SEVERE FIRE REGIMES SELECT FOR HIGHLY RESILIENT POPULATIONS IN ECTOTHERMS

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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

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Abstract (201 words)

Understanding species' responses to environmental change is crucial for mitigating the impact of human-induced disturbances. Because of human actions, fire regimes are increasing in frequency and intensity, including the occurrence of extreme severe events. 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. We use a Bayesian hierarchical framework to parameterize stochastic Integral Projection Models using 14 years of monthly, individual-level data from five sites along the Brazilian savannas that have historically been exerted to different fire regimes. We find that the most severe fire regimes select for populations with higher resistance or compensation (ability to benefit from disturbances). Generation time and reproductive output predict the general trends of the resilience components 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. Together, we evidence how constraints on reproductive effort (*e.g.*, viviparity, fixed clutch sizes) can have drastic consequences for the ability of natural populations of ectotherms to benefit from disturbances, an essential aspect that should be considered in conservation assessments.

Environmental change is causing the fast decline of biodiversity worldwide[1]. The most impactful drivers of this loss include habitat degradation[2] and the drastic modification of disturbance regimes[3], such as fires[4]. Understanding how species may respond to these impacts is at the core of ecology[5] and conservation biology[6]. Ecological resilience research in the last decades has obtained variable success regarding the extent to which species traits can predict their responses to disturbances[7,8]. Indeed, some organismal traits confer species with higher tolerance or susceptibility to perturbations. Examples include mobility[9], robustness[10], ability to acquire and allocate resources fast/efficientlyt[11], thermal performance[8], and reproductive output[12]. 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[13].

Ecological resilience, the ability of an ecological system to resist and recover, or move to a new stable equilibrium from disturbances[14], has been historically explored at the community and ecosystem levels[15]. Recently, though, key breakthroughs have been made unraveling the mechanisms behind population responses to disturbances[16]. Natural populations may respond to disturbances by avoiding decreases in size (resistance) or even by increasing in size (compensation) [16]. 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[16]. Thus, the full repertoire of resilience responses to a disturbance by a natural population can be quantified by 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[16].

Life history traits, the key moments along the life cycle of an organism[17], have received much attention in recent decades due to their potential to predict organismal responses[18]. These life history traits (*e.g.*, generation time, net reproductive output) are ultimately governed by the schedules of survival, growth, and reproduction, and are typically under strong selection to optimization[19]. Since these three vital rates operate under strong trade-offs, so do the emerging life history traits[17]. Importantly, because of their direct impact on fitness, life history strategies –the combination of life history traits in an organism– are a relevant proxy to predict population responses to environmental changes and disturbances[12,20]. For instance, recently, research has shown that plant species with high reproductive output tend to have high resistance and compensation to disturbances[21], while long-living animals have lower resistance and take longer to recover compared to fast-living species[12]. Despite these key findings, their generalization across the Tree of Life is challenging because organisms present diverse life history traits[22,23] and because quantifying trade-offs in natural populations under control conditions is difficult[24], let alone in a context of disturbance regimes[25]. Still, linking the mechanisms that regulate the vital rates to population-level responses to disturbances is essential to understand how these trade-offs constrain their portfolio, and ultimately shed light on their evolutionary processes.

Fire is a major disturbance that shapes ecosystems worldwide[26]. Fire consumes biomass, recycles nutrients, and triggers the renewal of the vegetation, leading to a burst of productivity and providing establishment opportunities for new individuals and species[27]. Despite regional heterogeneity in fire activity, average fire season had globally increased 18.7% in the last three decades, and in many regions fire frequency, intensity and spatial extent have increased presumably because of climate change and human management[4]. In fire-prone ecosystems, species typically develop adaptations to resist and recover from frequent fires[28]. Conversely, other species have evolved to take advantage of these disturbances. Examples include fire-adapted plants that only resprout[29] or whose seed dormancy only breaks[30] after a fire, thus benefiting from the open space in

temporarily less competitive environments. Historically, though, the fire ecology literature has focused more on plant responses than on animal ones (but see [29]), and so relatively little is still known regarding the mechanisms that confer animals with resilience to fire.

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 savanna[31], 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 underling 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 will select for more resilient populations (*i.e.*, higher resistance, higher compensation, 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.

Results

Vital rates

To test H1, we used mark-recapture models (see Supplementary Information for mark-recapture summary statistics). 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. As opposed to H1, ecophysiological traits were poor predictors of the vital rates, excepting for 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; Supplementary Table S4). In contrast, survival of *M. atticolus* and *T. itambere* was only affected by weather (*precip*, *tmed2m*, and *sol*; Fig. 1; Supplementary 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; Supplementary Table S4); Recruitment of *T. itambere* only varied with weather conditions (*tmed2m* and *sol*; Fig. 1; Supplementary Table S4). These patterns resulted in higher variation in the life-history traits in these two species—*M. atticolus* and *T. itambere* (Supplementary Fig. S8). We found significant differences in these vital rates among plots, which had been exerted to prescribed fire regimes for 18 years (Supplementary 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 (Supplementary 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; Supplementary Table S4).

Fire regimes and demographic resilience

To test H2, *i.e.* more severe fire regimes will select for more resilient populations, we built stochastic IPMs[32], estimated their species- and plot-specific resilience components of resistance, compensation, and recovery time, and then compared them using Bayesian linear mixed-effects models. Populations of *C. nigropunctatum* and *M. atticolus* presented high resistance but low compensatory abilities after fire disturbances (Figs. 2-3). In comparison, *T. itambere* displayed high

compensation at the cost of low resistance to fires (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.; *M. atticolus* - 1.516 ± 0.291 S.D.; *T. itambere* - 1.946 ± 0.200 S.D.). However, they followed clearly differentiated strategies depending on the fire severity, resulting in lowest 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) (Fig. 3): *C. nigropunctatum* displayed higher 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 disturbances in the most severe fire regime (Fig. 3).

Life history traits and demographic resilience

Using Bayesian mixed-effects models, we found that the differences of the demographic resilience components between fire regimes were strongly predicted by generation time and reproductive output (Supplementary Fig. S10), supporting H3 and H4. However, the direction of some of our predictions differed for the species with fixed clutch size, *M. atticolus*. We found that, in populations with higher generation times, resistance was higher, compensation 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 Supplementary 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 lower resistance to fire.

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 was lower, compensation higher, and recovery faster (Fig. 5). This pattern was consistent across species, with the exception of the fixed-clutch species *M. atticolus*, displaying higher resistance and lower compensation with increasing reproductive output (Fig. 5).

Vital rate parameters and demographic resilience

To test specific aspects of H4, that populations with higher body growth rate and higher thermal performance have higher compensation and faster recovery time and, at the same time, inspect which IPM vital rate parameters shaped the different demographic resilience components, we conducted a brute-force sensitivity analysis[33]. The analysis revealed that the demographic resilience components are most affected by the reproductive parameters (Table 1) and, to a lesser extent, by body growth. The relationships between probability of reproduction or number of newborns (except for the fixed-clutch size species *M. atticolus*) and SVL were significant for all of the resilience components in the three species (Table 1). This result indicates that reproduction among the largest individuals (usually the oldest[34]) is critical for demographic resilience of *C. nigropunctatum* and *T. itambere*. Higher vital rate parameter values describing investment on reproduction led to lower resistance and higher compensation (Table 1). However, complex results emerged regarding the vital rate parameters shaping recovery time. In *T. itambere*, a higher probability of reproduction and 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 reproduction of larger adult individuals shortened recovery times (Table 1). As we predicted, slower body growth rates led to slower recovery time, especially for the small-sized *M.*

atticolus (Table 1). Other parameters had negligible effects on the demographic resilience components across species and fire regimes.

Discussion

Using 14 years of monthly capture-mark-recapture data of three lizard species from the Brazilian Cerrado savannas, we show that severe disturbance regimes result in more resilient populations, supporting our primary hypothesis (H2). Indeed, our stochastic IPMs demonstrate that high severity fire regimes select for populations with high compensatory or resistance abilities. Accordingly, we also show that generation time and reproductive output strongly predict the differences of the demographic resilience components (resistance, compensation, recovery time) among fire regimes and species. Here, populations with higher generation time are characterized by a greater degree of resistance but slower recovery time (H3), whereas those populations with higher reproductive output tend to compensate more and recover faster (H4). The only species with different relationships between these life history traits and demographic resilience components is the small body-sized lizard *Micrablepharus atticolus*, which has a fixed clutch size of two eggs. Despite these differences, all species present a strong resistance *vs*. compensation trade-off to fires and climatic stochasticity. Partially supporting our hypothesis too, a species' probability and quantity of reproduction, but not its ecophysiology, are the main drivers of the demographic resilience in our three ectothermic species (H1), with body growth only being a strong predictor of recovery time in *M. atticolus*.

The most severe fire regime result in more resistant populations in our three species. However, our lizards display longer recovery times (~ two months) in response to this severe fire regime. This finding suggests that these populations surpass a tipping point in severe fire regimes, and achieve an alternative stable state to persist, as it has been shown in other systems, such as in shrubs and grasses from tallgrass prairies[35]. Here, the new state after intense fires is characterized

by strategies that allocate resources to either extreme along the fast-slow continuum[17] or the reproductive strategies continuum[36]. For instance, populations of *T. itambere* display longer generation times but lower reproductive output in the most severe fire regime. These findings further highlight the plasticity of species resilience strategies to cope with different levels of disturbance so populations may remain viable, an area that has received considerable attention in recent years[37]. Said plasticity seems to be particularly high in reptiles, which have not diminished their ability to respond to disturbances in the last decades compared to other vertebrates, such as mammals and birds[20].

Our findings align with recent examinations of the relationship between the demographic resilience of plants and animals with the fast-slow continuum[38,39]. Indeed, theoretical and empirical works have recently shown that populations with longer generation times tend to display a lower ability to compensate and are slower to recover after disturbances[39,40]. In addition, here we show a clear relationship between the demographic resilience and reproductive strategy, an orthogonal axis to the fast-slow continuum[22,36]. For instance, our populations with higher reproductive output compensate more (except the species with fixed clutch size, *M. atticolus*) and recover faster after disturbances. This reactive response to disturbances is in agreement with work showing that the ability to compensate, linked to reproductive output too, enhances colonizing and invasive potential among reptiles and amphibians[18], and even in plants[21].

Multiple calls have been made for a more mechanistic understanding of resilience in ecological systems[14-16]; these calls remain largely unanswered[41]. Here, we contribute to this gap of knowledge by mechanistically integrating into 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 understand demographic resilience, as recently highlighted in a synthesis across 69 animal and 232 plant species[12]. 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[12] 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[27] and enhances persistence in novel environments[18,25]. In line with these findings, we show that strategies leading to earlier reproduction are effective at conferring compensation and faster recovery against fires 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*. In contrast, we show that, in months when individuals allocate more resources to reproduction, populations lose the ability to resist disturbances. This pattern presumably results from individuals' reproductive costs[42]; thus, by delaying reproduction, individuals of indeterminate growth –most reptiles[34]– can continue to increase survival and reproductive rates at older ages[22,34], buffering the population against disturbances and environmental stochasticity[43]. 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[44] and plants[45] 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[46].

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*. In addition, we report a strong trade-off between the ability to resist and compensate after fires in all three species. Recently reported links between demographic buffering and transient dynamics after disturbances (demographic resilience[16]) may explain these patterns[39,40]. In reptiles, viviparity developed as an adaptation to increase reproduction success in cold climates[47], and might also confer species with the ability to buffer populations against environmental stochasticity, including resisting 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[48]. Indeed, these results provide the possible mechanisms on why, among 75,000 species of vascular plants and tetrapods, long-lived and low-reproductive species present higher extinction risks than fast-living and high-reproductive ones[13].

Our findings have key management and conservation implications. First, easily measureable traits such as probability of reproduction and clutch size predict species' resilience to environmental stochasticity and fires. Species with high generation time and low reproductive output, despite being more resistant, take longer to recover and cannot compensate as much as species with faster paces of life. In our study, more resistant species have higher abundances under extreme fire regimes, while species that recover faster from disturbances have higher abundances at intermediate fire severities. Therefore, these results support the pyrodiversity hypothesis, whereby higher heterogeneity in fire regimes increases the resilience of different populations and communities[49]. Second, despite species having certain plasticity to cope with highly severe fire regimes, populations can attain alternative stable states[35] and take longer to recover from disturbances. Thus, traditional ecological community studies probably underestimate disturbance impacts, since

populations may persist in severe regimes, but not in optimal conditions. Third, reproduction is a key mechanism conferring higher compensation and faster recovery time, both in our species and others[18,21]. Accordingly, species with constraints on reproduction (*e.g.*, viviparity, fixed clutch size) may have higher resistance but take longer to recover from disturbances. Taken together, these key findings imply that, to enhance viable strategies after disturbances, managers should focus on generating suitable and heterogeneous habitats to facilitate the reproductive aspects of populations. The ability to quantify and predict the resilience components of 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[4].

Methods

Study area

We conducted this study at Reserva Ecológica do IBGE, RECOR (15°56’41” S, 47°53’07” W; 1,141 m above sea level; Supplementary Fig. S1), situated approximately 15 km south of Brasília, Distrito Federal, Brazil, in the core of the Cerrado biome. The climate there corresponds to the Aw (tropical with dry winter) type in Köppen’s classification and has a high intra-annual predictability[50]. Mean temperatures are mild year-round (20.6 ± 1.4 °C S.D.), varying between 18.0–22.4 °C. Conversely, precipitation is markedly seasonal, with a wet season between October and April, when ~94% of the 1417.0 mm mean annual occurs. The vegetation consists of a complex mosaic of savannas, grasslands, and gallery forests[51].

Our study site is an ideal natural experiment where 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) [52]. 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 as a result of the prescribed fire regimes[53].

To acquire the necessary demographic data to test our hypotheses, we sampled lizards in five plots (Supplementary 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 I (Supplementary Fig. S1). Fire severity increased in the following order C < Q < EB < MB < LB. In addition to the costs and difficulties of replication typical of large-scale ecologic studies, our experiment could not be replicated because of legal issues associated with burning the vegetation inside protected areas. While this approach may reduce the statistical power in our study, doing so is the only way to ensure the availability of adequate treatment levels in such a large design[54].

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), heliotherm, viviparous skink that inhabits savannas and forests in Amazonia and Cerrado[55,56]. Females of this species may bear up to nine embryos per reproductive season, carrying them for 10-12 months[55]. *Micrablepharus atticolus* (Gymnophthalmidae) is a Cerrado endemic, small-sized (up to 50 mm SVL), and heliotherm that inhabits open savannas and grasslands[57,58]. Females have a fixed clutch of 1-2 eggs, but can produce multiple clutches per reproductive season[59]. *Tropidurus itambere* (Tropiduridae) is a Cerrado endemic, medium-sized (up to 100 mm SVL), and heliotherm that

inhabits savannas and grasslands from central Cerrado[60]. Its females may lay multiple clutches of 5-8 eggs per season[61]. All three species are generalists, with diets consisting primarily of small invertebrates, with ants as the main prey for *T. itambere*[55,59,62]. In general, most lizard species can persist through intense fire episodes[63], but each of our species responds differently to fire-induced changes in the vegetation structure, mainly driven by microclimate and microhabitat preferences[53]. While *C. nigropunctatum* had fewer captures in intermediate levels of fire severity and increased in abundance after prescribed fires ended in 2009 (Supplementary Fig. S2), *M. atticolus* and *T. itambere* displayed the opposite pattern, with more captures in intermediate fire severity levels and decreased abundance after 2011 (Supplementary Fig. S2).

Population monitoring

To acquire the individual-level data used in our analyses, we captured individual lizards in study plots using pitfall traps with drift fences[53]. From November 2005 to December 2019, we opened traps for six consecutive days every month and checked them daily during this period. We recorded snout-ventral length (SVL) with a ruler (1 mm precision) from each captured individual, followed by marking by toe-clipping (after the appropriate bioethics approval 33786/2016) and release at the capture site. We also assessed the reproductive state by palpation in females. This assessment is possible because, when female lizards bear eggs, embryos, or enlarged follicles, they display a significant enlargement in their abdomens[64].

Migration may bias the vital rates estimates and the underlying effects of the experimental plots[65], here fire regimes. However, considering the distance between transects in adjacent plots (*ca*. 200 m; Supplementary Fig. S1A), the small size, and the territorial behavior of some species[66], we assumed no significant lizard movements among plots that could affect our results. Indeed, there were no inter-site recaptures, supporting our assumption.

Ecophysiological traits

To test (H1) whether ecophysiological traits shape how underlying vital rates and emergent life history traits respond to fire regimes, we estimated locomotor thermal performance curves (TPC[67]) and hours of activity (*ha*[68]) based on preferred temperatures from at least 10 individuals by each species. To build the TPCs, we determined the minimum and maximum critical temperatures by submitting individuals to cold and hot temperatures until we observed no righting response, *i.e*. complex muscular movements in response to a stimulus[69]. Individuals ran twice in three temperatures: at ambient temperature (25-28°C), at 5°C below and 5°C above said ambient temperature. We recorded the runs with a Casio® EX-FH25 digital camera and calculated their velocity with the Tracker software (https://physlets.org/tracker/). Next, we built generalized additive mixed models (GAMMs) with package GAMM4[70] for each species relating maximum speed with body temperature, including individuals as a random factor (Figs. S3-S4). To determine the preferred temperatures, we placed the individuals in a ~15–50 °C temperature gradient made of MDF plywood (0.15 m wide × 0.3 m high × 1.0 m long). We placed a 60 W incandescent lamp to generate heat in one corner and ice packs to cool in the other. We left lizards in the gradient for 1 h and recorded their body temperatures every minute with a 1 mm thermocouple attached with tape to their abdomen and connected to a data logger. We used the range between the 5th and 95th temperature percentiles as the preferred temperature range for each species (Figs. S3 and S5). After the experiments, we returned the individuals to their sites.

Weather and microclimate

To estimate temperature and air humidity in the different fire regimes, we used a mechanistic model using the ERA-5 dataset from the European Center for Medium-Range Weather Forecasts (ECMWF[71] following Kearney, et al. [72]). We included the canopy closure estimates in the model to account for the microclimatic differences among the different fire regimes (see Supplementary

Information for details on the canopy closure estimates). We initially had 14 microclimatic and 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*). To predict *perf*, we used the GAMMs for each species. We considered the hours of activity (*ha*) as the hours when microclimate temperatures were within the preferred temperature ranges from each species (Figs. S3 and S5). As the three species are diurnal, we only considered hours of activity when insolation was greater than zero. Supplementary Information presents the correlations and relationships among the variables (Supplementary Fig. S7).

Data analyses

Using different datasets integrated into Bayesian hierarchical models, we estimated each species' monthly vital rates (survival, growth, and reproduction). For survival (σ), capture probabilities (p), and recruitment per-capita rates (f), we used a combination of two mark-recapture models: Cormack-Jolly-Seber (CJS) and Pradel Jolly-Sebber (PJS) [73,74]. The CJS model related the survival to the individuals' SVL, while the PJS incorporated the monthly environmental variation. The PJS model is a time-symmetric open model that estimates survival (σ) and recruitment per-capita rates (f) [74]. 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. Supplementary Information presents the details and formulas of the parameters estimated in each model.

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}). To estimate p_{rep}, we used the records of reproductive and non-reproductive females captured in the field and related them to the individual's SVL_i using a Bernoulli distribution (see Supplementary Information for formulas). To estimate n_b, we fitted a Poisson distribution relating the number of eggs or embryos produced per female to the individual's SVL_i (see Supplementary Information for formulas). Due to logistical limitations, data on the number of eggs or embryos came from *ex situ* locations, mainly specimens deposited in the Herpetological Collection of the University of Brasília (CHUNB). We derived p_{rec} from the PJS model (see Supplementary Information for details).

We implemented the models for each species with JAGS in R, using the packages JAGSUI, RUNJAGS, and RJAGS[75,76]. We initially used four Markov chains of 50,000 iterations in the JAGS adaptive phase, discarded 50,000 iterations as burn-in, and sampled 10,000 estimates by a thinning rate of 10. We assessed convergence within and between MCMC sequences with trace and density plots and the potential scale reduction factor ($\hat{R}$), considering that convergence was satisfactorily approached when $\hat{R}$ was smaller than 1.1 for all parameters[77]. However, we experienced convergence issues with some parameters in the CJS and PJS models of *C. nigropunctatum* (specifically, for $\overline{\sigma_{PJS}}$) and *T. itambere* (for *f*). We ran these models with different parameterizations and MCMC settings to improve convergence (Supplementary Information).

To test H2, H3, and H4 (See Introduction), we used the vital rates parameters estimates to build stochastic Integral Projection Models (IPMs) using the IPMR package[32]. 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 modelling density dependence; this is a common approach when analyzing long-term demographic data[23], as it is our case. IPMs are structured population models where the vital rates are influenced by a continuously varying

phenotypic trait[78] (*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. In our IPMs, the P sub-kernel was determined by the $logit\left(\sigma_{CJS}(SVL_i)\right)$ and the growth function by $g(x,y) \sim N(SVL_{it}, \tau^2)$, where τ^2 is the standard deviation of SVL_{it}, considering the parameter samples of the Von Bertalanffy function from the hierarchical Bayesian model. The F sub-kernel was determined by:

$$F(x,y) = \left(p_{rec}(plot,t) + \ p_{rep}(SVL_i)\right) \cdot \ n_b(SVL_i) \ \cdot dSVL_{nb} \qquad \text{(Eq. 2)}$$

Where $dSVL_{nb}$ is the normal size distribution of newborns, with mean and standard deviations measured with the newborn individuals we captured in the field.

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[79]. 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[80].

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[81] on our monthly, species- and site-specific IPMs. We used the first time-step amplification ($\log_{10}$(reactivity)) and $\log_{10}$(attenuation + 1) as the measures for compensation and resistance, respectively, following Capdevila *et al*[16]. Recovery time was estimated as follows:

$$t_K = \frac{\log\left(\frac{\lambda_1}{\|\lambda_2\|}\right)}{\log(10)} \qquad \text{(Eq. 3)}$$

In equation 3, λ_1 and λ_2 correspond the dominant and subdominant eigenvalues of the *K* kernel, respectively.

Next, to test (H2) whether more severe fire regimes select for more resilient 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[82]. We related the demographic resilience components with the two life history traits and among plots. For compensation and recovery time, we used exponential error distributions, and for resistance we used a beta distribution. For each species, we included plot, year, and month as nested random variables to control for pseudoreplication. 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[33]. To implement this sensitivity, 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 4, 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[83].

$$S_p = \frac{Transient\ metric_{\ original} - Transient\ metric_{perturbed}}{p_{original} - p_{perturbed}} \text{ (Eq. 4)}$$

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Table 1. Traits related to reproduction, rather than environmental and ecophysiological parameters shape demographic resilience components (resistance, compensation, and recovery time). 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}	-0.013 ± 0.001	0.111 ± 0.004	0.052 ± 0.001
$\beta_{prepSVL}$	-1.523 ± 0.167	13.836 ± 0.784	8.023 ± 0.264
$\beta_{prepSVL}^2$	-44.495 ± 43.141	86.673 ± 102.262	-173.243 ± 108.166
α_{nb}	-0.035 ± 0.001	0.2 ± 0.001	-0.21 ± 0.012
β_{nbSVL}	-5.132 ± 0.215	27.562 ± 1.194	-6.326 ± 0.745
μ_K	0.004 ± 0.001	0.004 ± 0.001	0.03 ± 0.005
		Micrablepharus atticolus	
α_{prep}	-0.017 ± 0.005	0.035 ± 0.005	-0.103 ± 0.182

$\beta_{prepSVL}$	-0.678 ± 0.224	1.603 ± 0.219	-4.227 ± 8.933
μ_K	0.005 ± 0.001	0.005 ± 0.001	0.654 ± 0.251
	Tropidurus itambere		
α_{prep}	-0.022 ± 0.004	0.127 ± 0.02	0.059 ± 0.005
$\beta_{prepSVL}$	-1.721 ± 0.309	10.516 ± 1.557	5.573 ± 0.342
α_{nb}	-0.081 ± 0.007	0.296 ± 0.003	-0.033 ± 0.004
β_{nbSVL}	-5.744 ± 0.469	24.955 ± 0.319	5.312 ± 0.914
β_{nbSVL}^2	-1071.617 ± 179.069	1655.239 ± 163.511	3.747×10^{10} ± 9.308×10^{10}
μ_K	0.005 ± 0.004	0.005 ± 0.004	0.005 ± 0.004

Figure legends

Fig. 1. Weather and microclimate shape the survival and recruitment of *Micrablepharus atticolus* and *Tropidurus itambere*, but not for *Copeoglossum nigropunctatum*. However, ecophysiological traits were poor predictors of the vital rates, excepting for recruitment of *M. atticolus*. We tested whether ecophysiological traits and weather/microclimate shape how vital rates and emergent life history traits of three lizard species respond to different fire timings and frequencies. Model coefficients (mean and 95% confidence intervals) of the effects of environmental covariates on vital rates of three species of lizards corresponding to: *tmed2m* = mean air temperature at 200 cm height; *tmin0cm* = minimum air temperature at 0 cm height; *tmed0cm* = mean air temperature at 0 cm height; *RHmax* = maximum relative air humidity; *sol* = solar radiation; *precip* = accumulated precipitation; *perf* = mean locomotor performance; *ha* = hours of activity; *random* = monthly random variation. We group-colored the covariates related to weather, microclimate, ecophysiological traits, fire, and randomness. Species' silhouettes from photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais (*T. itambere*).

Fig. 2. Three-dimensional space of the demographic resilience components (resistance, compensation, and recovery time) for three species of lizards from the Brazilian Cerrado savannas, showing distinct demographic resilience strategies, with a high tradeoff between resisting, compensating against, or recovering from disturbances. With a 14-year mark-recapture dataset, we derived demographic resilience components from monthly stochastic Integral Projection Models shaped by weather, microclimate, ecophysiological traits, and fire covariates. Species' silhouettes from photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais (*T. itambere*).

Fig. 3. High severity fire regimes selects for populations with high compensation or resistance. Raw data, density, mean estimates, and 95% confidence intervals of the demographic resilience components: (A,D & G) resistance; (B, E & H) compensation, and (C, F & I) recovery time of three species of lizards: (A-C) *Copeoglossum nigropunctatum*, (D-F) *Micrablepharus atticolus*, and (G-I) *Tropidurus itambere* from the Brazilian Cerrado 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). Species' silhouettes from photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais (*T. itambere*).

Fig. 4. Populations with high generation time are characterized by high resistance, low compensation, and long recovery times from fires. However, the small-bodied species with fixed clutch size (*M. atticolus*) has low resistance when its populations have high generation times. 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*' compensation and resistance, we also offer inserts in D and E with a narrower y-axis range. Species' silhouettes from photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais (*T. itambere*).

Fig. 5. Populations with high reproductive output are characterized by low resistance, high compensation, and short recovery times from fires. However, the small-bodied species with fixed clutch size (*M. atticolus*) has low compensation and high resistance when its populations have high

reproductive output. 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 D with a narrower y-axis range. Species' silhouettes from photos taken by Nicolás Pelegrin (*C. nigropunctatum* and *M. atticolus*) and Carlos Morais (*T. itambere*).

Figure 1

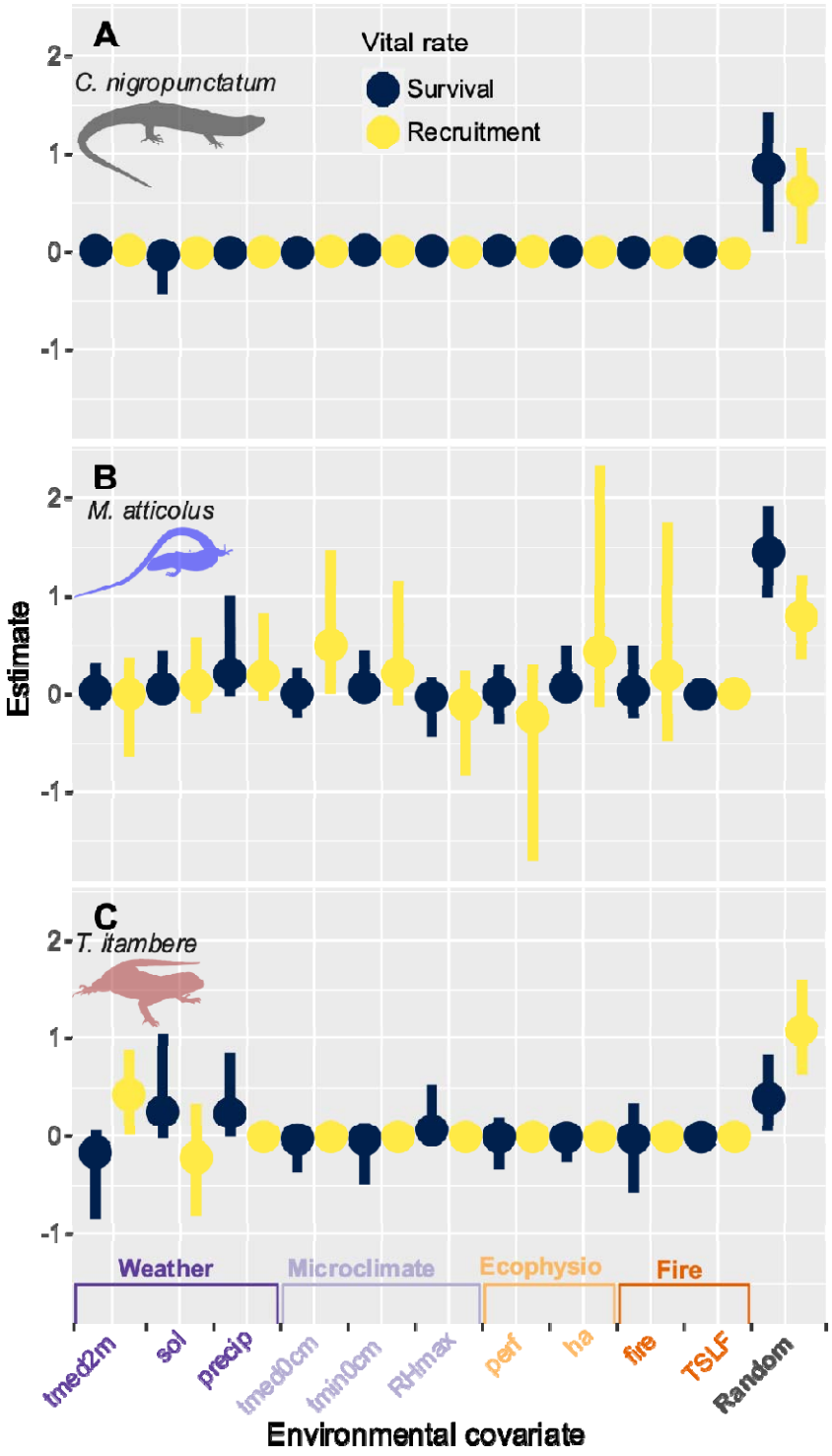

A
C. nigropunctatum
Vital rate
Survival
Recruitment
B
M. atticolus
C
T. itambere
Estimate
2
1
0
-1
Weather
Microclimate
Ecophysio
Fire
tmed2m
sol
precip
tmed0cm
tmin0cm
RHmax
perf
ha
fire
TSLF
Random
Environmental covariate

Figure 2

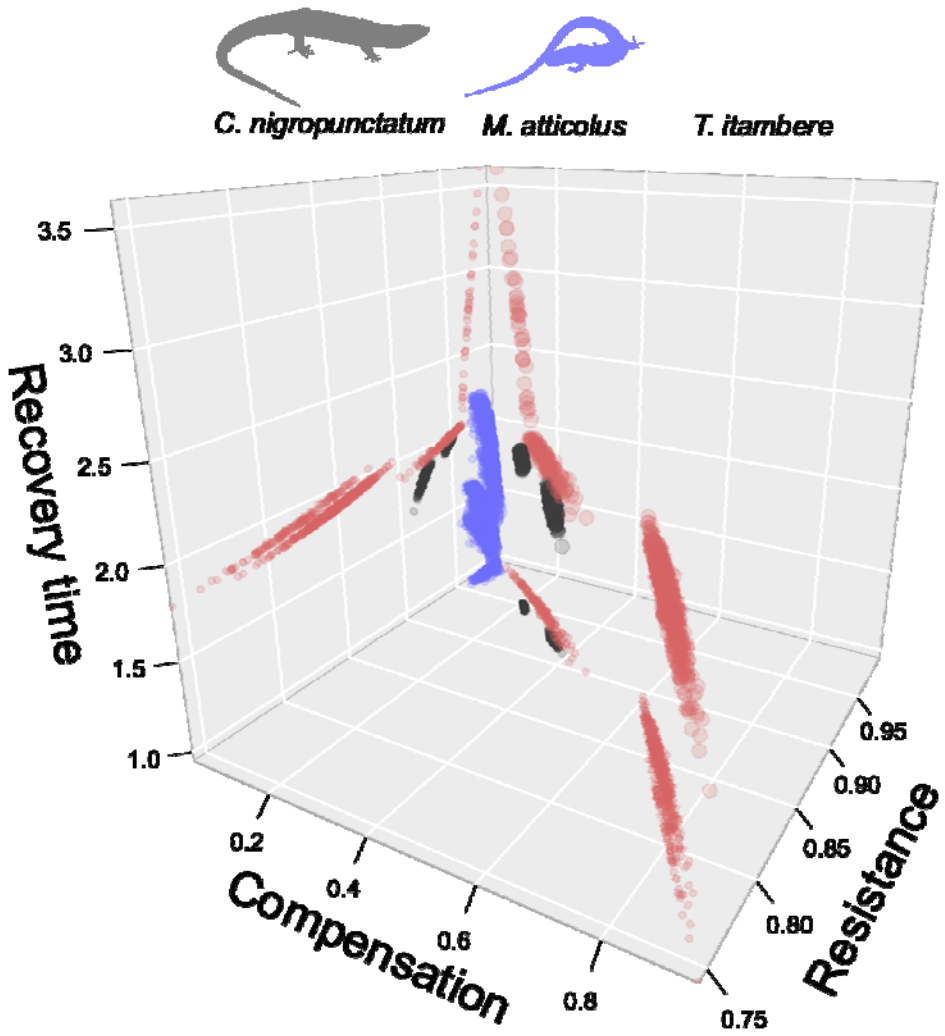

C. nigropunctatum
M. atticolus
T. itambere
Recovery time
3.5
3.0
2.5
2.0
1.5
1.0
Compensation
0.2
0.4
0.6
0.8
Resistance
0.95
0.90
0.85
0.80
0.75

Figure 3

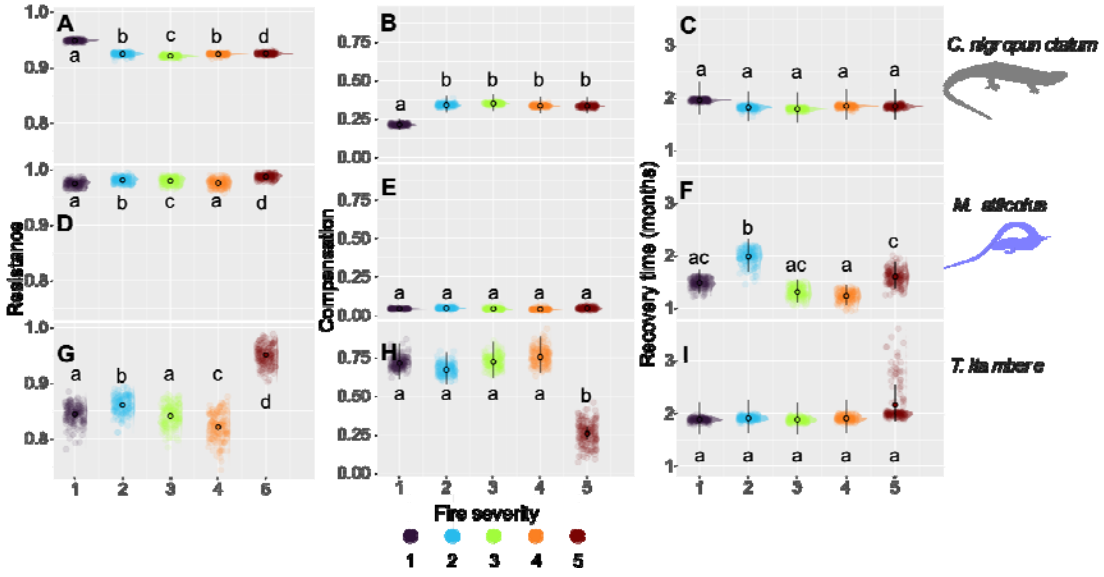

A
B
C
D
E
F
G
H
I
Resistance
Compensation
Recovery time (months)
Fire severity
C. nigropunctatum
M. atticolus
T. lambere

Figure 4

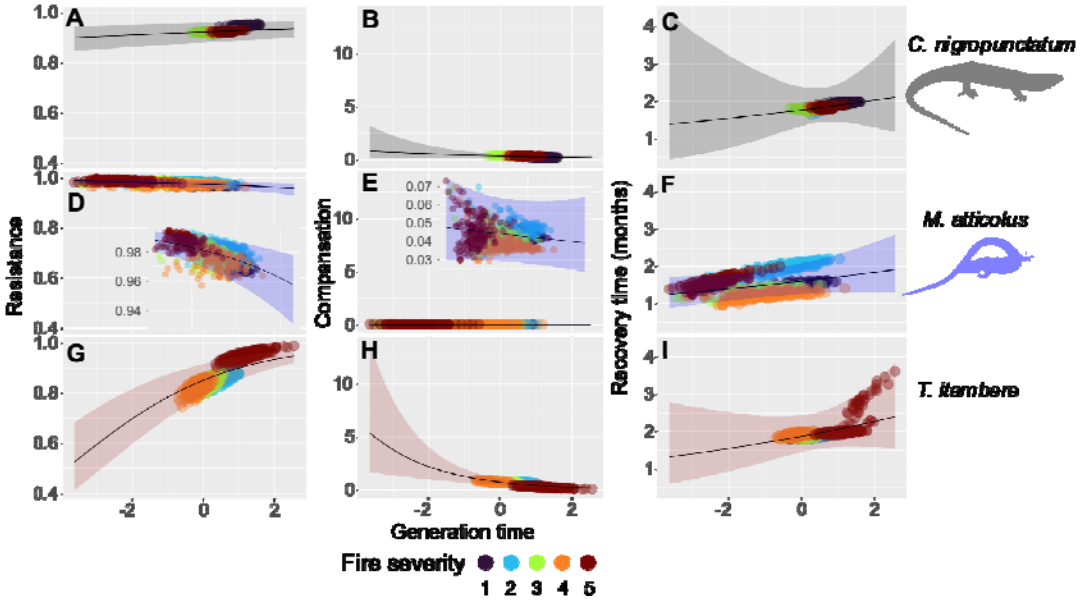
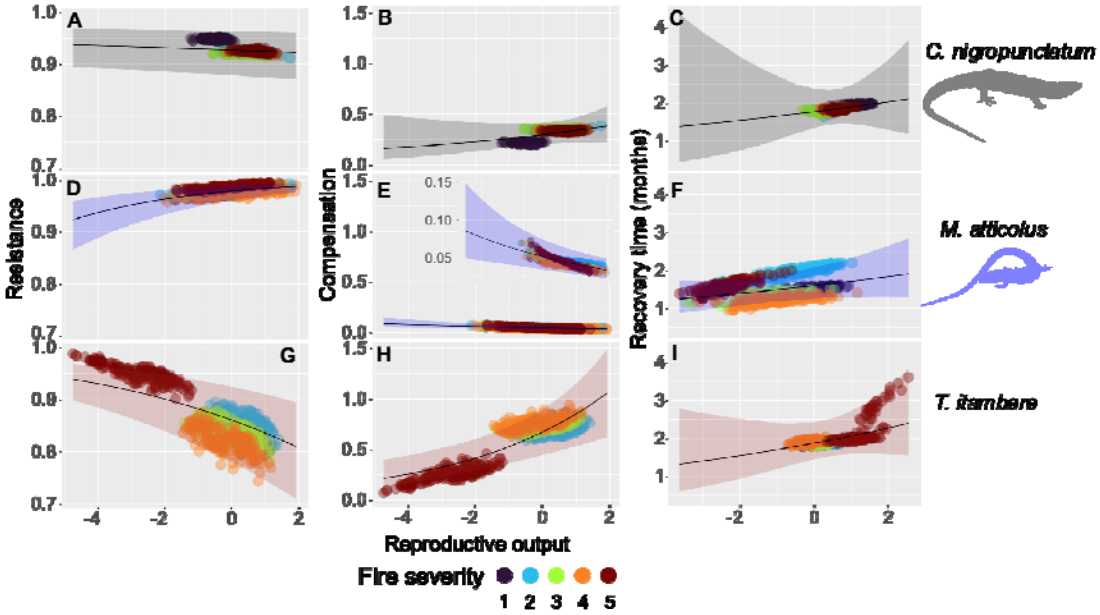

A
B
C
D
E
F
G
H
I
Resistance
Compensation
Recovery time (months)
Generation time
Fire severity
1 2 3 4 5
C. nigropunctatum
M. atticolus
T. itambere

Figure 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. alticolus
T. itambere