Natural disasters generate heterogeneity in individual life histories

Alexis A Diaz[1], Ulrich K Steiner[2], Shripad Tuljapurkar[3], WENYUN ZUO[3], and Raisa Hernández-Pacheco[4]

[1]California State University Long Beach College of Natural Sciences and Mathematics
[2]Freie Universität Berlin
[3]Stanford University
[4]California State University Long Beach

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Abstract

Extreme climatic events may influence individual-level variability in phenotypes, survival, and reproduction, and thereby drive the pace of evolution. Here, we quantify how experiencing major hurricanes influences individual life courses in the Cayo Santiago rhesus macaques. Our results show that major hurricanes increase heterogeneity in reproductive life courses despite an average reduction in mean fertility and survival, i.e. shortened life courses. In agreement with this, the population is expected to achieve stable population dynamics faster after a hurricane. Our work suggests that natural disasters force individuals into new niches to potentially reduce strong competition during poor environments where mean reproduction and survival are compromised. We also demonstrate that variance in lifetime reproductive success and longevity are differently affected by hurricanes, and such variability is mostly driven by survival.

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Alexis A. Diaz[1*], Ulrich K. Steiner[2], Shripad Tuljapurkar[3], Wenyun Zuo[3], Raisa Hernández-Pacheco[1]

[1] California State University-Long Beach, Long Beach, CA 90840

[2] Freie Universität Berlin, 14195 Berlin, Germany

[3]Stanford University, Stanford, CA 94305

*Corresponding author: Alexis.Diaz01@student.csulb.edu

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Abstract. Extreme climatic events may influence individual-level variability in phenotypes, survival, and reproduction, and thereby drive the pace of evolution. Here, we quantify how experiencing major hurricanes influences individual life courses in the Cayo Santiago rhesus macaques. Our results show that major hurricanes increase heterogeneity in reproductive life courses despite an average reduction in mean fertility and survival, i.e. shortened life courses. In agreement with this, the population is expected to achieve stable population dynamics faster after a hurricane. Our work suggests that natural disasters force individuals into new niches to potentially reduce strong competition during poor environments where mean reproduction and survival are compromised. We also demonstrate that variance in lifetime reproductive success and longevity are differently affected by hurricanes, and such variability is mostly driven by survival.

Introduction

Hurricanes are rare, yet their extreme acute nature can have profound impacts on life courses. They can reduce long-term population fitness through direct mortality (Batista & Platt, 2003; Wiley & Wunderle, 1993), suppressed fertility (Gannon & Willig, 1994; Luevano et al., 2022; Morcillo et al., 2020), increased physiological stress (Behie & Pavelka, 2014), increased social disorganization (Pavelka et al., 2003), and alterations in gene expression (Watowich et al., 2022). Climate models predict increases in the frequency of intense hurricanes (Bloemendaal et al., 2022; Holland & Webster, 2007), but how populations will respond to such sustained environmental change remains unclear. This reflects limitations in our current ecological and evolutionary understanding which mostly focuses on average population-level processes even though individual heterogeneity is what evolution acts on (Vindenes et al., 2008; Vindenes & Langangen, 2015). To predict the eco-evolutionary dynamics of populations under rapid environmental change, we must first investigate whether and how extreme climatic events affect the emergence and maintenance of individual heterogeneity (Caswell, 2001; Metcalf & Pavard, 2007). If adaptive, individual heterogeneity could support the persistence of populations by counteracting the negative effects of extreme environmental conditions (Chevin & Hoffmann, 2017). However, if the observed individual heterogeneity is neutral or fully stochastic, 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).

Here, we aim to understand how tropical cyclones influence individual heterogeneity in life courses by contrasting individual performance during years of major hurricanes with performance during ordinary years using a long-lived primate population. We first define individual heterogeneity as differences in individual life courses and characterize it using metrics of population entropy and stage persistence (Tuljapurkar et al., 2009). Starting at birth, life courses can be described by the sequence of stages an individual experiences until death (Caswell 2001). As life progresses through time, individuals may remain in the same stage (i.e., stasis) or transition among developmental, morphological, reproductive, behavioral, and physiological stages. Population entropy measures the rate at which these stage trajectories diversify with age (Hernández-Pacheco & Steiner, 2017; Tuljapurkar, 1982; Tuljapurkar et al., 2009). Persistence in any life stage instead measures the correlation time between an individual's current life stage and their stage at a later age. Contrary to stable environments which are expected to reduce individual heterogeneity because persistence of life stages is high (Tuljapurkar et al., 2009), extreme climatic events on animal populations leading to unfavorable conditions are expected to increase individual heterogeneity (Chambert et al., 2015; Jenouvrier et al., 2015). As major 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 or ecological niches increasing the expected rate of diversification in stage trajectories (i.e., high entropy, low stage persistence). Alternatively, major hurricanes may reveal potential 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.

Individual 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). As individuals age, their movement through the life cycle follows a random 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 (Tuljapurkar et al., 2020), and the variation in the lifetime number of visits to any transient state (i.e., individual stochasticity; Caswell 2009). Given the 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 individual heterogeneity 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 individual heterogeneity using annual stage-structured matrix population models. 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) during hurricane years and contrast it to ordinary years. Next, we measure persistence time of life stages to determine the correlation between an individual's current reproductive stage and its stage years later (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 revealed that major hurricanes influence eco-evolutionary processes by increasing entropy and lowering correlation time despite evidence of reductions in mean annual fertility and survival. We also find that the LRS and lifespan distributions are positively skewed and are mostly driven by survival.

Methods

Study population:

Cayo Santiago is a 15.2ha sub-tropical island located 1km Southeast of Puerto Rico (lat. 18°09’N, long. 65°44’W) that serves as a biological station for behavioral 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/day 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 includes 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) and Ruiz-Lambides et al. (2017)).

The Cayo Santiago rhesus macaque 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). Hugo and Georges were category 3 hurricanes with sustained wind speed of 201 km h^{-1} and 185 km h^{-1}, respectively (NOAA, 2014; USGS, 1999). Maria was a category 4 hurricane with sustained wind speed of 220 km h^{-1} (NOAA, 2019). Although food provisioning - and thus census taking - was resumed between 1 to 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), adverse demographic effects such as suppressed fertility (Luevano et al., 2022; Morcillo et al., 2020), as well as alterations in immune cell gene regulation (Watowich et al., 2022) associated to hurricanes have been reported.

Demographic analysis:

Our analysis was based on 46 years of individual data from 1973 to 2019. 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. Models were based on annual transition probabilities among developmental and reproductive stages (Hernández-Pacheco & Steiner, 2017; Morcillo et al., 2020). 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 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). 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. 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 individual 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, $s_{je} = \sum_{i}^{n} P_{ije} = 1 - d_{je}$, 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). As only stage B females contributed to reproduction, we set their fertility to 1 (100%) and NB and FB fertility to 0. 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 (Supporting Material, Table S1), we performed all analyses after adjusting the Hugo matrix by adding a 1% of total mortality rate to FB and B. For completion, we present the analysis using the empirical Hugo matrix in the Supporting Material (Table S2). 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). 95% confidence intervals for λ were estimated using bootstrap methods (Supporting Material). Transient dynamics can inform us on how strong a perturbation disequilibrates the stage structure of the population and how fast these effects can be reversed, i.e. 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 $\rho_e = \frac{\lambda}{\lambda_1}$, where λ_1 is the subdominant eigenvalue, for each matrix $\mathbf{P}_e$ (Caswell 2001).

Individual heterogeneity in stage trajectories:

Individuals differ in their sequence of reproductive stages making up their life course. This sequence defines an individual's reproductive trajectory (ω) and population entropy, *H*, describes the rate at which these trajectories diversify with age (Tuljapurkar et al., 2009; Table 1). We quantified this variation using matrix $\mathbf{R}_e$, a 3 x 3 submatrix of $\mathbf{P}_e$ including adult stages only, weighted by its corresponding quasi-stationary stage distribution, ω' (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. We also simulated heterogeneity in fitness estimates (survival and reproduction) using the mean population trajectory and the probability of observing a trajectory in transition matrices. Without heterogeneity in life courses, every individual would follow the same reproductive trajectory so that the populations reproductive variance becomes 0.

We estimated 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 indicates that an individual's current reproductive stage little predicts its future reproductive stage, and thus life trajectories are less deterministic.

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 Material). 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 **N** from matrix $\mathbf{P}_e$. Matrix **N** allows us to estimate the expected mean number of visits to transient state *i* an individual that starts in transient state *j* makes before death, regardless the order of occurrence (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 **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 **N**). We 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 short (negative skew) or long (positive skew) life. 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 (R Studio Team, 2022).

Results

Our analysis was based on 20,891 individual transitions from 4,075 females. During the 46-year period, λ was 1.119 (95% CI: 1.114, 1.123), for a mean annual population growth of 11.9%. During non-hurricane years, λ = 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 1.128 (1.099, 1.152), 1.101 (1.058, 1.119), and 1.087 (1.060, 1.113), respectively. On average, hurricane years revealed a higher proportion of NB and FB in the stable stage distribution relative to non-hurricane years (Fig. 1). 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; Fig. 1; Table 2). Moreover, FB showed the lowest survival during mean hurricane years compared to non-hurricane years (0.865 and 0.912, respectively; Table S3). Years of major hurricanes showed an increased damping ratio (Hugo = 1.532, Georges = 1.502, Maria = 1.504) relative to years of no hurricanes ($\rho = 1.482$), suggesting that the population takes a shorter time to converge into stable stage dynamics during poor environment years.

Population entropy increased during hurricane years ($H = 0.744$), relative to the non-hurricane environment ($H = 0.718$) and such increase was related to hurricane intensity defined by sustained wind speed. During Georges, the population entropy was $H = 0.663$, followed by Hugo with $H = 0.757$, and Maria with $H = 0.784$. The different entropies characterizing our population across environments can be further visualized with simulated cumulative reproduction (CR) trajectories which show a higher diversification in reproductive trajectories as a function of age (Fig. 2, top panel). Similarly, the corresponding simulated cumulative survival trajectories showed a higher diversification with hurricane intensity (Fig. 2, bottom panel). In agreement with this, stage persistence was reduced with increasing hurricane intensity (Georges = 0.014,Hugo = 0.009, Maria = 0.006), while ordinary years showed the lowest value ($\tau = 0.0005$).

The LRS distribution across all environments was positively skewed with rare females having an unusually high number of offspring (Fig. 3, top panel). This skewness was more pronounced for Georges and Maria where the probability of having no offspring was greater (33% and 35%, respectively) than that of the non-hurricane environment (23%). Visits to the breeder stage was reduced during hurricanes Georges and Maria where females were expected to have a mean LRS of 4 and 3 offspring, respectively (Table 3). During non-hurricane environments, females were expected to have a mean LRS of 5 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 offspring with the highest variance of 102.617. Immature stages 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 a low probability of mortality past maturity (≥3 years of age) and that there is no major differences in the likelihood to live long (Fig. 3, bottom panel). Hurricane Georges and Maria show the highest probability of dying early in life relative to Hugo and ordinary years. We observed a reduction in mean lifespan from birth during Georges (15.824 years) and Maria (15.555 years) relative to the non-hurricane environment (19.730 years). However, Hugo had a mean lifespan of 38.227 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 (Fig. S1).

Discussion

Our study revealed that major hurricanes generate heterogeneity in individual life courses despite an average reduction in mean fertility (i.e., decreased transitions to B) and survival (i.e., shortened life courses). Extreme climatic events may thus force individuals into new ecological niches increasing the rate of diversification in reproductive stage trajectories and decreasing reproductive stage persistence, while simultaneously shortening lifespans. By assessing life history trait distributions, 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.

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 shown the long-term effects on fertility and mortality (Luevano et al., 2022; Morcillo et al., 2020; Pavelka et al., 2007). The effects of hurricanes on the population dynamics of Cayo Santiago rhesus macaques are mostly driven by reductions in mean annual fertility, suggesting that survival is maintained at the expense of reproduction (Morcillo et al. 2020). Yet, these population-level processes reveal no information about the role of these climatic events and consequent environmental changes on the emergence and maintenance of individual heterogeneity and trait variances. Our analysis shows that population entropy increased with hurricane intensity, demonstrating that natural disasters generate heterogeneity in individual life courses and that such heterogeneity is independent of potential trade-offs between reproduction and longevity. In contrast to this, 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 (i.e., low correlation time). An increased population entropy and a decreased stage persistence during hurricanes could be the result of a strategy to avoid strong intraspecific competition during bad years through the exploration of ecological niches or demographic roles (Bolnick, 2001; Coulson et al., 2001). On the other hand, high-quality females (individuals that survive and breed successfully) could sustain breeding despite bad environmental conditions, whereas poor quality females might need to transition into other stages potentially contributing to the observed variability (Jenouvrier et al., 2022). In alignment with entropy, years of major hurricanes had the highest rate of convergence to a stable stage structure. This suggests that populations in which individuals explore stages that can maximize fitness at higher rates may reach equilibrium sooner than populations where individuals are performing less randomly.

Our findings also reveal that other unknown factors are contributing to individual heterogeneity as non-hurricane years had a relatively high entropy. For example, unmeasured physiology (Plard et al., 2015), as well as maternal and genetic (fixed) heterogeneity (Peripato et al., 2002) may contribute to differences in life history outcomes. Although our population exhibits negative density-dependence in fertility (Hernández-Pacheco et al., 2013), entropy was not found to be driven by density (Hernández-Pacheco & Steiner, 2017). We also found stage persistence to be the lowest during ordinary years. Such low correlation between current stage and a future stage could be due to individuals randomly exploring new stages to maximize the available variability for eco-evolutionary processes. Future research has yet to explore what other factors drive population entropy and stage persistence in ordinary environments.

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; Fig. 3). In our population, 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. The lifespan distributions revealed that the probability of mortality is highest before sexual maturity with one single large mortality schedule, in contrast 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 (Fig 3., 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 (Table 2), 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). The fact that Hugo showed high survival was not surprising as no evidence that hurricanes affect survival was found previously (Morcillo et al., 2020). Rather than a rare year, during Hugo females showed similar survival rates as many other years in the history of the population (Fig. S1).

Our findings support the hypothesis that intraspecific competition drives niche exploration, and this effect is more pronounced during extreme climatic events as seen by an increased heterogeneity in life histories following major hurricanes. Future studies investigating the viability of vulnerable populations should address the effects of extreme climatic events on individual heterogeneity. This will help to better understand in what direction significant environmental changes drive individual life courses and trait distributions, especially for traits (heritable or plastic) that have high adaptive potential (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 fitness of a population (i.e., growth of a stable population) at risk is shaped by the LRS distribution and the age-distribution of death.

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Tables

Table 1. Parameters and definitions. Taken from Caswell 2009 and Tuljapurkar et al. 2009.

Parameter	**Definition**
$\tau = \frac{-1}{ln(\lambda_1)}$	Correlation time Subdominant eigenvalue ($\lambda_1 \neq 1$; solves det(λ I- ***R)*** =0
$H = -\sum_{i=1}^{K}\sum_{j=1}^{K}\pi_i \boldsymbol{R}_{ij}\log\boldsymbol{R}_{ij}$ (with 0 log(0) = 0)	Population entropy
$V(v_{ij}) = (2\mathbf{N}_{diag} - I)\mathbf{N} - \mathbf{N}^2$	Variance in stage occupancy time LRS
$SD(v_{ij}) = \sqrt{V(v_{ij})^3}$	Standard deviation in LRS
$\eta_2 = (2\mathbf{N}_{diag} - I)\mathbf{N}$	Second moment in LRS
$\eta_3 = (6\mathbf{N}_{diag}{}^2 - 6\mathbf{N}_{diag} + I)\mathbf{N}$	Third moment in LRS
Skew = $(\eta_3 - 3\eta_2\mathbf{N} + 2\mathbf{N}^3)/SD(v_{ij})^3$	Skewness in LRS
CV = $SD(v_{ij})$/mean	Coefficient of variation

Table 2. Mean transition matrices $\mathbf{P}_e$ for environment e where the columns represent stage j at time t and rows represent stage i at time $t + 1$. I = immatures; Y = yearlings; J = juveniles; NB = nonbreeders; FB = failed breeders; B = successful breeders; q_x represents stage-specific mortality calculated after rounding. Bolded transition probabilities represent the 3x3 submatrix $\mathbf{P}_e$ used to estimate matrix $\mathbf{R}_e$.

	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	*0.011*	*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

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

Table 3. Mean, variance, skewness, and coefficient of variation of lifetime reproductive output. I = infants; Y = yearlings; J = juveniles; NB = nonbreeders; FB = failed breeders; B = successful breeders.

	I	Y	J	NB	FB	B
Non-hurricane years						
Mean	5.035	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

Figures

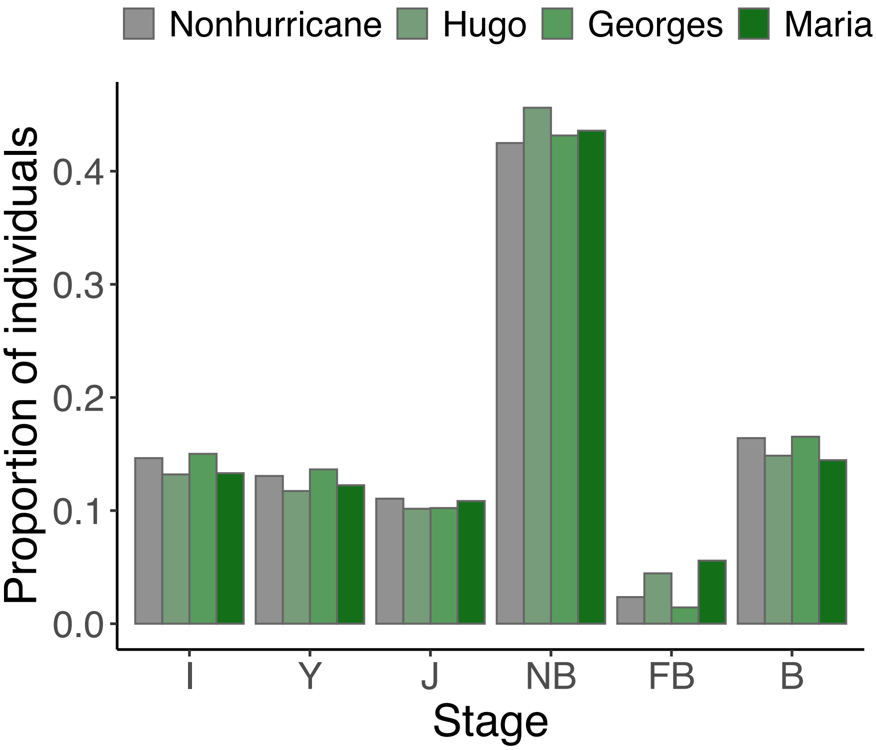

Figure 1. Stable stage distribution during non-hurricane and hurricane years.

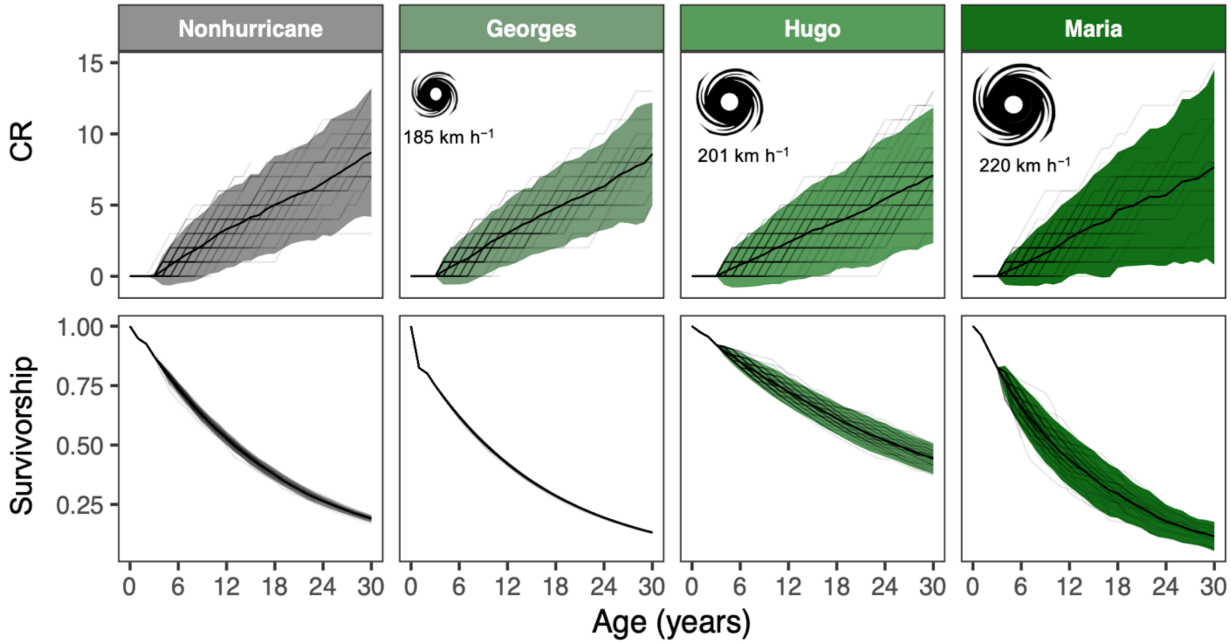

Figure 2. Simulated cumulative reproduction (CR, top panel) and survivorship (bottom panel) for non-hurricane and hurricane environments. Hurricanes are presented in increasing order of intensity (sustained wind speed; Georges: 185 km·h^{-1}; Hugo, 201 km·h^{-1}; Maria 220 km·h^{-1}). Lines represent mean trajectories (thick line) and individual trajectories (thin lines). Ribbons indicate 95% confidence intervals based on 1000 simulated trajectories.

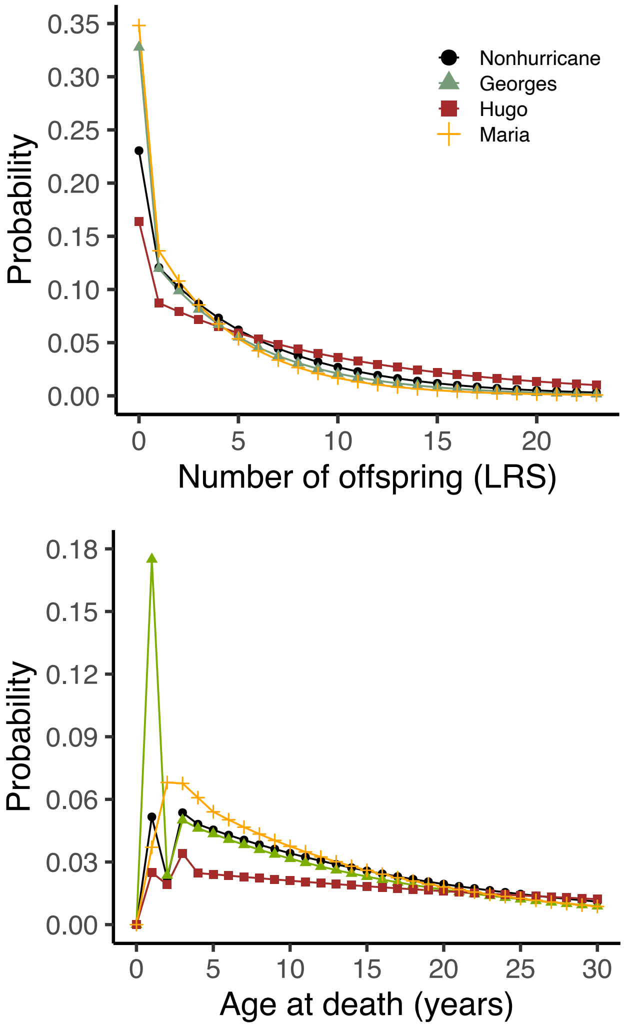

Figure 3. Probability distributions of lifetime reproductive success (LRS) and lifespan across environments.