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

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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 provide an opportunity for studying the biogeography of diversification and population fragmentation. Aotearoa (New Zealand) is an excellent location to investigate both phenomena due to alpine emergence and oceanic separation. While it would be expected that separation across oceanic and elevation gradients are major barriers to gene flow in animals, including aquatic insects, such hypotheses have not been thoroughly tested in these taxa. Here, we show that mountains and oceanic separation function as semi-permeable barriers for Kapokapowai (*Uropetala*) dragonflies. Although Te Moana o Raukawa (Cook Strait), is likely responsible for some of the genetic structure observed, speciation has not yet occurred in populations separated by the strait. We find no evidence that they are an impervious barrier, but Kā Tiritiri-o-te-Moana (the Southern Alps) significantly restrict gene flow between named species. Our data support the hypothesis of an active colonization of Kā Tiritiri-o-te-Moana by the ancestral population of Kapokapowai, followed by a recolonization of the lowlands. These findings suggest that aquatic insects could be an exciting new frontier in the study of the biogeography and population fragmentation in the landscape of Aotearoa.

Keywords

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

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 Te Moana o Raukawa (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 (Table 1).

Despite its young geologic age, Te Moana o Raukawa 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 tectonic uplift of the Kā Tiritiri-o-te-Moana mountain range 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 period, 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 uplift to higher altitudes (Heads, 2017).

Aquatic insects have been used to better understand the past climate and geology of Aotearoa, and are useful models in the study of evolution and ecology (Córdoba-Aguilar et al., 2022), but 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). 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 by Taylor (1855), italicizing "*Kapokapowai*" as to explicitly refer to a genus, three years prior to the first use of *Uropetala* by Selys (Grant, 2014; Taylor, 1855, 1870), and Kapokapowai 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.

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 1.2 km)
Kapokapowai Montane (KM)	*Uropetala chiltoni*, Kā Tiritiri-o-te-Moana

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 KS, and by black femur leg segments, which are brown in KN and KS. 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 (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 KN 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 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 we sequenced 31 new individuals, comprising 16 KM and 8 KN from Te Ika-a-Māui, as well as 8 KS from Te Waipounamu, including 7 *Phenes raptor* as an outgroup (Supplementary table 1), using a 20kb anchored-hybrid enrichment dataset (E. R. Tolman et al., 2024). We also utilized previously generated AHE reads for 2 KM, and 1 KN which were used in a molecular phylogeny of Petaluridae (E. R. Tolman et al., 2024). We mapped reads from all 41 AHE sequences to a previously compiled soft-masked whole genome assembly (NCBI GenBank assembly GCA_036926305.1) 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 v1.16.1 (Danecek et al., 2021). We called variants with bcftools v1.15.1 (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 (Goodman et al., 2023).

We then performed a PCA analysis on a covariance matrix generated from the called SNPs and additionally calculated the F_{ST} between and within each of the three putative species both using VCFtools v0.1.16 (Purcell et al., 2007). To generate admixture plots for populations we evaluated admixture models assuming 2-7 ancestral populations with ADMIXTURE v1.3.0 (Skotte et al., 2013) and compared model fit using a cross-validation approach. The admixture graph under the best fitting models and the PCA plots were generated in R v2024.04.2+764 using mapmixture v1.1.0 library (Jenkins, 2024).

To test for isolation by distance, we generated the pairwise genetic distance matrices with VCFtools v0.1.16 (Danecek et al., 2021), and then used the Mantel test in the vegan package in R v2024.04.2+764 (Oksanen et al., 2024), with 1,000 permutations to determine the significance of the correlation between geographic and genetic distance. We also tested for introgression between KM and KN and KS with an ABBA-BABA test from Dsuite v0.5 r57, which is optimized to work on lineages with shorter evolutionary time scales and utilize SNPs (Malinsky et al., 2021), using *P. raptor* as an outgroup (E. R. Tolman et al., 2024).

To determine species delimitation based on our SNP data, we used the SPEEDEMON v.1.1.1 (Douglas & Bouckaert, 2022) pipeline in BEAST2 v2.7.7 (Bouckaert et al., 2014), using 395 biallelic SNPs from our dataset, including all Kapokapowai and *P. raptor*. We used snapper v1.1.4 (Stoltz et al., 2021) to run this pipeline on SNPs as opposed to alignments, and BICEPS v1.1.2 (Bouckaert, 2022) to implement a Yule Skyline Collapse Model to test for species delimitations. We used a chain length of 10,000,000 to identify species delimitations using our dataset. In the species delimitation analysis we designated KM as a reference species, with KN and KS as putative species. We 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 the theta prior (Douglas & Bouckaert, 2022). We used an alpha of 2.0, and beta of 0.26942 to achieve this mean in the Gamma distribution of the theta prior (see Stoltz et al., 2021 for a full description of these options), and followed the developer's suggestions for all other parameters in the BEAST2 run (Stoltz et al., 2021) . 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 (later referred to as penes) 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 (> q30) and depth (10-350), 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's correlation coefficient $r = 0.02462$, $P = 0.322$), however, the ABBA-BABA test showed moderate evidence of gene flow from KM to KS ($P = 0.03$, Patterson's $D = 0.11$). All parameters in the Speedemon analysis showed adequate mixing (ESS > 400), and model convergence (see supplementary data). The species were recovered as currently described, specifically KM as *U. chiltoni* and KN and KS as *U. carovei*, with very high (99%) posterior support.

Figure 1: Population Genomics of Kapokapowai

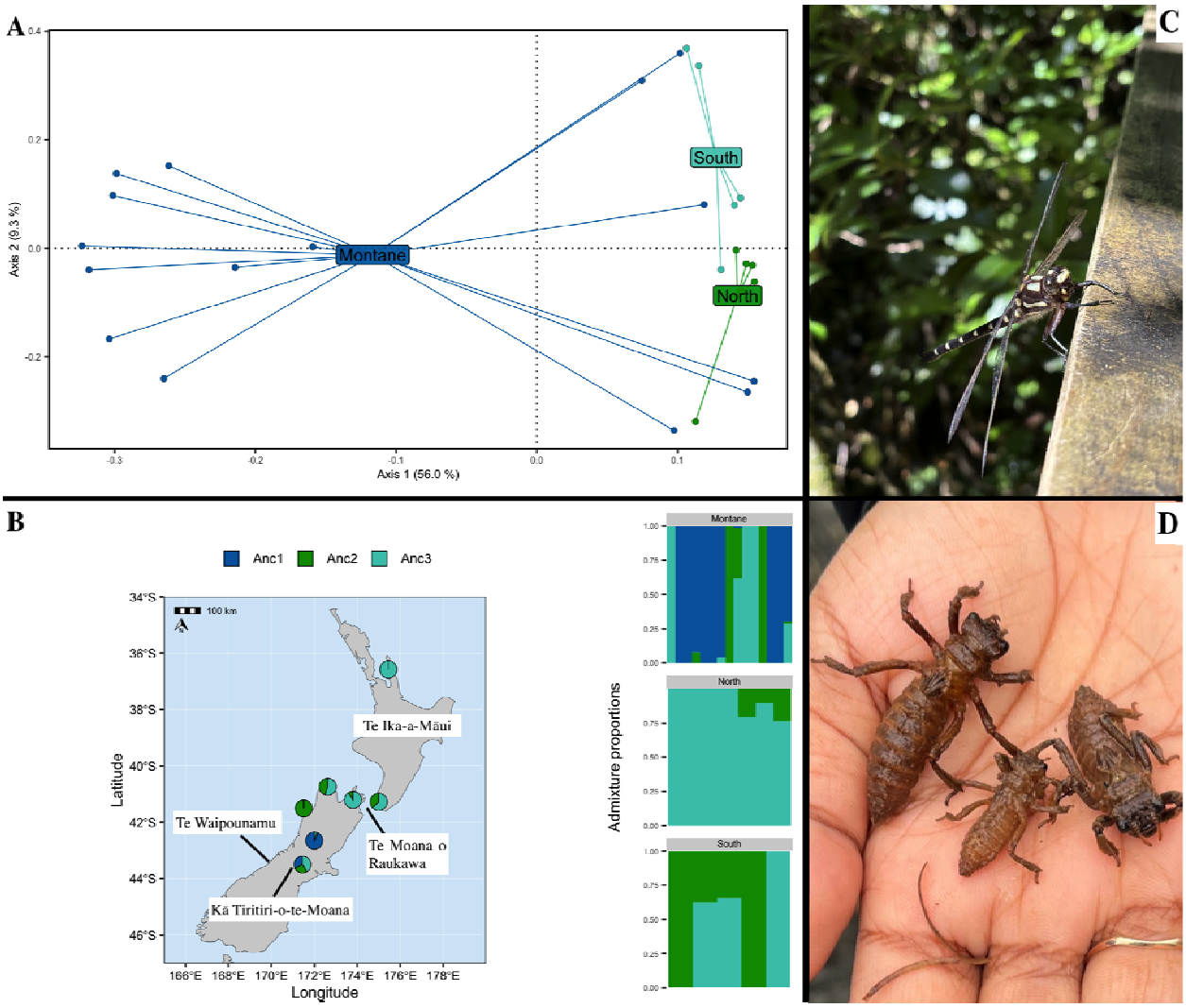

Fig. 1: (A) PCA of Kapokapowai, colored by putative species: Kapokapowai Montane (Blue), KN (Green) and KS (Teal). (B) Admixture analysis of Kapokapowai assuming three ancestral populations, with the ancestral populations 1-3 colored as blue, green, and teal respectively per each sampled individual (x-axis). Ancestral population 1 is only found in KM (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, using 365 called SNPs. Kapokapowai North (KN), Kapokapowai Montaine (KM), and Kapokapowai South (KS) are abbreviated. The results show stronger segmentation between KM and KN and KS.

Pairwise comparison	Mean F_{ST}	Weighted F_{ST}
KM-KS	0.20	0.23

KM-KN	0.27	0.29
KN-KN	0.05	0.11

Morphological analysis

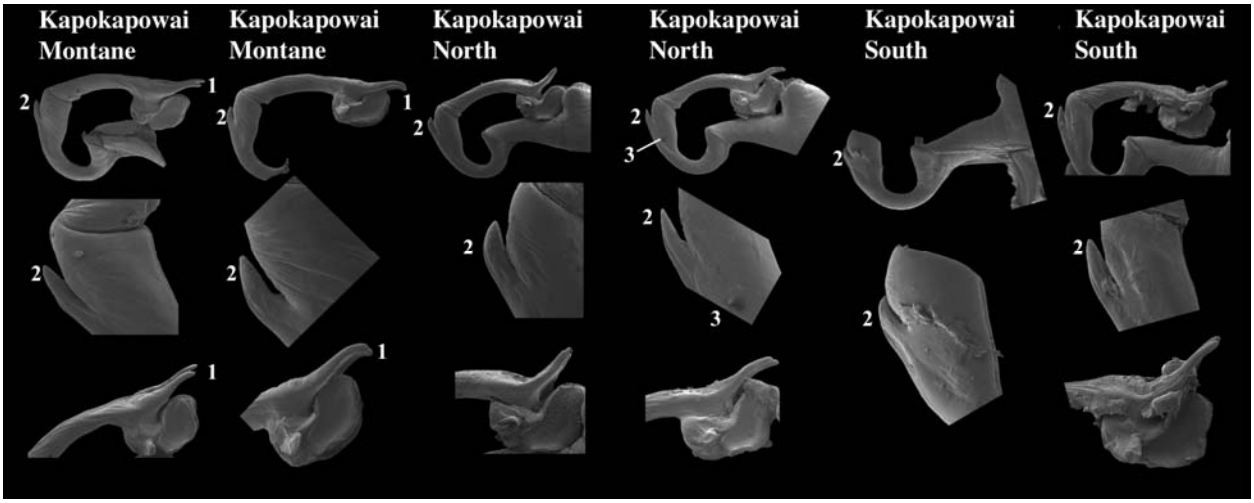

Figure 2: Male Secondary Genitalia of the Three Hypothesized Kapokapowai Species
Scanning electron microscopy. Images of male penes from six sampled Kapokapowai (two from each putative species). Divergent features include (1) curves at the end of the horns only found in Kapokapowai Montane, (2) the barb 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).

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.

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**

Bioclim Environmental Variable	PC1	PC2	PC3
	-0.51	**-0.27**	**-0.38**
Isothermality (Bio3)	**-0.51**	**-0.17**	**-0.48**
Temperature Seasonality (Bio4)	**0.11**	**0.47**	**-0.54**

Precipitation Seasonality (Bio15)	**0.24**	**0.49**	**-0.37**
Precipitation of Warmest Quarter (Bio18)	**0.38**	**-0.56**	**-0.20**
Precipitation of Coldest Quarter (Bio19)	**0.51**	**-0.35**	**-0.40**

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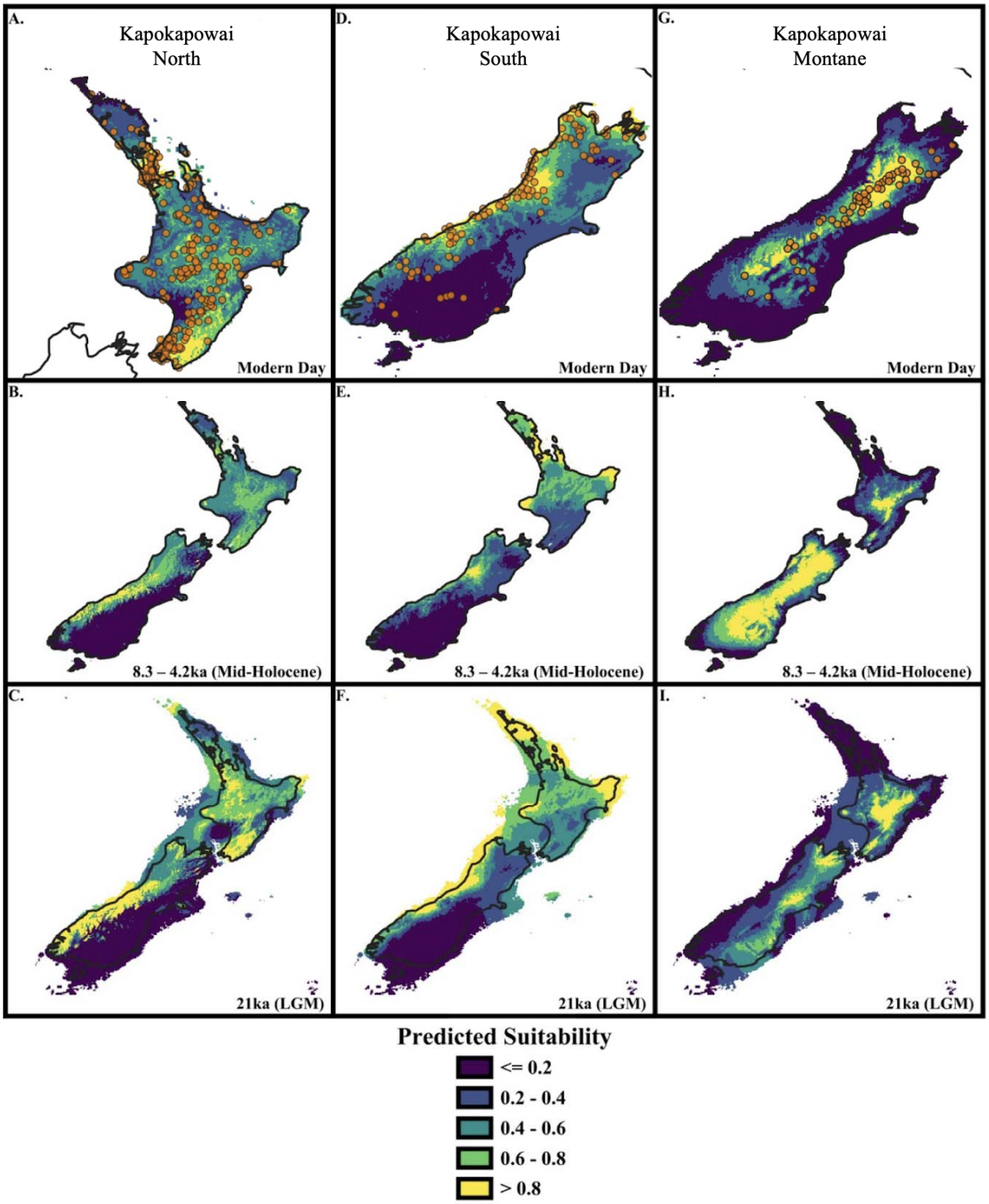

Figure 3: Niche Models of Kapokapowai Populations. MaxEnt predictions for Kapokapowai projected to the modern day using our 'Anthropocene variables', mid-Holocene (Northgrippian: 4.2 – 8.326ka) generated from the PaleoClim dataset (Brown et al. 2018), and Last Glacial Maximum (LGM)(21ka) and Last Interglacial (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).

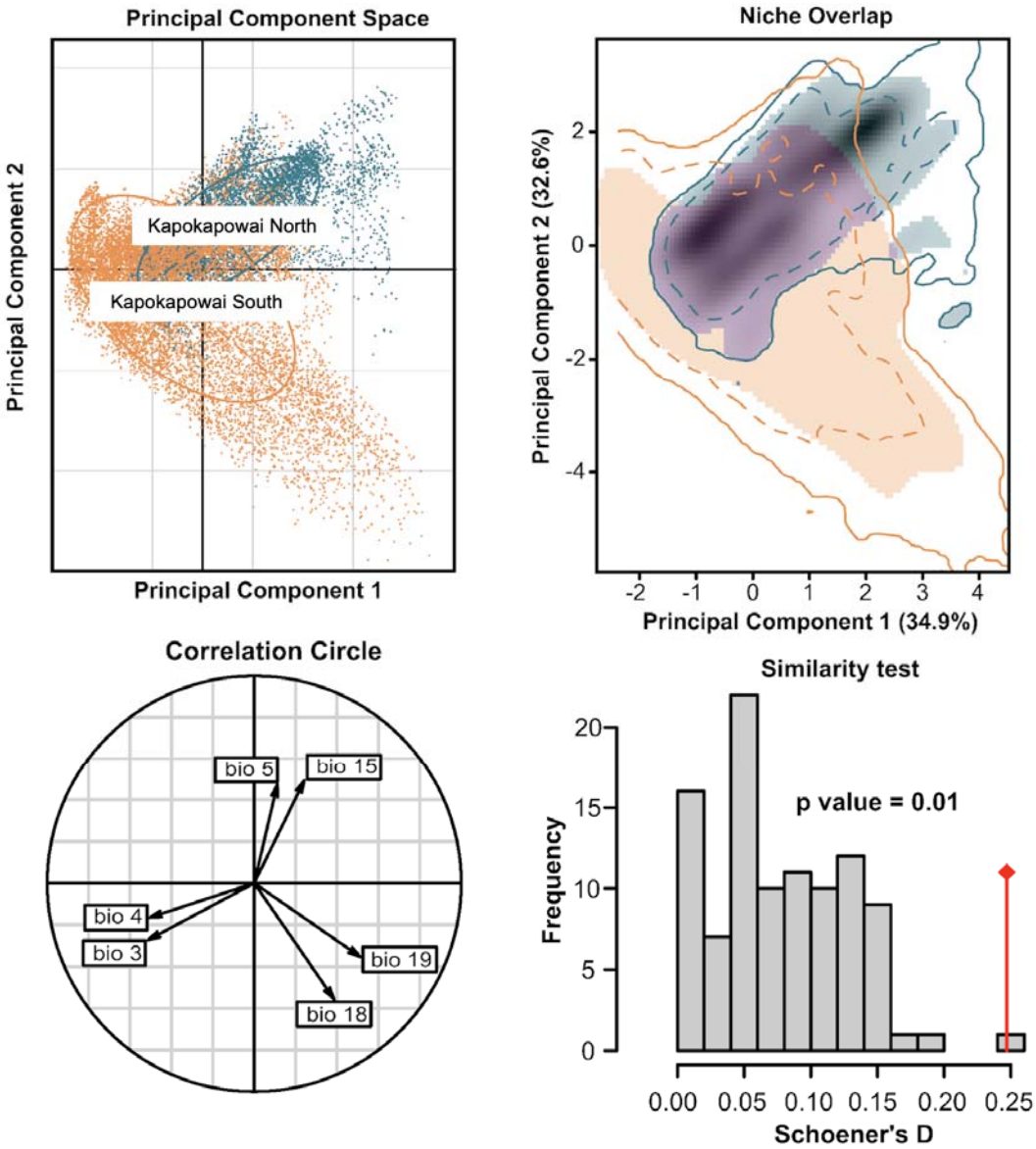

Figure 4: *Niche Overlap of Kapokapowai North and Kapokapowai South.* Ordination plot (PCA), niche overlap, correlation circle, and niche similarity tests showing niche differences between Kapokapowai North and South from Te Ika-a-Māui (North) and Te Waipounamu (South). Ordination plot represents principal 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 and barriers to gene flow

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 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 or 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), admixture (Fig. 1B), and introgression 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 latter 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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