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# Efeitos da Mudança Climática Rápida na Estrutura da Comunidade e Morfologia Craniana de Pequenos Mamíferos

## Effects of Rapid Climate Change on Community Structure and Cranial Morphology of Small Mammals

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**BELO HORIZONTE**

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Tese apresentada ao Programa de pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre (PPG-ECMVS), do Instituto de Ciências Biológicas, da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Ecologia.

**Orientador:** Adriano Pereira Paglia

**BELO HORIZONTE**

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Às minhas famílias, amigos e
todos amantes da ciência


FACTS ABOUT CLIMATE CHANGE # 6
TO QUESTION THE SCIENCE OF CLIMATE CHANGE AND OPPOSE ANY COMPREHENSIVE LEGISLATION TO DEAL WITH IT NOW WILL INCREASE THE COST OF FACING A PROBLEM THAT HUMANKIND WILL INEVITABLY FACE SOON.
AND ALL ANIMALS. AND EVERYTHING.
POLE The Comic Strip with Penguins © by Thomas Baehr http://PENGUINSFORFREE.COM
Bi,2013

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# SUMÁRIO

# RESUMO

Atividades antrópicas tem alterado drasticamente o ambiente nos últimos séculos. Uma dessas mudanças ambientais é a mudança climática, a qual tem sido relacionada a vários efeitos em diversos níveis da biodiversidade. Para os pequenos mamíferos, grupo que exerce grande influência na dinâmica florestal, existe lacunas de conhecimento sobre como essas mudanças climáticas afetam traços morfológicos e ecológicos, principalmente na região Neotropical. Assim, nós testamos os impactos das mudanças climáticas em escala individual e de comunidade. Primeiro, nós analisamos as mudanças temporais na estrutura da comunidade de pequenos mamíferos em dois fragmentos de Mata Atlântica, uma pequeno em regeneração (EPTEA Mata do Paraíso) e um fragmento florestal maduro (PERD). Ambos os fragmentos apresentaram mudanças significativas na estrutura da comunidade, sendo que o PERD apresentou maior dissimilaridade temporal. Mudanças direcionais na estrutura da comunidade parecem estar mais associadas a pequenos fragmentos, enquanto fragmentos grandes refletem um equilíbrio frouxo. Posteriormente, testamos a influência dessa variação biótica temporal, combinada com mudanças climáticas, na Variação Morfológica Rápida (VMR) de quatro espécies de roedores – *Akodon cursor*, *Cerradomys subflavus*, *Oligoryzomys nigripes* e *Oxymycterus dasytrichus* – da comunidade de pequenos mamíferos da EPTEA Mata do Paraíso. Testamos as diferenças no tamanho e forma craniana entre espécimes coletados em duas séries temporais. Também exploramos os melhores modelos entre as mudanças morfológicas e fatores ambientais. Nossas análises mostraram VMR em todas as espécies e essas variações foram fortemente influenciadas pela temperatura máxima, mostrando uma relação negativa com o tamanho. Além disso, a precipitação, umidade, riqueza de roedores e temperatura mínima tiveram uma relação positiva com o tamanho. A abundância também teve uma associação negativa com o tamanho em *Ol. nigripes* e *Ox. dasytrichus*. Adicionalmente, nós avaliamos os efeitos de variáveis climáticas na assimetria flutuante (AF) de diferentes populações. Foram criados 11 grupos espaço-temporais para *A. cursor* e 13 para *Ol. nigripes*. Cada grupo consistiu de espécimes de uma mesma localidade dividido em duas séries temporais. Cinco grupos de *A. cursor* apresentaram variação significativa na AF ao longo do tempo e, para *Ol. nigripes*, encontramos variação em seis grupos. O melhor modelo para explicar a AF em *A. cursor* incluiu apenas a temperatura máxima, enquanto para *Ol. nigripes* o modelo incluía apenas umidade. O aumento na AF geralmente afeta negativamente a aptidão das espécies. Desse modo, entender quais fatores afetam a estabilidade do desenvolvimento e também quais espécies tem maior potencial de adaptação é de grande importância para a biologia da conservação.

**Palavras chave:** Dinâmica de comunidades, Mamíferos neotropicais, Variabilidade temporal, Variação morfológica rápida, Variáveis ambientais.

# ABSTRACT

Human activities have altered drastically environments on Earth on the last centuries. One of these human-induced rapid environmental changes is climate change, which has been linked to many effects on different levels of biodiversity. In small mammals, group of animals that exerts great influence on the forest dynamics, there is a relative lack of knowledge on how climate changes affect morphological and ecological traits, especially on Neotropical region. To this end, we have tested the impacts of climate change that operate at individual and community scales. First, we analyzed temporal changes in the community structure of small mammal in two fragments of Atlantic forest, a small in regeneration (EPTEA Mata do Paraíso) and a large mature forest fragment (PERD). In both fragments we could see significant temporal changes in community structure. However, temporal dissimilarity was higher in PERD. Directional changes in the structure seem to be more associated with small fragments, while in larger fragment the community seems to reflect a loose equilibrium. Then, we tested the influence of these temporal biotic variations, combined with climatic changes, in Rapid Morphological Changes (RMCs) of four rodent species – *Akodon cursor*, *Cerradomys subflavus*, *Oligoryzomys nigripes* and *Oxymycterus dasytrichus* - of the small mammal community in EPTEA Mata do Paraíso. We tested differences in size and shape of the skull between specimens collected in two temporal series. We also explored the best relationships between cranial changes and environmental drivers. Our analysis showed RMCs in all species and theses changes were strongly influenced by maximum temperature, showing a negative association with size. Besides, precipitation, humidity, richness of rodents and minimum temperature had a positive association with size. Additionally, abundance also was negatively associated with size in *Ol. nigripes* and *Ox. dasytrichus*. After testing the temporal variation in size in this community, we analyzed how fluctuating asymmetry (FA), in different populations, is influenced by climatic drivers. We created 11 space-temporal groups for *A. cursor* and 13 for *Ol. nigripes*. Each group consisted of specimens from the same locality divided in two time series. Five groups of *A. cursor* showed significant variation on asymmetry over time and, for *Ol. nigripes*, we found variation in FA in six groups.  The best model to explain FA in *A. cursor* included only Maximum Temperature, while for *Ol. nigripes* the best model included only Humidity. Increased FA generally negatively affects fitness of the species. That way, understanding which factors most affect developmental stability and which species have the potential to adapt to changes is central for the future of biodiversity conservation.

**Key words:** Community dynamics, Environmental variables, Neotropical mammals, Rapid Morphological Change, Temporal Variability.

# INTRODUÇÃO GERAL

# Effects of Rapid Climate Change on Small Mammal Community Structure and Cranial Morphology

Human activities have altered drastically environments on Earth, affecting virtually all organisms (Sih et al., 2011). These activities often place organisms into new conditions that typically involve faster changes than organisms have experienced in their evolutionary past (Palumbi, 2001). Basically there are five types of human-induced rapid environmental change: fragmentation and habitat loss, the spread of exotic species, harvesting by humans, pollutants of various sorts, and climate change (Rohr et al., 2006; Lockwood et al., 2007; IPCC, 2007; Salo et al., 2007; Fabry et al., 2008). All these types of anthropogenic influence brings severe consequences for organisms. However, studies suggest that climate change could surpass habitat loss and fragmentation as the greatest global threat to biodiversity over the next several decades (Leadley et al., 2010).

Climate change have been linked to variation in feeding/foraging behavior (Nishizaki and Carrington, 2015; Hayford et al., 2015), reproductive activity (Neeman et al., 2015), body size (Gardner et al., 2011), morphological variation (Vishalakshi and Singh, 2008; Nishizaki et al., 2015), species distribution (Poloczanska et al., 2013) and other effects on different levels of biodiversity, as presented by Bellard et al. (2012) (Fig 01).

The effects of climate change on community structure have been reported for a long time (eg. Fitter and Fitter, 2002). Changes in abiotic and biotic processes affect the structure of ecological communities (Hastings et al., 1993; Wu and Loucks, 1995). These processes produce instabilities in the structure of communities and it can lead to change in a community over time (DeAngelis and Waterhouse 1987). The amount of change is buffered by the stability of a community structure. In more advanced stable communities, instabilities processes may be minimized as one process may reverse another (Ives and Carpenter, 2007).

Depending on the organism the structure of ecological communities can vary on the scale of days, months, or years (Collins, 2000; Gajer et al., 2012). For mammals, there are few long-term studies that describe temporal changes in the community structure, especially due to their long lifespan. Small mammals make a great model since their lifespan is short and they also have great influence on forest dynamics

(Gressler et al., 2006; Genrich et al., 2016). The number of small mammal species is mainly positively correlated with primary productivity, but species interactions and habitat selection are also important (Brown, 1987). The greatest drivers that affect structure of small mammal community are rainfall, food supply and disease; however these drivers greatly vary between species and domains (Korpimäki et al., 2004). Thus, dynamics of small mammal communities is still poorly understood (Korpimäki et al., 2004).

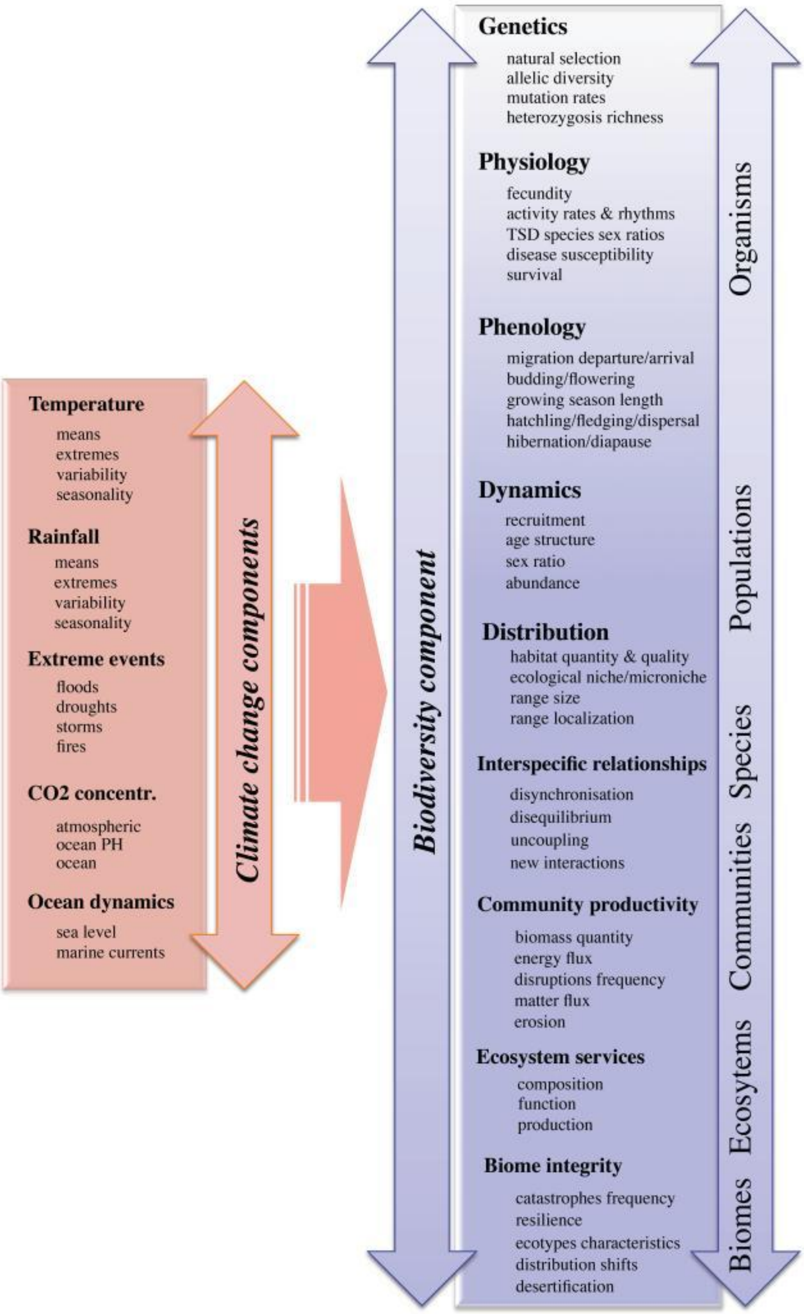

**Figura 1 -** Summary of some of the predicted aspects of climate change and some examples of their likely effects on different levels of biodiversity (Bellard et al., 2012).

Many rodent species have an evolutionary history that facilitates a rapid evolutionary response (e.g. short generation times, suitable genetic variation in key traits; Sih et al., 2011). That way, rapid climate changes may also drive rapid morphological changes on this group, including adaptive evolutionary responses (Gardner et al., 2011). Changes in body size or shape may develop rapidly and it is particularly easy to see in populations under pressure of fast environmental changes (Hoffmann and Sgrò, 2011; Doudna and Danielson, 2015).

Rise of global temperature seems to affect greatly body size of warm-blooded animals (Gardner et al., 2011). The premise for this hypothesis is described by Bergmann's rule. There is a positive relationship between body size and latitude, explained by the surface area-to-volume ratio. Thus, smaller individuals are found at lower latitudes where climates are generally warmer (Bergmann, 1847). Many scientists extrapolate this rule correlating body size with temperature. This extrapolation originates the prediction that current climate warming will lead to shifts in body size (Gardner et al., 2011). However, small mammals seem not to follow this rule (Gardner et al. 2011). Thermoregulation in rodents, in warm places, are made through nasal turbinates, since the amount of skin glands in these animals is insufficient for heat dissipation and their respiratory apparatus is inadequate for painting (Schmidt-Nielsen, 1975). That way, it is possible that rodents present a different response to global warming.

Besides rapid variation on size, another morphological responses caused by environmental changes are random variations of bilaterally symmetrical characters that deviate from perfect symmetry, known as fluctuating asymmetry (Kieser, 1993). This asymmetry is mainly associated with stress during development (Palmer and Strobeck, 1992; Dongen, 2006). This stress can affect bilateral development in two ways. First, it can lead to an increase in developmental noise, that is, increased incidence of random disturbances that tend to alter the development of the symmetrical form. Second, stress may decrease the level of development stability, which means reducing the buffering capacity or system robustness (Klingenberg & Nijhout, 1999). The measurement of fluctuating asymmetry may reflect how the stress during development affects a population. An increase in fluctuating asymmetry is usually attributed to the stressful effect of genetic or environmental variables (Palmer and Strobeck, 2003; Lazić et al., 2013).

In rodents, variations in temperature also have great impact on metabolism (Gordon, 1993). Temperature seems to have great metabolic influence during ontogenetic development (Harrison, 1958), resulting on morphological changes (Kieser, 1993; Klingenberg and Nijhout, 1999). Extreme cold temperatures as well as extreme heat increase cranial fluctuating asymmetry (Siegel and Doyle, 1975; Siegel et al., 1977). Maestri et al. (2015) also show a positive relation between temperature and fluctuating asymmetry in a sigmodontine rodent species, in Brazil. In this late study, fluctuating asymmetry was also associated to precipitation and environmental suitability.

However, association between fluctuating asymmetry and temperature in rodents is still not clear, since only extreme temperatures were tested on these animals (Siegel & Doyle, 1975; Siegel et al., 1977) and environmental variables have different impacts on fluctuating asymmetry depending on the species (Helle et al., 2011; De Coster et al., 2013).

Thus, due to the great influence of small mammals in forest dynamics as core components of forest food webs (Scheibler and Christoff, 2007) and seed dispersers (Gressler et al., 2006; Genrich et al., 2016); the relative lack of knowledge on how climate changes affect both the morphology and the ecology of this group, especially on Neotropical region; and most of data on morphological changes in small mammals present conflicting results; there is an urgent need to review our current understanding of the effects of rapid climate change on small mammal community structure and cranial morphology. To this end, we have tested the ranges of impacts of climate change that operate at individual and community scales.

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# CAPÍTULO 1

## MUDANÇAS TEMPORAIS NA ESTRUTURA DA COMUNIDADE DE PEQUENOS MAMÍFEROS EM REMANESCENTES DE MATA ATLÂNTICA

Artigo a ser publicado na Biota Neotropica

# Temporal changes in community structure of small mammals in Atlantic Forest remnants

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## ABSTRACT

Biotic and abiotic processes change the community structure over time producing instabilities. This is easier to see in primary ecological succession than in more advanced systems, because in the latter dissimilarities caused by perturbations are easily reversed. For small mammals, many studies associate community structure to the type of fragment and climate. However, there are few long-term studies that describe temporal changes in community structure of these mammals. Here we analyze temporal changes in the community structure of small mammal in two fragments, a small in regeneration and a large mature forest fragment. We hypothesized that (1) dissimilarity is associated with time only in the small fragment; and (2) the large fragment is more stable, thus, dissimilarity between its communities over time is lower than the dissimilarities in the small fragment. Data for the following analyses come from two forest fragments in southeastern Brazil, a small one in regeneration, sampled for 17 non-consecutive years and a large mature one, sampled for 6 consecutive years. We used months as sample unit and semesters as temporal groups. To test our hypotheses, we used the value of dissimilarity (R) given by ANOSIN between the first temporal group and each of others group. We explored potential associations between dissimilarity and time using a Generalized Linear Mixed Model (GLMM). We performed t-tests testing differences in dissimilarity between fragments to test our second hypothesis. In all areas we could see significant temporal changes in community structure. We found association between dissimilarity and time only in the small fragment. However, dissimilarity was higher in larger fragment. Our results clearly demonstrate changes in the community structure of small mammals over time. Furthermore, directional changes in the structure seem to be more associated with small fragments, while in larger fragment the community seems to reflect a loose equilibrium. Lastly, temporal dissimilarity may not be associated to fragment size, since differences between the fragment and the matrix can greatly interfere in community changes.

**Key words:** Community dynamics, Community stability, Neotropical mammals, temporal variability.

## INTRODUCTION

Structure of ecological communities is dynamic and it changes over time as a result of biotic and abiotic processes (Hastings et al., 1993; Wu and Loucks, 1995). These processes may affect birth, mortality and survival rates of each species differently, and also may lead to their potential replacement by other species better adapted to the new conditions (Lloret et al., 2012). Additionally, some species can be replaced by others with similar functional attributes (Naeem, 1998). Competition and predation are the two most prevalent biotic forces in communities (Abrams, 2000). Local extinctions and bioinvasions may act as a disruptive biotic process (Post and Pinn, 1983; Terborgh et al., 2001; Friman et al., 2014), while environmental perturbations, as those resulting from a high variability in temperature and precipitation, also can change community structure as abiotic factors (Lloret and Granzow-de la Cerda, 2013; Riva et al., 2016).

In the course of time, the occurrence probability of processes that may produce instabilities in the structure increases and it can lead to a directional change in a community over time (DeAngelis and Waterhouse 1987). That is easy to see in primary ecological succession, and the temporal change in the community structure (Pennanen et al., 2001; Hu and Liu, 2003). In more advanced systems, instabilities processes may not lead to a directional change as one process may reverse another (Ives and Carpenter, 2007). This is easily noticed in a predator-prey diagram (Abrams, 2000) or periodic fire in a forest (Collins, 2000).

Another factor that affects changes in the community structure is the stability. Holling's resilience, one of the most accepted concepts of stability, describes the ease with which systems can switch between alternative stable states, with more stable systems having higher barriers to switching (Holling, 1973). Fragmentation caused by the intensive use by men of the land has destroyed stable states in the last several decades (Donald, 2004; Clough et al., 2005). The increase of the interface between fragment and the matrix may alter wildlife communities within natural areas, with the increased edge effect (Laurance and Yensen, 1991; Laurance, 2000). The responses of wildlife communities to edge effects usually present a negative spatial relation (Fletcher, 2005), thus, larger fragments may exhibit greater stability.

Depending on the organism ecological communities can vary on the scale of days, for microbial communities (Gajer et al., 2012), or years, for vertebrates (Collins, 2000). For small mammals, many studies associate the community structure to the type of fragment and climate (eg. Kelt et al., 1996; Hurst et al., 2013). However, there are few long-term studies that describe temporal changes in the community structure of small mammal, and most of these are population studies of the most abundant species in the area and interactions among them (eg. Utrera et al., 2000; Krebs et al., 2001; Bonecker et al., 2009; Happold, 2015).

Small mammals are core components of forest food webs (Scheibler and Christoff, 2007). They also have great influence on forest dynamics through seed and mycorrhizal fungi dispersal (Gressler et al., 2006; Genrich et al., 2016). Rodents and small marsupials are also good indicators of both local habitat changes and landscape changes (Cunha and Vieira, 2002; Vieira and Monteiro-Filho, 2003). Despite the ecological importance of these animals, the dynamics of small mammal communities is still poorly understood (Korpimäki et al., 2004). The biggest problem in determining temporal patterns in community structure is the lack of a large number of samples to discriminate between temporal changes in the structure and changes that are related to spatial heterogeneity observed in a fragment (Lauber et al. 2013).

That way, here we examined how the structure of small mammal communities changed over time from different areas in two forest fragments, the first, a small fragment in regeneration, and the second, a large mature forest fragment. Given that larger fragments are more stable than small regenerating ones, we hypothesized that (1) in a long period of time, dissimilarity will be strongly associated with time only in the small fragment, since in the large fragment dissimilarities caused by perturbations are more likely to be reversed over time. Likewise, we hypothesized that (2) the large fragment is more stable, this way, dissimilarity between its communities over time is lower than the dissimilarity over time in the small fragment.

## MATERIAL AND METHODS

### Study area

Data for the following analyses come from two forest fragments in the state of Minas Gerais, southeastern Brazil, a small one in regeneration, and a large mature one. The first, known as Estação de Pesquisa, Treinamento e Educação Ambiental (EPTEA) Mata do Paraíso (central coordinates 20º48'S, 42º51'W), near Viçosa. The EPTEA Mata do Paraíso is a 194.36-ha, part of a larger fragment of Atlantic Forest reaching up to 384-ha. Altitude varies between 690 and 850 m and it has a warm temperate climate (Ribon, 2005). The EPTEA Mata do Paraíso's original vegetation was classified as Semideciduous Montane Forest (Pinto et al., 2007). The fragment is divided into a matrix of plant successional stages ranging from early up to advanced stages of secondary succession (Ribon, 2005). Two areas, 1 km distant from one another, in different stages of succession were sampled in the fragment. The first one, Anthropic Field, on early stage of regeneration, is a narrow strip area covered by molasses grass (*Melinis minutiflora*). It suffered a complete deforestation caused by pasture and subsequently colonization by grass (Paglia et al., 1995). At the end of 2006, the molasses grass was cut. It changed the land phytophysiognomy and led to the colonization of tree plant species. The second area, Secondary Forest, suffered little human interference over the years, and it consists of denser woods, especially of the Rubiaceae and Meliaceae families (Silva-Junior et al., 2004).

The second fragment is the Rio Doce State Park (PERD) (central coordinates 19º41'S, 42º32'W), established in 1944, and it is the largest fragment of Atlantic Forest in the state, which has an area of 35,973-ha (Andrade et al., 1997). The park occurs on topographic gradients that vary in elevation from 230 to 515 m above sea level and it also has a tropical wet and dry climate. The vegetation is predominantly forest (Semideciduous Submintane Forest), with areas of primary and secondary forests in different successional stages (Andrade et al., 1997). The park has several trails used for recreation and research (Pacheco, 2008), and two of them, 14 km distant from one another, were sampled in this fragment. The first area, Campolina, is a trail located outside the public visitation area of the park and it is open only to authorized researchers. This area of primary forest is near a road that cuts the park, and it ends in the Doce river. The area had little anthropic interference over the years, and it presents well preserver, with several species of large trees (Pacheco, 2008). The second area, known as Vinhático, is a patch of secondary forest in good condition of conservation, regenerating from a fire in the late 60s (Lopes et al., 2002). The trail of Vinhatico has allowed public visitation, and it is one of the most visited park trails. The number of trash and vandalized trees in this area are higher than in Campolina (Pacheco, 2008).

## Field Methods

In EPTEA Mata do Paraíso, each sampled area contained one trap line with 20 stations; while in PERD, each area had six trap lines with 10 stations each. Stations were located at 15-m intervals and consisted of a Sherman (8 x 9 x 23-cm) and a Tomahawk (15 x 16 x 42-cm) live traps, arranged alternately in the soil and understory. Traps were baited with peanut butter and banana on four consecutive nights per sampled month. Thus, sampling effort per month was different in the two fragments, 160 trap.night in EPTEA Mata do Paraíso and 480 trap.night in PERD.

The samples years were not consecutive in EPTEA Mata do Paraíso. Small mammals in both areas were sampled monthly from May 1992 to March 1993, thereafter from June to December 1997 and finally from April 2009 to September 2010. Additionally, small mammals were sampled in Anthropic Field in 2006, in May, June and July. In PERD, small mammals were sampled six months per year – three in the dry season and another three in the wet season - from 2001 to 2006 along permanently located trap lines in PERD.

Captured animals were identified, marked with numbered ear tags, and released at the site of capture. The species identification followed specific literature (Gardner 2007, Bonvicino *et al*. 2008, Patton *et al.* 2015). Additional details of small mammal communities at EPTEA Mata do Paraíso are given in Paglia et al. (1995), Lessa et al. (1999), and Lessa et al. (2014), and details of the composition of small mammals of the PERD can be found in Stallings et al. (1989), and Keesen et al. (2016).

## Data Analyses

We decided to use each sampled month as a sample unit in our analysis, once data collected from EPTEA Mata do Paraíso had no spatial replication. Wet and dry seasons apparently have a strong influence on the capture of small mammal (O’Connell, 1989). Differences between seasons can mask the differences in the temporal structure of the small mammal community. This occurs because the capture methodology uses bait, which attracts the species differently depending on the amount of resources that are affected by rainfall (Umetsu et al., 2006). Thus, we decided to test the existence of seasonal variation in each area, before calculating the temporal variation in the fragments. We made this using similarity analysis (ANOSIM) by comparing data of dry – all data collected in the months from April to September from an area – and wet season – data from October to March, using by Bray-Curtis similarity index. To avoid problems of temporal pseudoreplication, replicate samples were aggregated as described by Clarke (1993).

Temporal changes in community structure of each area was graphically represented by interpolated bar plots of relative abundance observed and non-metric multidimensional scaling (NMDS) obtained by Bray-Curtis similarity matrices. Each temporal group comprised all sample units included in a semester, corresponding to a season. Thus, we had seven temporal groups in Mata (four in dry season and three in wet season), eight groups in Anthropic Field (five in dry season and three in wet season) and twelve groups in both areas in PERD (six in each season).

To test our hypotheses, we used the value of dissimilarity (R) given by ANOSIN between the first temporal group and each of others group. In cases in which the community structure is different between seasons, we firstly calculated dissimilarity between the first temporal group in the dry season and each subsequent group within the same season, and then we made the same for the wet season groups.

We explored potential associations between dissimilarity and time using a Generalized Linear Mixed Model (GLMM) with a random effect of areas. This approach allows accounting for potential spatial pseudoreplication, linked to the hierarchical structure in the sampling design (Crawley, 2012). To test our first hypothesis we compared GLMM results of each fragment.

To test our second hypothesis we performed independent-samples t-tests to compare dissimilarity among EPTEA Mata do Paraíso and PERD. As we believe that time has a strong influence on dissimilarity (first hypothesis) we could not compare all semesters of both fragments, since in one 12 consecutive semesters were sampled, and in the other we have non-consecutive samples until the 36th semester. This way we used only temporal groups that had the same time gap from the first temporal group (i.e. 10th and 11th semester) from both areas of the sampled fragments

Type I error rate was set to 0.05 in all analyses and all statistical analyses were performed using the computing environment R (R Development Core Team, 2014) and the package “vegan”. Graphs were edited in GIMP 2.

## RESULTS

The results of all the sampled years summed up 18 species of small mammals captured in EPTEA Mata do Paraíso and 16 in PERD. The summary of the species collected and their relative abundances per area can be found in Online Resource 01. Three of four areas presented differences in community structure of small mammals between dry and wet season – Anthropic Field (R= 0.366; p=0.009); Secondary Forest (R= 0.484; p=0.003) and Campolina (R= 0.079; p=0.049). In Vinhático, there was no difference between the seasons. In addition, in this area, dissimilarity was greater within each season than between them (R= -0.016; p=0.288).

Community structure showed no major changes with time in Anthropic Field (Fig. 01A and 01C). *Oligoryzomys nigripes* was the dominant species during all sampled semesters, in some cases representing more than half of relative abundance. In the last three semesters, *Didelphis aurita* presented an expressive increase in abundance, with no major changes in the community structure (Fig. 01E). In Secondary Forest, community structure had larger temporal changes (Fig. 01B and 01D). Until the 11th semester *O. nigripes* was the most abundant species, from the 33rd semester relative abundance of *D. aurita* and *Akodon cursor* increased removing *O. nigripes* as the most abundant species (Fig. 01F). In both areas, changes in community structure were not abrupt.

In Campolina, small changes in community types were apparently cyclical. *Micoureus demerarae* was the most abundant species in all semesters. The other two most abundant species, *Metachirus nudicaudatus* and *D. aurita*, showed a strong temporal variation being the key of changes in community structure (Fig. 02A, 02C, and 02E). The greater temporal change in community structure happened in Vinhático. The beginning and ending are quite similar, there was a predominance of marsupials in the community. However, there were great changes in the middle. The species not recorded at the beginning or end, *A. cursor*, was the most abundant species in five of the central semesters (Fig. 02B, 02D, and 02F).

In all areas we could see significant temporal changes in community structure (Tab. 01), in some cases, the community structure changed significantly in one year. We found association between dissimilarity and time in EPTEA Mata do Paraíso (p=0.026), and no association in PERD (p=0.841) (Fig. 03).

Comparing the raw data of the first 10 semesters, the difference in dissimilarity between areas of PERD and the areas of EPTEA Mata do Paraíso is visible and t-test highlights that dissimilarity was higher in PERD than in EPTEA Mata do Paraíso (p=0.008).

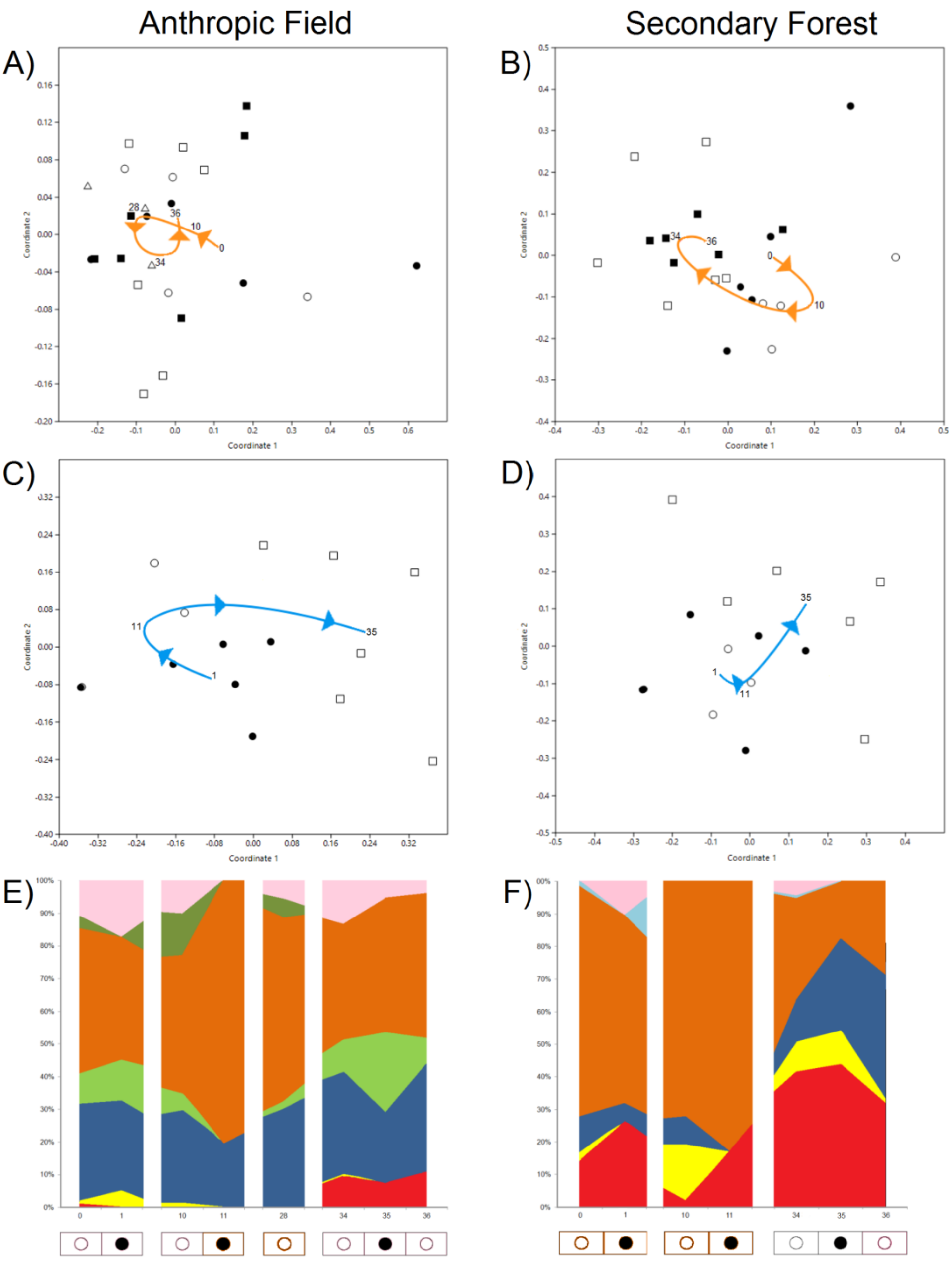

**Figure 01** Temporal changes in the community structure of small mammal in EPTEA Mata do Paraíso. **A**, **B**, **C** and **D)** Non-metric multidimensional scaling (NMDS) obtained by Bray-Curtis similarity matrices of the variation in the community structure in Anthropic Field and Secondary Forest. Arrows go through the mean distribution of each temporal group, represented by the number of the semester. Orange arrows represent the path followed by the community structure in dry season, while the blue arrows represent the path followed only during wet season. (Stress A = 0.131; Stress B = 0.192; Stress C = 0.159; Stress D = 0.155). ● – months sampled in the temporal group 0/1; ○ – temporal group 10/11; ∆ - temporal group 28; □ – temporal group 34/35; ■ – temporal group 36. **E** and **F)** Interpolated bar plots of small mammals relative abundance observed in each sampled area. ● – semesters sampled in wet season; ○ – semesters sampled in dry season. Red bar – *Didelphis aurita*; Yellow – other marsupial species; Dark Blue - *Akodon cursor*; Light Green – *Cerradomys subflavus*; Orange – *Oligoryzomys nigripes*; Dark Green – *Oxymycterus rufus*; Light Blue – *Rhipidomys mastacalis*; and Pink – other rodent species.

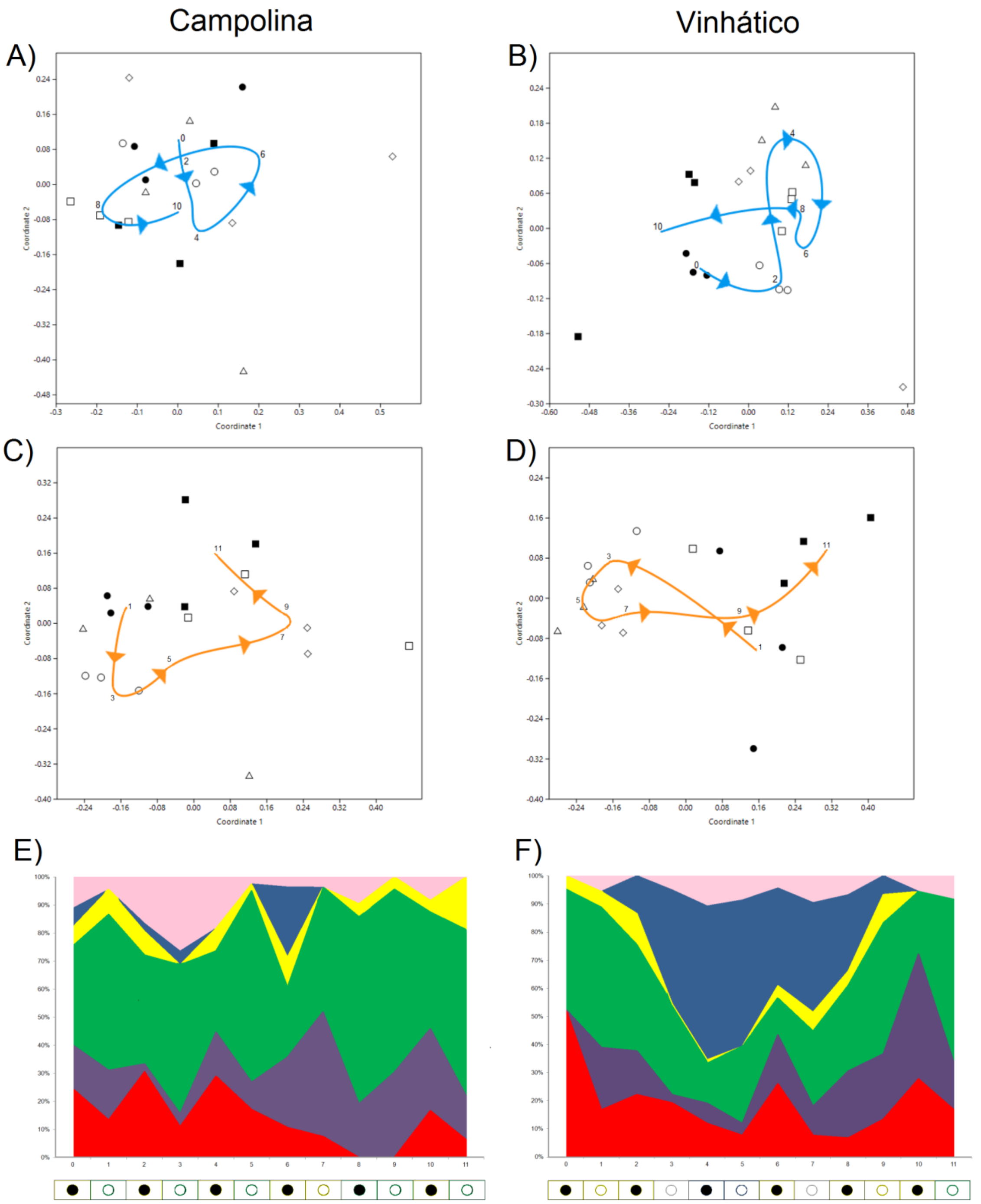

**Figure 02** Temporal changes in the community structure of small mammal in PERD. **A**, **B**, **C** and **D)** Non-metric multidimensional scaling (NMDS) obtained by Bray-Curtis similarity matrices of the variation in the community structure in Campolina and Vinhático. Arrows go through the mean distribution of each temporal group, represented by the number of the semester. Orange arrows represent the path followed by the community structure only during dry season, while the blue arrows represent the path followed only during wet season. (Stress A = 0.171; Stress B = 0.164; Stress C = 0.154; Stress D = 0.108). ● – months sampled in the temporal group 0/1; ○ – temporal group 2/3; Δ - temporal group 4/5; ◊ - temporal group 6/7; □ – temporal group 8/9; ■ – temporal group 10/11. **E** and **F)** Interpolated bar plots of small mammals relative abundance observed in each sampled area. ● – semesters sampled in wet season; ○ – semesters sampled in dry season. Red bar – *Didelphis aurita*; Purple – *Metachirus nudicaudatus*; Green – *Micoureus demerarae*; Yellow – other marsupial species; Dark Blue - *Akodon cursor*; and Pink – other rodent species.

**Table 01** ANOSIM and SIMPER test results for temporal variation in community structure of small mammals of all sampled areas in EPTEA Mata do Paraíso and PERD.

| **Fragment** | **Area** | **Season** | **R** | **P** | **Species that most contributed to temporal dissimilarity** | **Second species that most contributed to temporal dissimilarity** |
|---|---|---|---|---|---|---|
| Mata do Paraíso | Anthropic Field | Dry | 0.141 | 0.002 | *Oligoryzomys nigripes* (37.05%) | *Akodon cursor* (23.76%) |
| | | Wet | 0.536 | <0.001 | *Oligoryzomys nigripes* (33.06%) | *Cerradomys subflavus* (27.25%) |
| | Secondary Forest | Dry | 0.349 | <0.001 | *Oligoryzomys nigripes* (35.76%) | *Didelphis aurita* (28.59%) |
| | | Wet | 0.207 | <0.004 | *Didelphis aurita* (35.29%) | *Oligoryzomys nigripes* (24.24%) |
| PERD | Campolina | Dry | 0.542 | <0.001 | *Micoureus demerarae* (43.23%) | *Metachirus nudicaudatus* (16.63%) |
| | | Wet | 0.278 | <0.001 | *Micoureus demerarae* (22.51%) | *Didelphis aurita* (21.8%) |
| | Vinhático | - | 0.704 | <0.001 | *Akodon cursor* (35.36%) | *Micoureus demerarae* (22.7%) |

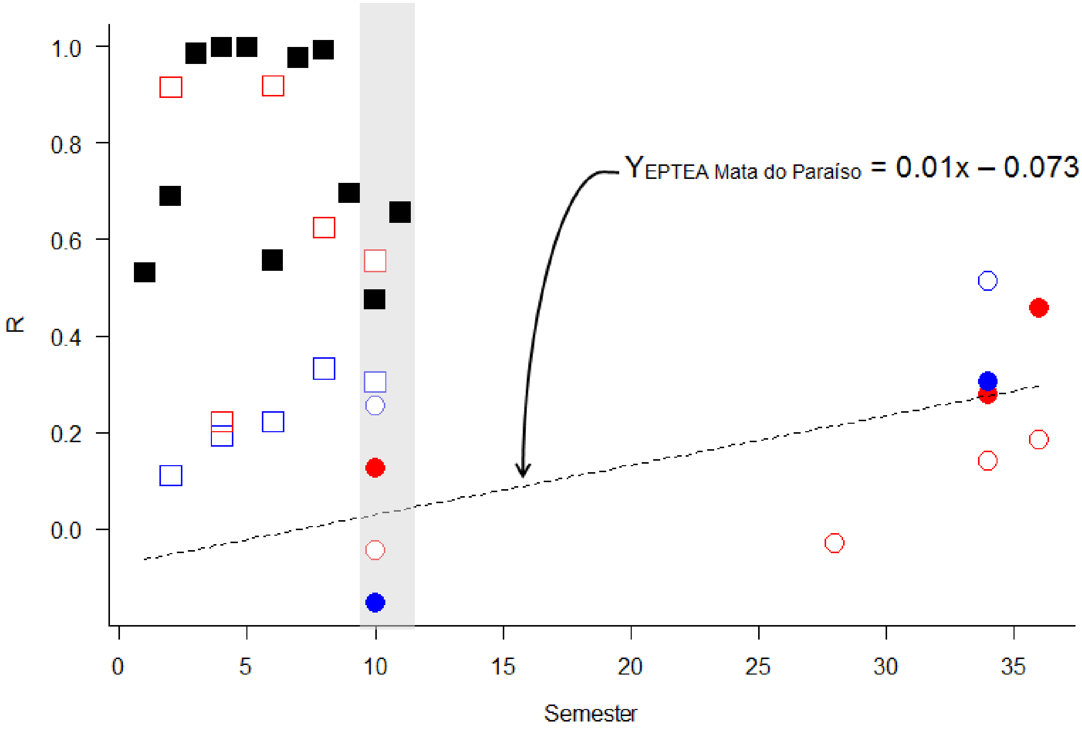

**Figure 03** Dissimilarity variation of the community structure of small mammals over time. Filled squares, Vinhático; Open squares, Campolina; Filled circles, Secondary Forest; and Open circles, Campo Atrópico. In red, dry season; blue, wet season; and black, indefinite season. The area in gray represents data used to test our second hypothesis.

## DISCUSSION

Results from our analyses demonstrate that, first, wet and dry seasons have great influence on the community structure evaluated by bait capture methods; second, tested small mammal communities significantly changed over time, and some of these changes came from one year to another; third, temporal changes in the community structure of small mammals in small fragments in regeneration are gradual and directional; and, finally, contrary to expectation, temporal dissimilarity in the small fragment was lower than in the large fragment.

The seasonal effects on capture success and composition of Neotropical small mammals have been documented in several studies (O'Connell, 1989; Feliciano et al., 2002; Carmignotto et al., 2014). In most cases, a higher density of rodents was found in dry season. A possible reason for the lower capture success in wet season, while using Sherman traps, is that availability of food resources to Neotropical small mammals is positively associated to rainfall, thus there is a decrease in the attractiveness of baits in this season (Umetsu et al. 2006). In most studies in Neotropical region, however, the evaluation of the small mammal community was carried out in one or two years. In our long-term sampling study, despite we did not test bias of baits in seasonal community structure of small mammals, our results showed that differences in the community structure between seasons are common.

In addition to seasonal changes in the community structure, our results also showed that temporal changes can be rapid. In all studied areas, there was at least one case where the community structure of small mammals significantly changed from one year to the next. In another long-term study conducted in the temperate zone, annual changes in the community structure of small mammal only occurred when preceded by fire (Collins, 2000). Temporal changes depends on the inherent dynamics of a system and the type of perturbation it experiences (Ivans et al., 2007). Although we have not tested potential disturbances, such as climate change, none of the areas studied here, during the sampled period, had experienced an event as extreme as fires. This may indicate that communities of Neotropical small mammals are more dynamic or more sensitive to disturbances than communities in temperate zones (Sheldon et al., 2011).

Regarding the hypotheses tested, we are aware that the differentiated use of sampling semesters, spaced in the EPTEA Mata do Paraíso and continuous in the PERD, may introduce more bias and limit the representativeness of our results for temporal changes in the community structure of small mammals. We understand that these datasets is not the most suitable for testing our hypotheses. However, due to lack of studies on the subject, and the high number of samples obtained, this was the first time we could test temporal changes in the community structure of small mammals in Neotropical region.

For the small mammals in EPTEA Mata do Paraíso, the community structure was undergoing a linear change. Compensatory changes in abundance of dominant species, as we could see in the last semesters of Anthropic Field and Secondary Forest, and lower spatial heterogeneity lead to strong directional change (Collins, 2000). Over the years vegetation's structure has changed in EPTEA Mata do Paraíso, mainly by natural regeneration (Higuchi et al., 2006), and this can be a potential explanation for changes in dominance of small mammals. The most abundant species in the early semesters, *O. nigripes*, feeds mainly on open field seeds even if it is living in mature forests (Galetti et al., 2016). Food limitation may stop increases in populations of small mammals (Korpimäki et al., 2004). Thus, the lower production of seeds of pioneer tree species may have limited food resources for *O. nigripes*, decreasing its population. The other two dominant species in the fragment do not have seeds as their base diet (Paglia et al., 2012), and they apparently have benefited from changes in vegetation structure.

The small mammal communities in PERD seem to reflect a loose equilibrium (DeAngelis et al., 1987). According to Ivens et al (2007) the absence of a statistically directional change in composition and abundance over time in response to disturbance indicates stability. That is, despite high year-to-year variability in composition and abundance, community structure remains stable, on average, over long time frames or large spatial scales (Bormann and Likens 1979). It is not uncommon to see stability in the community structure of small mammals in long-term studies conducted in mature areas, and the main reason for this is the high philopatry of these animals (Brown et al., 1986; Collins, 2000). This could be an explanation of the community dynamics in Campolina, where dominant species exhibit a fluctuation of individuals, but are relatively constant. However, in Vinhático, there is an outbreak followed by the disappearance of the generalist species *A. cursor*.

Population cycles and outbreaks of small mammals have been well recorded, but still poorly understood (Korpimäki et al., 2004). In some cases, population changes are associated with climate change (eg. Krebs et al., 2001; Klemola et al., 2003), however, only variations in climate do not seem to be the best explanation for the case of Vinhático, since *A. cursor* suffered almost the same environmental pressures in Campolina. The number of species of small mammals also seems to be regulated by primary productivity and also species interactions (Brown, 1987). Diet of the four dominant species in PERD is different. While *D. aurita* is omnivorous, with a very broad diet, *Me. nudicaudatus* and *Mi. demerarae* are mainly insectivore, occasionally feeding on small vertebrates and fruits (Santori et al., 2012). Diet of *A. cursor* is also predominantly insectivorous; however the species is also known to feed on large amounts of seeds (Carvalho et al., 1999). A potential explanation for the populational fluctuation of *A. cursor* in Vinhático is that population size of this rodent species is associated to seed production. The structure of the plant community in Vinhático is different from that found in Campolina, the first is still in medium stage of succession (Lopes et al., 2002). Many species of plants found near this area, including some species of bamboos, have a non-annual flowering, and when it blooms it gives a large number of seeds (Gonçalves, 2000; Lopes et al., 2002). The surge of rodents associated with bamboo floweting and subsequent mast seeding at periodic cycles, known as ‘ratadas’ have been related in South America since the 16th century (Jaksic and Lima, 2003). That way, the outbreak of *A. cursor* may be a result of seed rain of one or more of these non-annual flowering species.

Besides that, the area of Vinhático is open trail to public visitation, one of the most visited in PERD, and the volume of trash is greater than in Campolina (Pacheco, 2008). The opening and use of trails can affect the community of small mammals. Generalist species prefer track-borne habitats, while species more associated with mature forests tend to avoid such habitats (Adams & Geis, 1983). Additionally, *A. cursor* has high adaptive flexibility, and this species are abundant in fragmented or altered vegetation (Stallings et al., 1990; Paglia et al., 1995). In this way, it is possible that the garbage produced by the tourists also function as a source of food resource for the species, which may affect population fluctuations in the species.

In our late hypothesis, we expected that stability of small mammal communities would be greater in PERD, mainly because it is a large area and suffers less edge effect. However, temporal dissimilarity in EPTEA Mata do Paraíso was lower than in PERD. Populations of some generalist species of small mammals may be benefited by environmental changes adapting to adverse conditions, while forest-dependent species are more sensitive to microhabitat alterations (Vieira and Izar, 1999; Vieira et al., 2009). In some cases, especially in small fragments, the little difference between the forest fragment and the hospitable matrix favors generalist species due to the creation of open areas (Olifiers et al., 2005; Forero-Medina and Vieira, 2007). The absence of environmental filters may limit the edge effect, since both the fragment and the matrix communities are restricted to a small number of opportunistic species whose population density can increase dramatically due to the absence of competitive pressures (Ruedas et al., 2004). This may have been the case of EPTEA Mata do Paraíso. The matrix has a vegetation structure very similar to that found in Anthropic Field, where all dominant species has high adaptive flexibility (Paglia et al., 1995), and the community structure seems to be affected by border effect. Besides, a deforested area, that come into regeneration process and increases its size, needs gain of species from other fragments. These dispersal events might be retained in small fragments located close to larger, less defaunated areas (Galleti et al., 2006). However, EPTEA Mata do Paraíso has only smaller fragments nearby, that way the fragment will hardly be recolonized by other small mammal species in a short period of time.

The conclusions that can be drawn from this study are limited by the unequal collection of data between fragments. Despite this limitation, our results clearly demonstrate changes in the community structure of small mammals over time and between seasons. Furthermore, directional changes in the structure seem to be more associated with small fragments, while in larger fragment the community seems to reflect a loose equilibrium. Lastly, temporal dissimilarity may not be associated to fragment size, since differences between the fragment and the matrix can greatly interfere in community changes.

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# Online Resources 1

## Temporal changes in community structure of small mammal in Atlantic Forest remnants

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**Supplementary Table 1** Species of small mammals recorded during the sampling studied in this study. It is given the abundance rank of each species in that area, followed by its relative abundance in the same area. (Continue...)

| Taxa | Mata do Paraíso | | PERD | |
|---|---|---|---|---|
| | Anthropic Field | Secondary Forest | Campolina | Vinhático |
| **ORDER DIDELPHIMORPHIA** | | | | |
| **Family Didelphinae** | | | | |
| *Caluromys philander* (Linnaeus, 1758) | | | **4 (5.78%)** | 6 (2.43%) |
| *Didelphis aurita* (Wied-Neuwied, 1820) | 5 (4.1%) | **2 (24.59%)** | **3 (14.67%)** | **3 (14.35%)** |
| *Gracilinanus agilis* (Burmeister, 1854) | | | 11 (0.21%) | |
| *Gracilinanus microtarsus* (Wagner, 1842) | 15 (0.11%) | 5 (3.15%) | | 13 (0.37%) |
| *Marmosops incanus* (Lund, 1940) | | | | 14 (0.15%) |
| *Metachirus nudicaudatus* (Desmarest, 1817) | | | **2 (17.24%)** | **4 (12.05%)** |
| *Micoureus demerarae* (Thomas, 1905) | | | **1 (48.73%)** | **2 (29.43%)** |
| *Monodelphis americana* (Thomas, 1888) | 13 (0.21%) | 6 (1.59%) | 10 (0.43%) | 8 (0.66%) |
| *Philander frenatus* (Olfers, 1818) | 12 (0.28%) | 7 (1.21%) | | |

**Supplementary Table 1** (Continuation) Species of small mammals recorded during the sampling studied in this study. It is given the abundance rank of each species in that area, followed by its relative abundance in the same area.

| **Taxa** | **Mata do Paraíso** | | **PERD** | |
|---|---|---|---|---|
| | **Anthropic Field** | **Secondary Forest** | **Campolina** | **Vinhático** |
| **ORDER RODENTIA** | | | | |
| **Family Cricetidae** | | | | |
| *Abrawayaomys ruschii* Cunha & Cruz, 1979 | | | 11 (0.21%) | |
| *Akodon cursor* (Winge, 1887) | **2 (28.81%)** | **3 (18.14%)** | 5 (3.75%) | **1 (34.18%)** |
| *Bibimys labiosus* (Winge, 1887) | 10 (0.34%) | | | |
| *Calomys tener* (Winge, 1887) | 7 (1.85%) | 9 (0.35%) | | |
| *Cerradomys subflavus* (Wagner, 1842) | **3 (9.34%)** | 8 (0.69%) | 6 (3.1%) | 7 (1.47%) |
| *Holochilus sciureus* Wagner, 1842 | 14 (0.13%) | | | |
| *Hylaeamys laticeps* (Lund, 1840) | | | 7 (2.78%) | 11 (0.44%) |
| *Necromys lasiurus* (Lund, 1841) | 9 (0.81%) | | | |
| *Nectomys squamipes* (Brants, 1827) | 8 (1.09%) | | | |
| *Oecomys catherinae* Thomas 1909 | | | 8 (2.25%) | 5 (2.86%) |
| *Oligoryzomys nigripes* (Olfers, 1818) | **1 (44.13%)** | **1 (46.63%)** | | 11 (0.44%) |
| *Oxymycterus dasytrichus* (Schinz, 1821) | 6 (3.86%) | | | |
| *Oxymycterus rufus* (Fischer, 1814) | **4 (4.49%)** | | | |
| *Rhipidomys mastacalis* (Lund, 1940) | | | 9 (0.64%) | 8 (0.66%) |
| *Rhipidomys tribei* Costa, Geise, Pereira & Costa, 2011 | 15 (0.11%) | **4 (3.48%)** | | |
| **Family Echimyidae** | | | | |
| *Euryzygomatomys spinosus* (G. Fisher, 1814) | 10 (0.34%) | | | |
| *Phyllomys brasiliensis* Lund, 1940 | | | 11 (0.21%) | 10 (0.51%) |
| *Phyllomys pattoni*<br>Emmnons, Leite, Kock & Costa, 2002 | | 10 (0.17%) | | |

# CAPÍTULO 2

# FATORES AMBIENTAIS ATUANDO NA MUDANÇA MORFOLÓGICA RÁPIDA EM ROEDORES

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Stumpp R, Fuzessy L, Paglia AP (2016) Environment drivers acting on rodent rapid morphological change. J Mammal Evol. Doi: 10.1007/s10914-9369-2

# Environment drivers acting on rodent rapid morphological change

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## ABSTRACT

Rapid Morphological Changes (RMCs) in rodents has been frequently documented. However, relation between RMCs and potential environmental drivers has been understudied. Here, we utilized a museum collection of four rodent species, collected in the same Atlantic Forest fragment, to investigate variation in the skull morphology over time, and test the influence of environmental and diversity drivers in RMC. We tested differences in size and shape of the skull between specimens collected in two temporal series, 1992-1997 and 2009-2010. For size, we tested differences over time in 20 cranial measurements within each species with independent-samples t-tests. To test shape variation, we performed a PERMANOVA with data generated by 13 landmarks on the dorsal view and another 13 on the ventral view throughout two-dimensional geometric morphometrics. We also explored the best relationships between cranial changes and five drivers of climate and two of rodent diversity by Akaike model selection. Our analysis showed RMCs in all studied species and theses changes were strongly influenced by tested drivers. The best model included only maximum temperature showing a negative association with size. Other tested models that presented similar fit showed that precipitation, humidity, richness of rodents, and minimum temperature had a positive association with size. Additionally, abundance also was negatively associated with morphological changes in the most abundant and the largest of the sampled species. The results indicated these species seem to quickly respond to environmental changes. Understanding which species have the potential to adapt to changes is central for the future of biodiversity conservation.

**Key words:** Cricetidae, Climatic changes, Diversity drivers, Neotropical mammals, Skull morphology.

## INTRODUCTION

Rapid Morphological Change (RMC) is the variation of morphological characteristics in a population over a few generations. This event has been observed in many groups of living beings, such as plants, invertebrates, amphibians, reptiles, birds, and mammals (Holmes et al. 2016). Changes in morphology within a short period are the product of microevolution via natural selection and/or phenotypic plasticity (Valladares et al. 2014; Pergams et al. 2015; Holmes et al. 2016). As many studies focus on highly polygenic traits, like body size, which are also susceptible to environmental influences, it is hard to determine whether these changes are genetically and/or plastically controlled (Pergams and Lacy 2007; Gardner et al. 2011). In any case, the power of environmental influence on RMC is undeniable.

Several external factors may influence morphology, including nutrition during the growth period, competition for resources, habitat fragmentation, and climate change (Koontz et al. 2001; Schmidt and Jensen 2003; Yom-Tov et al. 2008; Kearney et al. 2009; Rode et al. 2010; Gardner et al. 2011; Hoffmann and Sgrò 2011). These changes in size or body mass may develop rapidly and it is particularly easy to see in populations under pressure of fast environmental changes (Barnett and Dickson 1989; Smith et al. 1998; Hoffmann and Sgrò 2011).

Body size is not the only morphological component that may change in a brief period. Many studies with RMC report changes of shape over time (e.g., Franssen 2011; Mallarino et al. 2011; Doudna and Danielson 2015). Because shape is multi-dimensional, it may have a high content of information regarding the ecological and evolutionary processes (Yazdi and Adriaens 2011).

In rodents, RMC is relatively well documented, mostly because they have a short generation time and also a great number of historical specimens in natural history collections against which modern samples can be compared (Holmes et al. 2016). Perhaps the first documented case of RMC in rodents, and also one of the first examples of microevolution, has been reported in the beginning of the last century. Clarke (1904) described changes in body size and coat color in island rodents in Western Europe after some decades of isolation. Since then, many advances have been made regarding RMC knowledge, mainly relating temporal variation on body size to climatic and anthropogenic factors (Pergams and Lawler 2009; Hoffman and Sgrò 2011).

Despite that much is known of RMC in rodents, there are still gaps. First, the influence of climatic factors may also be underestimated. Temperature change is a key factor in directing evolution of many warm-blooded vertebrate populations (Millien et al. 2006). Effects of global warming are leading mammals and birds to the miniaturization of body size (Gardner et al. 2011). The premise for this hypothesis is described by Bergmann’s rule (Bergmann 1847). However, the negative relationship between temperature and body size in small mammals seems not to be a rule (Meiri and Dayan 2003; Gardner et al. 2011). There are cases in RMC of rodents that conform to the rule (Smith et al. 1995), but also those that have opposite effects (Eastmann et al., 2012). Although this relationship is unclear, Maestri et al. (2016) showed the geographical variation of body size in sigmodontine rodents is strongly influenced by temperature.

Effects of rainfall are also intense on body size (Maestri et al. 2016). This driver may have an indirect impact on body size through food availability. Abundance of food may be related to nutritional quality, which may affect cranial size in rodents (Patton and Brysky 1987). Precipitation has a positive relationship with primary productivity; more rain can lead to more vegetation and thus potentially more food resources. Besides rainfall, humidity may also affect body size. In conditions when environmental temperature exceeds body heat, body temperature can be kept from rising by water evaporation (Schmidt-Nielsen 1975). Under conditions of low humidity, the evaporation rate of sweat from the skin increases, allowing a quick heat loss. In this way, local decrease in humidity should attenuate the effect of increasing temperature on body size. Thus, testing the influence of several environmental variables on RMC may help to understand the temporal variation.

Another gap is that most of these studies analyzed only one species (e.g., Ozgul et al. 2010; Nengovhela et al. 2015) or many species of multiple locations (e.g., Schmidt and Jensen 2003; Pergams and Lawler 2009; Yom-Tov et al. 2012). Studies on RMC with several rodent species of the same location are practically nonexistent. The relationship between rodent diversity and RMC is also unknown. Increased intra- and interspecific competition negatively affects food resources (Schmid-Araya et al. 2002; Amarilo-Suárez et al. 2011), which may indirectly lead to miniaturization due to low nutritional quality. Furthermore, the great majority of studies with RMC in rodents have been performed in temperate zones. In tropical zones, only a few analyses with specimens collected in Chile, Kenya, and Peru (Pergams and Lawler 2009).

In order to answer these outstanding issues, the main objective of this study is to analyze RMC in different species of rodents in a Neotropical forest fragment that has suffered great environmental and diversity changes over the past decades. Our base hypotheses are (1) cranial morphology varies over time and (2) it is influenced by rapid environment changes, (3) as well as quick variations in diversity of rodents.

We predicted that environmental drivers, especially temperature, would affect morphological variation, because microclimate changes will result in a different physiological effort spent during rodent development, which may lead to differences in shape and size of adults. Similarly, we predicted that biotic drivers, like richness and abundance, also would have a strong relationship with morphological change, because these directly affect competition for resources, leading to greater selection pressure.

## MATERIAL AND METHODS

### Study area

The study area, known as Estação de Pesquisa, Treinamento e Educação Ambiental (EPTEA) Mata do Paraíso, is located in Viçosa, Minas Gerais, Brazil (20º48'S, 42º51'W). Total area of EPTEA Mata do Paraíso is 195ha and it is inserted in a larger fragment of Atlantic Forest. Altitude varies between 690 and 850m (Ribon 2005) and it has a warm temperate climate (Vianello and Alves 1991). The original vegetation was classified as a Semideciduous Montane Forest (Pinto et al. 2007).

The EPTEA Mata do Paraíso was formerly a highly fragmented farmland used for coffee plantations and livestock. Since 1966, the fragment is the responsibility of Federal University of Viçosa (UFV). Hunting and timber removal ceased and the fragment started to regenerate (Ribon 2005). Structure and composition of vegetation has changed over this time, as well as the size of the fragment (Higuchi et al. 2006). Climate data also shows an apparent upward trend in average temperature and rainfall between 1991 and 2010, and an apparent decrease trend, in the same period, in humidity. Studies on small mammal communities also show a variation on structure and composition over time in EPTEA Mata do Paraíso (Paglia et al. 1995; Lessa et al. 1999). Environmental data are listed in Online resource 1.

### Specimen Selection

We chose two periods based on the years of collecting – Temporal Series 1 (TS1), with specimens collected in 1992-1993 and 1997; and Temporal Series 2 (TS2), with specimens collected in 2009-2010. We selected only species that had at least eight adult specimens collected in each Temporal Series. We considered adult only those rodents with three moderately worn molars.

Four Sigmodontinae species fulfilled these prerequisites: *Akodon cursor* (Winge, 1887), with 27 specimens of TS1 and 52 of TS2; *Cerradomys subflavus* (Wagner, 1842), with eight specimens of TS1 and 21 of TS2; *Oligoryzomys nigripes* (Olfers, 1818), with 33 specimens of TS1 and 51 of TS2; and *Oxymycterus dasythichus* (Schinz, 1821), with 11 specimens of TS1 and eight of TS2. All specimens are deposited in the Mastozoology Collection of João Moojen Zoology Museum at the Federal University of Viçosa (MZUFV). Specimens are listed in Online resource 2.

The cursorial grass mouse, *A. cursor,* is an akodontini rodent member of the forest and open area fauna in the Atlantic Forest of eastern Brazil. This species inhabits both primary and degraded forest fragments (Patton et al. 2015). Food preferences varied according to environmental conditions, but the species diet is mainly insectivore-omnivore (Paglia et al. 2012).

Another small rodent, the flavescent rice rat, *C. subflavus,* is a medium-sized oryzomyini rodent endemic to central Brazil. This rodent occurs in mesic habitats in the Cerrado, and in patches of semideciduous forest of the interior Brazilian highlands (Patton et al. 2015). It is a primarily frugivore-granivore rodent (Paglia et al. 2012).

The black-foot colilargo, *O. nigripes,* another member of the Oryzomyini tribe, is a small rodent common in eastern Brazil, Paraguay, Uruguay, and northeastern Argentina. This is the most habitat-generalist of all Brazilian *Oligoryzomys* species, occurring in primary and secondary vegetation (Patton et al. 2015). Its diet is basically frugivore-granivore (Paglia et al. 2012).

The last species, the northern Atlantic Forest hocicudo, *O. dasytrichus,* another akodontini, is a medium-sized small rodent. This species inhabits both coastal forests and isolated interior forest remnants in Brazilian Cerrado and Atlantic Forest (Patton et al. 2015). Its diet is basically insectivore-omnivore (Paglia et al. 2012).

## Size changes

We took twenty cranial measurements with a digital caliper, to the nearest 0.01 mm: greatest length of the skull (GLS), condylo-incisive length (CIL), nasal length (NL), breadth between occipital condyles (BOC), length of diastema (LDI), length of palatal bridge (LPB), length (LIF) and breadth of incisive foramina (BIF), length of maxillary molar row (LMR), breadth of upper first molar (BFM), breadth across molars (BAM), length of bulla (LBU), height of skull (HS), rostrum length (RL), rostrum width (ROW), least interorbital width (LIW), zygomatic breadth (ZIB), breadth of braincase (BBR), breadth of zygomatic plate (BZP), and length of mandible (LMA).

In order to reduce the effect of sex in our analysis, we tested sexual dimorphism within each species through t-tests for each measurement. Measurements that presented sexual differences had the effect of sex removed by summing up the difference between means of males and females to that sex which presented lesser values. Sexes were then pooled for all subsequent analyses, which were carried out on these transformed values (Geise et al. 2005). As sexual dimorphism in sigmodontine rodents is low (e.g., Carleton and Musser 1989; Voss 1991), we expect minor effects of sex on our results.

To determine morphological change, we performed independent-samples t-tests testing the significance of the difference between Temporal Series for each measurement. All analyzes were performed with the software Statistica v.10.1. We calculated the rates of change, as well as the rate of annual change for each significant trait. The first was done by dividing the difference in means by the mean of the most recent sample. The second was calculated dividing the rate of change by the number of years between time periods sampled. We also calculated rates of evolution in darwins with the equation:

$$d = \frac{|(lnX_2 - \ln X_1)|}{\Delta t}$$

in which $X_1$ and $X_2$ are the initial and final values of each measurement in the time classes and $\Delta$t is time interval per million years (Haldane 1949).

## Shape changes

We verified changes on cranial shape over time throughout two-dimensional geometric morphometric. We took dorsal and ventral digital photographs of the skull using a Canon EOS REBEL T3/1100D camera with 12.2 megapixel resolution (4272 x 2848) setting the macro function in an automatic mode and without flash or zoom. The photos were taken from a standard distance of 20 mm for all specimens. The total input data consisting of 13 landmarks on the dorsal view and another 13 on the ventral view (Fig. 1) were digitized using TpsDig2 software (Rohlf 2010). A description of all landmarks is given in Online resource 3.

We transformed a matrix based on landmark coordinates (x, y) using the Procrustes superimposition analysis in PAST v3.06, to remove the effects of translation, rotation, and scaling in our landmark data. All outliers were redigitized and tested again. The size of each specimen was accessed through the centroid size calculated as the square root of the sum of the squared distances from each of the 11 landmarks to their joint median using tpsRELW.

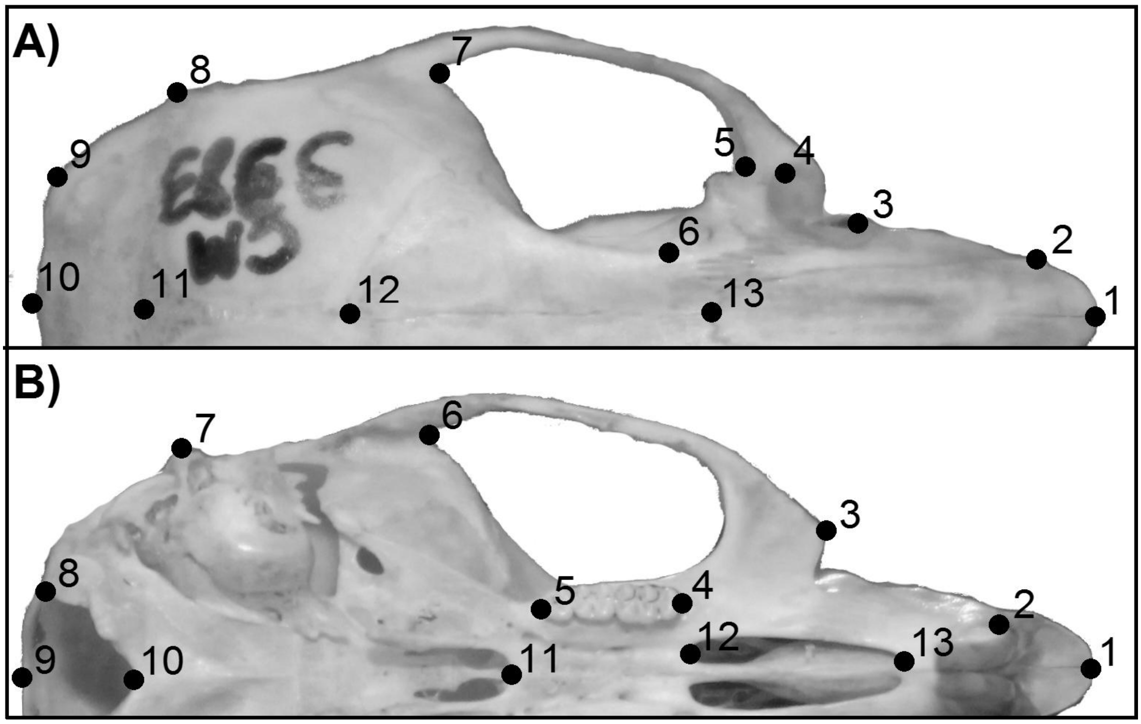

**Figure 01** Landmarks digitized in skull of all specimens. A description of each landmark is presented in Appendix III. A) 13 landmarks plotted in dorsal view; and B) 13 landmarks plotted in ventral view.

We tested differences between Temporal Series with a Permutational Multivariate Analysis of Variance (PERMANOVA) using the matrix genetared by Procrustes analysis. In cases where differences were significant, we proceed by performing the Relative Warp analysis in order to highlight changes in shape. We tested the influence of allometry with a linear regression of full shape space. In cases of correlation ($p < 0.05$), we compared shapes of the significant warp that most explained variation between mean shapes of each Temporal Series with deformation grids.

## Drivers of change

We tested the relationships between changes in cranial morphology and potential environmental drivers based on changes in climate and rodent diversity. As climate drivers, we used the following variables: Annual Mean Temperature (AMT), Mean Maximum Temperature of Warmest Quarter (MMTWQ), Mean Minimum Temperature of Coldest Quarter (MMTCQ), Annual Precipitation (AP), and Annual Humidity (AH). We obtained climate data from the meteorological station of Federal University of

Viçosa, located about 1,000m from EPTEA Mata do Paraíso. These data came from the year before specimens were collected, because environmental stress can lead to morphological changes caused by developmental instability (Kieser, 1993). Richness of Rodents (RR) and Abundance (Abd) of each species were variables used as drivers of rodent diversity. We took those data from previous studies (Paglia et al. 1995; Lessa et al. 1999) and unpublished data. As the sample effort was different between sampled years, we created an index of abundance - the ratio of total specimens captured in a determined year to total months sampled in that year.

We chose these seven drivers due to their direct or indirect effect on body size. As the relationship between temperature and body size for small mammals is unclear (Meiri and Dayan 2003; Gardner et al. 2011), but also temperature is the environmental driver that most affects body size in sigmodontine rodents (Maestri et al. 2016), we decided to use three drivers (AMT, MMTWQ, and MMTCQ) that represent temperature in order to make this relation clear.

We explored potential associations between measurements and drivers. For that, we made a principal component analysis of all measurements presenting significant difference over time using only species that had changed. We evaluated the potential effect of the six drivers that were constant for all individuals (AMT, MMTWQ, MMTCQ, AP, AH, and RR) on overall morphometric change in skull size, represented by the PC1 score. As units, we used individuals with driver's data associated with each individual specimen. After that, we determined the best fitted model by Akaike model selection (AIC— Akaike 1973) corrected for small sample sizes ($AIC_c$). We used the component ΔAICc to compare AICc between models and Akaike weights ($AICc_{(WT)}$) sensu Burnham and Anderson (2002) and Anderson (2008) to access level of support in favor of each model. We considered the best models those presenting low $\Delta AIC_c$ values, close to two, because they provide similar support (Burnham and Anderson 2002; Symonds and Moussalli, 2011). Abundance was a shifting driver between species, and it affects intraspecific competition. Therefore, seeking to evaluate the effect of this driver on morphometry, we fitted a general linear model accounting for abundance effects on PC1 score.

We also explored the association between changes in shape, represented by the first warp, and these drivers. Type I error rate was set to 0.05 in all analyses and all statistical analyses were performed using the computing environment R (R

Development Core Team, 2014) and additional packages (car, ape, psych, MuMin, and AICcmodavg)

## RESULTS

### Size changes

Sexual dimorphism was found only in one measurement in *A. cursor* from 2009-2010 (BAM), males smaller than females; and three measurements in *O. nigripes* from 1992-1993 (GLS, LIF, and LMA), males larger than females. Summaries of the raw data are given in Online resource 4.

Of all 80 possible size changes in species between Temporal Series, seven were significant at α<0.05, three for *O. nigripes*, two for *A. cursor*, and another two for *C. subflavus*. All of these increased with time. Four of these changes in measurements were linked to the rostral portion of the skull. The greatest change was 6.75% (0.41%/year) in the length of incisive foramen of *C. subflavus*. Rates of evolution varied from 1127.18d to 4308.62d (Fig. 2). No variation over time was found in *O. dasytrichus*.

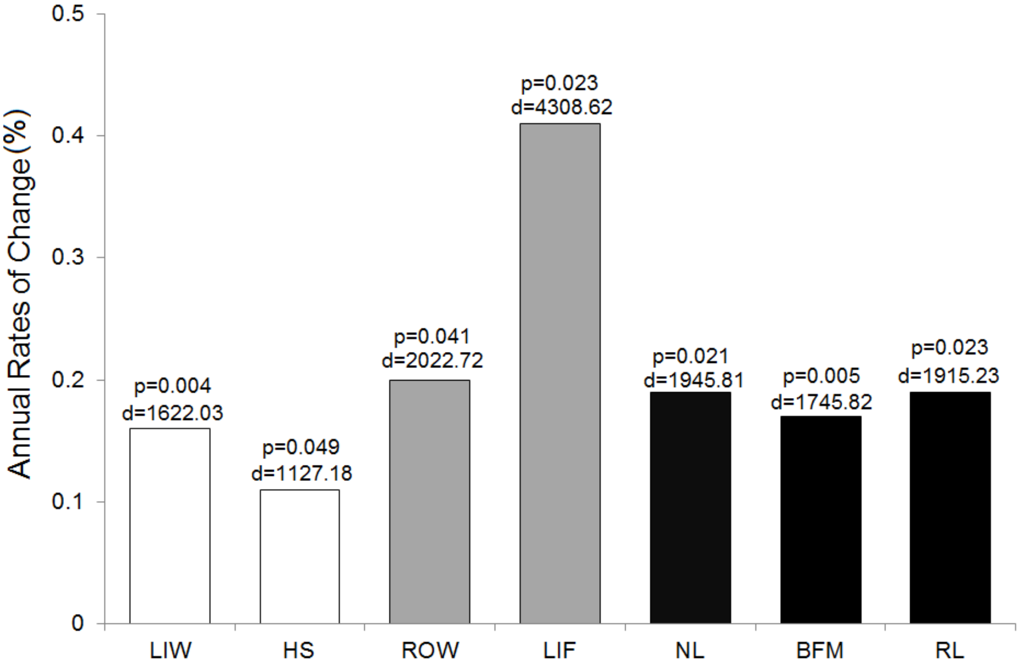

**Figure 02** Annual rates of change for all measurements that show significant difference over time at α<0.05. Above each bar is also given, in order, p-value and rate of evolution in darwins. White bars represent significant measurements of *Akodon cursor*, grey bars significant measurements for *Cerradomys subflavus*, and black bars significant measurements of *Oligoryzomys nigripes*.

## Shape changes

Results on PERMANOVA showed all four species had changes over time in ventral view; while in dorsal view, there were changes in *A. cursor* and *O. dasytrichus*. In all cases, the first relative warp better explained temporal changes in the cranium (Table 1).

**Table 01** Summary statistics for PERMANOVA and linear regressions of full shape space to test the influence of allometry in temporal changes in the cranium of the four species studied.

| **View** | **Species** | **PERMANOVA** | | **Linear regression** | |
|---|---|---|---|---|---|
| | | **F** | **P** | **$r^2$** | **P** |
| Ventral | *A. cursor* | 4.13 | **< 0.001** | 0.274 | < 0.001 |
| | *C. subflavus* | 2.72 | **0.019** | 0.187 | 0.001 |
| | *O. dasytrichus* | 2.94 | **0.002** | 0.421 | 0.002 |
| | *O.nigripes* | 1.94 | **0.036** | 0.593 | < 0.001 |
| Dorsal | *A. cursor* | 4.85 | **< 0.001** | 0.198 | 0.001 |
| | *C. subflavus* | 1.73 | 0.097 | 0.121 | 0.027 |
| | *O. dasytrichus* | 2.67 | **0.017** | 0.342 | < 0.001 |
| | *O. nigripes* | 1.61 | 0.096 | 0.184 | 0.003 |

Deformation grids showed two patterns of temporal changes in the ventral shape of the skull of the sampled species. In the first pattern, found in *A. cursor* and *C. subflavus*, there was an expansion of the zygomatic plate and most elements associated with the rostrum (nasal tip, incisive foramina, palate), and a strong retraction of the foramen magnum and a minor retraction of the maxillary molar row. The second, found in *O. nigripes* and *O. dasytrichus*, is almost the opposite of the first – there was a retraction of most elements associated with the rostrum, and a strong expansion of the foramen magnum and a minor expansion of the maxillary molar row. In dorsal view, we also found two almost opposite patterns. In *A. cursor* there was an overall retraction of the rostrum and the expansion of parietals, while in *O. dasytrichus* there was an expansion of the rostrum and a strong retraction of the parietals, as well as the retraction of the temporal fossa (Fig. 3).

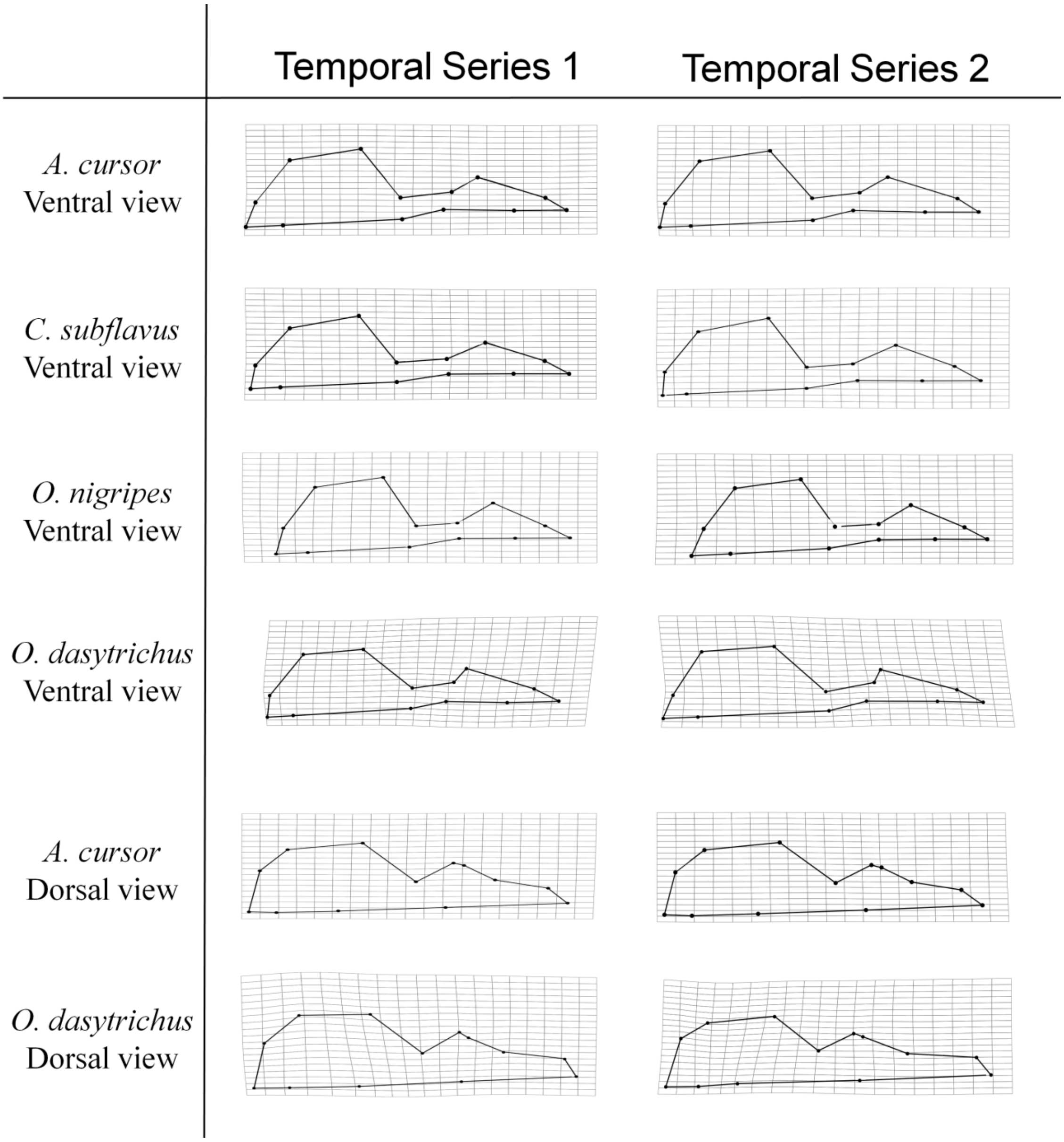

**Figure 03** Thin-plate corresponding to observed deformations between mean shapes of Temporal Series 1 and 2 along the first relative warp axis for the dorsal and ventral view of the skull of the studied species.

## Drivers of change

We performed principal component analysis to explore potential associations between measurements and drivers with the seven measurements that had significant differences over time – NL, LIF, BIF, BFM, HS, RL, and ROW – with all specimens of *A. cursor*, *C. subflavus*, and *O. nigripes*. All variables were positively correlated with PC1- which represented 63.18% of total explanation - indicating an index of structural size (Pimentel 1979). The correlation matrix of PC1 and the six drivers showed high correlation between MMTWQ, AP, and AH (>0.8). Under these circumstances the effect of those variables are highly reflected on each other, and we opted to maintain only MMTWQ. We made this choice because MMTWQ effects directly body size and it better explains the physiological mechanisms that affect body size. We also removed AMT because its correlation with PC1 was null (=0.0). Pearson's correlation coefficients between six analyzed drivers are given in the Online resource 5.

Model selection using the $AIC_c$ showed that for potential associations between measurements and drivers the best model included only MMTWQ. The best two following models had a $\Delta AIC_c$ very close to 2 and also a high *W*AIC (Table 2); thus we decided to use them to explain our results too. Given these three best models, MMTWQ represented 79% of total explanation and had a negative association with PC1 ($r=-0.2$), while RR, which explained 17% of changes in size, and MMTCQ, which explained 16%, had a positive association (respectively $r=0.12$; $r=0.11$). As AP and AH were highly correlated with MMTWQ, we also made linear regressions of these drivers onto PC1 of the three species. Both showed a positive association with PC1 (AP: $r=0.18$; $F=271$; $p<0.001$; AH: $r=0.21$; $F=252$; $p<0.001$).

In relation to changes in ventral and dorsal shape over the years, we kept AP and AH out of the model selection. However, we included AMT, because this driver had some correlation with RW1. The best model was the null model and no other had $\Delta AIC_c$ next to 2, which means no effect of drivers on shape.

In relation to abundance, the GLMs showed a relationship between PC1 and this driver only for *O. nigripes* ($F=5.89$; $p=0.017$), showing a negative association. The influence of abundance in shape was only observed in the dorsal view of *O. dasytrichus* ($F=4.66$; $p=0.049$). The increase in the number of individuals of this species leads to the shape of TS1.

**Table 02** Candidate models for the relationship between size changes in *A. cursor*, *C. subflavus*, and *O. nigripes* and environmental drivers. *K* is the number of parameters in the model, $AIC_c$ is Akaike's information criterion (AIC) corrected for small sample size, $\Delta AIC_c$ is the difference in AICc values between each model and the best model (i.e., lowest AICc), *W*AIC is the Akaike weight and Cum.W is the cumulative Akaike weight. MMTWQ - Mean Maximum Temperature of Warmest Quarter, MMTCQ - Mean Minimum Temperature of Coldest Quarter, RR - Richness of Rodents.

| Models | *K* | $AIC_c$ | ΔAICc | *W*AIC | Cum.W |
|---|---|---|---|---|---|
| MMTWQ | 3 | -427.91 | 0 | 0.46 | 0.46 |
| MMTWQ + RR | 4 | -425.89 | 2.01 | 0.17 | 0.63 |
| MMTWQ + MMTCQ | 4 | -425.81 | 2.1 | 0.16 | 0.79 |
| MMTWQ + MMTCQ + RR | 5 | -423.81 | 4.1 | 0.06 | 0.85 |
| RR | 3 | -423.27 | 4.64 | 0.04 | 0.9 |
| MMTCQ | 3 | -423.09 | 4.82 | 0.04 | 0.94 |
| Null | 2 | -423.03 | 4.88 | 0.04 | 0.98 |
| MMTCQ + RR | 4 | -421.45 | 6.46 | 0.02 | 1 |

## DISCUSSION

Our results clearly demonstrate Rapid Morphological Changes (RMCs) in the four studied species of EPTEA Mata do Paraíso. Furthermore, some of these changes appear to be driven by environmental drivers. Many species of rodents are highly adaptable to fit in a world in constant land use and climatic changes (Auffray et al. 2009) and one of the ways of suitability seems to be RMC.

Rates of change we found ranged from 1127.18d to 4308.62d, a similar range in cranial measurements for other cricetids, 586-5665d in Pergams and Lawler (2009), and 915-4772d in Pergams and Lacy (2007). Evolutionary rates are generally expected to be faster in warmer climates (Wright et al. 2006; Kozak and Wiens 2007), so we expected that rates of change would be greater than those of species that live in temperate zones. We also expected that island species would have a larger rate than continental species, usually attributed to selective release or founder events related to island settings (Palkovacs 2003). Nonetheless, rates of change in island rodents were lower than ours, ranging from 724d to 2567d (Pergams et al. 2015).

The absence of changes in measurements over time, as we find here for *O. dasytrichus*, is not rare in rodents, although they are poorly reported. According to Yom-Tov et al. (2012), these cases should be far more frequent than documented, but they are not published because authors, and particularly editors, are reluctant to publish negative results. In studies approaching RMC in various species of rodents, the percentage of species that have not changed over time ranged from 28% to 66% (Pergams and Lawler 2009; Yom-Tov et al. 2012). Changes in size are not the only morphological consequence caused by environmental stress (Yom-Tov et al. 2012), probably *O. dasytrichus* showed larger shape variation as a compensation for the lack of change in size.

Virtually all drivers tested here impacted on skull morphological changes, except for AMT. The influence of ecological drivers in sigmodontine rodents explains substantial components of the morphological variation (Tulli et al. 2015). Most changes we found in the analyzed species from 1992 to 2010 are related to the rostral part of the skull, as four of the seven measurements and most changes in shape are related to this part. In rodents, the rostral development may be associated with the nasal turbinates, which aid on thermoregulation and reduction of respiratory water loss (Hillenius 1992). Interestingly, the main functions of nasal turbinates are associated with three of the significant drivers, Mean Maximum Temperature of the Warmest Quarter (MMTWQ), Mean Minimum Temperature of Coldest Quarter (MMTCQ), and Annual Humidity (AH).

In tropical climates, average monthly temperature is at least 18ºC and maximum temperature easily exceeds 28ºC in the warmest months (McKnight and Hess 2000). Variations in temperature affects rodent metabolism, as they tolerate severe cold stress better than they withstand heat (Gordon 1993). Thus, it is easy to understand the reason, in tropical climates, that high temperature extremes affects physiology more than cold temperature. Our results showed the negative relationship between MMTWQ and body size, in accord with Bergmann’s Rule, as in many groups of mammals (Gardner et al. 2011). However, MMTCQ did not follow this rule and minimum temperature influenced the skull size differently, and perhaps it is a spurious correlation. Yet, according to our results it is not possible to state that changes on average temperature reflect on changes in size.

For small mammals, other studies showed uncertainty in the relationship between temperature increase and miniaturization (Ashton et al. 2000; Meiri and Dayan 2003; Gardner et al. 2011). However, in most of these studies, the researchers made only a few measurements, such as head and body length or greatest skull length. Those measurements only give a sense of the overall size of the animal, without showing variations in specific parts of the body. The environmental stress, as high temperatures, seems to influence animal physiology during ontogenetic development (Harrison 1958), then affecting their morphology (Kieser 1993; Klingenberg and Nijhout 1999). In rodents, the amount of skin glands is insufficient for heat dissipation and their respiratory apparatus is inadequate for painting (Schmidt-Nielsen 1975); therefore, thermoregulation through nasal turbinates is essential for these animals. The rostrum is presumably more affected by metabolic changes caused by climatic variation during development and then suffers greater morphological changes.

Effects of humidity in the rostrum also seem to follow this pattern. Humidity affects thermoregulation by limiting sweat evaporation and thus heat loss. The higher the humidity the harder is water evaporation. Also, mechanical forces caused by airflow are known to control morphological development of turbinates (Coppola et al. 2014), which is impacted by the temperature and humidity of the environment. Thus, it is possible that the high humidity during the development period of these rodents has influenced the increase of rostral region.

Besides nasal turbinates, the rostral development is also associated with chewing and the sense of smell (Myers and Hall 2000; Samuels 2009), and these are related to food. All indirect drivers - Annual Precipitation (AP), Richness of Rodents (RR), and Abundance (Abd) - had impact on body size. Rainfall is highly correlated with seed production (e.g., Joubert et al. 2013) and abundance of insects (e.g., Karuppaiah and Sujayanad 2012), the main food categories of our studied species. A larger amount of food resources may be associated with a richer diet, which may affect body size in rodents (Patton and Brysky 1987).

Our prediction about RR did not take place and this driver explained 17% of increase in some portions of the skull. It is possible that increased interspecific competition generated responses other than decrease in body size. Increased competition may imply diversification among species, decreasing niche overlap (Schmid-Araya et al. 2002). Allometric changes we found in the skull, especially in the rostral region, can be an effect of the selection pressure caused by this diversification. In addition, rostral stretching can also enhance the ability of foraging, as this part is strongly associated with olfactory sense (Gritti et al. 2002).

The last driver, Abd, negatively influenced *O. nigripes* body size. Amarilo-Suárez et al. (2011) tested the effects of population density and food resources on body size of beetles. They found that a greater number of specimens negatively affect body size. Nonetheless, this effect is attenuated in a large amount of resources. Here, species abundance seems to reflect this. In the EPTEA Mata do Paraíso, the most abundant species was always *O. nigripes* and the number of specimens of the other species was much lower (Paglia et al. 1995; Lessa et al. 1999). Increase in *O. nigripes* abundance could have raised further the intraspecific competition, and thus it could lead to miniaturization. On the other hand, due to low population density in *A. cursor* and *C. subflavus*, increased number of individuals did not seem to increase competition in order to diminish the nutritional quality and affect the morphology. In *O. dasytrichus*, Abd influenced the dorsal shape of the skull. Despite having the lowest population density, this species is the largest among the four studied species and the negative relationship between body size and abundance is greater in larger species (Amarilo-Suárez et al. 2011).

Changes over time in structure and composition of vegetation in EPTEA Mata do Paraíso, with dominant tree families more associated with mature forests (Higuchi et al. 2006), may also have led to morphological changes in the rostrum.  Seeds are the main food resource for *O. nigripes* (Pinotti et al. 2011), and this species feeds mainly on open field seeds even if it is living in mature forests (Galetti et al., 2016). Also, in our results the breadth of upper first molar (BFM) changed over time for this species. Significant changes in dentition might be driven by an alteration of food availability (Szuma 2003). The decreased production of seeds of pioneer tree species could have led to a selection of specimens that have better foraging capacity or individuals that eat different species of seeds. According to Samuels (2009), there is a strong relationship between cranial morphology and dietary habits of rodents. This also suggests that changes in food resources may have affected the morphology of the skull.

The influence of environmental as well as diversity drivers in RMC was clear in our results. Species we studied seem to quickly respond to changes and they are more likely to survive the rapid anthropic environmental changes of the last decades. Understanding which species have the greatest potential to adapt to these changes is one of the key pieces for the future of biodiversity conservation.

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# Online Resources 1

## Environment drivers acting on rodent rapid morphological change

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**Supplementary Table 1** Climatic data per year obtained climate data from the meteorological station of Federal University of Viçosa, located about 1,000m from EPTEA Mata do Paraíso.

| Year | Annual Precipitation (mm) | Annual Mean Temperature (ºC) | Mean Maximum Temperature of Warmest Quarter (ºC) | Mean Minimum Temperature of Coldest Quarter (ºC) | Annual Relative Humidity (%) |
|---|---|---|---|---|---|
| 1991 | 132.900 | 19.773 | 28.229 | 12.159 | 81.267 |
| 1992 | 121.325 | 19.616 | 27.279 | 11.861 | 84.206 |
| 1993 | 73.642 | 20.282 | 29.597 | 11.107 | 81.858 |
| 1994 | 95.920 | 19.389 | 29.144 | 10.194 | 81.802 |
| 1995 | 92.417 | 20.166 | 29.642 | 11.147 | 78.114 |
| 1996 | 94.825 | 19.703 | 30.011 | 10.093 | 79.159 |
| 1997 | 105.200 | 20.126 | 28.985 | 11.446 | 76.189 |
| 1998 | 95.442 | 20.485 | 30.210 | 11.859 | 80.577 |
| 1999 | 100.658 | 19.755 | 29.604 | 10.713 | 78.235 |
| 2000 | 103.473 | 20.040 | 29.121 | 11.138 | 83.872 |
| 2001 | 96.675 | 20.664 | 30.749 | 12.436 | 77.999 |
| 2002 | 106.142 | 20.836 | 30.163 | 12.527 | 78.333 |
| 2003 | 95.067 | 20.294 | 29.854 | 11.145 | 78.186 |
| 2004 | 149.833 | 19.721 | 27.920 | 11.580 | 81.244 |
| 2005 | 119.667 | 20.161 | 28.617 | 12.562 | 82.353 |
| 2006 | 100.242 | 19.987 | 29.552 | 11.145 | 84.301 |
| 2007 | 84.125 | 20.258 | 29.681 | 11.050 | 78.212 |
| 2008 | 140.800 | 19.892 | 28.227 | 11.551 | 81.360 |
| 2009 | 130.617 | 20.613 | 29.450 | 12.923 | 79.997 |
| 2010 | 112.633 | 20.203 | 30.553 | 10.718 | 76.517 |

**Supplementary Table 2** Diversity data per year obtained from other studies. Richness of rodents is the total of rodent species captured in that year, while Abundance represents an index of abundance - the ratio of total specimens captured in a determined year to total months sampled in that year.

| **Year** | **Richness of rodents (N)** | **Abundance (N)** | | | | **Reference** |
|---|---|---|---|---|---|---|
| | | ***Akodon cursor*** | ***Cerradomys subflavus*** | ***Oligoryzomys nigripes*** | ***Oxymycterus dasytrichus*** | |
| 1992 | 13 | 7.345 | 1.5 | 18.75 | 4 | Paglia et al.,1995 |
| 1993 | 13 | 8.25 | 2 | 17.25 | 3 | Paglia et al.,1995 |
| 1997 | 8 | 4.67 | 0.67 | 14 | 10 | Lessa et al., 1999 |
| 2009 | 10 | 8.11 | 2.55 | 12.33 | 3.67 | umpublished data |
| 2010 | 10 | 13.44 | 2.55 | 14.22 | 5.8 | umpublished data |

# Online Resource 2

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### LIST OF INVESTIGATED SPECIMENS:

Abbreviations: Mastozoology Collection of João Moojen Zoology Museum at the Federal University of Viçosa (MZUFV).

*Akodon cursor*: **Temporal Series 1 –** MZUFV 205, 214, 223, 225, 415, 418, 427, 428, 429, 430, 433, 437, 438, 439, 440, 442, 443, 592, 593, 635, 640, 645, 648, 663, 722, 726, 727. **Temporal Series 2** – MZUFV 2763, 2764, 2766, 2769, 2770, 2773, 2774, 2775, 2776, 2807, 2808, 2810, 2811, 2812, 2815, 2833, 2841, 2865, 2874, 2875, 2876, 2880, 2883, 2884, 2885, 2898, 2899, 2900, 2903, 2904, 2906, 2948, 2970, 2971, 2993, 2994, 3006, 3007, 3010, 3332, 3333, 3336, 3340, 3352, 3353, 3366, 3390, 3506, 3554, 3636, 3671, 3678.

*Cerradomys subflavus*: **Temporal Series 1** - MZUFV 202, 203, 219, 221, 222, 389, 451, 665. **Temporal Series 2** – MZUFV2785, 2800, 2801, 2805, 2806, 2827, 2856, 2879, 2882, 2911, 2917, 2947, 2978, 2979, 2982, 2996, 3000, 3190, 3368, 3375, 3670.

*Oligoryzomys nigripes:* **Temporal Series 1 –** MZUFV 206, 207, 413, 414, 419, 421, 422, 424, 435, 436, 441, 444, 449, 452, 580, 582, 583, 587, 604, 647, 650, 651, 653, 654, 666, 667, 668, 670, 671, 672, 673, 675, 706. **Temporal Series 3 –** MZUFV 2778, 2782, 2798, 2816, 2817, 2818, 2822, 2824, 2832, 2836, 2838, 2839, 2840, 2854, 2867, 2868, 2869, 2879, 2872, 2881, 2886, 2887, 2888, 2889, 2893, 2894, 2895, 2896, 2902, 2905, 2908, 2910, 1912, 2914, 2915, 2969, 2981, 2991, 2992, 3001, 3008, 3009, 3337, 3338, 3341, 3342, 3342, 3345, 3346, 3347, 3349.

*Oxymycterus dasythichus:* **Temporal Series 1** – MZUFV 204, 215, 226, 266, 432, 569, 589, 641, 703, 712, 715. **Temporal Series 2 –** MZUFV 2788, 2799, 2804, 2829, 2830, 2864, 2878, 2989.

# Online Resource 3

## Environment drivers acting on rodent rapid morphological change

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Landmarks in dorsal view were defined as:

1 - anterior tip of nasals;
2 - anterior point at suture between nasals and premaxilla;
3 - narrowest point of rostrum;
4 - posterior point of upper maxillary process;
5 - anterior point of interior orbit;
6 - least interorbital region;
7 - posterior point of interior orbit;
8 - exterior tip of external auditory meatus;
9 - edge of supraoccipital ridge;
10 - posterior point of supraoccipital;
11 - junction between interparietal, parietal, and midline;
12 - junction between parietal, frontal, and midline;
13 - junction between frontal, nasals, and midline;

Landmarks in ventral view were defined as:

1 - anteriormost point of the suture between nasals;

2 - outermost point of the alveolus of the incisor;

3 - rostral end of the zygomatic plate;

4 - anteriormost point of the molar row;

5 - posteriormost point of the molar row;

6 - posterior point of interior orbit;

7 - anteriormost external border of the ectotympanic.

8 - lateralmost point of the occipital condyle;

9 - posteriormost point of the foramen magnum;

10 - anteriormost border of the occipital condyle;

11 - posteriormost point of the suture between palatines and the anterior border of the mesopterygoid fossa;

12 - posteriormost point of the incisive foramen;

13 - anteriormost point of the incisive foramen;

# Online Resource 4

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**Supplementary Table 1** Craniodental measurements of the Akodontine species from EPTEA Mata do Paraíso separated by Temporal Series. Summary statistics: sample size (n), mean followed by standard deviation. Bold numbers show significant difference between temporal series.

| Measurements | *Akodon cursor* | | *Oxymycterus dasytrichus* | |
|---|---|---|---|---|
| | **Temporal Series 1 (27)** | **Temporal Series 2 (52)** | **Temporal Series 1 (11)** | **Temporal Series 2 (8)** |
| GLS | 28.73 ± 1.15 | 29.09 ± 1.03 | 36.52 ± 1.33 | 36.67 ± 1.54 |
| CIL | 27.97 ± 1.09 | 28.51 ± 1.17 | 33.76 ± 1.11 | 33.97 ± 1.34 |
| NL | 11.11 ± 0.64 | 11.13 ± 0.57 | 14.95 ± 1.37 | 14.44 ± 0.9 |
| BOC | 6.76 ± 0.25 | 6.74 ± 0.18 | 8.14 ± 0.14 | 8.12 ± 0.22 |
| LDI | 7.26 ± 0.42 | 7.36 ± 0.33 | 8.35 ± 0.5 | 8.6 ± 0.62 |
| LPB | 3.77 ± 0.37 | 3.84 ± 0.24 | 4.57 ± 0.37 | 4.44 ± 0.21 |
| LIF | 6.17 ± 0.37 | 6.31 ± 0.33 | 7.41 ± 0.34 | 7.62 ± 0.24 |
| BIF | 2.20 ± 0.13 | 2.23 ± 0.17 | 2.51 ± 0.15 | 2.6 ± 0.17 |
| LMR | 4.43 ± 0.11 | 4.44 ± 0.17 | 5.36 ± 0.26 | 5.36 ± 0.14 |
| BFM | 1.31 ± 0.12 | 1.28 ± 0.11 | 1.48 ± 0.08 | 1.45 ± 0.05 |
| BAM | 5.51 ± 0.18 | 5.58 ± 0.23 | 7.42 ± 0.22 | 7.39 ± 0.3 |
| LBU | 4.49 ± 0.17 | 4.54 ± 0.19 | 5.41 ± 0.22 | 5.35 ± 0.29 |
| HS | **8.8 ± 0.19** | **8.74 ± 0.32** | 10.6 ± 0.34 | 10.87 ± 0.51 |
| RL | 11.0 ± 0.75 | 12.05 ± 0.65 | 16.05 ± 0.73 | 16.09 ± 0.8 |
| ROW | 5.39 ± 0.29 | 5.34 ± 0.3 | 6.27 ± 0.33 | 6.12 ± 0.37 |
| LIW | **5.25 ± 0.16** | **5.38 ± 0.21** | 6.82 ± 0.31 | 6.91 ± 0.27 |
| ZIB | 15.15 ± 0.54 | 14.97 ± 0.45 | 16.89 ± 0.67 | 16.92 ± 0.64 |
| BBR | 12.75 ± 0.3 | 12.61 ± 0.25 | 15.12 ± 0.36 | 15.24 ± 0.31 |
| BZP | 2.92 ± 0.29 | 2.85 ± 0.25 | 2.6 ± 0.2 | 2.47 ± 0.22 |
| LMA | 14.54 ± 1.12 | 14.91 ± 0.70 | 17.93 ± 0.62 | 18.08 ± 0.78 |

**Supplementary Table 2** Craniodental measurements of the Oryzomyini species from EPTEA Mata do Paraíso separated by Temporal Series. Summary statistics: sample size (n), mean followed by standard deviation. Bold numbers show significant difference between temporal series.

| **Measurements** | ***Cerradomys subflavus*** | | ***Oligoryzomys nigripes*** | |
|---|---|---|---|---|
| | **Temporal Series 1 (8)** | **Temporal Series 2 (21)** | **Temporal Series 1 (33)** | **Temporal Series 2 (51)** |
| GLS | 33.27 ± 2.6 | 34.9 ± 2.2 | 23.98 ± 0.9 | 24.19 ± 0.75 |
| CIL | 26.01 ± 2.36 | 27.23 ± 1.86 | 22.32 ± 0.79 | 22.47 ± 0.71 |
| NL | 12.26 ± 1.49 | 12.94 ± 0.81 | **8.85 ± 0.47** | **9.1 ± 0.46** |
| BOC | 7.11 ± 0.15 | 7.21 ± 0.23 | 4.27 ± 0.18 | 4.25 ± 0.17 |
| LDI | 9.97 ± 0.52 | 10.13 ± 0.61 | 5.85 ± 0.32 | 5.87 ± 0.26 |
| LPB | 5.65 ± 0.24 | 5.74 ± 0.21 | 4.12 ± 0.22 | 4.13 ± 0.23 |
| LIF | **6.72 ± 0.56** | **7.17 ± 0.47** | 4.42 ± 0.2 | 4.44 ± 0.21 |
| BIF | 2.31 ± 0.06 | 2.35 ± 0.09 | 1.78 ± 0.09 | 1.77 ± 0.11 |
| LMR | 5.2 ± 0.14 | 5.35 ± 0.23 | 3.47 ± 0.09 | 3.47 ± 0.1 |
| BFM | 1.43 ± 0.09 | 1.51 ± 0.11 | **0.97 ± 0.03** | **0.99 ± 0.03** |
| BAM | 6.31 ± 0.24 | 6.27 ± 0.32 | 5.52 ± 0.17 | 5.54 ± 0.19 |
| LBU | 4.58 ± 0.15 | 4.72 ± 0.19 | 3.74 ± 0.14 | 3.75 ± 0.2 |
| HS | 11.06 ± 0.27 | 11.16 ± 0.38 | 7.86 ± 0.27 | 7.85 ± 0.28 |
| RL | 13.01 ± 1.58 | 13.66 ± 0.98 | **8.76 ± 0.47** | **9 ± 0.46** |
| ROW | **4.31 ± 0.19** | **4.45 ± 0.16** | 4.33 ± 0.21 | 4.35 ± 0.27 |
| LIW | 5.88 ± 0.44 | 5.92 ± 0.33 | 3.7 ± 0.15 | 3.71 ± 0.17 |
| ZIB | 16.94 ± 1.16 | 17.73 ± 1.01 | 12.66 ± 0.39 | 12.54 ± 0.41 |
| BBR | 14.70 ± 0.44 | 14.53 ± 0.58 | 11.08 ± 0.29 | 11.13 ± 0.33 |
| BZP | 3.82 ± 0.23 | 3.80 ± 0.26 | 2.42 ± 0.14 | 2.39 ± 0.15 |
| LMA | 17.29 ± 1.29 | 18.01 ± 0.93 | 11.63 ± 0.49 | 11.69 ± 0.46 |

# Online Resource 5

## Environment drivers acting on rodent rapid morphological change

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**Supplementary Table 1** Person's correlation coefficients between six analyzed drivers. AMT - - Annual Mean Temperature; MMTWQ - Mean Maximum Temperature of Warmest Quarter; MMTCQ - Mean Minimum Temperature of Coldest Quarter; AP - Annual Precipitation; AH - Annual Humidity; and RR – Richness of Rodents.

| | **AMT** | **MMTWQ** | **MMTCQ** | **AP** | **AH** | **RR** |
|---|---|---|---|---|---|---|
| **AMT** | | 0.09 | 0.64 | 0.3 | -0.05 | -0.04 |
| **MMTWQ** | 0.09 | | -0.56 | -0.91 | -0.99 | -0.66 |
| **MMTCQ** | 0.64 | -0.56 | | 0.72 | 0.57 | 0.73 |
| **AP** | 0.3 | -0.91 | 0.72 | | 0.89 | 0.52 |
| **AH** | -0.05 | -0.99 | 0.57 | 0.89 | | 0.64 |
| **RR** | -0.04 | -0.66 | 0.73 | 0.52 | 0.64 | |

# CAPÍTULO 3

## EFEITOS DO ESTRESSE TÉRMICO NA ASSIMETRIA FLUTUANTE DE ROEDORES SIGMODONTINEOS

Artigo a ser publicado na Ecological Indicators

# Effects of thermal stress on fluctuating asymmetry of sigmodontine rodents

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## ABSTRACT

Fluctuating asymmetry (FA) may reflect stressful effects of environmental changes, like the recent global warming. In rodents, variations in temperature seem to influence animal physiology during ontogenetic development, which may affect FA. That way, here we tested variation of FA over time in several populations of two rodent species, and the influence of temperature and other environmental variables on that. We created 11 space-temporal groups for *Akodon cursor* and 13 for *Oligoryzomys nigripes*. Each group consisted of specimens from the same locality divided in two time series, ranging from 10 to 32 years. To test asymmetry, 21 landmarks were digitized in the dorsal view of the skull of all individuals. FA was computed as the deviation of the original configuration of landmarks from the symmetric consensus. To test temporal variation of FA, we performed independent-samples t-test testing the asymmetry of skull between time series for each group for both species. We tested the relationships between FA and six potential environmental variables based on climate changes. For each group, we calculate the variation of each environmental variable over time. After that, we determined the best fitted model by Akaike model selection. Five groups of *A. cursor* showed significant variation on asymmetry over time, three presented an increase in mean FA. For *O. nigripes*, we found variation over time in FA in six groups, only in one there was a decrease in FA. The best model to explain FA in *A. cursor* included only Maximum Temperature, while for *O. nigripes* the best model included only Humidity. Increased FA generally negatively affects fitness of the species. That way, understanding which factors most affect developmental stability is of great importance to conservation biology.

**Key words:** Climatic changes, Environmental variables, Neotropical mammals, Rapid Morphological Change, Skull morphology.

## INTRODUCTION

Fluctuating asymmetry (FA) consists of subtle random variations of bilaterally symmetrical characters that deviate, right or left, from perfect symmetry (Graham et al., 2010). Increased levels of FA are mainly associated with stress during development (Palmer and Strobeck, 1992; Dongen, 2006). This stress can affect bilateral development in two ways. First, it can lead to an increase in developmental noise, that is, increased incidence of random disturbances that tend to alter the development of the symmetrical form. Second, stress may decrease the level of development stability, which means reducing the buffering capacity or system robustness (Klingenberg & Nijhout, 1999).

The measurement of FA may reflect how the stress during development affects a population. An increase in FA is usually attributed to the stressful effect of genetic or environmental variables (Palmer and Strobeck, 2003; Lazić et al., 2013). Many external factors, such as increased parasitism and predation (Møller, 1996; Thornhill and Møller, 1997), fragmentation and human land use (Lens et al., 1999; Marchand et al., 2003; Teixeira et al., 2006; Coda et al., 2016), pollution and radiation (Oleksyk et al., 2004; Yalkovskaya et al., 2016), and climate changes (Hódar, 2002; Servia et al., 2004; Nishizaki et al., 2015), may influence FA.

One of the overwhelming changes in climate is the recent global warming (Cook et al., 2016). Variation in temperature have been linked to changes in species distribution (Poloczanska et al., 2013), feeding/foraging behavior (Nishizaki and Carrington, 2015; Hayford et al., 2015), reproductive activity (Neeman et al., 2015), and body size (Gardner et al., 2011). There is much evidence that temperature also has a positive association with FA in invertebrates (Vishalakshi and Singh, 2008; Nishizaki et al., 2015).

In rodents, variations in temperature also have great impact on metabolism (Gordon, 1993), mainly due to its thermoregulatory apparatus is insufficient to eliminate excess heat (Schmidt-Nielsen, 1975). That way, temperature seems to influence animal physiology during ontogenetic development (Harrison, 1958), then affecting their morphology (Kieser, 1993; Klingenberg and Nijhout, 1999). In laboratory experiments, extreme cold (10°C) as well as extreme heat (33°C) has direct positive effect on FA (Siegel & Doyle, 1975; Siegel et al., 1977). Maestri et al. (2015) also show a positive relation between temperature and FA in a sigmodontine rodent species, in Brazil. In this late study, FA was also associated to precipitation and environmental suitability.

Despite these results, association between FA and temperature might not be clear. First, utmost metabolic stress, caused by extreme temperatures in the laboratory experiments above, always cause significant changes in development (Siegel & Doyle, 1975; Siegel et al., 1977). Thus, we do not know how small variations in temperature could affect the levels of development stability. Second, effects of FA can vary according to the taxon, analyzed component character or type of stress (Helle et al., 2011; De Coster et al., 2013). And third, the evolutionary history of each population is different, thus population genetic structure has different impact on how populations respond to environmental changes (Buj et al., 2015).

A potential solution for this last problem is comparing the same population over a few generations. The variation of morphological characteristics in a population in a short time, also known as Rapid Morphological Change (RMC), has detected changes in size and shape of many groups of living beings (Pergams et al., 2015; Holmes et al., 2016; Stumpp et al., 2016). Studies relating FA to RMC showed that asymmetry changes over time, however authors did not link these changes do any variable (Bechshøft et al., 2008; De Coster et al., 2013)

That way, here we combine the two approaches (FA and RMC) to determine whether the patterns of fluctuating asymmetry in sigmodontine rodents are associated with the temperature variation. Specifically, our hypotheses are (1) FA varies over time and (2) it is mainly influenced to temperature and it is negatively associated with this variable, (3) FA is also influenced by other environmental changes.

## MATERIAL AND METHODS

### Specimen Selection

We chose two species of sigmodontinae rodents, *Akodon cursor* (Winge, 1887) and *Oligoryzomys nigripes* (Olfers, 1818). These species have a large territorial distribution and they are abundant in faunistic inventories (Patton et al., 2015). Thus, there are several specimens from different locations collected in different years of these two species in museum collections.

We created space-temporal groups to test our hypothesis. Each group consisted of specimens from the same locality divided in two time series. Temporal gap of these series ranged from 10 to 32 years. Each group had at least five adult specimens collected in each time series. We considered adult only those rodents with three moderately worn molars. For *A. cursor* we created 11 groups, and for *O. nigripes* 13 groups (Fig. 01).

All specimens are deposited in the Mastozoology Collection of Federal University of Minas Gerais (UFMG), Mastozoology Collection of João Moojen Zoology Museum at the Federal University of Viçosa (MZUFV) and the Mastozoology

Collection of Minas Museum of Natural Sciences at the Pontifícia Universidade Católica of Minas Gerais (PUC-MG).

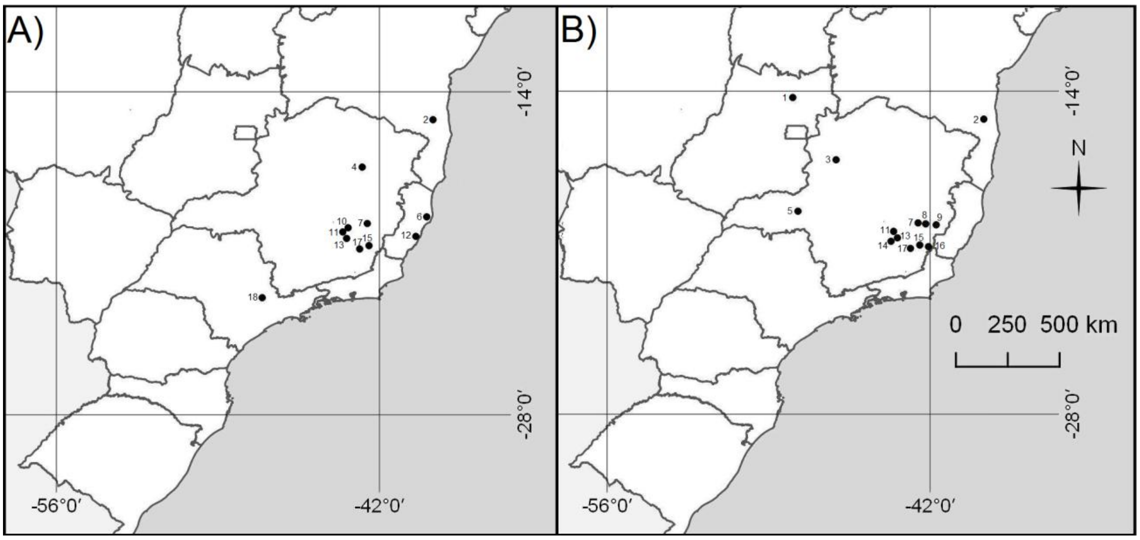

**Figure 01** Map of eastern Brazil showing locations of the space-temporal groups used in this study for both species. A) Sampling locations for *Akodon cursor*; B) sampling locations for *Oligoryzomys nigripes*. 1 – Flores de Goiás, GO; 2 – Una, BA; 3 – Brasilândia de Minas, MG; 4 – Turmalina, MG; 5 - Nova Ponte, MG; 6 – Linhares, ES; 7 – PERD, MG; 8 – Caratinga, MG; 9 – Ipanema, MG; 10 – PETI, MG; 11 – RPPN Serra do Caraça, MG; 12 – Cariacica, ES; 13 – Mariana, MG; 14 – Ouro Branco, MG; 15 – PESB, MG; 16 – Carangola, MG; 17 – Viçosa, MG; 18 – Campinas, MG.

## Geometric morphometrics procedures

We took digital photographs of the dorsal view of the skull of 282 specimens of *A. cursor* and 275 specimens of *O. nigripes* were taken using a Canon EOS REBEL T3/1100D camera with 12.2 megapixel resolution (4272 x 2848) setting the macro function in an automatic mode and without flash or zoom. Photos were taken from a standard distance of 100 mm for all specimens. A total of 21 landmarks were digitized in the dorsal view of the skull of all individuals using TpsDig2 software (Fig. 02). A description of all landmarks is given in Online resource 1.

After digitization, we transformed a matrix based on landmark coordinates (x, y) using a generalized Procrustes analysis (GPA) in MorphoJ software v1.06b (Klingenberg, 2011). The GPA removes effects of translation, rotation, and scaling in our landmark data, creating a new matrix with the shape coordinates only. After superimposition, we checked for outliers in the sample, and these were redigitized and tested again. The size of each specimen was accessed through the centroid size: the square root of the sum of squared distances of each landmark from the centroid of the configuration (Bookstein, 1991).

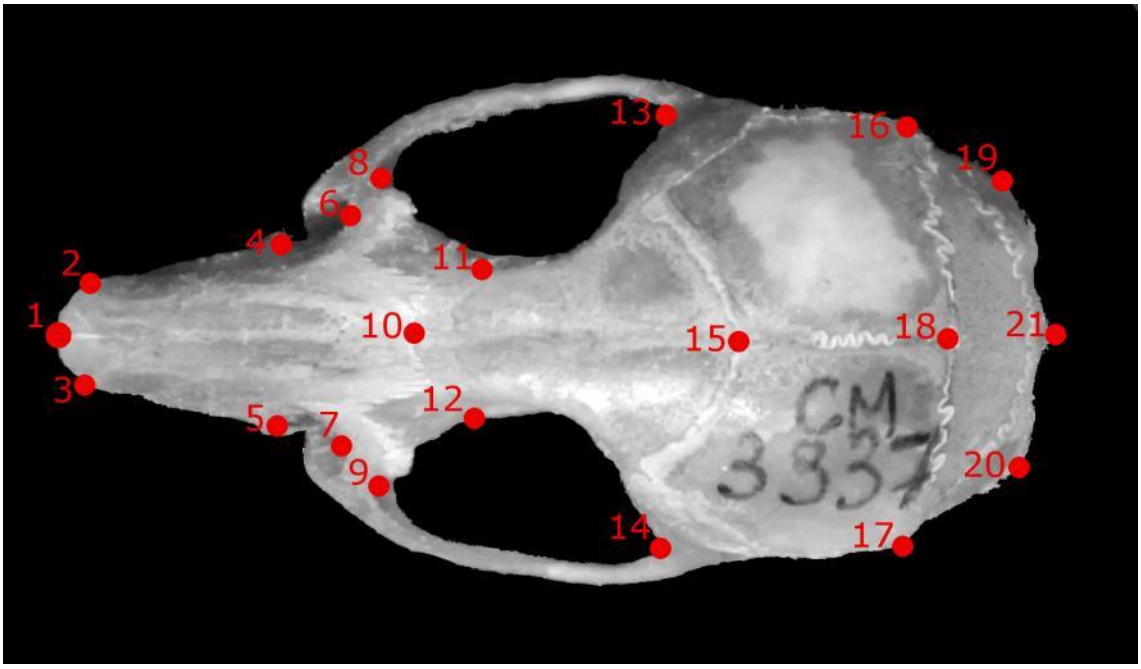

**Figure 02** Landmarks digitized in the dorsal skull of all studied specimens. A description of each landmark is presented in Online resource 2.

The measure of fluctuating asymmetry (FA), in units of Procrustes distance, was computed for each individual in MorphoJ software v1.06b (Klingenberg, 2011). First, we made a reflection of each of the original configurations of landmarks (each individual) to its mirror image, generating a reflected copy of each configuration. Then, using Procrustes fit, we generated an average of the original and mirrored configurations for each specimen, which is a perfectly symmetric configuration. Finally, the asymmetry of shape was computed, in units of Procrustes distance, for each individual as the deviation of the original configuration of landmarks from the symmetric consensus (Klingenberg and McIntyre, 1998).

To test RMC in FA, we performed independent-samples t-test testing the significance of asymmetry of cranial shape between time series for each group for both species. We also calculated the amount of asymmetry for each series of all groups, making an average of FA of all individuals within each series. Then, to assess the direction of FA over time for each group, we calculated the temporal variation of asymmetry, subtracting the mean value of FA of the older time series from the mean value of FA of the most recent series. A positive result in temporal variation of mean

FA indicates that asymmetry increased in that population over time, while a negative result indicates the asymmetry decreased.

## Environmental variables

We tested the relationships between FA and potential environmental variables based on climate changes. As environmental variables we used: Annual Mean Temperature (AMT), Mean Maximum Temperature of Warmest Quarter (MMTWQ), Mean Minimum Temperature of Coldest Quarter (MMTCQ), Annual Mean Precipitation (AMP), Mean Number of Days of Rain per Month (MNDRM), and Annual Mean Humidity (AMH). We chose these five environmental variables since they have direct or indirect influence in development stress (Maestri et al., 2015), which may affect asymmetry of the skull. For each sampled location, climate data were obtained from the nearest meteorological station provided by INMET (BDMEP, 2016). These data came from the year before specimens were collected, because environmental stress can lead to morphological changes caused by developmental instability (Kieser, 1993). For each group, we calculate the variation of each environmental variable over time, by subtracting the value of the variable corresponding to the previous year in which specimens of the oldest time series were collected from the same variable value corresponding to previous year in which specimens of the most recent series were collected.

In order to examine the multicollinearity in these environmental variables, we performed correlation matrix (Spearman's rank tests). Therefore, only uncorrelated variables (Spearman's rho, <0.4) were selected for statistical modeling. After that, we determined the best fitted model by Akaike model selection (AIC— Akaike 1973) corrected for small sample sizes ($AIC_c$). We used the component ΔAICc to compare AICc between models and Akaike weights ($AICc_{(WT)}$) sensu Burnham and Anderson (2002) and Anderson (2008) to access level of support in favor of each model. We considered the best models those presenting low $\Delta AIC_c$ values, close to two, since they provide similar support (Burnham and Anderson 2002; Symonds and Moussalli, 2011). Type I error rate was set to 0.05 in all analyses and all statistical analyses were performed using the computing environment R (R Development Core Team, 2014) and additional packages (car, ape, psych, MuMin and AICcmodavg).

## RESULTS

Five of the 11 space-temporal groups of *A. cursor* showed significant variation on asymmetry over time, three presented an increase in mean FA, while two presented a decrease. For *O. nigripes,* we found RMC in symmetry in six of 13 groups. In most of these groups asymmetry increased, only in one there was a decrease (Tab. 01). Four groups presented the same locality and the same time gap for the two species, and two of them – Una and Viçosa – showed variation on asymmetry for both, *A. cursor* and *O. nigripes*. However, while in Una, both species showed an increase in FA, in Viçosa, FA decreased for *A. cursor* and increased for *O. nigripes*.

The correlation matrix of the environmental variables, given in the Online resource 3, showed no high correlation between variables to the localities of the two species. Model selection using the $AIC_c$ showed that for potential associations between FA and environmental variables the best model for *A. cursor* included only Maximum Temperature of the Warmest Quarter (MMTWQ), and for *O. nigripes* the best model included only Annual Mean Humidity (AMH) (Tab. 02). The best following model for both species was the Null model, and no other model was fit for both species - $\Delta AIC_c$ far above 2. MMTWQ represented 36% of total explanation and had a negative association with FA (r=-0.62) in *A. cursor* (Fig. 03a), while AMH explained 44% of changes in FA in *O. nigripes,* also with a negative association (r=-0.61) (Fig. 03b)

**Table 01** Measures of mean fluctuating asymmetry (FA), in units of Procrustes distance, for both time series of each space-temporal group, followed by its sample size, for both sampled species. It is also given the FA variation over time, the time gap in years between the previous and posterior time series, and p-value of difference between series. Significant p-palues are highlighted in bold.

| **Locality** | **Previous time series** | **Posterior time series** | **Temporal Variation of FA** | **Time Gap (years)** | **p-value** |
|---|---|---|---|---|---|
| ***Akodon cursor*** | | | | | |
| Campinas – SP | 128.42 (14) | 134.67 (9) | 6.25 | 18 | 0.202 |
| Cariacica – ES | 125.43 (8) | 142.07 (14) | 16.64 | 17 | **0.023** |
| Linhares – ES | 130.83 (8) | 122.35 (5) | -8.48 | 13 | 0.203 |
| Mariana – MG | 131.43 (7) | 134.8 (12) | 3.37 | 19 | 0.456 |
| PERD – MG | 140.31 (21) | 131.72 (5) | -8.59 | 10 | **0.048** |
| PESB – MG | 141.51 (11) | 134.89 (9) | -6.62 | 15 | 0.275 |
| PETI – MG | 144.43 (16) | 136.72 (6) | -7.71 | 26 | 0.079 |
| RPPN Serra do Caraça - MG | 137.32 (7) | 151.23 (22) | 4.91 | 27 | **0.017** |
| Turmalina – MG | 141.37 (9) | 131.46 (7) | -9.91 | 14 | 0.051 |
| Una – BA | 131.69 (15) | 142.44 (11) | 10.75 | 14 | **0.042** |
| Viçosa – MG | 141.94 (24) | 127.07 (42) | -14.87 | 17 | **< 0.001** |
| ***Oligoryzomys nigripes*** | | | | | |
| Brasilândia de Minas – MG | 142.21 (8) | 146.83 (5) | 4.62 | 11 | 0.553 |
| Carangola – MG | 155.39 (11) | 136.17 (12) | -19.22 | 12 | **0.003** |
| Caratinga – MG | 141.4 (14) | 151.97 (9) | 10.57 | 16 | **0.029** |
| Flores de Goiás – GO | 146.69 (6) | 131.7 (5) | -14.99 | 13 | 0.066 |
| Ipanema – MG | 136.6 (5) | 136.38 (6) | -0.22 | 12 | 0.62 |
| Mariana – MG | 130.68 (8) | 145.43 (9) | 14.75 | 19 | **0.035** |
| Nova Ponte – MG | 136.93 (8) | 146.54 (13) | 9.61 | 11 | **0.033** |
| Ouro Branco – MG | 136.26 (12) | 138.23 (17) | 1.97 | 20 | 0.435 |
| PERD – MG | 151.55 (7) | 156.26 (9) | 4.71 | 32 | 0.242 |
| PESB – MG | 156.54 (5) | 156.65 (21) | 0.11 | 15 | 0.982 |
| RPPN Serra do Caraça - MG | 149.13 (6) | 157.03 (7) | 7.90 | 19 | 0.174 |
| Una – BA | 134.37 (9) | 149.43 (8) | 15.06 | 14 | **0.022** |
| Viçosa – MG | 147.32 (11) | 155.35 (45) | 8.03 | 17 | **0.04** |

**Table 02** Candidate models for the relationship between fluctuating asymmetry in *A. cursor*, and *O. nigripes* and environmental variables. *K* is the number of parameters in the model, $AIC_c$ is Akaike's information criterion (AIC) corrected for small sample size, $\Delta AIC_c$ is the difference in AICc values between each model and the best model (i.e. lowest AICc), *W*AIC is the Akaike weight and Cum.W is the cumulative Akaike weight. AMT - Annual Mean Temperature, MMTWQ - Mean Maximum Temperature of Warmest Quarter, MMTCQ - Mean Minimum Temperature of Coldest Quarter, AMP – Annual Mean Precipitation, Mean Number of Days of Rain per Month (MNDRM), and AMH - Annual Mean Humidity.

| **Models** | ***K*** | **$AIC_c$** | **ΔAICc** | ***W*AIC** | **Cum.W** |
|---|---|---|---|---|---|
| ***Akodon cursor*** | | | | | |
| MMTWQ | 3 | 87.02 | 0.00 | 0.36 | 0.36 |
| Null | 2 | 88.35 | 1.33 | 0.19 | 0.55 |
| MMTWQ + AMT | 4 | 89.96 | 2.95 | 0.08 | 0.63 |
| AMP | 3 | 90.02 | 3.00 | 0.08 | 0.72 |
| AMT | 3 | 90.21 | 3.20 | 0.07 | 0.79 |
| MMTCQ | 3 | 91.16 | 4.14 | 0.05 | 0.84 |
| AMP + MMTWQ | 4 | 91.46 | 4.44 | 0.04 | 0.88 |
| MMTWQ + MMTCQ | 4 | 92.02 | 5.00 | 0.03 | 0.90 |
| ***Oligoryzomys nigripes*** | | | | | |
| AMH | 3 | 98.85 | 0.00 | 0.44 | 0.44 |
| Null | 2 | 101.72 | 2.88 | 0.10 | 0.54 |
| MMTCQ + AMH | 4 | 101.98 | 3.14 | 0.09 | 0.64 |
| MNDRM + AMT | 4 | 102.58 | 3.73 | 0.07 | 0.70 |
| MNDRM + AMH | 4 | 102.99 | 4.15 | 0.06 | 0.76 |
| MNDRM | 3 | 103.18 | 4.33 | 0.05 | 0.81 |
| AMP | 3 | 103.31 | 4.46 | 0.05 | 0.86 |
| AMT | 3 | 103.50 | 4.65 | 0.04 | 0.90 |

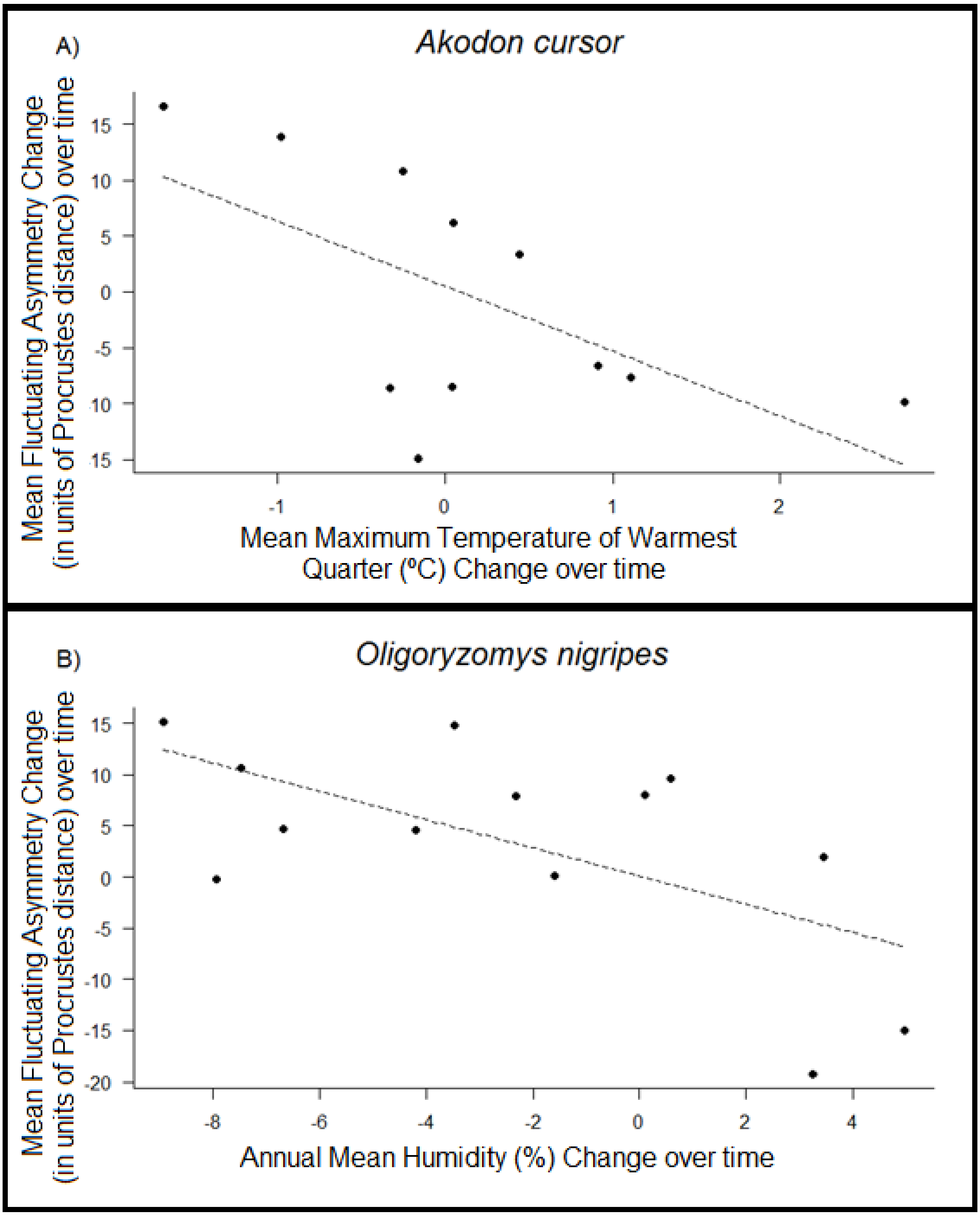

**Figure 02** The relationship between variation in fluctuating asymmetry and environmental variation. **A)** Negative association between fluctuating asymmetry and Mean Maximum Temperature of Warmest Quarter in *Akodon cursor* (r=-0.62). **B)** Negative association between fluctuating asymmetry and Annual Mean Humidity in *Oligoryzomys nigripes* (r=-0.61).

## DISCUSSION

The degree of FA can provide a valuable indicator of environmental and/or genetic stress in animal populations (Palmer and Strobeck, 2003; Lazić et al., 2013). A great number of studies have shown a positive relationship between FA and environmental stress in populations of rodents (Marchand et al., 2003; Oleksyk et al., 2004; Maestri et al., 2015). That way, 27% of tested populations of *A. cursor* and 38% of *O. nigripes* seems to have become progressively more stressed over time, while 18% of the populations of *A. cursor* and 8% of *O. nigripes* became less stressed. Variation in FA in a population over time has been reported before for polar bears (Bechshøft et al., 2008) and passerine birds (de Coster et al., 2013), and those variations were associated to processes that may produce instabilities over time.

The two species studied here presented different rates of increase and decrease of temporal stress, probably associated with different environmental pressures, as many localities were not common to both. However, of the common localities that presented significant differences in stress, half showed differences in direction, FA decreased for *A. cursor* and increased for *O. nigripes*. This indicates that distinct species may react differently to the same environmental conditions. Thus, the influence of specific factors related to species phylogeny plays no less important role than stress in determining the level of developmental instability in the cranium (Gileva et al., 2007).

This interspecific difference was also evident in the environmental variables that most influenced FA in each species. Maximum temperature (MMTWQ) had great influence and it was negatively associated with FA in *A. cursor*. And this is the opposite of what we hypothesize and also contradicts the findings of Maestri et al (2015) for the same species. In this late study, it was found that AMT and MMTCQ had a significant positive association with FA for *A. cursor*. MMTWQ was not significant. One explanation for this difference is the methodology for collecting variables. While Maestri et al (2015) used niche modeling climatic data, which comprises the average of 50 years for that particular point, we were more accurate, and we collected the exact climatic data from the year prior to the capture of the analyzed specimens.

Either way, this explains the mathematical difference of the results, not the biological one. As we said earlier, it is quite likely that different species will have distinct reactions to changes in the environment. *A. cursor* is a generalist rodent that inhabits both primary and degraded forest fragments mainly in the Atlantic Forest of eastern Brazil, from northeast to south, a span of about 18.58 in latitude (Geise, 2012). Species with great latitudinal distribution, although there is a great genetic difference between populations, appears to have high temperature tolerance (Calosi et al., 2010). Thus, it is likely that *A. cursor* presents high temperature tolerance, and, as the populations we studied are mainly in the middle of the species distribution, this way outside the limits of thermal stress of the species, our samples should be buffering the impacts of increased heat. In our case, negative association between FA and MMTWQ might means that the locations we sampled are close to the optimal temperature for the *A. cursor*.

The absence of temperature effects on FA of *O. nigripes* might have the same explanation we gave to *A. cursor*. This is also a generalist species of rodent, and it ranges from northeast Brazil to south Uruguay (Patton et al., 2015), and again, our sampled populations were in the middle of this distribution. These results show that to make more precise inferences about the biology of the species, it is more appropriate to sample populations in all their distribution or we will have specific responses on the species.

Other tested environmental variable had no effect on FA, but for humidity (AMH) in *O. nigripes*. By our results, the greater the humidity the greater is the stability of symmetry in this species. Under conditions of low humidity, the evaporation rate of sweat from the skin increases, allowing a quick heat loss, and also a great amount of loss of water. Desert rodents have many mechanisms to prevent water loss, and the amount of humidity directly affects the development of respiratory system and body size (Christian, 1978; Tracy and Walsberg, 2001). It is possible them that the greater amount of water loss in lower humidity may stress developmental stability of *O. nigripes*, enhancing FA.

Our results add important evidence that FA changes over time in a population, even over a few generations. We could also see that species have different response to the environmental variables tested, however climate changes seems to strongly influence developmental stability in all species tested. The relationship between FA and temperature is still not completely understood, as in the same species temperature indeed negatively affects stability (Maestri et al., 2015) while in our case happed the opposite.

Increased FA generally negatively affects fitness of the species (Reeves et al., 2016; Silva et al., 2016). That way, understanding which factors most affect developmental stability is of great importance to conservation biology. Upcoming studies, especially in the neotropics, with more species and covering a larger area, are needed to better understand the relationship between environment and biotic stresses.

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# Online Resource 1

## Effects of thermal stress on fluctuating asymmetry of sigmodontine rodents

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Landmarks in dorsal view were defined as:

1 - anterior tip of nasals;
2-3 - anterior point at suture between nasals and premaxilla;
4-5 - narrowest point of rostrum;
6-7 - posterior point of upper maxillary process;
8-9 - anterior point of interior orbit;
10 - junction between frontal, nasals, and midline;
11-12 - least interorbital region;
13-14 - posterior point of interior orbit;
15 - junction between parietal, frontal, and midline;
16-17 - exterior tip of external auditory meatus;
18 - junction between interparietal, parietal, and midline;
19-20 - edge of supraoccipital ridge;
21 - posterior point of supraoccipital;

# CONCLUSÕES GERAIS

# Effects of Rapid Climate Change on Small Mammal Community Structure and Cranial Morphology

Anthropogenic activity has led to giant changes in the environment over the last centuries, causing impacts both on individual and global scale. These changes led to an increase in the likelihood of disturbances, which generated fast responses. Here, we presented rapid changes in the structure of the small mammal communities as well as rapid morphological changes in rodents.

Our results showed that temporal changes in community structures of small mammals can be fast, changing from one year to another. This may indicate that communities of Neotropical small mammals are very dynamic or sensitive to disturbances. For the small mammals in EPTEA Mata do Paraíso, the community structure was undergoing a linear change in dominance. These changes are probably explained by the natural regeneration of the forest fragment, changes the plant composition and, consequently, food availability. The small mammal communities in PERD seem to reflect a loose equilibrium. Despite high annual variability in composition and abundance, community structure remains stable over long time periods.

Temporal dissimilarity of the small mammal communities in EPTEA Mata do Paraíso was unexpectedly lower than in PERD, which may be associated with the absence of environmental filters between the forest fragment and the hospitable matrix. Although we have not tested any environmental disturbances, our results clearly demonstrate rapid changes in the community structure of small mammals.

These rapid changes were also clear in the cranial morphological variation in the four studied species of EPTEA Mata do Paraíso – *Akodon cursor, Cerradomys subflavus, Oligoryzomys nigripes* and *Oxymycterus dasytrichus,* and most of these changes were related to the rostral part of the skull. Virtually all environmental variables tested impacted on cranial morphological changes. Maximum temperature, precipitation and humidity were the variables that most influenced the size, the first negatively and the other two positively. Although the maximum temperature is negatively related to body size in our work, in accord with Bergmann’s Rule, we cannot say that small mammals follow this rule, since the other environmental variables related to temperature presented different results.

Similar results were found for fluctuating asymmetry (FA) in *A. cursor* and *Ol. nigripes*. Our results add important evidence that FA changes over time in a population, even over a few generations. Considering that the degree of FA can provide a valuable indicator of environmental and/or genetic stress in animal populations, 27% of tested populations of *A. cursor* and 38% of *Ol. nigripes* seems to have become progressively more stressed over time, while 18% of the populations of *A. cursor* and 8% of *Ol. nigripes* became less stressed. These two species presented different responses in FA to the same environmental conditions. Thus, the influence of specific factors related to species phylogeny plays no less important role than stress in determining the level of developmental instability in the cranium.

This interspecific difference was also evident in the environmental variables that most influenced FA in each species. Maximum temperature had great influence and it was negatively associated with FA in *A. cursor*. In *Ol. nigripes,* by our results, the greater the humidity the greater is the stability of symmetry in this species.

The influence of environmental variables in RMC was clear in our results. Species we studied seem to quickly respond to changes and they are more likely to survive the rapid anthropic environmental changes of the last decades. Understanding which species have the greatest potential to adapt to these changes is one of the key pieces for the future of biodiversity conservation.