




RESEARCH ARTICLE

Hurricanes affect diversification among individual life courses of a primate population

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Abstract

1. Extreme climatic events may influence individual-level variability in phenotypes, survival and reproduction, and thereby drive the pace of evolution. Climate models predict increases in the frequency of intense hurricanes, but no study has measured their impact on individual life courses within animal populations.
2. We used 45 years of demographic data of rhesus macaques to quantify the influence of major hurricanes on reproductive life courses using multiple metrics of dynamic heterogeneity accounting for life course variability and life-history trait variances.
3. To reduce intraspecific competition, individuals may explore new reproductive stages during years of major hurricanes, resulting in higher temporal variation in reproductive trajectories. Alternatively, individuals may opt for a single optimal life-history strategy due to trade-offs between survival and reproduction.
4. Our results show that heterogeneity in reproductive life courses increased by 4% during years of major hurricanes, despite a 2% reduction in the asymptotic growth rate due to an average decrease in mean fertility and survival by that is, shortened life courses and reduced reproductive output. In agreement with this, the population is expected to achieve stable population dynamics faster after being perturbed by a hurricane ($\rho = 1.512$; 95% CI: 1.488, 1.538), relative to ordinary years ($\rho = 1.482$; 1.475, 1.490).
5. Our work suggests that natural disasters force individuals into new demographic roles to potentially reduce competition during unfavourable environments where mean reproduction and survival are compromised. Variance in lifetime reproductive success and longevity are differently affected by hurricanes, and such variability is mostly driven by survival.

KEYWORDS

Cayo Santiago, eco-evolutionary dynamics, extreme climatic events, hurricanes, individual heterogeneity, individual stochasticity, matrix population models, population entropy

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1 | INTRODUCTION

Hurricanes are rare, yet their extreme acute nature can have profound impacts on populations. Hurricanes increase mortality (Amezcua y Juárez et al., 2015; Batista & Platt, 2003; Wiley & Wunderle, 1993), suppress fertility (Gannon & Willig, 1994; Luevano et al., 2022; Morcillo et al., 2020), increase physiological stress (Behie & Pavelka, 2014), change social organization (Pavelka et al., 2003; Testard et al., 2021) and alter gene expression (Watowich et al., 2022). Although the accumulation of longitudinal data has contributed to our understanding of the effects of these events on average life-history traits, variation in such traits and not population averages, shape fitness and the resulting population response to environmental impacts (Jenouvrier et al., 2015; Vindenes et al., 2008; Vindenes & Langangen, 2015). Filling in this knowledge gap is important because climate models predict increases in the frequency of intense hurricanes (Bloemendaal et al., 2022; Holland & Webster, 2007). To accurately quantify the eco-evolutionary dynamics of populations under rapid environmental change, we must first investigate whether and how extreme climatic events drive the emergence and maintenance of heterogeneity in life courses (Metcalf & Pavard, 2007).

Here, we aim to understand how tropical cyclones influence heterogeneity in life courses and the resulting variation in life-history traits by contrasting individual performance during years of major hurricanes with performance during ordinary years using a long-lived primate population. We first define heterogeneity as differences in individual life courses that can vary temporally and characterize it using metrics of population entropy and stage persistence

(Tuljapurkar et al., 2009). We do not define population entropy as fixed heterogeneity (heritable variation) but consider it as one of the many measures of dynamic heterogeneity (also known as individual stochasticity) where individuals are defined with the same survival and reproduction rates though stochastic processes result in different sequences of stages as individuals age (Forsythe et al., 2021; Steiner & Tuljapurkar, 2023). Starting at birth, life courses can be described by the sequence of stages an individual experiences until death (Caswell, 2001; Figure 1: individual life courses). As life progresses through time, individuals may remain in the same stage (i.e. stasis) or transition among developmental, morphological, reproductive, behavioural and physiological stages. Population entropy measures the rate at which these stage trajectories are expected to diversify with age, and thus can take on a low value (slow increase in variability around the mean life course) or a high value (faster increase in variability around the mean life course; Hernández-Pacheco & Steiner, 2017; Tuljapurkar, 1982; Tuljapurkar et al., 2009; Figure 1: population entropy). Persistence in any life stage instead measures the correlation time between an individual's current life stage and their stage at a later age. Prior analyses did not find correlations between entropy and stage persistence for many species, implying that these two metrics describe independent features of the biology of individual life courses (Tuljapurkar et al., 2009).

The outcome of dynamic heterogeneity can also be described by the exact probability distributions of life-history traits and their higher moments, with life-history traits being evaluated at the end of life (Caswell, 2009, 2011; Tuljapurkar et al., 2020; van Daalen & Caswell, 2020; Figure 1: trait distribution). As individuals age, their movement through the life cycle follows a random

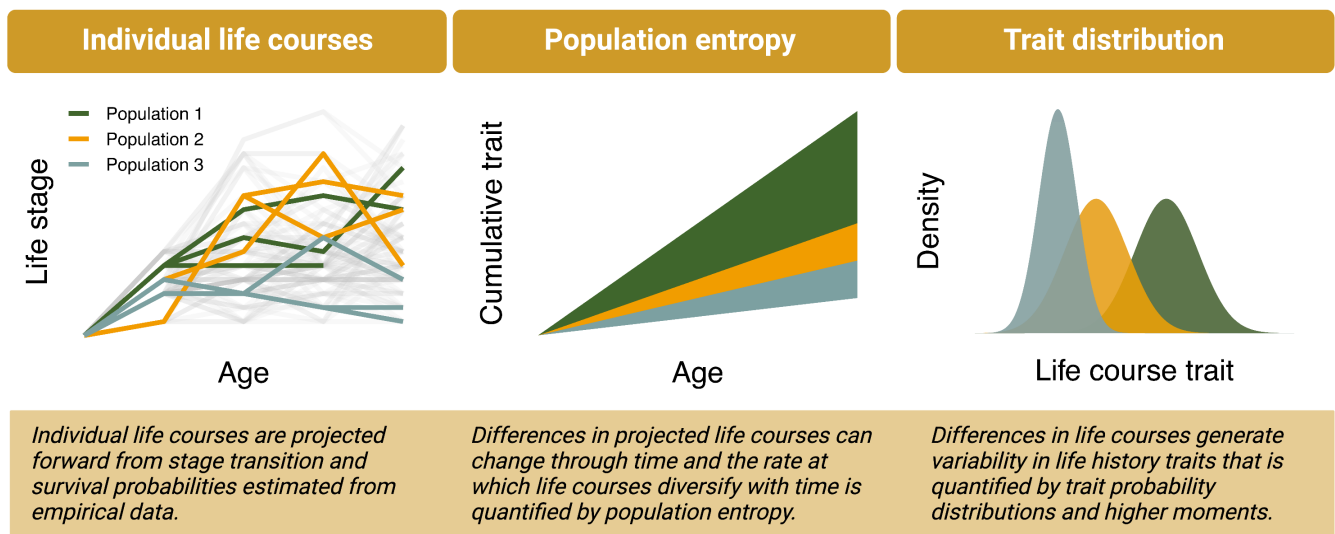


FIGURE 1 Dynamic heterogeneity metrics estimated from stage-based matrix population models. Individual life courses: life stage sequences across age are projected from stage-specific mean vital rates (three random life courses per population experiencing different vital rates are highlighted). Population entropy: variation in individual life courses result in different accumulation of fitness traits (e.g. cumulative reproduction) and such variation can have a fast increase over time (high entropy; Population 1) or a slow increase over time (low entropy; Populations 2 and 3). Trait distribution: stage-specific transition and survival probabilities defining life courses generate variation in life-history traits (e.g. reproductive output) that can be evaluated from their exact probability distributions and their higher moments (i.e. variance, skew). Entropy is independent from trait distribution variances (e.g. Population 1 and 2 differ in entropy but have the same trait variance).

process determined by transition rates that generates variation in life-history traits. We thus follow by defining the exact probability distributions of lifetime reproductive success (LRS) and lifespan (i.e. age at death, Tuljapurkar et al., 2020), and the variation in the lifetime number of visits (i.e. transitions into) to any transient state (i.e. individual stochasticity; Caswell, 2009). In contrast to population entropy and stage persistence, these distributions do not account for the order of stages through life (sequence) but provide information about the expected available variability in life-history traits within the population. In this way, two populations may present similar trait distributions, yet different entropies (Figure 1; Population 1 and 2).

To our knowledge, no study has investigated how hurricanes alter dynamic heterogeneity. Although prior work has established that high competition drives niche expansion (Bolnick, 2001) and that variable environments stimulate flexible life-history strategies with direct consequences on fitness (Chambert et al., 2015), we do not know if this translates into diversifying life courses and enlarge trait variances. As hurricanes result in extremely poor environments that lead to strong intraspecific competition (Schaffner et al., 2012), they may force individuals into new life-history strategies increasing the expected rate of diversification in stage trajectories over time (i.e. high entropy, low stage persistence). On the other hand, recent work on climate extremes shows that unfavourable years are associated with reductions in entropy (Jenouvrier et al., 2015). Thus, hurricanes may instead reduce life course heterogeneity due to potential life-history trade-offs between survival and reproduction. Here, individuals are driven to an optimal life-history strategy by either allocating more energy to maintenance processes to ensure future reproductive success after recovery (Morcillo et al., 2020) or by increasing reproduction and growth in certain life stages where survival is uncertain (Pascarella & Horvitz, 1998), thereby reducing entropy and increasing stage persistence. This latter scenario may also reveal individual intrinsic quality, where high-quality individuals who successfully reproduced are more likely to breed and reproduce again during the next season (i.e. high persistence), despite extremely harsh conditions (Jenouvrier et al., 2015). Similarly, hurricanes may influence life-history trait variances. Given the reported negative effects of hurricanes on mean annual fertility and survival across populations (Gannon & Willig, 1994; Morcillo et al., 2020; Wiley & Wunderle, 1993), we predict that hurricanes shape the distributions of LRS and lifespan by reducing variance and showing positive skewness (Tuljapurkar et al., 2020).

In this study, we evaluate the effects of major hurricanes on heterogeneity in life courses using the Cayo Santiago rhesus macaques, a population whose mean fertility is reduced during hurricane years likely to maintain high rates of survival (Morcillo et al., 2020). Here, we estimate multiple metrics of dynamic heterogeneity using annual stage-structured matrix population models over a period of 45 years. First, we estimate population entropy as a proxy of the expected annual rate of diversification in reproductive life courses of individuals (Hernández-Pacheco &

Steiner, 2017). Next, we measure persistence time of reproductive stages (Tuljapurkar et al., 2009). Lastly, we quantify within-trajectory variation in LRS and lifespan to obtain their exact probability distributions and higher moments (Caswell, 2009, 2011; Steiner et al., 2010; Tuljapurkar et al., 2020). Our analysis supports hypotheses on diversifying life courses as a potential mechanism to lessen severe competition following a climate extreme, and such finding is independent of the fact that hurricanes reduce life-history trait averages and variances.

2 | MATERIALS AND METHODS

2.1 | Study population

Cayo Santiago is a 15.2 ha subtropical island located 1 km Southeast of Puerto Rico (lat. 18°09' N, long. 65°44' W) that serves as a biological station for behavioural primate studies. The station was established in 1938 and is inhabited by free-ranging rhesus macaques (*Macaca mulatta*). Monkeys spend 50% of their daily activities foraging on natural vegetation on the island (Marriott et al., 1989) and are also provisioned ad libitum with water and approximately 0.23 kg animal⁻¹ day⁻¹ of commercial monkey chow. Since 1973 the entire population has been monitored and a reliable longitudinal demographic database on all individuals has been maintained. Individual data include date of birth, sex, mother identification, social group membership and date of death or permanent removal from the island for all individuals (for details on Cayo Santiago population data collection and management, see Hernández-Pacheco et al., 2016; Ruiz-Lambides et al., 2017). The population has experienced the direct impact of three major hurricanes (category ≥3) since the establishment of census records in 1956: Hugo (18 September 1989), Georges (21 September 1998) and Maria (20 September 2017; Kessler & Rawlins, 2016; Morcillo et al., 2020) with no other major hurricane or similar extreme climatic event occurring during the study period. Hugo and Georges were category 3 hurricanes with sustained wind speed of 201 and 185 km h⁻¹, respectively (Historical Hurricane Tracks, 1969; National Weather Service, 1998). Maria was a category 4 hurricane with sustained wind speed of 220 km h⁻¹ (National Hurricane Center, USA, 2017). Although food provisioning—and thus census taking—was resumed between 1 and 3 days after each hurricane (Morcillo et al., 2020), there is evidence of significant hurricane effects on several aspects of the population. Each hurricane caused 60%–90% of canopy loss immediately after the event (Morcillo et al., 2020), and changes in the social structure (Testard et al., 2021), as well as adverse demographic effects such as suppressed fertility (Luevano et al., 2022; Morcillo et al., 2020) and alterations in immune cell gene regulation (Watowich et al., 2022) were associated with these events. To better reveal how increasing hurricane-force winds affect heterogeneity in life courses and life-history trait distributions, we treat all three hurricanes as discrete events in our analysis.

2.2 | Demographic analysis

Our analysis was based on 45 years of individual data from 1973 to 2018. During this period, all individuals were followed over time for their entire life while at the biological station. Thus, there is no missing demographic data regarding date of birth, date of death or reproductive status. For each year, we parametrized female-only, birth-pulse matrix population models employing post-breeding censuses (Caswell, 2001). Following Hernández-Pacheco and Steiner (2017), we defined the annual structure in our analysis from 1 June at time t to 31 May at time $t+1$ to avoid significant overlap of birth seasons (Hernández-Pacheco et al., 2016). Models were based on annual transition probabilities among developmental and reproductive stages. In a given year, we classified sexually immature females in one of three age-specific developmental stages: infant (I; <1 year of age), yearling (Y; 1–2 years of age) and juvenile (J; 2–3 years of age). After reaching 3 years of age, we classified females in one of three reproductive stages: nonbreeder (NB), failed breeder (FB) and successful breeder (B). Nonbreeders were adult females who did not have an offspring in a given year (i.e. birth season skipping). Failed breeders were adult females whose offspring died before reaching 1 year of age. Successful breeders were adult females whose offspring survived to 1 year of age (recruitment). Thus, adult females either did not have offspring in a given year or had an offspring whose fate differed over the first year of life. Adult females transitioned among these three reproductive stages until death or until being right censored due to permanent removal from the population or if alive at the end of our study (life cycle graph in Figure S1). Reproductive senescence in this population appears at age 17 (Lee et al., 2021) but a low portion of the females give birth until age 24. Thus, we included all adult females in our analysis (oldest female on record reached 31 years of age). Although transitions from J to B or from J to FB are rare, they are expected to be non-zero as a small portion of 3-year-old females reproduce (Hernández-Pacheco et al., 2013). We only considered reproductive performance of females that survived to the census day, thus females dying during a given year were classified as transitioning to the absorbing death state independently of their reproduction.

To address hurricane effects on dynamic heterogeneity, we parameterized four stage-structured matrix models, one for each environment e , with stage-transition matrix, \mathbf{P}_e , and stage-specific survival rates, $s_{je} = \sum_i^n \mathbf{P}_{ije} = 1 - d_{je}$, where d_{je} is stage-specific mortality of stage j and environment e , and n is the number of stages. The four environments e were defined by the annual individual transitions belonging to (1) non-hurricane years (1973–1988, 1990–1997, 1999–2016, 2018–2019), (2) Hugo (1989–1990), (3) Georges (1998–1999) and (4) Maria (2017–2018). Transitions for hurricane years (1989–1990, 1998–1999 and 2017–2018) were also combined to create a hurricane matrix (Table S1). As only stage B females contributed to reproduction, we set their fertility to 1 (100%) and NB and FB fertility to 0 (Figure S1). Survival of infants was set to 1, as only surviving infants were recruited into the population (Morcillo et al., 2020). In our analysis, we assumed stage-specific mortality for

adults at any given time period to be non-zero. As no deaths were recorded among FB and B during hurricane Hugo (Table S2), we performed all analyses after adjusting the Hugo matrix by adding a 1% of total mortality rate to FB and B (an assumption commonly used for vital rate probabilities and elasticity analysis; Steiner et al., 2021). For completion, we present the analysis using the empirical Hugo matrix (Table S3). For each matrix model, we estimated the asymptotic growth rate (λ), the stable stage distribution (w) and the reproductive values (v) by computing the dominant eigenvalue, and the corresponding right and left eigen vectors, respectively (Caswell, 2001). The 95% confidence intervals for λ were estimated using bootstrap methods (Supporting Information). Transient dynamics can inform us on how strong a perturbation disequilibrates the expected stage structure of the population at demographic equilibrium and how fast these effects can be reversed, that is how fast a population reaches a stable equilibrium. To contrast each hurricane year with ordinary years, we compared the time the population takes to converge into stable equilibrium following each environment by estimating the damping ratio $\rho_e = \lambda / \lambda_1$, where λ_1 is the subdominant eigenvalue, for each matrix \mathbf{P}_e (Caswell, 2001). The 95% confidence intervals for ρ were estimated using bootstrap.

2.3 | Heterogeneity in life courses

Individuals differ in their sequence of reproductive stages making up their life course. This sequence defines an individual's reproductive trajectory (ω) and the entropy of the transition matrix, H , describes the rate at which individual trajectories diversify with age (Tuljapurkar et al., 2009; Table 1). We quantified this variation using matrix \mathbf{R}_e , a 3×3 submatrix of \mathbf{P}_e including adult transitions only, weighted by its corresponding quasi-stationary stage distribution, π , (Hernández-Pacheco & Steiner, 2017; Steiner et al., 2010). Here, we employed H as a proxy of the expected annual rate of diversification in life courses of mature individuals (Hernández-Pacheco & Steiner, 2017). If individuals follow the same sequence of reproductive stages across time, H is 0 (100% predictable stage trajectory). On the contrary, if individuals are equally likely to transition from any given state to any other state in the following year, then entropy increases up to its maximum value $\ln(K)$, where K is the number of reproductive stages (Tuljapurkar et al., 2009). For comparison across environments, we scaled H to its maximum value and presented relative H which is bounded between 0 and 1. To better illustrate heterogeneity in fitness estimates (survival and reproduction), we estimated the cumulative reproduction (CR) and survival based on 100 simulated individual trajectories using each \mathbf{R}_e . Without heterogeneity in life courses, every individual would follow the same reproductive and survival trajectory so that the population reproductive and lifespan variances become 0.

We estimated stage persistence time using the characteristic time τ and defined it as the correlation between an individual's current reproductive stage at time t and its stage $t+1$ years later (Table 1). In this way, τ is a timescale that measures the persistence of reproductive success or failure (Tuljapurkar et al., 2009). A low τ

Parameter	Definition
Entropy and persistence time	
Population entropy H	$-\sum_{j=1}^K \sum_{i=1}^K \pi_j \mathbf{R}_{ji} \log \mathbf{R}_{ji}$ (with $0 \log(0) = 0$)
Persistence time τ	$\frac{-1}{\ln(\lambda_1)}$, λ_1 is the subdominant eigen value ($\lambda_1 \neq 1$; solves $\det(\lambda \mathbf{I} - \mathbf{R}) = 0$), where \mathbf{I} is the identity matrix
Trait distributions	
LRS distribution	$\Gamma(f) = \Pr[\text{LRS}] = f$, where f is the number of offspring
Lifespan distribution	$\phi_{\mathbf{e}} = \mathbf{L}_{\mathbf{e}}(\mathbf{I} - \mathbf{Q}_{\mathbf{e}})\mathbf{e}$ (for parameters see Supporting Information)
Fundamental matrix \mathbf{N}	$\mathbf{N} = (\mathbf{I} - \mathbf{P})^{-1}$
First moment η_1 of stage j	$1\mathbf{N}$
Second moment η_2 of stage j	$\mathbf{N}(2\mathbf{N}_{\text{diag}} - \mathbf{I})$
Third moment η_3 of stage j	$\mathbf{N}(6\mathbf{N}_{\text{diag}}^2 - 6\mathbf{N}_{\text{diag}} + \mathbf{I})$
Variance V	$\mathbf{N} - \mathbf{N}^2(2\mathbf{N}_{\text{diag}} - \mathbf{I})$
Standard deviation (SD)	$\sqrt{V(v_{ij})}$
Skewness	$(\eta_3 - 3\eta_2\mathbf{N} + 2\mathbf{N}^3) / \text{SD}(v_{ij})^3$
Coefficient of variation (CV)	$\text{SD}(v_{ij})/\text{mean}$

Abbreviation: LRS, lifetime reproductive success.

indicates that an individual's current reproductive stage little predicts its future reproductive stage, and thus life trajectories are less deterministic. The 95% confidence intervals for H and τ were estimated using bootstrap.

2.4 | Probability distributions and higher moments of LRS and longevity

We computed the exact probability distributions of LRS and lifespan (i.e. age distribution of death) for each matrix \mathbf{P}_e following methods based on discrete convolutions and discrete Fourier transforms (Tuljapurkar et al., 2020; [Supporting Information](#)). The distributions were computed based on stage-only models where individuals may visit a stage any number of times before dying. To estimate higher moments in LRS and longevity, we computed the fundamental matrix \mathbf{N} from matrix \mathbf{P}_e ([Table 1](#)). Matrix \mathbf{N} allows us to estimate the expected mean number of visits (i.e. transitions into) to transient state i an individual that starts in transient state j makes before death, regardless the order of occurrence (i.e. sequence; [Table 1](#), Caswell, 2009). In this way, we defined stage-specific mean LRS as the expected mean number of visits (including stasis) an individual in stage j makes to the successful breeder stage before death (i.e. last row of \mathbf{N}). Similarly, we defined longevity as the mean number of visits an individual in stage j makes to all other stages before being absorbed in the death stage (i.e. the sum of each column of \mathbf{N}). This stage-based model approach does not estimate age-specific mortality but instead survival is fixed across all ages at any given stage so demographic senescence is not captured. However, we summed the estimated probabilities of mortality past 29 years of age to show differences in late-life survivorship across each environment. We

TABLE 1 Dynamic heterogeneity parameters and definitions. Taken from Caswell (2009), Tuljapurkar et al. (2020), and Tuljapurkar et al. (2009).

also estimated the variance, skewness and the coefficient of variation (CV) for LRS ([Table 1](#); Caswell, 2011, 2013; Varas Enríquez et al., 2022). A high magnitude in skewness indicates that rare individuals experience an unusually low (negative skew) or high (positive skew) number of offspring. A higher CV indicates that reproduction is highly spread over the life stages (more variation), relative to the mean expectation. All analyses were performed using the R software, version 4.1.3 (RStudio Team, 2022) with support from the popbio package (Stubben & Milligan, 2007).

3 | RESULTS

Our analysis was based on 20,891 individual transitions from 4075 females. During the 45-year period, λ was 1.119 (95% CI: 1.114, 1.123), for a mean annual population growth of 11.9% expected at demographic equilibrium. During non-hurricane years, $\lambda = 1.121$ (1.116, 1.125), while during hurricane years λ was reduced to 1.100 (1.084, 1.114). Specifically, during hurricanes Hugo, Georges and Maria λ was 1.125 (1.114, 1.152), 1.101 (1.058, 1.119) and 1.087 (1.060, 1.113), respectively. The relatively large λ estimates align with previous work on the Cayo Santiago rhesus macaques as this population has no predators and restoration of ad libitum water and food happened fast after each hurricane event (Blomquist et al., 2011; Morcillo et al., 2020). On average, hurricane years revealed a higher proportion of NB and FB in the stable stage distribution relative to non-hurricane years ([Figure 2](#)). Contrary to this, hurricane years show a lower proportion of B and I in the stable stage distribution (e.g. females transitioned less to the B stage and more to the NB and FB stage; [Figure 2](#); [Table 2](#)). Moreover, FB showed the lowest mean survival during hurricane years compared to non-hurricane years (0.865 and 0.912, respectively; [Table S4](#)).

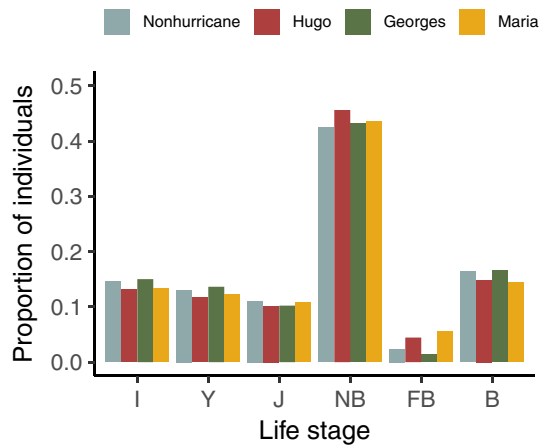


FIGURE 2 Stable stage distribution during non-hurricane and hurricane environments.

During non-hurricane years, ($\rho = 1.482$; 95% CI: 1.475, 1.490), while during hurricane years ρ increased to 1.512 (1.488, 1.538), suggesting that the population takes a shorter time to converge into stable stage dynamics during poor environment years. Specifically, during Hugo, Georges and Maria $\rho = 1.532$ (1.488, 1.587), 1.502 (1.471, 1.582) and 1.504 (1.469, 1.547), respectively.

Population entropy increased during hurricane years ($H=0.744$; 95% CI: 0.707, 0.775), relative to the non-hurricane environment ($H=0.718$; 0.707, 0.728) and such increase was related to hurricane intensity defined by sustained wind speed. During Georges, the population entropy was $H=0.663$ (0.597, 0.729), followed by Hugo with $H=0.757$ (0.652, 0.819) and Maria with $H=0.784$ (0.724, 0.824). The different entropies characterizing our population across environments can be further visualized with simulated CR trajectories that assume a constant environment. These trajectories show a higher

	I	Y	J	NB	FB	B
Non-hurricane years						
I	0	0	0	0	0	1
Y	1	0	0	0	0	0
J	0	0.948	0	0	0	0
NB	0	0	0.968	0.606	0.533	0.605
FB	0	0	0.003	0.042	0.070	0.039
B	0	0	0.006	0.294	0.310	0.311
q_x	0	0.052	0.023	0.058	0.087	0.045
Hurricane Hugo						
I	0	0	0	0	0	1
Y	1	0	0	0	0	0
J	0	0.975	0	0	0	0
NB	0	0	0.980	0.628	0.663	0.659
FB	0	0	0	0.071	0.163	0.069
B	0	0	0	0.265	0.163	0.262
q_x	0	0.025	0.020	0.036	0.010	0.010
Hurricane Georges						
I	0	0	0	0	0	1
Y	1	0	0	0	0	0
J	0	0.825	0	0	0	0
NB	0	0	0.971	0.583	0.643	0.694
FB	0	0	0	0.021	0.071	0.035
B	0	0	0	0.333	0.214	0.212
q_x	0	0.175	0.029	0.063	0.072	0.059
Hurricane Maria						
I	0	0	0	0	0	1
Y	1	0	0	0	0	0
J	0	0.963	0	0	0	0
NB	0	0	0.929	0.588	0.574	0.586
FB	0	0	0	0.110	0.019	0.080
B	0	0	0	0.227	0.241	0.310
q_x	0	0.037	0.071	0.075	0.166	0.024

TABLE 2 Mean transition matrices P_e for each environment e where the columns represent stage j at time t and rows represent stage i at time $t+1$. B, successful breeders; FB, failed breeders; I, immatures; J, juveniles; NB, nonbreeders; q_x represents stage-specific mortality calculated after rounding; Y, yearlings. Bolded transition probabilities represent the 3×3 submatrix of P_e used to define matrix R_e .

Note: Numbers in italics represent simulated mortality of 1% for NB and B stages.

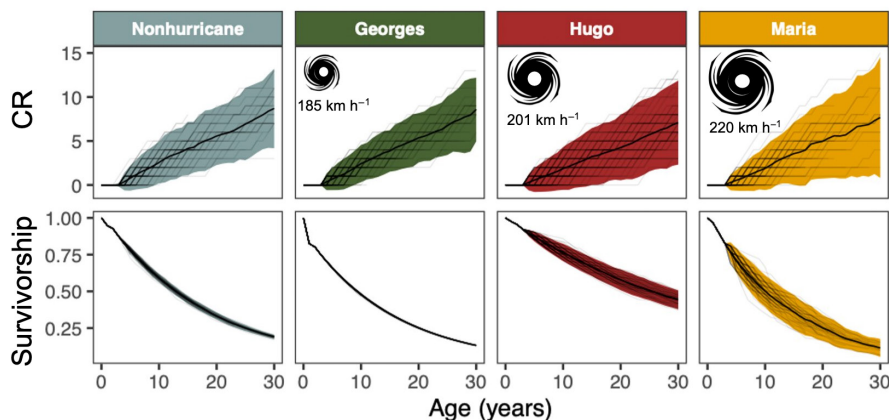


FIGURE 3 Simulated cumulative reproduction (CR, top panel) and survivorship (bottom panel) assuming a constant non-hurricane environment and constant hurricane environments. Hurricanes are presented in increasing order of intensity (sustained wind speed; Georges: 185 km h^{-1} ; Hugo, 201 km h^{-1} ; Maria 220 km h^{-1}). Lines represent mean trajectories (thick line) and individual trajectories (thin lines). Ribbons indicate 95% confidence intervals based on 1000 simulated trajectories.

variability in CR trajectories as a function of age (Figure 3, top panel). Similarly, the corresponding simulated cumulative survival trajectories showed a higher diversification with hurricane intensity (Figure 3, bottom panel). In agreement with this, stage persistence was reduced with increasing hurricane intensity where Georges had the highest value of $\tau = 0.014$ (95% CI: 0.001, 0.059) followed by Hugo with $\tau = 0.009$ (0.002, 0.210) and Maria with $\tau = 0.006$ (0.001, 0.034), while ordinary years showed the lowest value ($\tau = 0.0005$; 0.0002, 0.0031).

The LRS distribution across all environments was positively skewed with rare females having an unusually high number of offspring (Figure 4, top panel). This skewness was more pronounced during Georges and Maria where the probability of having no offspring was greater (33% and 35%, respectively) than that of the non-hurricane environment (23%). Transitions to the breeder stage were reduced during hurricanes Georges and Maria where females were expected to have a mean LRS of 3.827 offspring and 3.134 offspring, respectively (Table 3). During non-hurricane environments, females were expected to have a mean LRS of 5.035 offspring. Variance in LRS from birth was highest for non-hurricane years, followed by Georges and Maria (35.289, 25.003, 17.153, respectively, Table 3). In contrast, during hurricane Hugo females had a mean LRS of 9.040 offspring with the highest variance of 102.617. Immature stages across all environments showed the highest variability in LRS with respect to their mean (CV; Table 3).

The distribution of lifespan was also positively skewed across all environments revealing that individuals have the highest probability of mortality in the first year of life and this probability lowers past maturity (≥ 3 years of age; Figure 4, bottom panel). Individuals show the highest probability of dying early in life during Georges and Maria. We observed a reduction in mean lifespan since birth during Georges (15.8 years) and Maria (15.6 years) relative to the non-hurricane environment (19.7 years). However, during Hugo individuals experienced a mean lifespan of 38.2 years (Table 3). We found no evidence suggesting that Hugo was an unusually good year as mean vital rates in 1989 were similar to other years (Figure S2). By adding probabilities past 29 years of age, we can better visualize differences in later-life

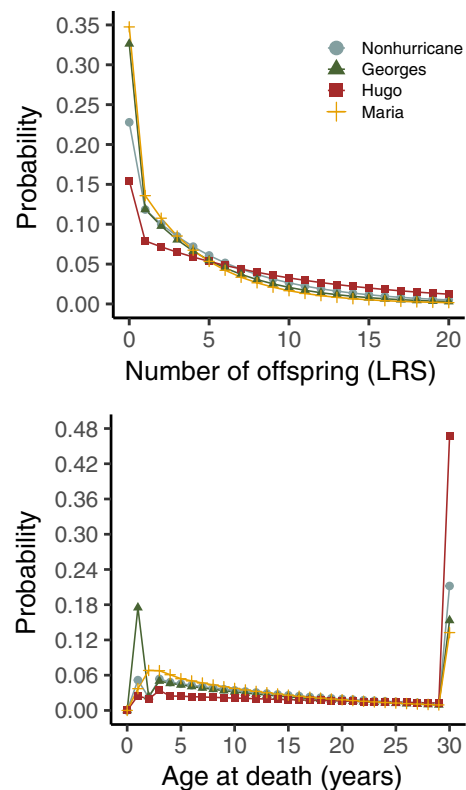


FIGURE 4 Probability distributions of lifetime reproductive success (LRS) and lifespan across environments. Survival probabilities past 29 years of age were summed.

mortality probabilities though they do not measure exact demographic senescence in our population (Lee et al., 2021). Individuals showed a higher mortality later in life during Hugo and ordinary years.

4 | DISCUSSION

Our study revealed that major hurricanes can generate heterogeneity in life courses despite an average reduction in mean fertility (i.e.

TABLE 3 Mean, variance, skewness and coefficient of variation of lifetime reproductive success.

	I	Y	J	NB	FB	B
Non-hurricane years						
Mean	5.036	5.036	5.310	5.430	5.282	6.522
Variance	35.288	35.288	35.754	35.911	35.714	36.011
Skew	2.062	2.062	2.027	2.015	2.030	2.007
CV	1.180	1.180	1.126	1.104	1.131	0.920
Hurricane Hugo						
Mean	9.040	9.040	9.271	9.457	9.586	10.696
Variance	102.617	102.617	103.099	103.407	103.581	103.703
Skew	2.032	2.032	2.019	2.011	2.006	2.002
CV	1.121	1.121	1.095	1.075	1.062	0.952
Hurricane Georges						
Mean	3.827	3.827	4.639	4.775	4.617	5.680
Variance	25.003	25.003	26.542	26.671	26.518	26.585
Skew	3.492	3.492	3.197	3.185	3.286	3.140
CV	1.307	1.307	1.111	1.082	1.115	0.908
Hurricane Maria						
Mean	3.134	3.134	3.255	3.502	3.227	4.804
Variance	17.153	17.153	17.420	17.878	17.361	18.270
Skew	2.177	2.177	2.138	2.072	2.147	2.014
CV	1.321	1.321	1.282	1.207	1.291	0.890

Abbreviations: B, successful breeders; CV, coefficient of variation; FB, failed breeders; I, infants; J, juveniles; NB, nonbreeders; Y, yearlings.

decreased transitions to B) and survival (i.e. shortened life courses). Extreme climatic events may thus force individuals to explore new life stages, increasing the rate of diversification in reproductive stage trajectories over time and decreasing reproductive stage persistence while reducing life-history trait averages and variances. We also demonstrate that hurricanes have different effects on the variation in LRS and lifespan and that such stochasticity is highly driven by survival in our long-lived primate population.

4.1 | Hurricane-induced impacts on population dynamics

Prior evidence show that hurricanes affect negatively the dynamics of animal populations mainly through changes in food and habitat structure (Klinger, 2006; Pavelka & Behie, 2005; Woolbright, 1991), but few studies have addressed individual-level changes and consequent long-term effects on the fertility and mortality of primates (Luevano et al., 2022; Pavelka et al., 2007). The effects of hurricanes on the population dynamics of rhesus macaques at Cayo Santiago are mostly driven by reductions in mean annual fertility, suggesting that survival is maintained at the expense of reproduction (Morcillo et al., 2020), a common life-history trade-off (Blomquist, 2009; Stearns, 1989). Our results showed relatively large population growth rate estimates which align with previous work on the Cayo Santiago rhesus macaques. This population has no predators and restoration of ad libitum water and food happened fast after each hurricane event (Hernández-Pacheco

et al., 2013; Morcillo et al., 2020). Yet, our analysis shows that hurricanes reduced the mean population growth rate due to a decreased proportion of non-breeders transitioning to successful breeders, as well as a decrease in the proportion of successful breeders remaining as such in consecutive years (stasis; Morcillo et al., 2020). Although the effect of major hurricanes on equilibrium dynamics was small, insights about transient dynamics (damping ratio) suggest a significant impact of hurricanes on population dynamics. Monkeys at Cayo Santiago rely partly on natural vegetation (50% of feeding time; Marriott et al., 1989) and their social stratification drives differential access to food (including ad libitum food). Thus, the amount of food consumed by individuals varies significantly according to their dominance rank (Balasubramanian et al., 2017). Our ability to find significant hurricane effects in this provisioned population (Morcillo et al., 2020) is indicative of the extreme nature of this perturbations and highlights multiple potential mechanisms underlying population response. For example, a higher density in proximity social networks and less social isolation was reported in Cayo Santiago following Maria, the most disruptive hurricane event (Testard et al., 2021). Strong social ties may reduce cortisol levels and improve immune responses following stressful events (Ellis et al., 2019; Gust et al., 1994; Sanchez et al., 2015). It is possible that a combination of food availability and re-arrangement of social connections contributed to the small reduction in population growth rate following each hurricane event. The small changes in population growth rates across hurricane years may also reflect demographic buffering, where λ is maintained relatively unchanged from reduced variability in vital rates which can potentially mitigate

increasing environmental variation (Hilde et al., 2020). Evolved traits allowing fast recovery after a significant perturbation may also play an important role, especially in populations under constant threat (Ameica y Juárez et al., 2015).

4.2 | Effects of major hurricane environments on the diversification of life courses

Our analysis shows that population entropy increased with hurricane intensity, suggesting that natural disasters generate heterogeneity in individual life courses and that such heterogeneity is independent of potential trade-offs between reproduction and longevity. An increased population entropy during hurricanes could be the result of a strategy to avoid strong intraspecific competition during unfavourable years through the exploration of demographic roles (Bolnick, 2001). Although we do not consider fixed (heritable) heterogeneity, such heterogeneity likely plays a role on overall variability. Unmeasured physiology (Plard et al., 2015), as well as maternal and genetic (fixed) heterogeneity (Peripato et al., 2002) may also contribute to differences in life-history outcomes. For instance, high-quality females (individuals that survive and breed successfully) could sustain breeding despite poor environmental conditions, whereas low-quality females (i.e. nonbreeders) might need to transition into other stages potentially contributing to the observed heterogeneity (Jenouvrier et al., 2015, 2022). This might be important to understand why during ordinary years entropy remained high. Other ecological processes, such as density-dependent dynamics, may be contributing to the observed entropy across environment; however, prior evidence indicates no association between entropy and density in this population (Hernández-Pacheco & Steiner, 2017). In alignment with entropy, years of major hurricanes had the highest rate of convergence to a stable stage structure. Assuming the newly explored stages during poor environments can maximize fitness, then populations in which individuals explore such stages at higher rates may reach equilibrium sooner than populations where individuals are performing less randomly in stage transitions during the same amount of time.

4.3 | Effects of major hurricane environments on life stage persistence

In contrast to entropy, stage persistence was reduced with increasing hurricane intensity; thus, the more extreme the environmental impact the more unpredictable life stages are given a female's current stage. This shows that rhesus macaque females are unlikely to remain in the same breeding stage as they age. Low breeding success persistence has also been reported for many other animal species but mostly during ordinary years (Tuljapurkar et al., 2009). These findings suggest that individuals randomly explore new stages to maximize the available variability for eco-evolutionary processes. In contrast to our findings, breeding stage persistence increased for a petrel population during unfavourable extreme climatic conditions, suggesting individual

intrinsic quality as those few able to reproduce in such environment were also able to reproduce during the following season (Jenouvrier et al., 2015). We also found stage persistence to be the lowest during ordinary years. Analysing whether such variability is potentially heritable would help to understand why individuals explore new stages at high rates. If adaptive, life course heterogeneity could support the viability of populations by counteracting the negative effects of extreme environmental conditions (Chevin & Hoffmann, 2017). For example, exploring the failed breeder stage during a bad year to ensure survival may be adaptive if it increases the speed of postpartum recuperation (Mas-Rivera & Bercovitch, 2008). Infant mortality can trigger an advance in the timing of estrus of females, shortening their inter-birth interval (Koford, 1965, 1966; Rawlins & Kessler, 1986; Rawlins et al., 1984). However, if the observed heterogeneity is neutral, its potential for selection is hindered, and the pace of evolutionary adaptation is significantly lowered, compromising the viability of populations at risk (Chevin & Lande, 2010; Steiner et al., 2021; Steiner & Tuljapurkar, 2012, 2023). Here, exploring a stage is merely by chance and does not contribute to selective processes. Future research has yet to explore what other factors drive population entropy and stage persistence in ordinary environments.

4.4 | Effects of major hurricane environments on life-history trait distributions

In agreement with previous studies, our analysis shows that life-history trait distributions are highly skewed (Colchero et al., 2016; Tatarenkov et al., 2008; Tuljapurkar et al., 2020; Figure 4). In our population, reproductive senescence increases sharply after 17 years (Lee et al., 2021) and only rare females produce a large number of daughters mainly because most females do not live their entire reproductive life (3–24 years of age) as they die at younger ages (Hernández-Pacheco et al., 2013). In particular, the LRS distributions show that hurricanes can increase the probability of having no offspring as Georges and Maria had the largest probability of 0 LRS, a larger skewness, and a reduced mean and variance, compared to ordinary years. Hurricane environments may be unfavourable for breeding as they can alter the physiological condition of individuals (e.g. expression of key immune genes in males; Watowich et al., 2022). Given that rhesus macaques have multiple reproductive events in life, physiological alterations may influence females to delay reproduction until the environment is favourable again. The distributions of age at death revealed that the probability of mortality is highest before sexual maturity but remains relatively constant in later-life, contrary to other mammal populations exhibiting one mortality schedule during juvenility and a second during old ages (belugas: Schindler et al., 2012; humans: Edwards & Tuljapurkar, 2005). This mortality schedule was more accentuated during Georges and Maria (Figure 4, bottom panel). However, this effect was eliminated when adult survival was not negatively affected as during Hugo. Similar to hurricanes Georges and Maria in which transitions into the breeder stage were reduced, the population suffered a reduction in mean annual fertility during hurricane Hugo, however during Hugo mortality was also

reduced among adults. As a result, this hurricane event showed a substantial increase in mean and variance of life-history traits, supporting prior evidence of the unbalanced contribution of survival and fertility to variability in this long-lived primate population (Morcillo et al., 2020). High variability among life-history traits increases the diversity needed for natural selection to select life-history outcomes that can support population viability. Rather than a rare year, during Hugo females showed similar survival rates as many other years in the history of the population.

5 | CONCLUSIONS

Our analysis supports the hypothesis that increased intraspecific competition drives temporal variation in reproductive stage trajectories and consequent trait distributions. The observed heterogeneity in life courses, coupled to the reduce stage persistence, may be a strategy to endure during poor environments. Hence, even a small increase in population entropy increases the opportunity for selection, assuming some portion of this variation is heritable. Understanding whether significant environmental changes generate or reduce the available heterogeneity in individual life courses and trait distributions is fundamental for managing populations (Conner & White, 1999). In particular, quantifying these changes may reveal if populations are at risk of extinction, especially if extreme events are drivers of evolutionary change (Grant et al., 2017). Future directions in modelling the effects of extreme climatic events on demography also include the description of probability distributions of life-history traits (Schindler et al., 2012). Such approach can be used to further understand how the long-term growth rate of a population at risk is shaped by the LRS distribution and the age-distribution of death.

AUTHOR CONTRIBUTIONS

Alexis A. Diaz performed all analyses and drafted all versions of the manuscript, Ulrich K. Steiner, Shripad Tuljapurkar and Wenyun Zuo contributed to the methodology design and manuscript revision, Raisa Hernández-Pacheco designed and supervised the study and contributed to manuscript revision. All authors discussed data interpretation and revised the final version.

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CONFLICT OF INTEREST STATEMENT

All authors agree with the contents of the manuscript and declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpnvx9b> (Diaz et al., 2023).

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SUPPORTING INFORMATION

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

Appendix S1. Information for estimating confidence intervals and the exact lifespan distribution. Supplemental information for hurricane Hugo and stage-specific survival across years are also included.

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