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Species biology and demographic history determine species vulnerability to climate change in tropical island endemic birds

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Tropical single-island endemic bird populations are particularly vulnerable to climate change. This study investigates genetic evidence of how such species dealt with climate change in the past as a possible predictor of how they will respond in the future, which could provide an **important** example for the fields of conservation genetics and island biogeography. The authors' integration of genomics and habitat modeling is commendable, but we find that the support for their conclusions is currently **inadequate**: some model parameter choices do not seem to reflect the biology of the studied species or to be well founded, which can cause misalignment of modeled dynamics with glaciation windows crucial for interpreting the study's results against its claims.

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Abstract

Climate change and associated habitat fluctuations can expedite the diversification of insular lineages or lead to isolation and extinction. Tropical island birds are a model system to assess responses to climate change owing to their insular nature and ability to diversify rapidly. While there is some understanding of the diversification of tropical island avian clades, we are yet to understand the vulnerability of these species to climate change. Long-term species genetic diversity and historical demography are critical predictors of this. Therefore, we investigated the sensitivity of tropical island endemic birds to climate change and analysed how species traits determine these responses by comparing species traits with demographic histories and paleohabitat fluctuations during the Last Glacial Period (LGP). From publicly available whole genome and paleoclimatic datasets, we reconstructed tropical island endemics' past demographic histories (effective population size (Ne)) using Pairwise Sequential Markovian Coalescent (PSMC) (n = 23) and suitable habitat (n = 29) during the LGP and the Holocene. We observed that most species experienced an increase in suitable habitat between the Last Interglacial and the Last Glacial Maximum. However, a concomitant increase in Ne was only observed in the hyper-diverse passerine clade, attesting to their ability to rapidly diversify. Overall, diet specialists and large-bodied species showed a decrease in Ne during the LGP. Our results indicate that species traits dictate tropical island endemics' demographic responses to climate, and a plastic response to habitat availability could be a consequence of clades' abilities to rapidly occupy new niches and diversify. Further, our analyses revealed that most species entered the Holocene with low effective population sizes. Given that tropical island endemics have small geographic ranges and are groups

vulnerable to climate change, special efforts are necessary to conserve them. We recommend that conservation management policies add components like historical demography and species traits while assessing extinction threats for island populations.

Introduction

Tropical islands of the Indo-Australian Archipelago (IAA), the Indo-Pacific, and the Caribbean and Atlantic have had complex geological pasts that have affected their species distribution patterns. While several Pacific islands are true oceanic islands arising *de novo* from the seafloor, many islands of the Caribbean and the IAA were once connected with each other or to the continental landmasses during periods of global sea-level fall in the Quaternary (Lohman et al., 2011; Voris, 2000). These land bridges and the additional habitat they offered during periods of sea-level fall facilitated on one hand colonisations among islands and between islands and the mainland (Andersen et al., 2015; Cros et al., 2020; Irestedt et al., 2013; Moyle et al., 2009; Ng et al., 2017; Pujolar et al., 2022) and on the other, range expansions within islands in response to fluctuations in suitable habitat space. The habitat type and quality of these intermittently exposed land bridges varied, ranging from open savannah biomes to lowland forests (Cannon et al., 2009; Lohman et al., 2011). In the case of stratified elevational gradients, with tropical upland montane forests expanding onto lower slopes during periods of global cooling, upland montane species might have been able to disperse across otherwise persistent dual barriers of land and sea (Cannon et al., 2009).

Tropical islands' geologic pasts make them an important natural system to study species responses to changing habitat at both ecological and evolutionary timescales. Birds are an ideal clade for this because they are taxonomically well-characterised, are ecologically well-studied, and charismatic. Avian lineages have arisen on tropical islands during the Pleistocene (Andersen et al., 2015; Garg et al., 2018; Irestedt et al., 2013; Moyle et al., 2009), concomitant with complex, clade-wise colonisation and recolonisation trajectories (Filardi and Moyle, 2005; Jønsson et al., 2008, 2011b, 2014) including colonisations of the mainland (Jønsson et al., 2011a) and repeated, independent colonisation events (Cibois et al., 2011). In birds, these responses to changing habitat are governed by species traits in several continental taxa and non-single-island endemics (Brüniche-Olsen et al., 2019, 2021), but responses in single-island endemics are poorly understood.

With such complex biogeographic pasts, tropical, single-island endemics represent either refugial populations, or *in-situ* diversifications as explained by taxon cycles (Ricklefs, 1970; Ricklefs and Cox, 1972, 1978). Being confined to single islands, these species are exceptionally vulnerable to ongoing anthropogenic climate change which is unprecedented and unlike the past Pleistocene and early Holocene climatic change (Crowley, 1990). This is exacerbated because we are currently experiencing a period of relatively high sea levels with reduced habitat availability for species resulting in population bottlenecks across taxa (Hewitt, 2000; Willis et al., 2004) including birds (Nadachowska-Brzyska et al., 2015; Smith et al., 2021). Information on tropical, single-island endemics' demographic responses to past climate change can inform conservation efforts, owing to the genomic signatures that predispose a species to extinction (Mays et al., 2018; Spielman et al., 2004) and the fact that demographic history is directly correlated to extinction risk and resilience (Wilder et al., 2023).

Pairwise Sequential Markovian Coalescent (PSMC) is a powerful method to reconstruct the effective population size (Ne) for a species using a single diploid genome (Li and Durbin, 2011) and has been used to infer demographic history across taxa (Chattopadhyay et al., 2019; Kim et al., 2016; Kozma et al., 2016; Murray et al., 2017; Nadachowska-Brzyska et al., 2015). Using this along with paleo-ecological niche modelling allows us to directly correlate the demographic history of a species with its distributional range at different time points (Chattopadhyay et al., 2019). We perform these analyses on a global panel of tropical single-island endemics to understand the effects of past climatic changes on species.

Results

Bird species panel

Our final species panel comprises 31 tropical single-island endemic bird species. Out of these, PSMC analyses were possible for 23 species and Ecological Niche Modelling (ENM) was possible for 29 species. Both PSMC and ENM analyses could be done successfully for 21 species (Table 1). These included eight Papuan species, five Philippine species, three Caribbean species, and three species from the Bismarck Archipelago. Of these 21 species, 14 species were passerines, with two from the white-eye family (Zosteropidae). Of the non-passerines, two species were parrots (family Psittacidae). All other families were represented by single species.

Paleo-habitat reconstruction

Among the 19 climatic variables used (Supplementary table S1), we observed precipitation of the warmest quarter (BIO18) to contribute the most for each island endemic bird species except for the Caribbean species *Amazona guildingii*. 25 out of the 29 bird species experienced an increase in suitable habitat from the Last Interglacial (LIG) to the Last Glacial Maximum (LGM) (Supplementary table S2). 12 out of 14 Papuan species showed an increase in habitat availability from the LIG to the LGM, with *Cicinnurus regius* and *Pseudorectus ferrugineus* as exceptions. All Philippine species showed an increase in habitat from the LIG to the LGM as well (Figure 1–2, Supplementary information S2). Two out of the three Caribbean species experienced a decline in suitable habitat during this period. Of the remaining species, all showed an increase in available habitat. Upland Papuan species remained confined to upland montane regions at all the time points we reconstructed available habitat, with *Rhagologus leucostigma* as a notable exception (Supplementary information S2). Papuan lowland species remained largely confined to regions which were not newly exposed land bridges at all times as well. From the LGM to the present day, habitat decreased for 20 out of the 29 bird species, and two species experienced no change (Supplementary table S2). For the present study, we primarily concentrate on habitat fluctuation between the LIG and the LGM as this is the period for which we have comparative evidence of fluctuations of both habitat as well as effective population size.

Strong Quaternary fluctuations in effective population size

PSMC analyses could be successfully done for 23 species (Table 1). Results indicate large effective population size (Ne) variations in almost all bird species, corresponding to Quaternary climate shifts (Figure 3). The demographic history of these species reconstructed using PSMC analyses extends back over a million years (Supplementary information S1). Reconstructed Ne values were generally concordant across the three PSMC settings used, except for five species (*Centropus unirufus, Dicaeum eximium, Irena cyanogastra, Sterrhoptilus dennistouni, Zosterops hypoxanthus*) where Ne values had large differences across PSMC settings measured at the LIG and LGM (Supplementary table S3). However, in three of these species as well, trends of Ne increase or decrease from the LIG to LGM were robust across all three PSMC models considered (*Centropus unirufus, Irena cyanogastra, Sterrhoptilus dennistouni*) (Supplementary table S4). We found no significant difference between the different sets of PSMC settings used to estimate the change in Ne during the LGP (Kruskal-Wallis test, $\chi^2 = 0.11$, DF = 2, p = 0.94).

The 14 passerine species we analysed showed overall lower Ne values in the LGM as compared to the LIG (Figure 1–2). We obtained similar results for non-passerines as well, with *Rhynochetos jubatus* as a notable exception using the –p “4 + 30 * 2 + 4 + 6 + 10” setting, displaying a large peak followed by a crash in Ne (Supplementary information S1). This is likely a PSMC artefact, because plots using other parameter settings did not show a peak (Supplementary information S1). Along with overall lower values, we also see a smaller range of Ne values in the LGM as compared to the LIG (Figure 1–2).

Species	PSMC	ENM	Endemic Region	Passerine	Family
Actenoides hombroni	y	y	Philippines	n	Alcedinidae
Aleadryas rufinucha	y	y	Papua New Guinea	y	Oreoicidae
Alectura lathami	y	y	Australia	n	Megapodiidae
Amazona guildingii	y	y	St Vincent	n	Psittacidae
Amazona vittata	y	y	Puerto Rico	n	Psittacidae
Amblyornis subalaris	y	n	Papua New Guinea	y	Ptilonorhynchidae
Cacatua alba	y	n	Indonesia	n	Cacatuidae
Centropus unirufus	y	y	Philippines	n	Cuculidae
Chaetorhynchus papuensis	n	y	Papua New Guinea	y	Rhipiduridae
Cicinnurus regius	y	y	Papua New Guinea	y	Paradisaeidae
Cnemophilus loriae	y	y	Papua New Guinea	y	Cnemophilidae
Dicaeum eximium	y	y	Bismarck	y	Dicaeidae

Table 1. Details of the taxa included in this study.

PSMC = Pairwise Sequential Markovian Coalescent, ENM= Ecological Niche Modelling, y = yes, n = no.

			Archipelago		
Diphyllodes magnificus	y	y	Papua New Guinea	y	Paradisaeidae
Eulacestoma nigropectus	n	y	Papua New Guinea	y	Eulacestomatidae
Ifrita kowaldii	n	y	Papua New Guinea	y	Ifritidae
Irena cyanogastra	y	y	Philippines	y	Irenidae
Machaerirhynchus nigripectus	y	y	Papua New Guinea	y	Machaerirhynchidae
Melanocharis versteri	y	y	Papua New Guinea	y	Melanocharitidae
Myiagra hebetior	y	y	Bismarck Archipelago	y	Monarchidae
Oreocharis arfaki	n	y	Papua New Guinea	y	Paramythiidae
Pachycephala philippinensis	y	y	Philippines	y	Pachycephalidae
Paradisaea raggiana	y	y	Papua New Guinea	y	Paradisaeidae
Paradisaea rubra	n	y	Indonesia	y	Paradisaeidae
Parotia lawesii	n	y	Papua New Guinea	y	Paradisaeidae

Table 1. (continued)

Pseudorectes ferrugineus	n	y	Papua New Guinea	y	Pachycephalidae
Ptilorrhoa leucosticta	n	y	Papua New Guinea	y	Cinclosomatidae
Rhagologus leucostigma	y	y	Papua New Guinea	y	Rhagologidae
Rhynochetos jubatus	y	y	New Caledonia	n	Rhynochetidae
Sterrhoptilus dennistouni	y	y	Philippines	y	Zosteropidae
Todus mexicanus	y	y	Puerto Rico	n	Todidae
Zosterops hypoxanthus	y	y	Bismarck Archipelago	y	Zosteropidae

Table 1. (continued)

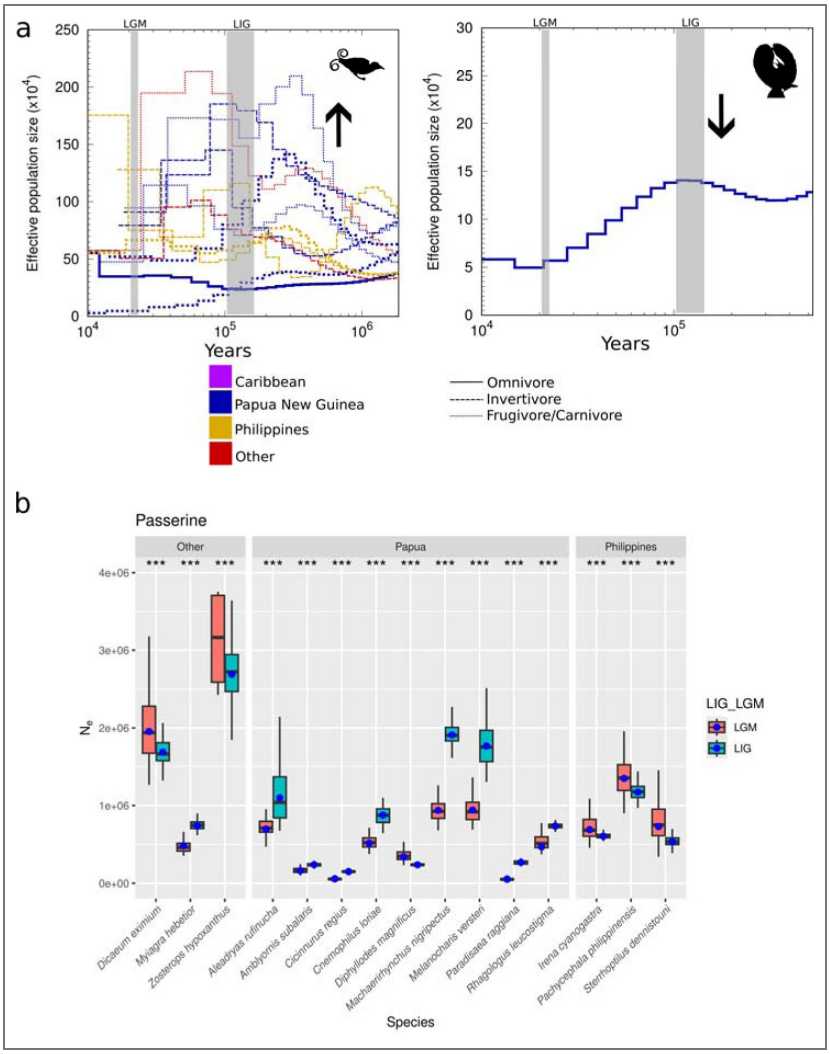

Figure 1. Effective population size for passerines.

(a) Pairwise Sequential Markovian Coalescent (PSMC) plots using the settings –p "2 + 2 + 30 * 2 + 4 + 6 + 10" displaying reconstructed effective population size values with time for passerines based on whether habitat availability increased (left) or decreased (right) during the Last Glacial Period (LGP). Colours indicate the archipelago the bird belongs to, and the line style indicates the dietary habit of the bird species. Bold lines indicate large (> 50 g body mass) bird species. The grey bands indicate the approximate durations of the Last Interglacial (LIG) and the Last Glacial Maximum (LGM). Black arrows indicate if habitat availability increased or decreased during the LGP. A mutation rate of 1.4 x 10e–9 years/site and a generation time of 2 years for passerines, and a mutation rate of 1.91 x 10e–9 years/site and a generation time of 1 year for non-passerines were used to generate plots. Only species for which both Ecological Niche Modelling and PSMC analyses were possible are shown. *Zosterops hypoxanthus* is not displayed because its Ne values far exceed those of the other species. (b) Comparisons of Effective Population Size (Ne) at the Last Interglacial (LIG) and Last Glacial Maximum (LGM) incorporating bootstrapped Ne values generated using the same PSMC settings. Boxplots display bootstrapped Ne values, and blue points display the non-bootstrapped Ne value. Outlying bootstrapped and non-bootstrapped Ne values are not displayed. "***" indicates $p < 0.001$.

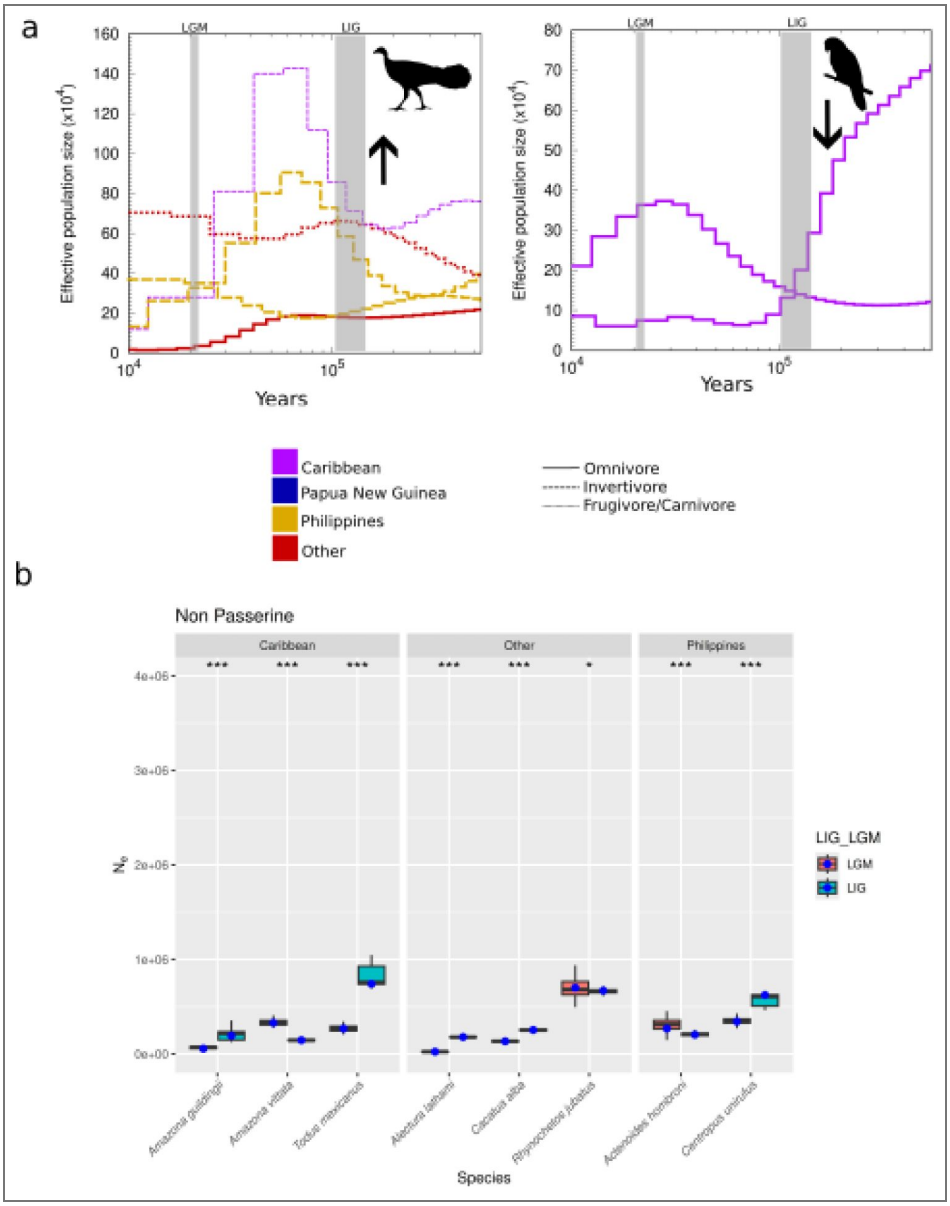

Figure 2. Effective population size for passerines.

(a) Pairwise Sequential Markovian Coalescent (PSMC) plots using the settings –p "2 + 2 + 30 * 2 + 4 + 6 + 10" displaying reconstructed effective population size values with time for non passerines based on whether habitat availability increased (left) or decreased (right) during the Last Glacial Period (LGP). Colours indicate the archipelago the bird belongs to, and the line style indicates the dietary habit of the bird species. Bold lines indicate large (> 50 g body mass) bird species. The grey bands indicate the approximate durations of the Last Interglacial (LIG) and the Last Glacial Maximum (LGM). Black arrows indicate if habitat availability increased or decreased during the LGP. A mutation rate of 1.4 x 10e–9 years/site and a generation time of 2 years for passerines, and a mutation rate of 1.91 x 10e–9 years/site and a generation time of 1 year for non-passerines were used to generate plots. Only species for which both Ecological Niche Modelling and PSMC analyses were possible are shown. (b) Comparisons of Effective Population Size (Ne) at the Last Interglacial (LIG) and Last Glacial Maximum (LGM) incorporating bootstrapped Ne values generated using the same PSMC settings. Boxplots display bootstrapped Ne values, and blue points display the non-bootstrapped Ne value. Outlying bootstrapped and non-bootstrapped Ne values are not displayed. "***" indicates $p < 0.001$, and "*" indicates $p < 0.05$.

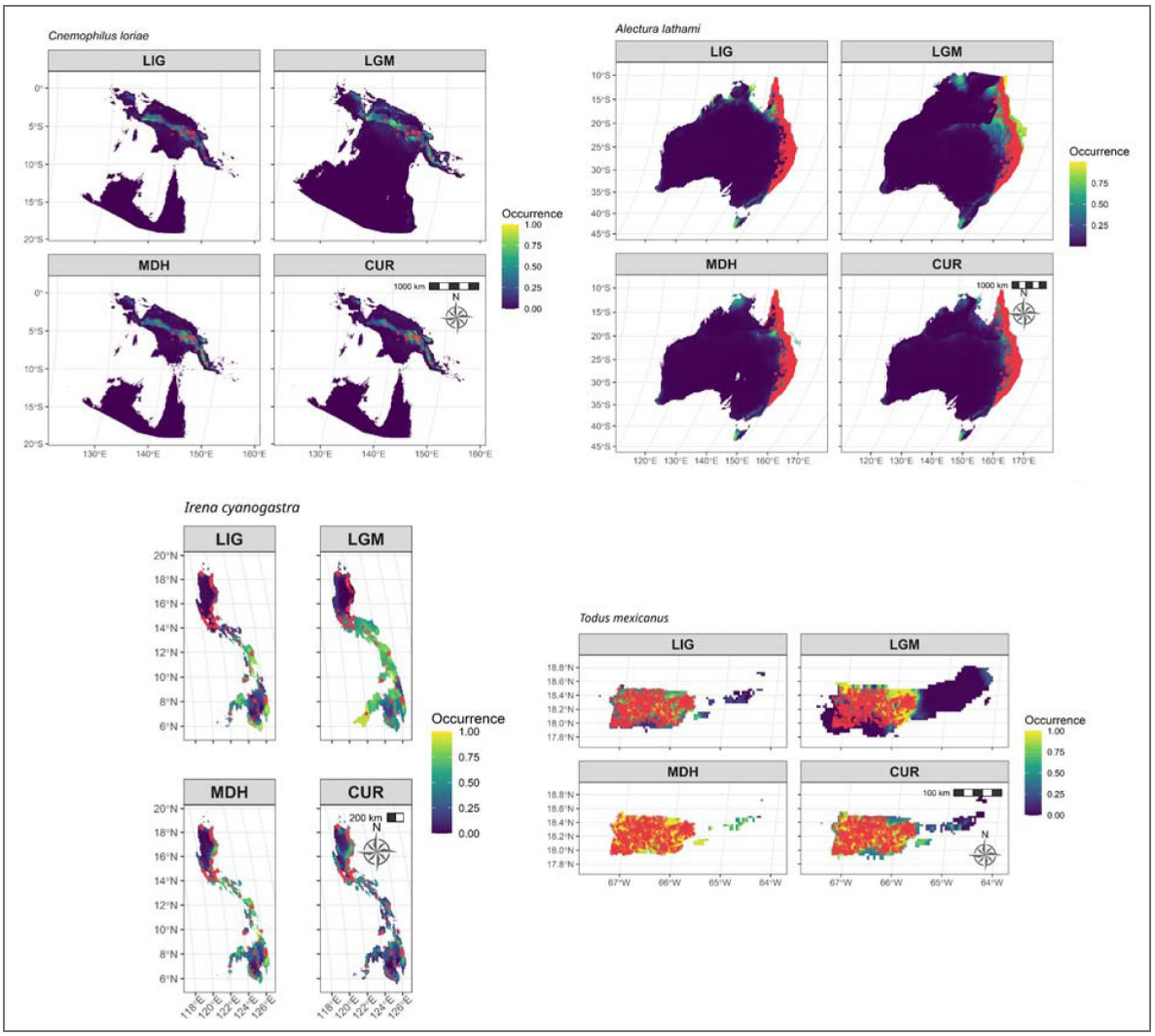

Figure 3. Example Ecological Niche Modelling plots for species from Papua (*Cnemophilus loriae)*, Australia (*Alectura lathami*), the Philippines (*Irena cyanogastra*), and the Caribbean (Puerto Rico, *Todus mexicanus*).

LIG = Last Interglacial. LGM = Last Glacial Maximum. MDH = Mid Holocene. CUR = Current. The continuous heatmap represents the probability of occurrence of the species and red points are known occurrences from GBIF. For all the plots see Figure S2.

Correlation between historical fluctuations in Ne and distribution

Habitat change was poorly associated with change in Ne for the 21 species for which both PSMC and ENM analyses were possible (Cramer's V = 0.11). However, when analysed separately, passerine species only showed a strong association (Cramer's V = 0.98), while non-passerines showed a weak negative association (Cramer's V = –0.15).

Bayesian multivariate regression models revealed that an overall fluctuation in Ne was associated with species biology and habitat change during the Last Glacial Period (LGP) even after controlling for geographical island group as a random effect (Figure 4). Most confidence intervals and beta coefficients did not overlap with zero (Figure 4) suggesting significant relationships. We found a positive association between change in habitat area (LIG to LGM) and Ne (β = 9.4, 95% CI: [1.95, 21.07]) and a negative relationship with body mass (β = −8.32, 95% CI: [–15.84, –2.59]). That is, large-bodied species showed decreases in Ne during the LGP. The change in Ne was positively correlated with the interaction term of habitat change and body mass (β = 10.28, 95% CI: [0.05, 25.18]). This suggests that habitat change and body mass act synergistically to predict the change in Ne. Diet specialists like frugivores (β = –11.89, 95% CI: [–22.57, –3.36]) and invertivores (β = –11.32, 95% CI: [–21.85, –2.85]) also showed significant negative associations with population change. However, omnivores (β = –1.28, 95% CI: [–12.77, 11.24]) did not show any association with population change. We found a marginally negative effect of clade identity as well (β = –3.64, 95% CI: [–7.91, –0.43]), that is, passerine status was associated with reducing Ne in the LGP in our dataset. Whether or not a species was a passerine was an important predictor of Ne in combination with the change in habitat from LIG to LGM (β = 8.01, 95% CI: [1.9, 17.11], suggesting that passerines respond positively to habitat change, as suggested by Cramer's V as well. Finally, the random effects parameter for country showed that there exists country-to-country variation (β = 0.86, 95% CI: [0.04, 2.25]) (Figure 4, Supplementary table S5).

Discussion

Island birds are vulnerable to the effects of climate change

Our results on the fluctuations in paleohabitat and Ne during the LGP highlight the vulnerability of island birds to climatic fluctuations. Climate fluctuations change habitat availability and, in turn, Ne, making these species particularly sensitive to a changing environment. In response to landmass expansion, several species in our panel across islands showed an increase in their Ne during the LGP (Figure 1–2, Supplementary information S1), although the overall relationship was weak (Cramer's V = 0.11). This could be because large amounts of intermittently exposed land bridge habitats remained uninhabited by the species in our panel (Supplementary figure S2). For example, we know that large amounts of exposed land bridge habitat available to our panel's Papuan species ranged from lowland evergreen to seasonal rainforest, with an expansion of upland habitats of evergreen to seasonal rainforest. Transitional hill forest formed an ecotone between these two (Cannon et al., 2009). However, most of our species inhabit dense forest (Supplementary table), which is unlikely to comprise newly exposed landbridge habitat. Moreover, rainfall is overall lower in the LGM in the tropics including South and Southeast Asia, where most of our species are from (McGee, 2020), indicating a possible explanation of why we observed precipitation of the warmest quarter to be the largest contributing bioclimatic variable for all but one Caribbean species.

Our results also reveal that both passerine and non-passerine island endemics have entered the Holocene with low Ne, based on the PSMC plots (Figure 1–2). A loss of Ne predisposes species to extinction (Mays et al., 2018; Spielman et al., 2004) with a potentially causal relationship for birds (Evans and Sheldon, 2008). The current climate crisis has greatly imperilled biodiversity with the documented loss of many vertebrate species (Steadman and Martin, 2003; Tan et al., 2023; Willis et al., 2004). Fossil evidence has revealed the extinction of several species in the Caribbean since the LGM (Morgan and Woods, 1986; Orihuela et al., 2020; Steadman et al., 1984), and many of the species in our panel are Southeast Asian where rapid

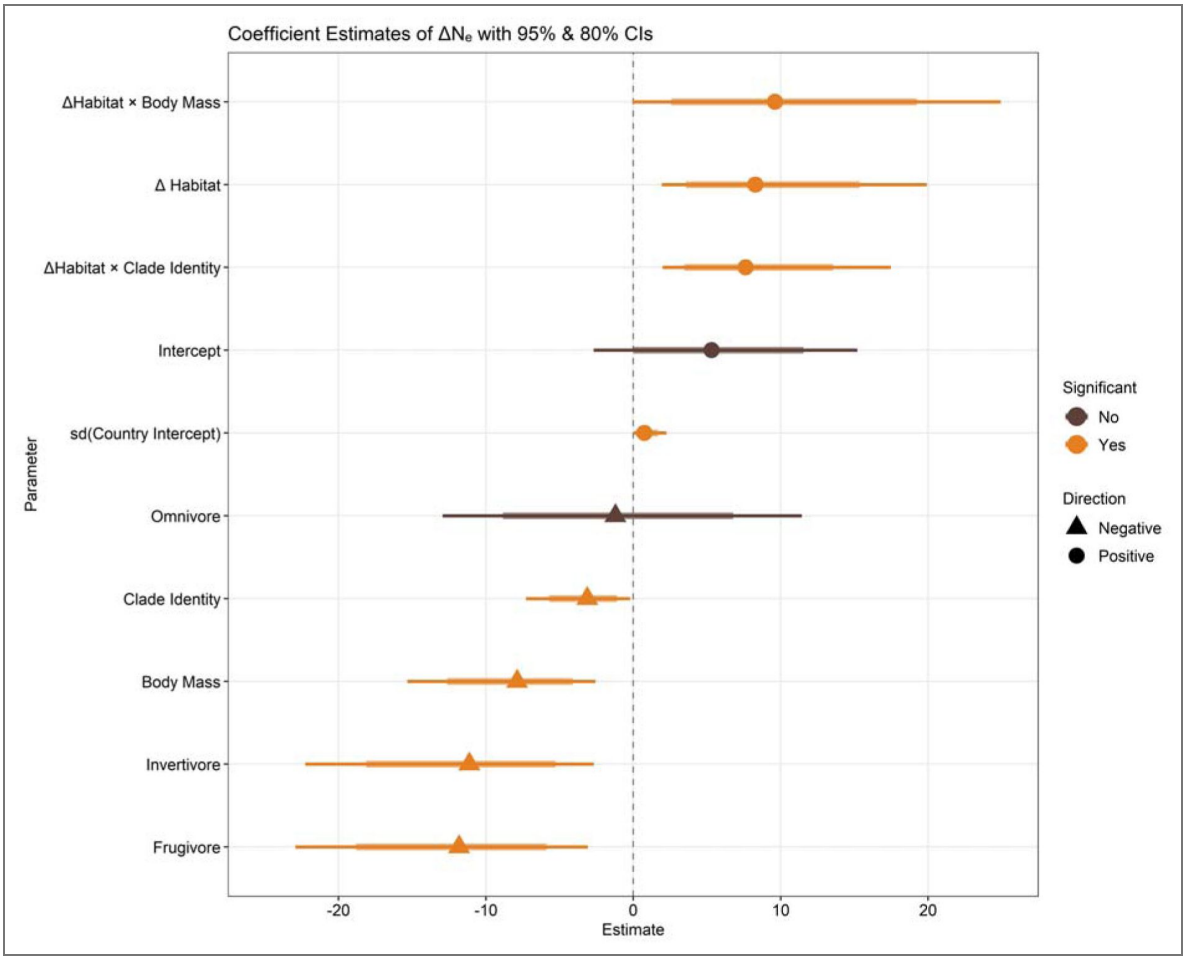

Figure 4. Results of the best Bayesian multivariate regression model performed.

The response variable represents the changes in effective population size (increased (=1) or decreased (=0)) during the Last Glacial Period. Shapes represent mean values, thick lines represent the 80% confidence intervals, and thin lines represent 95% confidence intervals. Model parameters and coefficients are provided in table S6. ΔHabitat = the change in suitable habitat from the Last Interglacial to the Last Glacial Maximum.

habitat loss is ongoing (Sodhi et al., 2004). Climate warming, sea level rise, and changes in vegetation are all associated with this loss, and flightless birds and endemics are particularly prone to extinction (Fromm and Meiri, 2021). Explicitly correlating past climate with demographic history—known to predict extinction risk (Wilder et al., 2023)—allows for a more robust validation of the latter.

Habitat loss, rise in sea level, and warming temperatures can rapidly accelerate species extinction, particularly in the tropics (Şekercioğlu et al., 2012). Effective population size, and in extension genetic diversity are associated with species survival and extinction risk (Frankham, 2005). Coalescent effective population size as used in PSMC is an important predictor of species vulnerability to extinction (Brüniche-Olsen et al., 2021; Wilder et al., 2023). Thus, an evolution-informed understanding of species vulnerability to climate change and their associations with paleohabitats can be an important tool to predict species vulnerability to the current climate crisis and future extinction risk (Brüniche-Olsen et al., 2021; Chattopadhyay et al., 2019; Gabrielli et al., 2024; Germain et al., 2023).

A strong passerine association might be driven by their rapid diversification

Passerines are a hyperdiverse clade representing over 60% of extant avian diversity. The most recent, fossil-calibrated passerine phylogeny (Oliveros et al., 2019) shows that passerines began diversifying in the Middle (47 mya) to Late Eocene (38–39 mya) with increasing diversification rates suggested as we move towards the present. Crown passerines originated in the Australo-Pacific region (Oliveros et al., 2019), and this places the many Papuan and Australian species in our panel close to the passerine diversification centre which is known to have rapid diversification rates (McCullough et al., 2022). Because bird lineages are known to have arisen on tropical islands in the Pleistocene (Andersen et al., 2015; Irestedt et al., 2013; Moyle et al., 2009), it is likely that the Southeast Asian species in our panel represent newly arisen lineages over refugia, possibly belonging to currently rapidly diversifying clades. This is supported by the fact that several of these species belong to small, often oligotypic families such as Oreoicidae (*Aleadryas rufinucha*), Ptilonorhynchidae (*Amblyornis subalaris*), Cnemophilidae (*Cnemophilus loriae)*, Eulacestomatidae (*Eulacestoma nigropectus*), Ifritidae (*Ifrita kowaldi*), Machaerirhynchidae (*Machaerirhynchus nigripectus*), and Rhagologidae (*Rhagologus leucostigma*). Many of these species belong to poorly-studied tropical genera for which species-level divergence times are unavailable. The strong passerine association between change in Ne and available habitat area (Cramer's V = 0.98; figure 4, $\beta = 9.4$) reveals that passerines are strongly plastic to the environment, most possibly as a consequence of their ability to rapidly diversify. This ability to diversify is reflected in their higher mutation rates as used in PSMC (Lanfear et al., 2010).

Non-passerines representing a paraphyletic outgroup do not show this trend (Cramer's V = – 0.15). The seven non-passerine species for which both ENM and PSMC analyses were possible belong to six different families (Table 1), representing a diverse sample across the avian phylogeny and precluding non-passerine phylogenetic insight. Notably, we confirm (Cramer's V = 0.11) that habitat area is positively correlated with genomic diversity in a clade non-specific manner for birds in general (Brüniche-Olsen et al., 2019, 2021).

Species traits influenced historic fluctuations in Ne during the LGP

The interplay of species traits and habitat availability determine how Ne values fluctuate with time in non-endemic birds (Brüniche-Olsen et al., 2021), and our results confirm this for tropical island endemics as well. Overall, habitat change in the LGP was positively associated with Ne fluctuations (Figure 4, $\beta = 9.4$). While diet generalists like omnivores showed no significant association with Ne fluctuations, specialists like frugivores (Figure 4, $\beta = –11.89$) and invertivores (Figure 4, $\beta = –11.32$) showed significant negative associations with fluctuation in Ne, implying that specialist species tended to show decreases in Ne in the LGP. Previous work has shown that large-bodied species have lower values of standing genetic diversity at a given time-point (Brüniche-Olsen et al., 2019, 2021; Eo et al., 2011). We find large-bodied species to

show a negative association with Ne fluctuations (Figure 4, β = –8.32) as well. Traits like body size and diet determine extinction risk (Ripple et al., 2017; Willis et al., 2004), and our results add to the understanding of how traits modulate Ne changes through time.

Assessing the relative contribution of species traits and habitat availability in determining Ne requires their quantitative measurements. Our methods generated values for available habitat at various time-points (Supplementary tableS2). However, Ne values can so far only be reconstructed using coalescent methods like PSMC. These values depend upon the parameter settings used. While we find these to be generally concordant across settings (Kruskal-Wallis, p = 0.94, Supplementary table S4), the precise, estimated values vary. We therefore chose to cautiously measure only the direction of change (increase or decrease) and not use numerical values.

Caveats of PSMC analyses

Coalescent methods for inferring demographic history like PSMC assume no operant selection. Our bootstrapped PSMC estimates partially account for this by subsampling from across the genome and potentially breaking any linked regions under selection. Further, PSMC traces a local population's demographic history rather than the entire species' history (Gattepaille et al., 2013; Heller et al., 2013; Ptak and Przeworski, 2002). Population structure is thus a confounding factor. For the majority of the species in our panel, modelled habitat areas in the LGM were largely contiguous (Supplementary figure S2), making panmixia and reduced population structure a possibility, with a subsequent increase in isolation and population structure towards present day. Moreover, Papua is the only island in our panel large enough to likely support population structure.

Large peaks followed by apparent collapses in Ne have also recently been shown to be an artefact of PSMC analyses (Hilgers et al., 2024). We addressed this caveat by using three different parameter combinations and tested for consensus amongst the different parameters (increase/decrease/no change). Finally, hybridization may also increase the estimates of Ne, due to increase in heterozygosity. However, we currently lack species specific studies to address this issue. With additional population genomic data on island endemics, we can address this caveat in the future. Because of these potential caveats, we only infer the direction of population size change rather than actual estimates of Ne.

Methods

Species selection

We queried Avibase (Lepage et al., 2014) for all species endemic to tropical islands and selected all species for which assembled whole genome sequences were available on GenBank using short-read data from the Illumina platform. We excluded genomes assembled from museum specimens. This resulted in a panel of 31 species (Table 1; Supplementary table S6–S7).

Pairwise Sequential Markovian Coalescent (PSMC) analyses

For each assembled diploid genome, we identified the contigs corresponding to the sex chromosomes using Satsuma ver. 2.0 (Grabherr et al., 2010) by aligning contigs to a *Gallus gallus* (chicken; BioSample: SAMN02981218) genome as a reference. All contigs mapping to the sex chromosomes were removed following standard practice (Hawkins et al., 2018; Liu and Hansen, 2016). Next, we obtained all available Illumina short reads for each species from the Sequence Read Archive (SRA) database of the NCBI, and checked them for errors using FastQC (Andrews, 2010). We used Trimmomatic (Bolger et al., 2014) for preprocessing and trimming the reads using the parameter settings "ILLUMINACLIP:TruSeq3-PE.fa:2:30:10:2:True LEADING:3 TRAILING:3 SLIDINGWINDOW:4:20 MINLEN:36".

The cleaned reads were aligned to the autosomes using BWA-MEM ver. 0.7.17 (Li, 2013) using default parameters. Next, we used SAMtools ver. 1.10 (Danecek et al., 2021) to merge all the resulting files to generate a single bam file for each species. We further sorted and removed

duplicates using SAMtools and estimated the depth of coverage for each species. We excluded species with a depth of coverage < 18x. This is a sufficient value of coverage for PSMC analyses (Li and Durbin, 2011). Next, we implemented the SAMtools mpileup-bcftools pipeline to identify SNPs. The minimum and maximum depths for calling SNPs was set to one-third and double the mean depth respectively following Nadachowska-Brzyska et al. (Nadachowska-Brzyska et al., 2015).

However, because sex chromosome reads could potentially map to other regions of the genome, we also performed PSMC using an alternate method. For this, we directly mapped raw reads files onto the genome and then called SNPs on only autosomal regions using the SAMtools mpileup-bcftools pipeline, after which we performed PSMC as above (Supplementary Information S3–4). This was done for five species. Results between the two methods were not significantly different (Supplementary information S3–4).

We used three sets of parameters for PSMC analyses and looked for consensus trends amongst them because PSMC analyses can result in spurious peaks of effective population size (Hilgers et al., 2024). We used the following parameter sets for PSMC analyses: –t5 –b –r1 –p "4 + 30 * 2 + 4 + 6 + 10", –t5 –b –r1 –p "2 + 2 + 30 * 2 + 4 + 6 + 10", and –t5 –b –r1 –p "1 + 1 + 1 + 1 + 30 * 2 + 4 + 6 + 10". These parameter options were chosen following Nadachowska-Brzyska et al. (2015). We performed 30 iterations for parameter optimisation and ran 100 bootstrap replicates using the "splitfa" PSMC utility on the psmcfa file to judge the uncertainty in our estimates. Bootstrapping was done by randomly sampling chromosome segments with replacement and running PSMC on them. To plot the results from the PSMC analyses, we used previously estimated values of mutation rates and generation times for passerines (1.4 x 10e–9 years/site and 2 years respectively; (Ellegren et al., 2012; Nadachowska-Brzyska et al., 2016) and non-passerines (1.91 x 10e–9 years/site and 1 year respectively) (Nam et al., 2010) (Supplementary material S1, supplementary table S3).

We extracted the precise values of the population scaled mutation rate (theta) from the bootstrapped and non-bootstrapped .psmc files and used these to calculate the precise values of Ne at the LIG and LGM (Supplementary information S5). We defined the LIG to be equal to 108,000–143,000 years ago, and the LGM to be equal to the atomic time interval closest to 20,000 years ago. We performed this for all three PSMC settings used and compared boxplots of bootstrapped PSMC values. We further performed the Kruskal-Wallis test for comparing across the three different PSMC settings using the "ggstatsplot" package in R (ver. 0.13.0; Patil, 2021).

Species and climate records

We performed reconstructions of paleohabitats through ecological niche models and reconstructed species distributions from four time periods: the Last Interglacial (LIG, approx. 110,000–130,000 years ago), the Last Glacial Maximum (LGM, approx. 20,000 years ago), the Mid-Holocene (MDH, approx. 6000 years ago) and Current (CUR, present day).

We used R (ver. 4.2.1; R Core Team, 2021) for all paleo-habitat modelling analyses. We accessed the location records of our bird species from the Global Biodiversity Information Facility (GBIF) in September, 2023 using the "rbgif" package (ver. 3.7.9) (Chamberlain and Boettiger, 2017) in R. We discarded duplicates and retained only human observed records using the "tidyverse" (v-2.0.0) package (Wickham and RStudio, 2023) followed by the 'CoordinateCleaner' package (v-3.0.1) (Zizka et al., 2023). We used the "spThin" package (Aiello-Lammens et al., 2014) to account for spatial autocorrelation and finally discarded spurious distribution records like records overlaying water bodies, buildings, roadways, and railways using QGIS (v-3.34+; *https://www.qgis.org/*). GBIF dataset keys used to access all the data points are in Supplementary table S8.

We used 19 climate variables (labelled BIO1 – BIO19; Supplementary table S4) for the four different time periods considered. We downloaded CHELSA (*https://chelsa-climate.org/*; Karger et al., 2021) climate predictors at a resolution of 2.5 arc-minutes (~5 km) for all regions.

We followed Chattopadhyay et al., (2019) and used a global dataset approach to account for idiosyncratic biases due to smaller datasets to extract the location points of each endemic-island group against each climatic variable. We tested for multicollinearity using variance inflation

factor (VIF) using the 'usdm' R package (Naimi, 2014) and considered variables for further analyses if their VIF value was ≤ 5 (Shrestha, 2020).

Habitat Suitability Modelling and Area Calculation

We used R to reconstruct paleo-climatic suitable habitat for 29 endemic island birds through ecological niche models for the four time-periods considered. For this, we accessed the Global Biodiversity Information Facility (GBIF) to extract our species' occurrence records. We could not perform ENM analyses for two species due to a paucity in the number of GBIF occurrence points for them (Table 1).

Data partitioning and model evaluation

For each species, we used available occurrence records from the present day to generate pseudo-absence data points. We generated 500–10,000 pseudo-absence/background points for each species depending upon the area of the island (Supplementary table S6), except for *Amazona guildingii* endemic to Saint Vincent where we generated 15 points. Saint Vincent's small land area could not accommodate more points than this. We used a subset of bioclimatic variables to generate a weighted average ensemble species distribution model (eSDM) for each island group. eSDMs were implemented in the R package "sdm" (v-1.2.37; Naimi and Araujo, 2016) applying the 'MaxEnt', 'GLM', and 'BRT' algorithms. eSDMs account for the limitations of different models by generating a weighted average of multiple models (Araújo and New, 2007; Dormann et al., 2018; Naimi and Araujo, 2016). We used k-fold cross-validation (CV) with replication for each method for training and test datasets across each endemic island group (Supplementary table S9). Model accuracy was measured using the Area Under the Curve (AUC) and True Skill Statistic (TSS) metrics. We first performed the above analyses for the present-day (CUR) distribution using the weighted-average of AUC and TSS. AUC and TSS values greater than 0.9 and 0.75 respectively have been shown to be indicators of superior model performance (Ahmad et al., 2019) and we chose a similar threshold (AUC ≥ 0.9 & TSS ≥ 0.8) to get the best ensemble model for most of the species except for 10 species for which data quality was poor (Supplementary table S9). Models for the other time points: the LIG, LGM, and MDH, were generated using the eSDM model generated based on CUR data.

Suitable area analysis

All spatial analyses were carried out using the R package 'terra' (ver. 1.7.13) (Hijmans et al., 2024). Equal area projections were used to calculate the absolute suitable area of each species across the four time-periods. To account for a spherical Earth and the limitations of landmass depiction of the original eSDM raster (World Geodetic System 1984) we reprojected it into a pseudocylindrical projection (Eckert IV). Further, we used the average quantile threshold pixels to measure the availability of absolute suitable areas for the LIG, LGM, MDH, and CUR periods (Supplementary table S2).

Statistical Analyses

We checked for associations between Ne and habitat change during the Last Glacial Period (from LIG to LGM) (LGP) using Cramer's V implemented in the"polycor" package in R (Fox, 2022). Cramver's V varies between –1 to 1, with values closer to 0 suggesting no-correlation. This was done for the entire dataset, and then for passerines and non-passerines separately.

We further explored the effects of species biology, habitat, and phylogenetic constraint on the fluctuation in Ne during the LGP using Bayesian Multilevel Models (MLMs), using the "brms" package in R (Bürkner, 2018). Our fixed effect predictors were habitat change from the LIG to LGM, diet (invertivore, frugivore, or omnivore; Supplementary table S6), body mass, and clade identity (passerine and non-passerine). The latter allows us to check if belonging to the rapidly diversifying passerine clade results in a signal. We also included country (the island/archipelago a species is endemic to) as a random effect variable for the analysis to account for country-specific effects. For the response variable i.e., the change in Ne, a Bernoulli distribution with a logit link

was used because it is a binary response variable. Thus, species traits, clade identity, and change in habitat were three sets of independent predictor variables, with the change in Ne as the response variable.

We ran a series of models (n=12) to find the best-fit model (brms11, Supplementary table S1 0) based on leave-one-out cross-validation. We generated a total of 16,000 posterior samples by using the No-U-Turn Sampler (Hamiltonian Monte Carlo) algorithm with 4 chains with 5000 iterations each (with 1000 warm-up iterations; supplementary Information S6). Further, we estimated the posterior parameters with 95% confidence intervals to find negative or positive associations between the Ne and its predictors. In addition, we assessed the posterior convergence of the sample through the R-hat statistic ($R\hat{} = 1$) where values close to 1 suggest an ideal convergence. We also reported the effective sample size for bulk and tail distributions (Supplementary table S9).

Data availability

The raw data used for this study are available on NCBI and details of the accession IDs are provided in Supplementary table S7 . All codes used in this study are provided on the Zenodo URL *https://doi.org/10.5281/zenodo.14603965* .

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Additional files

Supplementary figures

Supplementary tables

Additional information

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Peer reviews

Reviewer #1 (Public review):

Summary:

The authors combine PSMC and habitat modeling to try to connect habitat change during the Last Glacial Period to changes in Ne.

Strengths:

Observing how tropical single-island endemic bird species responded to habitat change in the past may help inform conservation interventions for these particularly vulnerable species. The combination of genomics and habitat modeling is a good idea-this sort of interdisciplinary thinking is what is needed to tackle these complex questions. Additionally, the use of PSMC makes it possible to perform this analysis on poorly-studied species with only a single genome available.

Room for Improvement:

A paper was cited to support the idea, but why coalescent Ne is a better predictor of extinction risk than current genomic diversity or current Ne isn't explicitly explained in this paper.

Differing PSMC parameters may also impact results: the differences between passerines and non-passerines was one of their main results. They explain why they chose different mutation rates for the two groups, but they do not provide any analysis to show this difference was not driven by the different mutation rates used for the two groups.

For five of the species tested, PSMC parameter differences led to different results, but the species shown in table S4 are different from what is listed in the manuscript.

Ecosystems are highly complex; there may also be other variables influencing past demographic change other than those explored here. Results should be interpreted with caution.

https://doi.org/10.7554/eLife.106369.2.sa2

Reviewer #2 (Public review):

Summary and strengths:

In this manuscript, Karjee and colleagues used coalescent based effective population size reconstruction (PSMC) from single genomes to understand past population trends in island birds and related this to life history traits and glacial patterns. In this analysis they chose to use a generation time of 2 years for passerines and 1 year for non-passerines. Non-passerine birds include Amazona vittata which only reaches sexual maturity at 3-5 years; Amazona guildingii which reaches sexual maturity at ~5 years; Amblyornis subalaris at 7 years etc. This means that the choice of generation time is very poorly matched to the species biology of many of the focal systems. What this will do is to "squash" the PSMC plot, meaning that population trends will not match with when they actually occurred. As a result, glaciation windows are not correctly placed. It is my opinion that the results are not interpretable in the current form.

The authors must adjust the generation time to roughly the median period between average age of sexual maturity and age of death. It should represent the time when an individual has had 50% of their offspring. After which all analyses must be repeated.

https://doi.org/10.7554/eLife.106369.2.sa1

Author response:

The following is the authors' response to the original reviews.

> ***eLife Assessment***
>
> *Tropical single-island endemic bird populations are particularly vulnerable to climate change. The authors investigate genetic evidence of how such species dealt with climate changes in the past as a possible predictor for how they will respond to change in the future, which could provide an important example for the fields of conservation genetics and island biogeography. The authors' integration of genomics and habitat modeling is commendable, but we find that the support for their conclusions is incomplete: at times, the results presented appear to contradict each other, the authors do not fully account for key variables, and the limited taxonomic scope may cause problematic biases for the conclusion.*

We thank the editors for supporting the premise of this study and highlighting the importance of the study approach. Based on the lacuna identified by the editors and the reviewers, we have modified the manuscript and details of the same are given below. We believe that these revisions have now substantially improved the flow and scope of the manuscript and have addressed the concerns raised by the reviewers.

> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *The authors combine PSMC and habitat modeling to try to connect habitat change during the Last Glacial Period to changes in Ne.*
>
> *Strengths:*
>
> *Observing how tropical single-island endemic bird species responded to habitat change in the past may help inform conservation interventions for these particularly vulnerable species. The combination of genomics and habitat modeling is a good idea - this sort of interdisciplinary thinking is what is needed to tackle these complex questions. Additionally, the use of PSMC makes it possible to perform this analysis on poorly-studied species with only a single genome available.*
>
> *Room for Improvement:*
>
> *Why coalescent Ne is a better predictor of extinction risk than current genomic diversity, or current Ne, isn't explicitly explained. PSMC in particular has many caveats, and some are not acknowledged or adequately addressed by the authors. For example, the authors note that population structure is a confounding factor with PSMC, but that it is not a problem in this instance. They do not provide compelling evidence for why this would be the case, they simply state that the species studied are all single-island endemics. However, single-island endemic species are not necessarily panmictic; this is even less likely to be true for species studied here that inhabit a large geographic area (ie, Australian species). Differing PSMC parameters may also impact results: the differences between passerines and non-passerines were one of their main results, but they do not provide any analysis to show that this difference was not driven by the different mutation rates used for the two groups.*
>
> *Parameters for many steps are not described, and choices that are described (such as the PSMC parameters) are not always fully explained. It is unclear why all data was mapped to the autosomes rather than removing reads that map to the sex chromosomes first. Using all the data, the reads belonging to the sex chromosomes could potentially map to other areas of the genome. It does not seem like a mapping quality filter was used, so these potential spurious alignments would not have been removed prior to analysis.*
>
> *There are points where the results are described in ways that appear to potentially differ from the supplementary figures. The authors state that even for species where PSMC results differed between models, "trends of Ne increase or decrease from the LIG to LGM were robust across all three PSMC models considered." The figures in the supplement for Pachycephala philippinensis, Rhynochetos jubatus, and Zosterops hypoxanthus appear to potentially contradict this statement, but it is difficult to tell, as the time period observed is not clearly marked on the graphs. How this robustness of trends was determined is not explained, leaving the precision of the analysis unclear.*
>
> *Table 1 also includes some information that contradicts what is in the Supplementary Tables, leading to a lack of clarity. Centropus unirufus, Chaetorhynchus papuensis, and Cnemophilus loriae are not included in Supplementary Table 4. Table 1 says Eulacestoma*

> *nigropectus, Paradisaea rubra, and Parotia lawesii did not undergo PSMC analysis, but Supplementary Table 4 says PSMC and modeling trends matched for these species. Table 1 says Rhagologus leucostigma underwent both PSMC and climate modeling, but Supplementary Table 4 says "NA" as if it was missing one of these analyses.*
>
> *Additionally, some of the results appear to contradict each other. For example, they show that there is no impact of habitat change in larger-bodied species, but also that larger-bodied species saw a decrease in Ne during the LGP. In another example, they state that when a species saw an increase in habitat during the LGP, they also had an increase in Ne. However, they also state that this was not the case for non-passerines.*
>
> *Ecosystems are highly complex; there may also be other variables influencing past demographic change other than those explored here. Results should be interpreted with caution.*

We thank the reviewer for their comments, which has helped us in improving the scope of the manuscript while also removing errors in the supporting information. We have improved the section of the manuscript which addressed the drawbacks of PSMC in our revised version. Details and rational for parameter choice are now included in the revised manuscript.

We performed additional PSMC analyses for a subset of the samples (n = 5), wherein the scaffolds mapping to the sex chromosome were removed only after mapping the reads. We compared the new approach suggested by the reviewer to our original approach and no differences in the PSMC pattern were observed, highlighting the robustness of the results (Supplementary Information Fig. S3).

Additionally, we have included multiple box-plot and tables in the revised manuscript that helps with interpreting the changes in effective population size. The details of the revisions are presented below in the “Recommendations for the authors” section. We believe that these changes have improved the scope of the manuscript and removed any redundancies and conflicts.

> ***Reviewer #2 (Public review):***
>
> *Summary and strengths:*
>
> *In this manuscript, Karjee and colleagues used coalescent-based effective population size reconstruction (PSMC) from single genomes to understand past population trends in island birds and related this to life history traits and glacial patterns. This concept is fairly new, as there are still relatively few multiple PSMC synthesis studies. I also thought that the focus on island endemics was unique and adds value to this paper. I enjoyed seeing a paper focused on South East Asia and think that this could help contribute to our knowledge of the important biodiversity within this region.*
>
> *Major weaknesses:*
>
> *My biggest concern with this paper is that the analyses are limited to 20-30 species, and significant taxonomic bias is present (there are multiple species of passerine but only 1-2 representatives of other groups). While this is not an issue alone, many of the life history traits or geographical traits are conflated with phylogenetic diversity (e.g., there are no large-bodied passerines). Thus, it is my opinion that the impact of these drivers of past population size is conflated and cannot be disentangled with the current data. The authors themselves state that the core hypothesis surrounding Ne and habitat availability is not supported by their entire dataset (only seen in Passerines). This was not clear enough in the abstract, and conclusions cannot be drawn here as the impact of taxonomy cannot be separated from data richness, traits, etc. The PSMC analysis was done according to the most recent recommendations, and this part of the manuscript is*

> *fairly robust. However, in several places, it is incorrectly stated that the PSMC measures or can infer genetic diversity; PSMC only infers past effective population size. It cannot measure genetic diversity in the past. I cannot review the habitat reconstruction modelling as I am a conservation genomics specialist.*
>
> *Appraisal:*
>
> *I am not convinced about the findings within the paper. I do not think that the results are sufficiently supported at this time, largely due to the conflation of taxonomy with other variables. As this type of comparison is new, I do think that there is a chance for reasonable impact on the field of genomics and island biogeography if the manuscript's constraints are addressed. I do not see scope for impact on conservation at this time and find the conclusions in the abstract regarding conservation relevance to be unfounded.*

We thank the reviewer for highlighting the unique and robust analytical approaches we have taken in this study. We agree with the reviewer that our sample size currently is small. However, we do observe a robust correlation between habitat fluctuation and change in effective population size. Further, the study also highlights the predicament of tropical island endemics, which are currently understudied and future studies are necessary to safeguard the biodiversity. We have highlighted this while also addressing the concerns in the revised version of the manuscript.

> ***Recommendations for the authors:***
>
> ***Reviewer #1 (Recommendations for the authors):***
>
> *Overall:*
>
> *This starts with a great premise - looking at how tropical single-island endemic bird species dealt with climate changes in the past may be a predictor of how they will respond to change in the future. Since these species are at high risk of extinction in the face of climate change, tailored approaches to conservation are a good idea. While the premise is solid, I have some questions and recommendations. At times while reading, I did feel a bit confused, which may be due to the fact that this isn't my exact area of expertise. However, if I'm confused, that means a reader from a general audience is also likely to be confused. Some results appear to be conflicting, some claims about data seem possibly inaccurate, and some major limitations are not acknowledged or fully addressed.*
>
> *Below I've noted areas that I feel could benefit from revisions. That being said, I liked the integration of habitat modeling and genomics! These sorts of multifaceted approaches are necessary when it comes to unraveling the complex dynamics involved in ecology and evolution.*
>
> *Crucial Issues to Address:*
>
> *(1) Line 75: With the lower sea levels and habitat change, you say animals can disperse across barriers of land and sea. When it comes to these single-island endemics, were they always confined to a single island? Is there no possibility of introgression with ancient populations of birds on other islands during these periods?*

We thank the reviewers for identifying the potential artifact in effective population size estimates that may occur due to hybridization/introgression. Most of our species belong to small and oligotypic families as has been addressed in the discussion section already, making them likely to be newly arisen lineages rather than refugial ones. There is scant information available in the literature on where the species in our dataset originated from, and further species-specific studies are required to identify signatures of hybridization/introgression.

However, we have included this caveat in the revised version of the manuscript (line numbers: 73-78 and 303–305).

> *(2) Lines 149-151 "However, in these species as well, trends of Ne increase or decrease from the LIG to LGM were robust across all three PSMC models considered." Please double-check this claim. Some of your figures in the supplement appear to contradict this. In particular, Pachycephala philippinensis, Rhynochetos jubatus, and Zosterops hypoxanthus appear to differ a bit in the time frame described, but it is difficult to tell-I would recommend adding some shading on the graphs to indicate the time period observed. If there was a way you determined this that is more precise than eyeballing the figures like I did, this should also be explained.*

We thank the reviewer for this comment and have reworded the sentence by cross verifying with the PSMC graphs. In addition, we have calculated the precise values of effective population size at the Last Interglacial (LIG) and Last Glacial Maximum (LGM) for each species using custom scripts and used these to evaluate whether the change in Ne during the Last Glacial Period (LGP) was significantly different for the three PSMC settings used. A table depicting these effective population size changes from LIG to LGM are also included in the revised version of the manuscript (Supplementary table S4; line numbers: 145-156 and 345-357).

> *(3) Lines 280-292: Issues with PSMC that are not acknowledged here are my largest concern. The situation being investigated does not necessarily meet all the assumptions PSMC makes (ie, neutral evolution and panmixia), which should be explained in this section. I'll point out the two issues I think should be acknowledged and addressed: First, selection is a confounding factor with PSMC, which is not mentioned here. While that's likely not an issue due to the size of the genome, this is still something that should be stated and explained. Second, the following statement is what I take the most issue with: "Population structure is thus a confounding factor. However, this is unlikely to be a problem given that all our species are single-island endemics". This needs justification. You state that in the past, islands could be connected (see my first comment regarding line 75), so it seems unlikely that 1) migration between past populations on other islands never happened, and 2) there is no population structure *on* the island.*

We thank the reviewer and have modified the PSMC caveats section of the revised version of the manuscript (line numbers: 289-307).

> *(4) Line 310: Mapping all the data to the autosomes seems inappropriate to me. The sex chromosome reads could potentially map to other areas of the genome. Unless this information was accidentally left out of the methods section, it doesn't seem like any mapping quality filter was used, so spurious alignments aren't being removed. To remove sex chromosome data, I would instead align data to the whole genome, remove all reads that map to the sex chromosomes, and then map the remaining reads to the autosomes.*

As mentioned earlier, for a subset of the species (n =5), we directly mapped raw reads files onto the genome and then called SNPs on only autosomal regions using the SAMtools mpileup-bcftools pipeline, after which we performed PSMC as above (Supplementary Information Fig. S3). We did not observe and significant difference between the two approaches. Further, only high-quality mapped reads were used for SNP calling as mentioned in the previous version of the manuscript (line numbers: 338-343; Supplementary Information Fig. S3).

> *(4) Table 1 includes some information that contradicts what is in the Supplementary Tables: Centropus unirufus, Chaetorhynchus papuensis and Cnemophilus loriae are not included in Supplementary Table 4. Table 1 says Eulacestoma nigropectus, Paradisaea*

> *rubra, and Parotia lawesii did not undergo PSMC analysis, but Supplementary Table 4 says PSMC and modeling trends matched for these species. "Pseudorectes ferrugineus" and "Rhynochetos jubatus" are spelled differently in Supplementary Table 4. Table 1 says Rhagologus leucostigma underwent both PSMC and climate modeling, but Supplementary Table 4 says "NA" as if it was missing one of these analyses.*

We thank the reviewer for identifying the errors and we have corrected for these in the revised version of the manuscript. Please see the detailed changes for these comments outlined below

Centropus unirufus, *Chaetorhynchus papuensis* and *Cnemophilus loriae* are not included in Supplementary Table S4 (Now Supplementary table S2): we have added these species to the revised table S2.

Table 1 says *Eulacestoma nigropectus*, *Paradisaea rubra*, and *Parotia lawesii* did not undergo PSMC analysis, but Supplementary Table 4 says PSMC and modeling trends matched for these species: The genomes for these samples were obtained from museums and exhibited high error rates. Hence, we excluded these samples from further analysis. However, the supplementary table S2 was not updated, and we have corrected this error in the revised version of the manuscript.

"*Pseudorectes ferrugineus*" and "*Rhynochetos jubatus*" are spelled differently in Supplementary Table 4 (Now table S2): we have corrected the typographical error in the revised manuscript.

Table 1 says *Rhagologus leucostigma* underwent both PSMC and climate modeling, but Supplementary Table 4 (Now table S2) says "NA" as if it was missing one of these analyses: This was a typographical error, and we have updated it to “mismatch”.

> *Major Issues to Address:*
>
> *(1) Lines 97-99: "Information on tropical, single-island endemics' demographic responses to past climate change can inform conservation efforts, owing to the genomic signatures that predispose a species to extinction". This needs more explanation. For example, why couldn't we just look at these genomic signatures instead of recreating demographic responses? I'm not sure I fully understand what you mean here.*

We thank the reviewer for this comment and have modified the introduction to highlight the importance of demographic history in predicting species extinction. Comparison of genomic diversity and demographic history of over 200 mammalian genomes, highlights the importance of demographic history in predicting species endangerment and extinction risk (Wilder et al., 2023) (line numbers: 99-104).

> *(2) Line 181-182: Whether or not a species was a passerine was an important predictor of Ne only in combination with the change in habitat from LIG to LGM". This is a major finding, but "respond positively to habitat change" (line 183) is a bit ambiguous. Were they responding to habitat expansion? Habitat contraction? Increase in rainfall? What is the change happening? Not all habitat changes are equal.*

We thank the reviewer for this comment and have modified this section for clarity in the revised results and discussion section of the manuscript. We observed a positive correlation between effective population size and availability of suitable habitat. Further, we observed precipitation of the warmest quarter to be the largest contributing bioclimatic variable for all but one Caribbean species (line numbers: 172-191; 196-211).

> *(3) Line 184-185: "The interaction between habitat change and body mass (β = 10.05, 95% CI: [-0.3, 24.41) suggests that there is no impact of habitat change in larger species."*

> *Doesn't this contradict the earlier finding of larger-bodied species seeing a decrease in Ne? Or do you mean the decrease in Ne was not due to habitat change?*

We have edited this section for clarity. With the inclusion of additional species, we observed a significant positive relationship between body size and effective population size (line number: 191-193).

> *(4) Lines 206-207: "Our results also reveal that both passerine and non-passerine island endemics have entered the Holocene with low genetic diversity." How does this align with the statement that passerines responded positively to habitat change?*

The observation that passerines respond positively to habitat change is based on a systematic analysis of the last glacial period. However, a close look at the entire species' demographic history reveals the often the Ne is at the lowest following the LGM, and coinciding with the advent of Holocene, the current interglacial. We have therefore modified the sentence in the revised version of the manuscript (line numbers: 213-214).

> *(5) Line 215: If we already know flightless birds and endemics are particularly prone to extinction, what is the benefit of this study? Be clear about how your method can be used in a way that is better than what people are already doing. It would be good to explicitly explain why coalescent Ne is a better predictor of extinction risk than current genomic diversity or current Ne.*

We thank the reviewer for this comment and have modified this section in the revised version of the manuscript (line numbers: 221-224).

> *(6) Line 259-261: "Habitat change in the LGP was positively associated with Ne fluctuations (Figure 3, β = 9.45), that is, species which showed an increase in habitat in the LGP also showed a concurrent increase in Ne." Is this true in all instances? I thought you found it had no effect for some, or did I misunderstand?*

We thank the reviewers for pointing this out. Species which showed an increase in habitat in the LGP did not always show a concurrent increase in Ne. Our results instead reflect an overall trend and this is clarified in the revised version of the manuscript (line numbers: 268-269).

> *Lines 328-330: Could the different mutation rates used for passerines and non-passerines be driving the differences found between the two groups?*

The difference in the mutation rate is low and using the passerine specific mutation rate for non-passerines only shifts the PSMC graph slightly. As our analysis is considering the change in Ne across the LGP, this shift is minimal and does not affect the overall results.

> *How are you connecting the demographic changes to species traits? I'm a bit confused about that, so I think some further explanation would be beneficial.*

We have modified the discussion to highlight the role of species traits in shaping the species response to habitat modification and ultimately the change in effective population size. We have included this in the revised version of the manuscript (line numbers: 437-439).

> *Minor Issues to Address:*
>
> *(1) Lines 165-168: "Habitat change was poorly associated with change in Ne for the 20 species for which both PSMC and ENM analyses were possible (Cramer's V = 0.15). However, passerine species only showed a strong association (Cramer's V = 0.96), while non-passerines showed a weak negative association (Cramer's V = -0.15)." This is phrased in a way that is a bit confusing. I'd consider rephrasing for clarity.*

We have modified this section in the revised version of the manuscript (line numbers: 167-170).

> *(2) Line 177: The confidence interval says "16.27, -2.61". I think it's supposed to be -16.27?*

We have corrected the typographical error in the revised version of the manuscript.

> *(3) Line 185-187: "Finally, the random intercept for Country (sd (Intercept)) showed a marginal positive influence (β = 0.85, 95% CI: [0.04, 2.24])". What does this mean? This needs further explanation.*

We modified this sentence in the revised version of the manuscript (line number: 189-191).

> *(4) Line 204: landbridge is misspelled as "landbride".*

We have fixed the typographical error.

> *(5) Line 310: What were your Trimmomatic parameters?*

We have included the parameters used for Trimmomatic in the revised version of the manuscript (line numbers: 324-326).

> *(6) Line 311: What were your bwa parameters?*

We used default parameters for bwa alignment and this is included in the revised version of the manuscript (line numbers: 328-329).

> *(7) Line 322-324: Why did you choose those specific parameters for PSMC? Splitting up the first time window makes sense (as shown in Hilgers 2025), but why did you choose t=5, r=1, and 84 atomic time intervals? Did you choose these parameters independently, or did you decide to use them because they were used by Nadachowska-Brzyska et al? Either way, that information is important to state.*

The parameter selection followed the suggestions based on both Hilgers et al. 2025 and Nadachowska-Brzyska et al. 2016. The information is included in the revised version of the manuscript (line numbers: 345-350).

> *(8) Lines 325-326: What did you use for bootstrapping? If not Psmcfa, why?*

We have used “splitfa” to generate files for bootstrap analysis and have included this information in the revised version of the manuscript (line numbers: 350-351).

> *(9) Lines 350-354: Please explain the reasoning behind using the different resolution and worldclim for Amazona guildingii.*

Based on the reviewer’s comment, we have re-run the habitat model with the same resolution for *Amazona guildingii* and include this in the revised version of the manuscript.

> *(10) Line 412-413: "For the response variable i.e., the change in Ne, a Bernoulli distribution with a logit link because it is a binary response variable." I think this sentence might be missing some words.*

We have fixed the typographical error in the revised version of the manuscript (line numbers: 444-445).

> *(11) Figure 1 is difficult to read, especially the top left panel. I would consider presenting this differently.*

We have supplemented Figure 1 with boxplots of effective population size values estimated during the Last Interglacial and the Last Glacial Maximum which should aid in clarity.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *The authors state that they intentionally chose to remove several avian species that would be suitable for this analysis, because they were subject to larger studies elsewhere. This seems like an unnecessary constraint, and it is my opinion that the authors need to add this data in. I am not aware of what species were excluded, but I hope this will increase the non-passerine proportion of their dataset to help them robustly address their questions. An alternative solution would be for the authors to only include passerines, but this will come at the expense of statistical power with the current dataset and so would also require an increase in sample size. Overall, I recommend including more non-passerine species with traits similar to your passerine species.*

This was a typographical error from the previous versions of the manuscript arising from the fact that we excluded museum species from our samples. We have modified this sentence in the revised version of the manuscript as well as included one new species (*Melanocharis versteri*) in our study panel (line number: 311-314).

> *It was not clear how or if PSMC bootstrapping was included in the comparisons across species, i.e. how did you include bootstrapping when you turned PSMC into a response variable within your statistical analysis? Failing to account for it would introduce measurement error into the data, and I would suggest that the authors explore how to incorporate this.*

We thank the reviewer for this comment and have calculated the precise values of effective population size during the LIG and the LGM using custom scripts to generate boxplots. These boxplots were used to investigate if effective population size values were significantly different during the LGP for all three PSMC parameter settings. Non-significant results were treated as “no change” in effective population size for further statistical analyses. The bootstrap values were used for this analysis, in addition to circumventing the issue of selection on the genome.

> *I would also like to see a greater discussion on what aspects of the PSMC curve were used for comparisons and the limitations therein. These cross-species comparisons are still relatively new, and I think they will add value to this paper.*

In our study, the change in Ne from LIG to LGM is considered. We have elaborated this in the revised version of the manuscript. Addition analysis, depicting the changes in Ne as box plots were also included to help understand the fluctuations in Ne.

> *Lines 164-168, which refer to your core hypothesis, are really unclear. What was actually found here? Please rephrase.*

We have rephrased the sentence for clarity in the revised version of the manuscript (line numbers: 169-172).

> *PSMC measures effective population size, not genetic diversity. Please change throughout.*

Based on the reviewer’s comment we have changed this in the revised version of the manuscript.

> *I was surprised to see some references to conservation within the abstract of the paper. It is important that this is also included in the discussion so that the authors ensure their*

> *logic is accessible to managers. It would also be good to discuss the risks of using PSMC to inform conservation from just one genome, as I see these being quite high.*

We thank the reviewer for this comment and have included both pros and cons of using PSMC in the revised version of the manuscript (line numbers: 229-237).

> *As this paper is based on public reference genomes, it is best practice that the original notes or reference genome papers are cited to acknowledge the data holders.*

We thank the reviewer for this comment and have included a supplementary table (Supplementary Table S7) acknowledging all the data holders.

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