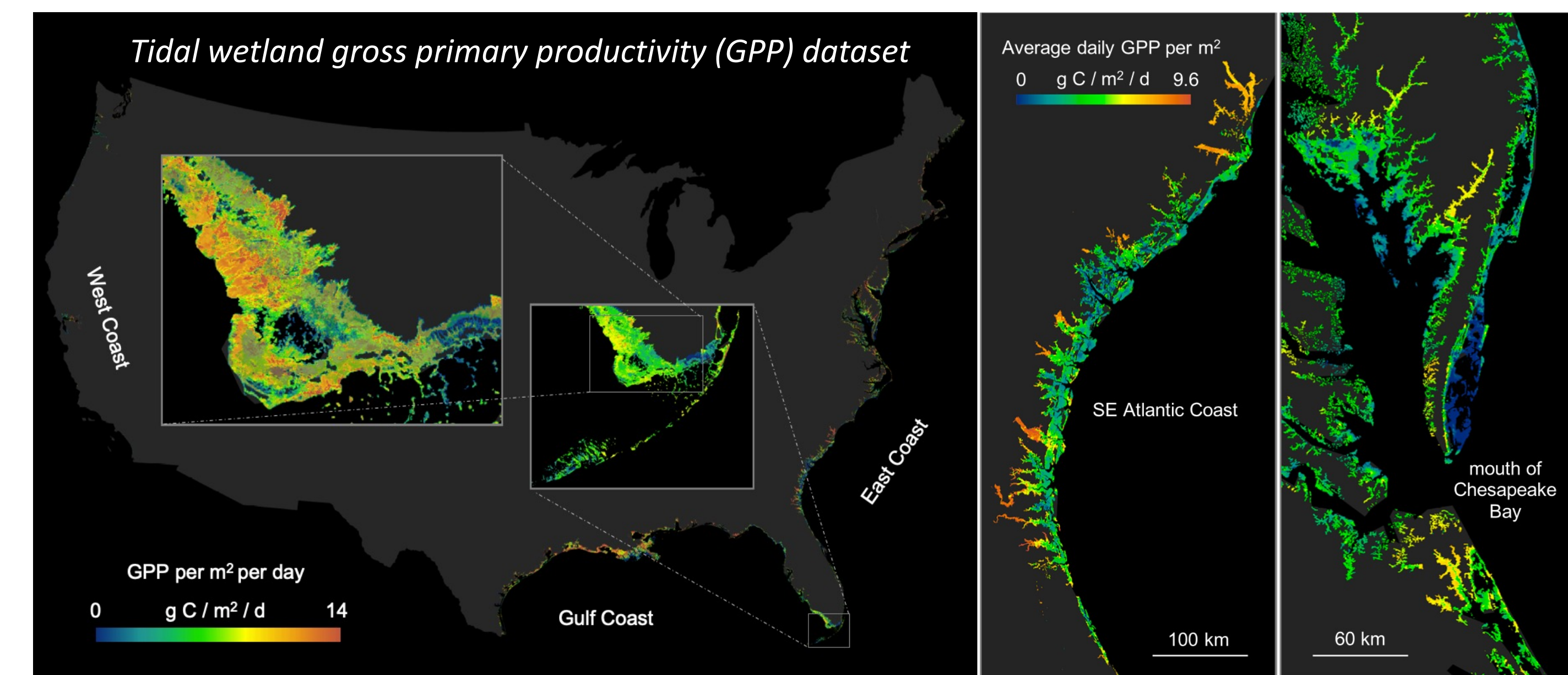


Introduction

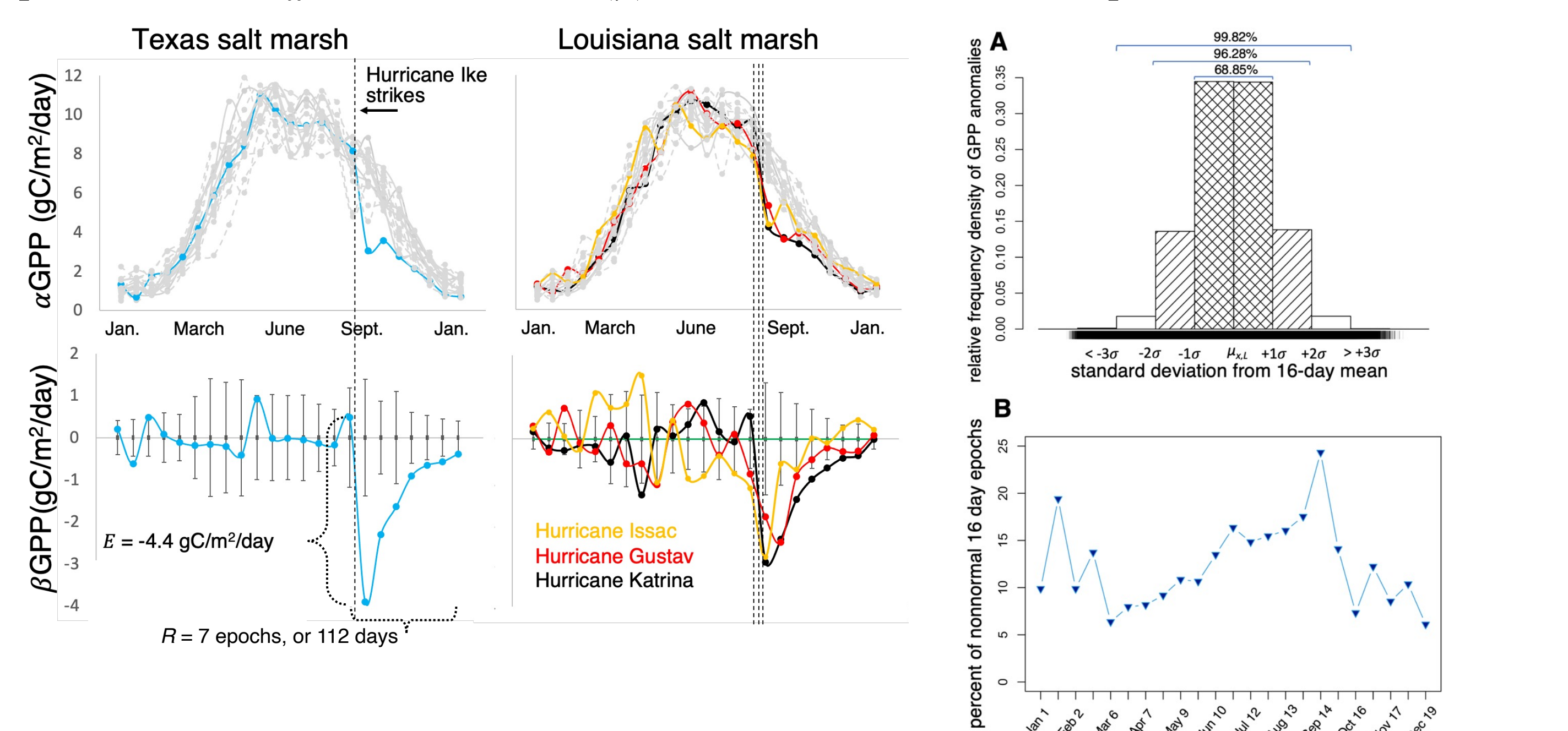
- The photosynthetic processes that capture and input energy into the ecosystem (measured as gross primary productivity or GPP) are vulnerable to environmental stresses and disturbances.
- Perturbations in ecosystem GPP can be quantified in terms of their resistance and resilience. These metrics were calculated from long-term GPP remote sensing datasets, using the effect size E and the return time R of perturbation events.

Methods

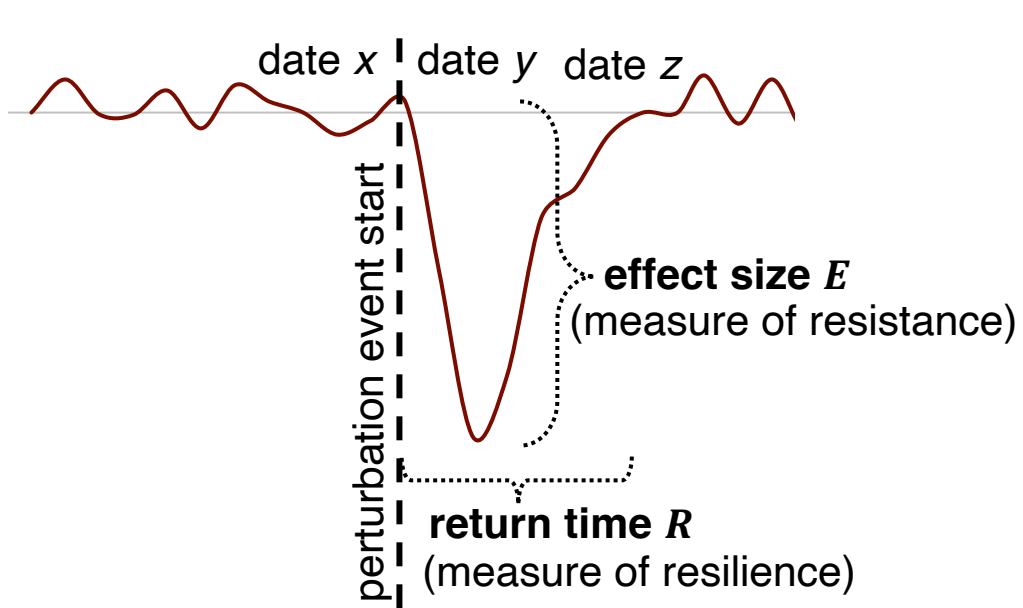
1) We used the MOD13Q1-derived tidal wetland GPP product from the NASA Oak Ridge National Laboratory DAAC to analyze the productivity of 145,871 tidal wetland pixel locations across the entire continental U.S., at 250 m resolution, every 16 days from February 18, 2000 to December 2, 2020. These include tidal salt marshes, tidal freshwater marshes, tidal forested swamps, and mangrove forests.



2) We standardized the data across locations and time by computing the anomaly of GPP from each location's 16-day epoch mean. The GPP anomaly, β_x , was quantified as the GPP product value, α_x , minus the mean (μ) GPP for all similar date x epochs at that location.

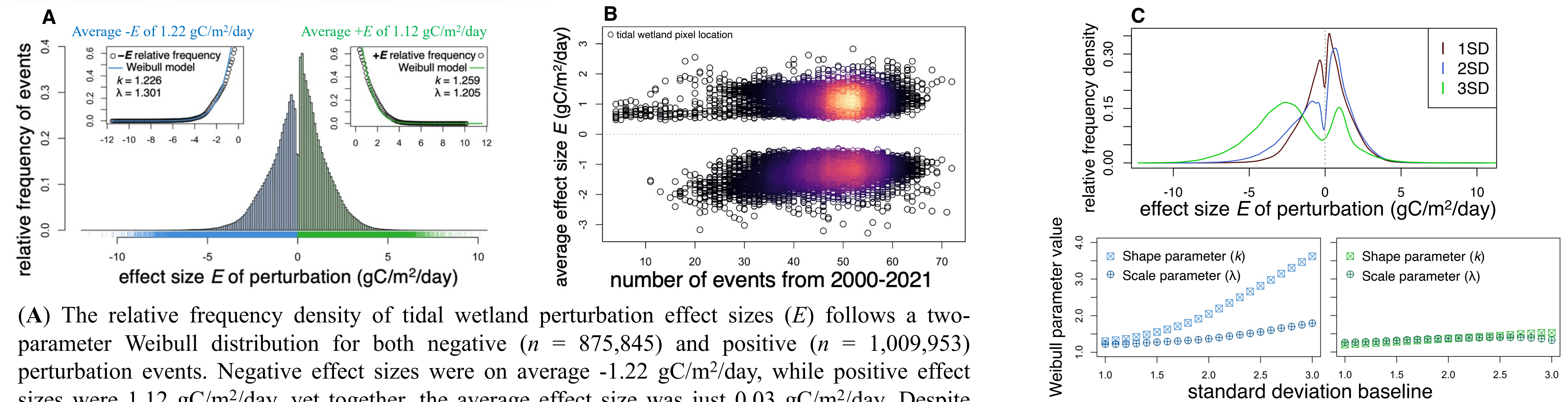


(A) Standardized GPP values ($n = 66,729,537$) were normally distributed around their 16-day means, and roughly conformed to the empirical (68-95-99.7%) rule. (B) Just 12.29% of 16-day epochs ($n = 3,354,719$) exhibited nonnormality.



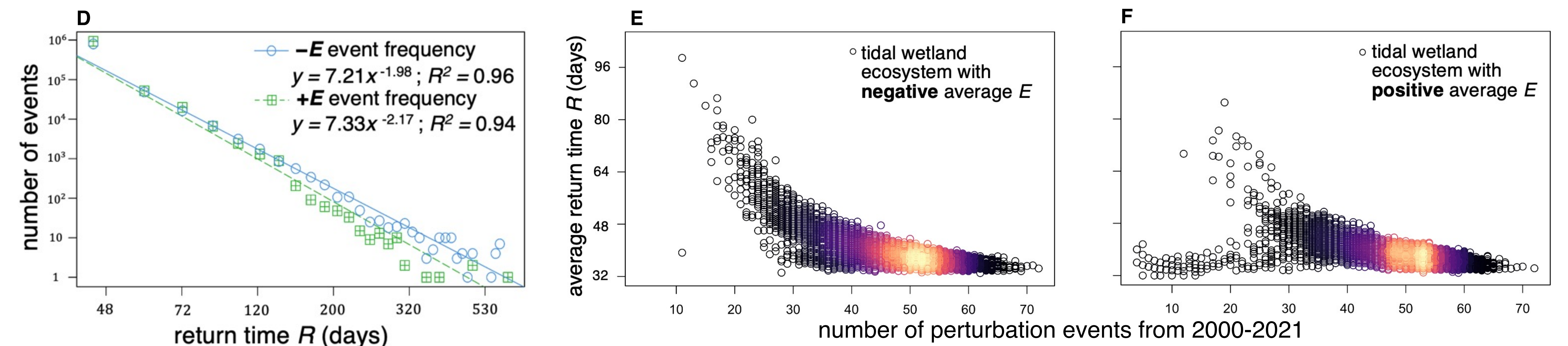
Ecosystem resistance of a perturbation event was estimated in terms of the effect size, E , in GPP, quantified using: $E = \beta_y - \beta_x$

Ecosystem resilience of a perturbation event was estimated as the return time, R , or the length of the GPP perturbation event. The return tolerance was set between $\mu_{z,L} \pm \sigma_{z,L}$ (the standard deviation from the mean GPP for values that composed epoch z for location L).

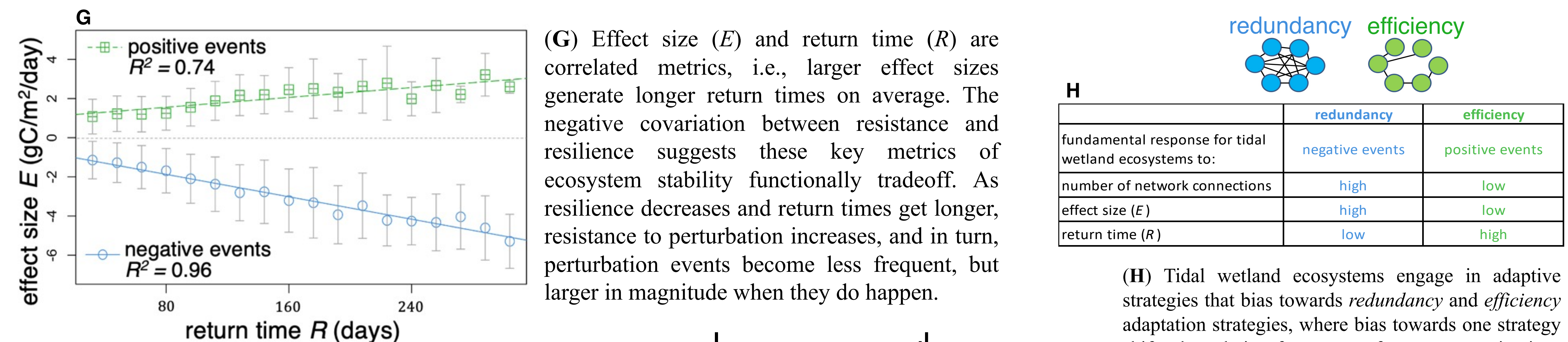


(A) The relative frequency density of tidal wetland perturbation effect sizes (E) follows a two-parameter Weibull distribution for both negative ($n = 875,845$) and positive ($n = 1,009,953$) perturbation events. Negative effect sizes were on average $-1.22 \text{ gC/m}^2/\text{day}$, while positive effect sizes were $1.12 \text{ gC/m}^2/\text{day}$, yet together, the average effect size was just $0.03 \text{ gC/m}^2/\text{day}$. Despite their vulnerability to frequent pulses of high intensity disturbance, tidal wetlands in the U.S. appear to reach a long term steady state, where positive perturbations are more frequent than negative perturbations, but negative perturbations are larger in magnitude. (B) Just 23% of pixel locations had a perturbation event. Locations with greater resistance to negative perturbation (less events) tended to have larger effect sizes, yet locations with less positive events often had small effect sizes.

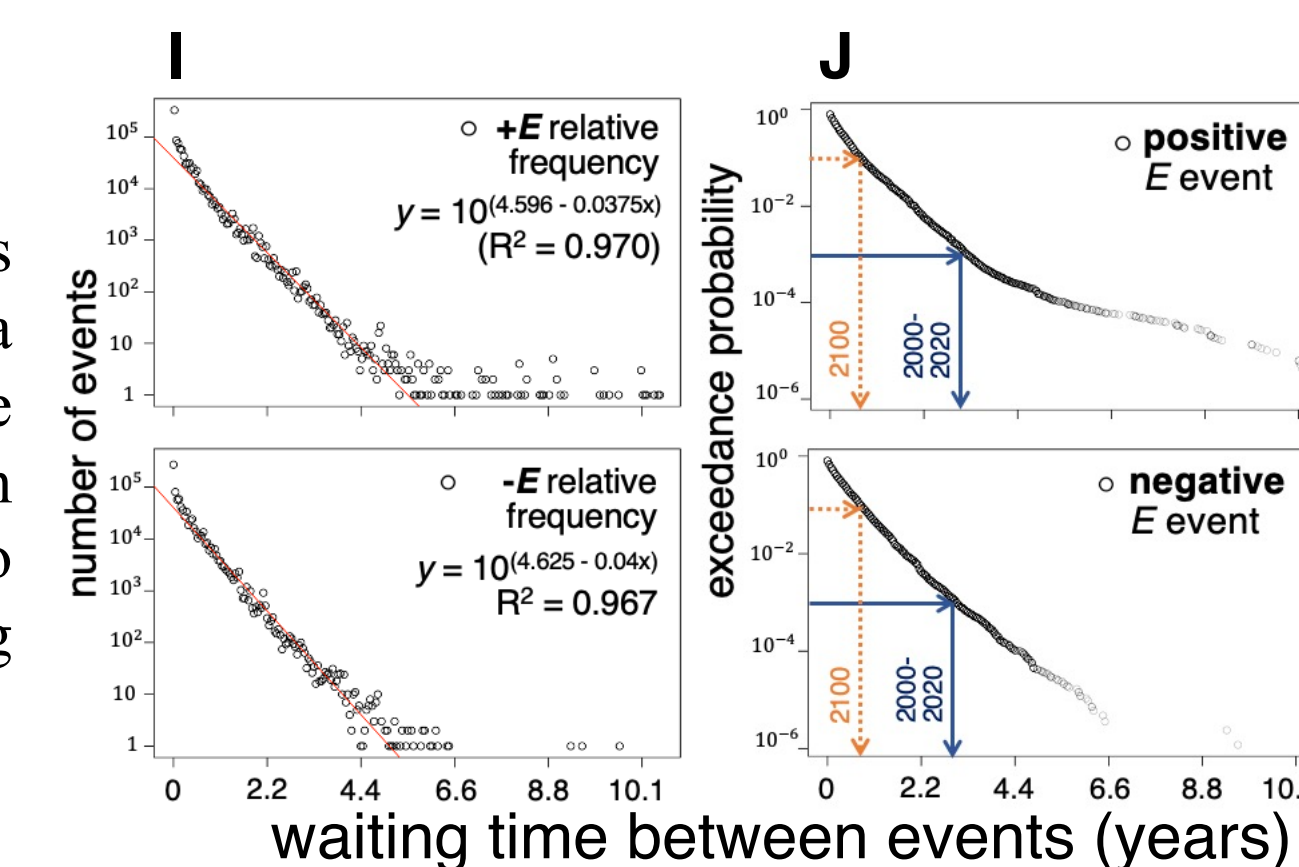
(C) Kernel density estimation of the effect size E of GPP perturbations with larger magnitude thresholds used to define events. At higher standard deviation baselines, extreme negative events became even more likely than extreme positive events. Weibull distribution parameters scaled consistently across the standard deviation thresholds used to define the perturbation events.



(D) Tidal wetland return times (R) are inverse power law distributed. For events more than half a year in duration, negative events are nearly ten-fold more common than positive events. (E) Tidal wetland locations with more negative perturbations were more resilient (they had shorter return times), and locations that are less resilient tended to be more resistant (they had fewer negative perturbations). (F) Some locations dampened positive perturbations by rapidly depleting resource pulses, but other locations amplified and prolonged positive perturbations. To take advantage of a positive event, the system would have to first construct and invest in new biophysical structure and function. This implicit thermodynamic start-up cost makes it more likely that the efficiency of these investments will be optimized if they can persist longer in time.



(I) The frequency distribution of the waiting times between events was exponential, and the ecosystem response therefore “memoryless”. For a memoryless system, the likelihood of experiencing the next event of a given size at any given point in time is independent of all other events (i.e., a Poisson process). (J) If 1 in 1000 probability events (blue arrows) are predicted to increase in frequency 100-fold by 2100, extreme events typically occurring about once every 3 years will instead occur about once per year (orange arrows).



(H) Tidal wetland ecosystems engage in adaptive strategies that bias towards *redundancy* and *efficiency* adaptation strategies, where bias towards one strategy shifts the relative frequency of events to maintain a long-term balance between negative and positive perturbations. The internal structure and function of the ecosystem must first reoptimize to meet its new frequency and magnitude of disturbance in order to produce the observed statistical distributions (i.e., the return interval between events is predictive of, and inversely correlated with, the ecosystem resistance and resilience).