Elevational and Oceanic Barriers Shape the Distribution, Dispersal and Diversity of Aotearoa's Kapokapowai (*Uropetala*) Dragonflies

Authors: Ethan R. Tolman*[1,2], Chris D. Beatty*[2,3], Aaron Goodman*[2,4,], Priscilla Ramchand*[2,5], Tara McAllister[6], Kelly Reyes[7], Akifa Zahara[7], Kassandra Taveras[7], Vincent Wade[7], John Abbott[8], Seth Bybee[9], Paul B. Frandsen[10], Robert Guralnick[11], Manpreet K. Kohli[1,12], Jessica Ware[†2], Anton Suvorov[†1]
*Equal contributing authors to the manuscript
[†]Senior authors
[1]Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia
[2]Division of Invertebrate Zoology, American Museum of Natural History, New York, New York
[3]Program for Conservation Genomics, Department of Biology, Stanford University, Stanford, California
[4]The Graduate Center, The City University of New York, New York, New York
[5] Brooklyn College, The City University of New York, Brooklyn, New York
[6]Te Wānanga o Aotearoa, New Zealand
[7]Science Research Mentorship Program, American Museum of Natural History, New York, New York
[8]Alabama Museum of Natural History and Department of Research and Collections, The University of Alabama, Tuscaloosa, Alabama
[9]Department of Biology, Brigham Young University, Provo, Utah
[10]Department of Plant and Wildlife Sciences, Brigham Young University, Provo, Utah
[11]Florida Museum of Natural History, University of Florida, Gainesville, Florida
[12]Department of Natural Sciences, Baruch College, New York, New York

Author Contributions

Ethan R. Tolman: Data acquisition, data analysis, funding, writing, editing.
Chris D. Beatty: Data acquisition, data analysis, writing, editing.
Aaron Goodman: Data acquisition, data analysis, writing, editing.
Priscilla Ramchand: Data acquisition, data analysis, funding, writing, editing.
Tara McAllister: Writing, editing.
John Abbott: Funding, writing, editing.
Kelly Reyes: Data analysis, writing, editing.
Akifa Zahara: Data analysis, writing, editing.
Kassandra Taveras: Data acquisition, data analysis, writing, editing.
Vincent Wade: Data acquisition, data analysis, writing, editing.
Paul B. Frandsen: Funding, writing, editing.
Robert Guralnick: Funding, writing, editing.
Seth Bybee: Funding, writing, editing.
Manpreet K. Kohli: Writing, editing, supervision.
Jessica Ware: Data acquisition, data analysis, funding, writing, editing, supervision.
Anton Suvorov: Data analysis, writing, editing, supervision.

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Data availability

Filtered vcf files with and without *P. raptor*, and log and xml files from the BEAST2 runs have been uploaded to figshare (10.6084/m9.figshare.27896910). The Raw reads have been uploaded to the sequencing read archive (bioproject PRJNA1190089).

Conflict of Interests Statement

The authors declare no conflicts of interest.

Abstract

Mountains and islands are both model systems for studying the biogeography of diversification and population fragmentation. Aotearoa is an excellent location to study both phenomena due to alpine emergence and oceanic separation. While it would be expected that separation across Te Moana o Raukawa and elevation gradients are major barriers to gene flow in aquatic insects, such hypotheses have not been thoroughly explored in these taxa. Here, we show that mountains and oceanic separation function as semi-permeable barriers for Kapokapowai dragonflies. We show that, although Te Moana o Raukawa, is likely responsible for some of the genetic structure observed, speciation has not yet occurred in populations separated by the strait. Although there is no evidence that they are an impervious barrier, Kā Tiritiri-o-te-Moana do represent a major barrier to gene flow between named species. The distribution of alpine Kapokapowai can also not be explained by the ancestral populations simply rising with the uplifted tectonic plates. Although further research is needed, our findings suggest that the ancestral Kapokapowai colonized alpine habitats after their formation, and then radiated back out to lowlands. These findings suggest that aquatic insects could be an exciting new frontier in the study of the biogeography of Aotearoa.

Keywords

Anisoptera, Epiprocta, biogeography, population genomics, Petaluridae, Islands, Odonata

Table 1: Reference table of colonial and Mãori names of localities and taxa.	
Geographic localities	
Māori name	Colonial name
Aotearoa	New Zealand
Te Moana o Raukawa	Cook Strait
Te Ika-a-Māui	North Island
Te Waipounamu	South Island
Kā Tiritiri-o-te-Moana	Southern Alps
Population Names	
Māori names used in this work	Scientific name and locality
Kapokapowai North (KN)	*Uropetala carovei*, Te Ika-a-Māui
Kapokapowai South (KS)	*Uropetala carovei*, Te Waipounamu (below 4000 ft)
Kapokapowai Montane (KM)	*Uropetala chiltoni*, Kā Tiritiri-o-te-Moana

Introduction

Islands are widely recognized for their unique role in shaping biodiversity (Barreto et al., 2021; Conway & Olsen, 2019; Gleditsch et al., 2022; Wilson, 2009). The Theory of Island Biogeography by MacArthur and Wilson (1963) summarized several of these phenomena, and this theory was later extended to mountaintop habitats (Wyckhuys et al., 2022). The islands of Aotearoa (New Zealand; see table 1 for nomenclature) have often been considered as a natural laboratory to study both island and mountain biogeography (Shepherd et al., 2024; Thomas et al., 2023; Wallis & Buckley, 2024; Waters & Craw, 2006). This is due to the opening and closing of the Te Moana o Raukawa, referred to by some post-European arrival as the Cook Strait, which separates Te Ika-a-Māui and Te Waipounamu (also known as the North and South Islands respectively) and last opened 500,000 years ago (Lewis et al., 1994), and the uplift of Kā Tiritiri-o-te-Moana (the Southern Alps), a relatively young mountain range on Te Waipounamu (South Island) (Table 1).

Despite its young age, Te Moana o Raukawa (the Cook Strait) has been proposed as a driver of allopatric speciation and population divergence in several taxa including amphipods (Stevens & Hogg, 2004), the Weka (terrestrial birds) and their ectoparasites (Trewick et al., 2017), and skink lizards (O'Neill et al., 2008). The uplift of the Kā Tiritiri-o-te-Moana mountain range, known colonially as the Southern Alps, likely opened niches and acted as a driver of diversification in flora (Thomas et al., 2023)

and fauna (Buckley et al., 2024) of Te Waipounamu. Most lineages of alpine flora arrived in the later Tertiary, and the environmental upheaval in the Pliocene and Pleistocene drove diversity in these lineages (Thomas et al., 2023). Most alpine invertebrate fauna are relatively young, with ages corresponding to the increased uplift of the Kā Tiritiri-o-te-Moana range 5 million years ago (Ma), and the development of a permanent snow line just over 1 Ma (Buckley et al., 2024). Similar to the flora, it is broadly understood that most invertebrate fauna evolved from lineages already on the island as niches opened with the increased elevation (Buckley et al., 2024), although it has been hypothesized that invertebrates rode tectonic lift to higher elevation (Heads, 2017).

Although aquatic insects have been used to better understand the past climate and geology of Aotearoa, they have been relatively underrepresented in biogeographic and broader biodiversity work (Leschen et al., 2023) and knowledge about their biogeography remains limited for many taxa. One such group of aquatic macroinvertebrates are the dragonflies first referred to as Kapokapowai (among other names) by Māori (Grant, 2014), and later, named *Uropetala* by colonial European scientists (Selys 1858).

According to Māori cosmology, dragonflies and other insects are considered the children of Tāne Māhuta (the god of forests, birds and insects). Dragonflies appear in whakaairo (traditional carvings which often adorn the walls of Māori meeting houses) and waiata (songs) of Māori (Indigenous Peoples of Aotearoa New Zealand). Stories about dragonflies also feature in pūrakau (legends) belonging to specific iwi (tribes) and hapū (subtribes). All insects, including dragonflies, were created before humans in Māori genealogical histories and are therefore tuakana (roughly translated as an elder family member) and are respected accordingly. Kapokapowai or Kapowai are names commonly-used for the Petaluridae of Aotearoa, which loosely translates to water snatchers, though there are other recorded names including Tītīwaiora, Kihihiwaru and Uruururoroa (Grant, 2014). As this work was conducted with the express permission of the iwi who own the lands of Aotearoa, we refer to these dragonflies by the Māori name, Kapokapowai, in our work here. We also note that the name Kapokapowai was used to describe these dragonflies in the literature, three years prior to the first use of *Uropetala* by Selys (Grant, 2014; Taylor, 1855, 1870), and it has continued to be used to refer to dragonflies in this genus in scientific literature (Durrant, 2024; Fong, 2024; E. R. Tolman et al., 2024). However, we are not making any change to the binary taxonomic nomenclature of this genus here.

Kapokapowai represent one of only five genera of Petaluridae, a family that comprises 11 currently described species (E. R. Tolman et al., 2024; Ware et al., 2014). Kapokapowai includes two currently described species, *Uropetala carovei* (Selys, 1843) which is thought to inhabit lower elevations of both Te Ika-a-Māui and Te Waipounamu (North and South Islands respectively), and *Uropetala chiltoni* (Tillyard, 1921), which inhabits higher elevations of Te Waipounamu (South Island). We refer to the populations by their Māori name in this work, referring to *U. chiltoni* as Kapokapowai Montaine (KM), and *U. carovei* from either island as Kapokapowai North (KN) and Kapokapowai South (KS)(Table 1), representing the three putative species in the Kapokapowai species complex.

Debate about whether this complex should appropriately be considered to have two species has been ongoing for decades (Andress, 1998; L. S. Wolfe, 1952; Winstanley & Rowe, 1980). According to Tillyard's original description, KM is characterized by large pale blotches on its labrum, which are not present in KN, and by black femur leg segments, which are brown in KN. However, variation in the splotches of the labrum have been used to suggest that hybrid populations between KM and KS can be found at the north end of Te Waipounamu (South Island) (Winstanley & Rowe, 1980). Behavioral work suggests that female KM lay all their eggs in one plant, and in repeating this egg laying process females tend to badly damage their wings; such damage has not been seen in KN or KS (W. J. Winstanley, 1981).

This behavioral work should be replicated to confirm that this is a species–wide behavior. It has also been suggested that KN and KS may be different species, as Kapokapowai North on Te Ika-a-Māui may have broader superior appendages and larger imagos than their counterparts on Te Waipounamu (L. S. Wolfe, 1952). Two different karyotypes have been identified for this genus, but it is unclear if this is due to laboratory error (Kuznetsova & Golub, 2020); no other attempts have yet been made to determine the number of species in this genus using molecular data. Based on known morphological variation and behavioral data (L. S. Wolfe, 1952; Winstanley & Rowe, 1980),, the dragonflies known as Kapokapowai are hypothesized here to comprise between one and three species, the diversification of which was shaped by both Te Moana o Raukawa (Cook Strait) and Kā Tiritiri-o-te-Moana (Southern Alps).

Here, we use population and functional genomics, alongside scanning electron microscopy and environmental niche models to determine the number of species and the population dynamics within Kapokapowai and to study how Kā Tiritiri-o-te-Moana and Te Moana o Raukawa may have driven speciation in this genus.

Materials and Methods

Population genomics

To determine the population structure of Kapokapowai using a sampling of individuals, we sequenced 31 individuals, comprising 16 KM and eight KN from Te Ika-a-Māui, as well as eight KS from Te Waipounamu, and seven *Phenes raptor* (Supplementary table 1), using a 20kb anchored-hybrid enrichment dataset (E. R. Tolman et al., 2024). We also utilized reads previously generated for this dataset for two KM from Te Waipounamu, and one KN from Te Ika-a-Māui (E. R. Tolman et al., 2024). We mapped these reads to the soft-masked assembly of an individual KS (E. R. Tolman et al., 2023) with bwa2 (0.7.17-r1188) (H. Li & Durbin, 2009), and calculated mapping statistics, average depth and converted the output to a sorted bam file with samtools (1.16.1) (Danecek et al., 2021). We called variants with bcftools (1.15.1) (Danecek et al., 2021), using the options: bcftools mpileup -a AD,DP,SP -Ou -f reference.fasta. Input_bam | bcftools call -f GQ,GP -mO z -o output. We then filtered the resulting vcf file for a minimum quality score of 30, and a minimum and maximum depth of 10 and 350 respectively to capture the region targeted with hybrid probes and the adjacent flanking region that is also sequenced and often more variable.

We then performed a PCA analysis and calculated the F_{ST} between and within each of the three putative species using vcftools (0.1.16) (Purcell et al., 2007). To visualize admixture among populations we generated admixture models assuming 1-7 ancestral populations with admixture v1.3.0 (Skotte et al., 2013) and evaluated the models with cross-validation error. The best fitting admixture-model and the PCA plots were generated in R using mapmixture (1.1.0) (Jenkins, 2024).

To test for isolation by distance, we used genetic differences calculated with VCFtools (Danecek et al., 2021), and performed a Mantel test using the vegan package in R v2024.04.2+764 (Oksanen et al., 2024), using 1000 permutations to determine the significance of the correlation. We also tested for introgression between KM and KN and KS from either island with an ABBA-BABA test from Dsuite v0.5 r57, which is optimized to work on lineages in shorter evolutionary time scales (Malinsky et al., 2021). In this test, seven sequenced individuals of *P. raptor* (the sister genus to *Uropetala* (E. R. Tolman et al., 2024)) were used as the outgroup taxa.

We used the speedemon v.1.1.1 (Douglas & Bouckaert, 2022) pipeline on 395 biallelic SNPs from our dataset, using snapper v1.1.4 (Stoltz et al., 2021) and BICEPS v1.1.2 (Bouckaert, 2022) in BEAST2 v2.7.7 with a chain length of 10,000,000 to identify species delimitations using our dataset. In

the analysis we designated KN, KS and KM as three separate populations, and used the mean pairwise percent genetic divergence between individuals of KM (~.54), as calculated with from the VCF file using the pandas (McKinney, 2010) library for data manipulations and numpy (Harris et al., 2020) for numerical computations, as the prior mean on theta, and used an alpha of 2.0, and beta of 0.26942 to achieve this mean in the Gamma distribution of the theta prior, and followed the developer's suggestions for all other parameters in the BEAST2 run (Douglas & Bouckaert, 2022). We independently ran the analysis two times to check for convergence, and tested for adequate mixing of and model convergence using Effective Sample Size (ESS), both in TRACER v1.7.2 (Rambaut et al., 2018).

Morphological analysis

To identify potential morphological synapomorphies between the putative species of Kapokapowai we evaluated the male secondary genitalia. We specifically looked at the vesica spermalis, or sperm pump. This structure is located on the ventral side of the second abdominal segment in male Odonata, to which sperm is transferred prior to copulation, and may provide informative morphological characters for species determination (Kennedy, 1922; May, 1997; Ware, 2008). The vesica spermalis of Odonata is composed of four segments that are variable between species in their relative size and shape. In Petaluridae, a barb on the second segment near the junction with the third segment and the horns on the lateral side of the third segment have been used to support intrageneric difference (E. Tolman, 2024). We imaged the vesica spermalis from two males from each putative species to try and identify more definitive diagnostic features for species delimitation. We followed the protocol for scanning electron microscopy outlined by Tolman et al. (2024). Briefly, penes were mounted laterally and dorsally on aluminum stubs and coated with gold palladium using a Cressington 108E sputter coater and specimens were then imaged using an S-7400 Hitachi scanning electron microscope.

Environmental niche modeling

Occurrence Records

We acquired occurrence records of adult KN, KS, and KM from the Global Biodiversity Information Facility (GBIF)(available in supplementary data). We selected occurrences from GBIF possessing preserved museum samples and research grade observations, which include verified latitude and longitude coordinates, a photograph of the sighting, observation date, and at least ⅔ agreement on species identification by the community. We filtered occurrences by removing sightings from erroneous localities (middle of the ocean, locations of large museums). We divided occurrences for KN and KS between Te Ika-a-Māui and Te Waipounamu (North and South Islands) to be used as individual models (Supplementary Table 3).

Environmental Data

We acquired averaged sets of environmental predictor variables for modeling consisting of purely bioclimatic variables. All analyses were conducted using the statistical programming language R v. 4.1.2. We acquired environmental rasters at 2.5 arc-second resolution (~5km at the equator) from the CHELSA climate database v2.1 (Karger et al., 2017, 2023) . We downloaded the 'Anthropocene' bioclimatic dataset (1979 – 2013) consisting of 19 bioclimatic variables which follow Worldclim v2 (Fick & Hijmans, 2017). We omitted bioclimatic variables 8 and 9 after visual inspection of interpolation discontinuities (Booth, 2022). Although such spatial artifacts were minor within our initial study extent,

we observed major breaks of climate smoothing when we extrapolated our model to a larger spatial extent within the last glacial maximum and interglacial periods.

Model Construction

We spatially thinned occurrences to the resolution of our environmental variables to reduce the effects of sampling bias and artificial clustering (Veloz, 2009). We thinned occurrences by 5km to match the spatial resolution of our environmental data. We chose study extents for occurrences of KN and KS found in Te Ika-a-Māui and Te Waipounamu, defined as polygons around all localities between both islands respectively; we chose the same study extent for occurrences of KM found in Te Ika-a-Māui. We chose these study extents to include potential suitable habitat, while excluding large areas outside the species' dispersal limitations (Peterson & Lieberman, 2012). Within this extent, we randomly sampled 50,000 background points for modeling and extracted their environmental values. We used these values to calculate correlations between variables using the 'vifcor' and 'vifstep' functions in the usdm package (Naimi, 2023) and filtered out variables with correlation coefficients higher than 0.7 and a Variance Inflation Factor (VIF) threshold of 10, both standard cutoffs in such analyses (Goodman et al., 2024).

To model the distribution of putative Kapokapowai species, we used the presence-background algorithm Maxent v3.4.4 (Phillips et al., 2017), using the R Package ENMeval 2.0.0 (Kass et al., 2021) for model building, parameterization, evaluation with different complexity settings, and reporting of results. We partitioned our data using the 'checkerboard2' strategy. To prevent our model from extrapolating beyond the bounds of training data, we clamped our models by omitting ranges of environmental data which fall outside of the training data. All final models were fitted to the full dataset. We tuned model complexity to find optimal settings using different feature classes, including linear (L), quadratic (Q), and hinge (H) as well as regularization multipliers 1 through 5 (higher numbers penalize complexity more) (Radosavljevic & Anderson, 2014; Warren & Seifert, 2011).

We assessed our model using averages of threshold-dependent (omission rate) and threshold-independent (Area Under the Receiver Operating Characteristic or AUC) discrimination performance metrics calculated on withheld validation data (Warren & Seifert, 2011). The 10th-percentile omission rate sets a threshold as the lowest suitability value for occurrences after removing the lowest 10% suitability values (Kass et al., 2021; Radosavljevic & Anderson, 2014). Validation AUC is a measure of discrimination accuracy that can be used to make relative comparisons between ENMs with different settings fit on the same data (Lobo et al., 2008; Radosavljevic & Anderson, 2014). Finally, we checked the results against the Akaike Information Criterion with correction for small sample sizes (AICc; calculated on the full dataset) (Warren & Seifert, 2011). To investigate model behavior, we examined marginal response to suitability. Marginal response curves show the modeled relationship of each variable individually with the occurrence data when all other variables are held constant (Phillips et al., 2017).

We made habitat suitability predictions for KM, and KN and KS from both islands using our 'Anthropocene' environmental predictor variables. We projected our modern-day models to a new study extent to encapsulate the potential habitat of Kapokapowai within the historic past, defined as a polygon around both Islands of Aotearoa. We generated thresholdless predictions by converting raw predictions to a scale of 0-1 to approximate probability of occurrence using the 'cloglog' transformation (Phillips et al. 2017). We also generated a threshold prediction, calculated from the 10-percentile omission rate from our model evaluation. To estimate habitat suitability of Kapokapowai within the geologic past, we generated predictions using environmental predictor variables from the PaleoClim dataset (Brown et al., 2018). We

generated predictions within three distinct time periods: Mid-Holocene (8.3 – 4.2ka), Last Glacial Maximum (21ka), and the Last Interglacial (130ka).

Ordination Analysis

To determine niche differentiation between putative species, we compared niche overlap in occurrences of KN and KS from Te Ika-a-Māui and Te Waipounamu using an ordination framework by first reducing dimensionality within the datasets via a Principal Component analysis (PCA). Using the 'espace_pca' function in the *Wallace* v2.0.5 and *ade4* package v1.7 in R (Dray & Dufour, 2007; Kass et al., 2018)), we generated a Principle Components Analysis (PCA) using environmental variables from Kapokapowai occurrences and plotted with correlation loadings to infer the degree of influence particular environmental variables possess in the distribution of background points within niche space; we chose bioclimatic variables which were uncorrelated and shared among both *Kapokapowai* maxent models. Using the 'espace_occDens' function in the package *ecospat* v3.2 (Di Cola et al., 2017, p. 2) an occurrence density grid was estimated for both the environmental values at each occurrence point and background extent points using a kernel density estimation approach. Niche overlap between occurrence density grids of environmental values at each occurrence point and background points were compared using Schoener's D (Schoener, 1968) 'espace_nicheOv' function. Finally, using the 'ecospat.plot.overlap.test' function, we conducted a niche similarity test in which Kapokapowai niches from both islands are randomly shifted in the background extent and permuted 1000 times, and the niche overlap between the two are recalculated. A p-value <0.05 indicates that the niches from both time periods are significantly similar with each other.

Results

Population genomics

After filtering for mapping quality and depth, we retained 365 SNPs for the population structure analysis. The weighted F_{ST} values were estimated at 0.23 between KM and KS, 0.29 between KM and KN and 0.11 between KN and KS (Table 2). We then separated the data into subsets as follows by their distributions along PC1 (Fig 1A): KM (all individuals), KM (negative PC axes), KN (Te Ika-a-Māui) and KS (Te Waipounamu). The F_{ST} values differed when only a subset of KM was used (Supplementary Table 3). The centroid of KM was distal from the centroids of KN and KS across PC1, while the centroid of KN and KS differed along PC2 (Fig. 1A). Despite the differing centroids across PC1 and PC2, there was overlap in the space occupied between all three putative species (Fig. 1A). Because of the low cross validation-error (Supplementary table 4), and the three clusters identified in the PCA analysis, we assumed three ancestral populations in our main admixture analysis (Fig. 1B), but also provide assumptions of K=2, and K=4 (Supplementary fig. 1). Ancestral population 1 was only present in KM, while ancestral populations 2 and 3 were present in all three putative species (Fig. 1B). There was no evidence that geographic separation was correlated with genetic distance in this dataset (pearson correlation coefficient r=0.02462, p=0.322), however, the ABBA-BABA test showed moderate evidence of gene flow from KM to KS (p=.03, f4-ratio=.45, D-statistic=.11). All parameters in the speedemon analysis showed adequate mixing (ESS>400), and model convergence (see supplementary data). The species were recovered as currently described with very high (99%) posterior support.

Figure 1: Population Genomics of Kapokapowai

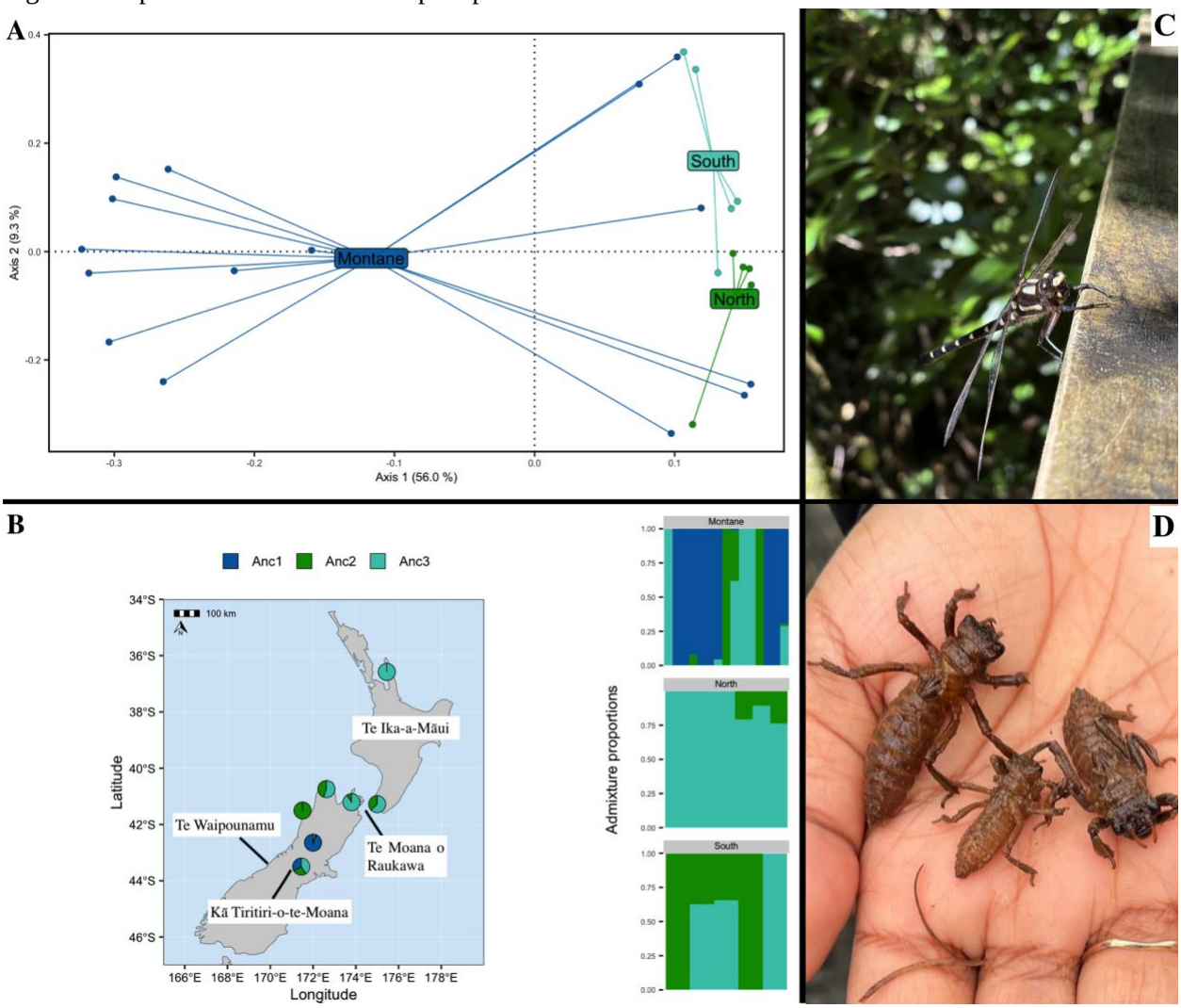

Fig. 1: (A) PCA of Kapokapowai, colored by putative species: Kapokapowai Montane (Blue), KN (Green) and KS (Teal). (B) Admixture analysis of Kapokapowai assuming three ancestral populations, with the ancestral populations 1-3 colored as blue, green, and teal respectively per each sampled individual. (C) Adult Female Kapokapowai North from Te Ika-a-Māui. (D) Nymphs of Kapokapowai Montane.

Table 2: F_{st} values between putative species of Kapokapowai			
Putative species 1	Putative species 2	Mean F_{ST}	Weighted F_{ST}
Kapokapowai Montane	Kapokapowai South	0.20	0.23
Kapokapowai Montane	Kapokapowai North	0.27	0.29
Kapokapowai North	Kapokapowai South	0.05	0.11

Morphological analysis

Figure 2: Male Secondary Genitalia of the Three Hypothesized Kapokapowai Species

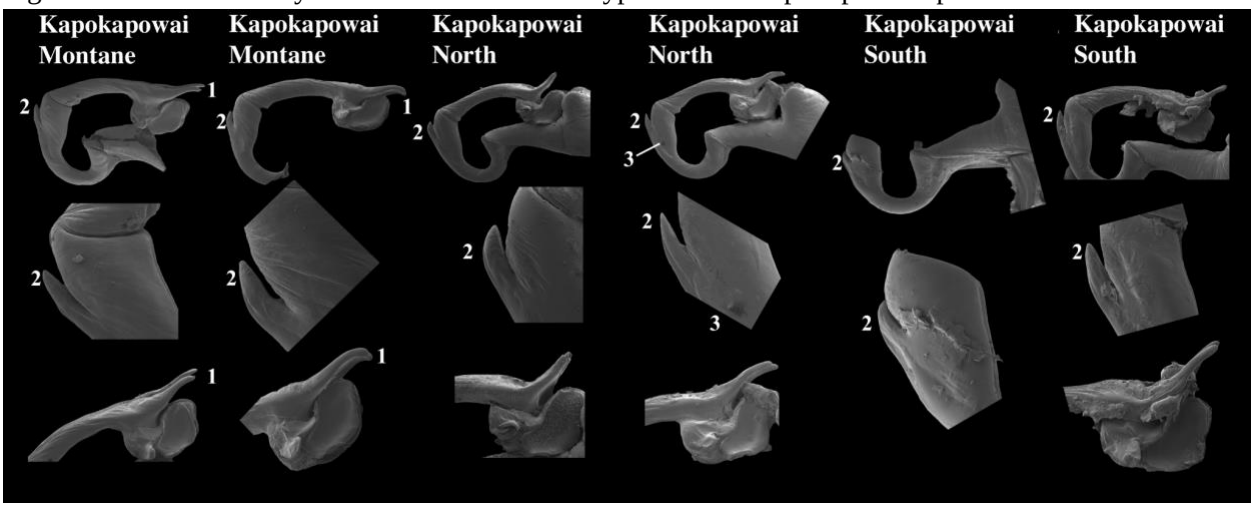

Fig. 2: SEM images of male penes from six sampled Kapokapowai (two from each putative species). Divergent features include (1) curves at the end of the horns only found in Kapokapowai Montane, (2) the barb near the joint of the second and third segments, and (3) a knob found near the barb from one individual from Kapokapowai North.

The "horns" of KM (see figure 2, feature 1) are down curved at the tips in a way not observed in any of the three KN or KS individuals (Fig. 3). The angle and curvature of the barb (figure 2, feature 2), and the presence of a "knob" near it (figure 2, feature 3) differs between individuals, but does not appear to be fixed between any populations. One individual of KN had a knob near the barb.

Ecological Niche Modeling

Optimal model settings varied considerably for Kapokapowai based on 10-percentile omission rate and mean validation AUC metrics. Based on the results of the collinearity analysis, we used the following six predictor variables to build all models: Isothermality (bio03), temperature seasonality (bio04), maximum temperature of the warmest month (bio05), precipitation seasonality (bio15), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19). Models varied in complexity with expressing either hinge-loss, or linear-quadratic feature classes with regularization multipliers of 3-4

(higher complexity penalty). Mean validation AUC was adequate for KS and KM (0.75 and 0.86 respectively), while 10% omission rate was low relative to its expected value of 0.1 (0.11 and 0.09 respectively) (Supplementary Table 2). Furthermore, optimal models for KS and KM possessed low amounts of non-zero lambdas (coefficients) and AICc values suggesting low amounts of model overinflation (Supplementary Table 2). Optimal models for KN performed poorly, possessing an unacceptably low AUC value (0.44) and high 10% omission rate (0.16) (Supplementary Table 2).

Optimal models retained 4 – 6 predictor variables after regularization, and relied mainly on contributions from Isothermality (bio03), temperature seasonality (bio04), maximum temperature of the warmest month (bio05), and precipitation of the wettest and driest quarters (bio18 and bio19 respectively) (See Supplemental Fig. 1). Response curves of climate variables revealed differing relationships with suitability among Kapokapowai models (Supplementary Fig. 1). Response curves for KN expressed jagged optimal ranges, with habitat suitability not following a smooth or continuous gadient. Temperature Seasonality (bio03) and precipitation of the coldest quarter expressed positive linear/hinge relationships with suitability among all three Kapokapowai models, while precipitation of the wettest quarter (bio18) expressed negative linear/hinge relationships with suitability for KN and KS; precipitation of the wettest quarter possessed no relationship in KM. Isothermality (bio03), and maximum temperature of the warmest month (bio05) expressed opposite relationships with suitability within Kapokapowai. Isothermality (bio03) expressed positive linear or linear/quadratic relationships with suitability within KM and KN, but a negative linear relationship with KS. Maximum temperature of the warmest month (bio05) expressed negative linear or quadratic/linear relationships with suitability within KM and KS but a positive linear relationship within Kapokaowai South (Supplementary Fig. 1).

Predictions using our ‘Anthropocene’ environmental variables for KS within Te Waipounamu revealed areas of high suitability along the coast (Westland, Nelson and Marlborough provinces) (Fig 3D). Suitability was highest for KM across the Southern Alps (interior Nelson and Marlborough provinces) (Fig. 3A). Predictions for Kapokaowai North within Te Ika-a-Māui revealed areas of high suitability within the interior (Wellington and Hawke’s Bay, along the Tararura, Ruahine, and Kaimanawa Mountain Ranges), as well as the Northern portion of the island within Auckland (Fig 3G). Threshold predictions reflect our ‘cloglog’ predictions (See Supplementary Fig. 2).

Predictions generated from our paleoclimate variables demonstrated variability in suitability over time for Kapokapowai compared to our modern-day ‘Anthropocene’ variables. For KM, suitability expands within the mid-Holocene (8.3 – 4.2ka), encompassing most of Te Waipounamu except for the coastal margins (Fig 3H.). Projection to the Te Ika-a-Māui within the mid-Holocene indicates suitable habitat within the island’s center (Te Ika-a-Māui Volcanic Plateau, Tararua Range, and Raukumara Range) (Fig 3H.). Within the LGM, suitability contracts within Te Waipounamu, with suitable habitat only being located within a small portion of the Kā Tiritiri-o-te-Moana (Southern Alps) and Kaikōura Mountain Ranges (Fig 3I.). Within Te Ika-a-Māui, suitability expands, encompassing most of the western and southern mountain ranges. Although a land bridge connected both Islands during the LGM (Te Moana o Raukawa), suitability was low (Fig 3I.) while our threshold predictions suggest suitable habitat across the strait (See Supplemental Figure 3).

For KS within Te Waipounamu, suitability contracts within the mid-Holocene, being restricted to a small portion of the coast (northern Westland) (Fig 3E.). When projected to Te Ika-a-Māui, suitability is high within the Northern Cape and southwestern cape (Taranaki Province), and Auckland (Fig 3E). Within the LGM, suitability expands encompassing the northern coastal regions of Te Waipounamu (Westland and Nelson), as well as the Northern Cape, Taranaki Province, and Auckland within Te Ika-a-

Māui (Fig 3F.). Suitability across the Te Moana o Raukawa is intermediate, with a few pockets of high suitability (Fig 3F.) while our threshold predictions suggest suitable habitat across the strait (See Supplemental Figure. 3).

For KN within Te Ika-a-Māui, suitability contracts within the mid-Holocene, with only a few pockets of high suitability within the southern coasts (Tararua Ranges), and Auckland (Fig. 3B.). When projected to Te Waipounamu, suitability is highest along the coastal ranges of southern Westland and Otago. Within the LGM, suitability expands to include most of the southern Mountain Ranges within Te Ika-a-Māui, as well as Kaimanawa Mountain Ranges within the middle of the Island (Fig 3C). Within Te Waipounamu, suitability slightly expands southward into the coastal ranges of Otago (Fig 3D). Suitability within the Te Moana o Raukawa remains intermediate with a small pocket of high suitability off the coast of Taranaki (Fig 3D.) while our threshold predictions suggest suitable habitat across the strait (See Supplemental Figure 3).

Ordination Analysis

Environmental variables for KN and KSwithin Te Ika-a-Māui and Te Waipounamu expressed an intermediate degree of overlap in ordination analysis, but were statistically more similar than random (Fig. 4). Within our PCA analysis, the first principal component explained ~34% of the variance with PC2 explaining ~32%. Isothermality (bio03), temperature seasonality (bio04), and precipitation of the coldest quarter (bio19) loaded strongly on PC1, while precipitation of the warmest and coldest quarters (bio18 and bio19) loaded strongly on PC2 (Table 3). Environmental niche overlap for Kapokapowai was intermediate between Te Ika-a-Māui and Te Waipounamu (Schoener's D = 0.24), with niche similarity tests showing observed overlaps being higher than 95% of simulated overlaps ($p = 0.01$), supporting niche similarity between both islands (Fig. 4).

Species	PC1	PC2	Overlap (%)	Unique North Island (%)	Unique South Island (%)	Schoener's D	Similarity test (p)
Kapokapowai (North and South)	**34.9**	**32.6**	**93**	**6.9**	**13.2**	**24.7**	**0.01**

Environmental Variable	PC1	PC2	PC3
bio 3	**-0.51**	**-0.27**	**-0.38**
bio 4	**-0.51**	**-0.17**	**-0.48**
bio 5	**0.11**	**0.47**	**-0.54**
bio 15	**0.24**	**0.49**	**-0.37**
bio 18	**0.38**	**-0.56**	**-0.20**
bio 19	**0.51**	**-0.35**	**-0.40**

Table 3: PCA loadings, importance of variables, percent overlap, percent of unique niche overlap from both islands, environmental similarity (Schoener's D), and results of similarity tests from our EcoSpat analyses.

Figure 3: Niche Models of Kapokapowai Populations

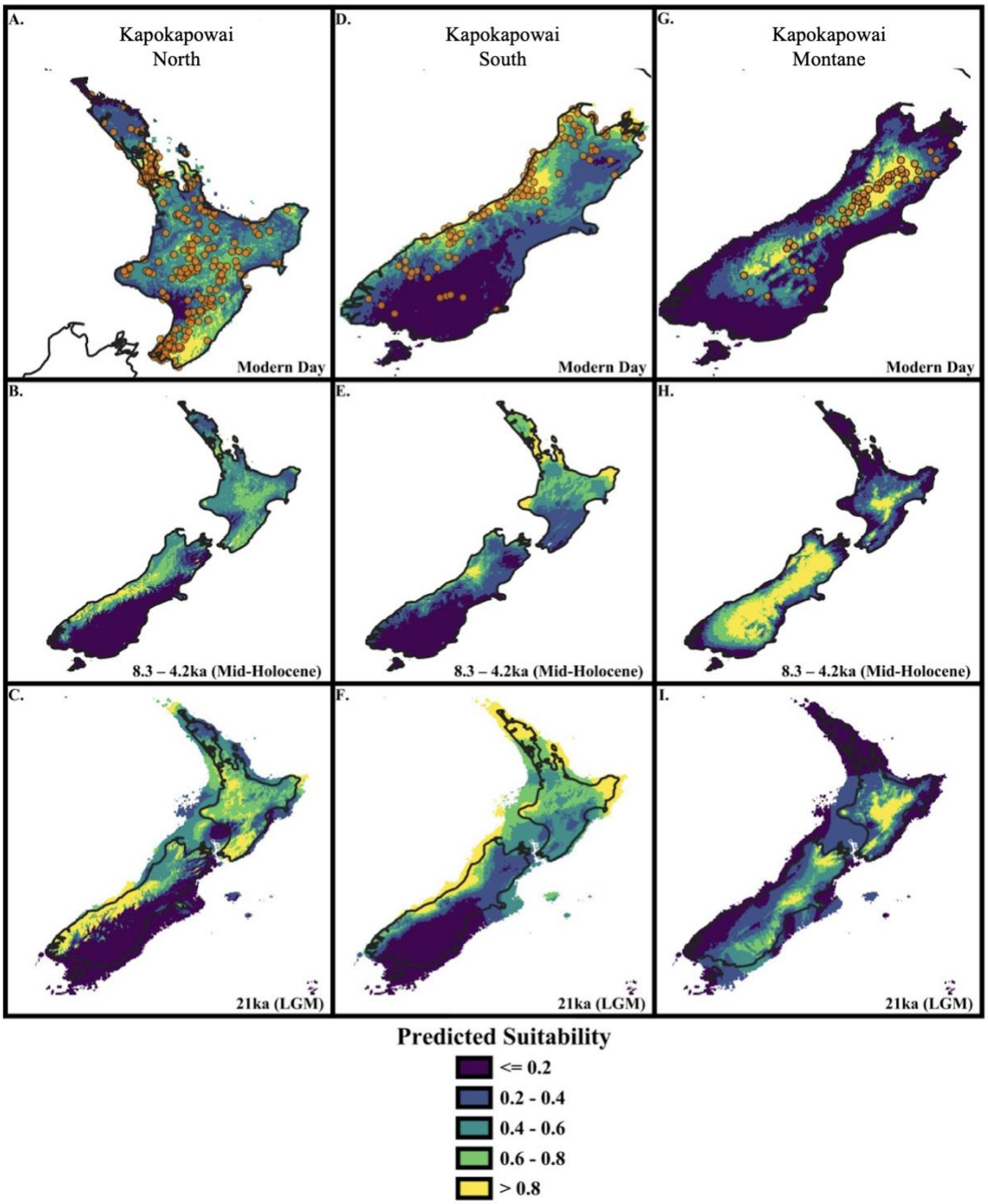

Figure 3: Maxent predictions for Kapokapowai projected to the modern day using our 'Anthropocene variables', mid-Holocene (Northgrippian: 4.2 – 8.326ka) generated from the PaleoClim dataset (Brown et al. 2018), and Last Glacial Maximum (LGM)(21ka) and Last Interglacial (LIG)(130ka) generated from the CHELSA database (Karger et al. 2017). Predictions were derived from the optimal model using the criterion of mean valuation AUC (AUC_{val}) values being the highest, and 10% omission rate being the

lowest. Predictions were transformed using the 'cloglog' function in Maxent v3.4.4 (Phillips et al., 2017), in which raw values are converted to a range of 0 - 1 to approximate a probability of occurrence. Brighter colors (yellow, green, blue) indicate areas of higher suitability (higher probability of occurrence), while darker colors (violet) indicate areas of lower suitability (lower probability of occurrence).

Figure 4: Niche Overlap of Kapokapowai North and Kapokapowai South

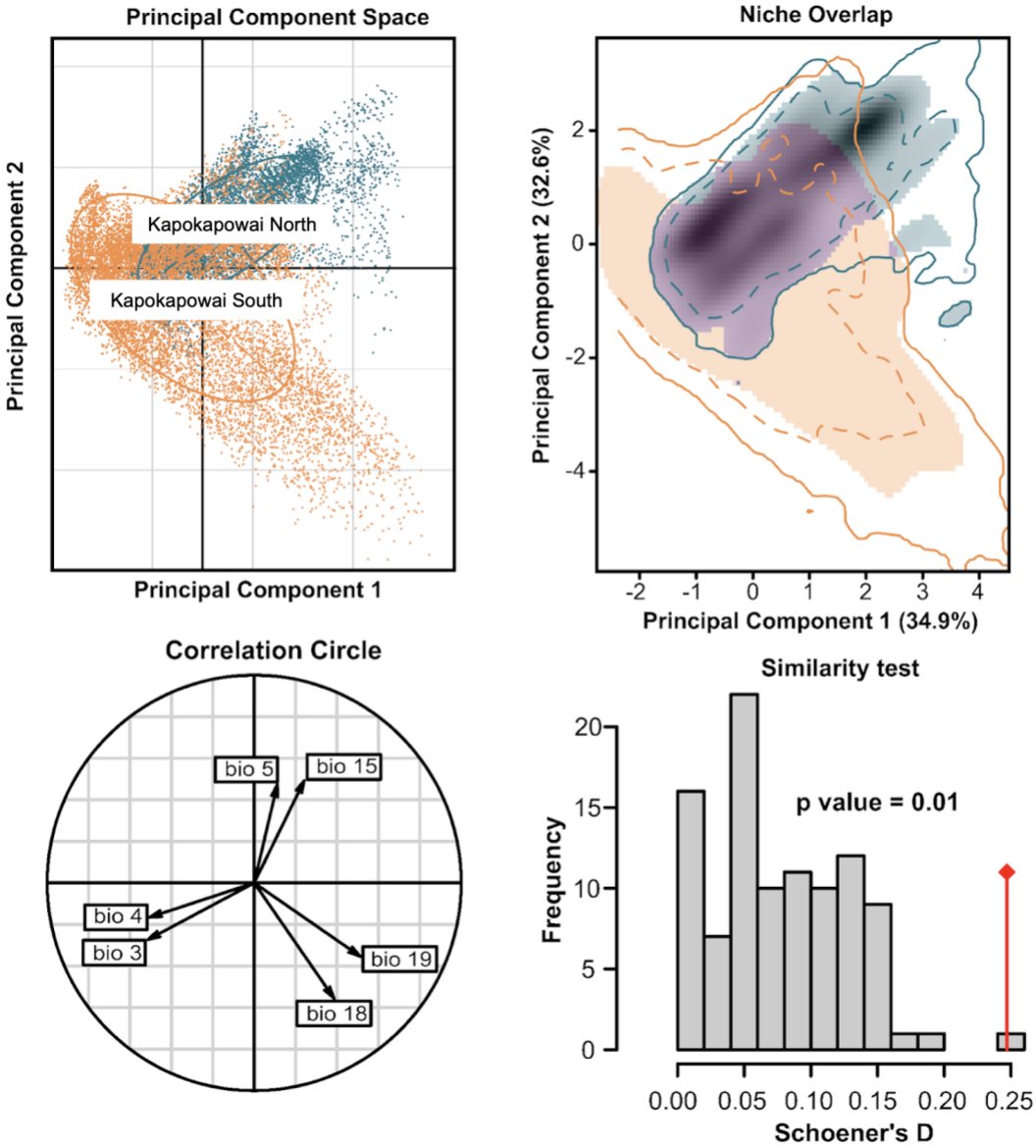

Figure 4: Ordination plot (PCA), niche overlap, correlation circle, and niche similarity tests showing niche differences between Kapokapowai North and South from Te Ika-a-Māui (North) and Te Waipounamu (South). Ordination plot represents principal component points of occurrence and background environmental values using type 2 scaling (Mahalanobis distance). PCA points for Te Waipounamu are in blue, while Te Ika-a-Māui is red. Solid contour lines in the niche overlap illustrate full range (100%) of climate space ('fundamental niche') while dashed lines indicate 50% confidence intervals. Contour lines of Te Waipounamu are in orange, and Te Ika-a-Māui is blue. Shading shows the

density of species occurrences per grid cell of kernel density analysis ('realized niche'), and violet pixels show niche stability (climate conditions occupied in both time periods). Orange shading indicates climate conditions only occupied by Te Waipounamu, while blue indicates climate conditions only occupied by Te Ika-a-Māui. Correlation circle indicates climactic variable loadings on the PCA space. Length and direction of arrows indicates influence and distribution of variables within PCA space. Bioclimatic variables which follow Worldclim v2 (Fick and Hijmans 2017). Histograms represent observed (red bar) and randomly simulated overlaps of niche similarity. The observed overlap is higher than 95% ($p < 0.05$) for both analyses supporting the niche similarity across both islands.

Discussion

Biogeography

The genetic differentiation between KM and KS is much higher than the differentiation between KN and KS (Table 2). Although Te Moana o Raukawa (Cook's Strait) is currently a barrier to the dispersal of Kapokapowai, our species distribution models suggest that this has not always been the case (Fig. 4, supplementary Fig. 2). Perhaps Te Moana o Raukawa has not been a barrier to the dispersal of Kapokapowai for a sufficient period of time for a strong genetic structure to evolve (Fig. 3). On the other hand, the peaks of Kā Tiritiri-o-te-Moana have not contained suitable habitat for KN and KS in any of the tested time periods, and have likely served as a longer barrier to the dispersal of these populations, shaping the genetic structure currently observed in Kapokapowai. The physical boundary of the mountains is further compounded by the fact that the alpine habitat has shortened the flight season of KM, compared to KN and KS (L. S. Wolfe, 1952). Despite this barrier, both the PCA (Fig. 1A) and admixture (Fig. 1B) analyses suggest there is some level of interbreeding and movement between populations, and neither barrier seems to be entirely restricting gene flow, as evidenced by the Fst values <.3, and the F4 ratios (Table 2).

Patterns of genetic diversity in Kapokapowai

Two main hypotheses have been posited to explain how alpine species evolved in Aotearoa: either the species arrived by passively being carried with tectonic uplift, (Heads, 2017)), or they actively colonized the mountains after their formation (Buckley et al., 2024). Our data offer support for the former in Kapokapowai. Both PCA (fig. 1A) and admixture (fig. 1B) analyses showed KM to have much higher genetic diversity than either KN or KS. This suggests that KM is closest to the ancestral state of all three populations, and has thus retained the highest amount of genetic diversity, while KN and KS lost diversity due to the founder effect, similar to many other systems (Anopheles gambiae 1000 Genomes Consortium et al., 2017; Auton et al., 2015; B. Li et al., 2024). A historical demographic model, generated from the reference genome of one individual of KS from Te Waipounamu using the Pairwise Sequential Coalescent (Liu & Hansen, 2017) shows a severe bottleneck in effective population size *after* alpine uplift (E. R. Tolman et al., 2023). Taken together with the population genomics presented here, a plausible explanation is that all sampled Kapokapowai are descendents of a population that colonized alpine habitats, while KN and KS descend from populations that later moved into lowland habitats. Such a model would reconcile the bottleneck of ancestral Kapokapowai observed in the PSMC, and patterns of genetic diversity as demonstrated by the PCA (Fig. 1A) and admixture (Fig. 1B) analyses, which show that KM maintains the highest genetic diversity, which would have been lost in KN and KS as the ancestral populations dispersed to lowlands. This hypothesis is not without precedent, as plant lineages have also been hypothesized to have colonized mountains, and then recolonized the lowlands of Aoteora

(Thomas et al., 2023). A demographic model for KM from a reference genome, and revisiting the specimens sampled here with genome-wide resequencing data could be used to generate a demographic model for all populations of Kapokapowai, and a historical demographic model of dispersal and gene flow between populations using the site-frequency-spectrum (Noskova et al., 2023), both of which could be used to robustly test this hypothesis.

Species delimitations

The genetic structure of the three putative Kapokapowai species demonstrate that incipient speciation (Fig. 1A,B) is underway in this genus, thus current species delimitations are difficult to make. Given the genetic differentiation between KM and KN and KS(F_{ST} >.23), our identification of a diagnostic characteristic of the curvature on the horns of KM (Fig. 2), and the strong posterior support (>99%) of the currently described species (*U. carovei* comprised of KN and KS and *U. chiltoni* comprised of KM) in our species delimitation analysis, we suggest that current species delimitations remain unchanged. Although KN and KS do show some genetic differentiation, they do not show evidence of niche divergence, and we do not believe that they merit a new species description at this point in time.

Conclusion

To look at species diversity and the potential for speciation in a group such as the petaltail dragonflies offers a unique perspective in evolutionary biology. Analyses suggest that this family is extremely old, even for an order as ancient as Odonata, with some extant species persisting as independent evolutionary lineages since the Cretaceous era (Kohli et al., 2021; Suvorov et al., 2022; E. R. Tolman et al., 2024). With their reliance on fen habitats, Petaluridae are also somewhat limited in their range, compared to more generalist dragonflies that use ponds or rivers to complete their life cycle. While Kapokapowai have potentially been separated for significant periods of time, either across islands or in different habitats within an island, it may be that their adaptations to these specialized habitats has limited the genetic variability that would lead to speciation. This may help to explain why this group, despite its age, continues to be the smallest family within Anisoptera.

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