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Adaptation of sea turtles to climate warming: Will phenological responses be sufficient to counteract changes in reproductive output?

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Abstract

Sea turtles are vulnerable to climate change since their reproductive output is influenced by incubating temperatures, with warmer temperatures causing lower hatching success and increased feminization of embryos. Their ability to cope with projected increases in ambient temperatures will depend on their capacity to adapt to shifts in climatic regimes. Here, we assessed the extent to which phenological shifts could

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mitigate impacts from increases in ambient temperatures (from 1.5 to 3°C in air temperatures and from 1.4 to 2.3°C in sea surface temperatures by 2100 at our sites) on four species of sea turtles, under a "middle of the road" scenario (SSP2-4.5). Sand temperatures at sea turtle nesting sites are projected to increase from 0.58 to 4.17°C by 2100 and expected shifts in nesting of 26–43 days earlier will not be sufficient to maintain current incubation temperatures at 7 (29%) of our sites, hatching success rates at 10 (42%) of our sites, with current trends in hatchling sex ratio being able to be maintained at half of the sites. We also calculated the phenological shifts that would be required (both backward for an earlier shift in nesting and forward for a later shift) to keep up with present-day incubation temperatures, hatching success rates, and sex ratios. The required shifts backward in nesting for incubation temperatures ranged from −20 to −191 days, whereas the required shifts forward ranged from +54 to +180 days. However, for half of the sites, no matter the shift the median incubation temperature will always be warmer than the 75th percentile of current ranges. Given that phenological shifts will not be able to ameliorate predicted changes in temperature, hatching success and sex ratio at most sites, turtles may need to use other adaptive responses and/or there is the need to enhance sea turtle resilience to climate warming.

KEYWORDS
adaptive response, climate change, ectotherms, marine turtles, phenology, reproductive output, sea turtles

1 | INTRODUCTION

The world's climate is changing at an unprecedented rate (Loarie et al., 2009). As a response, species, from polar terrestrial to tropical marine environments, have started to alter their phenology (e.g., timings of cyclical or seasonal biological events), shift their geographic distribution, and modify their trophic interactions (Dalleau et al., 2012; Parmesan & Yohe, 2003; Walther et al., 2002). Species' responses to climate change can occur through at least three contrasting but non-exclusive mechanisms: (1) range shifts, (2) phenotypic plasticity, and (3) microevolution via natural selection (Fuentes et al., 2020; Hulin et al., 2009; Waldvogel et al., 2020).

Range shifts might be observed by sea turtles responding to changes in climate by shifting their range to more climatically suitable areas (Abella Perez et al., 2016; Mainwaring et al., 2017). It is crucial that these areas provide the environment necessary for colonization and are conducive to egg incubation (Fuentes et al., 2020; Pike, 2013). However, it has been indicated that areas with climatically suitable environments might be impacted by other stressors (e.g., sea level rise, coastal development), which might hinder the potential adaptive capacity of sea turtles (Fuentes et al., 2020). Phenotypic plasticity allows individuals to cope with environmental changes and relates to the ability

of individuals to respond by modifying their behavior, morphology, or physiology in response to an altered environment (Hughes, 2000; Hulin et al., 2009; Waldvogel et al., 2020). Microevolution refers to adaptation occurring because of genetic change in response to natural selection (Lane et al., 2018). Phenotypic plasticity provides the potential for organisms to respond rapidly and effectively to environmental changes and thereby cope with short-term environmental change (Charmantier et al., 2008; Przybylo et al., 2000; Réale et al., 2003). However, phenotypic plasticity alone may not be sufficient to offset against projected impacts from climate change (Gienapp et al., 2008; Schwanz & Janzen, 2008). Microevolution, on the other hand, is thought essential for the persistence of populations faced with long-term directional changes in the environment. However, the ability of microevolutionary responses to counteract the impacts of climate change is unknown, because rates of climate change could outpace potential responses (Hulin et al., 2009; Morgan et al., 2020; Visser, 2008) although see Tedeschi et al. (2015).

It is unclear whether potential adaptive responses by turtles will be sufficient to counteract projected impacts from climate change (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Moran & Alexander, 2014; Morjan, 2003). For example, sea turtles have persisted through large changes in climate during the millions of years that

they have existed, demonstrating a biological capacity to adapt (Maurer et al., 2021; Mitchell & Janzen, 2010; Rage, 1998). Nevertheless, there is growing concern over the potential impacts that projected temperature increases might have on sea turtles (Patrício et al., 2021). Temperature plays a central role in sea turtle embryonic development, hatching success, hatchling sex ratios (Hays et al., 2017; Standora & Spotila, 1985), hatchling morphology, energy stores, and locomotor performance (Booth, 2017). Sea turtle eggs only successfully incubate within a narrow thermal range (25 and ~35°C), with incubation above the thermal threshold resulting in hatchlings with higher morphological abnormalities and lower hatching success (Howard et al., 2014; Miller, 1985). Furthermore, sea turtles have temperature-dependent sex determination, a process by which the incubation temperature determines the sex of hatchlings (Mrosovsky, 1980). The pivotal temperature (PT ~28.9–30.2°C for the species studied here, Figure S1), where a 1:1 sex ratio is produced, is centered within a transitional range of temperatures (~1.6–5°C, Figure S1), that generally produces mixed sex ratios. Values above the PT will produce mainly female hatchlings while values below produce mainly males (Mrosovsky, 1980).

Thus, projected increases in temperature may cause feminization of sea turtle populations and decrease reproductive success (Patrício et al., 2021). Many studies have suggested that sea turtles may adapt to increases in temperature by altering their nesting behavior, through changes in their nesting distribution, and nest-site choice (Kamel & Mrosovsky, 2006; Morjan, 2003), and by shifting nesting to cooler months (Almpanidou et al., 2018; Dalleau et al., 2012; Pike et al., 2006; Weishampel et al., 2004). Earlier nesting has already occurred in some turtle populations as a response to climatic warming (e.g., Pike et al., 2006; Weishampel et al., 2004). However, it is unclear whether phenological and behavioral shifts can sufficiently buffer the effects of rising temperatures (Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Lopez-Mendilaharsu, et al., 2019). Although two other studies (Almpanidou et al., 2018; Laloë & Hays, 2023) have explored whether earlier shifts in phenology can preserve the present-day thermal niche of sea turtle nesting environment in a changing climate, only one other study (Monsinjon, Lopez-Mendilaharsu, et al., 2019) explores the implications of phenological responses to sea turtle reproductive output (hatching success and primary sex ratio), of which they focused on loggerhead turtles (*Caretta caretta*). Given that different sea turtle species have different spatial–temporal nesting patterns, we expand from this study focused on loggerhead turtles to assess the extent to which phenological shifts by four different species of sea turtles could mitigate increases in temperature at different sea turtle nesting sites globally to maintain the reproductive output of affected populations. Furthermore, to build on previous work, we explore whether nesting populations could benefit from both an earlier and a later phenological shift. To do so, we calculated the shift (backward and forward, respectively) that would be required for incubation temperature, hatching success, and sex ratio to stay similar to current ranges. In doing so we are the first study to date to investigate the implications of a later nesting by sea turtles.

2 | MATERIALS AND METHODS

2.1 | Modeling framework

We considered the capacity of green (*Chelonia mydas, Cm*), loggerhead (*Caretta caretta, Cc*), hawksbill (*Eretmochelys imbricata, Ei*), and olive ridley (*Lepidochelys olivacea, Lo*) turtles to counteract the impacts of climate change on incubation temperature, hatching success, and sex ratio by temporally shifting their nesting season. We included 24 nesting sites globally which are part of 11 different regional management units (RMUs as per Wallace et al., 2010; Table S1). To predict overall hatching success and sex ratios at our study sites (scaling up spatially and temporally across levels: from the nest to the whole rookery; across the entire nesting period), we followed a method developed by Monsinjon, Wyneken, et al. (2019) for the loggerhead sea turtle (Figure 1). We calculated a seasonal indicator of mean incubation temperature (average weighted by the number of nests), hatching success (average survival proportion weighted by the number of nests), and sex ratio (average male or female proportion weighted by the hatching success and the number of nests). The approach consisted of six steps: (1) reconstruction of current (1979–2020) nest temperature at nesting sites, (2) modeling embryonic growth in clutches from the same RMU, (3) inferring thermal tolerances at the species level, (4) developing sex ratio thermal reaction norms at the species level, (5) describing nesting seasonality for each nesting site, and (6) forecasting nest temperature, hatching success and sex ratio under a scenario of climate warming, while considering a potential temperature-driven shift in nesting phenology (Figure 1). We give details on each step below and highlight any adjustments or improvements applied in the present study in relation to the Monsinjon, Wyneken, et al. (2019) analysis.

2.2 | Current clutch temperature

Based on a correlative approach with sea surface temperature and air temperature (Bentley et al., 2020; Fuentes et al., 2009; Girondot & Kaska, 2015; Laloë et al., 2020; Monsinjon, Jribi, et al., 2017), we reconstructed the daily nest temperature at each of our study sites between January 1979 and December 2020. For this, we obtained sea and air temperatures from the European Centre for Medium-Range Weather Forecasts (ECMWF) climate reanalysis v5 (ERA5; hourly time series at $0.25° \times 0.25°$ spatial resolution; Hersbach et al., 2020) at each site and fitted a linear mixed-effect model to our in situ daily nest temperatures using the R package "nlme" (Pinheiro et al., 2022) with nest identity as random effect and an ARMA correlation structure. To estimate metabolic heating (i.e., the increase in temperature within the egg chamber as compared to the surrounding incubation substratum), we used the proportion of incubation time as an additional predictor. This produces a proxy for metabolic heating specific to each nesting site (Monsinjon, Guillon, et al. (2017) for details). The values obtained (i.e., the increase in temperature at the end of incubation, Table S1) ranged from 0.46 to 5.55°C, which is similar to those presented by
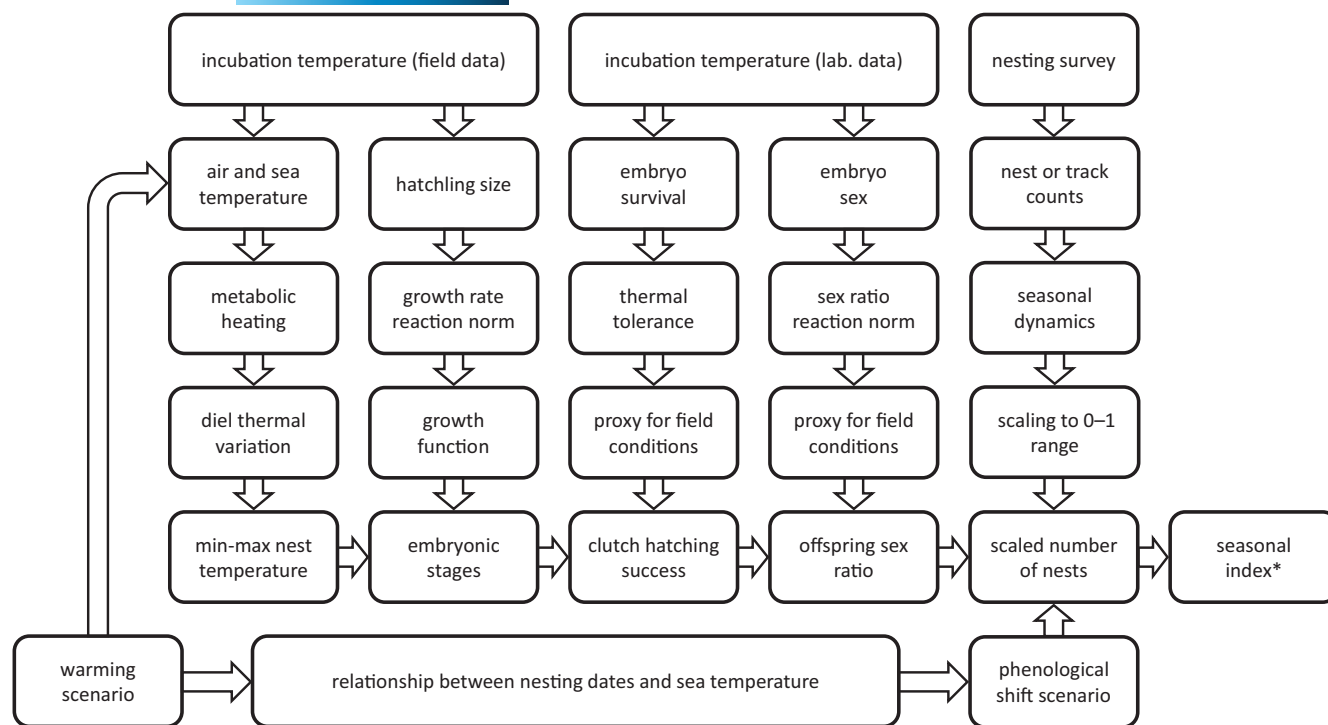
FIGURE 1 Modeling framework to predict overall hatching success and sex ratio at our study sites (scaling up from the day-nest level to the season-beach level), modified from Monsinjon, Wyneken, et al. (2019). * is to indicate seasonal index of incubtaion temperature, hatching success or sex ratio.

(Gammon et al., 2020). Based on the lowest Akaike information criterion (Burnham & Anderson, 2002), we selected the best model from a set of candidates using a daily lag with air or sea temperature varying from 0 (i.e., synchronous relationship with nest temperature) to 5 days (i.e., lagged relationship with nest temperature at day+5). Following (Monsinjon, Guillon, et al., 2017), we used the standard deviation of the coefficients of the random effect as a proxy of nest thermal heterogeneity at the nesting beach scale (see Monsinjon, Wyneken, et al., 2019) for its application in sea turtles. Finally, we estimated the coefficients of each predictor (sea surface temperature, air temperature, and proportion of incubation time) for the selected model within a standard generalized linear model framework using a Gaussian link function. To reconstruct diel thermal fluctuation, we computed daily maximum and minimum temperatures as follows: average daily temperature ± average daily amplitude (as defined by daily maxima − daily minima). We set daily maximum and minimum temperatures at the average time of day (decimal hours) when they occurred (mean daily amplitude and average time of day for minima and maxima are given in Table S1 along with the other parameters used to reconstruct nest temperatures).

2.3 | Embryonic development

To predict the progression of embryo size during incubation and hence estimate the dates of each embryonic stage along our nest temperature time series, we used two equations describing, respectively, the thermal reaction norm of embryonic

growth rate and a growth function of incubation time (Fuentes et al., 2017; Girondot et al., 2018; Girondot & Kaska, 2014; Monsinjon, Jribi, et al., 2017) using the R package "embryogrowth" (Girondot, 2022a). This method requires nest temperature data and measurements of the straight carapace length of hatchlings. Based on our field data (Table S1) and assuming a Gompertz model for embryo growth, we estimated the four parameters of the model (Schoolfield et al., 1981) using maximum likelihood (Girondot & Kaska, 2014). Here we identified the posterior distributions to compute confidence intervals using Bayesian Markov chain Monte Carlo (MCMC) with the Metropolis–Hasting algorithm (Chib & Greenberg, 1995) on 10,000 iterations. We used the values estimated with maximum likelihood as initial parameters and assumed a uniform distribution for priors. To ensure the acceptance rate across iterations was optimal, we followed the adaptive proposal distribution procedure (Rosenthal, 2011) implemented in the R package "HelpersMG" (Girondot, 2022b). Once calibrated, we ran the embryonic growth model along reconstructed nest temperatures to estimate, for any given day a clutch would be laid, the duration of incubation (i.e., when embryo size reaches hatchling size) and the position of the thermosensitive period of development for sex determination within that nest (Girondot et al., 2018).

2.4 | Thermal tolerance and hatching success

We used the flexible-logistic model described in Abreu-Grobois et al. (2020) and implemented in the R package "embryogrowth"

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(Girondot, 2022a) to describe the transition from maximal to 0% survival at temperatures where embryos fail to develop. This model allows for asymmetrical transitions in survival proportion at lethal temperatures (i.e., around 25°C and 33–35°C, with variation among species, Howard et al., 2014). We estimated the parameters of the thermal tolerance curve specifically for each species using literature data on hatching success measured at several controlled temperatures (i.e., held constant) during incubation experiments (Table S2). We first estimated the parameters using maximum likelihood and then we identified the posterior distributions to compute confidence intervals following the procedure described above (i.e., Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution) on 100,000 iterations assuming a uniform distribution for priors. Following Monsinjon, Wyneken, et al. (2019) and Laloë et al. (2020), we calculated hatching success from the mean temperature during the whole incubation after applying a correction parameter to control for deviations unrelated to temperature (Monsinjon, Wyneken, et al., 2019). The correction parameter was estimated by comparing in situ hatching success data (using data from the literature and the present study: see Table S3) with predicted ones (i.e., from mean temperature + correction factor) and searching for the value that minimizes the dispersion of residuals. As previous studies used +0.32°C for loggerhead turtles (Monsinjon, Wyneken, et al., 2019) and +0.82°C for green turtles (Laloë et al., 2020), we restricted our search between −1°C and +1°C.

2.5 | Sex ratio thermal reaction norm

To predict sex ratio (i.e., the proportion of males or females) at the scale of a clutch, we estimated the thermal reaction norm of sex ratio (i.e., the relationship between male proportion and temperature when held constant during incubation) using the logistic equation described in Monsinjon et al. (2022) and implemented in the R package "embryogrowth" (Girondot, 2022a). We estimated the equation parameters specifically for each species using literature data on sex ratio measured at several controlled temperatures (i.e., held constant) during incubation experiments (Table S4). We first estimated the parameters using maximum likelihood and then identified the posterior distribution of the parameters using Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution on 100,000 iterations assuming a Gaussian distribution for priors. We used a Gaussian distribution here since the values for the parameters do not vary much among sea turtle species. From our embryonic growth model, we estimated the position of the thermosensitive period of development (**BeginTSP** to **EndTSP** in the equation below), using the values estimated by Monsinjon et al. (2022) for sex determination during incubation and extracted temperature traces and increments of embryo size within this period (Girondot et al., 2018). As pointed out in previous research (Fuentes et al., 2017; Georges et al., 1994, 2005), the simple mean temperature is not an appropriate proxy

for sex ratio. Therefore, we calculated a growth-weighted average temperature (i.e., a constant temperature equivalent or CTE) and, following a recent improvement (Monsinjon et al., 2022), we added the level of sexualization (initially estimated for loggerhead turtles nesting in Florida, USA) to the weighting scheme. We calculated the growth-weighted sexualization-weighted average temperature (CTE) as follows:

$$\text{CTE} = \frac{\sum_{t=\text{BeginTSP}}^{\text{EndTSP}} (T_t \times \Delta\text{time} \times \textbf{Growth} \times \text{TRNS}(T_t) \times \text{S} - \text{TSP}(t))}{\sum_{t=\text{BeginTSP}}^{\text{EndTSP}} (\Delta\text{time} \times \textbf{Growth} \times \text{TRNS}(T_t) \times \text{S} - \text{TSP}(t))},$$

where T_t is the temperature at time t, Δtime is the time difference between two successive records, **Growth** is the size increment between two successive records, and $\text{TRNS}(T_t) \times \text{S} - \text{TSP}(t)$ is the level of sexualization defined by the thermal reaction norm of sexualization (**TRNS**) at T_t and the sensitivity of sexualization during the TSP (S − TSP) at time t.

2.6 | Nesting dynamics

To scale up incubation temperatures, hatching successes, and sex ratios at the scale of a clutch to the whole nesting season based on daily nest numbers, we estimated the overall nesting dynamics (i.e., the progression of nest number throughout any season) at our study sites (see Figure S2). To do this, we used the model described in Girondot (2010, 2017) available in the R package "phenology" (Girondot, 2020). This model uses a negative-binomial distribution for each ordinal day and has seven parameters that define nesting seasonality: (1) the date of the peak of nesting, (2) the average number of nests (or tracks) at the peak of the season, (3) its duration, (4) the minimum number of nests (or tracks) in periods out of the nesting season, (5) the duration from the beginning of the season to the peak and (6) from the peak to the end (the beginning and the end being estimated via the parameter 4), and (7) a negative-binomial parameter that controls for the dispersion around the mean. These parameters are components of a model described in Girondot (2010, 2017). This model uses all available nests (or tracks) to estimate the date of the beginning and the end of nesting seasons (via the parameters 1, 5, and 6, described above), which is more appropriate than using the first and the last nesting attempts that could be sporadic events not representative of the underlying nesting dynamics (e.g., if nesting occurs all year round). Here, we assumed that the maximum did not flatten out around the peak, which is consistent with the bell-shaped distribution of nest count data typically observed at our study sites. To minimize constraints on the parameters that control for the shape of nesting seasonality (i.e., when nesting begins, peaks, and ends), we estimated the maximum of each nesting season first while holding the "shape" parameters constant. Then we fixed the maximum to its estimated value, and we estimated the "shape" parameters in a second round. Finally, we standardized the overall nesting dynamics (number of nests or tracks per day) between 0 and 1 so that all nesting sites are treated the same way, assuming a

constant nesting success throughout the season. We treated the site Tetiaroa Atoll (French Polynesia) with a different set of equations (described in Laloë et al., 2020) derived from the aforementioned model (Girondot, 2010, 2017) because green turtles can attempt to nest on each of the 12 islets (see Laloë et al., 2020) which are not monitored with the same effort. Given the varying nesting proportion and monitoring effort at this site we estimated the maximum for each islet and each season to determine the overall nesting dynamics of this site. For computation efficiency purposes, we assumed the minimum number of nests was always zero during the low season, except for olive ridleys nesting at Las Cabras (Mexico). In this case, we also estimated season-specific minima because a non-negligible number of turtles came to nest sporadically all year round. We first estimated the parameters using maximum likelihood and then their distribution was estimated using Bayesian MCMC with the Metropolis–Hasting algorithm and the adaptive proposal distribution on 10,000 iterations assuming a Gaussian distribution for priors.

2.7 | Climate and phenology scenarios

We considered two climate scenarios: current (hindcasting between 2007 and 2020) and the IPCC's SSP2-4.5 "Middle of the road" scenario (IPCC, 2021); forecasting between 2059 and 2100. We predicted incubation temperature, hatching success, and sex ratio within the last two decades to stay representative of current day conditions and chose from 2007 onward as this period contains >97.5% of our hatching success field data (Table S5). We extracted mean temperature and sea surface temperature anomalies from the web interface (https://interactive-atlas.ipcc.ch/regional-information) of the IPCC's Atlas (Gutiérrez et al., 2021) with the following settings: Region set = WGI reference-regions (or Small islands for the Tetiaroa Atoll, French Polynesia), Uncertainty = Advanced, Season = Annual, Baseline period = 1981–2010, and Future period = 2081–2100. For both variables and within each region, we extracted the median change in temperature (Table S1). To forecast daily minimum and maximum nest temperatures between 2059 and 2100, we added those anomalies to our 1979–2020 baseline time series of air and sea surface temperature and applied the model calibrated on contemporary data. We then computed daily hatching success and sex ratio along forecasted nest temperatures by iterating the steps described earlier. Finally, we considered three plausible phenology scenarios: (1) no shift in nesting phenology, or (2) nesting dates will shift either 6.86 days earlier (hereafter referred to as the "mean" shift, ±SD = 4.23, n = 16; Table S6) or (3) 18.85 days earlier (hereafter referred to as the "maximum" shift, found in Mazaris et al., 2008) for every 1°C rise in sea surface temperature at nesting sites. We calculated the mean and maximum shifts based on an extensive search of previous studies that reported a significant negative relationship between nesting dates and seawater temperature in sea turtles (Table S6). We did not consider non-significant or positive relationships between the proxy for nesting phenology and the environmental cue (i.e., a delay of nesting dates with increasing temperatures instead of a shift earlier as assumed in the present

study). Based on these relationships and the expected regional anomalies in sea surface temperature under the SSP2-4.5 warming scenario, we estimated the expected number of days shifted in the future at our study sites (Table S1) and forecast our seasonal indicators of incubation temperature, hatching success, and sex ratio accordingly. When considering if sites would remain within current rates we considered conditions within a 2.5% of the present-day values for hatching success and sex ratio shift (i.e., difference between 25th percentile of current and median of future <2.5% reduction) and within 0.5°C buffer for incubating temperature (i.e., difference between median of future and 75th percentile of current <0.5°C). To complement this analysis, we also calculated earlier and later phenological shifts that would be required in the future to stay within current conditions. To do so, we shifted nesting seasons backward (from −1 to −365 days) and forward (from +1 to +365 days) and we retained the minimum number of days earlier or later when the following conditions are met for each indicator: (1) median incubation temperature index ≤75th percentile of current indices, (2) median hatching success index ≥25th of current indices, and (3) median sex ratio (male proportion) index ≥25th percentile of current indices.

2.8 | Sensitivity analysis and fit quality

As sufficient data were not available specifically for each RMU, we fitted thermal tolerance curves and sex ratio thermal reaction norms at the species level (i.e., pooling all available data, individually for each species) to benefit from the existent extensive literature data (Tables S2 and S4). This approach allowed us to predict hatching success and sex ratio for sites where data were unavailable or too scarce at the RMU level (i.e., lack of data at low or high temperatures, Table S1). For our sensitivity analysis, we compared our predicted hatching success and sex ratio seasonal indices using either species-wide or RMU-wide data when available for both hatching success and sex ratio laboratory data. This allowed us to compare the outputs for loggerheads from the "Atlantic, Northwest" RMU (2/6 loggerhead sites; 1/4 RMUs), hawksbills from the "Atlantic, Western Caribbean/USA" RMU (4/7 hawksbill sites; 1/4 RMUs), and olive ridleys from the "Pacific, East" RMU (2/3 olive ridley sites; 1/2 RMUs), but we could not compare the outputs for green turtles (eight green turtle sites; five RMUs) because there were no data available for any of the RMUs (thermal tolerance curves and sex ratio thermal reaction norms are presented in Figure S1 and details on sites and RMUs can be found in Table S1). We evaluated the robustness of our predictions by comparing predicted daily mean nest temperatures with recorded ones. We calculated the R^2 coefficient of determination as a measure of fit quality.

3 | RESULTS

Under a "middle of the road" warming scenario (SSP2-4.5), the air temperature will increase on average by 1.5–3°C, and local sea surface temperature will increase by 1.4–2.3°C by 2100 across our

study sites, resulting in a 0.58–4.17°C increase in sand temperatures (Table S1). According to the maximum expected phenological shift (18.85 days earlier for every 1°C rise in local sea surface temperature), nesting seasons could shift from 26 to 43 days earlier on average by 2100 at our study sites (n = 24, Table S1).

Currently (2007–2020), the median incubation temperature at our study sites is 30.1°C (25th–75th percentiles = 29.1–30.8°C), ranging from 26.1 to 32.1°C (Cc 26.1–32.1°C, Cm 28.8–32.1°C, Ei 28.5–31.6°C, Lo 30.3–30.7°C; Figure 2; Figure S3). Under a "middle of the road" scenario (2059–2100), the median incubation temperature will rise to 31.7°C (25th–75th = 30.7–32.8°C), ranging from 28 to 35.7°C (Cc 28–35.7°C, Cm 29.9–34.4°C, Ei 30.3–33.7°C, Lo 32.3–33.1°C). With a maximum expected shift in phenology, the median decreases to 31°C (25th–75th = 30.1–32.5°C), ranging from 26.6 to 34.2°C (Cc 26.6–33.9°C, Cm 29.7–33.6°C, Ei 28.8–33.8°C, Lo 31.9–34.2°C; Figure 2). With a maximum shift in phenology only seven sites would be able to maintain current incubation temperature or lower. To keep up with present-day incubation temperature the required shifts backward, for an earlier nesting, ranged from −20 to −191 days (Figure S3; Table S7), whereas the required shifts forward, for a later nesting, ranged from +54 to +180 days. To note for half of the sites no matter the shift the median temperature will always be warmer than the 75th percentile of current ranges. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved are presented in Table S7.

Currently, the median hatching success rate at our study sites is 80.1% (25th–75th = 74.3%–82.7%), ranging from 53.5% to 84.5% (Cc 76.1%–84.5%, Cm 73.2%–82.6%, Ei 65.7%–84%, Lo 53.5%–68.9%; Figure 3; Figure S4). Under a "middle of the road" scenario, hatching success rates will drop to 67.4% (25th–75th = 46.3%–78.2%), ranging from 1% to 84.5% (Cc 1%–84.5%, Cm 50.4%–81%, Ei 42.6%–75.2%, Lo 26.5%–57.5%), and with the maximum expected shift in phenology hatching success rates increases to 69.1% (25th–75th = 50.8%–79.9%), ranging from 15.3% to 84.5% (Cc 27.5%–84.5%, Cm 59.1%–81.3%, Ei 41.1%–83.1%, Lo 15.3%–58.2%), with 10 of the 24 nesting sites being able to maintain similar hatching success rates to current values (Figure S4; Table S8). To keep current hatching success rates, the required shifts backward for an earlier nesting ranged from −1 to −172 days (Figure S4; Table S7), whereas the required shifts forward for a later nesting ranged from +1 to +252 days. With half of the sites being unable to maintain current hatching success rates no matter the shift undertaken. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved is presented in Table S7.

Currently 6 of the 24 nesting sites produce more than 90% of female hatchlings and 6 of the 24 sites produce at least 50% male hatchlings (Figure 4; Figure S5). We predicted that under a "middle of the road" scenario, 16 of the 24 nesting sites will produce clutches comprising more than 90% female hatchlings, with only one site (Lepidochelys olivacea in las Cabras, Mexico) producing clutches with more than 50% male hatchlings. However, with the maximum expected phenological shifts, the number of sites producing more than 90% of females will reduce to 11, and three sites would produce more than 50% of males. Overall, with the maximum expected phenological shift, half of the sites will be able to maintain current sex ratios (Figure S5; Table S8) of which seven are expected to produce more than 25% males (loggerheads in Wassaw Island and Dalyan Turtle beach, greens in Akyatan and Alagadi Turtle beaches, hawksbills in Fuwairit, and olive ridleys in Rushikulya and Las Cabras). The required shifts backward to keep current male proportions ranged from −1 to −149 days (Figure S5; Table S7), whereas the required shifts forward ranged from +1 to +160 days. With eight sites being unable to keep current sex ratio no matter the shift undertaken. The relationship between nesting dates and SSTs (i.e., the phenological rates) that would allow the required phenological shifts to be achieved is presented in Table S7.

3.1 | Model robustness

Overall, there is good agreement between predicted and recorded daily incubation temperatures with a R^2 of .71 (Figure 5) that ranges from .2 to .91 when temperatures are compared individually for each site (Figure S6). Our sensitivity analysis shows that seasonal indicators of hatching success can be different for hawksbills (i.e., hatching success always higher under the warming scenario considered here when using data at the species level) when using either species-wide or RMU-wide laboratory data to adjust the model for thermal tolerances (Figure S7). On the other hand, we did not detect substantial differences for loggerheads and olive ridleys, for both indicators of hatching success and sex ratio.

4 | DISCUSSION

The maximum expected shift in nesting phenology will allow for some sites to maintain similar incubation temperatures (n = 7), hatching success (n = 10), and sex ratio (n = 12) to current values (2007–2020). However, for half of the sites no matter the shift in phenology current rates of incubation temperature and hatching success will not be able to be maintained, with eight sites being unable to keep current male production no matter the shift undertaken. These results align with similar studies which found variability in the ability of phenological shifts to maintain current temperature levels and consequently productivity (Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Wyneken, et al., 2019), with nesting sites further from the equator (>30° latitude) showing to have the greatest capacity to buffer impacts of predicted increases in nest temperatures (this study and Laloë & Hays, 2023). The inability for nesting phenology to counteract predicted changes in temperature and productivity is of concern.

Several studies, including this one, have predicted a reduction in hatchling production as temperatures increase, which would impact population growth and stability (Laloë et al., 2017; Montero et al., 2019; Montero, Ceriani, et al., 2018; Santidrián Tomillo
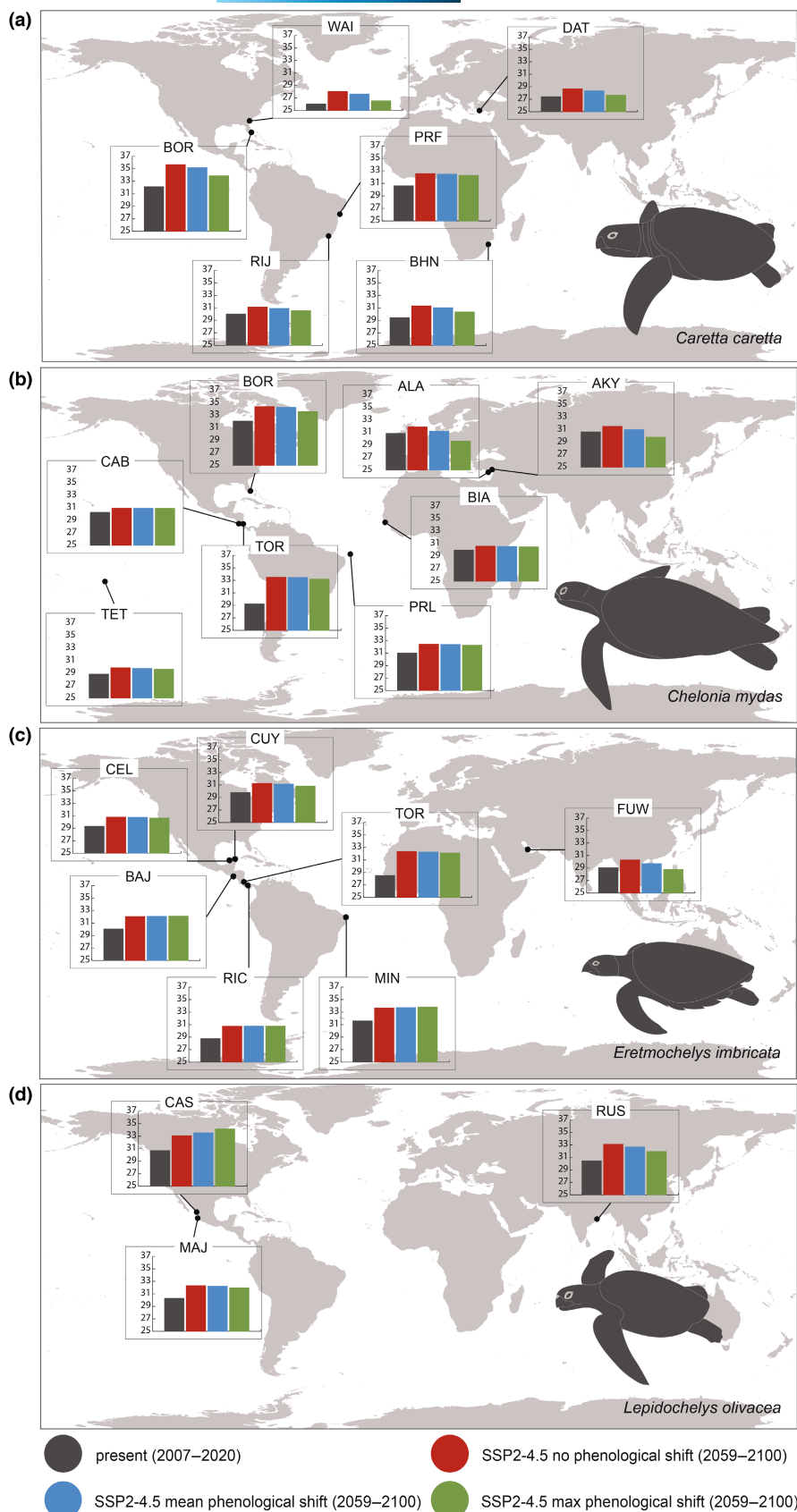
FIGURE 2 Current (2007–2020) absolute mean incubation temperature, and future (2059–2100) incubation temperature across the whole incubation period under a middle of the road scenario (SSP5-48.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), (d) olive ridley (*Lepidochelys olivacea*). AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA.

et al., 2015). Furthermore, even though sea turtle populations are typically female bias (Hays et al., 2014), greater production of female hatchlings in relation to current rates (median female proportion across our study sites between 2007 and 2020 ≈ 70%) may ultimately result in unbalanced sex ratios of breeding adults (Schwanz et al., 2010), which might alter reproductive dynamics, reducing
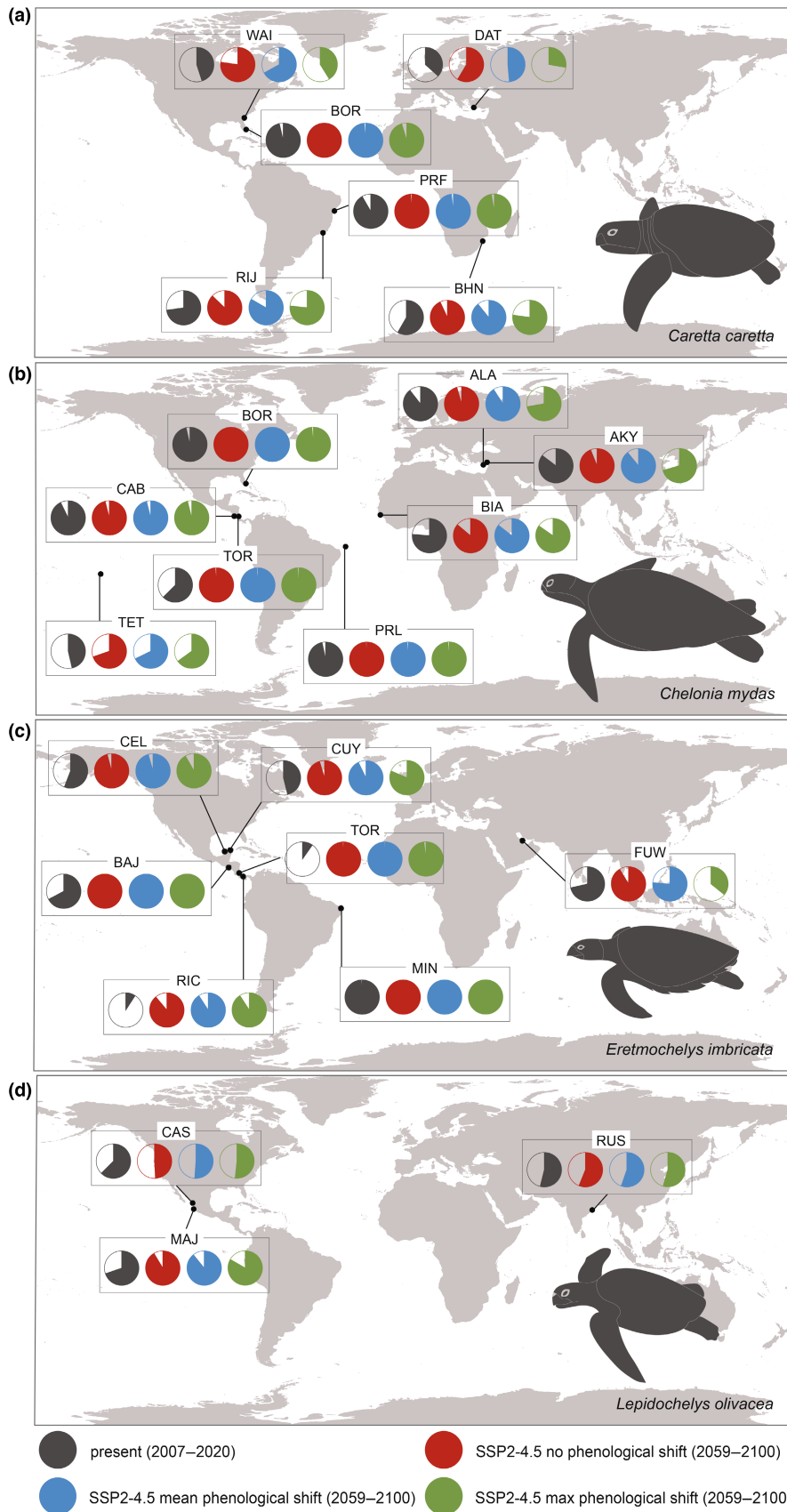
FIGURE 3 Current (2007–2020), and future (2059–2100) hatching success projections under a middle of the road scenario (SSP2-4.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), and (d) olive ridley (*Lepidochelys olivacea*). Full charts indicating 100% hatching success AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA.
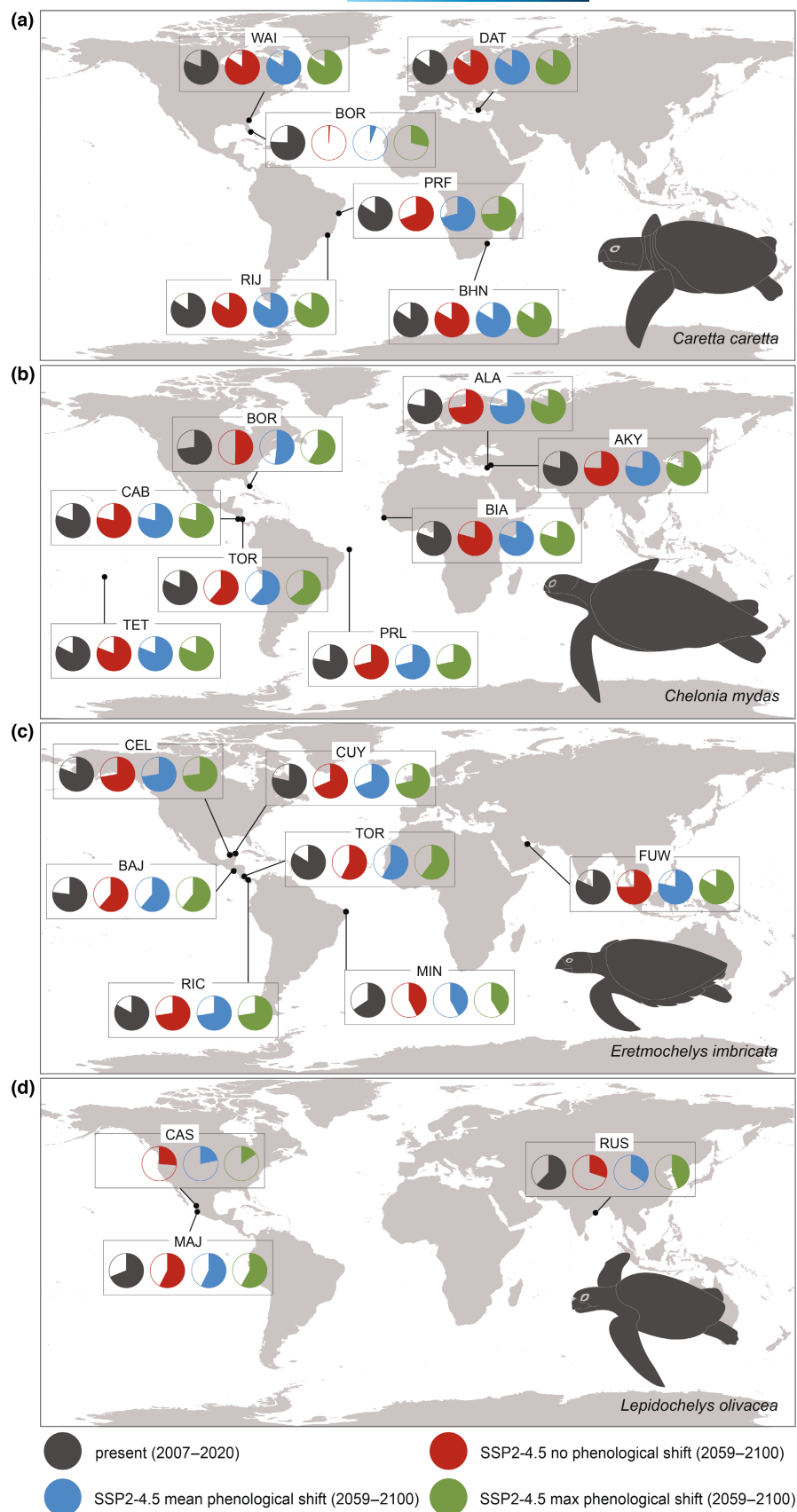
the incidence of multiple paternity and fertilization rates, as well as resulting in loss of genetic variation (Booth et al., 2021; Fuller et al., 2013; Hays et al., 2023; Manning et al., 2015). Feminization

of populations may lead to demographic collapses (Mitchell & Janzen, 2010), although some evidence suggests that a shorter period between breeding bouts in males and promiscuous breeding

FIGURE 4 Current (2007–2020), and future (2059–2100) projections of female hatching production under a middle of the road scenario (SSP2-4.5) with and without an earlier phenological shift (26–43 days) for (a) loggerhead turtles (*Caretta caretta*), (b) green turtles (*Chelonia mydas*), (c) hawksbill turtles (*Eretmochelys imbricata*), and (d) olive ridley (*Lepidochelys olivacea*). Full charts indicate 100% female production. AKY, Akyatan beach, Türkiye; ALA, Alagadi Beach, Cyprus; BAJ, Bahía de Jiquilisco, El Salvador; BHN, Bhanga Nek, South Africa; BIA, Bijagós Archipelago, Guinea-Bissau; BOR, Boca Raton, Florida, USA; CAB, Cabuyal, Costa Rica; CAS, Las Cabras, Mexico; CEL, Celestún, Mexico; CUY, El Cuyo, Mexico; DAT, Dalyan Turtle Beach, Türkiye; FUW, Fuwairit, Qatar; MAJ, Majahuas, Mexico; MIN, Minas, Brazil; PRF, Praia do Forte, Brazil; PRL, Praia do Leão, Brazil; RIC, Rio Caña, Panama; RIJ, Rio de Janeiro, Brazil; RUS, Rushikulya, India; TET, Tetiaroa, France; TOR, Tortuguero, Costa Rica; WAI, Wassaw Island, USA. To note estimation is not directly obtained from Figure 2, but rather derived from temperatures during the TSP.

behavior may help balance operational sex ratios in warmer climates (Hays et al., 2023). The long-term consequences of skewed primary and adult sex ratios on population dynamics and the proportion of

males required to sustain populations need to be fully understood for more robust assessments of the impacts of climate change on sea turtles (Boyle et al., 2014, 2016; Heppell et al., 2022). Similarly,
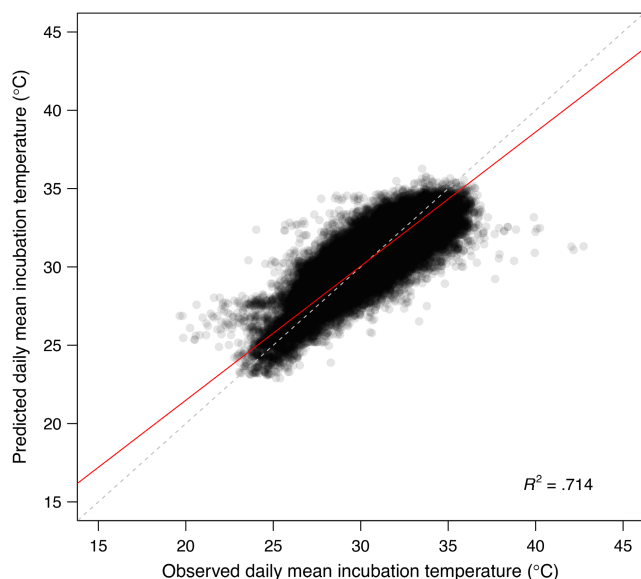
FIGURE 5 Predicted versus observed daily mean incubation temperatures (all study sites pooled together). The gray dashed line is the line of equality, and the red line shows the orthogonal regression.

for studies that aim to predict future hatchling production, such as this one, lack of data on the relationship between constant temperatures and hatching success remains problematic as well as lack of knowledge of how to integrate varying temperatures into constant equivalent temperatures and a lack of understanding on metabolic heating and its contribution to hatching success (Gammon et al., 2020, 2021). Such data gaps hindered our ability to include leatherback (*Dermochelys coriacea*) and flatback (*Natator depressus*) turtles in our assessment. For these species, we lack hatching success data below lower and above upper lethal temperatures (i.e., ~25 and ~35°C, respectively, Howard et al., 2014) to properly estimate thermal tolerance limits from laboratory experiments although see Gammon et al. (2021).

It is also important to consider that our study focuses on temperature-driven hatching success whereas other environmental factors, such as precipitation and moisture have also been found to influence hatching success (Montero, Marcovaldi, et al., 2018; Rafferty et al., 2017). For instance, embryos can die from suffocation if the nest is flooded from heavy rainfall for an extended period or from desiccation in the opposite case. Moreover, precipitation can cause incubation temperatures to drop via direct cooling or evaporation (Lolavar & Wyneken, 2021; Tezak et al., 2018), which has resulted in the suggestion that nest watering could potentially be used as management strategy to reduce heat-induced egg/hatchling mortality and to manipulate hatchling sex ratios (e.g., Gatto et al., 2023; Hill et al., 2015; Jourdan & Fuentes, 2015; Smith et al., 2021). However, human-assisted cooling of nests comes with a series of costs and benefits. Costs include the persistent need of human resources if temperatures continue to increase and a potential slowdown of natural selection via the retention of deleterious alleles. Benefits include a demographic boost if rescued embryos

make it to adulthood and reproduce as well as the maintenance of appropriate genetic mixing if primary sex ratios translate into an optimal balance between reproductive males and females (Patrício et al., 2021). Nevertheless, if managers decide to manipulate the incubation of eggs, it is crucial to evaluate the consequences and define a strategy that requires the least human resources. Based on controlled incubation experiments, Porter et al. (2021) mimicked the effect of heavy rainfall by dropping incubation temperatures for 3 or 7 days during the thermosensitive period for sex determination (TSP). For eggs incubating at constant, female-producing temperatures, the results suggest that short temperature drops below the pivotal temperature can be sufficient to trigger the development of males and that the sensitivity to these drops throughout the TSP varies between green and loggerhead turtles. As discussed by the authors, this can be useful to target when to cool down the nests in natural conditions. A potential research avenue would be to refine the results presented in Patrício et al. (2021) by determining what would be the smallest drop in both temperature difference and duration sufficient to reach a specific proportion of males at any given temperature throughout incubation.

Our sensitivity analysis suggests that hatching success predictions for hawksbill turtles can differ when using data at the RMU level when compared to the species level, especially under the "middle of the road" (SSP2-4.5) warming scenario (Figure S7). This likely reflects a lack of data at the RMU level for this species. Although we did not detect substantial differences for olive ridley and loggerhead turtles, it is recommended to use hatching success and sex ratio data at the RMU level to account for local adaptation (or maladaptation) in thermal tolerances and pivotal temperatures. We encourage further research to obtain such data to refine the results presented here and extend our assessment of adaptive capacity to other sites and species. Furthermore, other limitations must also be taken into consideration when interpreting our results. First, we forecast future incubation temperatures based on a correlative model (i.e., via generalized linear models) whereas a mechanistic one (i.e., based on thermodynamics and biophysics principles) would be more appropriate (Bentley et al., 2020). We found an overall good agreement between incubation temperature predictions and observations, except for some sites for which high temperatures are largely underestimated (Figure S6). This is problematic when projecting warming impacts as we might underestimate exposure to female-producing and lethal temperatures. On the other hand, a mechanistic microclimate model (e.g., NicheMapR; Kearney & Porter, 2017) requires extensive information on sand physical properties, beach topography, vegetation, and local weather, which makes it difficult to apply extensively and globally (Fuentes & Porter, 2013). Second, we projected hatching success solely based on temperature, but future studies must integrate the combined effect of other climatic variables such as temperature and humidity, and consider uncertainties related to climate-driven changes in these variables. Third, we predicted clutch sex ratios using a recent, more sophisticated approach, namely the thermal reaction norm for sexualization (Monsinjon et al., 2022). However, this method requires extensive data on hatchling sex

ratios under fluctuating temperature regimes and thus was applied so far only for loggerhead turtles nesting in Florida. Further research must be undertaken to investigate potential variations among species and populations in the timing of the TSP and the sensitivity of sexualization. Finally, we assumed that earlier phenological shifts are driven by temperature at nesting sites, in which case turtles would be waiting for optimal conditions for nesting after their arrival, with higher temperatures speeding up egg maturation (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Pike, 2009; Schofield et al., 2009). However, sea turtle nesting phenology is yet to be fully understood as other studies suggest that the environmental cue turtles respond to might be sensed before their departure from foraging areas (Mazaris et al., 2009; Monsinjon, Lopez-Mendilaharsu, et al., 2019). We did not investigate this because the location of foraging areas connected to our nesting sites was unknown for most of the sites considered here. In addition, it is sometimes unclear whether other factors are involved (e.g., demography) in observed phenological shifts (Monsinjon, Lopez-Mendilaharsu, et al., 2019; Robinson et al., 2014), which makes it difficult to disentangle the effect of temperature. We encourage further studies to finetune the calculation of expected phenological shifts, specifically for each nesting population, by considering multiple factors (e.g., temperature, demography, migratory connectivity, and foraging habitat productivity).

Even though some work is still necessary to improve the spatio-temporal scale of our results, and that some improvements can be potentially made with our modeling approach our study provides another step toward a multi-species evaluation of climate change impacts on sea turtles' embryonic stage and sets the baseline for future research on this topic. For example, even though we only considered the influence of temperature on hatchling success, our results allow us to identify which sites might be more vulnerable/resilient to changes in temperature and that will suffer from warming-related shortage of hatchlings (i.e., the sites potentially at risk from rising temperatures only), which is particularly relevant for ectothermic species like sea turtles. Ultimately, the broad geographic span of our study sites, and consideration of four of the seven species of sea turtles, indicate that the impacts of climate change and the ability of phenological shifts to counteract potential feminization of sea turtles and decreases in hatching success will vary spatially and among species with some populations being unable to take advantage of phenological shifts, as previously indicated by similar studies (see Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon, Wyneken, et al., 2019). Having said this, we identified five sites (Wassaw Island, USA, Daylan beach, and Akyatan beach in turkey, Alagadi Beach in Cyprus and Fuwairit, Qatar) in which a maximum phenological shift will result in more males being produced than currently without a reduction in hatching success as observed at Las Cabras, Mexico. Ultimately, the impact of climate change on sea turtles and their resilience to it will depend on several factors such as population size, genetic diversity, non-climate-related threats, foraging plasticity, the availability of climatically suitable habitat, and their capacity to adapt (Fuentes et al., 2013, 2020; Patrício et al., 2021). Here, we only considered the ability of sea turtles to adapt through shifts in nesting phenology, which alone will likely not be sufficient to counteract the projected impacts of climate change on sea turtle reproduction (Almpanidou et al., 2018; Monsinjon, Wyneken, et al., 2019). It might be that several other processes need to take place for sea turtles to be able to adapt to climate change. Other behavioral adaptations may include changes in the spatial distribution of sea turtle nesting sites, as well as changes in their nest-site choice on nesting beaches (Cardona et al., 2022; Girard et al., 2021; Hochscheid et al., 2022; Mancino et al., 2022; Tomillo et al., 2022). Since spatial and temporal adaptations may occur simultaneously (Chuine, 2010), future studies should develop a multi-faceted framework to explore the adaptive potential of sea turtles in response to contemporary climate change. It is also important to consider the potential implications of adaptations and, to the extent possible, account for known non-climate-related threats which will occur concurrently and potentially synergistically so that an adaptive management approach can be undertaken in impact assessments (Fuentes et al., 2016).

Shifts in nesting phenology may result in changes in the exposure of sea turtles to threats that have a seasonal nature (e.g., specific fisheries, recreational activities). Similarly, shifts in nesting range may result in turtles being more exposed to other threats such as coastal development and sea level rise (Fuentes et al., 2020). Clearly, there are several interlinked factors affecting the ability of sea turtles to adapt and survive projected climate changes, highlighting the need for a better understanding of the cumulative and interacting nature of these factors in conjunction with animal behavior. While we address the current knowledge gaps, which hinder a more comprehensive understanding of the impacts of climate change on sea turtles (Patrício et al., 2021), there remains a need to enhance sea turtle resilience to climate change by mitigating other threats that they currently face (Brander, 2008; Fuentes et al., 2012). Such an approach will give vulnerable and depleted populations greater resilience to resist these disturbances.

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CONFLICT OF INTEREST STATEMENT

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.