Universidade de Brasília

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EFEITO DE DESVIOS CLIMÁTICOS EM UMA POPULAÇÃO DE LAGARTOS DE UMA SAVANA ALTAMENTE ESTACIONAL

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Índice

Resumo

Os ciclos de vida dos organismos de savanas tropicais refletem o clima estacional e previsível de seu habitat. Nós investigamos os efeitos de desvios do clima típico do Cerrado em uma população de um organismo modelo, o lagarto *Tropidurus torquatus*. Identificamos quais componentes demográficos são afetados por esses desvios e qual sua influência no crescimento dessa população. Populações que evoluíram em ambientes estacionais têm seus ciclos de vida ajustados à estacionalidade, e podem não possuir mecanismos para lidar com imprevisibilidade no clima. Para ter um quadro mais completo de como mudanças climáticas afetam essas populações, é necessário avaliar a complexidade das relações de suas dinâmicas com o ambiente. Nós decompusemos seis variáveis climáticas locais em componentes estacionais e não-estacionais e, por meio de seleção de modelos usando dados de um monitoramento populacional de 12 anos de duração, avaliamos quais desses componentes, juntamente com componentes representando efeitos de fogo em curto e longo prazo, melhor descreviam as taxas vitais da população (sobrevivência e recrutamento). Então calculamos a sensibilidade do crescimento populacional a essas taxas. Descobrimos que a taxa de sobrevivência não está atrelada aos ciclos estacionais do clima, sofrendo apenas pequenas flutuações associadas a extremos climáticos. O efeito do fogo em longo prazo teve um efeito positivo sobre a taxa de recrutamento, que também mostrou uma forte influência dos ciclos climáticos estacionais. Estes foram responsáveis pela maior parte da variação no crescimento populacional. O recrutamento também foi afetado por desvios climáticos que causaram severas flutuações no número de recrutas entre ciclos reprodutivos. Isso resultou em uma influência negativa do recrutamento sobre o crescimento populacional, causando um acentuado declínio populacional ao longo do período de estudo. Essa espécie de lagarto, e provavelmente outros animais que evoluíram em condições similares, podem compensar os

efeitos sobre a população causados pelo fogo, uma alteração ambiental familiar a eles, porém não possuem mecanismos para lidar com desvios climáticos que não estiveram presentes em sua história evolutiva.

Introdução Geral

Em populações sob um regime aleatório de taxas de crescimento, espera-se que a taxa de crescimento total diminua conforme a variabilidade das taxas para cada ocasião aumenta (Lewontin & Cohen, 1969; Orzack, 1985; Tuljapurkar, 1989). A variação das taxas de crescimento pode ser minimizada ao diminuir-se a sensibilidade ambiental das taxas vitais, como sobrevivência e recrutamento (Pfister, 1998). Para que algumas características permaneçam constantes, outras podem ter que variar (Cannon, 1932; West, 2010). Plasticidade em características individuais que determinem taxas vitais podem atenuar a influência de fatores externos nestas, diminuindo sua variabilidade, isso é conhecido como tamponamento ambiental (Caswell, 1983; Pfister, 1998).

Um ambiente suficientemente variável pode reduzir a adaptabilidade de estratégias de vida que de outra forma seriam estáveis (Benton & Grant, 1996). Isso é conhecido como “crossover effect” (Tuljapurkar, 1989). É mais provável que plasticidade evolua em ambientes imprevisíveis (Bradshaw, 1965), a pressão seletiva para essa característica em espécies de ambientes previsíveis como savanas tropicais pode ser fraca, portanto mecanismos de tamponamento podem não ser fixados. Manter mecanismos que tornam a plasticidade possível, como genes e enzimas regulatórios, tem um custo energético (Moran, 1992). Portanto, a plasticidade reduzirá a aptidão de um organismo em um ambiente muito estável, e espera-se que a característica sofra seleção estabilizante nesses casos. Modelos atuais de mudanças climáticas predizem que climas locais tornar-se-ão mais variáveis e alcançarão extremos mais frequentemente (Easterling et al., 2000).

Enquanto mudanças climáticas recentes representam alterações atípicas em muitos ambientes, alguns fatores que alteram profundamente o habitat já ocorrem historicamente. O fogo ocorre naturalmente no Cerrado e é um fator ecológico importante para organismos locais (Coutinho, 1990; Miranda, Bustamante, & Miranda, 2002). O fogo pode ter efeitos positivos ou negativos sobre populações de lagartos, dependendo das características das espécies (Faria, Lima, & Magnusson, 2004; Fenner & Bull, 2007; Griffiths & Christian, 1996; Mushinsky, 1985).

Tropidurus torquatus Wied, 1820 é um lagarto heliotérmico, territorial e típico forrageador senta-e-espera, localmente abundante e tem a maior distribuição do gênero, ocorrendo no Brasil, Uruguai, Paraguai e Argentina (Rodrigues, 1987). Em populações desse lagarto, tamanho populacional, recrutamento e estrutura etária variam estacionalmente, refletindo o ciclo reprodutivo da espécie (Wiederhecker, Pinto, Paiva, & Colli, 2003). Essas são características de espécies com alto investimento em reprodução, baixo investimento em sobrevivência e ciclos de vida curtos (Tinkle, Wilbur, & Tilley, 1970; Tinkle, 1969). Aqui, investigamos se uma população de *T. torquatus* no Cerrado é sensível a variação climática além daquela típica da estacionalidade local, e também a efeitos em curto e longo prazo de queimadas. Como a população habita um ambiente cíclico, previsível e propenso a queimadas, nós esperamos que ela apresente mecanismos de tamponamento para lidar com efeitos imediatos do fogo e com a alteração de habitat resultante, porém que não seja capaz de lidar com desvios do ciclo climático típico causados por mudanças climáticas globais.

Materiais e Métodos

Nós monitoramos uma população de *Tropidurus torquatus* na mata de galeria do córrego Monjolo na Reserva Ecológica do Roncador (RECOR), em Brasília, Distrito Federal, na região central do Cerrado (15°55'51.37" S, 47°53'1.99" W). A área era protegida de fogos desde 1975, quando foi criada a reserva, até uma queimada em 1994. Duas outras queimadas ocorreram em Julho de 2005 e Outubro de 2012. Nós capturamos os lagartos com 20 armadilhas de interceptação e queda, que eram checadas duas vezes por semana, de Junho de 2000 a Maio de 2012 e demos a cada um uma marcação permanente e individual por meio de corte de falanges.

Dados climáticos para o período de estudo foram medidos na estação meteorológica da RECOR. Os parâmetros usados foram médias mensais de temperatura mínima, temperatura média, temperatura máxima, precipitação, umidade e insolação. As séries temporais de dados climáticos foram divididas em componentes estacionais e não-estacionais por meio de decomposição por LOESS (Cowpertwait & Metcalfe, 2009).

Nós usamos os históricos de captura dos lagartos para estimar parâmetros demográficos usando o pacote *RMark* (Laake, 2013) que constrói modelos para o Programa MARK (White & Burnham, 1999). Nós ajustamos modelos do tipo Pradel (que produzem estimativas para probabilidade de sobrevivência, recrutamento e taxa de crescimento populacional) aos componentes da decomposição das series climáticas e a componentes representando os efeitos em curto e longo prazo das queimadas. Baseado no critério de informação de Akaike (AIC), nós selecionamos os melhores modelos, aqueles com diferença de AIC para o melhor modelo menor que 7 (Burnham & Anderson, 2002). Em seguida, fizemos a média dos parâmetros desses modelos, ponderada pelo AIC de cada modelo, e somamos a frequência de cada variável nos modelos selecionados, ponderada pelo AIC de cada modelo, para determiner a importância das variáveis (Cooch & White, 2006).

Nós calculamos a taxa de crescimento total para cada ciclo reprodutivo, para compará-los sem interferência da variação interna dos ciclos. Esse cálculo foi feito pelo produto das taxas de crescimento em cada ciclo. Para ter uma estimativa da taxa de crescimento média dos ciclos, calculamos a media geométrica de todas as taxas de crescimento mensais elevada ao comprimento de um ciclo em meses (Lewontin & Cohen, 1969). Depois de decompor cada taxa vital (sobrevivência e recrutamento) por LOESS, calculamos a sensibilidade da taxa de crescimento a cada componente, dividindo a variação de cada componente pela variação da taxa de crescimento (Cooch & White, 2006).

Resultados e Discussão

A probabilidade de sobrevivência nessa população diminuiu em meses em que os componentes não-estacionais de temperatura mínima atingiam valores muito baixos e em que os de temperatura máxima atingiam valores muito altos. Isso sugere que permanecer em certa faixa de temperatura é o fator ambiental mais importante para esses lagartos permanecerem vivos. Porém, a análise de sensibilidade mostrou que essas restrições à sobrevivência são de menor importância para o crescimento populacional quando comparadas com o recrutamento. Recrutamento foi afetado por componentes estacionais e não-estacionais e também por um componente de fogo, reflexo do ajustamento do ciclo reprodutivo da espécie à estacionalidade climática, influência positiva de efeitos do fogo em longo prazo e sensibilidade a desvios climáticos. A taxa de crescimento foi muito mais sensível ao recrutamento, somando-se os componentes estacionais e não-estacionais, (0.99) do que à sobrevivência (0.01). É compreensível que o crescimento populacional seja mais afetado pela repentina entrada de indivíduos a cada ciclo reprodutivo, porém a sensibilidade do crescimento ao componente não-estacional do recrutamento (0.24), ainda é muito maior do que à sobrevivência (0.01), mostrando que são flutuações no número de recrutas a cada ciclo reprodutivo que determina o crescimento populacional. O fogo teve um efeito benéfico para a população em longo prazo, porém não o suficiente para compensar os efeitos dos desvios climáticos sobre o recrutamento.

A instabilidade e mudanças abruptas nas taxas de crescimento entre ciclos reprodutivos evidenciam alta resiliência na população, permitindo-a recuperar-se rapidamente se houverem condições adequadas. Porém, a magnitude da instabilidade ambiental a que essa população está submetida parece estar além dessa capacidade de resiliência. Com uma taxa de crescimento média de 0.79 por ciclo reprodutivo, essa população está em severo declínio. Instabilidade no número de recrutas a cada ciclo está fazendo essa população encolher, o que é coerente com estudos anteriores (Pfister, 1998). Como os componentes estacionais são idênticos entre anos, a instabilidade parece ser causada por desvios do clima típico local.

Como a espécie evoluiu em um ambiente historicamente sujeito a fogo, a população foi capaz de tamponar os efeitos das queimadas, até mesmo se beneficiando dos efeitos em longo prazo. Isso mostra que eles têm mecanismos para lidar com alterações ambientais, desde que estas sejam familiares à história evolutiva da espécie. Isso contrasta com a incapacidade que a população apresenta em lidar com desvios climáticos, que causaram efeitos muito negativos sobre o crescimento populacional. A alta previsibilidade do clima do Cerrado pode não ter imposto pressão seletiva suficiente durante a história evolutiva de seus organismos para que esses evoluíssem mecanismos para lidar com mudanças rápidas e imprevisíveis. Com o clima global tornando-se mais imprevisível e alcançando extremos mais frequentemente (Easterling et al., 2000), e populações tornando-se menores devido a fragmentação de habitat, estas podem tornar-se mais instáveis e declinar. Se os padrões aqui encontrados repetirem-se em outras espécies do Cerrado ou qualquer outro ambiente, isso pode acontecer ainda mais rápido. Além disso, esses resultados contribuem para recentes descobertas que indicam que um declínio mundial da fauna de lagartos (Sinervo et al., 2010).

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Climate deviation effects on a lizard population from a highly seasonal savanna

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Summary

1. Tropical savannas present seasonal and predictable climate, which reflects on the life cycle of its wildlife. We investigated the effects of deviation from typical climate of the Brazilian Cerrado on the population dynamics of a model organism, the lizard *Tropidurus torquatus*, identifying demographic components that are affected by those deviations and determining their influence on population growth.

2. Populations that evolved in seasonal environments have their life cycles attuned to this seasonality, and might not have mechanisms to deal with unpredictability. To get a complete picture of how climate change affects those populations, it is necessary to address the complexity underlying the relation of their dynamics with the environment.

3. We decomposed six local climate variables into seasonal and non-seasonal components and, through model selection with data from a 12-year mark-and-recapture survey, assessing which of those factors, along with long and short term fire effects, better accounted for variation in population vital rates (survival and recruitment) and calculated the sensitivity of population growth to those vital rates.

4. We found that survivability was not attuned to climate seasonality; instead, it suffered minor fluctuations associated with temperature extremes. Recruitment benefitted from long-term fire effects and had a strong seasonal effect that accounted for most of the variation in population growth. It was also affected by climate deviations, which led to severe fluctuations in the number of recruits each year, with an overall negative effect to population growth, which was much more sensitive to recruitment than to survival, resulting in a sharp population decline over the study period.

5. This lizard species, and probably other animals that have evolved in similar conditions, can buffer the demographic effects of fire, an environmental alteration familiar to them, but lack mechanisms to deal with climate deviation that was not present in their evolutionary history. Recruitment sensitivity can be very important to population dynamics in the context of climate change, and that it is a key aspect to be addressed on population persistence studies and extinction predictions.

Key-words: Cerrado, climate predictability, demography, environmental buffering, evolution, global warming, life history, population ecology, Squamata, tropical savannas

Introduction

Population growth is the result of entries and departures of individuals, often expressed as vital rates such as survival, recruitment or fecundity (Bogue, 1969). Vital rates are outcomes of the interaction of individual traits, such as life history characteristics and physiological limitations, with external factors, such as climate or species interactions (Moss, Watson, & Ollason, 1982) or of inherent aspects of population dynamics, such as the Allee effect (Allee, 1978; Courchamp, Berec, & Gascoigne, 2009; Stephens, Sutherland, & Freckleton, 1999). In populations under a regime of random growth rates, the overall growth rate is expected to decrease as the variability in growth rates for each occasion increases (Lewontin & Cohen, 1969; Orzack, 1985; Tuljapurkar, 1989). In other words, in randomly varying environments the extinction probability of populations may eventually approach unity if they can't cope with variability in vital rates. However, serial autocorrelation in growth rates will slow this convergence down, especially in cyclic environments with fixed frequencies (Lewontin & Cohen, 1969; Orzack, 1985; Tuljapurkar, 1989). The variation in growth rates can be minimized by decreasing the sensitivity in vital rates and their underlying traits, especially life history traits (Pfister, 1998).

Stochasticity in demographic rates may arise from sampling effects, because they are a by-product of individual probabilities of survival and reproduction. But these effects are only significant in very small populations, as variation in larger populations is governed by factors influencing all individuals, such as climate, interacting species or random catastrophes (Lande, 1993, 1998). The influence of environmental fluctuations and random catastrophes will depend on the mean and variance of environmental factors and the magnitude and frequency of catastrophes, and even small populations subject to these factors can persist if their growth rate is large enough (Lande, 1993). Too much sensitivity of vital rates to external factors is non-adaptive, as population growth rate can be interpreted as average *per capita* fitness (Cole, 1954; Fisher, 1930).

In order for some organism traits to remain constant, others might have to vary (Cannon, 1932; West, 2010). It has been argued that, for a given character, genotypes with wider ranges of expression would be most often selected than genetic polymorphism (Lewontin, 1957; Orzack, 1985) and that selection would act as to buffer species from environmental changes (Hartl & Cook, 1973). However, the advantage of buffering will depend on the frequency and autocorrelation of environmental changes (Orzack, 1985). Plasticity in individual traits underlying sensitive vital rates might attenuate the influence of external factors on those, reducing their variation. This is known as environmental buffering (Caswell, 1983; Pfister, 1998) and has been demonstrated for both long (Gaillard & Yoccoz, 2003) and short-lived organisms (Reed & Slade, 2012).

Different life history traits can be selected, depending on environment variation and correlation structure (Benton & Grant, 1996), i.e., a sufficiently variable environment might reduce the fitness of otherwise stable life history strategies. This is called the “crossover effect” (Tuljapurkar, 1989). As plasticity is more likely to arise in unpredictable environments (Bradshaw, 1965), selection on species from predictable environments like tropical savannas may be weak, so that efficient environmental buffering mechanisms may not be fixed. Organisms from such environments have life cycles adjusted to climate seasonality (Martins, Bonato, Da-Silva, & dos Reis, 2006; Ribeiro, Rocha, & Marinho-Filho, 2011; Vasconcellos & Colli, 2009) and demographic sensitivity can be evaluated as departures from these typical cycles. Maintaining the mechanisms that make plasticity possible, such as regulatory genes and enzymes, has an energetic cost (Moran, 1992). Further, plasticity genes may have more complex consequences and interactions, such as negative pleiotropic and epistatic effects, links to other genes that might cause low fitness and developmental instability (DeWitt, Sih,

& Wilson, 1998). Therefore, plasticity will reduce fitness under stabilizing selection, such as in less variable environments, and is likely to be selected away.

Current models of climate change predict that local climates will become more variable and reach extremes more often (Easterling et al., 2000). Thus, it is important to understand if organisms from predictable environments can cope with new climate patterns. Apparently, demography is more important than genetics to determine minimum viable population size (Lande, 1998). As habitat fragmentation makes populations smaller and more isolated, it is crucial to understand population dynamics, as small populations will be more affected by stochastic demographic factors (Lande, 1993). Environmental variation will affect both large and small populations (Lande, 1993), and human influence might make this variation exceed the capacity organisms have evolved to deal with (Chevin, Lande, & Mace, 2010).

Contrasting with the unpredictable alterations recent limate change might bring, some environments are subject to events present in their history that can alter habitats profoundly. Fire occurs naturally in the Cerrado and is an important ecological factor to local organisms (Coutinho, 1990; Miranda et al., 2002). Natural fires are caused by lightning in the beginning of the wet season (Miranda et al., 2002; Ramos-Neto & Pivello, 2000), whereas human–induced fires tend to be more frequent and intense, and to occur during the dry season (Miranda et al., 2002; Mistry, 1998). In gallery forests, fire will cause high tree mortality, creating clearings that will favor colonization by pioneer species, like grasses (Seeliger, Cordazzo, & Barbosa, 2002). Fire can have positive or negative effects on lizard populations, depending on species characteristics (Faria et al., 2004; Fenner & Bull, 2007; Griffiths & Christian, 1996; Mushinsky, 1985). Many Cerrado lizards are well-adapted to fire and do not suffer from direct and short term effects (Costa, Pantoja, Vianna, & Colli, 2013).

Tropidurus torquatus Wied, 1820 is one of the most abundant and conspicuous lizards in Brazil. It is very common in urban areas, but in natural vegetation sites it inhabits mostly forest edges and glades, being notably absent from adjacent open areas, where it is replaced by other congeneric species like *T. itambere* (Nogueira, Valdujo, & França, 2005). It is a heliothermic and territorial lizard. A typical ambush hunter, it feeds mostly on arthropods and occasionally on plant items, it is locally abundant and has the widest distribution in its genus, occurring in Brazil, Uruguay, Paraguay and Argentina (Rodrigues, 1987). In Brazil it occurs through most part of the Cerrado, and in some areas of the Atlantic Forest (Rodrigues, 1987). Population size of this lizard, recruitment and age structure vary seasonally, reflecting the species reproductive cycle (Wiederhecker et al., 2003). Populations show high turnover rates, for even though lifespan reaches three years, most individuals don't live beyond one year (Wiederhecker et al., 2003). Those are characteristics of species with high investment in reproduction, low investment in survival and short life cycles (Tinkle et al., 1970; Tinkle, 1969).

Herein, we investigate if a Cerrado population of a model organism, *T. torquatus*, is sensitive to climatic variation beyond that typical of local seasonality and to the short and long-term effects of fire. Lizards are considered good models for ecological studies because they are ectothermic and generally small-bodied. Since the population inhabits a very predictable, cyclic and fire-prone environment, we predict it should present buffering mechanisms to cope with the immediate effects of fire and the resulting habitat alteration, but lacks this capacity to deal with deviations from climate seasonality caused by global climate change. We expect the population to be attuned to the typical weather cycle and to be sensitive to non-seasonal weather fluctuations, as well as being immune to short and long-term fire effects.

Materials and Methods

STUDY AREA

We monitored a population of *Tropidurus torquatus* in the gallery forest of Monjolo creek at Reserva Ecológica do Roncador (RECOR), a 13.6 km² wide ecological preserve at Brasília, Distrito Federal, at the central region of the Brazilian Cerrado (15°55' S, 47°53' W). Local climate is Aw in Köppen’s classification (Haffer, 1987), it has a marked seasonality, with a wet season from October to April, followed by a dry season from May to September (Nimer, 1979). The forest follows the creek from its headspring, ranging from 120 m to 160 m width throughout its extension. The creek’s bed is well defined, with no flooding areas. The soil is mainly dark-red latosol with spots of red-yellow latosol with plinthite outcrops. The topography is plane on the creek’s headspring, sloping downstream. The area was protected from fires since 1975, when of the preserve creation, until a fire in 1994, which caused retreat of the forest border, death of trees, opening of glades and densification of shrub and herb layers. Two other fires occurred in July 2005 and October 2011, further defacing the forest. The fires have also favored an alien grass, *Melinis minutiflora*, which forms very dense shrubs, outcompeting local species and making the site more fire-prone.

DATA COLLECTING

We trapped lizards with 20 arrays of pitfall traps, visiting the site twice a week, every week, from June 2000 to May 2012. Each array consisted of one 30 l central plastic bucket buried to the ground, surrounded by three more 30 l buckets 6 m away from the center. The peripheral buckets are connected to the central one by 6 m long and 0.5 m high galvanized foil fences, angled 120º from each other, giving an “Y” figure to the array. We measured the snout-vent length (SVL) of captured lizards with a ruler (1 mm precision) and gave them a permanent, individual numerical identity by toe clipping, so individuals could later be identified if recaptured. The capture history of individuals was kept in a binomial record, by assigning the value “1” to each individual in the months they were captured and “0” in the months they were not captured.

Climate data for the study period was measured at RECOR's weather station. The weather parameters we used were monthly means of minimum daily temperature (*tmin*), mean daily temperature (*tmed*), maximum daily temperature (*tmax*), relative air humidity (*humid*), daily precipitation (*precip*) and daily hours of insolation (*sun*). We also used climate normals from 1960-1990 for the same weather parameters (Ramos, Santos, & Fortes, 2009).

STATISTICAL ANALYSES

To determine the length and timing of the population’s reproductive cycle, we plotted the SVL at each capture against the time (month) of capture. To check for seasonality in the climate time series, we searched for seasonal patterns on autocorrelation plots. An autocorrelation plot will show the correlation of the time series with itself on different lags, effectively showing the correlation between observations inside the series at any point. A consistent pattern of correlation in regular intervals indicates a cyclical pattern. To determine the length of seasonal cycles we plotted the spectral density of each time series, which will indicate which wave frequency has the highest spectral density for that time series, that is, the wave of a frequency that better explains the cyclical variation in the series (Cowpertwait & Metcalfe, 2009). We checked for the presence of an overall downward or upward trend in the climate through model selection, using linear mixed-effect models (LME) to control for temporal pseudoreplication. We built one model with a trend component and one without it for each variable, using package *lme4* (Bates, Maechler, & Bolker, 2012) of R (Team, 2005), and compared them with the Pearson χ^2 statistic to test the significance of the reduction in scaled deviance (Crawley, 2012). Next, we separated the seasonal, trend, and stochastic components of each time series via seasonal decomposition by LOESS (Cowpertwait &

Metcalfe, 2009). If the time series had a significant overall trend, it was accounted in the model selection as a directional shift in the climate cycles and the stochastic component accounted for climate deviation from the typical cycle. If the time series did not have a significant overall trend, the trend component was added to the stochastic component and treated as a residual non-seasonal component, accounting for climate deviation. After that, we determined the percent of variation summarized by each component by dividing the component variation by the total variation. We also performed Granger tests (Granger, 1969), using package *lmtest* (Zeileis & Hothorn, 2002), to check the predictability between the seasonal component of each climate series and the 30-years climate normals, repeated yearly, to assess whether the seasonal component is representative of historical climate.

We used the capture histories from June 2000 to May 2012 to estimate demographic parameters using package *RMark* (Laake, 2013), which builds models for Program MARK (White & Burnham, 1999). We fitted Pradel models to the decomposed components of climate time series and also components for short-term (*sfire*) and long-term (*lfire*) fire effects: *sfire* was a categorical effect at every month for one year after each burn occasion, and *lfire* was a categorical effect at every month after the first burn until the end of the study period. These models estimate probabilities of survival (Φ), recapture (p), *per capita* recruitment (f) and, by derivation, population growth rate (λ). The results concerning recapture probabilities (p) are not reported here, as they are not relevant to the questions we posed.

Before proceeding with the model selection, we first tested the goodness-of-fit of a fully time-dependent Cormack-Jolly-Seber model [there are no available goodness-of-fit tests for Pradel models (Cooch & White, 2006)] with U-CARE v2.3.2 (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). If this more general model fits well the data, any other time variant model with the same structure should fit as well. Based on the Akaike information criterion corrected for finite sample sizes (AIC_c), we selected the best models, those with ΔAIC_c (distance to best model AIC_c) smaller than 7 (Burnham & Anderson, 2002). Then, we averaged the parameters from the selected models, weighting them by their AIC_c, and also recorded the frequency of each environmental variable among selected models, weighting by their AIC_c, to determine variable importance (Cooch & White, 2006).

We derived population growth rate (λ) simply by adding survival probability (Φ) and *per capita* recruitment (f) for each occasion (Cooch & White, 2006). We calculated the overall growth rate for the length of each reproductive cycle, to compare them without interference from intra cycle variation. We assessed the growth rate for each reproductive cycle by the product of the growth rates from that cycle, and the mean growth rate by calculating the geometric average of all month growth rates to the power of a cycle length (Lewontin & Cohen, 1969). After decomposing the vital rates via LOESS decomposition, we calculated the sensitivity of the growth rate to each component of the decomposed vital rates dividing the variance of the component by the variance of the growth rate (Cooch & White, 2006).

Results

Throughout the study period, we made 752 captures, marked 420 individuals and had 332 recaptures. The number of captures varied seasonally, peaking in September–October, the onset of the rainy season (Fig. 1a). There was a great variation in the number of captures in each annual peak, but these peaks always occurred at the same time of the year, in the wet season. Peaks were mostly due to capture of juveniles (SVL < 65mm, Wiederhecker, Pinto & Colli 2002), most of which disappeared after November. Occasionally, even smaller individuals (SVL < 40mm) were captured in April or May and adults (SVL > 65mm) were captured year-round (Fig. 1b). So we delimited the reproductive cycle to begin in November, when all individuals at the population are sexually mature, and end in October, when recruits from that cycle are reaching sexual maturity. This way, each cycle should comprehend the mating period, gestation, laying, incubation and hatching of eggs and the growth until sexual maturity of the recruits born in that cycle.

As expected, all climate variables showed a cyclical autocorrelation pattern (Fig. 2) and all had their highest spectral density near the frequency of 0.083 (Fig. 3), the frequency of a 12-month cycle, indicating that climate is constant in its annual seasonality. The time series for mean and maximum temperature had a more irregular autocorrelation pattern and showed a secondary peak of spectral density near 0.166, the frequency of a 6-months cycle. Those two series were also the only ones not predictable by historical climate series (Granger test, $P > 0.05$, Table 1), so seasonal components of those two time series cannot be interpreted as representative of historical climate, and if selected in the demographic model selection, should be viewed as the effect of this new abnormal cycle in the lizard's demography. We found no overall upward or downward trend among climate variables (Table 1), indicating no clear directional shift in climate cycles, so trend and stochastic components were added for all of them and treated as a non-seasonal residual component in the demographic model selection. The seasonal components were responsible for most of the variation in all climate variables, ranging from 62.6% to 86% (Table 1).

The goodness-of-fit test showed no overdispersion of the data in relation to the most general model ($\chi^2_{190} = 96.88$, $P \sim 1.00$), therefore the structure of the general model comprehends the variation in data and there was no need to adjust the AICc of models for lack of fit. A total of 71 models with ΔAIC < 7 were selected for averaging (Table 2). Only residual components were selected for survival probability (*tmin* and *tmax*), while recruitment was explained both by seasonal (*humid* and *precip*) and residual components (*tmin*, *sun* and *precip*) and by long-term fire effects (*lfire*). As such, survival showed a constant pattern with minor variations, while recruitment occurred only from June to September, peaking in July, with severe year-to-year variations (Fig. 4a). Mirroring recruitment, growth rates for each reproductive cycle (November to October) varied markedly, sometimes going from sharp decline to increase in adjacent cycles (Fig. 4b). Total population growth rate for the November-October period each year was very unstable, ranging from 0.49 to 1.66, but rarely staying close to 1. Mean growth for the population over a seasonal cycle of a year was 0.79, indicating a decline through the study period. Survival probability could not be decomposed to calculate the sensitivity of the growth rate to it, because it had no seasonal component, so it was treated as a residual component itself. Growth rate was more sensitive to the seasonal component of recruitment (0.75), next to the residual component of recruitment (0.24) and then to survival (0.01).

Discussion

The SVL patterns agree with those observed in a population of *T. torquatus* in an urban area from another site in Brasília (Wiederhecker et al., 2003), with population age structure varying seasonally, in consonance with the species reproductive cycle. Juveniles were present from April to October, and virtually disappeared after November, due to the species early age of maturity, approximately five months (Pinto, 1999). The similarity between those areas may indicate lack of plasticity in the lizard’s life cycle, as those sites differ greatly in every habitat aspect and are separated by over 10 km of urban and open Cerrado areas.

Survival in the population was reduced in months when minimum temperature was too low and in those when maximum temperature was too high (coefficients: *tmax*=-0.38, *tmin*=0.20). This suggests that staying in a certain temperature range is the most important environmental factor for those lizards to stay alive. But the sensitivity analysis showed that those constraints in survival are of minor importance for population growth in face of recruitment.

Recruitment was affected by seasonal and non-seasonal components, and also by a fire component. This shows an attunement of the reproductive cycle with climate seasonality, positive influence of long-term fire effects and sensibility to small departures from typical climate seasonality. Recruitment, as a vital rate, might represent the success in several stages of the lizard reproduction, such as the number of females reproducing, number of eggs laid, survival of eggs or hatchlings. So, the residual climate variables selected might be affecting recruitment in any of those stages. Examining the coefficients of the most important residual climate variables, we are presented with an odd figure: recruitment will decrease in months that won't reach low enough temperatures (*tmin*=-0.17), that are too sunny (*sun*=-0.94) and too rainy (*precip*=-0.06). Trying to explain those figures in a *post hoc* approach might prove a naïve effort, as the effects might operate in far more complex levels, considering all the possible stages of reproduction that might be affected in different ways and the lags between effect and consequence in recruitment, opposed to probability of survival, which might suffer more direct and immediate effects of climate. But it is enough to say that departures in climate are affecting the dynamics of this population, and their effect upon recruitment was the most important to population growth rate, which had a sensitivity of 0.99 to recruitment, summing the seasonal and residual components. It is understandable that population growth will be mostly affected by the sudden entrance of individuals every reproductive cycle, but the sensitivity of growth to the residual component of recruitment (0.24) is still much higher than to survival (0.01), showing that it is truly deviations in the number of recruits every year that drive population growth. The long-term fire effect was beneficial to this population (coefficient: *lfire*=0.29). The change in microhabitat structure caused by fire might have benefited recruitment in many ways: it may have excluded hatchlings' predators or competitors, improved microhabitat condition for eggs or increased resources availability, but its beneficial effect was not enough to compensate for the effects of climate upon recruitment.

Even though the seasonal pattern for maximum and minimum temperature series did not correspond to historical climate, those variables were not very important to vital rates (Table 2). This suggests that lizards might be able to buffer for those changes if there is enough regularity, and only truly unpredictable changes would affect them. The instability and abrupt shifts in growth rates between reproductive cycles show that this population is highly resilient and can recover quickly given the adequate conditions, probably due to their life history characteristics, such as short life cycle and high investment in reproduction. But the magnitude of environmental instability this population is going through seems to be too much for their inherited capacities. With a mean growth rate of 0.79 per year, this population is in sharp decline. Instability in the annual number of recruits is causing this population to shrink (Fig. 4), which is coherent with previous findings for animal and plant species (Pfister, 1998). As the seasonal components are identical between years, this decline seems to be caused by the climate departures, despite the positive effects of fire.

Because the species evolved in a fire-prone environment, the population was able to buffer the effects of the catastrophe and the resulting severe habitat alteration on its survival, and even took advantage of long-term alterations to improve recruitment, showing they have mechanisms to cope with environmental change, if the species is familiar with the type of change. This, and the fact that they were not affected by the seasonal components of climate variables that did not correspond to historical climate, contrasts with their inability to deal with climate deviation, which had detrimental effects that could even compensate for the positive effect of fire in recruitment. It seems that through high resilience associated with life history characteristics, this population can endure great habitat alterations and even climate shifts, given that there is a historical presence or certain regularity and predictability in those disturbances. On the other hand, rapid and unpredictable changes in climate might grievously impair reproductive efforts, frustrating whole recruitment occasions. High predictability and seasonality in the Cerrado climate may not have imposed enough selective pressure during the evolutionary history of its organisms to evolve rapid variability control mechanisms. Even though, the population still struggles and takes advantage of appropriate conditions to try and compensate for previous bad recruitment occasions, sometimes presenting very high growth rates. However, in the end this instability seems to be driving the population to extinction.

Our results also highlight an important feature that might have been overlooked in climate driven extinction risk projections: the role of reproduction. That is in fact the most critical aspect for population's persistence: surviving individuals will do no good if they do not reproduce. Predictions based purely on adult survival might be underestimating those risks, as any additional effect on reproduction will only accelerate population decrease. There are already several local studies about the effect of environmental conditions on the reproduction of reptiles (Clarke & Zani, 2012; Dubey & Shine, 2011; Lu, Wang, Tang, & Du, 2013; Telmeco, Radder, Baird, & Shine, 2010; Warner, Moody, Telemeco, & Kolbe, 2012), and it is important to incorporate that data in the macro scale projections.

As global climate grows more unpredictable, reaching extremes more often (Easterling et al., 2000), and populations grow smaller due to habitat loss and fragmentation, populations might become more unstable and decline. If the patterns we discovered here repeat themselves in other species from the Cerrado or any other environment, this might happen even faster. Furthermore, these results contribute to recent findings that a climate induced worldwide decline in lizard populations is already on its way (Sinervo et al., 2010). Global efforts for the reduction of carbon dioxide emissions might be coming too late for some groups that are already facing mass extinction, such as lizards and amphibians (Barnosky, Matzke, & Tomiya, 2011). Because CO_2 stays a long time in the atmosphere, any change in emissions now will take decades to reduce warming (Hare & Meinshausen, 2006). A potential path to decelerate climate change is the reduction of short lived climate forcers, which are pollutants that may have greater warming potential than CO_2 but stay on the atmosphere much shorter (Sasser & Chappell, 2011).

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Table 1. Tests and descriptive statistics of climate time series between 2000 and 2012 at Distrito Federal, Brazil: Chi-square test for significance of overall trend; Granger test for predictability test with historical climate series; proportion of variation associated with seasonal and residual components, *tmax*=maximum daily temperature, *tmed*=mean daily temperature, *tmin*=minimum daily temperature, *humid* =day relative humidity, *sun*=total daily hours of sunlight, *precip*=total daily precipitation.

	Trend test	Granger test	Seasonal component	Residual component
tmax	$P = 0.99$	$P = 0.11$	0.63	0.37
tmed	$P = 0.79$	$P = 0.48$	0.72	0.28
tmin	$P = 0.59$	$P < 0.01$	0.86	0.14
humid	$P = 0.49$	$P < 0.01$	0.79	0.21
sun	$P = 0.65$	$P < 0.01$	0.72	0.28
precip	$P = 0.65$	$P = 0.05$	0.73	0.27

Table 2. Average importance and coefficients (β) for a selection of Pradel models relating the probability of survival (*Φ*) and *per capita* recruitment (*f*) to residual and seasonal components of climate variables (*tmax* = maximum daily temperature, *tmed* = mean daily temperature, *tmin* = minimum daily temperature, *humid* = daily relative humidity, *sun* = total daily hours of sunlight, *precip* = total daily precipitation) and fire effects (*sfire* = short term fire effect, *lfire* = long term fire effect) for a population of *Tropidurus torquatus* from a gallery forest in Brasília, Distrito Federal, Brazil.

		Φ		*f*	
		Importance	β	Importance	β
Residual					
	tmax	0.853	-0.382	0.007	0.001
	tmed	0.000	0.000	0.008	0.001
	tmin	0.976	0.203	0.892	-0.172
	humid	0.000	0.000	0.029	0.001
	sun	0.000	0.000	1.000	-0.938
	precip	0.000	0.000	1.000	-0.064
Seasonal					
	tmax	0.000	0.000	0.007	0.011
	tmed	0.000	0.000	0.007	0.009
	tmin	0.000	0.000	0.008	0.022
	humid	0.000	0.000	1.000	-0.179
	sun	0.000	0.000	0.008	-0.004
	precip	0.000	0.000	1.000	-0.070
Fire					
	sfire	0.000	0.000	0.077	0.019
	lfire	0.000	0.000	0.978	0.294

Figure labels

Figure 1. (a) Monthly captures of *Tropidurus torquatus* in a gallery Forest site at Brasília, Brazil between June, 2000 and May, 2012. (b) Monthly Snout-Vent Length distribution of *Tropidurus torquatus* captured in a gallery Forest site at Brasília, Brazil between June, 2000 and May, 2012. Orange vertical lines indicate the events of fire.

Figure 2. Autocorrelation plots of climate time series for monthly means of minimum daily temperature (ºC), mean daily temperature (ºC), maximum daily temperature (ºC), total daily precipitation (mm), daily relative humidity (%), and daily insolation (h) at Brasília, Brazil, from June 2000 to May 2012.

Figure 3. Spectral density of climate time series of monthly means for minimum daily temperature (ºC), mean daily temperature (ºC), maximum daily temperature (ºC), total daily precipitation (mm), daily relative humidity (%), and daily insolation (h) at Brasília, Brazil, from June 2000 to May 2012. The red lines mark the frequencies of highest spectral densities.

Figure 4. (a) Survival probability and *per capita* recruitment of a *Tropidurus torquatus* population at Monjolo creek gallery forest, Brasília, Brazil, from June 2000 to May 2012. (b) Growth rate variation for the same population. Orange vertical lines indicate the events of fire. On the bottom it is indicated the total growth for each reproductive cycle, from November to October (λ).

Figure 1

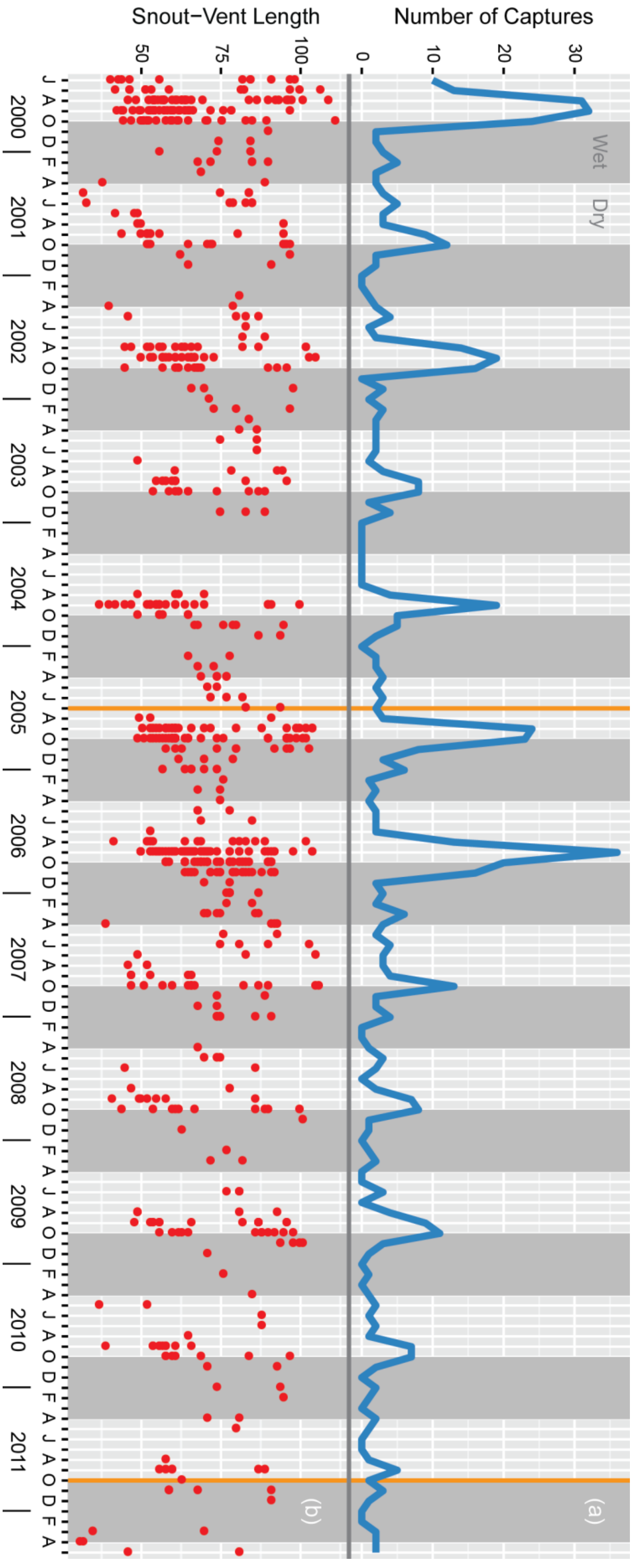
Number of Captures
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Figure 2

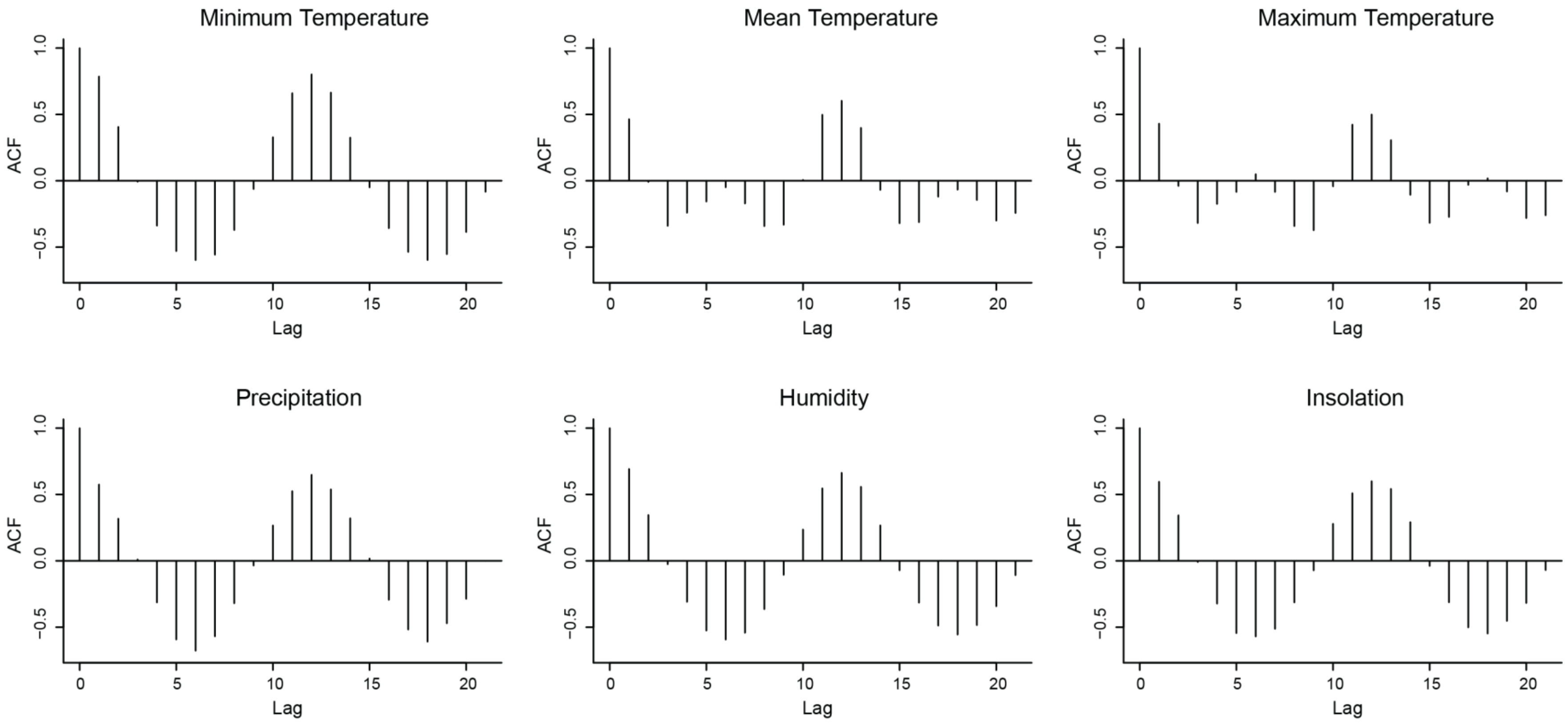
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Figure 3

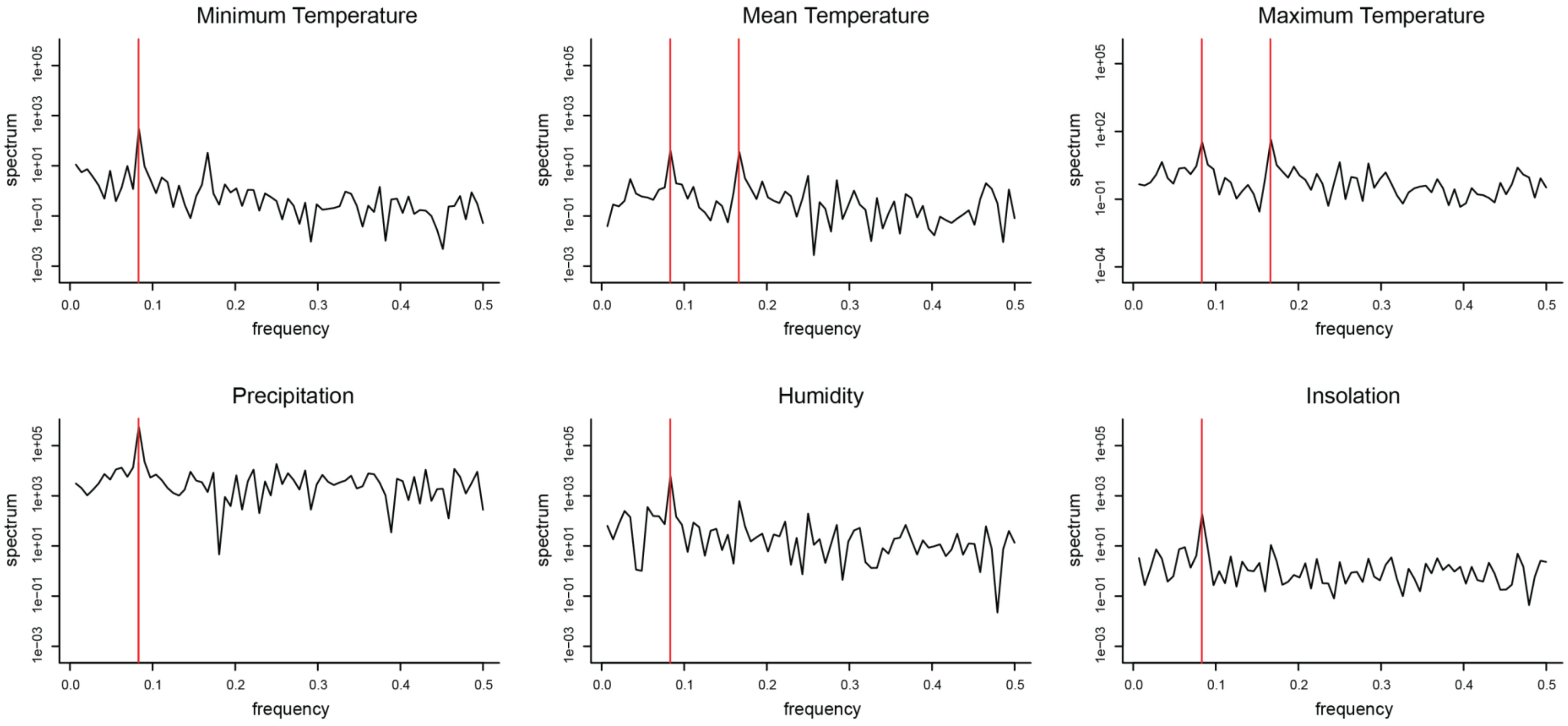
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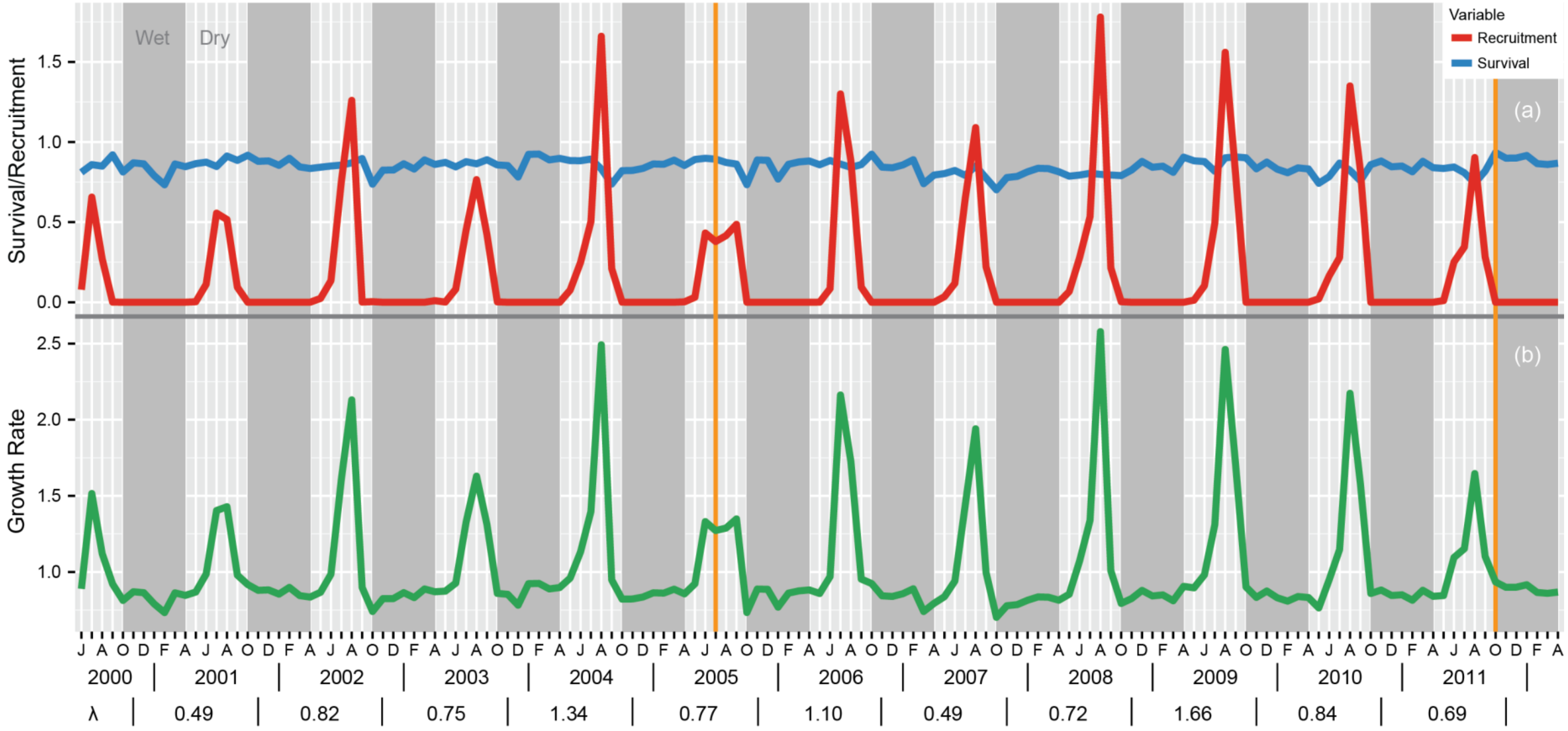
Figure 4


Survival/Recruitment
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