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RESEARCH ARTICLE

Drivers of unique and asynchronous population dynamics in Malagasy herpetofauna

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Abstract

Aim: A long history of isolation coupled with complex landscapes makes Madagascar ideal for exploring the historical factors that have shaped patterns of population diversity and endemism. Many species-level studies have suggested Late Quaternary climate change may have influenced population dynamics in the tropics, but unique biomes and individual species properties may have driven idiosyncratic responses to these shifts. Here, we use community-scale population genetic data to investigate the impact of Quaternary climate cycles on shared demographic response and investigate the contributions of both biotic and abiotic factors which shape these demographic trajectories.

Location: Madagascar.

Taxon: Reptiles and Amphibians.

Methods: Using community-scale population genetic data, we implement a hierarchical approximate Bayesian computation approach to evaluate the degree of synchronous population expansion during glacial cycles across herpetofaunal assemblages both within and across discrete biomes and taxonomic groups. We use Bayesian model averaging to identify intrinsic and extrinsic conditions predictive of individualistic demographic change.

Results: We find that demographic responses are not uniform across groups, with more than 50% of all populations showing signal of recent expansion. Our explanatory models indicate species occupying narrow elevational ranges had a higher probability of expansion, while amphibian assemblages showed higher genetic diversity and greater departures from population neutrality. Expansion events were largely asynchronous, with coexpansion found in less than half of all populations. Exceptionally, 69%–74% of all humid-restricted populations coexpanded during the start of the Last Glacial Period at around 100 kya, supporting the hypothesis of a more extensive humid forest cover for Madagascar during this time.

Main conclusions: We show that differences in life history and regional biogeography have contributed to patterns of richness and endemism found across Madagascar, and historical connectivity across humid forests has been an important factor in shaping present-day diversity and endemism on Madagascar, particularly for amphibians.

KEYWORDS
biodiversity hotspot, coexpansion, comparative phylogeography, hierarchical approximate Bayesian computation, historical demography, Quaternary climate change

1 | INTRODUCTION

Madagascar is a large, isolated island characterized by extreme habitat heterogeneity, a well-defined tectonic history and massive in situ diversification, exemplary even among other species-rich continental biomes (Ganzhorn et al., 2001; Pyron & Burbrink, 2014). More than 90% of the amphibians, reptiles, terrestrial mammals and plants are found nowhere else on earth and remain highly threatened by anthropogenic deforestation (Vieilledent et al., 2018). Studies framed within the confines of a single tropical island present a unique opportunity to examine the already complex interactions among traits, climate and demography as they contribute to generating patterns of elevated diversity and endemism (Wilmé et al., 2006). Madagascar's long-term isolation, biotic and topographic heterogeneity, and diverse species radiations make it an ideal system for exploring how population dynamics influence community assemblage and persistence through time and across elevational gradients.

The climatic and topographic turnover between Madagascar's ecoregions has long since been invoked as a causal mechanism of the unique biodiversity gradients across the island (Raxworthy & Nussbaum, 1997). As Madagascar separated from India along its eastern coastline ~80 million years ago (Ma), moist trade winds from the Indian Ocean and a gradual equatorial shift contributed to the formation of extensive eastern rainforest biomes (Wells, 2003). Palaeoecological reconstructions indicate that this region, particularly the northeastern extent, acted as a major refugium during glacial periods (Matsumoto & Burney, 1994; Rakotoarinivo et al., 2013). Today, west of these humid and evergreen forests, Madagascar becomes increasingly arid, with deciduous forests and a high central plateau covered by a mosaic of evergreen forest and savannah grassland (Burgess et al., 2004). The southernmost biome of Madagascar is also arid, characterized by highly endemic spiny desert and xeric scrubland flora and fauna (Gautier & Goodman, 2003; Henkel & Schmidt, 2000). Throughout the Plio-Pleistocene, fossil pollen deposits indicate these arid habitats were less stable than those in the humid east (Burney et al., 2004; Virah-Sawmy et al., 2010). In particular, vegetative community turnover was especially high in the southern portions of this biome (Matsumoto & Burney, 1994). Topographic heterogeneity along the eastern escarpment has been established over 180 Mya, with more recent uplift events occurring throughout the mid-Miocene (de Wit, 2003). While sharp climatic gradients over short geographical distances across the island have contributed to patterns of endemism, these discrete differences in stability and the location of historical refugia over the Late Quaternary also contributed to the patterns of genetic diversity and associated demographic dynamics (Brown et al., 2016; Rakotoarinivo et al., 2013; Wilmé et al., 2006).

Many groups in Madagascar originated via transoceanic dispersal throughout the Cenozoic (e.g. Vences et al., 2003, 2004; Yoder & Nowak, 2006), although some geological data suggest transient Cenozoic land bridges actually facilitated many of these immigration events (Masters et al., 2021). In addition to these colonization events, more recent population dynamics have also influenced observed patterns of species richness and community diversity. Divergence for many contemporary endemics dates to the Plio-Pleistocene (Burbrink et al., 2019; Crottini et al., 2012; Goodman & Ganzhorn, 2004; Kremen et al., 2008; Wilmé et al., 2006; Yoder & Nowak, 2006), a period of intense climate change and corresponding global vegetation shifts (Hewitt, 2000, 2004; Provan & Bennett, 2008). Palynological and recent biogeographical evidence from discrete sites across the island suggest that Madagascar followed this global trend of historical climate and vegetation changes over the Late Quaternary, with historical connectivity between isolated montane rainforests via lowland and mid-elevation rainforest corridors during glacial cycles (Burney, 1987; Burney et al., 2004; Rakotoarisoa et al., 2012; Yoder et al., 2016). In particular, frequent vegetational shifts identified over Quaternary time scales in the eastern and northwestern humid forests suggest these events have been important for promoting elevated speciation rates and richness (Gasse & Van Campo, 1998; Townsend et al., 2009). Interpolations from these paleoclimatic data do not render a complete picture of Madagascar's past, especially given the dearth of vertebrate fossils from the Pleistocene (Burney et al., 2004).

Climatic change during the Late Quaternary is the paradigm for explaining the diversity across many biomes (Hewitt, 2000, 2004). In Madagascar, several studies based on single species or closely related species groups implicate Quaternary climate change as a significant force structuring populations (e.g. Crottini et al., 2012; Florio & Raxworthy, 2016; Rakotoarisoa et al., 2012, 2013; Ratsoavina et al., 2010). As population-level studies have expanded in geographical and taxonomic breadth over the last decade, it has become clear that many codistributed populations have unique demographic histories (e.g. Gehring et al., 2013; Olson et al., 2009; Rakotoarisoa et al., 2012, 2013). Although often invoked to explain these patterns, historical climate is not always causally related to patterns of endemism and richness (Brown et al., 2016). One approach successful in disentangling the relative influence of climate and intrinsic biotic traits is the study of whole assemblage responses (Chan et al., 2014). When evaluated in the context of ecological differences or similarities across assemblages, demographic responses can grant further insight to mechanisms generating community level patterns, as well as how traits accelerate or inhibit population responses to historical climate (Papadopoulou & Knowles, 2016; Sgarlata et al., 2018). Studies that incorporate both the responses of entire faunal assemblages and the biotic traits of independent populations provide an opportunity to explore the unique effects of Quaternary climate change on shaping patterns across Madagascar's biomes (Prates, Xue, et al., 2016).

If dynamic abiotic factors have significantly influenced population demographic trajectories at community levels, we expect to observe assemblage-wide population events that temporally coincide with the glacial cycling of the Late Quaternary if biomes have since remained stable and occupy similar geographical extents in present day (Burbrink et al., 2016; Chan et al., 2014; Gehara et al., 2017; Xue & Hickerson, 2017). Vertebrate assemblages on Madagascar are uniquely characterized by extreme microendemism (Goodman & Benstead, 2003), resulting in higher incidence of constrained responses for populations with limited geographical ranges and small effective sizes during periods of unfavourable climatic conditions (Gehring et al., 2013; Rakotoarisoa et al., 2013; Zenboudji et al., 2016). Alternatively, Madagascar's disparate ecoregions may be operating as continental microcosms, with taxa responding uniquely and adapting locally to disparate climatic histories (Brown et al., 2014; Vences et al., 2009; Wilmé et al., 2006). In these examples, the landscape heterogeneity of the island or habitat affinities of endemic populations may have played a significant role in community assembly. If this is the case, the elevated species richness of Madagascar may have been driven by a composite of evolutionary and ecological processes.

We therefore hypothesize that if Quaternary climate change has been an important factor shaping modern community structure across Madagascar's diverse biomes, assemblage-wide (and ecoregion wide) demographic responses on Madagascar will show temporally congruent expansion histories coinciding with the most recent global Quaternary glacial cycles. Because Quaternary climate change may uniquely affect different ecoregions in Madagascar, we do not expect these responses to be synchronous across the entire island, but rather within discrete biomes. If Quaternary climate change is not the primary driver of community structuring on Madagascar, we hypothesize that assemblage-wide demographic responses will be idiosyncratic, with little or no temporal synchronicity across expansion histories (see Figure 1). Should a non-Quaternary effect hypothesis be supported, then other factors related to biogeographical history (e.g. dispersal, isolation), ecological thresholds (e.g. tracking prey responses), biotic interactions (e.g. competition) or the ability of a population to track suitable habitat (e.g. specialists from high elevation regimes) may have structured assemblages on the island, and we hypothesize to find greater synchronicity in demographic response across biologically similar groups.

To test these hypotheses, we examine the degree of historical demographic synchronicity among herpetofaunal populations distributed across the island of Madagascar using hierarchical approximate Bayesian computation (hABC) and coalescent methods.

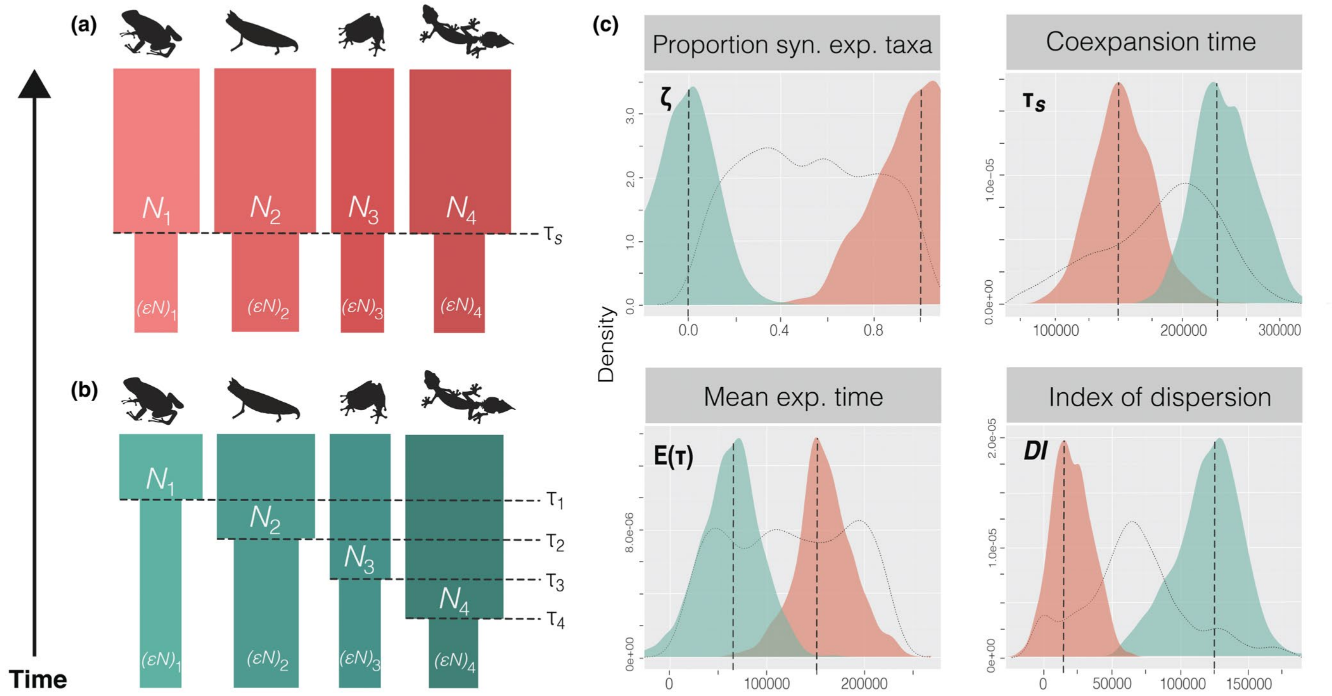

FIGURE 1 Schematic of codemographic models where each vertical pipe represents an independent population trajectory with a contemporary effective population size (N_i) that experiences instantaneous expansion ε_i the current size at time τ_i or τ_s. Demographic hypotheses are adapted from Chan et al. (2014): (a) synchronous expansion and (b) fully asynchronous expansion. (c) Comparative inference of concerted demographic response associated with each model displayed as density distributions. The following hyperparameters of interest are indicated: the proportion of taxa that expand synchronously (ζ), coexpansion time (τ_s), mean time of expansion ($E(\tau)$) and time-DI ($\mathrm{Var}(\tau)/E(\tau)$), represented here as DI. For each hyperparameter, the prior distribution is displayed as a dotted line, the distribution for the synchronous model in (a) is pink and marked with an asterisk, the asynchronous model is light blue and the dashed vertical lines are median values. Animal silhouettes by A. Kuhn.

We further explore the contribution of abiotic and biotic variables, such as life history, endemism and ecoregion distribution, on demographic response and genetic diversity using linear regression and Bayesian model averaging (BMA). In the arid biomes of Madagascar, we find that demographic responses across populations are idiosyncratic, primarily due to the landscape heterogeneity and the diverse ecologies of endemic constituents. Conversely, in the montane and lowland humid forests of eastern Madagascar, we discover that historical connectivity and refugia have resulted in shared population expansion events, ultimately contributing to the elevated diversity and endemism of regionally restricted species despite intrinsic species-specific differences.

2 | MATERIALS AND METHODS

2.1 | Data

We first compiled publicly available sequence data from GenBank and other data repositories (see Burbrink et al., 2019; Ruane et al., 2018) for 106 previously named Malagasy reptile and amphibian species for a mixture of six different mitochondrial loci (16S, ND1/2/4, COI, CYTB). Datasets with ambiguous native status (e.g. *Hemidactylus frenatus*, Vences et al., 2004; $N = 2$), locality data that could not be georeferenced ($N = 6$), or <10 individuals were removed prior to the filtering steps outlined below. For our study, we first examined the codemographic history of all populations under the justification that historical ranges are unknown, contemporary knowledge of historical climate across various biomes is not complete, and populations vary in levels of endemism to span single or multiple habitats. From here, we partitioned this population dataset into geographical groups (see 2.4 below) to enforce a more rigorous application of codistribution sensu stricto (Figure 2).

2.2 | Filtering

After initial sequence assembly and alignment (Clustal W, Thompson et al., 1994), 106 mitochondrial single-locus species-level datasets were manually inspected for gaps and overall sequence quality. Missing sequence data were trimmed from the beginnings and ends of sequence alignments, and resulting alignments varied in length from 345 to 1400 base pairs. A maximum clade credibility (MCC) tree was inferred for each species using BEAST 1.8.4 under a phylogenetic clock model using the Bayesian Skyline Plot (BSP) tree prior from 5000 post burn-in trees (Drummond et al., 2012). All trees were checked for post burn-in convergence and proper mixing using Tracer (1.6.0). Using these MCC trees and the Bayesian implementation of the generalized mixed Yule-coalescent model through the R package 'bGMYC' (Pons et al., 2006; N. M. Reid & Carstens, 2012), we partitioned the data into population-level units independently for each species-level mitochondrial dataset. Following the approach of Gehara et al. (2017), we used the single-threshold model to assign probabilities indicating conspecificity of lineages and retained only those at >0.5 probability of conspecificity, which allowed us to distinguish between deep intraspecific divergences and extensive population genetic structure from each species-level phylogeny in accordance with the assumptions of all coalescent models employed downstream (Hudson, 2002, see Appendix S1, for additional detail). These independent clusters are herein referred to as 'populations' (e.g. Gehara et al., 2017; Prates, Xue, et al., 2016).

2.3 | Single population demographic analyses

We performed demographic model selection to distinguish between three probable demographic models (constant size, bottleneck and expansion) for each individual population and obtained median estimates of parameter values of interest (e.g. effective population size, N_e) with 95% highest posterior density (HPD) intervals around these values to inform prior intervals in downstream analyses. For this step, we used ABC, which allowed us to fit a highly specific statistical model across independently evolving populations and loci for which the parameterization quickly becomes too complex to be evaluated via the likelihood function (Beaumont, 2010). Briefly, ABC analyses involved drawing parameters from pre-specified prior distributions under which simulated data were generated for a given model. This simulated data and our observed data were reduced into descriptive summary statistics to reduce computational time (e.g. number of segregating sites, nucleotide diversity, Tajima's D statistic, see Table S5 for full list of summary statistics). Using a *rejection* algorithm, a proportion of simulations within a set Euclidean distance (designated by tolerance) of the observed were accepted. Posterior model probabilities and parameter values were approximated using this proportion of accepted simulations.

For the simulation and posterior approximation of demographic parameters, uniform priors were set for effective population size and scaled by generation time, magnitude of the population size change (N_eA/N_e: 0.1–0.001, for expansion model; 2–20, for the bottleneck model) and expansion time (τ: 10,000–500,000). The broad priors on N_e were derived from the 95% HPD intervals from BSP analyses, a practice that is common in the demographic inference literature (Burbrink et al., 2016; Gehara et al., 2017; Reid et al., 2019; see Appendix S1, for details). To account for rate variation across loci and taxa when sampling an approximate per-generation mutation rate for our simulations, we drew from a normal distribution with a mean of 1×10^{-8}/site/generation and a wide standard deviation of 1.5×10^{-9} for each population. This mean mutation rate was based on previous studies that have estimated mutation rates for amphibians and reptiles (Bromham, 2002; Eo & DeWoody, 2010). While an exact mutation rate is not available for the majority of Malagasy herpetofauna, this standard deviation encompasses mitochondrial mutation rate estimates for closely related herpetofaunal groups reported in the literature (Daza et al., 2010; Gehring et al., 2013; Kurabayashi et al., 2008; Wollenberg et al., 2011; see Table 1; Table S1 for summary of prior values). We generated 500,000 simulations per model

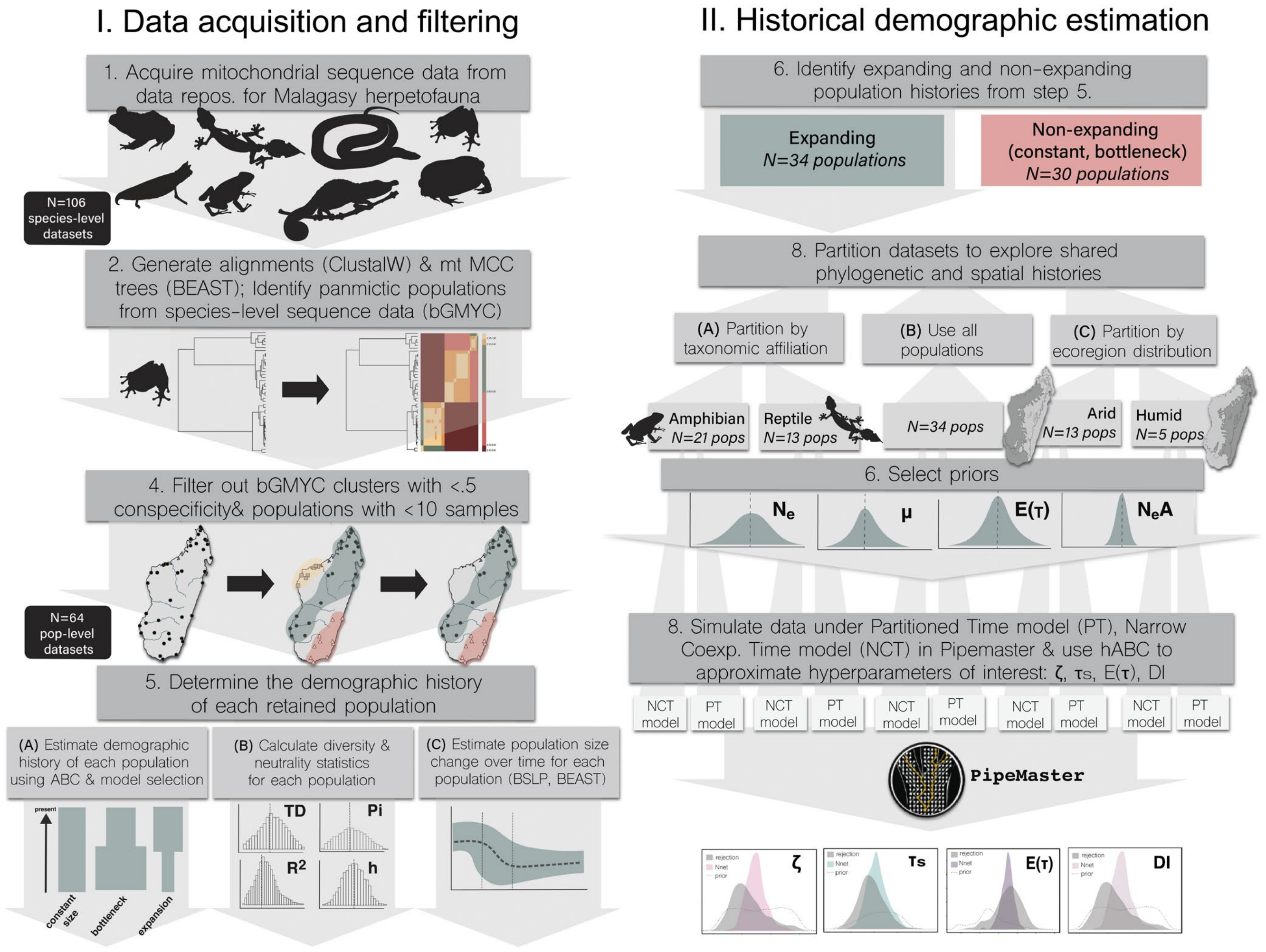

FIGURE 2 Workflow schematic from initial data acquisition to partitioned ABC analyses. For all data filtration steps and partitioning schemes, the total number of species or populations, where applicable, are listed. Animal silhouettes by A. Kuhn. DI, dispersion index; hABC, hierarchical approximate Bayesian computation; MCC, maximum clade credibility

(expansion, constant and bottleneck) for all observed populations, with number of base pairs and number of individuals specific to each observed dataset (see Table S1) under random parameter draws from the aforementioned priors in *PipeMaster* (Gehara et al., 2017; Gehara et al., 2019). We reduced our observed sequence data into the following summary statistics per population: nucleotide diversity (π), number of segregating sites (ss), haplotype diversity (H), Tajima's D and the first three bins of the site frequency spectrum (ss1, ss2 and ss3); see Table S5 for full descriptions of summary statistics. Because the ability of ABC to accurately approximate posterior distributions is partially limited by the quality of user-specified summary statistics (Burr & Skurikhin, 2013), we used principal component analysis to graphically check the simulated summary statistics and plotted the first two principal components (PCs) of the simulated data with the observed to assess model fit and optimize prior distributions for downstream codemographic analyses (Cornuet et al., 2010). Using the aforementioned summary statistics and the *rejection* algorithm via the R package 'abc' (Csilléry et al., 2012), the closest 500 simulations were retained and posterior distributions for parameters of interest were approximated for N_e, N_eA and expansion time, and posterior probabilities were inferred for each of the three models. Non-expanding populations were not further classified as having a constant versus contracting population growth history due to the limited ability of mitochondrial data to detect loss of heterozygosity when sample sizes are small (Cornuet & Luikart, 1996).

2.4 | Codemographic analyses

To determine the degree of synchronicity among expanding herpetofauna, we followed the hABC multispecies coexpansion inference procedure from Chan et al. (2014) where the following hyperparameters are approximated to describe the degree to which populations coexpand synchronously: the proportion of taxa that expand synchronously (ζ), the coexpansion time (τ_s), the mean time of expansion among all populations ($E[\tau]$) and the time-dispersion index (DI) of expansion times ($\mathrm{Var}(\tau)/E(\tau)$), represented herein as DI. We expected to recover only the most recent expansion events, occurring in

TABLE 1 Results of the model selection (using the *neuralnet* algorithm) to evaluate which of the three simulated models for various degrees of proportional synchronous population size changes (ζ) better fit our pseudoreplicated data. Models are as follows: minimum (min.) ζ (asynchronous expansion), middle (mid.) ζ (partially synchronous expansion) and maximum (max.) ζ (synchronous expansion).

	Posterior model probabilities			
Partition	**Max.**	**Mid.**	**Min.**	**Accuracy, %**
Complete	0.00	**0.89**	0.11	80
Amphibian	0.02	**0.90**	0.07	78
Reptile	0.01	0.10	**0.89**	66
Humid	0.21	**0.69**	0.11	68
Arid	0.00	0.34	**0.66**	53

response to either the Last Glacial Maximum (LGM), that is, between 26,500 and 19,000 years ago (Clark et al., 2009; Davis, 2008; Sandel et al., 2011), or prior to that, at the onset of the Last Glacial Period. Therefore, we considered that a species could have expanded due to LGM-associated climate change if the estimated expansion time was <19 kya. Because single population analyses suggested some expansion events were non-overlapping (Table S4; Figure S1), we implemented two time-prior modifications from the Gehara et al.'s (2017) study that best fit these assumptions (Figure S2). Both modifications force the coexpansion time (τ_s) and the individual population expansion times (τ_n) to be sampled from independent, non-overlapping priors, resulting in confined and more evenly sampled parameter space. The Narrow Coexpansion Time (NCT) model requires τ_s to be sampled from a narrow prior and τ_n sampled from a separate, wider prior, implementing a threshold (see 'buffer' parameterization in *multiDICE*, Xue & Hickerson, 2017) so that τ_s and τ_n must be *n*-years apart. The Partitioned Time model (PT) model forces τ_n and τ_s to be drawn from independent time block priors (where nblocks = number of populations for which τ_n is estimated), which are randomly assigned to τ_s and τ_n each simulation cycle. Because these blocks are evenly spread out over the expansion time prior, when values of ζ are dispersed and <1.0, the variance in hyper summary statistics (hSS) should also reflect these differences.

We ran a total of 16×10^6 simulations under wide uniform priors for the hyperparameters ζ [0.0–1.0] and coexpansion time, τ_s [10,000–500,000]; see Table S8 for a summary prior values. For the NCT model, a 50 kyr threshold was set around the coexpansion time (Xue & Hickerson, 2017). For the PT model, no buffer was set, and the number of time prior blocks from which τ_s was sampled was set to the number of populations in the dataset. We again reduced our observed sequence data using the summary statistics indicated in Table S5. To construct posterior distributions from accepted simulations for hSS of interest, we used both the *rejection* algorithm and an algorithm that uses a neural network to perform a regression-based correction (*neuralnet*) implemented in the R package 'abc' (Blum & François, 2010; Csilléry et al., 2012). Tolerance rates were adjusted to accept 100 points nearest the target values for *rejection* methods and the nearest 1000 for the *neuralnet* to allow for more training observations. Studies have shown that neural network regression correction may improve posterior estimates by differentially weighting simulations that are closest to the observed summary statistics, reducing dimensionality of the summary statistics, and ultimately increasing the accuracy of accepted and observed summary statistics matches (Blum & François, 2010). We used 20 neural networks with 10 nodes in one hidden layer with all parameters optimized and no heteroscedastic correction, using a log transformation of the hyperparameters of interest. To test the goodness of fit of both models to the observed data, we used the *gfit* function (Csilléry et al., 2012). We conducted ABC model selection between the NCT and PT models on the first 500,000 simulations to determine which was a better fit for our data. Prior checks are an important step in preventing biased inference in any ABC analysis due to the high dimensionality of parameter sampling. While priors that are too wide can result in falsely synchronous estimates due to inefficient sampling, overly narrow priors can conversely result in the true parameter values never being sampled (Hickerson et al., 2014; Leaché et al., 2007; Oaks et al., 2014). We performed both statistical and graphical checks on different priors by performing tests of goodness of fit of data simulated under all models for all dataset partitions and our observed data. Our null distributions were generated from simulated data using 200 replicates for use as pseudo-observed data to calculate the median of the distance between observed and accepted summary statistics and a tolerance rate of 0.2 and the *rejection* algorithm (Cornuet et al., 2010; Csilléry et al., 2012; Gelman et al., 2004). We also carried out a priori goodness of fit for NCT and PT models and performed principal component analysis with retained simulated summary statistics, visually checking the 90% envelope of simulated data to ensure that the observed summary statistics were contained within these envelopes.

Taxon-specific life-history traits could be responsible for differences in demographic response (Burbrink et al., 2016). Additionally, if the ecoregions of Madagascar experienced independent biogeographical histories, assemblages occupying dry and humid biomes will have responded differently to Pleistocene cycle phases (Wells, 2003). In particular, glacial–interglacial precipitation and temperature oscillations (in contrast to temperature) have been important for driving population dynamics in tropical latitudes (Prates, Rivera, et al., 2016). For this reason, we repeated the above steps independently for four alternative population groupings to examine extrinsic conditions or intrinsic traits that may have contributed to synchronous responses, specifically, taxonomic history (amphibian populations only, reptile populations only) and biogeographical history (populations endemic to humid and arid ecoregions of Madagascar only). For taxonomic partitions, we classified populations as either non-avian *reptiles* (e.g. family Testudinae, order Squamata, order Crocodilia; $N = 13$ populations) or *amphibians* (order Anura; $N = 21$ populations). To sort populations by biogeographical history, we used broad ecoregion assignments (see Section 2.5 for classification details). Populations restricted to the evergreen rainforest, Sambirano rainforest and central highlands were identified as *humid* taxa ($N = 13$ populations) and tested for synchronous expansion. Taxa confined to the dry deciduous forest and arid spiny bush were identified as *arid*, and separately tested for coexpansion ($N = 5$ populations) although we note that small sample sizes have less power to detect synchronous demographic change. Unless otherwise stated, these five partitioning strategies (*complete*, *amphibian*, *reptile*, *humid* and *arid*) were explored for all codemographic analyses. Finally, we evaluated the accuracy of our codemographic model selection and hyperparameter estimation procedures using leave-one-out cross validation and pseudo-observed datasets (see Appendix S1, for detail).

2.5 | Determinants of demographic history

To address alternative hypotheses that demographic change was not primarily influenced by historical climate change, we used multiple linear regression to model the predictive power of several intrinsic traits and ecological conditions on demographic history, population neutrality and genetic diversity for Malagasy herpetofauna. We assembled a suite of predictors based on the best available trait data to represent physiology, life history, taxonomy and ecology for all populations examined (detailed below). Using these predictors, we explored two continuous response variables describing population neutrality, Tajima's D (Tajima, 1989) and Ramos-Onsins and Rozas's R_2 (Ramos-Onsins & Rozas, 2006), and one continuous response variable related to the type of demographic event, expansion probability, obtained from the three-model probability results estimated in the single population ABC inference (see Table S1). Because historical fluctuations of population size and species' ranges can influence genetic differentiation, we also investigated the ability of these same variables to predict two continuous response variables (H and π) as measures of genetic diversity (Knowles & Alvarado-Serrano, 2010). We used a Pearson's correlation to determine the strength of the relationship between demographic and diversity response variables to eliminate highly correlated response variables from our final analyses.

In the absence of complete data on body mass, we examined body size (snout-vent length [SVL]). We also examined behavioural traits—activity pattern (‘diurnal’, ‘nocturnal’) and microhabitat use (‘terrestrial’, ‘arboreal’)—that are related to other ecological preferences (Keller & Taylor, 2008). Generation time was also used as a predictor, as it is representative of ecological strategies that directly impact population dynamics. Phylogenetic history could also produce shared responses in demographic history and diversity (Burbrink et al., 2016); therefore, we included taxonomy as a predictor as well (‘amphibian’, ‘reptile’). Physical landscape features can also influence demographic history and genetic diversity of populations (Wang, 2013); therefore, we also included elevational range index of dispersion as a predictor (for a detailed explanation and justification see Supporting Information and Table S1).

To address differences in biogeographic history and endemism, we classified all populations by ecoregion. We used five of the six major terrestrial ecosystems of Madagascar: ‘arid spiny bush’, ‘central highlands’, ‘dry deciduous forest’, ‘vergreen rainforest’ and ‘Sambirano rainforest’ (Goodman & Benstead, 2003; Yoder & Nowak, 2006), and a simplified classification of ‘humid’ when partial or total locality data were restricted to the evergreen rainforest, Sambirano rainforest, and central highlands and ‘arid’ when confined to the dry deciduous forest and arid spiny bush ecoregions. To determine whether any ecoregion had independent association with population neutrality or diversity, we selected among the best models across two groups of possible explanatory variables: the first with populations classified as being present or absent in each of the five ecoregions mentioned above, and a second with the simplified humid versus arid classification due to the non-independence of these two predictor variable sets.

We explored all possible combinations of predictors using two predictor variable sets to prevent redundancy, one including all ecoregions (11 predictor variables) with a total of 2048 models visited, and a simplified predictor set including only arid and humid classifications with eight predictors and thus 256 total models visited. For both the 11 and 8 predictor sets, we created global models considering all variables and possible two-way interactions between them to investigate the association between the ecology of populations and their demographic history or genetic diversity (Feldkircher et al., 2015). To perform model selection and comparison, we used BMA. Unlike standard model selection, BMA is able to account for model uncertainty and the direct comparison of non-nested models by assigning a weighted average to candidate models containing unique combinations of predictor variables representing the proportional ability of the model to predict response variables (Hoeting et al., 1999; Raftery et al., 1997). BMA over all candidate linear regression models was performed using the R package ‘BMS’ (Zeugner & Feldkircher, 2015). We assumed uniform priors over model size and applied a unit information prior on Zellner's g (Zellner, 1986). All numeric data were standardized to have a mean of 0 and standard deviation of 1. We averaged coefficients over all possible models, including models where the variable was not contained.

To ensure that intrinsic qualities of sourced data were not biasing outcomes, we regressed properties of the mitochondrial samples used, specifically, fragment size ($M = 621$, $SD = 312$) and number of individuals sampled ($M = 40$; $SD = 48$) as null predictors of the probability of population expansion prior to final analyses.

3 | RESULTS

3.1 | Population-level analyses

We obtained sequence data for 106 reptile and amphibian species from data repositories (for references and accession numbers, see Table S3). We filtered the total dataset, which resulted in a total of 64 identified panmictic populations (35 amphibian populations across 19 species, 29 reptile populations across 19 species), ranging from 15 to 200 samples/population for the following mitochondrial markers: 16S, COI, CYTB, ND4, ND2 and ND1 (avg. seq. length = 526 base pairs, see Tables S1 and S3). Our single-population ABC inference classified 34 of the 64 populations examined as expanding (13 reptiles, 21 amphibians) and 30 as non-expanding (16 reptiles, 14 amphibians, Table S1). The distribution of expanding and non-expanding taxa across the island did not show any obvious patterns with respect to ecoregion (Figure 3a), or taxonomic group (Figure 3b), but we address these components of demographic history explicitly in our predictive modelling results and discussion (Figure 5).

3.2 | Coexpansion analyses

After we tested the fit of our observed data to each time-prior model, we found that both the NCT and the PT models provided a good fit for our data across all partitions (see Figure S3). For our model selection, the best model for our *complete*, *amphibian*, *humid* and *arid* observed data partitions using the *rejection* algorithm was always NCT (posterior model probability, PMP: 0.76, 0.81, 0.68, 0.25, respectively). For the *reptile* partition, the PT model was selected over the NCT model (PMP: 0.67).

For the *complete* analyses run under the NCT model (see Figure 4), we obtained a posterior density estimate for ζ that suggested partially synchronous expansion (*rejection* mode: 0.5–0.6). The mode for the posterior distribution of the coexpansion time was consistent with late Quaternary climate change, but credible intervals were wide. The average expansion time was greater than the coexpansion time, but the credible interval encompassed the coexpansion time, $E(\tau)$ (*rejection* mode: 168 kyr; CI: 143–238 kyr). The DI was high, due to the proportion of the taxa not sharing expansion histories, which instead show older expansion times than the synchronous expansion pulse group.

Results for both the *amphibian* and *reptile* datasets simulated under the NCT model were similar (see Table 2; Figure S4); for *amphibian*, the *rejection* mode for ζ was 0.3–0.5, and for reptiles, 0.2. The posterior distribution of expansion time (τ_s) was older for reptiles (156 kyr) and $E(\tau)$ had a comparable credible interval in comparison to the amphibian dataset but with less overlap to the coexpansion credible intervals (*rejection* mode: 211 kyr; CI: 152–279, nnet mode 251 kyr; CI: 205–319). The DI for expansion times was also higher for *reptiles* for both *rejection* and *neuralnet* estimates. For both partitions, DI estimates were smaller when using the *neuralnet* regression correction. Estimates for ecoregion-restricted taxa (*humid*, *arid*) varied. *Arid* partitions indicated asynchronous population expansion and posterior distributions obtained with both *rejection* and *neuralnet* algorithms showed high density around low values of ζ (*rejection* mode: 0.2). Contrastingly, *humid* taxa had high posterior densities for ζ (*rejection* mode: 0.69, *neuralnet* mode: 0.74) and suggested the greatest proportional synchronicity of all data partitions examined (Figure S5).

Under the PT model, we obtained comparable results (Table 2; Figure S4). When examining all herpetofaunal populations (*complete*), our approximation for ζ showed nearly half of all populations had congruent demographic histories. Values for τ_s and $E(\tau)$ were still non-overlapping under this model, and the DI was high (19 kyr). Values of ζ for both assemblages were low, but not greater for either group (*amphibian* ζ: 0.27; *reptile* ζ: 0.24). Values for τ_s and $E(\tau)$ were consistent across all datasets as well. DI approximations

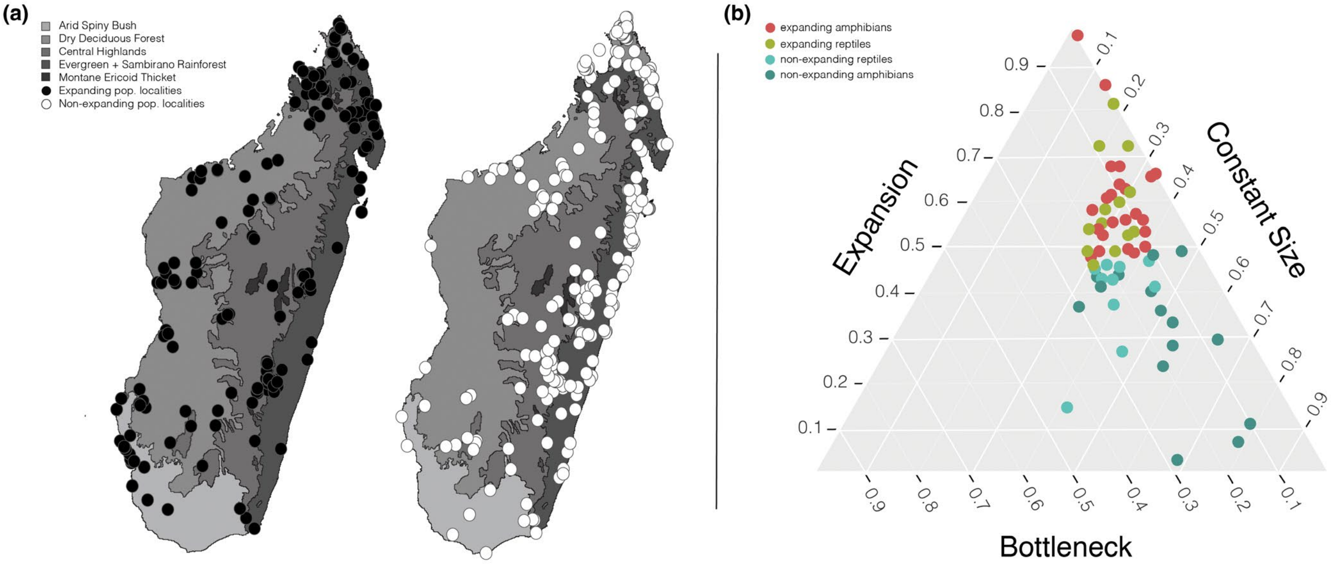

FIGURE 3 (a) Major ecoregions of Madagascar where light shades represent arid ecoregion classification (Arid Spiny Bush, Dry Deciduous Forest) and dark shades represent humid ecoregions (Central Highlands, Evergreen and Sambirano Rainforest). The 64 populations examined in this study occur across multiple localities, with individual dots representing sampling localities from which these panmictic populations were identified using the bGMYC method. Localities for populations ultimately classified as expanding (left) are coloured pink, and non-expanding populations (right) are coloured teal; (b) demographic model probabilities (listed on axes) from single population inference for the most probable model. Colouration of closed circles indicates final demographic designation of a given reptile or amphibian population. For probabilities of alternate models (see Table S1)

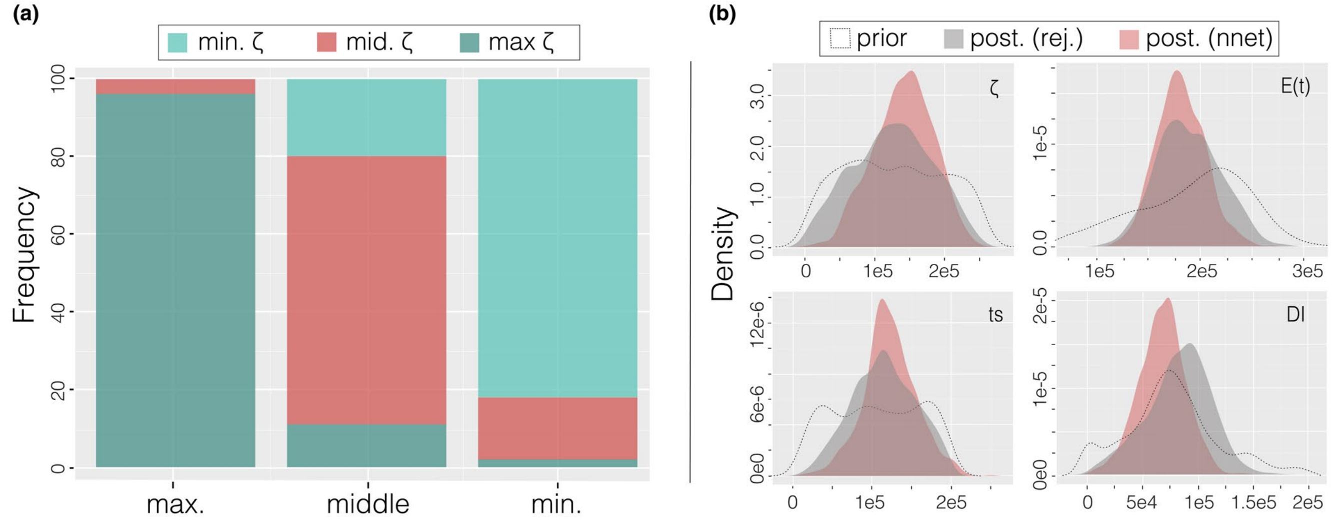

FIGURE 4 (a) Graphical representation of the confusion matrix used to evaluate the accuracy of coexpansion model classification using *K*-fold cross-validation. True models are indicated on the *x*-axis, and coloured proportions indicate the frequency of model misassignment on the *y*-axis (light teal: minimum (min.) ζ = fully asynchronous model; pink: middle (mid.) ζ = partially synchronous model; dark teal: maximum (max.) ζ = fully synchronous model). (b) Posterior densities approximated under the Narrow Co-expansion Time prior using the complete dataset for the following hyperparameters: the proportion of synchronously expanding taxa (ζ), the coexpansion time (τ_s), the mean time of expansion ($E(\tau)$) and the time-dispersion index (DI). For each hyperparameter, the prior distribution is displayed as a dotted line, the rejection algorithm posterior (rej) is in grey and the neuralnet (nnet) posterior is in pink

were lower for *reptiles* in comparison to *amphibians* (*amphibian* DI: 28 kyr; *reptile* DI: 2 kyr). For the *humid* dataset, parameter estimates were less informative than those obtained via the NCT model and showed support for greater asynchronicity. Our co-demographic inference cross-validation simulation experiments showed reasonably high model selection (Table 1; Figure 4; Figure S6) and parameter estimation accuracy (Table 1; Figure S7). See Appendix S1, for full details.

3.3 | Determinants of demographic history

When included as predictors, marker characters were never included in the best models in isolation or in combination with other variables for expansion probability (posterior inclusion probabilities [PIP] = 2.5%, 9.2% for fragment size and sample size, respectively). Thus, variability in marker length and sample size were not driving observed patterns, and we performed our final BMA excluding these predictors to reduce model space. Tajima's *D* and R_2 ($r = 0.76$; $p = 0.005$) and π and *H* ($r = 0.84$; $p = 0.003$) were all significantly correlated. For this reason, only Tajima's *D*, expansion probability and π are reported in the main text as independent response variables (for results examining *H* and R_2 as response variables (see Figures S8 and S9; Table S2).

Using BMA, we found that taxonomy was the main predictor of genetic diversity (Figure 5; Table S9). This measure alone had the highest posterior inclusion probability (91%, 86% for broad ecoregion and five-ecoregion analyses, respectively). Most of the posterior model mass contained variables that would include classification as a reptile or an amphibian; taxonomy was the only variable contained in the model with the highest posterior probability (35%) (Figure 5; Table S9). Depending on the model, taxonomy always had either a positive (Tajima's *D*) or a negative (π) coefficient.

The highest posterior predictive model for expansion probability included a combination of elevation dispersion and habitat use (14% PIP), with less influential models including activity pattern as well. Both broad ecoregion (humid/arid) and five-ecoregion predictor regressions included elevation dispersion as a significant predictor of non-neutral population history, accounting for 72%–82% of total model mass. While the highest posterior predictive model for Tajima's *D* contained a combination of taxonomy, body size, broad ecoregion classification and elevation dispersion (14% PIP, Table S9), the next best model excluded elevation dispersion (20% PIP). Less supported models included some combination of these variables, but mostly included taxonomy (86% PIP). Body size and taxonomy were negatively correlated among models predicting population neutrality and expansion probability (Figure 5; Figures S8 and S9). While we found arid-ecoregion distribution was a moderately important predictor of Tajima's *D* in the broad ecoregion predictor set (66% PIP), the dry deciduous forest was more important than in the five-ecoregion predictor set than the arid spiny bush (48% PIP, Figure S4).

4 | DISCUSSION

4.1 | Demographic expansion across and within ecoregions

Population expansion has been associated with Late Quaternary post-glacial periods globally, when climatic shifts altered habitat distribution in temperate and tropical latitudes (Richardson, 2001;

TABLE 2 Mode and credible intervals of posterior distributions of parameters estimated under each of the four models using the *rejection* (left columns) and *neuralnet* approximate Bayesian computation (ABC) algorithms. Between parentheses is the 2.5%–97.5% highest posterior density. Values of τ_s, $E(\tau)$ and DI are shown in Kyear. Hyper summary statistics approximated using all populations, amphibian-only populations and reptile-only populations. Values provided are the mode, with the 95% credible interval indicated in brackets. For each dataset partition, only results from the Narrow Coexpansion Time (NCT) model are displayed. ζ is the degree of proportional synchronicity, τ_s is the coexpansion time, $E(\tau)$ is the average expansion time and DI is the dispersion index in expansion times (var $E(\tau)/E(\tau)$).

	Rejection			Neuralnet		
	Mode	CI	R^2	Mode	CI	R^2
ζ						
Complete	0.50	(0.06–0.91)	*0.61*	0.60	(0.51–0.68)	*0.56*
Amphibians	0.34	(0.05–0.83)	*0.62*	0.52	(0.18–0.81)	*0.62*
Reptiles	0.21	(0.08–0.89)	*0.25*	0.20	(0.02–0.42)	*0.37*
Humid	0.69	(0.23–1.00)	*0.48*	0.74	(0.27–0.92)	*0.47*
Arid	0.20	(0.20–0.80)	*0.22*	0.21	(0.02–0.64)	*0.18*
τ_s						
Complete	107	(46–186)	*0.45*	121	(107–133)	*0.57*
Amphibians	78	(201–185)	*0.40*	99	(34–177)	*0.47*
Reptiles	156	(17–194)	*0.44*	127	(23–175)	*0.37*
Humid	79	(36–166)	*0.37*	106	(58–177)	*0.44*
Arid	146	(14–198)	*0.17*	120	(190–186)	*0.32*
$E(\tau)$						
Complete	168	(143–238)	*0.74*	182	(168–195)	*0.81*
Amphibians	187	(139–235)	*0.81*	166	(134–228)	*0.83*
Reptiles	211	(152–279)	*0.60*	251	(205–319)	*0.63*
Humid	155	(89–210)	*0.75*	151	(112–220)	*0.75*
Arid	214	(154–371)	*0.47*	283	(232–372)	*0.52*
DI						
Complete	86	(15–127)	*0.59*	61	(54–67)	*0.65*
Amphibians	101	(18–139)	*0.58*	85	(41–123)	*0.58*
Reptiles	765	(11–144)	*0.32*	92	(45–139)	*0.41*
Humid	791	(10–176)	*0.39*	60	(10–120)	*0.45*
Arid	95	(28–204)	*0.16*	83	(27–175)	*0.28*

Smith et al., 2014). In Madagascar, several studies have found similar correlations between recent climate change and genetic diversity, demography and species' ranges, but this has never been investigated across whole assemblages (e.g. Florio & Raxworthy, 2016; Markolf & Kappeler, 2013; Rakotoarisoa et al., 2013; Ratsoavina et al., 2010; Wilmé et al., 2006). The individual ecoregions of Madagascar are discrete and sharply juxtaposed, exhibiting distinct seasonal patterns, biotic compositions and biogeographical origins (Du Puy & Moat, 1996; Humbert, 1955; Lowry et al., 1997). Here, we find support that these steep environmental gradients have uniquely influenced historical demographic dynamics, with extreme synchronicity in expansion (ζ: 0.69–0.74) across assemblages in the humid rainforest biome of eastern Madagascar (Gehring et al., 2013; Rodríguez et al., 2015). While synchronicity is not found in our other partitions, humid-region taxa are likely the source of the partially synchronous signal we detect in the *complete* dataset (ζ: 0.5–0.6), which we recover when examining these biomes independently. Given the high DI estimated for the *humid* subset, it is likely that a few outlier taxa, such as *Heterixalus betsileo* and *Mantella baroni*, expanded earlier than the estimated coexpansion pulse, while most taxa in this region shared a single coexpansion event around the onset of the Last Glacial Period, about 100 kya.

During this time, palynological evidence shows that montane humid forests were more widespread, with greater connectivity at lower elevations and cool, dry conditions found throughout the interior (Burney et al., 2004; Gasse & Van Campo, 1998; Goodman & Rakotozafy, 1997; Matsumoto & Burney, 1994). These major vegetation shifts could have produced departures from genetic equilibrium as populations expanded from refugia to occupy suitable habitat (Davies et al., 2009; Hewitt, 2004). Our regression analyses showed that the coefficient associated with broad ecoregion distribution was significantly negative, and this predictor was included in a large proportion of models for Tajima's *D* (PIP: 0.662), reinforcing our finding that populations restricted to the eastern humid ecoregions of Madagascar experienced greater departures from equilibrium. During the Late Quaternary, interglacial periods resulted in reduced forest cover across the island, and these humid regions in the east likely acted as refugial zones for forest-adapted taxa and also provided corridors between suitable regions, ultimately facilitating expansion into novel habitat (Rakotoarisoa et al., 2013; Raxworthy & Nussbaum, 1995; Vences et al., 2009; Weyeneth et al., 2011). In particular, pollen-based palaeoecological reconstructions indicate LGM the persistence of rainforest and increased precipitation during dry period in the northeastern humid forests of Madagascar (Rakotoarinivo et al., 2013). Vegetative turnover

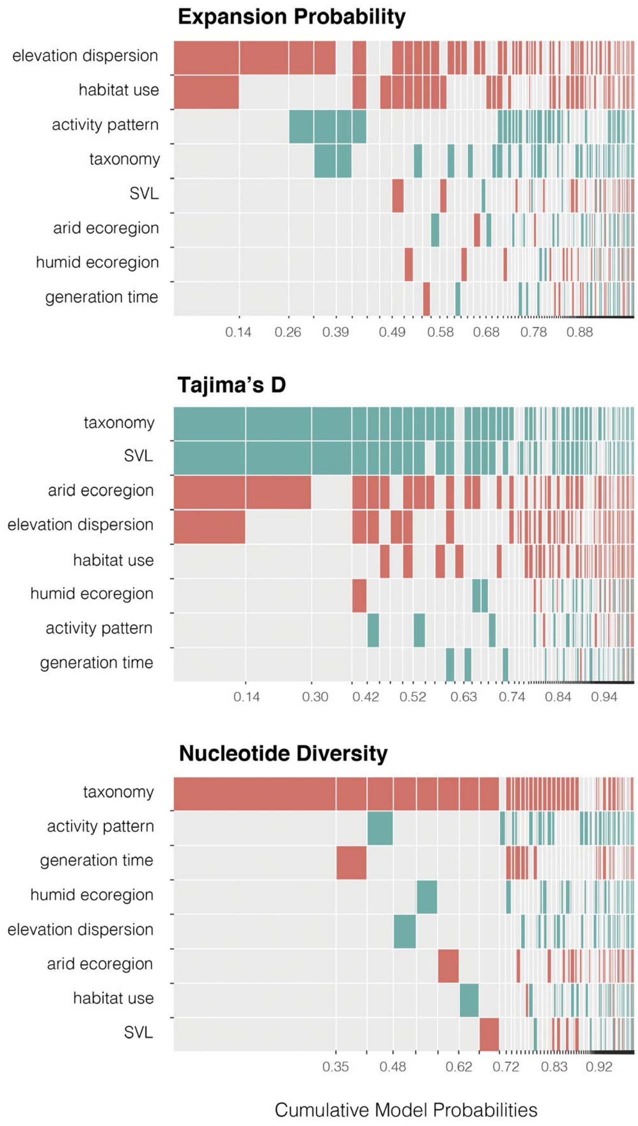

FIGURE 5 Relative importance of ecological and life-history trait predictors to the response variables expansion probability (pr[exp]), Tajima's *D* and nucleotide diversity (π). Teal blocks correspond to positive coefficients, pink blocks represent negative coefficients and grey indicates non-inclusion. Best models are shown on the x-axis; the size of each block is scaled by the posterior model probability (PMPs). Predictors are listed on the y-axis, ordered by their posterior inclusion probabilities (the sum of all predictor PMPs for all models that included a covariate)

and connections between suitable habitats may have provided opportunities for species to shift and expand during interglacial periods, which may explain the exceptional endemism and elevated herpetofaunal species richness found in this eastern rainforest zone relative to elsewhere on Madagascar (Brown et al., 2016; Burney, 1996; Vences et al., 2009; Wilmé et al., 2006). Specifically, overall herpetological species richness is lower in the western arid ecoregion of Madagascar when compared to the eastern humid forests (Andreone et al., 2005; Brown et al., 2016), potentially due to the relative habitat instability of these regions throughout the Late Pleistocene (Matsumoto & Burney, 1994). Given this, we expect species would have tracked limited ecological refugia during dryer periods, resulting in more genetic bottlenecks in this region than the humid east. Yet, we see a lack of concerted responses across communities in the arid western region, indicating that species did not respond uniformly to a single event at this time, such as increased aridity during a glacial period, or that turnover during these unstable periods was so extreme that many population-level lineages went extinct and were not sampled in our study. Alternate evidence suggests that the western arid and semiarid regions did not experience drastic vegetative changes throughout the Late Quaternary, but rather remained relatively stable since the Oligocene (Burney, 1987). Although this is another possible explanation for the lack of expansion synchronicity, further investigation with more arid endemics is required.

4.2 | Role of intrinsic traits in community-wide response

We found extrinsic environmental factors, such as distribution in the humid ecoregion, were important contributors to synchronous expansion response. Additionally, we recovered evidence that intrinsic biotic traits also played an important role in driving individualistic responses and population expansion events among Madagascar's many microendemic specialists (Papadopoulou & Knowles, 2016; Potter et al., 2018; Ricklefs, 2015). We found that elevational disparity––a proxy for the ability to occupy a large range of environmental (and therefore climatic) conditions––was an important predictor of expansion probability (PIP: 0.724), and the coefficient associated with this predictor was significantly negative (CI: −0.406 to −0.052). This indicates that species occupying larger elevational ranges are less likely to expand, while species occupying narrow elevational ranges had a higher probability of expansion. This trend was also recovered for models predicting Tajima's *D*, with elevational disparity as a moderately important predictor (PIP: 0.422); however, this coefficient estimate minimally overlaps with zero and is not significantly negative. These trends suggest that population sizes of taxa occupying large climatic ranges are buffered against environmental fluctuations in a way that species with narrow climatic niches are not, as has been seen in Malagasy bats (Weyeneth et al., 2011). Strong dispersers with generalist traits are expected to fill ranges and maintain stable effective population sizes during periods of significant climate change (Gaston, 2009). These species should tolerate a wide range of environmental conditions and therefore should display reduced signal of climate- and habitat-induced demographic fluctuation (Davis, 2008). Alternatively, species with limited dispersal capabilities, specialized traits and restricted ranges, such as those with distributions spanning limited elevational zones, are particularly sensitive to rapid climate change (Raxworthy et al., 2008) and may undergo rapid boom and bust population dynamics (Sandel et al., 2011).

Inclusion in reptilia versus amphibia was included in a large proportion of models for Tajima's *D* (PIP: 0.862) and nucleotide diversity (PIP: 0.911), in agreement with current theory which shows that more closely related species tend to have similar physiologies and life histories (Kozma et al., 2016). Here, several key differences between reptiles and amphibians, especially those related to dispersal capabilities and environmental tolerances likely explain the importance of this distinction in our BMA. The coefficients associated with these variables were significantly positive for Tajima's *D*, and significantly negative for π, suggesting more demographic stability but reduced genetic diversity for reptile populations. This result is in line with theory, as amphibians tend to be more explosive breeders, and this life-history trait is associated with larger effective population size, and thereby increased genetic diversity (Romiguier et al., 2014). For herpetofaunal communities, although amphibians had a higher probability of expansion and higher genetic diversity than reptile lineages, both *amphibian* and *reptile* partitions had comparably low proportional synchronicity (0.34 and 0.21, respectively). This indicates that, while Malagasy amphibian species showed greater propensity for coexpansion, numerous differences in life-history traits and biogeographical histories among them have reduced synchronicity in their response to past environmental conditions. Our results additionally show that the ability to tolerate a wide range of environmental conditions can promote population stability under fluctuating climatic conditions, regardless of levels of standing genetic variation.

4.3 | Drivers of idiosyncratic responses

We show that demographic expansion coinciding with changes in temperature and precipitation during the Late Quaternary climate change is not ubiquitous across all herpetofaunal assemblages in Madagascar, although 53% of all populations do reveal a signature of population expansion. Across all expanding populations, we find that total temporal synchronicity is always strongly rejected regardless of the model implemented or taxonomic group studied (Figures 1 and 4). Importantly, while inappropriate priors can result in false signal of synchronicity in ABC analyses, we show our data have substantial power to detect asynchronous divergence under informed divergence time priors (Hickerson et al., 2014; Oaks et al., 2014). In agreement with our results, several studies have shown that glacial cycles across Madagascar's ecoregions were not ubiquitous, and island-wide patterns are at least partially influenced by species-specific responses even in shared environments (Burney, 1987, 1996; Burney et al., 2004; Crowley et al., 2017; Gasse & Van Campo, 1998; Goodman & Jungers, 2014).

Historical population trajectories were less uniform across Malagasy assemblages than for those from homogeneous landscapes with comparable climatic histories (Burbrink et al., 2016; Delrieu-Trottin et al., 2017; Gehara et al., 2017; Mastretta-Yanes et al., 2018). Yet, in other systems spanning comparably diverse habitats, agreement in demographic signal across communities was still more consistent than for Madagascar (Potter et al., 2018; Reid et al., 2019; Weyeneth et al., 2011; see Table S6). Several alternative explanations may account for this outcome. No single hypothesis can entirely explain the diversity of higher taxonomic groups in Madagascar (Brown et al., 2014) and lack of temporal concordance without trait-based assessment does not entirely reject shared history (Papadopoulou & Knowles, 2016). Differences in species' physiological tolerances and ecological thresholds can cause temporal incongruence in response to the same historical event (Bai et al., 2018; Burbrink et al., 2016; Potter et al., 2018), or cause entirely different responses (e.g. expansion or bottleneck) to the same event. Thus, while species' responses could still be influenced by climate instability during the Last Glacial Period, individualistic life-history traits can attenuate this response (Bai et al., 2018; Ruane et al., 2015). Additionally, changes in vegetation across the island are unique within different ecoregions (Burney et al., 2004), further altering population dynamics as species respond to entirely different ecological events. Although these are possible explanations for non-uniform responses, species may have also been responding to alternate events occurring at this time that were not accounted for in our analyses, or they may have had no response to the event. While controversial evidence of transient land bridges throughout the Late Cenozoic (66–5 Ma) may have contributed to greater genetic variation in younger island lineages, the population dynamics investigated here are too recent to support this geological and biological evidence (Masters et al., 2021). These stochastic differences in biogeographical and assemblage histories can contribute to asynchronicity as well.

4.4 | Future directions

Intraspecific genetic diversities from community-scale mitochondrial metabarcoding studies are available for many groups of organisms (Elbrecht et al., 2018), offering a powerful tool for assessing community-wide past population dynamics using new inference tools (Overcast et al., 2019, 2021). However, we note that mtDNA sequences represent one sampled genealogy which may only partially reflect the 'true' history of a population (but see Bowen et al., 2014). The inclusion of nuclear genomic DNA could reveal alternate demographic histories, such as older expansion events, that mitochondrial data will not recover (Zhang & Hewitt, 2003). Codemographic inference using multiple markers with known mutation rate variation can bias the estimated timing of synchronous events (Nabholz et al., 2009). Although we addressed this potential bias by sampling mutation rates with mean and standard deviation informed by previous literature, multi-locus or sub-genomic nuclear sampling would lend greater power to our inference. This work provides testable hypotheses for estimating the sensitivity of target populations to future climate and land use change. In the future, this framework should be implemented with increased sampling for understudied arid regions, genome-wide data, and more detailed life-history traits to provide further insight into the historical and demographic processes responsible for the observed distribution of genetic variation and species diversity (e.g. Rakotoarisoa et al., 2013). Hindcast niche models for populations with extensive occurrence data should improve a priori predictions of historical range and assemblage response in areas like Madagascar where our understanding of Quaternary climatic history is incomplete. As more genome-wide sampling from vertebrate assemblages becomes available, we will be able to detect synchronicity in population response across multiple population pulses during historical glacial cycling events, regardless of the trajectory, providing further insight to how populations not only respond, but recover and persist through unstable conditions.

4.5 | Conclusions and implications for Madagascar

In summary, we show population expansions represent more than half of the demographic histories of Malagasy herpetofauna, with complex patterns of temporal congruence among expanding populations. Because expansions cannot be linked to a single instance of environmental change, it is likely that groups of species were either affected differently by unique events within microhabitats or responded at different temporal scales due to variability in life-history traits. Additionally, ecological interactions within communities are complex, but we see here that such biotic factors are influential to the direction and timing of species-level responses. We also show that historical connectivity across expansive humid forests has been an important factor in shaping present-day diversity and endemism on Madagascar, with species from this biome, especially amphibians, responding strongly to environmental fluctuations. The extensive forests that allowed the island's exceptional biodiversity to survive past climate changes are largely gone. Madagascar has lost almost 50% of its natural forest cover over the last six decades alone, resulting in highly fragmented habitat that will provide little buffer for large-scale species range shifts (Vieilledent et al., 2018). The impacts of current and future climate change may follow very different trajectories in comparison to past events, with extensive implications for biodiversity. This work provides testable hypotheses for predicting ecoregion-wide responses to climatic and vegetative change, which can be modified to estimate the sensitivity of entire assemblages to future climate change and capture full ecosystem turnover from an assemblage-wide perspective.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Supporting Information (Table S3) contains all GenBank accession numbers and references for all previously published data compiled for analyses, (Table S1) contains georeferenced population locality information. To access species-level fasta alignments compiled for all downstream analyses, code and associated methodological implementation with example files for assemblage and analysis of data used in this paper, see Dryad repository (https://doi.org/10.5061/dryad.573n5tb90).

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BIOSKETCH

Arianna Kuhn is interested in bringing big data approaches to understudied at-risk tropical systems. This study represents a portion of her dissertation work at the City University of New York and American Museum of Natural History on spatial patterns of biodiversity and underlying evolutionary and ecological processes driving these patterns in herpetofaunal species on Madagascar.

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SUPPORTING INFORMATION

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