

LETTER

Recent exposure to environmental stochasticity does not determine the demographic resilience of natural populations

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Editor: Ian Donohue**Abstract**

Escalating climatic and anthropogenic pressures expose ecosystems worldwide to increasingly stochastic environments. Yet, our ability to forecast the responses of natural populations to this increased environmental stochasticity is impeded by a limited understanding of how exposure to stochastic environments shapes demographic resilience. Here, we test the association between local environmental stochasticity and the resilience attributes (e.g. resistance, recovery) of 2242 natural populations across 369 animal and plant species. Contrary to the assumption that past exposure to frequent environmental shifts confers a greater ability to cope with current and future global change, we illustrate how recent environmental stochasticity regimes from the past 50 years do not predict the inherent resistance or recovery potential of natural populations. Instead, demographic resilience is strongly predicted by the phylogenetic relatedness among species, with survival and developmental investments shaping their responses to environmental stochasticity. Accordingly, our findings suggest that demographic resilience is a consequence of evolutionary processes and/or deep-time environmental regimes, rather than recent-past experiences.

KEYWORDS

demographic compensation, matrix population models, partial least squares regression, phylogenetic signal, recovery, resistance, transient demography

INTRODUCTION

Ongoing global shifts in the timing and magnitude of environmental variation warrant an understanding of the processes underlying the capacity for populations to resist and recover from disturbances (Angeler & Allen, 2016; Standish et al., 2014) (i.e. their resilience; Holling, 1973). However, half a century since Holling first defined resilience in ecological systems (Holling, 1973), we still do not know whether and how past environmental regimes shape the resilience of extant species (Walker, 2020).

Resolving this knowledge gap is pivotal for identifying those species most vulnerable to future increases in environmental stochasticity (Gaillard, 2010; McLeod et al., 2021), and thus, for designing effective ecosystem management strategies (Pressey et al., 2007).

While the resilience of ecological systems has attracted much attention for decades (Capdevila et al., 2021; Kéfi et al., 2019), approaches to evaluate the resilience of natural populations and communities often overlook its short-term nature (Cant, Salguero-Gómez, et al., 2022; Hastings et al., 2018; although see McDonald

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et al., 2016). Classic life-history theory posits that organisms operate under a strong trade-off coordinating their investments across the vital rates of survival, progression (e.g. growth and development), retrogression (e.g. shrinkage [Salguero-Gómez & Casper, 2010] and rejuvenation [Salguero-Gómez et al., 2013]) and reproduction (Stearns, 1989, 1992). Indeed, considerable attention has been directed at using these vital rates to describe how energetic trade-offs shape population performance when exposed to disturbances (Boyce et al., 2006; Jonzén et al., 2010; Tuljapurkar, 1982; Tuljapurkar et al., 2009; Tuljapurkar & Orzack, 1980). Yet, this attention has largely focused on the use of derivatives of long-term (i.e. asymptotic) population characteristics (such as stochastic population growth rate, λ_s) as measures of population performance in the face of recurrent disturbances (Crone et al., 2011). Thus, these assessments assume that natural populations can reach a stable, stationary, structural composition (i.e. the relative frequency of individuals at different stages along the life cycle of a species does not change with time) (Stott et al., 2011). Yet, in a demographic context, disturbances are typically defined as any external, discrete (a)biotic event that modifies the structural composition of a population (Capdevila et al., 2020). For example, susceptibility to drought-induced mortality increases with tree size across forests worldwide (Bennett et al., 2015), while seasonal declines in food availability increases juvenile mortality rather than that of mature fish in populations of Atlantic Salmon (*Salmo salar*; Kennedy et al., 2008). Thus, in natural environments, populations are frequently pushed away from their stationary equilibria, where a stable structural composition would be achieved (Koons et al., 2005). Instead, disturbances can, and oftentimes do, displace populations into a transient (i.e. short-term) phase, where their dynamics vary considerably from their asymptotic trajectories (Hastings, 2001; Figure 1). Long-term measures of population performance are, therefore, unlikely to reveal how environmental stochasticity influences the resilience of populations (Cant, Salguero-Gómez, et al., 2022). Alternatively, transient population metrics, describing how the dynamics of populations can change following disturbance relative to their long-term characteristics (Koons et al., 2005; Stott et al., 2011), offer greater insight into the inherent resilience (i.e. intrinsic capacity to respond to different disturbances) of different populations and species.

Natural populations exposed to greater environmental stochasticity are expected to undergo a selection for traits and vital rates that enhance their resilience (Boyd et al., 2016; Lande & Arnold, 1983). Within stochastic environments, populations endure greater abiotic variability and, thus, are more likely to experience more frequent alterations to their structural composition away from their stationary equilibrium (Kendall, 1998; Tuljapurkar et al., 2009). Thus, greater environmental stochasticity constitutes increased demographic disturbance.

Following these disturbance events, characteristics that inhibit transient declines in population growth, or those promoting short-term increases, are likely more beneficial than those maximizing long-term growth (Cant, Cook, et al., 2022; McDonald et al., 2016). Logically, therefore, one would expect increased environmental stochasticity to select for populations with increased *resistance* (i.e. a population's ability to avoid a decline in size after disturbance), and/or *compensation* (the ability to increase in size after disturbance), and shorter *recovery time* (henceforth recovery, the time needed for converging back to a stationary equilibrium after disturbance) (Capdevila et al., 2020; Hodgson et al., 2015; Figure 1). Evaluating how variation in the transient characteristics of populations is shaped across a gradient in environmental stochasticity, therefore, presents a unique opportunity for assessing how past exposure to disturbance shapes the ability for populations to tolerate future increases in environmental stochasticity.

Here, we provide a macroecological assessment of the environmental determinants of demographic resilience, examining how short-term environmental drivers mediate long-term evolutionary outputs. Specifically, we quantify the inherent capacity for resistance, compensation, and recovery, of 2242 natural populations across 61 animal, 305 plant, and three algae species, from two extensive demographic databases (Salguero-Gómez et al., 2015, 2016; Figure 1; Table S1). Building on the expectation that greater exposure to recurrent disturbances enhances demographic resilience (Boyd et al., 2016; Rivist et al., 2017), we anticipated that (H1a) exposure to higher frequency environmental stochasticity will select for faster recovery, while (H1b) exposure to broader spectra environmental stochasticity would select for increased resistance and reduced compensation. The vital rates of survival, progression, retrogression and reproduction describe how trade-offs in individual-level fitness translate into population-level performance (Metcalf & Pavard, 2007). Thus, we also expected patterns in demographic resilience to correspond with the underlying vital rates of populations. Specifically, we predicted that (H2a) greater investment into individual survival will minimize the impact of shifts in the compositional structure of populations on their realized growth rates, therefore enhancing their resistance, whereas (H2b) greater reproductive investment will enable faster population growth and, therefore, promotes enhanced compensatory and recovery potential.

METHODS

Demographic data extraction

To evaluate the selection pressures on the resilience attributes of natural populations, we extracted matrix population models (MPMs) from the open-source

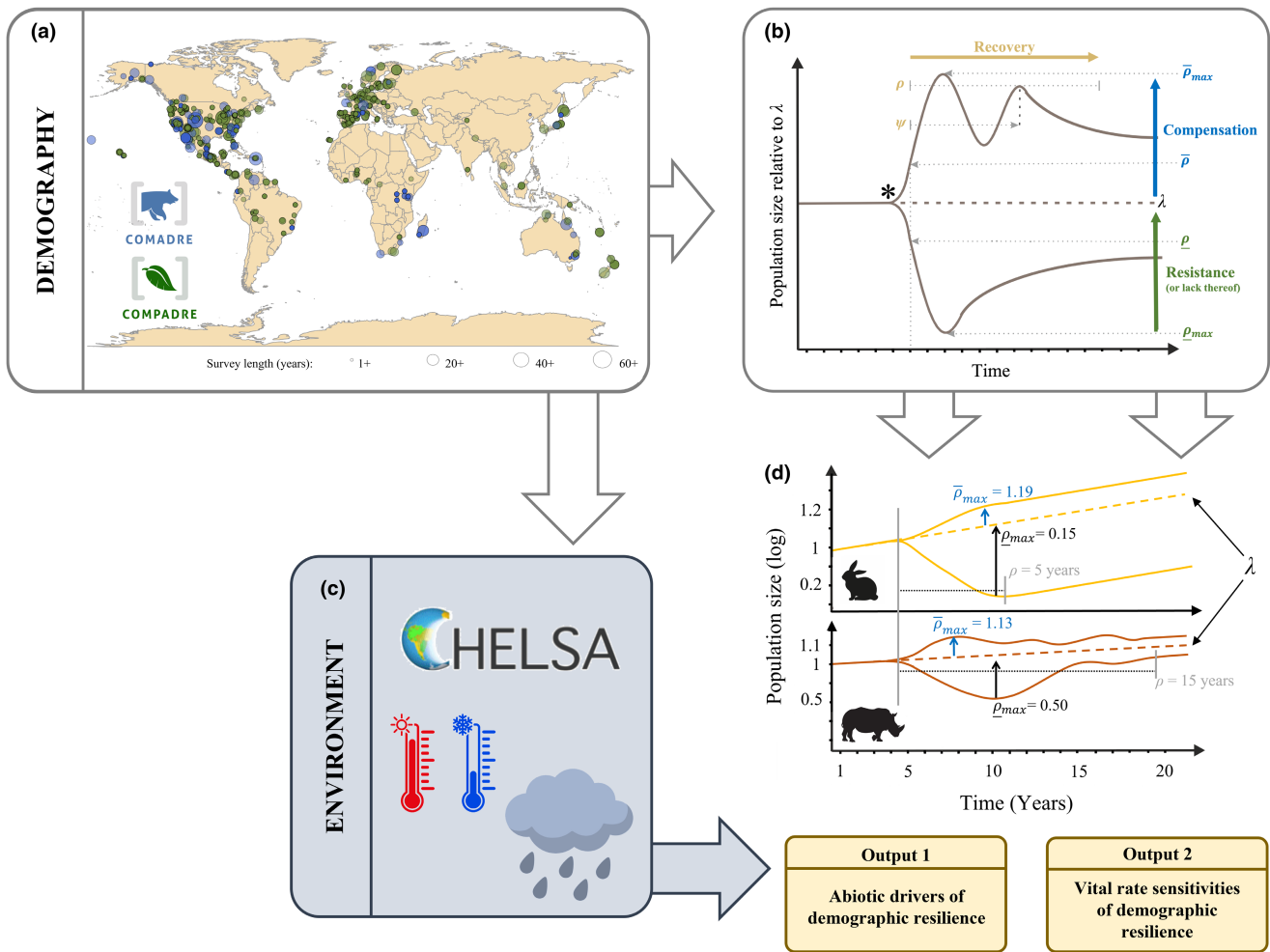


FIGURE 1 Using demographic data sourced for various natural populations we evaluated the (a) biotic drivers of demographic resilience. (a) Following a series of strict selection criteria (see Methods) we extracted matrix population models (MPMs) for 2242 populations across 305 plant, 61 animal and 3 algae species, from the COMPADRE (green; plants and algae) and COMADRE (blue; animal) databases. From each of these MPMs, we extracted various measures describing different aspects of each population's inherent demographic resilience. (b) Under stable stationary conditions, populations display asymptotic (i.e. long-term) growth trajectories whereby the size of a population changes at a constant rate (λ). However, following a disturbance (*), populations can enter a transient state during which their growth rate can differ significantly from asymptotic expectations. The duration and form of this transient phase depend, in addition to key moments of disturbances (e.g. magnitude, frequency, etc.), on a population's resilience attributes of resistance, compensation and time to recovery. Here, *resistance* is the ability of a population to avoid a decline in size following a disturbance, whereas *compensation* is the extent to which a population may increase in size following a disturbance, relative to its pre-disturbance condition. Meanwhile, the time of recovery (henceforth *recovery*) is the duration needed for a population to converge back to its stationary equilibrium following a disturbance. Metrics of transient dynamics allow for the characterization of these short-term dynamics in natural populations. Thus, transient metrics unlock the potential for macroecological studies exploring patterns and plausible mechanisms of demographic resilience. Transient increases in population size (N) can be evaluated using metrics of population reactivity ($\bar{\rho}$; increase in N within a one-time step following a disturbance) and maximal amplification ($\bar{\rho}_{max}$; maximum increase in N during the transient period). Equally, the magnitude of transient declines in population size can be assessed using the metrics of first-step attenuation (ρ ; decrease in N within a one-time step following a disturbance) and maximal attenuation (ρ_{max} ; maximum decrease in N during the transient period). Finally, the damping ratio (ρ ; rate of convergence back to stationary stability) and period of oscillation (ψ ; time between corresponding phases of the largest oscillatory cycle in N) of populations offer insights into their capacity to transition back to a stationary stable equilibrium. (c) We linked the transient dynamics of each population to their corresponding exposure to environmental stochasticity. To do so, we quantified environmental stochasticity using temporal records of maximum and minimum monthly temperature ($^{\circ}\text{C}$) and mean monthly precipitation (kgm^{-2}), obtained from the CHELSA climate database. (d) Using the transient and environmental stochasticity metrics obtained for each population, we subsequently tested whether demographic resilience is moulded by past exposure to recurrent disturbance and a population's vital rates of survival, progression, retrogression and reproduction. Here, we include a hypothetical example to demonstrate how comparing estimates of the damping ratio (ρ) and maximal attenuation (ρ_{max}) obtained from a fast- (rabbit, yellow) and slow-growing (Rhino, Orange) population can offer insight into their differing resilience characteristics. At equilibrium, both populations would be expected to exhibit a constant rate of growth (dashed line, λ). Yet, following a disturbance to their respective population structures, each population may exhibit differing growth trajectories (solid lines, showing possible transient increases and decreases in population size). Comparatively, the fast-growing population exhibits a lower resistance ($\rho_{max} = 0.18$) than the slow-growing population ($\rho_{max} = 0.50$), with the size of population dropping to a greater extent, relative to its asymptotic condition. However, the fast-growing population requires less time to reobtain its stable structural composition ($\rho = 5$ years), and therefore, reattain its stable growth rate, and thus displays more enhanced recovery compared to the slow-growing population ($\rho = 15$ years). Meanwhile, neither population displays a high capacity for demographic compensation ($\bar{\rho}_{max} = 1.19$ and 1.13 for the fast- and slow-growing populations respectively).

COMPADRE Plant Matrix Database (v. 5.0.1; Salguero-Gómez et al., 2015) and COMADRE Animal Matrix Database (v. 3.0.1; Salguero-Gómez et al., 2016). Categorizing populations into a sequence of discrete life stages or states (i.e. age, size classes and/or developmental stages), MPMs consist of a series of elements ($a_{i,j}$) reflecting the probability of individuals in a given state (i) transitioning into another state (j , i.e. growth/progression, stasis or shrinkage/retrogression) or the per capita production of individuals of state j by individuals of state i (i.e. sexual reproduction or clonality; van Groenendael et al., 1988). Using this framework, it is then possible to obtain estimates of population performance, such as long-term population growth rate (λ), and measures of demographic resilience (Caswell, 2001; Stott et al., 2011). Combined, COMPADRE and COMADRE contain over 12,000 MPMs from more than 1100 animal and plant species. However, here we tested our hypotheses using only MPMs satisfying a series of strict criteria. Briefly, among other criteria (see Supplementary SI for further details), we retained only MPMs describing the demographic characteristics of wild, un-manipulated populations recorded annually over a single continuous period of time. Following these criteria, we retained 3890 MPMs across 556 species, representing 3204 populations from 438 plant species, 665 populations from 112 animal species, and 21 populations from six brown and red algae species (Table S1).

We further refined this initial list of MPMs according to their transient, asymptotic and species-specific properties. All MPMs were tested for irreducibility (i.e. all life cycle stages are either directly or indirectly connected to one another), ergodicity (i.e. asymptotic dynamics are independent of the initial population structure) and primitivity (i.e. MPMs consist of non-negative elements) (Caswell, 2001). We carried out these tests using the corresponding *isErgodic*, *isIrreducible*, and *isPrimitive*, diagnostic functions from the R package '*popdemo*' (Stott et al., 2012). A total of 1203 reducible, imprimitive and/or non-ergodic MPMs were excluded from further analyses on the basis that they represent untenable life cycles that defy logical biological processes (Stott et al., 2010). MPMs with population growth rates (λ) >2 , indicating that the population is projected to increase twofold or more every year, were also rejected as they represent unlikely realizations of population performance in our experience. Equally, MPMs from highly migratory species (home ranges >1000 km) were discarded, since their vital rate schedules are unlikely to be solely shaped by the environment in which they were measured. We also note here that, across our initial population sample, the vital rate of clonality was rare, with only 140 populations across 37 plant species, and two populations from one animal species (*Amphimedon compressa*; see Mercado-Molina et al., 2011) explicitly exhibiting this demographic process. Thus, to focus our analyses on common demographic currencies, we excluded all populations

exhibiting clonality. Overall, this refinement resulted in a final sample of 2242 MPMs, corresponding with 369 species: 402 populations from 61 animal species, 1830 populations from 305 plant species, and 10 populations from three species of algae (Table S1).

Quantifying demographic resilience

We quantified demographic resilience using various transient metrics that describe a population's inherent ability to resist (i.e. not decline in size following a disturbance), compensate (i.e. increase in size following a disturbance) and recover (i.e. the time required to return to a stationary equilibrium after a disturbance) (Capdevila et al., 2020). In essence, these transient metrics outline the best- and worst-case scenarios in the size of a population, relative to its trajectory at equilibrium (Capdevila et al., 2020; Stott et al., 2011; Figure 1). Accordingly, transient metrics describe the capacity for different populations to exhibit particular responses to demographic perturbation by resisting, compensating and/or recovering quickly. To calculate these transient metrics, we standardized all MPMs by dividing each matrix element by the MPM's dominant eigenvalue (λ), thus detrending their transient and asymptotic properties (Caswell, 2001; Koons et al., 2005). Next, we estimated resistance (using the measures of first-timestep attenuation, $\underline{\rho}$ and maximal attenuation, $\underline{\rho}_{\max}$), compensation (reactivity, $\bar{\rho}$ and maximal amplification, $\bar{\rho}_{\max}$) and recovery (damping ratio, ρ and period of oscillation, ψ) from each MPM (see Supplementary SI for further details).

Next, to explore how the fitness components of individuals mediate the selection gradients placed on demographic resilience by environmental stochasticity, we calculated the sensitivity of each transient metric towards each of the vital rates of survival (σ), progression (γ), retrogression (τ) and fecundity (φ). First, we calculated the sensitivity of each transient metric to changes in each matrix element (s_{ij}). Individual elements within an MPM are typically comprised of combinations of multiple vital rates (i.e. the production of offspring involves aspects of reproduction and adult survival). Subsequently, calculating the vital rate sensitivities of each transient metric (s_{λ}) requires the decomposition of element-level sensitivities into their vital rate components (Franco & Silvertown, 2004). This decomposition requires the estimation of state-specific survival probabilities (σ_j) for each MPM. These estimates of σ_j are then used to determine the proportion of each matrix element, and thus, each element-level sensitivity, corresponding with survival (σ), progression (γ), retrogression (τ), and fecundity (φ) (Franco & Silvertown, 2004). The vital rate sensitivities of each transient metric can then be calculated through the summation of corresponding proportional element-level sensitivities (see Supplementary SI for further details).

The distributions of each transient metric and its corresponding vital rate sensitivities were checked prior to subsequent regression analyses. To ensure normality across each distribution, outliers, defined as values outside the 95% confidence intervals of the distribution, were omitted, with the remaining estimates then transformed if necessary. For each transient metric, power transformations (y^x) were used to achieve approximate normality using the Box–Cox transformation functions of the R package ‘*caret*’ (Kuhn, 2020) to estimate x . The distributions of damping ratio, period of oscillation, reactivity and maximal amplification raised negative x values and so their transformations took the form $1/y^{|x|}$. Inverse and log transformations were also necessary for several of the vital rate sensitivity variables (see Table S2 for further details).

Phylogenetic correction

Evaluating the selection pressures exerted on attributes of demographic resilience across multiple species requires an explicit consideration for how traits are expected to covary due to phylogenetic relationships (Freckleton, 2009; Freckleton et al., 2002; Revell, 2010). To account for such relationships in our analyses, we constructed a population-within-species-level phylogenetic tree using phylogenetic data extracted from the Open tree of Life for the animal, plant and algae species, across our population sample (OTL, Hinchliff et al., 2015; Supplementary S3). Our approach here also allowed us to accommodate studies that included multiple, separate populations for the same species (see below). First, the scientific names of each species associated with our extracted MPMs were checked against current taxonomy records using the R package ‘*taxize*’ (Chamberlain et al., 2020). Next, we extracted information regarding the taxonomic classification and phylogeny of each species from the OTL database with the R package ‘*rotl*’ (Michonneau et al., 2016). Subsequently, using the ‘*ape*’ (Paradis & Schliep, 2018) and ‘*phytools*’ packages (Revell, 2012), this phylogenetic information was used to construct a species-level phylogenetic tree corresponding with the 369 unique species within our MPM list.

Beyond accounting for phylogenetic signals in trait variance–covariance across our population sample, it was necessary to ensure that our phylogenetic tree reflected the influence of spatial signals in the development of traits within species. Thus, we expanded our phylogenetic tree by adding branch tips to incorporate multiple population entries per species (sensu Freckleton & Jetz, 2009), generating a population-level tree comprising our full sample of 2242 populations (Supplementary S3). Finally, we computed the branch lengths for our phylogenetic tree using the function *compute.brLen* in the R package ‘*ape*’ (Paradis & Schliep, 2018). These branch

lengths were estimated using Grafen's arbitrary branch lengths (Grafen, 1989), assuming a Brownian motion model with the variance between species directly proportional to time since divergence (Revell et al., 2008). Importantly, we constrained branch lengths between populations of the same species to approximately zero (0.0000001) under the assumption of negligible phylogenetic distance between species replicate populations.

Quantifying environmental stochasticity

To investigate the role of environmental stochasticity in defining the resistance, compensation and recovery components of demographic resilience, we determined the exposure of each population to environmental stochasticity. Using the latitude and longitude of each natural population in COMPADRE and COMADRE, we linked the transient metrics of each MPM to the population's local abiotic environment.

We quantified environmental stochasticity by focusing on extremes of temperature and mean precipitation. We selected these abiotic variables because they are important biodiversity drivers across all ecoregions (Howard et al., 2020), except in marine environments, which are not directly affected by precipitation (although see Haapkylä et al., 2011). Accordingly, we excluded MPMs associated with marine populations (29 populations from six animal species and 10 populations from three red/brown algal species) from this section of our analyses. For the retained 2184 terrestrial and 19 freshwater populations, we sourced high-resolution (1 km²) monthly temperature and precipitation records from the CHELSA climate database (Karger et al., 2017). For each population, we extracted records of maximum and minimum monthly temperature (°C) and mean monthly precipitation (kgm⁻²) for a timeframe equal to the period during which the population was surveyed plus an additional 50 years prior to survey onset, to account for the effects of environmental legacy (Evers et al., 2021). Within our sample, there were a total of two freshwater and 277 terrestrial populations for which no environmental data could be sourced. Subsequently, these 279 populations were excluded from this specific analysis.

We used five metrics to quantify the autocorrelation, range and frequency characteristics of the environmental stochasticity regimes experienced by each population: thermal autocorrelation (a_T), thermal range (m), thermal frequency spectrum (β_T), precipitation autocorrelation (a_p), and precipitation frequency spectrum (β_p). We arranged our extracted abiotic variables into time series depicting the 50+ year abiotic regimes to which each population had been exposed. We then estimated the temporal autocorrelation of each temperature (a_T) and precipitation (a_p) time series, using the ‘*colorednoise*’ package (Pilowsky, 2019). Next, we calculated the frequency spectrum of each time series. This metric is often

referred to as the colour of environmental variation and is typically represented on a red to blue colour scale, with blue describing higher frequency variation and red variation dominated by low frequencies (Ruokolainen et al., 2009). The frequency spectrum of a time series is expressed by its spectral exponent (β), which we calculated as the slope coefficient of the linear regression between the log spectral density and log frequency of the time series (Gilljam et al., 2019). We calculated the spectral exponent of the temperature (β_T) and precipitation (β_P) regimes experienced by each population using the *spectrum* command from the 'stats' package (R Core Team, 2019). Finally, we calculated thermal range (m) as the mean difference between maximum and minimum monthly temperatures throughout a time series, providing a measure of the magnitude of any environmental stochasticity. Prior to further analyses, we discarded outliers outside of the 95% confidence intervals for each of the aforementioned metrics of environmental stochasticity, before testing each variable for normality (Table S2) and collinearity (Supplementary S4).

Evaluating the association between resilience and environmental stochasticity

We used phylogenetically corrected partial least squares regression (pPLS) to test our hypotheses that the resistance, compensatory capacity, and recovery of natural populations, correspond with gradients in environmental stochasticity and how this is mediated by fitness investments. Using a pPLS, we evaluated the relationship between our estimates of demographic resilience and both their associated environmental stochasticity regimes and vital rate sensitivities. The pPLS technique is considered a more powerful comparative tool than other multivariate regression methods (Carrascal et al., 2009), as it simultaneously condenses the variation among numerous predictors while maximizing the variance explained among response variables. Subsequently, we investigated the selection pressures on the resistance, compensation, and recovery attributes of natural populations, and therefore, the capacity for environmental legacies, and vital rate characteristics, to serve as predictors of resilience attributes.

We first applied a phylogenetically corrected Pearson's test of correlation and pPLS to analyse the correlation between environmental stochasticity and our metrics of demographic resilience. This approach enabled us to test for covariation between the transient characteristics of populations and gradients in their exposure to environmental stochasticity. pPLS tests were carried out for each transient measure with the predictor variable set comprised of our five metrics of environmental stochasticity. From each test, we then extracted component scores and loadings describing the arrangement of the environmental predictor variables within a multivariate space. To

estimate the strength of any association between environmental stochasticity and the transient dynamics of our population sample we also obtained the percentage variance ($\%var$) among the predictors explained by each regression component, and the proportion of variance in the transient response variables explained by each component (r^2).

Next, we again used phylogenetically corrected correlation tests and pPLS analyses to examine for patterns between each transient characteristic and its associated vital rate sensitivities. Again, we calculated test coefficients (r), component scores, loadings, $\%var$, and r^2 values, to quantify the influence of the fitness components of survival, progression, retrogression, and reproduction, towards the transient characteristics of natural populations. Using the 'pls' R package (Mevik et al., 2019) with pertinent modifications included to ensure our analyses accounted for any evolutionary covariance (Adams & Felice, 2014; Revell, 2009, 2012) (see *Data Availability Statement* for a link to our code), we carried out all pPLS analyses using only complete entries, omitting populations with missing estimates for any one variable. To test that missing data were not obscuring any correlation between our measures of demographic resilience and environmental stochasticity, we repeated our analyses using phylogenetic imputation to estimate missing demographic measures (James et al., 2021; see Supplementary S5). Using the *phylosig* function from the 'phytools' package (Revell, 2012), we also calculated the phylogenetic signal (Pagel's λ [Pagel, 1999]; not to be confused with long-term population growth rate, λ) for each of our transient and sensitivity variables. Pagel's λ ranges between $0 < \lambda < 1$, with 0 indicating that the trait under examination has evolved independently of phylogeny and 1 representing a high phylogenetic signal across any pattern observed in the trait (Pagel, 1999), thus allowing us to explore the extent to which demographic resilience is determined by ancestral history.

RESULTS AND DISCUSSION

Sourcing climate records at the necessary temporal and spatial resolution for quantifying deep-time environmental legacies presents a considerable challenge (Dixon et al., 2021; Kwiatkowski et al., 2014). Thus, a population's resilience to future global change is more often inferred from its exposure to more contemporary conditions (Foden et al., 2019; Walker, 2020). Here, however, using phylogenetically-corrected pPLS and Pearson's tests of correlation, we found that no measure of environmental stochasticity constitutes a strong predictor of variation in the resistance, compensation, and recovery attributes, of populations (Figure 2; Table 1). This finding was insensitive to both phylogenetic imputation (Figure S2) and the length of time used to quantify recent-past exposure to environmental stochasticity (Figures S5 and S6).

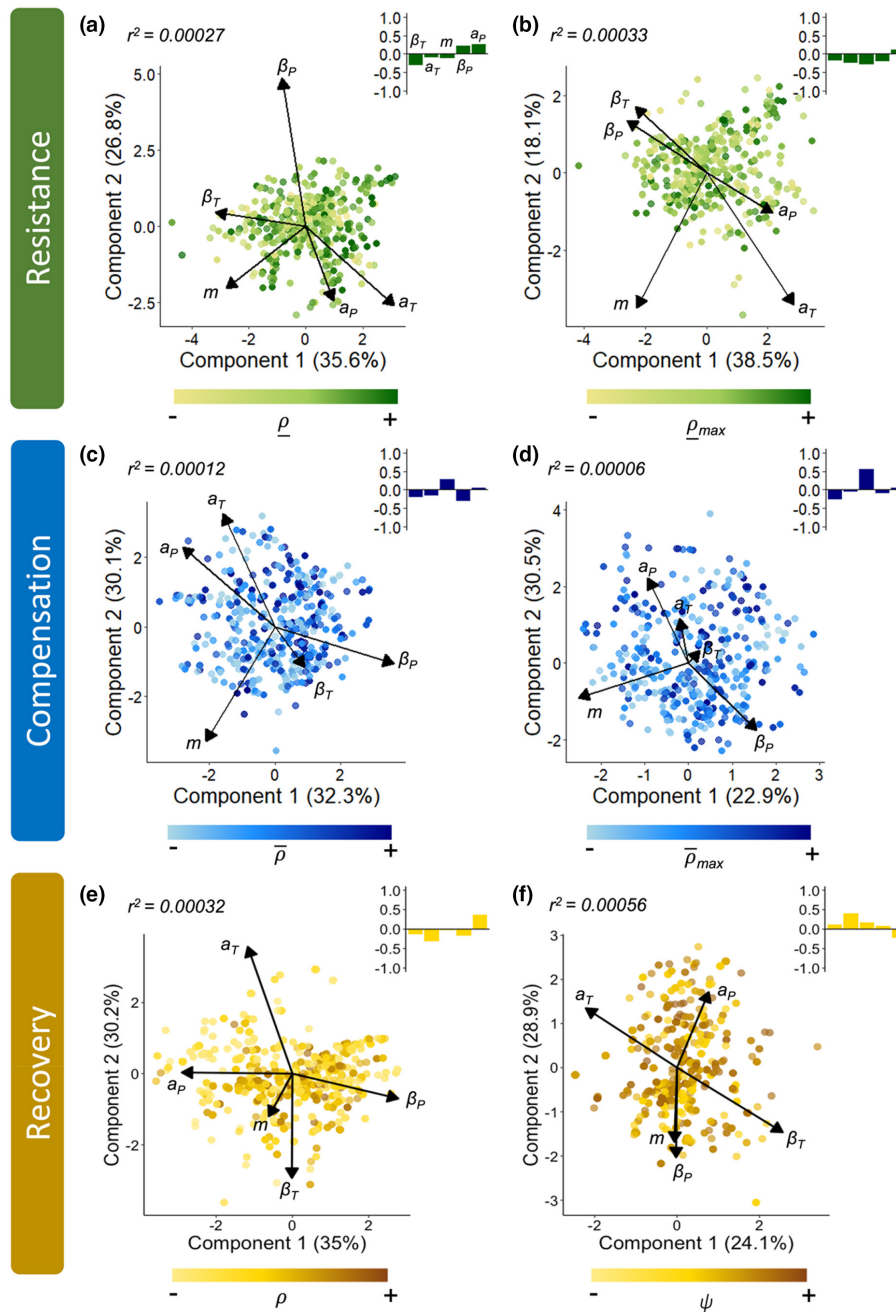


FIGURE 2 Variation across metrics of demographic resilience: resistance (green), compensation (blue) and recovery (orange) does not correspond with patterns in the exposure of populations to environmental stochasticity. Scores and loadings of a phylogenetically weighted partial least squares (pPLS) regression analysis exploring the correlation between patterns in the variation of the six transient metrics of (a) first-step attenuation ($\underline{\rho}$), (b) maximal attenuation ($\underline{\rho}_{\max}$), (c) reactivity ($\bar{\rho}$), (d) maximal amplification ($\bar{\rho}_{\max}$), (e) damping ratio (ρ) and (f) period of oscillation (ψ) and the five metrics of environmental stochasticity: temperature frequency spectrum (β_T), temperature autocorrelation (a_T), thermal range/magnitude (m), precipitation frequency spectrum (β_P) and precipitation autocorrelation (a_P). The component scores along each axis display the percentage variance in the environmental stochasticity variables captured by each component, with the first two components alone explaining $>50\%$ of the variance across all models. The gradation in point colour then reflects patterns in the relative magnitude of each transient metric recorded for each population, with darker shades indicating higher estimates. Inset barplots are the standardized regression coefficients (b) highlighting the relative weighting of each abiotic variable in the overall capacity of each pPLS model to explain variation in a given transient metric (r^2).

Using a novel framework, based on punctual disturbances altering population structure, to quantify demographic resilience (Capdevila et al., 2020), we estimated the six transient metrics comprising resistance (first-step

attenuation, $\underline{\rho}$ and maximal attenuation, $\underline{\rho}_{\max}$), compensation (reactivity, $\bar{\rho}$ and maximal amplification, $\bar{\rho}_{\max}$), and recovery (damping ratio, ρ and period of oscillation, ψ), in each population following disturbance (Caswell,

TABLE 1 The resilience attributes of resistance (green), compensation (blue) and recovery (orange) of natural populations do not correlate with their relative exposure to environmental stochasticity. Using phylogenetically-corrected Pearson's tests of correlation, we explored the association between transient metrics of demographic resistance (first-timestep attenuation, $\underline{\rho}$ and maximal attenuation, $\underline{\rho}_{\max}$), compensation (reactivity, $\bar{\rho}$ and maximal amplification, $\bar{\rho}_{\max}$) and recovery (damping ratio, ρ and period of oscillation, ψ ; Figure 1b) and five metrics of environmental stochasticity: temperature frequency spectrum (β_T), temperature autocorrelation (a_T), thermal range (m), precipitation frequency spectrum (β_P) and precipitation autocorrelation (a_P). Correlation displayed using Pearson's correlation coefficient (r).

Transient metric	Resilience attribute	β_T	a_T	m	β_P	a_P
$\underline{\rho}$	Resistance	-0.0106	0.0060	-0.0094	-0.0024	0.0042
$\underline{\rho}_{\max}$		-0.0071	0.0031	-0.0121	-0.0093	0.0068
$\bar{\rho}$	Compensation	-0.0026	0.0007	0.0070	-0.0080	0.0041
$\bar{\rho}_{\max}$		-0.0016	<0.0001	0.0069	-0.0026	0.0009
ρ	Recovery	0.0012	-0.0007	0.0026	-0.0124	0.0147
ψ		-0.0071	0.0133	0.0052	0.0037	-0.0070

2001; Stott et al., 2011; Capdevila et al., 2020; Figure 1b). Next, we quantified the exposure of these populations to environmental stochasticity using measures of mean thermal range (m), as well as the spectral frequency and autocorrelation of temperature (β_T and a_T) and precipitation regimes (β_P and a_P) they experienced during the 50-years preceding the beginning of each study (Supplementary S4). Over any given timeframe, shorter-lived populations (mean life expectancy ≤ 10 years) are likely to have had a larger number of generations exposed to local environmental stochasticity, thereby offering greater opportunity for adaptive change. Yet, our finding persists irrespective of mean life expectancy, with recent-past exposure to environmental stochasticity having an equally negligible influence on the resilience attributes of populations of both long- and short-lived species (Figure S4).

Resistance and compensation, but not recovery, are determined by energetic investments across somatic maintenance/development and reproduction. Using pPLS across our 2242 populations, we evaluated the relationship between our six measures of demographic resilience (Figure 1b) and their sensitivities to each of the vital rates of survival (σ), progression (γ), retrogression (τ) and fecundity (φ ; Figure 3). These vital rate sensitivities reflect how much each transient metric would change following perturbations in each vital rate (Caswell, 2001). Thus, these sensitivities highlight how investments into any one vital rate influence a population's capacity to resist, compensate and recover following a disturbance and so provide a measure of the absolute importance of each vital rate in shaping demographic resilience. We focused on sensitivities here, rather than elasticities (proportional sensitivities; de Kroon et al., 2000), as the former provide a closer representation of selection gradients (van Tienderen, 2000).

Corroborating recent evidence that the resistance and compensation attributes of populations are constrained by individual-level fitness investments (Capdevila et al., 2022), we illustrate how greater investment in survival enhances population resistance,

whereas greater reproductive investment reduces resistance potential (Table 2). Being able to rely upon the survival of the most viable individuals enables populations to mitigate any negative effects arising from the loss of individuals due to temporal variability in resource availability (Gaillard & Yoccoz, 2003), thereby bolstering their demographic resistance. With the energetic costs associated with enhanced reproductive investment known to reduce investment into somatic maintenance (Stearns, 1989), it is unsurprising that greater reproductive investment opposes population resistance. Meanwhile, enhanced investment into individual progression minimizes a population's capacity for compensation, a capacity that can instead be enhanced by adopting retrogressive strategies (e.g. shrinking [Salguero-Gómez & Casper, 2010] or rejuvenation [Salguero-Gómez et al., 2013]; Table 2). Populations of fast-growing individuals typically exhibit shorter generation times, equipping them with the high turnover rates characteristic of fast colonizers of novel environments (Gaillard et al., 2005). Yet, the development of fast-growth strategies suggests a need to escape vulnerable early life stages (Arendt, 1997). Alternatively, retrogressive strategies, such as vegetative dormancy and the fission of corals into smaller fragments, can facilitate the rapid replenishment of natural populations following fires and storm events (Connell, 1997; Miller & Chesson, 2009). We found, however, no evidence of demographic selection pressures upon the attribute of recovery (Figure 3; Table 2). Again, these findings are insensitive to phylogenetic imputation (Figure S3).

A strong phylogenetic signal across energetic investments into resistance, compensation, and recovery, suggests that demographic resilience is not shaped by recent environmental patterns, but by phylogenetic ancestry. Using estimates of phylogenetic signal (Pagel's λ) we demonstrate a strong phylogenetic signal (Pagel's $\lambda > 0.940$, $p < 0.001$) across the transient metrics of resistance (first-timestep attenuation and maximal attenuation) and compensation (reactivity and maximal amplification) and their corresponding vital rate

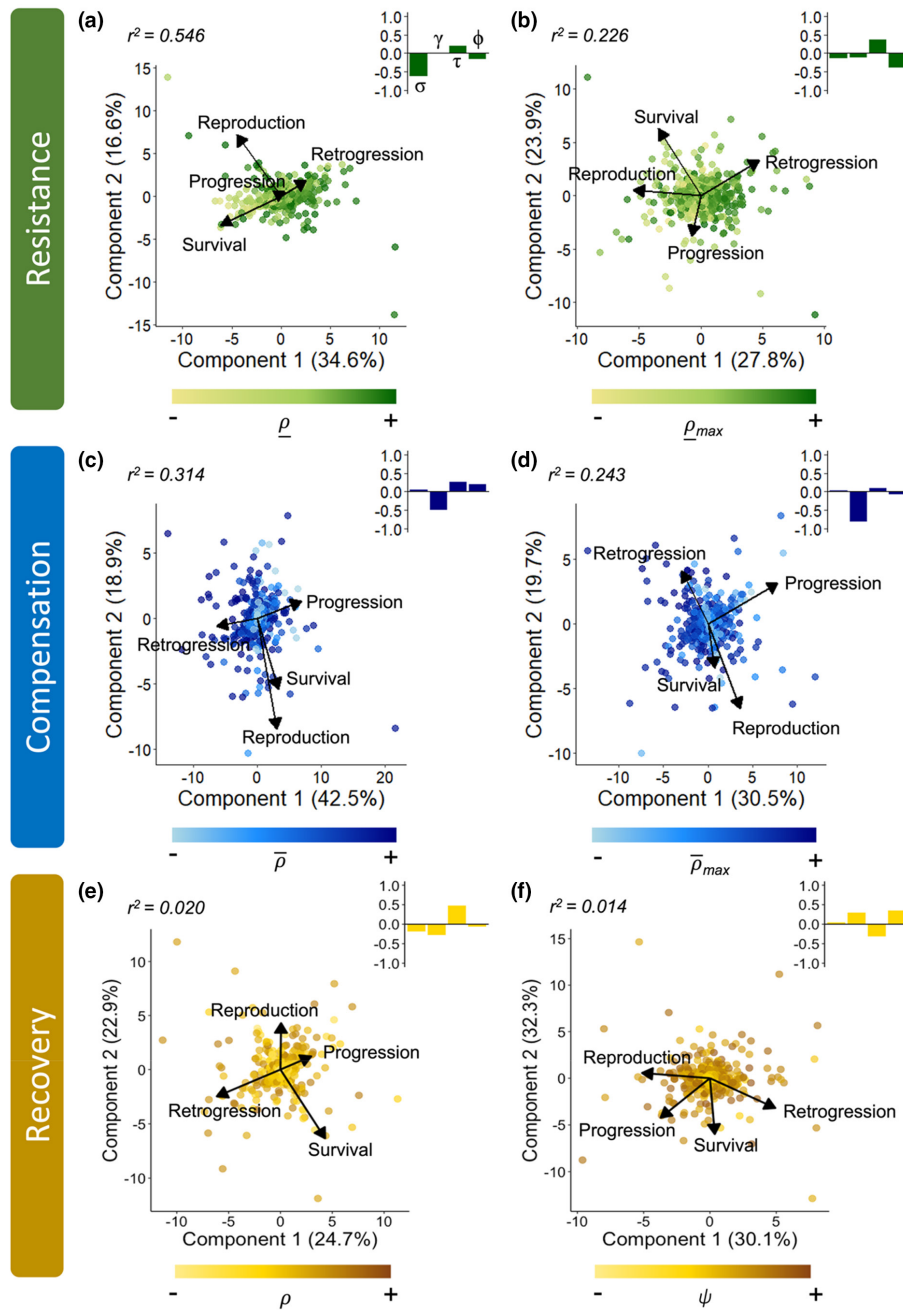


FIGURE 3 The resilience attributes of resistance (green), compensation (blue) and recovery (orange), in natural populations are determined by the relative energetic investments of their individuals. Scores and loadings of a phylogenetically weighted partial least squares regression analysis exploring the sensitivity patterns of the six transient metrics of (a) first-step attenuation (ρ), (b) maximal attenuation (ρ_{max}), (c) reactivity ($\bar{\rho}$), (d) maximal amplification ($\bar{\rho}_{max}$), (e) damping ratio (ρ) and (f) period of oscillation (ψ), towards the vital rates of survival (σ), progression (γ), retrogression (τ) and reproduction (ϕ). The component scores along each axis display the percentage variance in the environmental stochasticity variables captured by each component, with the first two components alone explaining >47% of the variance across all models. The gradation in point colour then reflects patterns in the relative magnitude of each transient metric recorded from each population, with darker shades indicating higher estimates. Inset barplots are the standardized regression coefficients (b) highlighting the relative weighting of each vital rate in the overall capacity of each PLS model to explain variation in a given transient metric (r^2).

sensitivities (Table 3). Phylogenetic signal reflects the proportion of variation in a trait across different species that can be explained by their shared evolutionary history (Freckleton et al., 2002; Pagel, 1999). As such, this analysis quantifies the extent to which evolution may have shaped the observed resilience attributes of

natural populations. We observed little association between the phylogenetic patterns of resilience and the environmental stochasticity regimes to which our examined natural populations were exposed. Selection pressures constrain how individuals allocate finite resources across survival, somatic development and

TABLE 2 Variation across resistance (green) and compensation (blue) of natural populations corresponds with the energetic investments of their individuals, but characteristics of recovery (orange) do not. Using phylogenetically-corrected Pearson's tests of correlation, we explored the association between the transient metrics of resistance (first-timestep attenuation, $\underline{\rho}$ and maximal attenuation, $\underline{\rho}_{\max}$), compensation (reactivity, $\bar{\rho}$ and maximal amplification, $\bar{\rho}_{\max}$) and recovery (damping ratio, ρ and period of oscillation, ψ ; Figure 1b) and their sensitivities to the vital rates of survival (σ), progression (γ), retrogression (τ) and reproduction (ϕ). Correlation displayed using Pearson's correlation coefficient (r), with darker colour gradations used to highlight stronger associations (irrespective of direction) between each transient metric and its vital rate sensitivities.

Transient metric	Resilience attribute	Survival σ	Progression γ	Retrogression τ	Reproduction ϕ
$\underline{\rho}$	Resistance	-0.70	-0.07	0.28	-0.39
$\underline{\rho}_{\max}$		-0.17	0.07	0.31	-0.34
$\bar{\rho}$	Compensation	-0.11	-0.49	0.39	-0.04
$\bar{\rho}_{\max}$		-0.02	-0.49	-0.13	-0.14
ρ	Recovery	-0.06	-0.06	0.11	-0.01
ψ		<0.01	0.06	-0.08	0.08

TABLE 3 Variation in resistance (green), compensation (blue) and recovery (orange) is strongly predicted by phylogenetic association. However, while a strong phylogenetic signal is also evident across the vital rate sensitivities of measures of resistance and compensation, there is a negligible phylogenetic signal across the vital rate sensitivities of measures of recovery. To quantify the strength of statistical non-independence in the resilience attributes of natural populations due to species' common ancestry, we estimated the phylogenetic signal (Pagel's λ ; Pagel, 1999) across our transient metrics of demographic resistance (first-timestep attenuation, $\underline{\rho}$ and maximal attenuation, $\underline{\rho}_{\max}$), compensation (reactivity, $\bar{\rho}$ and maximal amplification, $\bar{\rho}_{\max}$) and recovery (damping ratio, ρ and period of oscillation, ψ ; Figure 1b), as well as their sensitivities to the vital rates of survival (σ), progression (γ), retrogression (τ) and reproduction (ϕ). Pagel's λ ranges between 0, indicating that traits have evolved independently of phylogeny, and 1, representing a high phylogenetic signal. Colour gradation highlights the likelihood that the phylogenetic signal observed across each transient metric and its vital rate sensitivities differs significantly from 0 ($p < 0.05$), with darker shades representing stronger signals.

Transient metric	Resilience attribute	Pagel's λ	Survival σ	Progression γ	Retrogression τ	Reproduction ϕ
$\underline{\rho}$	Resistance	0.997	0.997	0.989	0.967	0.985
$\underline{\rho}_{\max}$		$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
$\bar{\rho}$	Compensation	0.998	0.990	0.999	0.995	0.996
$\bar{\rho}_{\max}$		$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
ρ	Recovery	0.996	0.003	<0.001	0.005	<0.001
ψ		$p < 0.001$	$p = 0.344$	$p = 0.686$	$p = 0.094$	$p > 0.999$
		0.992	<0.001	0.179	<0.001	<0.001
		$p < 0.001$	$p > 0.999$	$p < 0.001$	$p > 0.999$	$p > 0.999$

reproduction, thus mediating the capacity for populations to exploit and prevail within their local environments (Lande & Arnold, 1983; Stearns, 1989). Over time, these selective forces have moulded the resilience attributes of populations, but not in response to the environmental stochasticity regimes they currently endure (Bell, 2013; Bell & Gonzalez, 2011). It is necessary, therefore, to highlight the limitations associated with using the recent exposure of populations to environmental stochasticity as a predictor of their continued resilience to future disturbances.

Caution is necessary when interpreting our results regarding the selection pressures maintained by environmental stochasticity. Our exploration into the environmental drivers of demographic resilience focuses only on terrestrial populations. Compared with

marine systems, terrestrial environments afford organisms with more opportunities for seeking out tolerable microclimates (Sunday et al., 2014), thereby reducing the susceptibility of terrestrial taxa to environmental shifts. By contrast, marine species inhabit conditions closer to their physiological limits (Pinsky et al., 2019), rendering them more sensitive to abiotic shifts. It was also not possible to include a measure of monthly precipitation range within our calculations of environmental stochasticity. With characteristics such as the size and timing of individual rainfall events a key driver of performance in plant communities (Griffin-Nolan et al., 2021), it would be pertinent to expand our work in the future to incorporate a measure of monthly precipitation variability, alongside other important abiotic variables, as the data becomes available. Although

remediating data biases was beyond the scope of this study, we must also acknowledge geographic and taxonomic biases implicit within our sources of demographic data (see Paniw et al., 2021; Römer et al., 2021; Salguero-Gómez et al., 2021; Figure 1a). Environmental stochasticity plays a crucial role in regulating species range boundaries (Benning et al., 2022; Feldman et al., 2015), and indeed, the transient dynamics of coral assemblages in southern Japan and eastern Australia mediate their capacity for persisting outside of their core ranges (Cant et al., 2021; Cant, Cook, et al., 2022). Yet coral populations represent a taxonomic group for which there is not yet extensive demographic data available (Edmunds & Riegl, 2020). Most importantly, however, here we quantify past exposure to environmental stochasticity using maximum exposure legacies of 100 years. It is plausible, however, that deep-time environmental regimes would offer greater predictive potential. Indeed, deep-time studies have demonstrated how the latitudinal diversity gradient, a prominent pattern underlying contemporary ecological understanding, has only persisted during the past 30 million years (Mannion et al., 2014). While environmental stochasticity is known to influence population dynamics (Lande et al., 2003), its observable effects on population characteristics can remain negligible until compounded by external factors such as changing habitat configurations (Fraterrigo et al., 2009). Any direct impacts of environmental stochasticity on the resilience of natural populations may, therefore, become more detectable with time.

Despite the potential influence of historical climate legacies on the resilience of natural populations, our results show a robust lack of influence of recent-past climate on demographic resilience, even after explicitly accounting for lifespan and legacy time. Adaptation is the accumulation of beneficial, heritable characteristics within a population over multiple generations. Therefore, populations exposed to specific conditions over extended timeframes, or those that turn over multiple generations within a short period of time, are more likely to display trait characteristics adapted to those conditions (Bell, 2013; Bell & Gonzalez, 2011; Compagnoni et al., 2021). To evaluate the implications of different exposure periods on our observations, we first repeated our pPLS analyses exploring the relationship between demographic resilience and environmental stochasticity focusing on only populations of short-lived species (Supplementary S6). We determined population longevity using estimates of mean life expectancy (η_e), with populations of $\eta_e \leq 10$ years defined as short-lived ($n=1606$ populations). Next, we repeated our analyses using only populations for which 100-year abiotic legacies could be sourced (Supplementary S7). Neither approach improved our ability to predict the demographic resilience attributes of natural populations using measures of environmental stochasticity (Figures S5–S7).

CONCLUSIONS

Global change is changing the periodicity of phenological drivers (Cordes et al., 2020; Paniw et al., 2019), reducing return times between severe disturbance events (Hughes et al., 2018; Thornton et al., 2014). Natural populations worldwide are, thus, being exposed to increasingly stochastic environments, with many facing imminent collapse (Lenton et al., 2019). Here, we illustrate, however, that the recent-past exposure (last 50–100 years) of natural populations to environmental stochasticity does not constrain, nor guarantee, their resilience towards future climatic shifts. This realization that demographic resilience appears constrained by the adaptation of species over longer-term evolutionary timeframes, not the conditions experienced by populations following their dispersal, is not trivial. Rather, this key insight can help to focus the current debate surrounding the concept of resilience (Hodgson et al., 2015; Ingrisch & Bahn, 2018; Kéfi et al., 2019), enabling our attention to be directed towards identifying populations with high adaptive potential and maintaining the high genetic diversity necessary to enhance the resilience of natural populations. Reliant on preserving and enhancing the earth's natural capital, initiatives such as the United Nations Sustainable Development Agenda are interwoven with the conservation-orientated goals of our responsibility for environmental stewardship (Seddon et al., 2020; Walker, 1995). Accordingly, a detailed understanding of the mechanisms that do and do not promote the resilience of natural populations is imperative for not only achieving conservation success but also for securing our socio-economic future.

AUTHOR CONTRIBUTIONS

James Cant, Roberto Salguero-Gómez, Maria Beger and Pol Capdevila conceived the ideas and methodology for the project. James Cant, Pol Capdevila and Roberto Salguero-Gómez carried out data extraction and analysis. James Cant led the writing of the manuscript, with close support from Roberto Salguero-Gómez, and all authors contributed critically to the writing and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare there are no conflicts of interest associated with this work.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All demographic data used in this study are permanently archived within the open access COMADRE and COMPADRE demographic databases (<https://compadre-db.com/>). Meanwhile, all taxonomic information used in the construction of our phylogenetic trees can be sourced from the Open Tree of Life (<https://tree.opentreeoflife.org/>), whilst all temperature and precipitation records used in this study can be downloaded from the CHELSA climate database (<https://chelsa-climate.org/>). Finally, the R code used for all data extraction and the analyses presented throughout this manuscript are available on Zenodo (<http://doi.org/10.5281/zenodo.7828862>).

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SUPPORTING INFORMATION

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

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