Evolutionary processes, not environmental drivers, determine the resilience of natural populations

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Abstract

Escalating climatic and anthropogenic pressures expose ecosystems worldwide to increasingly frequent disturbances. Yet, our ability to forecast the responses of natural populations to global change is impeded by a limited understanding of how exposure to environmental change shapes population resilience. Here, we test the association between local regimes of environmental change and the resilience to disturbance of 2,242 natural populations across 369 terrestrial and aquatic animal and plant species. Unexpectedly, we find that recent abiotic disturbance regimes (<50 years) do not predict the inherent ability of populations to resist and recover from disturbances. Instead, population resilience carries a strong evolutionary signal, with survival and developmental investments playing a key role in shaping population responses to disturbance. Contrary to assumptions that exposure to more frequent disturbances confers a greater ability to cope with future global change, population resilience relies on evolutionary processes that have shaped species characteristics over many generations.

Introduction

Predicting the outcomes of ongoing shifts in the timing and severity of environmental variability challenges ecologists to identify the processes underlying the capacity for populations to resist and recover from disturbances[1,2] (*i.e.*, their resilience[3]). However, half a century since Holling first defined resilience in ecological systems[3], we still do not know whether and how past environmental regimes shape the resilience of extant species[4]. Resolving this knowledge gap is pivotal for identifying those species most vulnerable to future increases in the frequency of disturbance regimes[5,6] and for designing effective ecosystem management strategies[7].

Resilience is far from a neglected concept[8,9], but approaches used to evaluate resilience often overlook its short-term nature[10]. Classic life-history theory argues that organisms operate under a strong trade-off coordinating their biological investment across survival and reproduction[11,12]. Indeed, considerable focus has been applied towards using the vital rates of survival, progression (*e.g.*, growth, development), retrogression (*e.g.*, shrinkage[13], rejuvenation[14]), and reproduction, to describe how these trade-offs then shape population performance in stochastic environments, characterised by frequent disturbances[15–19]. Yet, attention has still largely remained focused on the use of stochastic 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. Instead, disturbances, defined here as external (a)biotic forces with the capacity to modify the structural composition of natural populations, can displace populations into a transient (*i.e.*, short-term) phase during which their dynamics can vary considerably from their asymptotic trajectories[20] (Fig. 1A). Amid this transient phase, characteristics that inhibit short-term declines in population growth, or those promoting a short-term elevation are likely more beneficial than those maximising long-term performance[21].

Within stochastic environments, with populations exposed to repeated disturbances, it is logical that natural selection would act upon heritable traits enhancing their overall resilience[22,23]: increasing *resistance* (*i.e.*, a population's ability to avoid a decline in size after disturbance) and/or *compensation* (*i.e.*, ability to increase in size after disturbance), and/or shortening *time of recovery* (henceforth recovery; *i.e.*, the time needed for converging back to a stationary equilibrium after disturbance) following disturbances[24,25] (Fig. 1A). Long-term measures of population performance cannot, therefore, reveal how environmental stochasticity shapes the resilience of populations to disturbances[10]. Alternatively, metrics of short-term (*i.e.*, *transient*) population dynamics, describing how the dynamics of populations within a transient state can be expected to change relative to their long-term characteristics[26,27], can provide greater insight into the resilience of natural populations[25,28,29]. These transient metrics thus represent a unique opportunity for exploring the responses of natural populations to disturbances (their resilience)[24,25], and how these might have been influenced by past-disturbance regimes.

Here, to better understand the mechanisms underpinning resilience, we provide a global assessment of the environmental and phylogenetic determinants of population resilience. Specifically, we quantify the inherent capacity for resistance, compensation, and recovery of 2,242 natural populations across 61 animal, 305 plant, and 3 algae species from global demographic databases[30,31] (Fig. 1B & Supplementary Table S1). Building on the expectation that past disturbance regimes have shaped current resilience[23,32], we anticipate that (H1a) exposure to a higher disturbance frequency will select for faster recovery, whilst (H1b) exposure to broader spectra in environmental stochasticity selects for increased resistance and reduced compensation. With the vital rates of survival, progression, retrogression, and reproduction describing how trade-offs in individual-level fitness translates into population-

level characteristics[33], we expect that (H2) the effects of environmental stochasticity on population resilience will manifest through the underlying vital rates of populations.

Results and Discussion

It is often assumed that past periodic exposure to disturbance will promote the resilience of ecological systems towards future disturbances[4]. Here, however, using phylogenetically-corrected partial least squares regression (pPLS) we found no relationship among the resilience attributes of populations (*i.e.*, resistance, compensation, and recovery; Fig. 1A) and their recent-past exposure to varying degrees of environmental stochasticity (Fig. 2). We used six transient metrics to quantify resistance (first-step attenuation, $\underline{\rho}$ & maximal attenuation, $\underline{\rho}_{max}$), compensation (reactivity, $\overline{\rho}$ & maximal amplification, $\overline{\rho}_{max}$), and recovery (damping ratio, ρ & period of oscillation, ψ) in each population following disturbance[25,27,34] (Fig. 1A). 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 & a_T) and precipitation regimes (β_P & a_P) they experienced during the 50-years preceding the beginning of each study (Supplementary S4). Overall, no measure of environmental stochasticity constituted a strong predictor of variation in resistance, compensation, or recovery (r^2 <0.001 in all cases; Fig. 2).

The limited association between exposure to environmental stochasticity and the resilience attributes of natural populations is further evident in phylogenetically-corrected Pearson's tests of correlation between our transient metrics and our estimates of environmental stochasticity ($|r|$ <0.015 in all cases; Table 1). Importantly, this finding is insensitive to phylogenetic imputation[35] (Fig. S3) and the length of time used to quantify recent-past exposure to environmental stochasticity (Fig. S6 & S7). Our finding also persists regardless of mean life expectancy (η_e), with both long- and short-lived populations displaying an equally negligible influence of recent-past exposure to environmental stochasticity on their resilience

attributes (Fig. S5). This similarity occurs over equivalent 50-year intervals, even though short-lived populations ($\eta_e \leq 10$ years) are likely to have had a larger number of generations exposed to local stochasticity, thereby offering greater opportunity for adaptive change.

Resistance and compensation, but not recovery, are however, determined by selection pressures shaping their energetic investments across somatic maintenance/development, and reproduction. Using pPLS across our 2,242 populations, we evaluated the relationship between our six measures of demographic resilience (Fig. 1A) and their sensitivities to each of the vital rates of survival (σ), progression (γ), retrogression (τ), and fecundity (φ; Fig. 3). These vital rate sensitivities reflect how much each transient metric would change following alterations in each vital rate[34]. Thus, these sensitivities highlight how investments into any one vital rate influence a populations' capacity to resist, compensate, and recover following a disturbance, and 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[36]), as they provide a closer representation of selection gradients across populations possessing traits with negative values or no natural zero level[37]. Patterns across the vital rate sensitivities of each transient characteristic corroborate recent evidence of an association between population resistance and compensation[38], revealing that the resistance and compensation attributes of populations are constrained by individual-level investments on survival, progression, retrogression, and reproduction, whilst there is no evidence for demographic selection pressures on the attribute of recovery (Fig. 3 & Table 2). Again, these findings are insensitive to phylogenetic imputation (Fig. S4).

Using estimates of phylogenetic signal (Pagel's λ[39]; not to be confused with long-term population growth rate, λ) we further demonstrate a strong phylogenetic signal (Pagel's $\lambda > 0.94$ & $p < 0.001$) across the transient metrics of resistance (first-timestep attenuation & maximal attenuation) and compensation (reactivity & maximal amplification), and their

corresponding vital rate sensitivities (Table 3). Phylogenetic signal reflects the proportion of variation in a trait that can be explained by species' shared evolutionary history, and so represents the extent to which evolution constraints the expression of that trait[39,40] (here the ability of a natural population to respond to disturbances). That resistance, compensation, and recovery have evolved regardless of whether populations endure frequent disturbances or not is indicative of indirect selection and may undermine the capacity for many populations to persist with future increases in environmental stochasticity. Indirect selection occurs when selective forces operate simultaneously upon multiple traits[22,41,42]. When population characteristics rely on similar underlying mechanisms, such as enhanced individual survival, directional selection can promote covariance across a combination of trait characteristics[22]. Accordingly, non-adaptive and maladaptive trait characteristics can appear contrary to expected selection pressures due to responses driven by selective forces acting upon other trait characteristics[42].

Caution is necessary, however, when interpreting observations regarding the selection pressures maintained by environmental stochasticity. Our exploration into the environmental drivers of demographic resilience focuses only on terrestrial populations. Physiological adaptations, such as thermoregulation, that serve to broaden abiotic tolerance, are more prevalent across terrestrial taxa, whilst the ability to seek out tolerable microclimates further reduces the susceptibility of terrestrial populations to environmental stochasticity[43]. Marine species often inhabit conditions close to their physiological limits, rendering them more sensitive to abiotic shifts than terrestrial species[43,44]. More importantly, though, 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[45]. Whilst environmental stochasticity is known to influence population dynamics[46], its observable effects on population characteristics can remain negligible until compounded by external factors such as changing habitat configurations[47]. Any direct impacts of 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 populations, we illustrate how our observations here persist even when explicitly accounting for lifespan and legacy time. Our findings illustrate that through evolutionary time, adaptation plays an important role in the development of resilience traits. Adaptation is the accumulation of beneficial, heritable characteristics within a population over multiple generations[48]. 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[49–51]. To evaluate the implications of differing 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 = 1,606 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 (Figs. S5, S6 & S7).

Conclusions

Climate shifts and anthropogenic activities are impacting upon the periodicity of phenological drivers[52,53], and reducing the return times between severe disturbance events[54,55]. Natural populations worldwide are thus being exposed to increasingly stochastic environments, with

many facing imminent collapse[56]. Here, we illustrate, however, that the past exposure of natural populations to environmental stochasticity does not limit, nor guarantee, their resilience towards future disturbances. ~~[1,2]~~Resilience is a complex and heavily debated concept[9,24,57]. Yet, the realisation that population resilience is mediated by the adaptation of species over evolutionary timeframes, not the conditions experienced by populations following their dispersal, is not trivial. Rather, this understanding enables attention to be better focused towards identifying populations with high adaptive potential, whilst maintaining the high genetic diversity necessary to enhance the resilience of natural populations.

Sourcing climate records at the necessary temporal and spatial resolution for quantifying deep-time environmental legacies presents a considerable challenge[58,59]. Thus, the susceptibility, and resilience, of species to future global change is more often inferred from their exposure to more contemporary conditions[60–62]. It is necessary, therefore, to highlight the limitations associated with using the recent exposure of populations to environmental stochasticity to predict their continued resilience. Instead, we argue that selective forces acting upon other adaptive population characteristics have indirectly refined the ability for natural populations to resist, compensate, and recover from disturbances. Selection pressures constrain how individuals allocate finite resources across survival, somatic development, and reproduction, thus mediating the capacity for populations to exploit and prevail within their local environments[12,22]. Over time, these selective forces have moulded the resilience attributes of populations, but not necessarily in response to the current disturbance regimes they endure.

Methods

Demographic data extraction & transient indices

To evaluate the selection pressures on the resilience attributes of natural populations, we extracted Matrix Population Models (MPMs) from the open-source COMPADRE Plant Matrix Database[31] (v. 5.0.1) and COMADRE Animal Matrix Database[30] (v. 3.0.1). MPMs are discrete

time, structured population models where the lifecycle is categorised into discrete state classes (*i.e.*, age, size, and/or developmental stages)[34]. Combined, COMPADRE and COMADRE contain over 12,000 MPMs from more than 1,100 animal and plant species. However, here we only retained MPMs satisfying the following six criteria to test our hypotheses: (1) MPMs reflecting the demographic characteristics of individual populations recorded across a single time period (*Individual* MPMs). We did, however, select MPMs consisting of demographic information averaged across multiple populations and/or time periods (*mean* MPMs), for populations for which no individual matrices were available (330 populations after applying the additional criteria below); (2) MPMs based on annual surveys to ensure all subsequent metrics obtained reflected identical units of time, thus allowing for their comparability; (3) MPMs representing wild, un-manipulated populations, to guarantee investigating the selection pressures underpinning the resilience of natural populations and the possibility to link their dynamics to their local environmental regimes; (4) MPMs comprised of three or more life stages, as lower dimension MPMs typically lack the necessary resolution for estimating vital rates[63] and transient dynamics[64]; (5) MPMs from populations with known latitude and longitude information to allow us to link their demographic properties to local environmental regimes; and finally (6) MPMs describing full life cycles (e.g., no missing data on survival, progression, retrogression, and reproduction) to ensure the correct calculation of vital rates and transient metrics. Following these criteria, we retained 3,890 MPMs corresponding with 3,204 populations across 438 plant species, 665 populations across 112 animal species, and 21 populations across six algae species (Supplementary Table S1).

We further refined our 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)[34]. We carried out these tests using the corresponding *isErgodic*, *isIrreducible*, and *isPrimitive*, diagnostic functions from the R package '*popdemo*'[65]. A total of 1,203 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[66]. MPMs with population growth rates $\lambda>2$, indicating that the population is projected to increase two-fold or more every year, were also rejected as they represent unlikely realisations of population performance in our experience. Equally, MPMs from highly migratory (e.g., > 1,000 km) species were discarded, since their vital rate schedules are unlikely to be mostly shaped by the environment in which they were measured. We also note here that, across our initial population sample, the vital rate of clonality (κ) was rare, with only 140 populations across 37 plant species, and two populations from one animal species (*Amphimedon compressa*[67]) explicitly exhibiting this demographic process. Thus, to focus our analyses on common demographic currencies, we excluded all populations exhibiting clonality. Overall, our strict selection criteria resulted in a final sample of 2,242 MPMs, corresponding with 369 species: 402 populations from 61 animal species, 1,830 populations from 305 plant species, and 10 populations from three species of algae (Supplementary Table S1).

For each retained MPM, we calculated six transient metrics quantifying each population's potential for demographic resistance (first-timestep attenuation, $\underline{\rho}$ & and maximal attenuation, $\underline{\rho}_{max}$), compensation (reactivity, $\overline{\rho}$ & maximal amplification, $\overline{\rho}_{max}$), and recovery (damping ratio, ρ & period of oscillation, ψ), following a disturbance[25] (Fig. 1). Firstly, with estimates of transient dynamics known to be contingent on the reproductive strategies of populations, it was necessary to convert all post-reproductive matrices into a pre-reproductive format by adjusting patterns of reproduction to include a measure of adult survival[68]. All MPMs were then standardised to separate their transient and asymptotic properties by dividing each matrix element by the MPM's dominant eigenvalue, λ[26,34]. Following standardisation, from

each MPM we obtained estimates of reactivity and first-timestep attenuation as the upper and lower bounds returned by the function *reac*, and calculated maximal amplification and maximal attenuation indices using their respective functions *maxamp* and *maxatt*, all within the R package '*popdemo*'[65]. Meanwhile, we calculated the damping ratio of each MPM using *eigen.analysis* from the '*popbio*' package[69]. Finally, we calculated the period of oscillation (ψ) for each MPM using its subdominant eigenvalue (λ_2) (equation 1)[34].

$$\psi = \frac{2\pi}{\theta_2} \qquad \text{Where: } \theta_2 = \tan^{-1}\left(\frac{I(\lambda_2)}{R(\lambda_2)}\right) \tag{1}$$

To explore how the fitness components of individuals mediate the selection gradients placed on demographic resilience by environmental variability, we calculated the sensitivity of each transient metric towards the vital rates of survival (σ), progression (γ), retrogression (τ), and fecundity (φ). For each MPM, we first estimated all vital rate sensitivities from their element-level constituents. Individual elements a_{ij} within the MPM $\boldsymbol{A}$ typically describe combinations of multiple vital rates[70]. Subsequently, calculating the sensitivity of each transient metric (s_x) with respect to underlying vital rates requires the decomposition of element-level sensitivities into their vital rate components[70]. Briefly, this decomposition requires the estimation of stage-specific survival probabilities (σ_j) for each MPM. These estimates of σ_j are then used to determine the proportion of each matrix element a_{ij} corresponding with survival (σ), progression (γ), retrogression (τ), and fecundity (φ)[70]. Accordingly, we initially calculated the sensitivity of each transient metric at the matrix element-level (s_{ij}). The sensitivities of the damping ratio (ρ) and period of oscillation (ψ) were determined using equations 2 & 3, with s_{ij}^1 and s_{ij}^2 as the matrix element-level sensitivity matrices of the dominant and subdominant eigenvalues, respectively[34].

$$s_{\rho_{ij}} = \frac{1}{|\lambda_2|}\left(s_{ij}^1 - \frac{\rho}{|\lambda_2|}\left[R\left(s_{ij}^2\right) + I\left(s_{ij}^2\right)\right]\right) \tag{2}$$

$$s_{\psi_{ij}} = \frac{-2\pi}{\theta_2|\lambda_2|^2}\left[I\left(s_{ij}^2\right) - R\left(s_{ij}^2\right)\right] \tag{3}$$

The sensitivities of reactivity, amplification, and attenuation (s_{ij}) with respect to element a_{ij} were then estimated as the magnitude of change (δ) in each transient metric (x) following a small change (here 0.01) in a_{ij} (Equation 4)[71].

$$s_{ij} = \frac{\delta x}{\delta a_{ij}} = \frac{x_{Perturbed} - x_{Original}}{a_{ij}^{Perturbed} - a_{ij}^{Original}} \quad (4)$$

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*'[72] 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[40,73,74]. 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[75]; Supplementary S3). Our approach here also allowed us to accommodate studies that included multiple, separate populations for the same species (*see below*). Firstly, the scientific names of each species associated with our extracted MPMs were checked against current taxonomy records using the R package '*taxize*'[76]. Next, we extracted information regarding the taxonomic classification and phylogeny of each species from the OTL database with the R package '*rotl*'[77]. Subsequently, using the '*ape*'[78] and *'phytools'*

packages[79], 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*[80]), generating a population-level tree comprising our full sample of 2,242 populations (Supplementary S3). Finally, we computed the branch lengths for our phylogenetic tree using the function *compute.brlen* in the R package '*ape*'[78]. These branch lengths were estimated using Grafen's arbitrary branch lengths[81], assuming a Brownian motion model with the variance between species directly proportional to time since divergence[82]. 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 variability

To investigate the role of environmental selection pressures on the resistance, compensation, and recovery components of resilience in natural populations, we used a pPLS regression exploring the association between transient characteristics and metrics of environmental variability. We quantified the magnitude and frequency of environmental variation to which each population was exposed using the GPS location information extracted with each MPM from COMPADRE & COMADRE[30,31] (Supplementary S4). Since temperature and precipitation rates are universal drivers of biological community assembly across terrestrial environments[83], we selected data describing temporal trends in thermal and precipitation regimes as a measure of the environmental variability experienced by each population. Crucially, however, with precipitation not directly influencing marine environments (although

see[84]), we excluded marine populations (29 populations from six animal species, and 10 populations from three algal species) from this portion of our analyses.

We quantified environmental variance through the metrics of autocorrelation, abiotic range, and frequency spectrum using long-term temperature and precipitation records sourced from the CHELSA climate database[85]. For each population, we extracted monthly records of maximum and minimum temperatures (°C) and mean precipitation rates (kg m^{-2}) corresponding with the specific period during which the population was surveyed as detailed in COMPADRE and COMADRE, plus an additional 50-years prior to the onset of censusing to account for environmental legacy effects[86]. We condensed maximum and minimum temperature readings into monthly estimates of mean temperatures and thermal range. Next, as a gauge of disturbance magnitude (m), we estimated the mean thermal range experienced by each population across their associated temporal records. We then arranged our monthly mean temperature and precipitation estimates into time series depicting the temporal environmental regimes to which each population was exposed. Using the '*colorednoise*' package[87], we calculated the autocorrelation of each temperature (a_T) and precipitation (a_P) time series as a measure of environmental predictability[88].

The colour of environmental variation is depicted on a red to blue colour scale, from lower to higher frequencies, respectively[88]. The frequency spectrum of a time series is expressed by its spectral exponent (β), which is calculated as the negative slope of the linear regression between the log spectral density and log frequency of the time series[89]. We calculated the frequency spectrum of each precipitation (β_P) and temperature (β_T) time series as an indicator of the colour of environmental variation experience by each population[89]. The spectral exponent for each time series was estimated using the spectrum function from the R package '*stats*'[90].

Partial Least Squares Regression

We utilised a phylogenetically corrected Partial Least Squares regression (pPLS) framework to test our hypothesis that the resistance, compensatory, and recovery of natural populations correspond with gradients in environmental variability and evaluate how this is mediated by fitness investments. Using a pPLS, we evaluated the relationship between our estimates of population resilience, and both associated environmental variability regimes and their vital rate sensitivities. The pPLS technique is considered a more powerful comparative tool than other available multivariate regression methods[91], as it simultaneously condenses the variation among numerous predictors whilst maximising 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 variability and transient demographic characteristics. This approach enabled us to test for covariation between the transient characteristics of populations and gradients in their exposure to environmental variability. pPLS tests were carried out for each transient measure with the predictor variable set comprised of our five metrics of environmental variability. From each test, we then extracted component scores and loadings, which describe the arrangement of the environmental predictor variables within a multivariate space. We also obtained the percentage variance (*%var*) among the predictors explained by each regression component and the proportion of variance in the transient response variable explained by each component (r^2) to estimate the strength of any association between environmental variability and the transient dynamics of our population sample.

Phylogenetically corrected correlation tests and pPLS analyses were used to examine for patterns between each transient characteristics and its associated vital rate sensitivities. Again, test coefficients (*r*), component scores, loadings, *%var*, and r^2 values were calculated to quantify the influence of the fitness components of survival, progression, retrogression, and reproduction towards the transient characteristics of natural populations. All pPLS analyses were conducted using the *'pls'* R package[92], with modifications included to ensure our analyses accounted for any evolutionary covariance between the sensitivity patterns and transient characteristics of different populations[79,93,94].

We carried out all pPLS analyses using only complete entries, omitting populations missing estimates for any one variable. To provide further clarity regarding any patterns we observed between our measures of population resilience, their environmental legacies, and their vital-rate sensitivities, we repeated each analysis twice. During these repeated tests, we first evaluated whether considering the life expectancies of populations influenced any observed patterns (Supplementary S6). Within a given time period, long-lived species will likely experience fewer generations than shorter-lived species diminishing the relative impact of existing selection pressures on their trait characteristics[95]. Thus, it was necessary to ensure that the inclusion of long-lived species within our population sample did not limit our capacity for exploring environmental selection pressures. We categorised each population within our sample as either long- or short-lived according to their associated mean life expectancy (η_e), calculated from each extracted MPM using the R package '*IPMpack*'[96]. Next, we repeated our pPLS analyses using only 'short-lived' populations for which $\eta_e \leq 10$ years (n = 1606 populations). This threshold was selected as a balance between maximising the number of generations experienced by populations during the multi-year time series used in calculating environmental legacies and maximising our sample size.

Understanding patterns in the responses of natural populations to environmental change is often impeded by gaps in available data linking population characteristics to abiotic regimes[97]. To ensure that missing data was not obscuring any correlation between our measures of population resilience and environmental stochasticity we repeated our analyses using phylogenetic imputation to estimate any demographic measures of resilience missing across our population sample[35] (Supplementary S5). We calculated the phylogenetic signal (Pagel's λ[39]) of each transient and sensitivity variable using the *phylosig* function from the '*phytools*' package[79]. Pagel's λ exists on the scale $0 < \lambda > 1$, with 0 indicating traits have evolved independently of phylogeny, and 1 representing a high phylogenetic signal[39]. For any variable exhibiting a strong phylogenetic signal (*i.e.*, Pagel's $\lambda \geq 0.65$) that differs significantly from zero ($p < 0.05$), we imputed all missing values assuming a Brownian motion evolutionary model, before repeating our pPLS analyses.

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Author Contributions

JC, RS-G, MB, and PC conceived the ideas and methodology for the project. JC, PC, and RS-G carried out data extraction and analysis. JC led the writing of the manuscript, with all authors contributing critically to the writing and giving final approval for publication.

Data Accessibility

All Matrix Projection Models used within this study are available from the COMADRE and COMPADRE demographic databases (https://compadre-db.com/). Equally, all taxonomic information used in the construction of our phylogenetic trees can be sourced from the Open Tree of Life (https://tree.opentreeoflife.org/), and 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 the data extraction and analyses presented throughout this manuscript have been uploaded to GitHub and will be made publicly available following publication.

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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, $\overline{\rho}$ & maximal amplification, $\overline{\rho}_{max}$), and recovery (damping ratio, ρ & period of oscillation, ψ; Fig. 1A) 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
$\overline{\rho}$	Compensation	-0.0026	0.0007	0.0070	-0.0080	0.0041
$\overline{\rho}_{max}$		-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

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, $\overline{\rho}$ & maximal amplification, $\overline{\rho}_{max}$), and recovery (damping ratio, ρ & period of oscillation, ψ; Fig. 1A) 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 the colour gradation highlighting the strength of the absolute correlation between each transient metric and its vital rate sensitivities, with darker shades representing stronger associations.

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
$\overline{\rho}$	Compensation	-0.11	-0.49	0.39	-0.04
$\overline{\rho}_{max}$		-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, whilst 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[39]) across our transient metrics of demographic resistance (first-timestep attenuation, $\underline{\rho}$ & and maximal attenuation, $\underline{\rho}_{max}$), compensation (reactivity, $\overline{\rho}$ & maximal amplification, $\overline{\rho}_{max}$), and recovery (damping ratio, ρ & period of oscillation, ψ; Fig. 1A), as well as their sensitivities to the vital rates of survival (σ), progression (γ), retrogression (τ), and reproduction (ϕ). Pagel's λ[39] 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 p <0.001	0.997 p <0.001	0.989 p <0.001	0.967 p <0.001	0.985 p <0.001
$\underline{\rho}_{max}$		0.997 p <0.001	0.993 p <0.001	0.985 p <0.001	0.952 p <0.001	0.989 p <0.001
$\overline{\rho}$	Compensation	0.998 p <0.001	0.990 p <0.001	0.999 p <0.001	0.995 p <0.001	0.996 p <0.001
$\overline{\rho}_{max}$		0.998 p <0.001	0.988 p <0.001	0.998 p <0.001	0.946 p <0.001	0.996 p <0.001
ρ	Recovery	0.996 p <0.001	0.003 p = 0.344	<0.001 p = 0.686	0.005 p = 0.094	<0.001 p >0.999
ψ		0.992 p <0.001	<0.001 p >0.999	0.179 p <0.001	<0.001 p >0.999	<0.001 p >0.999

Figure captions

Figure 1. Demographic resistance, compensation, and time of recovery across 2,242 natural populations show how population resilience corresponds with exposure to environmental stochasticity. (A) Within stochastic environments, the dynamics of populations can vary considerably from long-term (*i.e.*, asymptotic) expectations. Under stable stationary conditions, populations display asymptotic 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 depends, 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 for 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. Meanwhile, time of recovery (henceforth *recovery*) is the duration needed for a population to converge back to its stationary equilibrium following a disturbance. Transient demographic theory offers the opportunity to quantify the short-term dynamics of natural populations, thus unlocking the potential for macroecological studies exploring patterns and plausible mechanism of demographic resilience worldwide. Transient increases in population size (N) can be evaluated using metrics of population reactivity ($\overline{\rho}$; increase in N within a one-time step following a disturbance) and maximal amplification ($\overline{\rho}_{max}$; 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 ($\underline{\rho}$; decrease in N within a one-time step following a disturbance) and maximal attenuation ($\underline{\rho}_{max}$; maximum decrease in N during 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 go back to a stationary stable equilibrium. **(B)** We quantified the aforementioned transient metrics of demographic resilience for 2,242 populations from 369 species for whom Matrix Population Models (MPMs) are available from the global COMPADRE[25] (Blue; plants & algae) and COMADRE[24] databases (Orange; animals). Point size illustrates the relative length of time over which each population was surveyed to parameterise the MPMs deposited within COMPADRE and COMADRE.

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 ($\overline{\rho}$), **(D)** maximal amplification ($\overline{\rho}_{max}$), **(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. A gradation in point colour is then used to reflect patterns in the relative magnitude of each transient metric recorded from each population, with darker shades indicating higher estimates. Insert barplots are the standardised 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).

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 ($\underline{\rho}$), **(B)** maximal attenuation ($\underline{\rho}_{max}$), (**C**) reactivity ($\overline{\rho}$), **(D)** maximal amplification ($\overline{\rho}_{max}$), **(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. A gradation in point colour is then used to reflect patterns in the relative magnitude of each transient metric recorded from each population, with darker shades indicating higher estimates. Insert barplots are the standardised regression coefficients (*b*) highlighting the relative weighting of each vital rate in the overall capacity of each pPLS model to explain variation in a given transient metric (r^2).

Figure 1

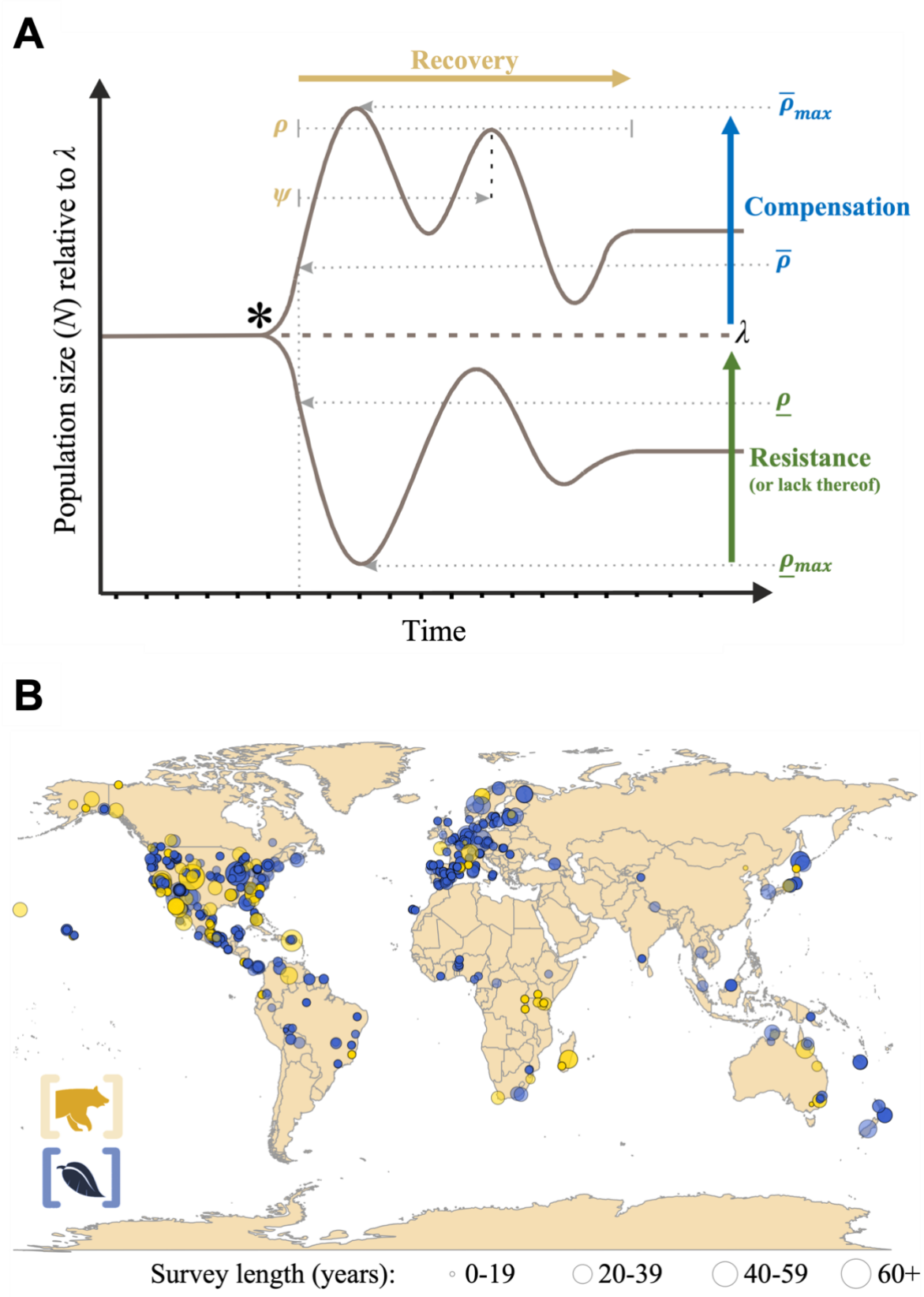

A
Recovery
ρ
ψ
$\bar{\rho}_{max}$
Compensation
$\bar{\rho}$
*
λ
$\underline{\rho}$
Resistance
(or lack thereof)
$\underline{\rho}_{max}$
Population size (N) relative to λ
Time
B
Survey length (years):
0-19
20-39
40-59
60+

Figure 2.

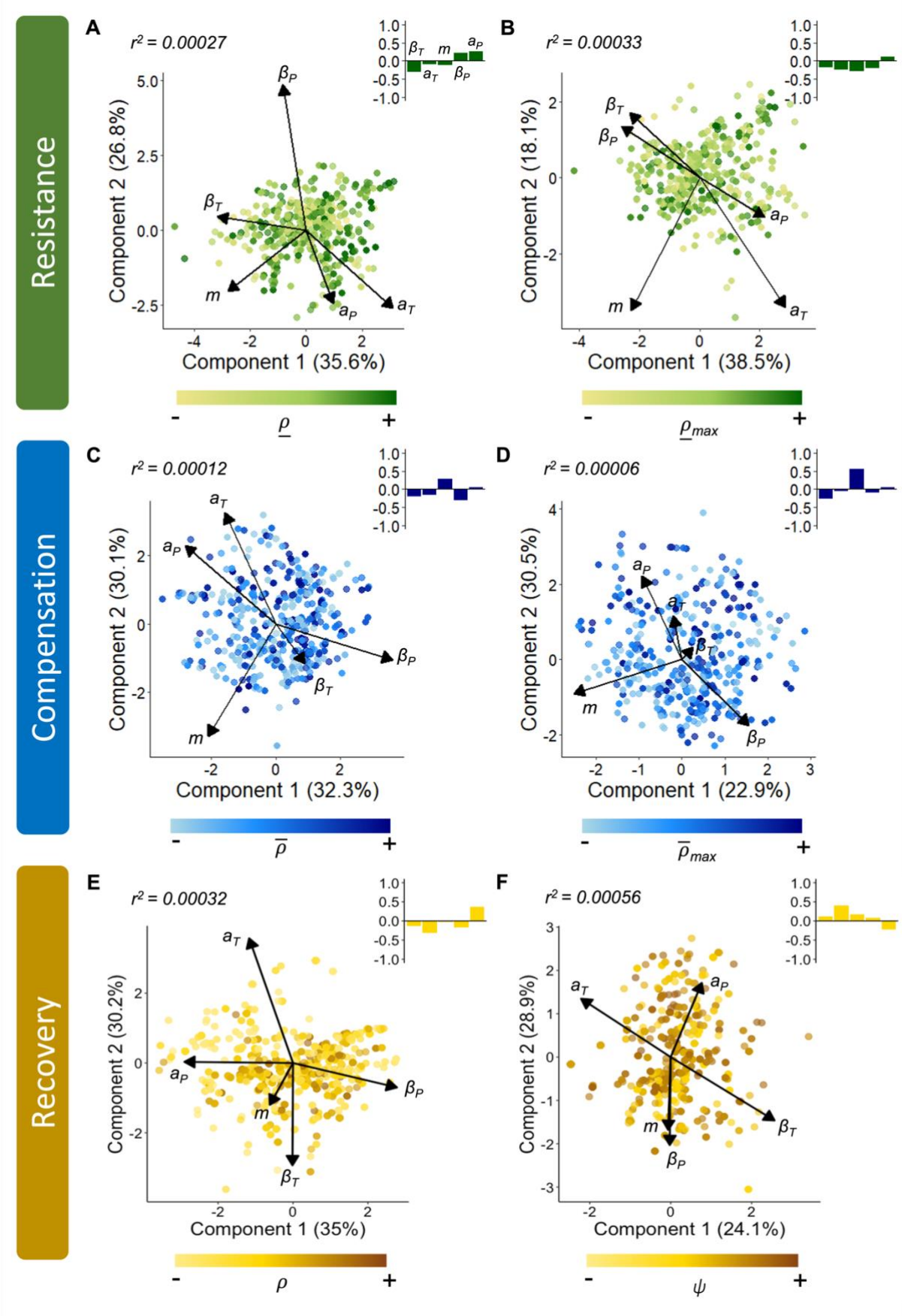
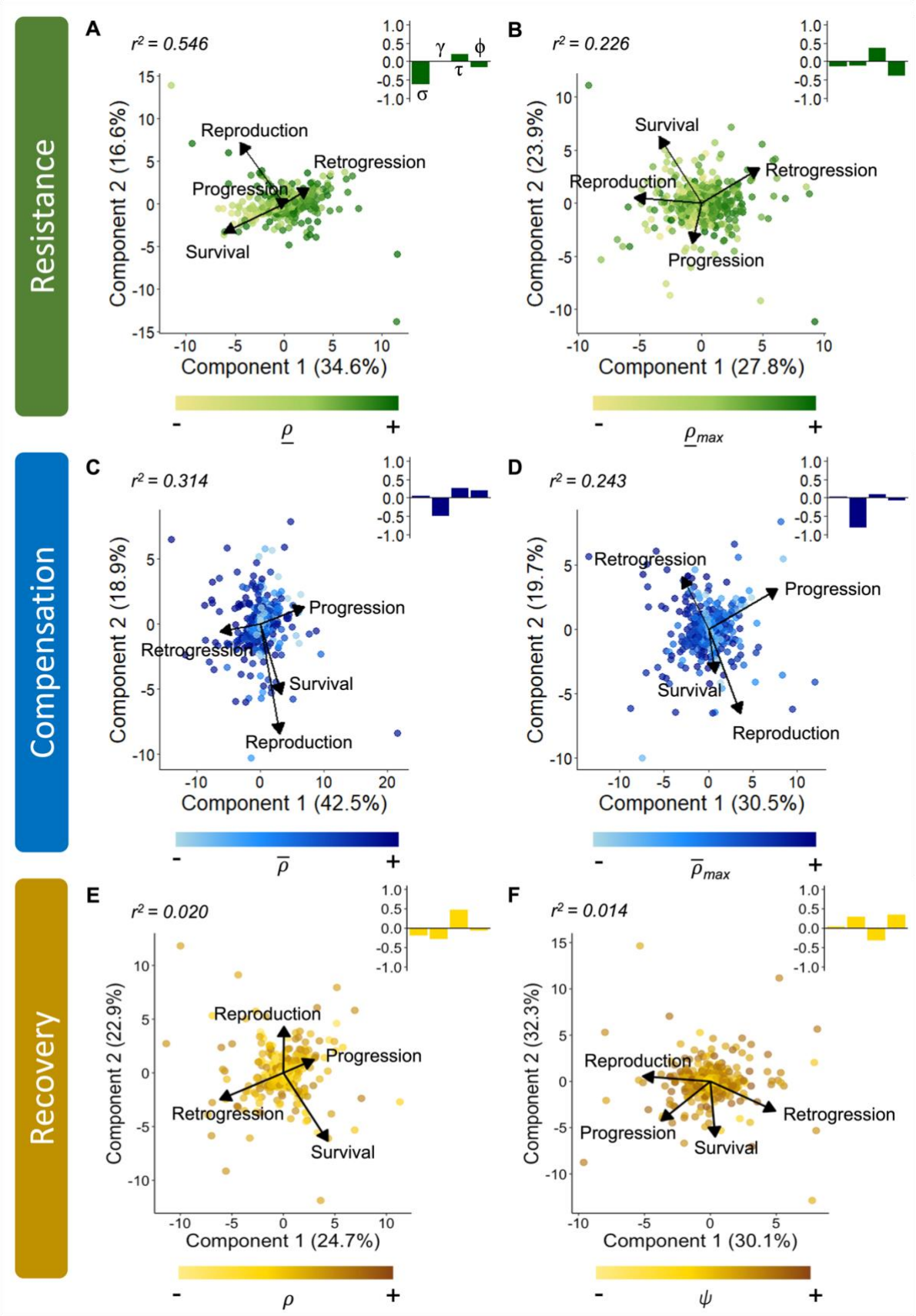

Resistance
Compensation
Recovery
A
r^2 = 0.00027
Component 1 (35.6%)
Component 2 (26.8%)
$\underline{\rho}$
B
r^2 = 0.00033
Component 1 (38.5%)
Component 2 (18.1%)
$\underline{\rho}_{max}$
C
r^2 = 0.00012
Component 1 (32.3%)
Component 2 (30.1%)
$\overline{\rho}$
D
r^2 = 0.00006
Component 1 (22.9%)
Component 2 (30.5%)
$\overline{\rho}_{max}$
E
r^2 = 0.00032
Component 1 (35%)
Component 2 (30.2%)
ρ
F
r^2 = 0.00056
Component 1 (24.1%)
Component 2 (28.9%)
ψ

Figure 3.


Resistance
Compensation
Recovery
A
r² = 0.546
Component 2 (16.6%)
Component 1 (34.6%)
Reproduction
Retrogression
Progression
Survival
σ
γ
τ
ϕ
B
r² = 0.226
Component 2 (23.9%)
Component 1 (27.8%)
Survival
Reproduction
Retrogression
Progression
C
r² = 0.314
Component 2 (18.9%)
Component 1 (42.5%)
Progression
Retrogression
Survival
Reproduction
D
r² = 0.243
Component 2 (19.7%)
Component 1 (30.5%)
Retrogression
Progression
Survival
Reproduction
E
r² = 0.020
Component 2 (22.9%)
Component 1 (24.7%)
Reproduction
Progression
Retrogression
Survival
F
r² = 0.014
Component 2 (32.3%)
Component 1 (30.1%)
Reproduction
Retrogression
Progression
Survival
ρ
ρmax
ψ