SEVERE FIRE REGIMES DECREASE ECTOTHERMIC POPULATIONS' RESILIENCE

A manuscript in preparation as a *Research Letter* for submission to *Journal of Animal Ecology*

Heitor Campos de Sousa[1,*], Adriana Malvasio[1], Guarino Rinaldi Colli[4,**] & Roberto Salguero-Gómez[2,3,**]

[1] Universidade Federal do Tocantins – UFT, Quadra 109 Norte Av. NS-15, ALCNO-14, Plano Diretor Norte, CEP: 77001-090, Palmas, Tocantins, Brasil.

[2] Department of Zoology, University of Oxford, 11a Mansfield Rd, OX1 3SZ, UK.

[3] Evolutionary Demography Laboratory, Max Planck Institute for Demographic Research, Konrad Zuße straße 1, DE 18057, Germany.

[4] Universidade de Brasília – UnB, Departamento de Zoologia, Instituto de Ciências Biológicas, Avenida L4 Norte, Asa Norte, CEP: 70910-900, Brasília, Distrito Federal, Brasil.

* Contact author: heitor.sousa@uft.edu.br

** Shared senior authors

Type of article: Research article

Short running title: Demographic resilience of Cerrado lizards

Word count in abstract: 165; Word count in main text: 8,458; Number of figures: 5; Number of tables: 1; Number of references: 74.

Acknowledgments: This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and by a NERC Independent Research Fellowship to RSG (NE/M018458/1). HCS was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) [grant numbers 88887.484511/2020-00 and 88881.623332/2021-01]. GRC thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Apoio à Pesquisa do Distrito Federal (FAPDF) and the USAID's PEER program under cooperative agreement AID-OAA-A-11-00012 for financial support.

Conflict of interest: Authors declare no conflict of interest.

Statement of authorship:

Conceptualization: HCS, AM, GRC, and RSG; Data curation: HCS and GRC; Formal analysis: HCS with assistance by RSG; Funding acquisition: GRC and RSG; Investigation: HCS and GRC; Methodology: HCS,

GRC, and RSG; Project administration: GRC; Resources: GRC and RSG; Software: HCS and GRC; Supervision: AM, GRC, and RSG; Validation: AM, GRC, and RSG; Visualization: HCS with assistance by RSG; Writing - original draft: HCS; Writing - reviewing and editing: AM, GRC, and RSG.

Data availability statement: We confirm that the data and code supporting the results will be archived in an appropriate public repository such as Dryad or Figshare, and the data DOI will be included at the end of the article.

Abstract (165 words)

1. Understanding species' responses to environmental change is crucial for mitigating human-induced disturbances.
2. Here, we test hypotheses regarding how three essential components of demographic resilience (compensation, resistance, and recovery) co-vary along the distinct life histories of three lizard species exposed to variable, prescribed fire regimes.
3. Using a Bayesian hierarchical framework, we parameterize stochastic Integral Projection Models with 14 years of individual-level data from five sites in Brazilian savannas, each historically subjected to different fire regimes.
4. Our findings reveal that severe fire regimes reduce populations' resistance, compensation, or recovery abilities. Additionally, we identify generation time and reproductive output as predictors of resilience trends across fire regimes and climate. Our analyses demonstrate that the probability and quantity of monthly reproduction are the proximal drivers of demographic resilience across the three species.
5. We emphasize how reproductive constraints, such as viviparity and fixed clutch sizes, significantly impact the ability of ectothermic populations to resist to and benefit from disturbances, underscoring their relevance in conservation assessments.

Keywords: Demography, Disturbance, Ecophysiology, Environmental stochasticity, Environmental change, Integral Projection Model, Life history, Reptile, Transient dynamics.

1 | INTRODUCTION

Environmental change is causing a fast decline in biodiversity worldwide (Newbold *et al.* 2020). The most impactful drivers of this loss include habitat degradation (Gonçalves-Souza, Verburg & Dobrovolski 2020) and the drastic modification of disturbance regimes (Hale *et al.* 2016), such as fires (Bowman *et al.* 2020). Understanding how species may respond to these impacts is at the core of ecology (Sutherland *et al.* 2013) and conservation biology (Sutherland *et al.* 2009). Ecological resilience research in the last decades has obtained variable success regarding how species traits can predict their responses to disturbances (Halpern 1989; Hu, Doherty & Jessop 2020). Indeed, some organismal traits confer species with higher tolerance or susceptibility to perturbations. Examples include mobility (Merrien *et al.* 2022), robustness (Dantas *et al.* 2013), rapid growth (Hoffmann *et al.* 2012), thermal performance (Hu, Doherty & Jessop 2020), and reproductive output (Capdevila *et al.* 2022). Therefore, deciphering which traits confer species the ability to resist and recover is critical to understanding and predicting how populations will respond to disturbances in the Anthropocene (Carmona *et al.* 2021).

Ecological resilience, the ability of an ecological system to resist and recover, or move to a new stable equilibrium from disturbances (Hodgson, McDonald & Hosken 2015), has been historically explored at the community and ecosystem levels (Kefi *et al.* 2019). Recently, though, key breakthroughs have been made in unraveling the mechanisms behind population responses to disturbances (Capdevila *et al.* 2020). Natural populations may respond to disturbances by avoiding decreases in size (resistance) or even by increasing in size (compensation) (Capdevila *et al.* 2020). Following a transient period caused by the disturbance, populations may recover from said disturbance by transitioning back to the previous or a new stable stationary structure, at which point the composition of stages (*e.g.*, age, size classes) in the population remains relatively constant over time (Capdevila *et al.*

2020). Thus, we can quantify the full repertoire of resilience responses to a disturbance by a natural population with three essential components: (1) resistance, (2) compensation, and (3) recovery time. This novel demographic resilience framework has the advantage of quantifying resilience based on the species' vital rates (*i.e.*, survival, growth, and reproduction), allowing for inter- and intra-specific comparisons, and providing a mechanistic understanding of the processes and trade-offs involved in species' responses to disturbances (Capdevila *et al.* 2020).

Life history traits, key moments in an organism's life cycle (Stearns 1976), have gained attention for their predictive potential in organismal responses (Allen, Street & Capellini 2017). These traits, including generation time and net reproductive output, are governed by survival, growth, and reproduction schedules, and are subject to strong selection for optimization (Stearns 2000). As these vital rates involve trade-offs, so do the emerging life history traits (Stearns 1976). Understanding the combination of these traits, known as life history strategies, is valuable in predicting population responses to environmental changes and disturbances (Capdevila *et al.* 2021a). For instance, recent research has shown that plant species with high reproductive output exhibit greater resistance and compensation to disturbances (Iles *et al.* 2015), while longer-lived animals have lower resistance and longer recovery times compared to fast-living species (Capdevila *et al.* 2022). Despite these key findings, their generalization across the Tree of Life is challenging because organisms present diverse life history traits (Salguero-Gómez *et al.* 2016a; Healy *et al.* 2019) and because quantifying trade-offs in natural populations under control conditions is difficult (Metcalf 2016), let alone in a context of disturbance regimes (Lytle 2001). Still, linking mechanisms regulating vital rates to population-level responses to disturbances is crucial for understanding how these trade-offs shape evolutionary processes.

Fire is a major disturbance that shapes ecosystems worldwide (Pausas & Parr 2018). Fire consumes biomass, recycles nutrients, and triggers the renewal of vegetation, leading to a burst of productivity and providing establishment opportunities for new individuals and species (Pausas & Bond 2020). Despite regional heterogeneity in fire activity, the average fire season had globally increased by 18.7% in the last three decades, and in many regions, fire frequency, intensity, and spatial extent have also increased, presumably because of climate change and human management (Bowman *et al.* 2020). In fire-prone ecosystems, species typically develop adaptations to resist and recover from frequent fires (Keeley *et al.* 2011). Conversely, other species have evolved to take advantage of these disturbances. Examples include fire-adapted plants that only resprout (Pausas, Keeley & Schwilk 2017) or whose seed dormancy only breaks (Paniw *et al.* 2016) after a fire, thus benefiting from the open space in temporarily less competitive environments. Historically, though, fire ecology research has primaly focused on plant responses, leaving the mechanisms that confer animals with resilience to fire poorly understood (but see Pausas, Keeley & Schwilk 2017).

To fill this knowledge gap, we investigate how the demographic resilience components (resistance, compensation, and recovery time) co-vary with generation time, reproductive output, and their underlying vital rates. To do so, we parameterize hierarchical Bayesian Integral Projection Models (IPMs) with a 14-years of monthly mark-recapture data from 3,538 individuals of three lizard species (*Copeoglossum nigropunctatum, Micrablepharus atticolus*, and *Tropidurus itambere*) from the Brazilian Cerrado savannas (Oliveira & Marquis 2002), with multiple populations exposed to prescribed fires with varying frequencies and timings. Our three species have rather distinct life-history strategies, but co-exist in all of the study sites, thus creating a perfect *in situ* experimental laboratory to explore how their life history traits and resilience components change in response to fire regimes. We test (H1) whether ecophysiological traits, such as thermal locomotor

performance and daily activity, and weather/microclimatic data shape how underlying vital rates and emergent life history traits respond to fire regimes. We then quantify the extent to which vital rates and life history traits drive demographic resilience. We hypothesize that: (H2) more severe fire regimes increase populations' resilience (*i.e.,* higher resistance, higher compensation, and faster recovery); (H3) species' populations with greater generation time will have higher resistance but slower recovery time; and (H4) populations with greater reproductive output, higher body growth rate, and higher thermal performance will have higher compensation and faster recovery time.

2 | MATERIALS AND METHODS

2.1 | Study species

Here we focus on the three most abundant lizard species from the assemblage to examine the traits that confer higher resilience to climate, microclimate, and fire regimes. Of critical importance to test our hypotheses, each species presents different life history strategies. *Copeoglossum nigropunctatum* (Scincidae) is a medium-sized (up to 150 mm snout-vent length; SVL) viviparous skink found in Amazonia and Cerrado (Vitt & Blackburn 1991; Vitt, Zani & Lima 1997); its females can carry up to nine embryos for 10-12 months (Vitt & Blackburn 1991). *Micrablepharus atticolus* (Gymnophthalmidae) is a small-sized (up to 50 mm SVL) Cerrado endemic with a fixed clutch of 1-2 eggs (Vitt & Caldwell 1993; Rodrigues 1996), but capable of producing multiple clutches (Vieira *et al.* 2000). *Tropidurus itambere* (Tropiduridae) is a medium-sized (up to 100 mm SVL) species from central Cerrado that lays multiple clutches of 5-8 eggs per season (Van Sluys & Henderson 1993). All three species have generalist diets, primarily feeding on small invertebrates, with ants being the main prey for *T. itambere* (Vitt & Blackburn 1991; Van Sluys 1993; Vieira *et al.* 2000). While most lizard species can withstand intense fires (Costa *et al.* 2013), our species respond

differently to fire-induced vegetation changes, influenced by microclimate and microhabitat preferences (Costa *et al.* 2021). *C. nigropunctatum* showed fewer captures in intermediate fire severity levels but increased abundance after prescribed fires ended in 2009, while *M. atticolus* and *T. itambere* displayed the opposite pattern (Supporting Information-SI; Fig. S2).

2.2 | Population monitoring

Our study site (*Reserva Ecológica do IBGE*, RECOR; see more details in the SI) is an ideal natural experiment to test our hypotheses regarding the drivers of demographic resilience. From 1972 to 1990, RECOR was protected from fires. In 1989, a long-term experiment was initiated to evaluate the responses of animals and plants in 10 ha plots, each submitted to unique fire regimes characterized by a combination of timing (early dry season, in late June; mid dry season, in early August; and late dry season, in late September) and frequency (biennial and quadrennial) (Miranda 2010). Plots were placed in the cerrado *sensu stricto* physiognomy and shared a common recent fire history before the experiment's onset. Thus, differences between plots over time are likely to have arisen due to the prescribed fire regimes (Costa *et al.* 2021).

To acquire the individual-level data used in our analyses, from November 2005 to December 2019, we captured individual lizards in study plots using pitfall traps with drift fences in five plots (Fig. S1): three under prescribed biennial fires (early biennial – EB, middle biennial – MB, and late biennial – LB), one under prescribed quadrennial fires (middle quadrennial – Q), and one control plot (C) (Fig. S1). Considering the number of fires each plot was submitted and their canopy cover (Fig. S6), fire severity increased in the following order C < Q < EB < MB < LB. We opened traps for six consecutive days every month and checked them daily during this period. We recorded snout-vent length (SVL) with

183 a ruler (1 mm precision) from each captured individual, followed by marking by toe-clipping
184 (after the appropriate bioethics approval 33786/2016) and release at the capture site. Toe-
185 clipping is a widely used system to mark individuals in amphibians and reptiles, where each
186 toe has a unique code to set the identity for each individual (Hero 1989). We also assessed
187 the reproductive state by palpation in females. This assessment is possible because, when
188 female lizards bear eggs, embryos, or enlarged follicles, they display a significant
189 enlargement in their abdomens (Meiri, Brown & Sibly 2012).

190 Migration may bias the vital rates estimates and the underlying effects of the
191 experimental plots (Paquet *et al.* 2020), here fire regimes. However, considering the distance
192 between transects in adjacent plots (*ca.* 200 m; Fig. S1A), the small size, and the territorial
193 behavior of some species (Van Sluys 1997), we assumed no significant lizard movements
194 among plots that could affect our results. Indeed, there were no inter-site recaptures,
195 supporting our assumption. In addition to the costs and difficulties of replication typical of
196 large-scale ecological studies, our experiment could not be replicated because of legal issues
197 associated with burning the vegetation inside protected areas. While this approach may
198 reduce the statistical power in our study, doing so is the only way to ensure the availability
199 of adequate treatment levels in such a large design (Driscoll *et al.* 2010).

200

201 **2.3 | Ecophysiological traits, weather, and microclimate**

202 To test (H1) whether ecophysiological traits and weather/microclimate shape how
203 underlying vital rates and emergent life history traits respond to fire regimes, we estimated
204 locomotor thermal performance curves (TPC) (Huey & Stevenson 1979) and hours of
205 activity (*ha*) (Sinervo *et al.* 2010) based on laboratory experiments from at least 10
206 individuals by each species (see SI for more details). We initially had 14 microclimatic and
207 weather variables. However, after excluding highly correlated variables (using the stepwise

procedure *vifcor* from package USDM with cor > 0.8), we retained: mean air temperature at 200 cm height (*tmed2m*), minimum air temperature at 0 cm height (*tmin0cm*), mean air temperature at 0 cm height (*tmed0cm*), maximum relative air humidity (*RHmax*), solar radiation (*sol*), and accumulated precipitation (*precip*). With the hourly microclimate temperature estimates at 10 cm height, we predicted monthly mean locomotor performance (*perf*) and the hours of activity (*ha*). SI presents the correlations and relationships among the variables (Fig. S7) and the details of the microclimatic and thermal physiological estimates.

2.4 | Data analyses

We estimated each species' monthly vital rates (survival, growth, and reproduction) using different datasets integrated into Bayesian hierarchical models and a combination of Cormack-Jolly-Seber (CJS) and Pradel Jolly-Seber (PJS) mark-recapture models (Pradel 1996; Tenan *et al.* 2014). The CJS model related the survival (σ) to the individuals' SVL, while the PJS incorporated the monthly environmental variation (weather, ecophysiological, microclimate, months with fire, and time since last fire – *TSLF*) into survival (σ) and reproduction (probability of recruitment, p_{rec}). For the changes in the body size through time (growth, γ), we combined a Von Bertalanffy body growth function with the individuals' records of SVL and capture history. For reproduction, we considered three different processes: the probability of reproduction (p_{rep}), the production of newborns (clutch size; n_b), and the probability of recruitment (p_{rec}). We used Bayesian generalized linear models to relate p_{rep} and n_b to the individuals' SVL. We implemented the models for each species with JAGS in R, using the packages JAGSUI, RUNJAGS, and RJAGS (Kellner 2019; Plummer 2019). SI presents the details of the parameterizations estimated in each model, including their formulas.

To test H2, H3, and H4 (see Introduction), we used the vital rates (σ, γ, p_{rep}, n_b, and p_{rec}) parameters estimates to build stochastic Integral Projection Models (IPMs) using the IPMR package (Levin *et al.* 2021). Although we have not parameterized the IPMs with explicit density-dependent parameters constraining their vital rates, we assumed that the environmental covariates and plots represented the primary resources the lizards use (habitat, thermal niche, and food), thus indirectly modeling density dependence; this is a common approach when analyzing long-term demographic data (Salguero-Gómez *et al.* 2016a), as it is our case. IPMs are structured population models where the vital rates are influenced by a continuously varying phenotypic trait (Easterling, Ellner & Dixon 2000) (*e.g.*, body size), instead of discrete stages or ages. In a population structured by a continuous variable body size (SVL), as in our three study species, the IPM describing the number of individuals of size y at time $t + 1$ is:

$$n(y, t+1) = \int_{\mathrm{L}}^{U} [P(x,y) + F(x,y)]n(x,t)dx$$

$$= \int_{\mathrm{L}}^{U} K(x,y)n(x,t)dx \qquad \text{(Eq. 1)}$$

In equation 1, L and U specify the lower and upper body size limits in the model, respectively; $P(x,y)$ describes the changes in size conditional on survival; $F(x,y)$ quantifies fecundity; and $K(x,y) = P(x,y) + F(x,y)$ is the *kernel* surface, representing all possible transitions and per-capita sexual contributions from size x to size y between t and t+1. The P sub-kernel incorporates both survival and growth components, such that $P(x,y) = s(x) \cdot g(x,y)$, where $s(x)$ is the survival probability of a size-x individual and $g(x, y)$ is the probability of a size-x individual growing to size y (see SI for the IPMs' implementation).

To test whether populations with greater (H3) generation time and (H4) reproductive output attain higher demographic resilience, we estimated those two life history traits with the monthly IPM kernels of each plot and species using the package RAGE (Jones *et al.* 2022). We also estimated other life history traits from these IPMs, but we decided to focus our analyses on generation time and net reproductive output only, as they describe the principal axes of the life history variation in our species (Figs. S8-S9), as well as in other reptiles (Rodriguez-Caro *et al.* 2023).

To test our hypotheses regarding the demographic resilience components (H2-H4), we estimated the resistance, compensation, and recovery time from our IPMs. To do so, we used the package POPDEMO (Stott, Hodgson & Townley 2012) on our monthly, species- and site-specific IPMs. We used the first time-step amplification (reactivity) and attenuation as the measures for compensation and resistance, respectively, following Capdevila *et al.* (2020). First time-step amplification and attenuation are the highest population increase, and the lowest population decrease possible in the next month, respectively. Attenuation values vary from 0 to 1, where 0 means high resistance and 1 means low resistance. To facilitate interpretation, we considered resistance as 1 - first time-step attenuation. Thus, given the species, sites, and monthly environmental covariates (weather, microclimate, ecophysiological, fire-related, and randomness), resistance and compensation estimates represent the monthly potential of each population to maintain and increase its size in the next month, respectively. Recovery time was estimated as follows:

$$t_K = \frac{\log\left(\frac{\lambda_1}{\|\lambda_2\|}\right)}{\log(10)} \qquad \text{(Eq. 2)}$$

In equation 3, λ_1 and λ_2 correspond to the dominant and subdominant eigenvalues of the K kernel, respectively. This measure estimates the time (months) required to reach stable stationary structure every month.

Next, to test (H2) whether more severe fire regimes increase populations' resilience populations, and populations with (H3) greater generation time and (H4) reproductive output have higher demographic resilience, we built Bayesian linear mixed-effects models using BRMS (BÜRKNER 2017). We related the demographic resilience components with the two life history traits and among plots. We used exponential error distributions for compensation and recovery time, and for resistance, we used a beta distribution. For each species, we included species, plot, year, and month as nested random variables to control for pseudoreplication. We $\log_{10}$-transformed the compensation values prior to analyses. In addition to the $\log_{10}$ transformation, we z-scaled the life history traits values before performing the analyses.

To test specific aspects of H4, that populations with higher body growth rate and higher thermal performance will have higher compensation and faster recovery time and, at the same time, inspect which IPM vital rate parameters affected the different demographic resilience components, we conducted a brute-force sensitivity analysis (Morris & Doak 2002). To implement the brute force sensitivity analysis, we added values from 0.01 to 0.1 to each of the parameters specifying our vital rates, and recalculated the differences in the demographic resilience components. Our parameter sensitivities (S_p) were estimated as in equation 3, where the numerator describes the difference in the transient metric of choice (*e.g.*, reactivity for amplification) resulting from perturbing a vital rate parameter p at a time, in the denominator, following Cant *et al.* (2023).

$$S_p = \frac{Transient\ metric_{\ original} - Transient\ metric_{perturbed}}{p_{original} - p_{perturbed}} \qquad \text{(Eq. 3)}$$

3 | RESULTS

3.1 | Vital rates

Overall, we found that weather and microclimate shape the survival and recruitment of *Micrablepharus atticolus* and *Tropidurus itambere*, but not of *Copeoglossum nigropunctatum* (Fig. 1), partially supporting our hypothesis (H1). As opposed to H1, ecophysiological traits were poor predictors of the vital rates, except for the recruitment of *M. atticolus*. For instance, the vital rates of survival and recruitment of *C. nigropunctatum* were better explained by random monthly variation than environmental covariates (Fig. 1; Table S4). In contrast, survival of *M. atticolus* and *T. itambere* was only affected by weather (*precip*, *tmed2m*, and *sol*; Fig. 1; Table S4). Partially supporting our predictions (H1), weather (*tmed2m*), microclimatic (*tmin0cm*), and ecophysiological (*perf* and *ha*) conditions affected the recruitment of *M. atticolus* (Fig. 1; Table S4); Recruitment of *T. itambere* only varied with weather conditions (*tmed2m* and *sol*; Fig. 1; Table S4). These patterns resulted in higher variation in the life-history space in these two species—*M. atticolus* and *T. itambere* (Fig. S8). We found significant differences in these vital rates among plots, which had been exposed to prescribed fire regimes for 18 years (Table S4). The differences in vital rates were most apparent under both extremes of fire severity (absence of fire and frequent late-dry season fires), suggestive of the long-term effects of the fire regimes (Table S4), in addition to differences in microclimate and ecophysiological traits (H1). However, the other fire-related variables (*fire* and *TSLF*) were poor predictors of the vital rates, except for the recruitment of *M. atticolus* (Fig. 1; Table S4). See SI for mark-recapture summary statistics.

3.2 | Fire regimes and demographic resilience

Contrary to H2, populations of the three species presented low resistance ability in severe fire regimes (Figs. 2-3). Populations of *T. itambere* also displayed low compensation in the most severe fire regime (Figs. 2-3). In average, the three lizard species recover rather fast to their stable stationary structure (Figs. 2-3; *C. nigropunctatum* - 1.844 ± 0.064 S.D. months; *M. atticolus* - 1.516 ± 0.291 S.D. months; *T. itambere* - 1.946 ± 0.200 S.D. months). However, they followed clearly differentiated strategies depending on the fire severity, resulting in highest resistance to fire at intermediate levels of severity (Fig. 3). The most striking differences, though, occurred at the extremes of fire severity (absence of fire and frequent late-dry season fires): *C. nigropunctatum* displayed lower resistance in the least severe fire regime, and *M. atticolus* and *T. itambere* in the highest (Fig. 3). Interestingly, *M. atticolus* and *T. itambere* lost the ability to recover fast (*i.e.*, < 1.5 months) from fire and climate disturbances in the most severe fire regime (Fig. 3).

3.3 | Life history traits and demographic resilience

Using Bayesian mixed-effects models, we found that the differences in the demographic resilience components between fire regimes were significantly predicted by generation time and reproductive output (Fig. S10), supporting H3 and H4. However, the direction of some of our predictions differed for the resistance component and the species with fixed clutch size, *M. atticolus*. We found that, in populations with higher generation times, resistance and compensation was lower, and recovery longer (Fig. 4). This striking pattern was consistent across the three examined species, but with a weaker relationship in *C. nigropunctatum* due to its constrained vital rate variation in response to the environment, and thus lower variance in life history traits (see Figs. S8-S10 for different life history traits among the species). An important exception to the overall pattern was again *M. atticolus*,

with its fixed clutch size, where populations with higher generation times also displayed higher resistance to fire and climate variation.

Reproductive output also shaped the demographic resilience components of the three species, supporting H4. The opposite pattern regarding the relationship between resilience components and life history traits was found with reproductive output (Fig. 5). Indeed, in populations with higher reproductive output, resistance and compensation was higher, and recovery faster (Fig. 5). This pattern was consistent across species, with the exception of the fixed-clutch species *M. atticolus*, displaying lower resistance and compensation with increasing reproductive output (Fig. 5).

3.4 | Vital rate parameters and demographic resilience

The brute-force sensitivity analysis revealed that the demographic resilience components are most affected by the reproductive parameters (Table 1) and, to a lesser extent, by body growth; but not by thermal physiology as we predicted (H4). The relationships between probability of reproduction or number of newborns and SVL regulated all the resilience components in the three species (Table 1). This result indicates that reproduction among the largest individuals (usually the oldest, Reinke *et al.* (2022)) is critical for the demographic resilience of *C. nigropunctatum* and *T. itambere*. Higher vital rate parameter values describing investment in reproduction led to higher resistance and compensation (Table 1). However, complex results emerged regarding the vital rate parameters shaping recovery time. In *T. itambere*, a higher probability of reproduction and a higher number of newborns resulted in a displacement of the population structure further away from the stable size distribution, leading to longer recovery times (Table 1). In *C. nigropunctatum*, we found the opposite pattern, except for the probability of reproduction (which presented complex non-linear relationships). In *M. atticolus,* a higher probability of

375 reproduction of larger adult individuals shortened recovery times (Table 1). As we predicted,
376 slower body growth rates led to slower recovery time, especially for the small-sized *M.*
377 *atticolus* (Table 1). Other parameters had negligible effects on the demographic resilience
378 components across species and fire regimes.
379

380 **4 | DISCUSSION**

381 Using 14 years of monthly mark-recapture data of three lizard species from the Brazilian
382 Cerrado savannas, we show that severe disturbance regimes result in less resilient
383 populations, opposing our primary hypothesis (H2). Indeed, our stochastic IPMs
384 demonstrate that high-severity fire regimes decrease the compensatory, resistance, or
385 recovery abilities. Accordingly, we also show that generation time and reproductive output
386 predict the differences in the demographic resilience components (resistance, compensation,
387 recovery time) among fire regimes and species. Here, populations with higher generation
388 times are characterized by a lower degree of resistance and slower recovery time (H3),
389 whereas those with higher reproductive output tend to compensate more and recover faster
390 (H4). The only species with different relationships between these life history traits and
391 demographic resilience components is the small body-sized lizard *Micrablepharus atticolus,*
392 which has a fixed clutch size of two eggs. Despite these differences, all species present a
393 strong positive correlation among resistance, compensation, and fast recovery time to fires
394 and climatic stochasticity. Partially supporting our hypothesis too, the species' probability
395 and quantity of reproduction, but not its ecophysiology, are the main drivers of the
396 demographic resilience in our three ectothermic species (H1), with body growth only being
397 a strong predictor of recovery time in *M. atticolus*.

398 The most severe fire regime results in less resistant populations in our three species.
399 Additionally, our lizards display longer recovery times (~ two months) or lower

400 compensation in response to this severe fire regime. This finding suggests that these
401 populations surpass a tipping point in severe fire regimes, and achieve an alternative stable
402 state to persist, as shown in other systems, such as in shrubs and grasses from tallgrass
403 prairies (Collins *et al.* 2021). Here, the new state after intense fires is characterized by
404 strategies that allocate resources to either extreme along the fast-slow continuum (Stearns
405 1976) or the reproductive strategies continuum (Salguero-Gómez *et al.* 2016b). For instance,
406 populations of *T. itambere* display longer generation times but lower reproductive output in
407 the most severe fire regime. Similarly, *M. atticolus* also presents lower reproductive output
408 in this regime. These findings further highlight the plasticity of species resilience strategies
409 to cope with different levels of disturbance so populations may remain viable, an area that
410 has received considerable attention in recent years (Vinton *et al.* 2022). Said plasticity seems
411 particularly high in reptiles, which have not diminished their ability to respond to
412 disturbances in the last decades compared to other vertebrates, such as mammals and birds
413 (Capdevila *et al.* 2021a).

414 Our findings align with recent examinations of the relationship between the
415 demographic resilience of plants and animals with the fast-slow continuum (Stott *et al.* 2010;
416 Jiang *et al.* 2022). Indeed, recent studies have recently shown that populations with longer
417 generation times tend to display a lower ability to compensate and are slower to recover after
418 disturbances (Stott *et al.* 2010; McDonald *et al.* 2016). In addition, here we show a clear
419 relationship between the demographic resilience and reproductive strategy, an orthogonal
420 axis to the fast-slow continuum (Salguero-Gómez *et al.* 2016b; Healy *et al.* 2019). For
421 instance, our populations with higher reproductive output resist and compensate more
422 (except the species with fixed clutch size, *M. atticolus*) and recover faster after disturbances.
423 This reactive response to disturbances agrees with work showing that the ability to
424 compensate, linked to reproductive output too, enhances colonizing and invasive potential

among reptiles and amphibians (Allen, Street & Capellini 2017), and even in plants (Iles *et al.* 2015).

Multiple calls have been made for a more mechanistic understanding of resilience in ecological systems (Hodgson, McDonald & Hosken 2015; Kefi *et al.* 2019; Capdevila *et al.* 2020); these calls remain largely unanswered (Capdevila *et al.* 2021b). Here, we contribute to this knowledge gap by mechanistically integrating into the local population dynamics of each species their ecophysiology, size structure, environmental factors, and varying disturbance regimes. Indeed, one of our key findings is that probability and quantity of monthly reproduction are key drivers of demographic resilience. The lack of predictive power of ecophysiological characteristics (*e.g.*, thermal performance, preferred temperature) on resilience reinforces the idea that life history traits constitute an excellent approach to understanding demographic resilience, as recently highlighted in a synthesis across 69 animal and 232 plant species (Capdevila *et al.* 2022). In addition, our results suggest that resilience components exhibit strong intra- and inter-specific variation, and that these relationships are strongly modulated by species' vital rates and life history characteristics. Thus, we argue that existing macroecological and comparative approaches (Capdevila *et al.* 2022) likely mask some of the intraspecific trade-offs we disentangle here using 14 years of monthly mark-recapture data under five levels of fire disturbances. Future studies will likely deliver important insights by testing the predictive power of various kinds of traits (*e.g.*, morphological, physiological, life history) across a wider range of species and disturbance levels.

Fast growth increases resilience after disturbances (Pausas & Bond 2020) and enhances persistence in novel environments (Lytle 2001; Allen, Street & Capellini 2017). In line with these findings, we show that strategies leading to earlier reproduction are effective at conferring resistance, compensation and faster recovery against fires and climate variation

in our three lizard species. We suggest that this strategy may be particularly important for small animals, as it may allow them to achieve sexual maturity earlier, like in the case of *M. atticolus*. Additionally, we show that in months when individuals allocate more resources to reproduction, populations increase the ability to resist, compensate, and recover after disturbances. The timing of disturbances may affect population resilience and explain why timing of reproduction (*i.e.*, phenology) has a critical effect on the responses of lizards (Braithwaite 1987) and plants (Zirondi, Ooi & Fidelis 2021) to fires prescribed in different seasons. This connection between phenology and timing of disturbances is increasingly relevant to other highly-seasonal environments, where species' vital rates are adapted to predictable environmental changes (Prather *et al.* 2023).

Since reproduction is a critical vital rate conferring resilience, species with morphological and physiological constraints on reproduction (*e.g.*, viviparity and fixed clutch sizes) have limited ability to benefit from disturbances. This prediction is precisely what we show in *C. nigropunctatum* and *M. atticolus*. However, both species relatively sustained their resilience strategies in varying degrees of fire severity. Recently reported links between demographic buffering and transient dynamics after disturbances (demographic resilience) (Capdevila *et al.* 2020) may explain these patterns (Stott *et al.* 2010; McDonald *et al.* 2016). In reptiles, viviparity developed as an adaptation to increase reproduction success in cold climates (Zimin *et al.* 2022), and might also confer species with the ability to buffer populations against environmental stochasticity, including resilience to disturbances. Therefore, demographically buffering species may outcompete others in the most extreme fire regimes (total absence of fire *vs.* frequent and severe fires), as we show here. However, because of the constraints on their reproductive schedules, individuals from viviparous and fixed clutch size species need to perform other strategies to increase their reproductive output and to compensate after fires, such as reproducing more often (Cayuela

475 *et al.* 2022). Indeed, these results provide the possible mechanisms for why, among 75,000
476 species of vascular plants and tetrapods, long-lived and low-reproductive species present
477 higher extinction risks than fast-living and high-reproductive ones (Carmona *et al.* 2021).

478 Our findings have key management and conservation implications. First, easily
479 measurable traits such as probability of reproduction and clutch size predict species'
480 resilience to environmental stochasticity and fires. Species with high generation time and
481 low reproductive output take longer to recover, and cannot resist and compensate as much
482 as species with faster paces of life. In our study, populations have higher resilience at low
483 and intermediate degrees of fire severity. Therefore, these results support the pyrodiversity
484 hypothesis, whereby higher heterogeneity in fire regimes increases the resilience of different
485 populations and communities and avoids high severity regimes that homogenize the
486 environment (Jones & Tingley 2021). Second, despite species persist in highly severe fire
487 regimes, populations can attain alternative stable states (Collins *et al.* 2021), with limited
488 resistance, compensation, and recovery abilities after disturbances. Thus, traditional
489 ecological community studies probably underestimate disturbance impacts, since
490 populations may persist in severe regimes, but not in optimal conditions. Third, reproduction
491 is a key mechanism conferring higher resistance, compensation and faster recovery time,
492 both in our species and others (Iles *et al.* 2015; Allen, Street & Capellini 2017). Accordingly,
493 species with constraints on reproduction (*e.g.*, viviparity, fixed clutch size) have lower
494 resistance and compensation, taking longer to recover from disturbances. Taken together,
495 these key findings imply that, to enhance viable strategies after disturbances, managers
496 should focus on generating suitable and heterogeneous habitats to facilitate the reproductive
497 aspects of populations. The ability to quantify and predict the resilience components of
498 natural populations based on their vital rates and life history traits will be increasingly critical

for conservation biology in the coming decades, when climate change and disturbances are projected to increase in frequency and intensity (Bowman *et al.* 2020).

REFERENCES

Allen, W.L., Street, S.E. & Capellini, I. (2017) Fast life history traits promote invasion success in amphibians and reptiles. *Ecology Letters,* **20,** 222-230.

Bowman, D.M.J.S., Kolden, C.A., Abatzoglou, J.T., Johnston, F.H., van der Werf, G.R. & Flannigan, M. (2020) Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment,* **1,** 500-515.

Braithwaite, R.W. (1987) Effects of fire regimes on lizards in the wet-dry tropics of Australia. *Journal of Tropical Ecology,* **3,** 265-275.

Bürkner, P.-C. (2017) brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software,* **80**.

Cant, J., Capdevila, P., Beger, M. & Salguero-Gomez, R. (2023) Recent exposure to environmental stochasticity does not determine the demographic resilience of natural populations. *Ecology Letters*.

Capdevila, P., Noviello, N., McRae, L., Freeman, R. & Clements, C.F. (2021a) Global patterns of resilience decline in vertebrate populations. *Ecology Letters***,** 1-12.

Capdevila, P., Stott, I., Beger, M. & Salguero-Gómez, R. (2020) Towards a comparative framework of demographic resilience. *Trends in Ecology & Evolution,* **35,** 776-786.

Capdevila, P., Stott, I., Cant, J., Beger, M., Rowlands, G., Grace, M. & Salguero-Gómez, R. (2022) Life history mediates the trade-offs among different components of demographic resilience. *Ecology Letters*.

Capdevila, P., Stott, I., Oliveras Menor, I., Stouffer, D.B., Raimundo, R.L.G., White, H., Barbour, M. & Salguero-Gómez, R. (2021b) Reconciling resilience across

ecological systems, species and subdisciplines. *Journal of Ecology,* **109,** 3102-3113.

Carmona, C.P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-M, R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M. & Toussaint, A. (2021) Erosion of global functional diversity across the tree of life. *Science Advances,* **7,** eabf2675.

Cayuela, H., Monod-Broca, B., Lemaitre, J.F., Besnard, A., Gippet, J.M.W., Schmidt, B.R., Romano, A., Hertach, T., Angelini, C., Canessa, S., Rosa, G., Vignoli, L., Venchi, A., Carafa, M., Giachi, F., Tiberi, A., Hantzschmann, A.M., Sinsch, U., Tournier, E., Bonnaire, E., . . . Lena, J.P. (2022) Compensatory recruitment allows amphibian population persistence in anthropogenic habitats. *Proceedings of the National Academy of Sciences, USA,* **119,** e2206805119.

Collins, S.L., Nippert, J.B., Blair, J.M., Briggs, J.M., Blackmore, P. & Ratajczak, Z. (2021) Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters,* **24,** 636-647.

Costa, B.M., Pantoja, D.L., Sousa, H.C., de Queiroz, T.A. & Colli, G.R. (2021) Long-term, fire-induced changes in habitat structure and microclimate affect Cerrado lizard communities. *Biodiversity and Conservation,* **29,** 1659-1681.

Costa, B.M., Pantoja, D.L., Vianna, M.C.M. & Colli, G.R. (2013) Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. *Journal of Herpetology,* **47,** 502-510.

Dantas, V.d.L., Pausas, J.G., Batalha, M.A., de Paula Loiola, P. & Cianciaruso, M.V. (2013) The role of fire in structuring trait variability in Neotropical savannas. *Oecologia,* **171,** 487-494.

548 Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J.,
549 Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G.,
550 Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams,
551 R.J. & York, A. (2010) Fire management for biodiversity conservation: Key
552 research questions and our capacity to answer them. *Biological Conservation,* **143,**
553 1928-1939.
554 Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: Applying a
555 new structured population model. *Ecology,* **81,** 694-708.
556 Gonçalves-Souza, D., Verburg, P.H. & Dobrovolski, R. (2020) Habitat loss, extinction
557 predictability and conservation efforts in the terrestrial ecoregions. *Biological*
558 *Conservation,* **246,** 108579-108579.
559 Hale, S., Nimmo, D.G., Cooke, R., Holland, G., James, S., Stevens, M., De Bondi, N.,
560 Woods, R., Castle, M., Campbell, K., Senior, K., Cassidy, S., Duffy, R., Holmes,
561 B. & White, J.G. (2016) Fire and climatic extremes shape mammal distributions in
562 a fire-prone landscape. *Diversity and Distributions,* **22,** 1127-1138.
563 Halpern, C.B. (1989) Early successional patterns of forest species: interactions of life
564 history traits and disturbance. *Ecology,* **70,** 704-720.
565 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R. & Buckley, Y.M. (2019)
566 Animal life history is shaped by the pace of life and the distribution of age-specific
567 mortality and reproduction. *Nature Ecology and Evolution,* **3,** 1217-1224.
568 Hero, J.M. (1989) A simple code for toe clipping anurans. *Herpetological Review,* **20,** 66-
569 69.
570 Hodgson, D., McDonald, J.L. & Hosken, D.J. (2015) What do you mean, 'resilient'? *Trends*
571 *in Ecology & Evolution,* **30,** 503-506.

572 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,
573 Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-forest
574 boundary: How plant traits, resources and fire govern the distribution of tropical
575 biomes. *Ecology Letters,* **15,** 759-768.
576 Hu, Y., Doherty, T.S. & Jessop, T.S. (2020) How influential are squamate reptile traits in
577 explaining population responses to environmental disturbances? *Wildlife Research,*
578 **47,** 249-259.
579 Huey, R.B. & Stevenson, R.D. (1979) Integrating thermal physiology and ecology of
580 ectotherms: a discussion of approaches. *American Zoologist,* **19,** 357-366.
581 Iles, D.T., Salguero-Gómez, R., Adler, P.B., Koons, D.N. & Zuidema, P. (2015) Linking
582 transient dynamics and life history to biological invasion success. *Journal of*
583 *Ecology,* **104,** 399-408.
584 Jiang, S., Jaggi, H., Zuo, W., Oli, M.K., Coulson, T., Gaillard, J.M. & Tuljapurkar, S.
585 (2022) Reproductive dispersion and damping time scale with life-history speed.
586 *Ecology Letters,* **25,** 1999-2008.
587 Jones, G.M. & Tingley, M.W. (2021) Pyrodiversity and biodiversity: A history, synthesis,
588 and outlook. *Diversity and Distributions***,** 1-18.
589 Jones, O.R., Barks, P., Stott, I., James, T.D., Levin, S., Petry, W.K., Capdevila, P., Che-
590 Castaldo, J., Jackson, J., Römer, G., Schuette, C., Thomas, C.C. & Salguero-
591 Gómez, R. (2022) Rcompadre and Rage—Two R packages to facilitate the use of
592 the COMPADRE and COMADRE databases and calculation of life-history traits
593 from matrix population models. *Methods in Ecology and Evolution,* **13,** 770-781.
594 Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.a. (2011) Fire as an
595 evolutionary pressure shaping plant traits. *Trends in Plant Science,* **16,** 406-411.

Kefi, S., Dominguez-Garcia, V., Donohue, I., Fontaine, C., Thebault, E. & Dakos, V. (2019) Advancing our understanding of ecological stability. *Ecology Letters,* **22,** 1349-1356.

Kellner, K. (2019) jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses.

Levin, S.C., Childs, D.Z., Compagnoni, A., Evers, S., Knight, T.M. & Salguero-Gómez, R. (2021) ipmr: Flexible implementation of Integral Projection Models in R. *Methods in Ecology and Evolution,* **2021,** 1826-1834.

Lytle, D.A. (2001) Disturbance regimes and life-history evolution. *The American Naturalist,* **157,** 525-525.

McDonald, J.L., Stott, I., Townley, S. & Hodgson, D.J. (2016) Transients drive the demographic dynamics of plant populations in variable environments. *Journal of Ecology,* **104,** 306-314.

Meiri, S., Brown, J.H. & Sibly, R.M. (2012) The ecology of lizard reproductive output. *Global Ecology and Biogeography,* **21,** 592-602.

Merrien, T., Davis, K.J., Di Marco, M., Capdevila, P. & Salguero-Gómez, R. (2022) Human disturbances erode the diversity of species resilience strategies. *BioRxiv*.

Metcalf, C.J. (2016) Invisible trade-offs: Van Noordwijk and de Jong and life-history evolution. *American Naturalist,* **187,** iii-v.

Miranda, H.S. (2010) *Efeitos do regime do fogo sobre a estrutura de comunidades de cerrado: Resultados do Projeto Fogo*. IBAMA, Brasília, Brasil.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates Inc., Sunderland, USA.

Newbold, T., Bentley, L.F., Hill, S.L.L., Edgar, M.J., Horton, M., Su, G., Şekercioğlu, Ç.H., Collen, B. & Purvis, A. (2020) Global effects of land use on biodiversity differ among functional groups. *Functional Ecology,* **34,** 684-693.

Oliveira, P.S. & Marquis, R.J. (2002) *The cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York.

Paniw, M., Quintana-Ascencio, P.F., Ojeda, F. & Salguero-Gómez, R. (2016) Accounting for uncertainty in dormant life stages in stochastic demographic models. *Oikos,* **126,** 900-909.

Paquet, M., Arlt, D., Knape, J., Low, M., Forslund, P. & Pärt, T. (2020) Why we should care about movements: Using spatially explicit integrated population models to assess habitat source-sink dynamics. *Journal of Animal Ecology,* **89,** 2922-2933.

Pausas, J.G. & Bond, W.J. (2020) On the three major recycling pathways in terrestrial ecosystems. *Trends in Ecology & Evolution,* **35,** 767-775.

Pausas, J.G., Keeley, J.E. & Schwilk, D.W. (2017) Flammability as an ecological and evolutionary driver. *Journal of Ecology,* **105,** 289-297.

Pausas, J.G. & Parr, C.L. (2018) Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology,* **32,** 113-125.

Plummer, M. (2019) rjags: bayesian graphical models using MCMC.

Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics,* **52,** 703-709.

Prather, R.M., Dalton, R.M., Barr, B., Blumstein, D.T., Boggs, C.L., Brody, A.K., Inouye, D.W., Irwin, R.E., Martin, J.G.A., Smith, R.J., Van Vuren, D.H., Wells, C.P., Whiteman, H.H., Inouye, B.D. & Underwood, N. (2023) Current and lagged climate affects phenology across diverse taxonomic groups. *Proceedings of the Royal Society of London, Series B: Biological Sciences,* **290,** 20222181.

Reinke, B.A., Cayuela, H., Janzen, F.J., Lemaitre, J.F., Gaillard, J.M., Lawing, A.M., Iverson, J.B., Christiansen, D.G., Martinez-Solano, I., Sanchez-Montes, G., Gutierrez-Rodriguez, J., Rose, F.L., Nelson, N., Keall, S., Crivelli, A.J., Nazirides, T., Grimm-Seyfarth, A., Henle, K., Mori, E., Guiller, G., . . . Miller, D.A.W. (2022) Diverse aging rates in ectothermic tetrapods provide insights for the evolution of aging and longevity. *Science,* **376,** 1459-1466.

Rodrigues, M.T. (1996) A new species of lizard, genus *Micrablepharus* (Squamata: Gymnophtalmidae), from Brazil. *Herpetologica,* **52,** 535-541.

Rodriguez-Caro, R.C., Gracia, E., Blomberg, S.P., Cayuela, H., Grace, M., Carmona, C.P., Perez-Mendoza, H.A., Gimenez, A. & Salguero-Gomez, R. (2023) Anthropogenic impacts on threatened species erode functional diversity in chelonians and crocodilians. *Nature Communications,* **14,** 1542.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F.n., Hartmann, A., Henning, A., Hoppe, G., R??mer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., . . . Vaupel, J.W. (2016a) COMADRE: A global data base of animal demography. *Journal of Animal Ecology,* **85,** 371-384.

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., de Kroon, H. & Buckley, Y.M. (2016b) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences, USA,* **113,** 230-235.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Victoriano Sepulveda, P., Rocha, C.F.D., Ibargüengoytía, N., Aguilar Puntriano,

C., Massot, M., Lepetz, V., . . . Sites, J.W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science,* **328,** 894-899.

Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *The Quarterly review of biology,* **51,** 3-47.

Stearns, S.C. (2000) Life history evolution: successes, limitations, and prospects. *Naturwissenschaften,* **87,** 476-486.

Stott, I., Franco, M., Carslake, D., Townley, S. & Hodgson, D. (2010) Boom or bust? A comparative analysis of transient population dynamics in plants. *Journal of Ecology,* **98,** 302-311.

Stott, I., Hodgson, D.J. & Townley, S. (2012) Popdemo: An R package for population demography using projection matrix analysis. *Methods in Ecology and Evolution,* **3,** 797-802.

Sutherland, W.J., Adams, W.M., Aronson, R.B., Aveling, R., Blackburn, T.M., Broad, S., Ceballos, G., CÔtÉ, I.M., Cowling, R.M., Da Fonseca, G.A.B., Dinerstein, E., Ferraro, P.J., Fleishman, E., Gascon, C., Hunter, M., Hutton, J., Kareiva, P., Kuria, A., MacDonald, D.W., MacKinnon, K., . . . Watkinson, A.R. (2009) One hundred questions of importance to the conservation of global biological diversity. *Conservation Biology,* **23,** 557-567.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., . . . Gibson, D. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology,* **101,** 58-67.

Tenan, S., Pradel, R., Tavecchia, G., Igual, J.M., Sanz-Aguilar, A., Genovart, M. & Oro, D. (2014) Hierarchical modelling of population growth rate from individual capture-recapture data. *Methods in Ecology and Evolution,* **5,** 606-614.

Van Sluys, M. (1993) Food habits of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. *Journal of Herpetology,* **27,** 347-351.

Van Sluys, M. (1997) Home range of the saxicolous lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. *Copeia,* **1997,** 623-628.

Van Sluys, M. & Henderson, R.W. (1993) The reproductive cycle of *Tropidurus itambere* (Sauria: Tropiduridae) in Southeastern Brazil. *Journal of Herpetology,* **27,** 28-32.

Vieira, G.H.C., Mesquita, D.O., Péres Jr, A.K., Kitayama, K. & Colli, G.R. (2000) *Micrablepharus atticolus* (NCN). Natural History. *Herpetological Review,* **31,** 241-242.

Vinton, A.C., Gascoigne, S.J.L., Sepil, I. & Salguero-Gomez, R. (2022) Plasticity's role in adaptive evolution depends on environmental change components. *Trends in Ecology & Evolution,* **37,** 1067-1078.

Vitt, L.J. & Blackburn, D.G. (1991) Ecology and life-history of the viviparous lizard *Mabuya bistriata* (Scincidae) in the Brazilian Amazon. *Copeia***,** 916-927.

Vitt, L.J. & Caldwell, J.P. (1993) Ecological observations on Cerrado lizards in Rondônia, Brazil. *Journal of Herpetology,* **27,** 46-52.

Vitt, L.J., Zani, P.A. & Lima, A.C.M. (1997) Heliotherms in tropical rain forest: The ecology of *Kentropyx calcarata* (Teiidae) and *Mabuya nigropunctata* (Scincidae) in the Curua-Una of Brazil. *Journal of Tropical Ecology,* **13,** 199-220.

Zimin, A., Zimin, S.V., Shine, R., Avila, L., Bauer, A., Böhm, M., Brown, R., Barki, G., de Oliveira Caetano, G.H., Castro Herrera, F., Chapple, D.G., Chirio, L., Colli, G.R., Doan, T.M., Glaw, F., Grismer, L.L., Itescu, Y., Kraus, F., LeBreton, M.,

Martins, M., . . . Meiri, S. (2022) A global analysis of viviparity in squamates highlights its prevalence in cold climates. *Global Ecology and Biogeography,* **31,** 2437-2452.

Zirondi, H.L., Ooi, M.K.J. & Fidelis, A. (2021) Fire-triggered flowering is the dominant post-fire strategy in a tropical savanna. *Journal of Vegetation Science,* **32,** 1-11.

Table 1. Probability and quantity (number of newborns) of monthly reproduction are the main proximal drivers of the demographic resilience components. Sensitivity (mean ± S.D.) of the demographic resilience components to parameters' perturbation in three species of lizards from the Brazilian Cerrado savannas: *Copeoglossum nigropunctatum*, *Micrablepharus atticolus*, and *Tropidurus itambere*. Cell colors vary from white to dark orange, indicating absolute sensitivity values of demographic resilience component with respect to different plausible drivers: $\alpha_{vitalrate}$ = intercept of the vital rate function; $\alpha_{vitalrateSVL}$: slope of the linear relationship with body size (snout-vent length—SVL); $\beta_{vitalrateSVL}^2$: slope of the quadratic relationship with body size (SVL); μ_K = mean body growth constant, *i.e.*, time required to reach asymptotic size, thus higher μ_K values means slower body growth rates. Ony parameters related to probability of reproduction (prep), number of newborns (nb), and body growth were higher than zero. The sensitivity values of the other vital rates were null and not shown.

Parameter	Resistance	Compensation	Recovery time
		Copeoglossum nigropunctatum	
α_{prep}	0.026 ± 0.002	0.111 ± 0.004	0.052 ± 0.001
$\beta_{prepSVL}$	2.909 ± 0.315	13.836 ± 0.784	8.023 ± 0.264
$\beta_{prepSVL}^2$	71.366 ± 69.583	86.673 ± 102.262	-173.243 ± 108.166
α_{nb}	0.067 ± 0.002	0.2 ± 0.001	-0.21 ± 0.012
β_{nbSVL}	9.58 ± 0.219	27.562 ± 1.194	-6.326 ± 0.745
μ_K	-0.007 ± 0.001	0.004 ± 0.001	0.03 ± 0.005
		Micrablepharus atticolus	
α_{prep}	0.037 ± 0.011	0.035 ± 0.005	-0.103 ± 0.182
$\beta_{prepSVL}$	1.475 ± 0.462	1.603 ± 0.219	-4.227 ± 8.933

μ_K	-0.012 ± 0.003	0.005 ± 0.001	0.654 ± 0.251
	Tropidurus itambere		
α_{prep}	0.036 ± 0.008	0.127 ± 0.02	0.059 ± 0.005
$\beta_{prepSVL}$	2.740 ± 0.608	10.516 ± 1.557	5.573 ± 0.342
α_{nb}	0.128 ± 0.005	0.296 ± 0.003	-0.033 ± 0.004
β_{nbSVL}	8.806 ± 0.201	24.955 ± 0.319	5.312 ± 0.914
β_{nbSVL}^2	186.827 ± 141.564	1655.239 ± 163.511	3.747×10^{10} ± 9.308×10^{10}
μ_K	-0.008 ± 0.006	0.005 ± 0.004	0.005 ± 0.004

739 **Figure legends**

740

741 **Fig. 1.** Model coefficients (mean and 95% confidence intervals) of the effects of
742 environmental covariates on vital rates of three species of lizards corresponding to: *tmed2m*
743 = mean air temperature at 200 cm height; *tmin0cm* = minimum air temperature at 0 cm
744 height; *tmed0cm* = mean air temperature at 0 cm height; *RHmax* = maximum relative air
745 humidity; *sol* = solar radiation; *precip* = accumulated precipitation; *perf* = mean locomotor
746 performance; *ha* = hours of activity; *fire* = month with fire; *TSLF* = time since last fire;
747 *random* = monthly random variation. We group-colored the covariates related to weather,
748 microclimate, ecophysiological traits, fire, and randomness. Species' silhouettes from
749 photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais
750 (*T. itambere*).

751

752 **Fig. 2.** Three-dimensional space of the demographic resilience components (resistance,
753 compensation, and recovery time) for three species of lizards from the Brazilian Cerrado
754 savannas, showing distinct demographic resilience strategies. With a 14-year mark-recapture
755 dataset, we derived demographic resilience components from monthly stochastic Integral
756 Projection Models shaped by weather, microclimate, ecophysiological traits, and fire
757 covariates.

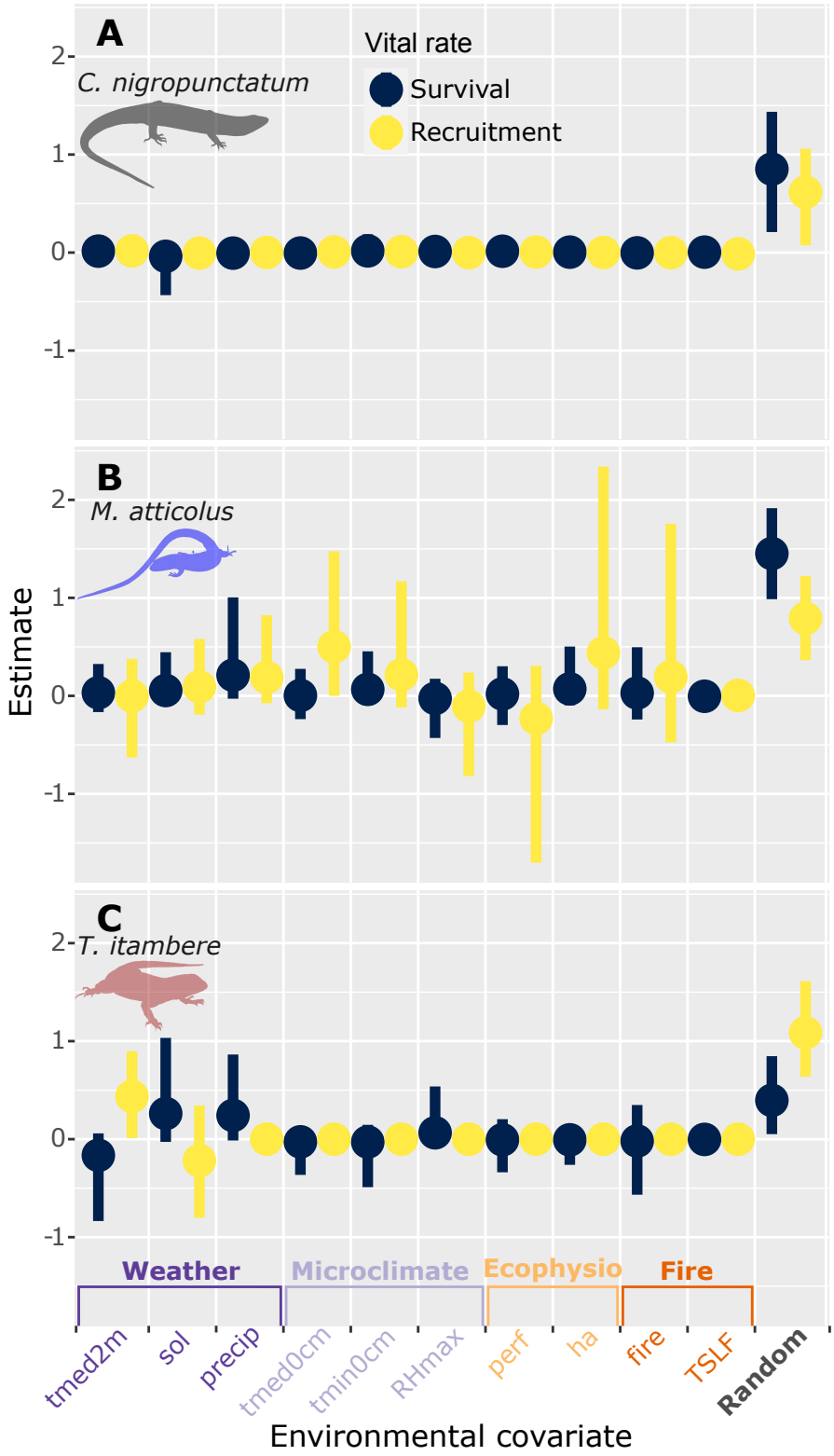
758

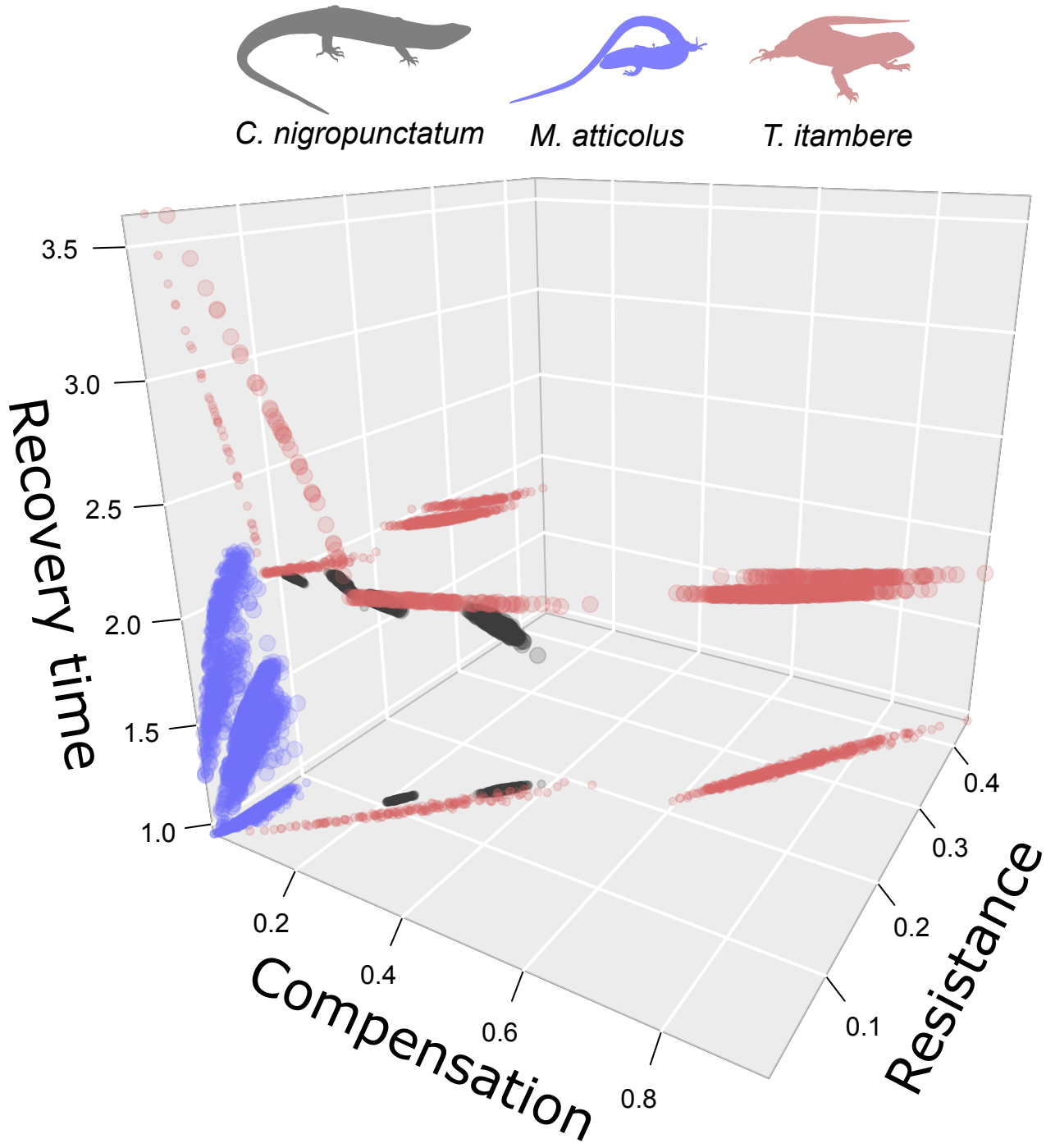
759 **Fig. 3.** Raw data, density, mean estimates, and 95% confidence intervals of the demographic
760 resilience components: (A,D & G) resistance; (B, E & H) compensation, and (C, F & I)
761 recovery time of three species of lizards: (A-C) *Copeoglossum nigropunctatum*, (D-F)
762 *Micrablepharus atticolus*, and (G-I) *Tropidurus itambere* from the Brazilian Cerrado
763 savannas under different fire regime severity. Within each panel, we show high posterior

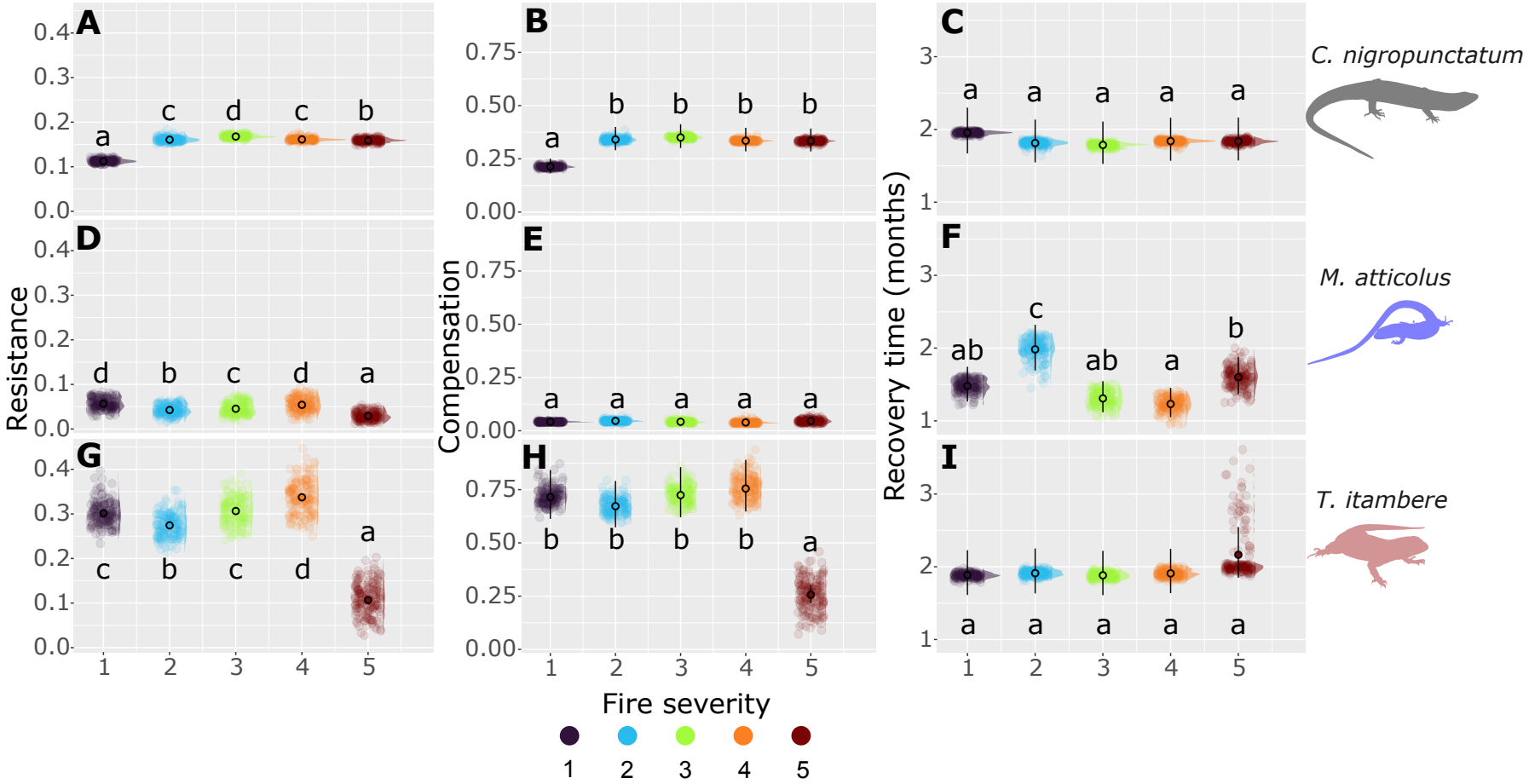
density (95% probability) contrast letters corresponding to groups that are not significantly different (overlapping zero difference). Later letters in the alphabet mean higher values (d > c > b > a).

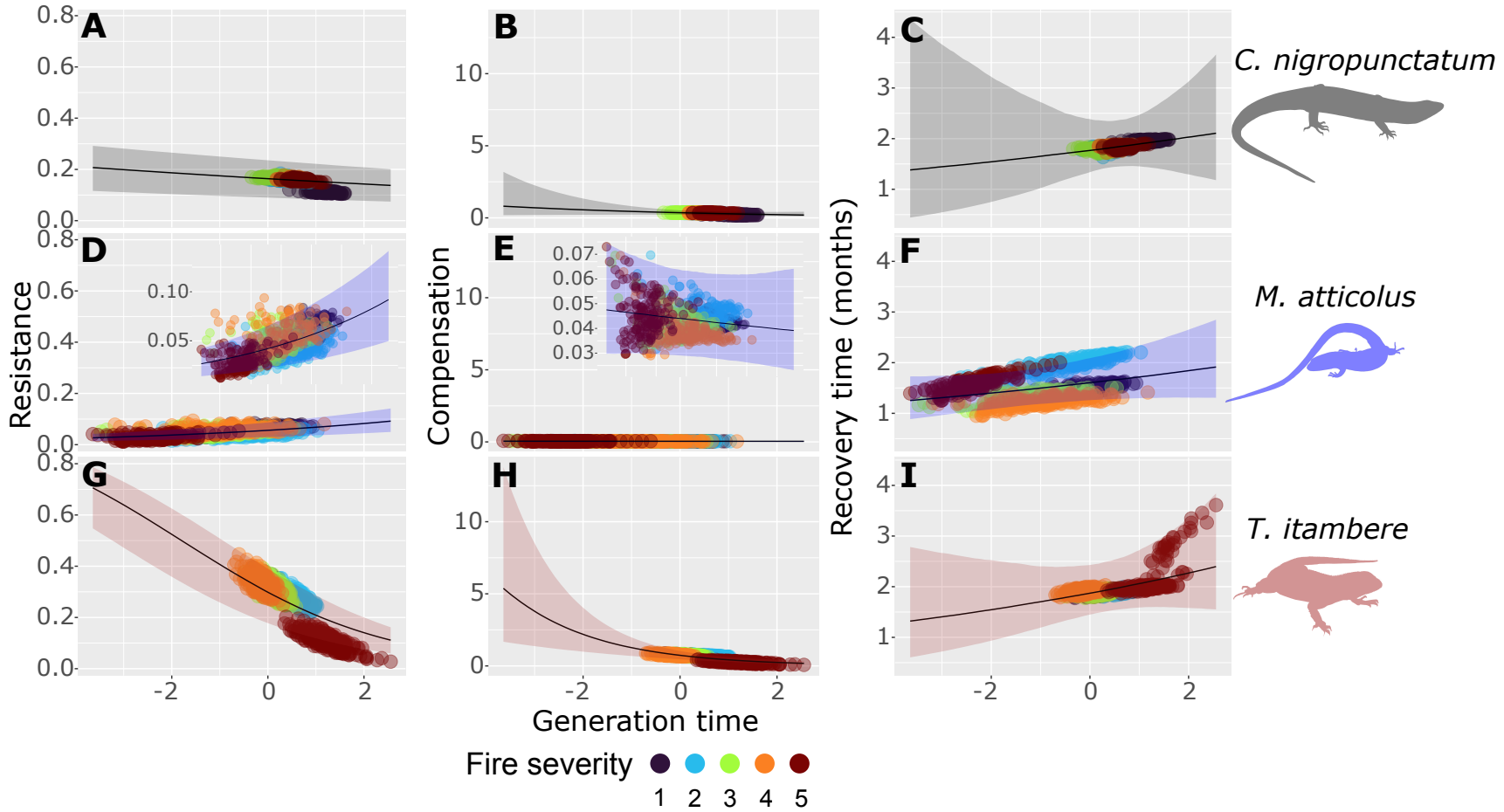
Fig. 4. Relationship between generation time (log_{10}-transformed and z-scaled) and the demographic resilience components: (A, D & G) resistance, (B, E & H) compensation, and (C, F & I) recovery time of three lizard species: (A-C) *Copeoglossum nigropunctatum*, (D-F) *Micrablepharus atticolus*, and (G-I) *Tropidurus itambere* under fire regimes of varying severity. Lines and shades represent mean estimates and 95% confidence intervals derived from Bayesian mixed-effects models, respectively. To offer higher resolution for *M. atticolus*' resistance and compensation, we also offer inserts in D and E with a narrower y-axis range.

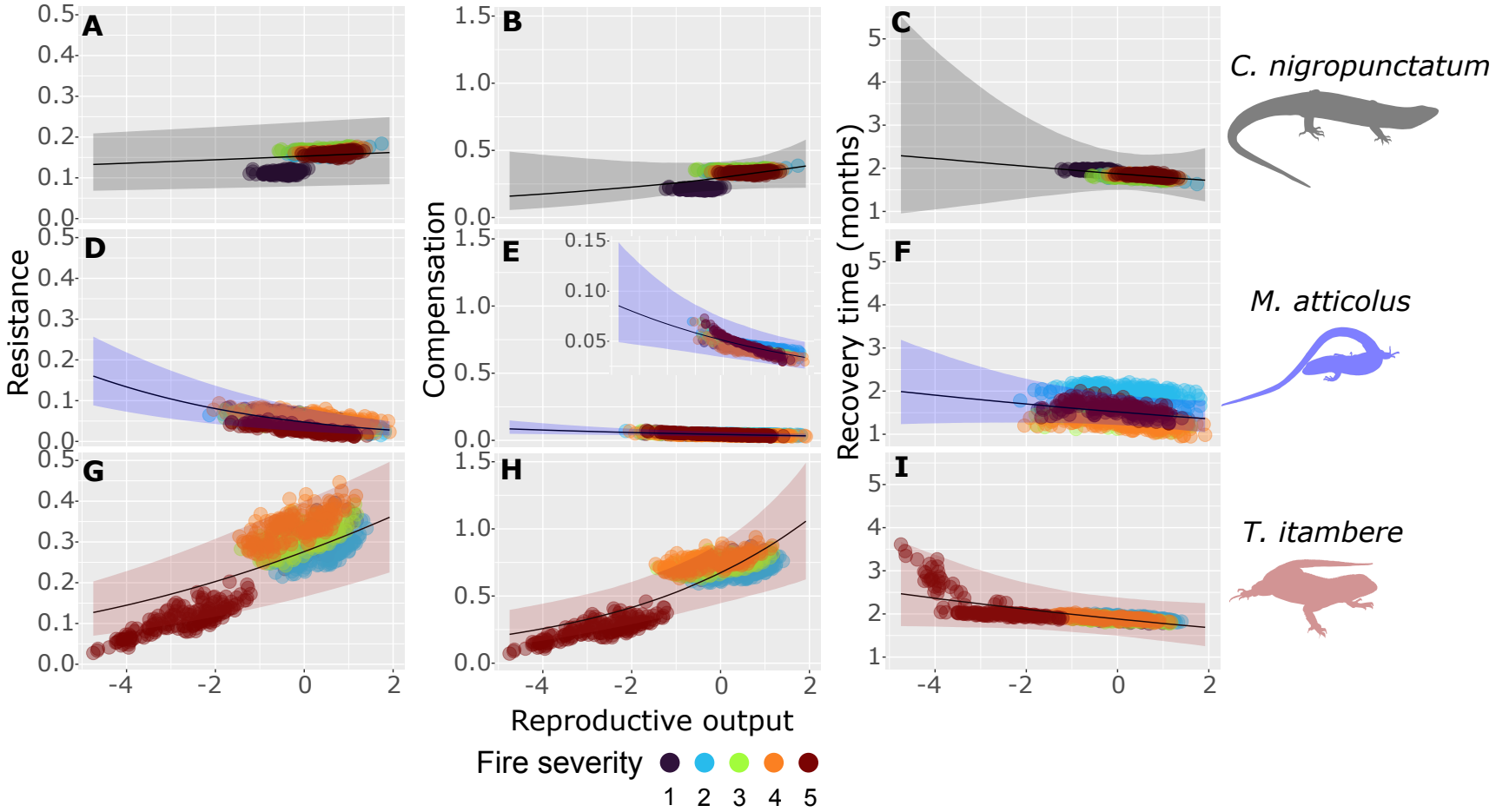
Fig. 5. Relationship between reproductive output (log_{10}-transformed and z-scaled) and the demographic resilience components (A, D & G) resistance, (B, E & H) compensation, and (C, F & I) recovery time of three lizard species (A-C) *Copeoglossum nigropunctatum*, (D-F) *Micrablepharus atticolus*, and (G-I) *Tropidurus itambere* under fire regimes of varying severity. Lines and shades represent mean estimates and 95% confidence intervals derived from Bayesian mixed-effects models, respectively. To offer higher resolution for *M. atticolus*' compensation, we also offer an insert in E with a narrower y-axis range.


A
C. nigropunctatum
Vital rate
Survival
Recruitment
B
M. atticolus
C
T. itambere
Estimate
2
1
0
-1
Weather
Microclimate
Ecophysio
Fire
tmed2m
sol
precip
tmed0cm
tmin0cm
RHmax
perf
ha
fire
TSLF
Random
Environmental covariate


C. nigropunctatum
M. atticolus
T. itambere
Recovery time
3.5
3.0
2.5
2.0
1.5
1.0
Compensation
0.2
0.4
0.6
0.8
Resistance
0.1
0.2
0.3
0.4


A
B
C
D
E
F
G
H
I
Resistance
Compensation
Recovery time (months)
Fire severity
1
2
3
4
5
C. nigropunctatum
M. atticolus
T. itambere


A
B
C
D
E
F
G
H
I
Resistance
Compensation
Recovery time (months)
Generation time
C. nigropunctatum
M. atticolus
T. itambere
Fire severity
1 2 3 4 5


A
B
C
D
E
F
G
H
I
Resistance
Compensation
Recovery time (months)
Reproductive output
Fire severity
1 2 3 4 5
C. nigropunctatum
M. atticolus
T. itambere