1 **Geography best explains global patterns of genetic diversity and post-glacial co-**
2 **expansion in marine turtles**

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Abstract

For many species, climate oscillations drove cycles of population contraction during cool glacial periods followed by expansion during interglacials. Some groups, however, show evidence of uniform and synchronous expansion while others display differences in the timing and extent of demographic change. We compared demographic histories inferred from genetic data across marine turtle species to identify responses to post-glacial warming shared across taxa and to examine drivers of past demographic change at the global scale. Using coalescent simulations and approximate Bayesian computation (ABC), we estimated demographic parameters, including the likelihood of past population expansion, from a mitochondrial dataset encompassing 23 previously identified lineages from all 7 marine turtle species. For lineages with a high posterior probability of expansion, we conducted a hierarchical ABC analysis to estimate the proportion of lineages expanding synchronously and the timing of synchronous expansion. We used Bayesian Model Averaging to identify variables associated with expansion and genetic diversity. Approximately 60% of extant marine turtle lineages showed evidence of expansion, with the rest mainly exhibiting patterns of genetic diversity most consistent with population stability. For lineages showing expansion, there was a strong signal of synchronous expansion after the Last Glacial Maximum. Expansion and genetic diversity were best explained by ocean basin and the degree of endemism for a given lineage. Geographic differences in sensitivity to climate change have implications for prioritizing conservation actions in marine turtles as well as for

- 42 identifying areas of past demographic stability and potential resilience to future climate
- 43 change for broadly distributed taxa.

Introduction

Climatic cycles over the Quaternary period shaped extant species' ranges and evolutionary trajectories (Dynesius & Jansson, 2000). These climate changes forced many species into warm refugia during colder glacial periods in both terrestrial (Hewitt, 2000) and marine environments (Maggs *et al.*, 2008). The signature of later release from these refugia is evident in synchronous demographic expansion after the Last Glacial Maximum (LGM) exhibited by some groups, including Australian birds (Chan *et al.*, 2014). In northeastern Pacific rocky-shore communities (Marko *et al.* 2010), Pacific reef fish (Delrieu-Trottin *et al.*, 2017), and eastern Nearctic vertebrates (Burbrink *et al.*, 2016), however, responses to warming were more individualistic, resulting in asynchronous or partially synchronous patterns of demographic change. Understanding assemblage responses to past climate change is crucial for predicting the consequences of current climate change for biodiversity (Prates *et al.*, 2016) and for effectively allocating resources for biological conservation (Graham & Grimm, 1990). For instance, species in areas that were climatically more stable over time should have high genetic diversity and deeper within-species divergences due to lower extinction rates and larger population sizes, and species inhabiting regions of historic climate instability should exhibit low genetic diversity and low within-species divergences (Grant and Bowen, 1998). Areas harboring species with higher genetic diversity can be identified with comparative demographic analysis and represent high conservation priorities (Carnaval *et al.*, 2009).

To better understand patterns of past demographic change and more accurately predict potential future changes, it is necessary to assess the role of abiotic drivers as well as species-specific characteristics that may have influenced demographic trajectories. Large-scale responses to climate change in globally-distributed marine species can be especially useful case-studies. Paleoclimatic marine research suggests that the Indo-Pacific region maintained the warmest temperatures among all global oceans and experienced less temperature variation than the Atlantic during the Pleistocene (Annan & Hargreaves, 2013). If temperature variability caused demographic fluctuations in the marine realm, Indo-Pacific populations should then be more stable and genetically diverse than Atlantic populations. Furthermore, if changing climate were the main driver of demographic change, population expansions should exhibit high synchrony corresponding with warming (e.g. Gehara *et al.*, 2017). Alternatively, if species traits such as life history, body size, or degree of diet specialization primarily explain the demographic trajectory of populations during the late Pleistocene (as observed in bats; Carstens *et al.* 2018), there should be a stronger association between population trajectory and these species-level predictors, rather than geographic factors.

Marine turtles (superfamily Chelonioidea) are an ideal group in which to conduct comparative demographic tests of these alternate hypotheses. Because of their global distribution, these chelonians can be used to identify large-scale responses to climate change. Marine turtle diversity is composed of seven recognized species (Table 1), six in the family Cheloniidae (hard-shelled sea turtles) and one forming the monotypic family Dermochelyidae, containing the leatherback turtle (*Dermochelys coriacea* Vandelli). All

species except the flatback turtle (*Natator depressus* Garman) inhabit open-ocean habitat during the juvenile period (Bolten, 2003), and most adult females periodically migrate between feeding grounds and nesting beaches (Plotkin, 2003). Most marine turtles, except leatherback turtles, experience adverse physiological consequences when exposed to waters colder than approximately 15°C, and as such they are mainly limited to tropical and warm temperate waters (Davenport, 1997). Temperature also affects embryonic development and hatchling sex in all species, and these characteristics constrain the distribution of suitable nesting habitat to tropical or subtropical areas (Davenport, 1997). It is therefore plausible to hypothesize that warming following the LGM would increase suitable marine and nesting habitat and thus result in synchronous increases in marine turtle population sizes.

Despite their considerable dispersal ability, most marine turtle species exhibit spatial genetic structure among populations, as evidenced by their mitochondrial DNA (mtDNA) (Bowen and Karl 2007, Jensen et al. 2013). Genetic structure among ocean basins represents both ancient vicariance between the Atlantic-Mediterranean and the Indo-Pacific caused by the uplift of the Isthmus of Panama and a historical barrier to gene flow (the cold-water Benguela current) between the Indian and Atlantic oceans at Cape Agulhas, South Africa (Bowen & Karl, 2007), as well as more recent colonization events between the Indian and Atlantic oceans (Bowen *et al.*, 1997; Dutton *et al.*, 2013). Within the Indo-Pacific, gene flow between the western Pacific and the Indian Ocean was limited during glacial periods during which the Sahul and Sunda Shelves became exposed (Dethmers et al. 2006). Additional structure within basins is likely due to natal philopatry

by breeding females and population contraction and expansion in response to Pleistocene climatic cycles (Reece et al. 2005, Bowen and Karl 2007). Genetic studies focused on individual species have found signatures of population expansion in some, but not all, mitochondrial lineages (Leroux *et al.*, 2012; Naro-Maciel *et al.*, 2014; Shamblin *et al.*, 2014; Vargas *et al.*, 2016, Hahn unpublished). However, no study to date has attempted a quantitative comparison of historic changes in population size across these species in different ocean basins, and the degree to which global change in population size in response to Quaternary climate change in marine turtles was uniform or synchronous remains unknown.

Here, we compile mitochondrial DNA sequences from all seven species to estimate parameters relating to demographic history for individual lineages and for marine turtles as a whole. We employ coalescent simulations and approximate Bayesian computation (ABC) to make inferences in a cohesive, model-based framework. Our primary research questions are: (1) What proportion of lineages show evidence of expansion? (2) Was population expansion synchronous across expanding lineages, and did expansion occur subsequent to the Last Glacial Maximum? (3) What factors drove lineages to either expand, decline, or remain stable in the face of past climate change? and (4) Do particular geographic regions exhibit evidence of historic demographic stability and high genetic diversity across marine turtle species?

Materials and Methods

Data compilation

We obtained publicly available mitochondrial control region sequence data from Genbank for six of the seven sea turtle species, as well as unpublished sequence data for the flatback turtle and for Atlantic olive ridley turtles (*Lepidochelys olivacea* Eschscholtz) (Supplementary Materials 1). We grouped haplotypes according to “clades”, “lineages”, or “haplogroups” previously identified in the literature, resulting in 23 total lineages (Figure 1). These lineages mainly represent groups of haplotypes with pre-LGM origins, ranging from the late Pleistocene to the Pliocene (Shanker *et al.*, 2004; Leroux *et al.*, 2012; Naro-Maciel *et al.*, 2014; Shamblin *et al.*, 2014; Vargas *et al.*, 2016). In several species, some Atlantic haplotypes are closely related to Indo-Pacific haplotypes due to recent colonization (2 *Dermochelys* lineages, Dutton *et al.* 2013; one hawksbill turtle (*Eretmochelys imbricata* Linnaeus) lineage, Monzón-Argüello *et al.* 2011; and one *L. olivacea* lineage; Shanker *et al.* 2004). As these Atlantic populations could have experienced different climatic conditions than Indo-Pacific source populations, we also split these into separate lineages. For leatherback and loggerhead turtles (*C. caretta* Linnaeus), we grouped sequences from South Africa with Atlantic-Mediterranean sequences in accordance with previous studies (Shamblin *et al.*, 2014; Dutton *et al.*, 2013).

To generate a population genetic dataset for each lineage we used haplotype frequency data available in the literature mainly from studies of nesting females at rookeries (see Supplementary Materials 1 for sources and additional details). We excluded lineages with

<30 samples as these contained too little information for downstream analyses. We randomly sampled 200 sequences from each larger dataset using an R script (available at github.com/gehara) to represent each of these lineages to reduce the computational resources needed and to standardize the amount of sequence data used per lineage. Haplotype frequencies for the subsampled datasets were representative of the original datasets (Supplementary Materials 2). After subsampling, the final dataset consisted of 3955 sequences representing 23 lineages (between 80 to 200 sequences per lineage). The length of the control region fragment used ranged from 353 to 810 base pairs (Table 2).

Lineage-specific analyses

We estimated the most likely demographic model for each lineage as well as the demographic parameters associated with that model using Approximate Bayesian Computation (ABC) in the *abc* package (Csilléry *et al.*, 2012) in R (R Core Team 2018). In brief, ABC consists of a simulation step and a rejection step. In the simulation step, datasets are simulated under one or more generative models using a range of parameter values (the prior distribution). In the rejection step, summary statistics are calculated for the simulated datasets and the observed data, and the simulated datasets most similar to the observed data are selected based on a rejection criterion. The distribution of parameter values and models used to generate these “accepted” simulations then constitute the posterior model probabilities and posterior parameter distributions.

We conducted coalescent simulations under three simple demographic models: an expansion model, a bottleneck model, and a constant population size model. All models include a parameter for current female effective population size (N_e). The bottleneck and expansion models also include a parameter for ancestral female effective population size (N_{eA}) and assume an instantaneous population size change at the time of expansion (T_e) or contraction (T_c). For each model, we used a wide prior distribution for effective population size (N_e ; Uniform: 1,000 – 100,000). The upper limit for the effective population size prior was set to a value approximately equal to the upper 95% credible limit of recent effective population size estimated for Atlantic green sea turtle lineages (*Chelonia mydas* Linnaeus) based on Bayesian skyline plots (Naro-Maciel et al. 2014). We also used wide prior distributions for the timing of expansion or contraction (T_e or T_c ; Uniform: 5,000-500,000 years before present (YBP)) and for the magnitude of expansion or contraction, expressed as the ratio of current to ancestral effective population size (N_e/N_{eA} ; Uniform: 0.01-0.1). For each lineage, we simulated datasets with the same number of sequences and the same sequence length as the observed lineage dataset (Table 2) to ensure the generation of comparable summary statistics. We calculated an approximate per-generation lineage mutation rate for each species as half the estimated per-year control region divergence rate for marine turtles (1.75×10^{-8}) (Formia et al., 2006) multiplied by generation time for each species (Table 1). To accommodate potential uncertainty in actual mutation rates relative to this reported rate, mutation rates used in simulations were drawn from a normal distribution with mean equal to the per-generation mutation rate (ranging between 2×10^{-7} and 4×10^{-7} depending on species) and a wide standard deviation relative to this mean (1×10^{-7}). Simulations were performed via

the PipeMaster package (Gehara *et al.*, 2017) in R (R Core Team 2018) available in github (github.com/gehara/PipeMaster). We conducted 500,000 simulations of each model for each lineage.

In PipeMaster, we calculated seven summary statistics for each simulated dataset as well as for the observed dataset. These summary statistics were nucleotide diversity (π), number of segregating sites (S), haplotype diversity (h), Tajima's D (D), and the first three bins of the site frequency spectrum ($ss1$, $ss2$, and $ss3$, corresponding to the frequency of the three most common alleles in a given lineage). To confirm that the observed data were within the parameter space of the simulated data, we conducted a principal component (PC) analysis using these summary statistics for the simulated and observed data, plotted the first two PC axes, and verified that the PC scores for the observed data fell within the range of PC scores for the simulated data (Supplementary Materials 3). We tested the fit of the models using the "gfit" function and estimated the posterior probability of the three demographic models for each lineage via the "postpr" function in package abc. We identified all lineages for which the expansion model had the highest posterior probability across all estimation methods as "expanding lineages". We then estimated posterior distributions for N_e , magnitude of expansion, and timing of expansion for each expanding lineage using the "abc" function in abc. For ABC inferences, we used simple rejection with a tolerance level (equal to the proportion of simulations used to calculate the posterior distribution) of 0.001. We checked model posterior probabilities using a lower tolerance level (0.0001) and the neural net method implemented in abc as well, which gave highly similar results (data not shown).

We identified all lineages for which the expansion model had the highest posterior probability as candidates for inclusion in co-expansion analyses. To corroborate evidence for lineage expansion from ABC with more traditional estimators, we also calculated two statistics from aligned sequence data for each lineage (Tajima's D and Ramos-Onsins and Rozas' R_2), with significance determined by randomization tests, in the R package *pegas* (Paradis, 2010). Candidate lineages exhibiting negative values for D and values of $R_2 < 0.05$ were then included in the coexpansion analysis.

Coexpansion analysis

To determine the proportion of lineages expanding synchronously and the timing of synchronous expansion, we used the hierarchical ABC method developed by Chan et al. (2014). The demographic model used in this method simulates expansion in multiple lineages, with a proportion of those lineages (ζ) expanding synchronously at a certain time (τ_s) and the remaining lineages expanding asynchronously. Values of ζ close to 1 indicate highly synchronous expansion, while values close to 0 indicate highly asynchronous expansion. We used wide prior distributions for the hyperparameters ζ (Uniform: 0–1) and τ_s (Uniform: 5,000–500,000). To obtain better model fit to the expanding lineages, we set priors for ancestral population size and magnitude of expansion to the posterior distributions of these parameters estimated for the expanding lineages in the lineage-specific analyses described above (Supplementary Materials 4). As in the lineage-specific ABC analyses, we simulated data using the observed number of

sequences and sequence length for each individual lineage included in the coexpansion analysis. We conducted six million simulations and calculated 16 hyper-summary statistics (mean, variance, skew and kurtosis for π , S , H , and D) for simulated and observed datasets in PipeMaster (Gehara *et al.*, 2017). We assigned asynchronous expansion times based on two different buffering models (the narrow coexpansion model NC and the partitioned-time model PT; Gehara *et al.*, 2017). We then estimated posterior distributions for ζ , τ_s , and the dispersion of expansion times in abc using the simple rejection method and a tolerance of 0.0001. The rejection method and tolerance parameters used here are similar to those used in simulations conducted by Gehara *et al.* (2017), who found that the rejection method provided more accurate estimates of the hyperparameters than the neural net for coexpansion analyses.

We also conducted a separate exploratory coexpansion analysis for which we excluded Atlantic lineages representing recent colonization from the Pacific, as these lineages could have much shallower evolutionary histories by default than lineages that have occupied an ocean basin for longer time periods. This analysis used the narrow coexpansion model only, and we used a smaller number of simulated datasets (100,000) and a higher tolerance (0.001) than in the primary coexpansion analysis.

Determinants of expansion and diversity

Present-day vulnerability to climate change is influenced by both life history traits and spatial factors (Pearson *et al.* 2014), and past responses to climate change may have been

determined by a similar suite of characteristics. To evaluate factors associated with demographic change and genetic diversity in sea turtle lineages, we identified a set of six potential predictor variables that included species-level traits and lineage-level geographic factors. Body size is intimately associated with many life history and ecological traits that could potentially affect demographic responses to climate change (Carstens *et al.*, 2018). We used the average straight-line carapace length (SCL) reported for adults of each species (Spotila, 2004) as an index of body size. We also used generation time as a potential predictor variable, as this characteristic is an important predictor of present vulnerability to climate change (Pearson *et al.* 2014). Sea turtle species include several diet specialists as well as generalists (Bjorndal, 1997), and species that consume a broad range of invertebrate prey are thought to be less sensitive to climate-driven changes in prey availability than those with strong dietary preferences for a particular type of prey (Hawkes *et al.* 2009). As such, we also included degree of diet specialization as a binary predictor variable in our analyses, coding species that consume a variety of invertebrate prey as “generalists” and those with distinct preference for particular items as “specialists” (Table 1).

Sensitivity to Pleistocene climate change may also be related to differing climate tolerances among species that are reflected in present distributions. We used seasonality (temperature of warmest quarter minus temperature of coldest quarter) as an index of lineage-level climate tolerance, with higher values of seasonality indicating preference for nesting in more temperate areas and lower values indicating preference for nesting in tropical areas. We calculated seasonality for each rookery using Bioclim data and

averaged the seasonality values for each rookery at which a lineage is found to produce a lineage-specific seasonality value. We also used ocean basin (defined broadly as either Atlantic-Mediterranean or Indo-Pacific) as a categorical predictor of demographic responses, since populations in these two areas were isolated from one another during most of the Pleistocene and climatic conditions differed between these areas. Finally, as area of occupancy is a strong predictor of present-day vulnerability to climate change (Pearson et al. 2014), we included within-basin extent of occurrence as a coarse-grained indicator of geographic range in this analysis. Lineages occurring at rookeries across multiple continents were classified as “broadly distributed”, while lineages found only at a single rookery or on a single continent/continental shelf were classified as “endemic”.

We used a Bayesian model averaging (BMA) methodology to identify which of these variables best explained variability in summary statistics related to either demographic change (D and R_2) or genetic diversity (H and π). BMA analyses were carried out using the R package BMS (Zeugner and Feldkircher 2015). Before conducting BMA analyses, we centered and standardized all continuous variables by subtracting the mean value for each variable and dividing by the standard deviation. We conducted a separate BMA analysis using each of these summary statistics as the response variable and all linear combinations of predictor variables plus an intercept-only model as potential explanatory models (64 models total). Each BMA analysis was run for 10,000 iterations, with the first 1,000 iterations discarded as burn-in, using a uniform model prior. Posterior inclusion probabilities, posterior mean coefficient values, and posterior standard deviations for these coefficient values were used to evaluate the relative importance of each predictor

variable and the size and direction of the effect on the response variables. We included all lineages in this analysis, but conducted a separate analysis excluding the four Atlantic lineages representing recent colonization from the Pacific to determine whether these lineages influenced the results due to potentially strong founder effects in these lineages compared.

Results

Lineage-specific analyses

Expansion was consistently supported as the most likely of the three demographic models in ABC analyses for 14 of the 23 sea turtle lineages (9 Atlantic lineages, including all lineages representing recent colonization from the Pacific, and 5 Indo-Pacific lineages; Figure 2). The probability of expansion was ≥ 0.487 and the probability of the two other models was ≤ 0.321 for all of these lineages. Tajima's D , R^2 , and posterior probability of expansion were all correlated with one another across lineages ($|r| \geq 0.8$), and most lineages for which expansion was the most likely demographic mode also exhibited negative values for D ($D < -0.8$) and low R^2 values ($R^2 \leq 0.05$; Table 2), although these values were not always statistically different from expectations under neutrality. For one lineage (*D. coriacea*, lineage DcA2) with low diversity that likely represented recent colonization from the Indo-Pacific (Dutton et al. 2013), relative support for the expansion model was weak, D was close to 0, and R^2 was > 0.05 , which is more consistent with long-term stability than expansion. We excluded this lineage from co-expansion analyses

in favor of lineage DcA1, another lineage resulting from recent colonization that showed stronger evidence of recent expansion. The estimated magnitude of expansion (as measured by the mode of N_e divided by the mode of N_{eA}) was >10-fold for all the lineages included in co-expansion analyses (Supplementary Materials 4). The bottleneck model was only the best model for one lineage (*C. caretta* lineage CcP1), although the posterior probability of stability (0.367) was similar to the posterior probability of a bottleneck (0.404) in this case. Probability densities for estimates of the times of expansion from lineage-specific analyses were skewed toward recent expansion, although there was considerable uncertainty in expansion time especially for Indo-Pacific lineages (Figure 3).

Coexpansion analysis

The estimate for ζ was consistent with highly synchronous expansion. The mode for the posterior distribution of zeta was 1 for both buffering models (model NC ζ credible interval: 0.692–1, and model PT ζ credible interval: 0.615–1; Figure 4). The posterior distribution of expansion times was consistent with post-LGM expansion (model NC τ_s : mode 11,565 YBP, credible interval: 6,089–37,945 YBP, model PT τ_s : mode 10847 YBP, credible interval: 5,003–50,674 YBP), and the estimate of dispersion index for expansion times was low, although the credible interval was wide (model NC dispersion index: mode 2,945, credible interval: 0–311,177; model PT dispersion index: mode 1,971, credible interval: 0–300,562). Posterior distributions and parameter estimates from the exploratory analysis excluding Atlantic lineages that represent recent colonization from

the Pacific were similar, and the mode for ζ was again close to 1 (Supplementary Materials 5).

Determinants of expansion and genetic diversity

Across all BMA analyses, geographic variables (ocean basin and within-basin range) had higher posterior inclusion probabilities than variables related to climate, body size, or generation time (Figure 4; Table 3). For the two response variables related to demographic change (D and $R2$), the coefficient associated with range size was positive and the coefficient associated with the Atlantic was negative, suggesting more demographic stability for widely distributed lineages and lineages in the Indo-Pacific; however, coefficient estimates overlapped zero for both (Table 3). There was stronger association between geographic variables and diversity statistics. Ocean basin had a posterior inclusion probability of 0.969 (for H) and 0.981 (for π), and coefficient estimates were negative and significantly different from zero for each (indicating lower haplotype and nucleotide diversities in the Atlantic). Range size was also included in a large proportion of models for H (0.615) and π (0.895), and the coefficient associated with range for π was significantly positive. None of the other variables had estimated coefficients that were significantly different from zero. Variable inclusion probabilities were similar for analyses conducted without lineages representing recent colonization of the Atlantic (Supplementary Materials 6).

Discussion

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389 The present-day distribution of biological diversity is, in part, a function of both temporal
390 fluctuations in global climate and local variability in the magnitude of these fluctuations
391 over time. Understanding how temporal and spatial variability in climate interact is a
392 major challenge for ecologists, but has the potential to explain broad-scale patterns in
393 biodiversity (Klopfer, 1960) as well as diversity within species and groups (Carnaval *et*
394 *al.*, 2009). The patterns of demographic change and genetic diversity described here
395 provide a window into understanding this relationship. We see strong evidence of a
396 synchronous demographic response to the last glacial transition across the majority of sea
397 turtle lineages. Differences among lineages were not in the timing of expansion but in the
398 magnitude of demographic change, with some lineages apparently stable or relatively
399 stable since the LGM, and others showing signatures of dramatic shifts in population
400 size. Lineages in the Indo-Pacific tended to show more demographic stability and more
401 genetic diversity than those in the Atlantic, suggesting greater stability overall in the
402 Indo-Pacific area.

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404 *Expansion of marine turtle lineages across ocean basins and limits of inference*

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406 Our ABC analyses indicated that a majority of marine turtle lineages likely expanded
407 after the LGM (assuming glaciers attained their maximum extent 26,500 ybp and
408 remained at this extent until approximately 19,000–20,000 ybp; Clark *et al.* 2009) and did
409 so in a highly synchronous fashion, suggesting a rapid response to changes in the marine
410 environment. Quaternary climate cycles produced many changes, ranging from

fluctuations in sea surface temperatures to rising and falling sea levels (Lowe and Walker 2014), that may have affected availability of suitable marine habitat, nesting habitat, and prey for marine turtles. Our BMA analyses also indicated that demographic stability and genetic diversity were largely independent of diet preferences, body size, and generation time, but depended on ocean basin and range size, indicating a stronger influence of abiotic geographic factors than biotic factors on the demographic history of marine turtle populations. These coordinated impacts across globally distributed taxa suggest that, although some populations and species may remain relatively stable, changes in climate can cause synchronous reorganizations in communities across the globe.

It is important to note that although we partitioned the data into “expanding” versus “constant” lineages for the purposes of identifying synchronous expansion, lineages identified as “constant” may have experienced some demographic change over the late Quaternary period. Indeed, while the posterior probabilities of the “constant” or “bottleneck” demographic modes were close to zero for some lineages, the posterior probability of the “expansion” model was greater than 0.2 for all lineages, indicating that expansion cannot be completely ruled out for any lineage. Additionally, the dataset used excluded some rarely detected lineages, including rare *C. mydas* lineages in the Pacific (Dethmers et al. 2006), as well as haplotypes that are not represented in current rookery databases but have been detected in other datasets (see for example Jensen et al. 2013). Sampling these lineages and including them in future analyses would enable a more complete characterization of mtDNA patterns in marine turtles. The results presented

here indicate that, for sampled lineages with the strongest signature of expansion, expansions were most likely synchronous.

We used the large existing database of mtDNA data already available for marine turtles here. Inferences based on this single-locus database could be confirmed and further refined by incorporating next-generation sequencing data. Komoroske *et al.* (2019) recently developed a high-throughput method for generating population genomic data in marine turtles using a hybrid of RAD-seq and sequence capture (Rapture). Combined with the PipeMaster approach described here or other related methods (e.g. MULTI-DICE; Xue and Hickerson 2017), these genomic data could be used to clarify population histories by testing models of more complex demographic histories, including models incorporating multiple size changes and alternate modes of expansion and contraction (e.g. exponential rather than instantaneous change).

Geographic factors influencing expansion

While lineage-level demographic expansions appear to have been synchronous, these expansions were not homogenous across space. Specifically, Atlantic lineages were somewhat more likely to show evidence of expansion than Indo-Pacific lineages, and most Indo-Pacific lineages were more genetically diverse than Atlantic lineages. Sea surface temperatures in the western Pacific warm pool, an area centered around equatorial Melanesia and Micronesia, but extending into the Indian Ocean (Supplementary Material 7), were relatively stable over the course of the Pleistocene

456 compared to other oceanic regions (de Garidel-Thoron *et al.*, 2005), and this stability may
457 have contributed to demographic stability and higher overall genetic diversity in this area.

458 There is some support for the importance of the warm pool in long-term stability of
459 marine turtle species, as all Indo-Pacific lineages that showed little evidence of recent
460 expansion had present-day ranges that overlapped broadly with the Pacific warm pool.

461
462 Reduced climatic variation in the Indo-Pacific means that this region may have served as
463 a stable “source” for some tropical marine taxa that then recolonized the more unstable
464 Atlantic. Several species of reef fish, for example, colonized the Atlantic during
465 interglacial periods preceding the LGM (Rocha *et al.*, 2005; Bowen *et al.*, 2006).

466 Interestingly, three marine turtle lineages representing recent colonizations of the Atlantic
467 from the Indo-Pacific (*D. coriacea* lineage DcA, *Eretmochelys imbricata* lineage EiA,
468 and *L. olivacea* lineage LoA1) appear to have expanded at the same time as lineages that
469 experienced *in situ* expansion at the LGM based on the observed synchrony of co-
470 expansion. Bowen and Karl (2007) suggested that the colonization of the Atlantic from
471 the Pacific in marine turtles is normally prevented during glacial periods by the cold-
472 water Benguela current running north along East Africa, and this barrier likely becomes
473 permeable during interglacial periods due to leakage of the warm-water Agulhas current
474 from the Indian ocean (Peeters *et al.*, 2004). As such, synchronous colonization events
475 and *in situ* expansion after the LGM can be explained by climatic change resulting in the
476 simultaneous elimination of environmental limits to both spatial and demographic
477 expansion.

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Within ocean basins, marine turtle lineages occur over both broad and narrow ranges; some lineages are found in rookeries spread across the entire Pacific, while others are confined to small areas (Vargas et al. 2016). In widely-distributed lineages, some haplotypes are found across an entire ocean basin, suggesting rapid range expansion (Shanker 2004). However, we found little evidence for expansion in lineages with extremely broad distribution in haplotypes. Instead, endemic lineages (including *Natator depressa* and the Kemp's ridley turtle, *Lepidochelys kempii* Garman) were more likely to show strong evidence for expansion than broadly-distributed lineages. This can potentially be explained by the fact that broadly-distributed lineages would be more likely to inhabit areas of relative climatic stability compared to endemic lineages, which would have been at the mercy of local climatic conditions. Previous work in terrestrial environments has shown higher genetic diversity in widespread species compared to range-restricted species (Hamrick et al. 1992) and lower genetic diversity in endemics inhabiting areas with a history of climate instability compared to more widespread species with access to stable refugia (Carnaval et al. 2009). In a study comparing demographic histories of reef fish, however, Delrieu-Trottin (2017) found that population expansions were common across both widespread and range-restricted species, indicating that this pattern may not be universal in marine species.

While lineage-level seasonality did not predict expansion or genetic diversity, our results also indicate some evidence for a role of species' thermal preferences in demographic expansion. In the two species (*Dermochelys coriacea* and *Caretta caretta*) showing the least evidence for population expansion, their distributions shift and spatial expansion

may have occurred without substantial increase in population size. *Dermochelys* nests in the tropics but have a much broader temperature tolerance range than other marine turtle species due to their size-based thermal inertia (“gigantothermy”; Paladino *et al.*, 1990). In leatherback turtles, expansion was limited to a lineage that colonized the Atlantic, and the single lineage in the Pacific showed stability in the Late Pleistocene. *Caretta* is tolerant to seasonality and nest mainly in warm-temperate rather than tropical regions. The one loggerhead turtle lineage showing evidence of expansion is the only lineage found in the Mediterranean. In this case, a post-LGM expansion into the Mediterranean Sea (following similar patterns in other Mediterranean biota; Emig & Geistdoerfer, 2005) may be driving the genetic signature of population expansion.

Implications for conservation

The concept of biodiversity “hotspots”, identified via species-level diversity and endemism, has been applied to both marine and terrestrial realms to identify priority areas for efficient conservation of biodiversity (Myers *et al.*, 2000; Roberts *et al.*, 2002). An alternative approach is to define hotspots using genetic data and to identify areas of reduced historic climatic variation that may be particularly relevant to conserving biodiversity in the face of ongoing climate change (Prates *et al.*, 2016). The patterns of population change and genetic diversity described here for marine turtles suggest that the Indo-Pacific, particularly regions associated with the Western Pacific warm pool, has served as a particularly stable reservoir for marine biodiversity. This is supported by studies of paleodiversity that indicate high species richness in the Indo-Australian

Archipelago, which has persisted since the early Miocene (Renema *et al.*, 2008). As this region has likely served as a stable refuge in times of past climate change, preservation may be crucial to maintaining marine biodiversity in the future.

Whether relatively high population stability in the equatorial Pacific translates to greater resilience to future climate change will depend on the mode of future climate change. Many climate models predict enhanced warming in the equatorial Pacific, although these predictions depend on numerous feedbacks involving ocean currents and atmospheric circulation cycles that may themselves be altered by projected warming (DiNezio *et al.* 2009). Given the importance of the Indo-Pacific to marine biodiversity in the past and current uncertainty regarding the impacts of projected change in this area, future work integrating both history and fine-scale projections of change in this area (including change in thermal characteristics and flooding risk at nesting beaches; Butt *et al.* 2016) could be useful in optimizing the design and implementation of marine sanctuaries that maximize the preservation of future biodiversity.

Preserving the full range of diversity in marine turtles will also require addressing the particular issues facing individual species. Knowledge of past changes in population size can also be instructive in this regard. Based on our analyses, lineages in the Atlantic and narrowly-distributed lineages were most sensitive to past climate change. If these patterns also hold for future climate change, some rare and narrowly-distributed Atlantic lineages that are already at risk of extinction (such as *L. kempii*, which nests only along the coast of the Gulf of Mexico, and *Eretmochelys* lineage EiA3) may be especially threatened.

Indian Ocean lineages of olive ridley turtles and hawksbill turtles may also be at risk, as well as the flatback turtle, which is restricted to the continental shelf around northern Australia. Future work using next-generation sequencing to robustly characterize past population history and current trajectories in these populations may be especially useful for conservation planning in these lineages. The combined effects of anthropogenic stressors, such as rapid ocean acidification and submergence of nesting habitats due to sea level rise, could also change marine turtle habitats in ways that differ from previous episodes of warming (Hawkes *et al.* 2009). It is therefore important to consider the possibility that responses to ongoing climate change could be dramatically different from past responses and to develop new methods for predicting these responses (Brown *et al.*, 2016; Prates *et al.*, 2016). However, quantifying past changes in species and assemblages, as we have done here, is crucial to contextualizing these predictions. By examining past change in this widely-distributed group, we hope to contribute to the establishment of a baseline for conservation of global biodiversity and to inform strategies for the management of biodiversity in the face of future change.

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References

- Annan, J. & Hargreaves, J. (2013). A new global reconstruction of temperature changes at the Last Glacial Maximum. *Climate of the Past*, 9, 367–376.
- Bjorndal, K. (1997). Foraging ecology and nutrition of sea turtles. *The Biology of Sea Turtles, Volume I* (ed. by P.L. Lutz and J.A. Musick), pp 199 - 231. CRC Press, Boca Raton, FL, USA.
- Bolten, A. (2003). Variation in sea turtle life history patterns. *The Biology of Sea Turtles, Volume II* (ed. by P.L. Lutz, J.A. Musick, and J. Wyneken), pp 243-258. CRC Press, Boca Raton, FL, USA.
- Bowen, B.W., Clark, A.M., Abreu-Grobois, F.A., Chaves, A., Reichart, H.A. & Ferl, R.J. (1997). Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica*, 101, 179–189.
- Bowen, B.W. & Karl, S.A. (2007). Population genetics and phylogeography of sea turtles. *Molecular Ecology*, 16, 4886–4907.
- Bowen, B.W., Muss, A., Rocha, L.A. & Grant, W.S. (2006). Shallow mtDNA Coalescence in Atlantic Pygmy Angelfishes (Genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity*, 97, 1–12.
- Brown, J.L., Weber, J.J., Alvarado-Serrano, D.F., Hickerson, M.J., Franks, S.J. & Carnaval, A.C. (2016). Predicting the genetic consequences of future climate change: The power of coupling spatial demography, the coalescent, and historical landscape changes. *American Journal of Botany*, 103, 153–63.
- Burbrink, F.T., Chan, Y.L., Myers, E.A., Ruane, S., Smith, B.T. & Hickerson, & M.J.

- 594 (2016). Asynchronous demographic responses to Pleistocene climate change in
595 Eastern Nearctic vertebrates. *Ecology Letters*, *19*, 1457–1467.
- 596 **Butt, N, Whiting, S, & Dethmers, K (2016). Identifying future sea turtle**
597 **conservation areas under climate change. *Biological Conservation*, *204*, 189-196.**
- 598 Carstens, B.C., Morales, A.E., Field, K., & Pelletier, T.A. (2018). A global analysis of
599 bats using automated comparative phylogeography uncovers a surprising impact of
600 Pleistocene glaciation. *Journal of Biogeography*, *45*, 1795-1805.
- 601 Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009).
602 Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. *Science*,
603 *323*, 785–789.
- 604 Chan, Y.L., Schanzenbach, D. & Hickerson, M.J. (2014). Detecting concerted
605 demographic response across community assemblages using hierarchical
606 Approximate Bayesian Computation. *Molecular Biology and Evolution*, *31*, 2501–
607 2515.
- 608 Clark, P.U., Dyke A.S., Shakun J.D., Carlson A.E., Clark J., Wohlfarth B., Mitrovica
609 J.X., Hostetler S.W. & McCabe, A.M. (2009). The last glacial maximum. *Science*,
610 *325*, 710-714.
- 611 Csillery, K., Francois, O. & Blum, M. (2012) abc: an R package for approximate
612 Bayesian computation (ABC). *Methods in Ecology and Evolution*, *3*, 475-479.
- 613 Davenport, J. (1997). Temperature and the life-history strategies of sea turtles. *Journal of*
614 *Thermal Biology*, *22*, 479–488.
- 615 Dethmers, K.E.M., Broderick, D., Moritz, C., FitzSimmons, N.N., Limpus, C.J., Lavery,
616 S., Whiting, S., Guinea, M., Prince, R.I.T., and Kennett, R. (2006). The genetic

- 617 structure of Australasian green turtles (*Chelonia mydas*): exploring the geographical
618 scale of genetic exchange. *Molecular Ecology*, 15, 3931–3946.
- 619 Delrieu-Trottin, E., Mona, S., Maynard, J., Neglia, V., Veuille, M. & Planes, S. (2017).
620 Population expansions dominate demographic histories of endemic and widespread
621 Pacific reef fishes. *Scientific Reports*, 7, 40519.
- 622 DiNezio, P.N., Clement, A.C., Vecchi, G.A., Soden, B.J., Kirtman, B.P., and Lee, S.
623 (2009). Climate response of the equatorial Pacific to global warming. *Journal of*
624 *Climate*, 22, 4873–4892.
- 625 Dutton, P.H., Roden, S.E., Stewart, K.R., LaCasella, E., Tiwari, M., Formia, A., Thomé,
626 J.C., Livingstone, S.R., Eckert, S., Chacon-Chaverri, D., Rivalan, P. & Allman, P.
627 (2013). Population stock structure of leatherback turtles (*Dermochelys coriacea*) in
628 the Atlantic revealed using mtDNA and microsatellite markers. *Conservation*
629 *Genetics*, 14, 625–636.
- 630 Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species'
631 geographical distributions driven by Milankovitch climate oscillations. *Proceedings*
632 *of the National Academy of Sciences of the United States of America*, 97, 9115–20.
- 633 Emig, C. & Geistdoerfer, P. (2005). The Mediterranean deep-sea fauna: historical
634 evolution, bathymetric variations and geographical changes. *Carnets de Geologie*
635 2004, 1-10.
- 636 Formia, A., Godley, B.J., Dontaine, J.-F. & Bruford, M.W. (2006). Mitochondrial DNA
637 diversity and phylogeography of endangered green turtle (*Chelonia mydas*)
638 populations in Africa. *Conservation Genetics*, 7, 353–369.
- 639 de Garidel-Thoron, T., Rosenthal, Y., Bassinot, F. & Beaufort, L. (2005). Stable sea

- 640 surface temperatures in the western Pacific warm pool over the past 1.75 million
641 years. *Nature*, 433, 294–298.
- 642 Graham, R.W. & Grimm, E.C. (1990). Effects of global climate change on the patterns of
643 terrestrial biological communities. *Trends in Ecology & Evolution*, 5, 289–292.
- 644 Grant, W.A.S., & Bowen, B.W. (1998). Shallow population histories in deep
645 evolutionary lineages of marine fishes: insights from sardines and anchovies and
646 lessons for conservation. *Journal of Heredity*, 89: 415–426.
- 647 Hamrick, J.L., Godt, M.J.W., and Sherman-Broyles, S.L. (1992). Factors influencing
648 levels of genetic diversity in woody plant species. *New Forests*, 6, 95–124.
- 649 Hawkes, L.A., Broderick, C.A., Godfrey, M.H., and Godley, B.J. (2009). Climate change
650 and marine turtles. *Endangered Species Research*, 7, 137–154.
- 651 Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913.
- 652 Jensen, M.P., FitzSimmons, N.N., and Dutton, P.H. (2013). Molecular genetics of sea
653 turtles. In *The Biology of Sea Turtles, Volume III*. (ed. by J. Wyneken, K.J.
654 Lohmann, and J.A. Musick,) pp 135–162. CRC Press, Boca Raton, FL, USA.
- 655 Klopfer, P.H. (1960). Environmental Determinants of Faunal Diversity. *The American*
656 *Naturalist*, 93, 337–342.
- 657 Komoroske, L.M., Miller, M.R., O'Rourke, S.M., Stewart, K.R., Jensen, M.P., & Dutton,
658 P.H. (2019). A versatile Rapture (RAD-Capture) platform for genotyping marine
659 turtles. *Molecular Ecology Resources*, 19, 497–511.
- 660 Leroux, R.A., Dutton, P.H., Abreu-Grobois, F.A., Lagueux, C.J., Campbell, C.L.,
661 Delcroix, E., Chevalier, J., Horrocks, J.A., Hillis-Starr, Z., Troëng, S., Harrison, E.,
662 and Stapleton, S. (2012). Re-examination of population structure and

- 663 phylogeography of hawksbill turtles in the wider Caribbean using longer mtDNA
664 sequences. *Journal of Heredity*, 103, 806–820.
- 665 Lowe, J. and Walker, M. *Reconstructing Quaternary Environments*. Routledge, New
666 York, NY, USA.
- 667 Maggs, C.A., Castilho, R., Foltz, D., Henzler, C., Jolly, M.T., Kelly, J., Olsen, J., Perez,
668 K.E., Stam, W., Väinölä, R., Viard, F. & Wares, J. (2008). Evaluating signatures of
669 glacial refugia for north Atlantic benthic marine taxa. *Ecology*, 89, S108–S122.
- 670 Marko, P.B., Hoffman, J.M., Emme, S.A., McGovern, T.M., Keever, C.C. & Cox, N.L.
671 (2010). The “Expansion-Contraction” model of Pleistocene biogeography: rocky
672 shores suffer a sea change? *Molecular Ecology*, 19, 146–169.
- 673 Monzón-Argüello, C., Loureiro, N.S., Delgado, C., Marco, A., Lopes, J.M., Gomes, M.G.
674 & Abreu-Grobois, F.A. (2011). Príncipe island hawksbills: Genetic isolation of an
675 eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology*, 407,
676 345–354.
- 677 Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000).
678 Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- 679 Naro-Maciel, E., Reid, B.N., Alter, S.E., Amato, G., Bjørndal, K.A., Bolten, A.B.,
680 Martin, M., Nairn, C.J., Shamblin, B. & Pineda-Catalan, O. (2014). From refugia to
681 rookeries: Phylogeography of Atlantic green turtles. *Journal of Experimental*
682 *Marine Biology and Ecology*, 461, 306–316.
- 683 Paladino, F., O’Connor, M. and Spotila, J.R. (1990). Metabolism of leatherback turtles,
684 gigantothermy, and thermoregulation of dinosaurs. *Nature*, 344, 858–860.
- 685 Paradis, E. (2010). pegas: an R package for population genetics with an

- 686 integrated-modular approach. *Bioinformatics*, 26, 419-420.
- 687 Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J.,
688 Horning, N., Fordham, D.A., Raxworthy, C.J., Ryue, H.Y., McNees, J., and
689 Akçakaya, H.R. (2014). Life history and spatial traits predict extinction risk due to
690 climate change. *Nature Climate Change*, 4, 217-221
- 691 Peeters, F.J.C., Acheson, R., Brummer, G.-J.A., de Ruijter, W.P.M., Schneider, R.R.,
692 Ganssen, G.M., Ufkes, E. & Kroon, D. (2004). Vigorous exchange between the
693 Indian and Atlantic oceans at the end of the past five glacial periods. *Nature*, 430,
694 661–665.
- 695 Plotkin, P. (2003) Adult Migrations and Habitat Use. In *The Biology of Sea Turtles*,
696 *Volume II*, (ed. by P.L. Lutz, J.A. Musick, and J. Wyneken), pp 225-242. CRC
697 Press, Boca Raton, FL, USA.
- 698 Prates, I., Xue, A.T., Brown, J.L., Alvarado-Serrano, D.F., Rodrigues, M.T., Hickerson,
699 M.J. & Carnaval, A.C. (2016). Inferring responses to climate dynamics from
700 historical demography in neotropical forest lizards. *Proceedings of the National*
701 *Academy of Sciences of the United States of America*, 113, 7978–85.
- 702 R Core Team. (2018). R: a language and environment for statistical computing. R
703 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- 704 Reece, J.S., Castoe, T.A. & Parkinson, C.L. (2005). Historical perspectives on population
705 genetics and conservation of three marine turtle species. *Conservation Genetics*, 6,
706 235–251.
- 707 [dataset]Reid, B.R., Naro-Maciel, E., Torres Hahn, A, FitzSimmons, N.N., & Gehara, M.

- 708 (2019). Data from: [Geography best explains global patterns of genetic diversity and](https://doi.org/10.5061/dryad.5d2nv88)
709 [post-glacial co-expansion in marine turtles](https://doi.org/10.5061/dryad.5d2nv88). <https://doi.org/10.5061/dryad.5d2nv88>
- 710 Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt,
711 P., Meyer, C.P., McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A.,
712 Wesselingh, F.P., Wilson, M.E.J. & Pandolfi, J.M. (2008). Hopping hotspots: global
713 shifts in marine biodiversity. *Science*, *321*, 654–657.
- 714 Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister,
715 D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. &
716 Werner, T.B. (2002). Marine biodiversity hotspots and conservation priorities for
717 tropical reefs. *Science*, *295*, 1280–1284.
- 718 Rocha, L.A., Robertson, D.R., Rocha, C.R., Tassell, J.L., Craig, M.T. & Bowen, B.W.
719 (2005). Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish.
720 *Molecular Ecology*, *14*, 3921–3928.
- 721 Shamblin, B., Bolten, A., Abreu-Grobois, F., et al. (2014). Geographic patterns of genetic
722 variation in a broadly distributed marine vertebrate: new insights into loggerhead
723 turtle stock structure from expanded. *PLoS One*, e85956.
- 724 Shanker, K., Ramadevi, J., Choudhury, B.C., Singh, L. & Aggarwal, R.K. (2004).
725 Phylogeography of olive ridley turtles (*Lepidochelys olivacea*) on the east coast of
726 India: implications for conservation theory. *Molecular Ecology*, *13*, 1899–1909.
- 727 Spotila, J.R. (2004) *Sea turtles: a complete guide to their biology, behavior, and*
728 *conservation*. Johns Hopkins University Press, Baltimore, MD, USA.
- 729 Vargas, S.M., Jensen, M.P., Ho, S.Y.W., Mobaraki, A., Broderick, D., Mortimer, J.A.,
730 Whiting, S.D., Miller, J., Prince, R.I.T., Bell, I.P., Hoenner, X., Limpus, C.J.,

Santos, F.R. & FitzSimmons, N.N. (2016). Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. *Journal of Heredity*, 107, 199–213.

Xue, A.T. & Hickerson, M.J. (2017). MULTI-DICE: R package for comparative population genomic inference under hierarchical co-demographic models of independent single-population size change. *Molecular Ecology Resources*, 17, e212–e224.

Zeugner, S. and Feldkircher, M. (2015). Bayesian model averaging employing fixed and flexible priors: The BMS Package for R. *Journal of Statistical Software*, 68, 1–37.

Data Accessibility Statement

Previously unpublished sequence data are available on Genbank for Atlantic *L. kempii* (accession numbers MN047281 – MN047285) and for *N. depressus* (accession numbers MN029076 – MN029107). All other genetic sequences are available either on Genbank or other publicly accessible databases specific to marine turtles, and haplotype frequency data compiled for this paper is available from the sources given in Supplementary Materials 1. Lineage-specific FASTA files and the R script used to subsample these files can be obtained from Dryad:

<https://datadryad.org/review?doi=doi:10.5061/dryad.5d2nv88>

Author contributions

754 B.N. Reid and M. Gehara conceived and designed the study. A. Torres Hahn, E. Naro-
755 Maciel, and N.N. Fitzsimmons provided datasets. B.N. Reid and M. Gehara conducted
756 the analyses and wrote the manuscript. All authors edited and provided feedback on the
757 manuscript.

Table 1. Names and species traits for the marine turtles included in this study. Approximate generation times in years are based on IUCN Red List entries for species except for Data Deficient *N. depressa*, where generation time was calculated based on Parmenter and Limpus (1995). Approximate adult straight-line carapace length, body mass, and diet are based on Spotila (1995).

Species name	Common name	Generation Time (years)	Body Mass (kg)	Carapace Length (cm)	Diet
<i>Caretta caretta</i>	Loggerhead turtle	40	140	104.5	Generalist
<i>Chelonia mydas</i>	Green turtle	40	134.5	101	Specialist (sea grass, algae)
<i>Dermochelys coriacea</i>	Leatherback turtle	30	578.5	155	Specialist (jellyfish)
<i>Eretmochelys imbricata</i>	Hawksbill turtle	40	59	81.5	Specialist (sponges, algae)
<i>Lepidochelys kempii</i>	Kemp's Ridley turtle	20	40.5	68.5	Generalist
<i>Lepidochelys olivacea</i>	Olive Ridley turtle	20	39.5	65.5	Generalist
<i>Natator depressa</i>	Flatback turtle	30	80	87	Generalist

764 Table 2. Characteristics of the 23 marine turtle lineages included in this study. The 13 lineages shown in bold were included in co-
765 expansion analyses. # = sequences were thinned to 200 for final analyses, *D* = Tajima’s *D*, *R*2 = Ramos-Onsins and Roza’s *R*2, *P*(*Exp*)
766 = posterior probability of expansion model, * = significant (*p* < 0.05).

Lineage	Species	Basin	Distribution	Seasonality	Sequences	Base Pairs	<i>D</i>	<i>R</i> 2	<i>P</i> (<i>Exp</i>)
CcA1	<i>C. caretta</i>	Atlantic	broad	18.419	1635 [#]	659	-0.624	0.059	0.397
CcA2	<i>C. caretta</i>	Atlantic	endemic	12.135	162	659	0.574	0.111	0.369
CcA3	<i>C. caretta</i>	Atl-Med	broad	21.058	1629 [#]	659	-2.086*	0.018*	0.965
CmA1	<i>C. mydas</i>	Atlantic	broad	10.710	502 [#]	491	-0.881	0.049	0.491
CmA2	<i>C. mydas</i>	Atl-Med	broad	14.518	675 [#]	491	-1.613*	0.034	0.918
DcA1	<i>D. coriacea</i>	Atlantic	broad	11.213	283 [#]	695	-1.312	0.022*	0.531
DcA2	<i>D. coriacea</i>	Atlantic	broad	12.090	133	695	-0.122	0.085	0.406
EiA1	<i>E. imbricata</i>	Atlantic	broad	10.584	283 [#]	746	-1.501	0.029*	0.588
EiA2	<i>E. imbricata</i>	Atlantic	broad	10.867	408 [#]	746	0.324	0.023*	0.360
EiA3	<i>E. imbricata</i>	Atlantic	endemic	8.828	102	746	-1.313	0.040*	0.531
LkA1	<i>L. kempii</i>	Atlantic	endemic	21.977	158	764	-1.003	0.050	0.524
LoA1	<i>L. olivacea</i>	Atlantic	broad	10.994	147	689	-1.649	0.022*	0.611
CcP1	<i>C. caretta</i>	Pacific	broad	22.050	553 [#]	808	2.167	0.162	0.229
CmP1	<i>C. mydas</i>	Indo-Pacific	broad	11.410	1401 [#]	353	-0.310	0.071	0.447
CmP2	<i>C. mydas</i>	Pacific	endemic	11.116	112	354	-0.809	0.049	0.570
CmP3	<i>C. mydas</i>	Indo-Pacific	broad	10.905	1083 [#]	353	0.730	0.114	0.309
DcP1	<i>D. coriacea</i>	Pacific	broad	10.548	175	496	-0.129	0.082	0.387
EiP1	<i>E. imbricata</i>	Indo-Pacific	broad	15.005	534 [#]	765	-1.656	0.033	0.863
EiP2	<i>E. imbricata</i>	Indian	endemic	7.099	80	766	-1.565	0.042*	0.748
EiP3	<i>E. imbricata</i>	Indo-Pacific	broad	9.301	144	766	0.024	0.085	0.380
LoP1	<i>L. olivacea</i>	Indian	endemic	14.356	86	395	-1.928*	0.034*	0.879
LoP2	<i>L. olivacea</i>	Indo-Pacific	broad	14.813	266 [#]	470	1.057	0.086	0.275
NdP1	<i>N. depressus</i>	Pacific	endemic	17.837	305 [#]	810	-0.971	0.049	0.487

Table 3. Bayesian Model averaging results. For each combination of predictor and response variable, the posterior inclusion probability (PIP), posterior mean coefficient value (β), and 95% credible interval for β are provided.

Predictor	Response	PIP	β	95% CI (β)
Ocean Basin	<i>D</i>	0.513	-0.369	[-1.337 to 0.598]
	<i>R2</i>	0.723	-0.650	[-1.674 to 0.375]
	<i>H</i>	0.969	-1.144	[-1.923 to -0.365]
	π	0.981	-1.157	[-1.853 to -0.461]
Range Size	<i>D</i>	0.562	0.490	[-0.676 to 1.655]
	<i>R2</i>	0.410	0.279	[-0.586 to 1.144]
	<i>H</i>	0.615	0.467	[-0.459 to 1.393]
	π	0.895	0.879	[0.007 to 1.751]
Seasonality	<i>D</i>	0.195	0.021	[-0.186 to 0.227]
	<i>R2</i>	0.230	0.036	[-0.21 to 0.282]
	<i>H</i>	0.374	0.103	[-0.258 to 0.465]
	π	0.232	0.031	[-0.164 to 0.226]
Generation Time	<i>D</i>	0.192	0.020	[-0.201 to 0.242]
	<i>R2</i>	0.271	0.067	[-0.275 to 0.409]
	<i>H</i>	0.355	0.086	[-0.228 to 0.401]
	π	0.312	0.069	[-0.184 to 0.323]
Carapace Length	<i>D</i>	0.195	0.020	[-0.187 to 0.228]
	<i>R2</i>	0.277	0.060	[-0.224 to 0.344]
	<i>H</i>	0.181	-0.003	[-0.128 to 0.122]
	π	0.186	-0.010	[-0.156 to 0.137]
Diet Specialization	<i>D</i>	0.222	-0.074	[-0.593 to 0.444]
	<i>R2</i>	0.328	-0.198	[-1.004 to 0.609]
	<i>H</i>	0.292	0.135	[-0.538 to 0.808]
	π	0.205	0.032	[-0.348 to 0.412]
Sequence Length	<i>D</i>	0.177	0.001	[-0.181 to 0.182]
	<i>R2</i>	0.180	-0.004	[-0.186 to 0.179]
	<i>H</i>	0.265	0.046	[-0.186 to 0.278]
	π	0.457	-0.117	[-0.444 to 0.209]

Figure 1. Map of sampling sites and geographic distributions of mitochondrial control region data for marine turtle species. Colors in haplotype network correspond to lineages used in this study, and size of circles in haplotype network is proportional to haplotype frequency in each thinned dataset. Spatial distribution of these haplotypes is shown by concentric circles with colors corresponding to lineages present at each rookery.

Figure 2. Triangle plot of posterior model probabilities for each of the three potential demographic modes (expansion, bottleneck, constant) for each marine turtle lineage. Symbol type indicates species, while colors correspond to the colors used in haplotype networks and maps in figure 1. Populations in the top portion of the triangle have a >50% posterior probability of expansion.

Figure 3. Prior (dotted line) and posterior (solid line) probability distributions for parameters included in co-expansion analyses. Priors and posteriors from the narrow expansion time model are shown in black, while priors and posteriors for the partitioned-time model are shown in red. ζ = proportion of populations expanding, T_s = time of synchronous expansion, $E(t)$ = expected expansion time, DI = dispersion index of expansion times. Note that priors for ζ overlap for the two co-expansion models.

Figure 4. Results of Bayesian Model Averaging analyses in grid form. Each column of rectangles represents one of 64 possible models, and column width indicates posterior model probability. Predictor variables are arranged from top to bottom by posterior inclusion probability. Blue indicates a positive coefficient for a given variable, violet indicates a negative coefficient, and white indicates that a variable was not included in a given model. Empty columns represent the intercept-only model.

Figure 1a.

Figure 1b.

Figure 2.

Figure 3.

Figure 4.

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Prior (narrow coexpansion)
Prior (partitioned-time)
Posterior (narrow coexpansion)
Posterior (partitioned-time)

D

R^2

h

π

Cumulative Model Probability

Table 1. Names and species traits for the marine turtles included in this study. Approximate generation times in years are based on IUCN Red List entries for species except for Data Deficient *N. depressa*, where generation time was calculated based on Parmenter and Limpus (1995). Approximate adult straight-line carapace length, body mass, and diet are based on Spotila (1995).

Species name	Common name	Generation Time (years)	Body Mass (kg)	Carapace Length (cm)	Diet
<i>Caretta caretta</i>	Loggerhead turtle	40	140	104.5	Generalist
<i>Chelonia mydas</i>	Green turtle	40	134.5	101	Specialist (sea grass, algae)
<i>Dermochelys coriacea</i>	Leatherback turtle	30	578.5	155	Specialist (jellyfish)
<i>Eretmochelys imbricata</i>	Hawksbill turtle	40	59	81.5	Specialist (sponges, algae)
<i>Lepidochelys kempii</i>	Kemp's Ridley turtle	20	40.5	68.5	Generalist
<i>Lepidochelys olivacea</i>	Olive Ridley turtle	20	39.5	65.5	Generalist
<i>Natator depressa</i>	Flatback turtle	30	80	87	Generalist

Table 2. Characteristics of the 23 marine turtle lineages included in this study. The 13 lineages shown in bold were included in co-expansion analyses. # = sequences were thinned to 200 for final analyses, *D* = Tajima’s *D*, *R*2 = Ramos-Onsins and Roza’s *R*2, *P*(*Exp*) = posterior probability of expansion model, * = significant (*p* < 0.05).

Lineage	Species	Basin	Distribution	Seasonality	Sequences	Base Pairs	<i>D</i>	<i>R</i> 2	<i>P</i> (<i>Exp</i>)
CcA1	<i>C. caretta</i>	Atlantic	broad	18.419	1635 [#]	659	-0.624	0.059	0.397
CcA2	<i>C. caretta</i>	Atlantic	endemic	12.135	162	659	0.574	0.111	0.369
CcA3	<i>C. caretta</i>	Atl-Med	broad	21.058	1629 [#]	659	-2.086*	0.018*	0.965
CmA1	<i>C. mydas</i>	Atlantic	broad	10.710	502 [#]	491	-0.881	0.049	0.491
CmA2	<i>C. mydas</i>	Atl-Med	broad	14.518	675 [#]	491	-1.613*	0.034	0.918
DcA1	<i>D. coriacea</i>	Atlantic	broad	11.213	283 [#]	695	-1.312	0.022*	0.531
DcA2	<i>D. coriacea</i>	Atlantic	broad	12.090	133	695	-0.122	0.085	0.406
EiA1	<i>E. imbricata</i>	Atlantic	broad	10.584	283 [#]	746	-1.501	0.029*	0.588
EiA2	<i>E. imbricata</i>	Atlantic	broad	10.867	408 [#]	746	0.324	0.023*	0.360
EiA3	<i>E. imbricata</i>	Atlantic	endemic	8.828	102	746	-1.313	0.040*	0.531
LkA1	<i>L. kempii</i>	Atlantic	endemic	21.977	158	764	-1.003	0.050	0.524
LoA1	<i>L. olivacea</i>	Atlantic	broad	10.994	147	689	-1.649	0.022*	0.611
CcP1	<i>C. caretta</i>	Pacific	broad	22.050	553 [#]	808	2.167	0.162	0.229
CmP1	<i>C. mydas</i>	Indo-Pacific	broad	11.410	1401 [#]	353	-0.310	0.071	0.447
CmP2	<i>C. mydas</i>	Pacific	endemic	11.116	112	354	-0.809	0.049	0.570
CmP3	<i>C. mydas</i>	Indo-Pacific	broad	10.905	1083 [#]	353	0.730	0.114	0.309
DcP1	<i>D. coriacea</i>	Pacific	broad	10.548	175	496	-0.129	0.082	0.387
EiP1	<i>E. imbricata</i>	Indo-Pacific	broad	15.005	534 [#]	765	-1.656	0.033	0.863
EiP2	<i>E. imbricata</i>	Indian	endemic	7.099	80	766	-1.565	0.042*	0.748
EiP3	<i>E. imbricata</i>	Indo-Pacific	broad	9.301	144	766	0.024	0.085	0.380
LoP1	<i>L. olivacea</i>	Indian	endemic	14.356	86	395	-1.928*	0.034*	0.879
LoP2	<i>L. olivacea</i>	Indo-Pacific	broad	14.813	266 [#]	470	1.057	0.086	0.275
NdP1	<i>N. depressus</i>	Pacific	endemic	17.837	305 [#]	810	-0.971	0.049	0.487

Table 3. Bayesian Model averaging results. For each combination of predictor and response variable, the posterior inclusion probability (PIP), posterior mean coefficient value (β), and 95% credible interval for β are provided.

Predictor	Response	PIP	β	95% CI (β)
Ocean Basin	<i>D</i>	0.513	-0.369	[-1.337 to 0.598]
	<i>R2</i>	0.723	-0.650	[-1.674 to 0.375]
	<i>H</i>	0.969	-1.144	[-1.923 to -0.365]
	π	0.981	-1.157	[-1.853 to -0.461]
Range Size	<i>D</i>	0.562	0.490	[-0.676 to 1.655]
	<i>R2</i>	0.410	0.279	[-0.586 to 1.144]
	<i>H</i>	0.615	0.467	[-0.459 to 1.393]
	π	0.895	0.879	[0.007 to 1.751]
Seasonality	<i>D</i>	0.195	0.021	[-0.186 to 0.227]
	<i>R2</i>	0.230	0.036	[-0.21 to 0.282]
	<i>H</i>	0.374	0.103	[-0.258 to 0.465]
	π	0.232	0.031	[-0.164 to 0.226]
Generation Time	<i>D</i>	0.192	0.020	[-0.201 to 0.242]
	<i>R2</i>	0.271	0.067	[-0.275 to 0.409]
	<i>H</i>	0.355	0.086	[-0.228 to 0.401]
	π	0.312	0.069	[-0.184 to 0.323]
Carapace Length	<i>D</i>	0.195	0.020	[-0.187 to 0.228]
	<i>R2</i>	0.277	0.060	[-0.224 to 0.344]
	<i>H</i>	0.181	-0.003	[-0.128 to 0.122]
	π	0.186	-0.010	[-0.156 to 0.137]
Diet Specialization	<i>D</i>	0.222	-0.074	[-0.593 to 0.444]
	<i>R2</i>	0.328	-0.198	[-1.004 to 0.609]
	<i>H</i>	0.292	0.135	[-0.538 to 0.808]
	π	0.205	0.032	[-0.348 to 0.412]
Sequence Length	<i>D</i>	0.177	0.001	[-0.181 to 0.182]
	<i>R2</i>	0.180	-0.004	[-0.186 to 0.179]
	<i>H</i>	0.265	0.046	[-0.186 to 0.278]
	π	0.457	-0.117	[-0.444 to 0.209]