. Clade ages

This study represents the most comprehensive phylogeographic history of endemic taxa in Vanuatu. We estimated the age of Vanuatu's endemic damselflies as ~ 7.25 Ma, using all available calibration points. This age predates the formation of the Central Chain but after the origin of the oldest landmasses, the Western Chain. Excluding geologic constraints to calibrate the phylogeny, we recovered a congruent but slightly older (8–9 Ma) age for the crown of the genus. The few studies that have previously provided faunal ages for clades from Vanuatu are largely in disagreement. Liebherr (2005) suggested a Miocene age for ground beetles found in Vanuatu using the geologic estimates for the older islands (22–25 Ma). In contrast, using a standard substitution rate for gastropods, the age of snails in Vanuatu indicated a Pliocene origin (~5 Ma) (Zielske and Haase, 2014). The age for centipedes in Vanuatu was young (~2 Ma), estimated using geologic constraints (Colo orogeny in Fiji), with the Vanuatu taxa nested within a clade of Fijian taxa (Murienne et al., 2011).

The crown age of the clade encompassing *Nesobasis* + *Nikoulabasis* + *Vanuatubasis* was estimated to be older than the breakup of the Vitiaz arc (10–12 Ma; Meffre and Crawford, 2001; Martin, 2013). However, the crown age of *Nikoulabasis* (~12 Ma) and both major clades within the *Nesobasis* (~10 Ma) largely coincide with this fragmenting arc. Results of the lineage-through-time plot illustrate an increase in the rate of accumulation of lineages shortly after Fiji and Vanuatu separated from one another. These data suggest that the Vitiaz arc played a significant role in the generic-level divergences that we see today–especially in the Fijian damselflies. This finding is consistent with Lucky and Sarnat (2010) who found that ant diversification aligned with the fragmentation of the Vitiaz arc.

4.2. Biogeography of the Vitiaz arc

We performed two different sets of biogeographical analysis based on the number of geographic areas coded. Using our two area models, we recovered an ancestral range for all three genera as (AB), which encompasses both Fiji and Vanuatu. These genera then begin to diverge with *Nesobasis* + *Vanuatubasis* splitting from *Nikoulabasis*. *Nesobasis* + *Vanuatubasis* (node 43, ~16 Ma) remain distributed across the Vitiaz arc while *Nikoulabasis* becomes extinct in the northern region that, once separated, will become Vanuatu. A vicariance event is reconstructed when *Vanuatubasis* diverged from *Nesobasis* (after 16 Ma) with the former retaining its range in the northern portion of the Vitiaz arc (Vanuatu) and the latter in the southern portion (Fiji). Our results are less clear when we consider our 11 area models. Both the null model and the area-restricted model reconstructed dispersal events from Fiji Islands to Vanuatu islands. When we exclude islands not habitable prior to their estimated age (i.e., area-restricted model), the dispersal was reconstructed as Viti Levu / Ovalau to Espiritu Santo. This dispersal event would have taken place some time during the breakup of the Vitiaz arc (after ~ 16 Ma) and likely occurred when the islands were much closer together then they are today.

While including additional areas is beneficial in that it provides more information for the model, it suffers from decreased phylogenetic signal due to fewer lineages sharing the same ancestral areas (Ree and Sanmartin, 2009). This matter is further complicated by the fact that oceanic arcs are known to have formerly habitable islands now submerged in the ocean due to volcanic eruptions, shifting plates, and sea-level changes (Nunn, 2006; Whittaker and Fernández-Palacios, 2007). In some cases, knowledge of these "vanishing" islands are passed down in local oral traditions (Nunn, 2006; 2009). The subsequent geographic extinction from these islands can lead to inaccurate reconstructions of ancestral ranges (Sanmartín and Meseguer, 2016). Because of the dynamic system oceanic islands represent, it is often better to take a broader-scale view and examine biogeographic patterns at the archipelagic scale rather than the island scale (Triantis et al., 2016; Valente et al. 2015). In doing so, we are accounting for the plasticity of island systems and missing data associated with extinct areas. Due to these factors, in addition to our two-area preferred model reconstructing both Fiji and Vanuatu as the ancestral range of the common ancestor for all three genera, we suggest that vicariance is the best explanation for the extant range and diversity of these genera.

4.3. Biogeography of Vanuatu

In order to explore biogeographical patterns within Vanuatu, we reconstructed the biogeography using 11 areas. The weakness of this approach is that it does not account for dynamic island systems that have undergone various periods of emergence and submersion (see above). However, geographic areas need to be adjusted for the scale of questions. By looking at individual islands we increase our resolution to explore questions of individual island colonization while keeping in mind the limitations of the model.

We recovered Espiritu Santo as the ancestral range for *Vanuatubasis* in our area-restricted preferred model (Fig. 4). Espiritu Santo is one of the oldests islands in Vanuatu and has the largest land area (Hadden et al., 2020) making it an unsurprising source for later dispersal events to other parts of the country. Most of the models recovered dispersal from Espiritu Santo to Malekula, Maewo, Pentecost and Aneityum. All of these dispersal events, except for one, occur between reasonably close islands with the exception of Aneityum. From Malekula, an additional dispersal event is predicted to Efate under all the models. The Western chain's Espiritu Santo was colonized first (~7 Ma), followed by dispersal within this chain to Malekula (~1 Ma), next dispersing to to the central chain's Efate (after ~ 1 Ma), and finally to the Eastern chain (~0.4 Ma).

Vanuatubasis bidens on Aneityum, however, appears to represent a much longer dispersal event. The model lacking area-restriction often

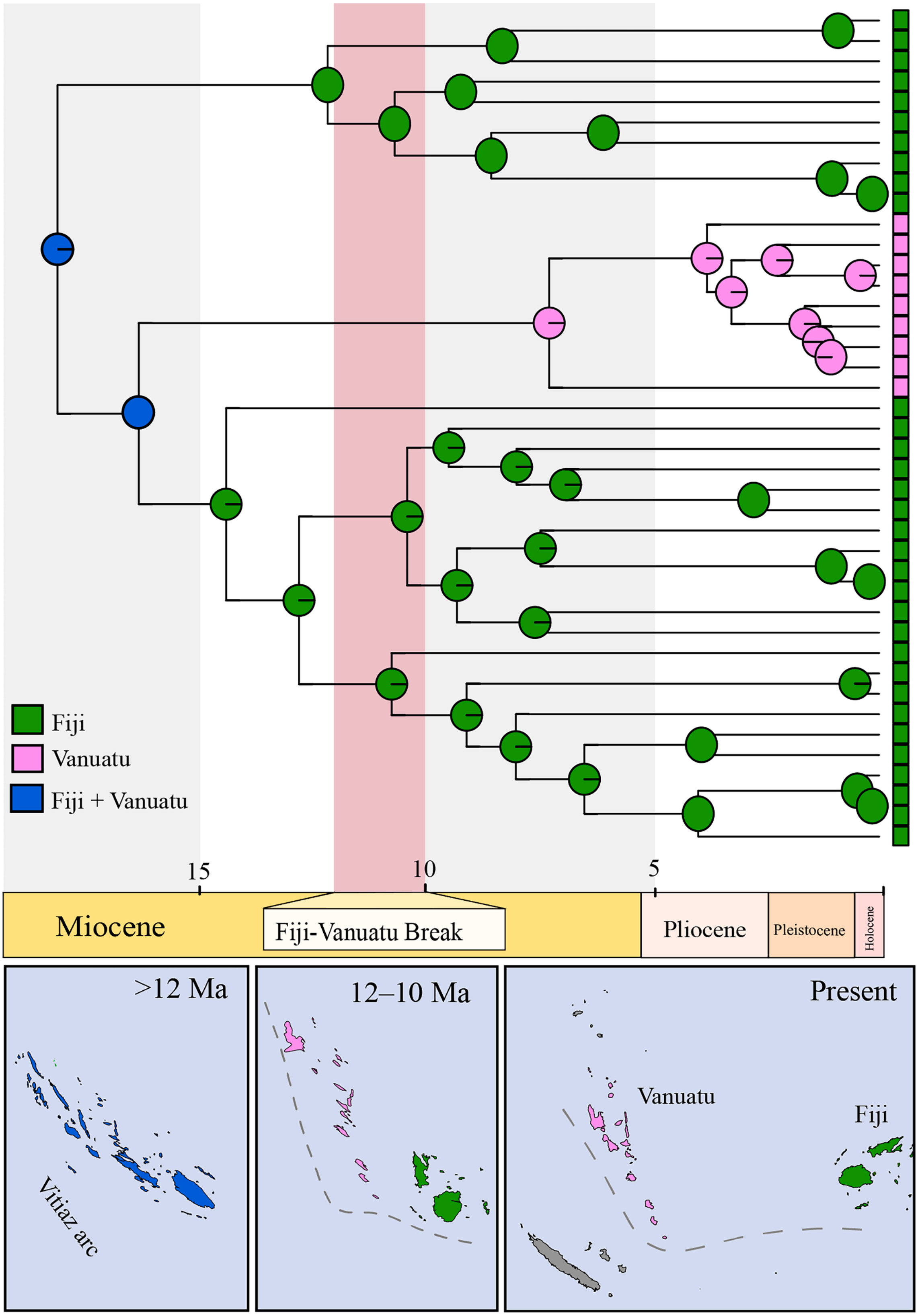

Fig. 3. Results of BioGeoBEARS favored model (DEC) analysis using 2 coded areas.

recovered Aneityum as an equally probable ancestral area for *Vanuatubasis* or recovered the node as both Espiritu Santo and Aneityum (FK). However, geologic evidence suggests Aneityum is younger than the crown age of the genus (Greene et al., 1994). These results are a consequence of *V. biden*'s basal phylogenetic position relative to the rest of the genus. *Vanuatubasis bidens* is also the only species found south of Cheesmen's line, on the Southernmost island, and was noted as having the most unique morphology of the genus (Saxton et al. 2022). Due to

Table 3
BioGeoBEARS analysis results for all models tested using eleven areas both without (Null) and with area-restrictions based on the estimated ages of islands.

Model	# areas	n	d	e	j	LnL	AIC
Null							
DEC	11	2	7.59e-03	1.00e-12	0	−117.69	239.4
DEC + J	11	3	5.10e-03	1.00e-12	0.0203	−110.84	241.4
DIVAlike	11	2	8.95e-03	1.00e-12	0	−118.19	240.4
DIVAlike + J	11	3	5.80e-03	1.00e-12	0.0168	−112.46	242.4
Bayarealike	11	2	0.01	0.01	0	−164.52	333
Bayarealike + J	11	3	0.0021	0.0071	0.0281	−104.90	215.8
Area-restricted							
DEC	11	2	0.0184	0.0594	0	−151.95	307.9
DEC + J	11	3	0.0151	0.0150	0.0169	−149.15	304.3
DIVAlike	11	2	0.0194	0.0577	0	−152.30	308.6
DIVAlike + J	11	3	0.0160	0.0490	0.0143	−150.33	306.7
Bayarealike	11	2	0.0198	0.1093	0	−163.15	330.3
Bayarealike + J	11	3	0.0130	0.0540	0.0217	−148.88	303.8

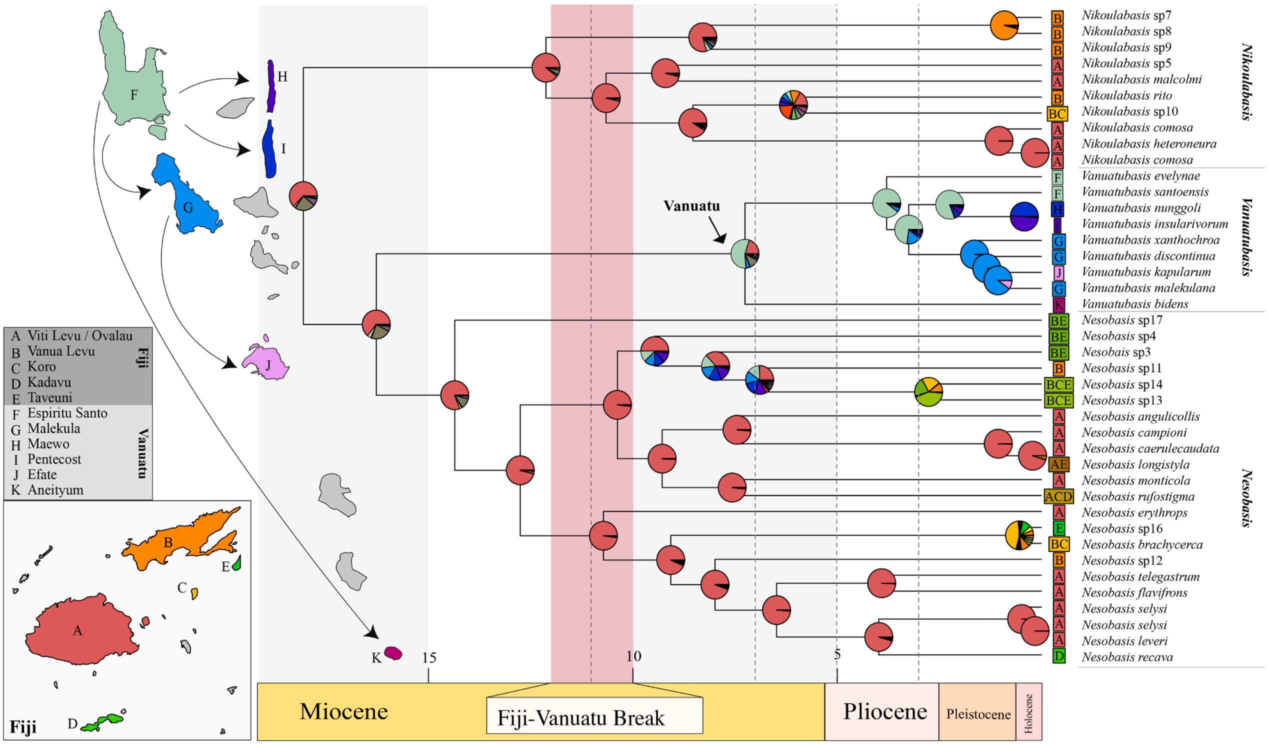

Fig. 4. Results of BioGeoBEARS favored model (BAYAREALIKE + J) analysis using 11 coded areas and area-restrictions imposed based on time. Dashed lines indicate time slices used to constrain the model.

these factors, we explored the small probability (~20%) indicated in our favored, time-constrained model that the ancestral area for *Vanuatubasis* is the Fijian islands of Viti Levu / Ovalau. This result would suggest that there were two independent dispersal events to Vanuatu *after* the breakup of the Vitiaz arc. Other explanations of this pattern include considering extinct or undiscovered lineages that inhabited other southern islands such as Tanna and Erromongo. Although it should be noted that extensive fieldwork on those islands, particularly Tanna, failed to recover any specimens (Saxton et al. 2021). It is also possible that damselflies have occasionally dispersed between Espiritu Santo and southern islands but only persisted in Aneityum.

5. Conclusions

In this study we were able to explore biogeographical patterns in the South Pacific using three endemic damselfly genera with a specific focus on those patterns within Vanuatu. We found that the Vitiaz arc likely played an important role in the divergence of these genera. The origin of *Vanuatubasis* appears to be due to a vicariance event during the breakup of the Vitiaz arc that split the southern portion of the arc from the northern portion. Within Vanuatu, Espiritu Santo acted as an important source for dispersal events to the rest of the archipelago with some island hopping occurring from here to the Central chain's island of Efate. We note that extinct or undiscovered species, in addition to extinct geographical areas (i.e., sunken islands), likely impact the results of our biogeographical constructions.

CRediT authorship contribution statement

Natalie A. Saxton: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization, Validation. **Gareth S. Powell:** Conceptualization, Methodology, Writing – review & editing, Validation. **Seth M. Bybee:** Conceptualization, Writing – review & editing, Funding acquisition, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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***Data** Accessibility*

All genetic sequences are available on GenBank. All additional data is available in the supplementary files that accompany this study.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107831.

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