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Thaís Flores Battistella

VARIAÇÃO DO TAMANHO CORPORAL EM PEQUENOS MAMÍFEROS NEOTROPICAIS

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria (UFSM), como requisito parcial para a obtenção do título de **Mestre em Ciências Biológicas − Área Biodiversidade Animal**.

Orientador: Dr. Nilton Carlos Cáceres

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Aprovada em 17 de Fevereiro de 2020:

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RESUMO

VARIAÇÃO DO TAMANHO CORPORAL EM PEQUENOS MAMÍFEROS NEOTROPICAIS

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Variações intraespecíficas podem ser melhor observadas em populações amplamente distribuídas ao longo de gradientes heterogêneos. As hipóteses de Bergmann e de recursos são importantes regras ecogeográficas que buscam explicar a variação no tamanho corporal. No presente estudo, os padrões de variação do tamanho corporal foram analisados em populações de oito espécies de pequenos mamíferos (marsupiais e roedores). Análises de regressão linear entre tamanho corporal, e quatro variáveis respondendo pelas duas principais hipóteses ecogeográficas, foram realizadas para acessar as principais causas dessa variação. Das oito espécies, três espécies (marsupiais) apresentam tamanhos corporais maiores em baixas latitudes (converso de Bergmann), e duas espécies (roedores) seguem a regra de Bergmann. De acordo com o encontrado, as três espécies de marsupiais que apresentam uma relação significativa e negativa com a latitude mostram também um aumento no tamanho em locais com altas temperaturas. Já nas duas espécies de roedores os tamanhos aumentam, mas a baixas temperaturas. Em relação à hipótese do Recurso, duas espécies (roedores) mostram uma relação positiva com a precipitação e apenas uma destas com produtividade primária líquida. Nossos resultados indicam que marsupiais e roedores parecem ter padrões divergentes quanto a respostas às regras ecogeográficas. Assim, mostramos que há mais variáveis determinando a variação de tamanho em pequenos mamíferos, que a regra de Bergmann e do Recurso.

Palavras-chave: Clina de temperatura. Gradientes latitudinais. Regras ecogeográficas. Restrições de tamanho. Tamanho corporal. Variação de tamanho intraespecífica.

ABSTRACT

SMALL MAMMALS ONLY PARTIALLY FOLLOW BERGMANN'S OR RESOURCE'S RULES: A POPULATION LEVEL APPROACH

AUTHOR: Thaís Flores Battistella
ADVISOR: Nilton Carlos Cáceres

With this study we aim to examine the ecogeographic patterns of body size variation in populations of small mammals of the Atlantic Forest in eastern South America. For this we use body mass data from a mammal morphological trait dataset. The analyses comprise data for 8 species of marsupials and rodents, with adequate sampling throughout their distributions. We used linear regression analyses between body size and four predictor variables, accounting for the two main ecogeographic hypotheses, Bergmann's and Resource rules. Considering the eight species studied, three marsupial species showed larger body sizes at lower latitudes, corresponding to the converse of Bergmann, and two rodent species follow Bergmann's rule. Three marsupial species that present a significant and negative relationship with latitude also show an increase in size towards sites with higher mean temperatures. Conversely, the same occurs for two rodent species whose sizes increase with latitude but at lower temperatures. Regarding the resource hypothesis, three rodent species showed positive relationships with precipitation and one species with net primary productivity. Overall, marsupial species showed negative relationships with net primary productivity, decreasing body mass in more productive sites. Our results shed light into the divergent responses of marsupial and rodent species to ecogeographic rules. While some species follow Bergmann's or Resource's rules, we acknowledge that there are other environment or neutral factors determining the size variation in small mammals other than common predictors such as temperature, precipitation, and net primary productivity.

Keywords: Ecogeographic rules. Intraspecific size variation. Latitudinal gradient. Marsupial size constraints. Rodent body mass. Temperature cline.

SUMÁRIO

INTRODUÇÃO GERAL

O tamanho corporal é um exemplo de fenótipo com ampla variação tanto entre clados quanto entre populações de uma mesma espécie (MEIRI et al., 2007). Tal variação pode ser observada tanto em escalas espaciais, ao longo de gradientes heterogêneos, quanto temporais (ASHTON, 2000; YOM-TOV e GEFFEN, 2006; MEIRI et al., 2007; COOPER e PURVIS, 2010). Existem importantes hipóteses ecogeográficas que buscam indicar padrões causadores de tal variação (BERGMANN, 1847; OSOVITZ e HOFMANN, 2007; KOPSOVÁ-STORCHOVÁ et al., 2017). Em face à importância da caracterização dos processos adaptativos nas espécies é necessário a identificação de tais padrões ecológicos ao longo de gradientes geográficos, climáticos e/ou ambientais.

Em seu estudo sobre economia térmica e sua relação com o tamanho corporal de animais, Bergmann (1847) debate sobre a influência da temperatura na variação do tamanho corporal. Esta hipótese, conhecida como regra de Bergmann, postula que em climas mais frios, animais homeotérmicos apresentam tamanhos maiores quando comparados a espécies proximamente relacionadas habitando áreas com temperaturas mais elevadas. Tal observação é sugerida pela menor razão entre área superficial e volume em animas com maior tamanho corporal, o que permitiria maior retenção do calor gerado. Também podemos esperar que este padrão seja mais aparente no nível populacional que entre níveis taxonômicos superiores (BERGMANN, 1847; JAMES, 1970; MEIRI, 2004; MEIRI, 2011). Desse momento em diante diversos estudos testaram a hipótese proposta por Bergmann a fim de evidenciar padrões na clina de tamanho corporal (BLACKBURN, 1999; ASHTON, 2000; RODRÍGUEZ et al., 2006; MEDINA, et al., 2007).

Muitos destes estudos, na busca por associar a variação do tamanho corporal com a regra de Bergmann, corroboram a influência da latitude e temperatura sobre o tamanho do corpo (ASHTON, 2000; FRECKLETON et al., 2003). Por outro lado, o contrário também é observado (MEDINA, 2007). O número de estudos que encontram o oposto ao esperado por Bergmann é significativo e torna-se evidente que não há consenso sobre qual o padrão principal para a variação do tamanho corporal nas espécies (RODRIGUEZ ET AL., 2008; MAESTRI, 2016). Frente a tal divergência outras hipóteses se fazem necessárias na tentativa de caracterizar os fatores responsáveis pela variação do tamanho corporal observada.

Com intuito de elucidar o que o gradiente de temperatura sozinho não explica a disponibilidade e abundância de recursos (inferidas através de variáveis como: precipitação, produtividade primária líquida e evapotranspiração) foram sugeridas para explicar as clinas de tamanho observadas ao longo de gradientes geográficos (ROSENZWEIG, 1968; YOM-TOV e GEFFEN, 2006; MCNAB, 2010). A hipótese do Recurso propõe que as clinas de tamanho corporal são resultado da variação na disponibilidade de recursos, gerada pela heterogeneidade ao longo de gradientes geográficos, climáticos ou ambientais (MACNAB, 2010).

Apesar do número relevante de estudos comprometidos a explicar a variação no tamanho do corpo, independentemente se estes corroboram a regra de Bergmann ou adequam-se a hipótese de recursos, há falta de estudos para certos grupos, a exemplo os pequenos mamíferos, como roedores e marsupiais (MEIRI e DAYAN, 2003). Estudos focando na variação do tamanho corporal de pequenos mamíferos não voadores neotropicais mostram não haver consenso sobre os processos ecogeográficos que regem variação fenotípica no tamanho do corpo (CERQUEIRA e WEBER, 2016; MAESTRI et al., 2016; MAGNUS, MACHADO e CÁCERES, 2017). Tal fato aliado à ampla diversidade e distribuição comportadas por estes animais os tornam um grupo ideal para estudos da variação geográfica em características como o tamanho corporal (MEIRI & DAYAN, 2003; MAESTRI et al., 2016).

O objetivo geral deste estudo é elucidar quais fatores ecogeográficos melhor explicam a variação do tamanho corporal em populações de pequenos mamíferos neotropicais. Especificamente objetiva-se testar se quatro espécies de marsupiais e quatro espécies de roedores, endêmicos da Floresta Atlântica, seguem ou não as principais hipóteses ecogeográficas quanto à variação do tamanho corporal.

Estrutura da dissertação

A dissertação está estruturada no formato de *research paper*, de acordo com as normas da revista Mammalian Biology.

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Small mammals only partially follow Bergmann’s or Resource’s rules: a population level approach

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ABSTRACT

With this study we aim to examine the ecogeographic patterns of body size variation in populations of small mammals of the Atlantic Forest in eastern South America. For this we use body mass data from a mammal morphological trait dataset. The analyses comprise data for 8 species of marsupials and rodents, with adequate sampling throughout their distributions. We used linear regression analyses between body size and four predictor variables, accounting for the two main ecogeographic hypotheses, Bergmann’s and Resource rules. Considering the eight species studied, three marsupial species showed larger body sizes at lower latitudes, corresponding to the converse of Bergmann, and two rodent species follow Bergmann’s rule. Three marsupial species that present a significant and negative relationship with latitude also show an increase in size towards sites with higher mean temperatures. Conversely, the same occurs for two rodent species whose sizes increase with latitude but at lower temperatures. Regarding the resource hypothesis, three rodent species showed positive relationships with precipitation and one species with net primary productivity. Overall, marsupial species showed negative relationships with net primary productivity, decreasing body mass in more productive sites. Our results shed light into the divergent responses of marsupial and rodent species to ecogeographic rules. While some species follow Bergmann’s or Resource’s rules, we acknowledge that there are other environment or neutral factors determining the size variation in small mammals other than common predictors such as temperature, precipitation, and net primary productivity.

Keywords: Ecogeographic rules. Intraspecific size variation. Latitudinal gradient. Marsupial size constraints. Rodent body mass. Temperature cline.

1 | INTRODUCTION

Many ecogeographical hypotheses were postulated to explain intra and interspecific trait variation across geographic, climatic, or environmental (Bergmann 1847; Osovitz and Hofmann 2007; Kopsová-Storchováe et al. 2017). Body size is an example of a phenotypic trait that presents variation among individuals and species, in spatial and temporal scales (Ashton et al. 2000; Cooper and Purvis 2010). In his study of thermal economy and its relation to animal body size, Bergmann (1847) discusses the influence of temperature on body size variation. This hypothesis, known as the "Bergmann’s rule", states that in colder climates, endothermic animals present larger sizes when compared to closely related species inhabiting areas with higher temperatures. The explanation suggested for the inherent mechanism is that the lower ratio of surface area to volume in larger body sizes would allow a better heat retention in cold climates. Provided that the Bergmann’s rule was postulated to a size variation across related species, we can also expect this pattern to be more apparent at the population level (Bergmann 1847; James 1970; Meiri et al. 2004).

Mammals in general tend to follow the Bergmann’s rule, especially the large species. Primates, Lagomorpha, Carnivora, and Artiodactyla are examples of orders that follow this rule, although several exceptions do exist, as succeeds with Mustelidae (Carnivora) and rodents in general (Ashton and Tracy 2000; Freckleton et al. 2003; Meiri and Dayan 2003). American and Australian marsupials show opposite trends, while Australian ones seem to conform to Bergmann’s rule (Ashton and Tracy 2000), American marsupials, in general, do not (Cerqueira and Weber 2016; Magnus et al. 2017). Therefore, there is still a discussion whether small mammals conform to Bergmann’s rule or the converse of it. In face of such divergence, other hypotheses have arisen in an attempt to shed light to the process responsible for the observed patterns of body size variation in mammals (McNab, 2010).

In order to elucidate which mechanism explains geographical size variation other than temperature (Bergmann’s rule), resources availability was suggested as a competing driver of size clines (Rosenzweig 1968; Yom-Tov and Geffen 2006; McNab 2010). The distribution of resources can be inferred through proxies such as precipitation and evapotranspiration (Rosenzweig 1968). The Resource hypothesis proposes that body size clines are a result of variation of resources availability, generated by environmental heterogeneity (McNab 2010).

Regarding this hypothesis, mammal body size in general appears to be affected by regional availability of resources. Thus, larger amounts of resources will favor larger body size, as demonstrated by Meiri et al. (2007) for the brown bear. This also can be seen in the hartebeest clade *Alcelaphus buselaphus*, which tends to increase size in arid areas with higher precipitation rates (Capellini and Gosling 2007). This pattern also succeeds for the molina's hog-nosed skunk *Conepatus chinga*, with an increase of body size following a gradient of primary productivity (Schiaffini 2016). Even small-mammal species like the rodent *Peromiscus melanotis* (García-Mendoza et al. 2018), the ground squirrel *Urocitellus richardsonii* (Gür and Gür 2012), and the common brush-tailed possum *Trichosurus vulpecula* (Correll et al. 2016) increase their body sizes in more productive areas, as well as the pallid bat *Antrozous pallidus* (Kelly et al. 2018)

Marsupials and rodents have a wide diversity and global distribution making them ideal for ecogeographic studies (Meiri and Dayan 2003; Maestri et al. 2016). There is no general pattern of size cline for both small-mammal clades in a first overview (Ashton and Tracy 2000; Meiri and Dayan 2003). However, in South America, rodents appear to follow the converse of Bergmann at community level, where the average species size tends to increase towards lower latitudes (Medina et al. 2007; Maestri et al. 2016). Therefore, we do not know how South American marsupial and rodent species size respond to the latitudinal, climatic, and resource variation at population level.

We aim to elucidate the drivers of body size variation, at population level, for marsupial and rodent species endemic to the Atlantic Forest in eastern South America, for which there are available samples. To evaluate body size variation, we used data comprising eight small mammal species and tested with a set of predictors representing Bergmann's rule and Resource rule. As seem in Maestri et al. (2016) at community level rodents follow the converse of Bergmann's Rule and so we test if such a cline is held intraspecifically for rodents and also for marsupials. This is based also in the findings of Cerqueira and Weber (2016) and Magnus et al. (2017) who found the converse of Bergmann for marsupials (Fig. 1). Furthermore, we expect that the resource rule will play a positive and significant role in structuring the body size variation in such Neotropical small mammals (Rosenzweig 1968; Correll et al. 2016) at the population level (Fig. 1). We expect that these clines will be stronger for marsupials, regarding temperature gradient, compared to rodents due to physiological restrictions of the formers (Sánchez-Villagra 2013).

2 | MATERIALS AND METHODS

2.1 | Body mass data

We used a subset of the Atlantic mammal trait dataset (Gonçalves et al. 2018) corresponding to four species of marsupials and four of rodents, endemic to the Atlantic Forest which ranges from 3°S to 30°S (SOS Mata Atlântica and INPE 2019; Table 1; Fig. 2, 3, 4). The species were chosen based on the number of adequate samples for analyses and their even distribution along the ecoregion. We considered body mass as a proxy of body size. Although the dataset provides other traits, such as body length, we consider that it could have inadequate accuracy since it is often measure in alive animals. Such lack of accuracy does not occur when measuring body mass of alive or recently dead animals. We used adult specimens only and if necessary (because sample size) we included individuals of unknown age after a thorough reclassification. We considered as adults those individuals classify as "NA" (not available in the dataset) regarding age and with body mass greater than the average of the 10 lighter known adult specimens for each species. Moreover, juveniles, pregnant females, and extreme values (i.e. body mass measures that did not correspond with what it is expected for the mass range of the species; Paglia et al. 2012) were excluded from the analyses. This exclusion was used for standardization purposes and also to exclude possible sampling errors common in such extensive datasets with so many collaborators (Gonçalves et al. 2018).

2.2 | Predictor variables

The Atlantic Forest is a rich and diverse tropical to subtropical ecoregion which encompasses a high latitudinal variation and thus having a great environmental heterogeneity (Fonseca et al. 1999; Fig. 2).

Data regarding geographical coordinates of each specimen were extracted from the Atlantic Forest dataset which were provided with a good precision by the different authors (Gonçalves et al. 2018). Annual mean temperature and annual precipitation were extracted with 2.5 arc-min resolution from the 'WorldClim' raster database (Fick and Hijmans 2017). Net primary productivity was obtained from the 'Atlas of the Biosphere' (https://nelson.wisc.edu/sage/data-andmodels/atlas/maps.php). The variables were extracted using the program QGIS v. 3.10.2.

2.4 | Data analysis

We performed an analysis of variance to access if there was a significant sexual size dimorphism in each species. In the case of existence of a significant difference, females and males were treated separately in the subsequent analyses (Table 1). We control heteroscedasticity, through log transformation, for species whose data did not meet the parametric assumptions. We used linear regressions to examine the relationships of the predictor variables on the body size variations for each species at the population level. We used body mass as a response variable and a set of four predictors: latitude (as a proxy for environmental variation), mean annual temperature, annual precipitation, and net primary productivity.

3 | RESULTS

Within the dataset we selected eight species of small mammals, four marsupials and four rodents for which we had available samples for statistical analyses (Table 1). All marsupials belong to the Didelphidae family, subfamily Didelphinae, comprising the Didelphini (*Philander quica*), Marmosini (*Marmosa paraguayana*), and Thylamyni (*Gracilinanus microtarsus* and *Marmosops incanus*) tribes. For rodents, all of them belong to the Cricetidae family, subfamily Sigmodontinae, including Akodontini (*Thaptomys nigrita*) and Oryzomyini (*Euryoryzomys russatus*, *Nectomys squamipes*, and *Sooretamys angouya*) tribes. For the selected species, the ones with the highest number of data available were respectively *M. incanus* (N = 187) and *T. nigrita* (N = 219). The highest marsupial mean body mass (from the Atlantic Forest dataset) was for *Philander quica* with 296 g, and the lowest was for females of *Gracilinanus microtarsus* averaging 22 g. Males of *N. squamipes* presented the highest mean body mass with 220g and females of *Thaptomys nigrita* had the lowest mean body mass with 18g (Table 1).

Of the eight species, two showed sexual size dimorphism and thus were analyzed separately (Table 1). Among the four marsupial species, three followed the converse of Bergmann’s rule (Table 2; Fig. 5) being negatively correlated with latitude. For rodents, two species followed the Bergmann’s rule (Table 2; Fig. 5) and for the other species no significant relationship with latitude was found. The number of samples for each species decreased, compared to the original dataset, due to the exclusion of juveniles, outliers, and specimens lacking data (e.g. lacking age or sex).

3.1 | Marsupials

Gracilinanus microtarsus presents sexual size dimorphism, therefore, females and males were treated separately. No significant pattern of body mass variation was observed with latitude for both sexes (Table 2). Among all predictor variables, only precipitation had a negative and significant influence on body mass variation of *Gracilinanus* males (Fig. 6). Both males and females of *Marmosa paraguayana* seems to follow the converse of Bergmann's rule (Fig. 5); the female size also showed a positive relationship with temperature (Fig. 7) and a negative with precipitation (Fig 6), and both sexes presented a negative association with NPP (Fig 9). *Marmosops incanus* showed a significant pattern with latitude, following the converse of Bergmann's (Fig. 5). It also exhibited a significant and positive relationship with temperature (Fig. 7). This species also showed significant and negative relationships with precipitation (Fig. 6) and NPP (Fig. 9), respectively. *Philander quica* showed the converse of the expected by the Bergmann's rule (Fig. 5), with a significant and positive relationship with temperature (Fig. 7), and negative associations with precipitation (Fig. 6) and NPP (Fig. 9).

3.2 | Rodents

Euryoryzomys russatus follows the Bergmann's rule (Fig. 5). Among the other predictors, this species showed a positive relationship only with precipitation (Fig. 8). *Sooretamys angouya* follows the Bergmann's rule (Fig. 5). While temperature showed a significant and negative influence on body mass (Fig. 7), both precipitation (Fig. 8) and NPP (Fig. 9) showed positive influences on its body mass variation. *Nectomys squamipes* presents sexual size dimorphism and neither sexes followed the Bergmann's rule or its converse (Table 2). Also, none of the sexes presented significant relationships with the predictor variables, the exception being the negative association of female body mass with precipitation (Fig. 8) and NPP (Fig. 9). Finally, *Thaptomys nigrita* has sexual dimorphism and both sexes do not follow Bergmann's rule or its converse. Among all variables only precipitation had a significant and positive relationship with *T. nigrita* male size (Fig. 8).

4 | DISCUSSION

Our results show that, at the population level, marsupials and rodents present divergent body mass variation patterns (Table 2). We found that while marsupials increase body size at low latitudes, part of rodents follows an inverse pattern. Specifically, three of the four marsupial species presented higher body mass values at low latitudes, being the converse of Bergmann’s rule, and two of the four rodent species presented an increase in size at high latitudes, conforming to the Bergmann’s rule. No species of marsupials follow the Bergmann’s rule and no rodent species follow the converse. For marsupials these results corroborate our hypothesis that small mammals would present larger body sizes at low latitudes (Fig. 1). The fact that just two species (*E. russatus* and *S. angouya*) out of eight conformed to the Bergmann Rule is consistent with the findings in an assemblage-based approach by Maestri et al. (2016) and the ones from Freckleton et al. (2003) which state that small mammals are less likely to conform to Bergmann’s rule. *Euryoryzomys russatus* and *S. angouya* are relatively large sized species of cricetid rodent (85 g and 140 g, respectively; Paglia et al., 2012) and so we wonder if there is a size limit in which below that species tend to not follow the Bergmann rule (Vieira et al. 2019; Bubadué et al. 2020). Moreover, it seems that, at the population level, overall marsupials and rodents reveal divergent adaptations (Sánchez-Villagra, 2013; Table 2) to cope with differences along an environmental gradient (CS Dambros et al. unpublished).

Regarding temperature, our predictions were confirmed for marsupials (Fig. 1 and 7) since this variable has a positive and significant relationship with the variation of body mass for three species. The positive relationship of temperature with body size is the opposite of what is expected for the Bergmann’s rule, as was observed the wholly opossum species from the genus *Caluromys* (Magnus et al. 2017) and for the water opossum *Chironectes minimus* (Cerqueira and Weber 2016). On the other hand, only one species of rodent presents a significant and negative relationship associated with temperature (*S. angouya*), following a typical Bergmann trend. Overall, marsupial body mass is under influence of temperature (Fig. 7), and this is most probably due to different physiological responses of marsupials when compared to eutherians, such as rodents (Sánchez-Villagra 2013). Conversely, eutherians use brown adipose tissue (BAT) for heat generation, linked to survival in cold temperatures (Cannon and Nedergaard 2004), and have higher metabolic rates which favor persistence in colder climates, more than marsupials (Jastroch et al. 2008). Furthermore, rodent species in our study have wider distributions towards higher latitudes and colder climates than marsupials (Fig. 3 and 4), which could be a direct result of the better ability of rodents to live in cold climates due to the specialized heat generation mechanism that is not found in marsupials (Cannon and Nedergaard 2004; McNab 2008).

Our overall results regarding the resource hypothesis showed the opposite of our previous predictions (Fig. 1). In our data, four marsupial and one rodent (*N. squamipes*) species show decrease in size with the increase of precipitation or productivity (Fig. 6, 8, 9; Table 2). However, three rodent species (*E. russatus*, *S. angouya* and *T. nigrita*) show an increase in size with the increase in precipitation and net primary productivity (Fig. 8, 9), corroborating the resource hypothesis (Table 2). Interestingly, these rodent species (*E. russatus* and *S. angouya*) conform also to the Bergmann rule. Considering all species, the overall result was not expected given the known relationship of these predictor variables with body size (Yom-Tov and Geffen 2006; McNab 2010; Formoso et al. 2011), specially for marsupials that follow the converse of Resource rule according to our results (Table 2). Given the lower ability of marsupials to cope with colder climates (Sánchez-Villagra 2013), it would be expected that this group would be more dependent on resource availability for increasing body size in cold temperatures (Formoso et al. 2011). However, we did not find this pattern in our dataset but the converse. We suggest that local heterogeneity in a finer scale on habitat structure or ecological interaction along the Atlantic Forest could explain the lack of a positive association between productivity and marsupial (plus *N. squamipes*) body mass. The same association was seen for females of the Western hartebeest (Bovidae) which show smaller sizes with increasing precipitation (Capellini and Gosling 2007).

A possible overall explanation for the negative relationship of body size and environmental resources (Table 2) would be if character displacement does exist among Atlantic Forest small mammals, with marsupials being smaller in size at higher productive sites which are places supporting more competing (e.g. rodents) and predatory (e.g. felids) species. Similar trend was recently observed in *Marmosops incanus*, to which interspecific competition have negative effects on local abundance (Braz et al. 2020). Thus, population size of *M. incanus* is constrained by the degree of interspecific competition in resource-rich sites (Braz et al. 2020), which bring more ecological similar competing species; Jones 1997). The hypothesis of competition and character displacement is corroborated by the fact that the narrow feeding ecological niche of marsupials is totally nested in the broader ecological niche of cricetid rodents from the Atlantic Forest (Galletti et al. 2016). This observed pattern (decrease of size with increase resources) is also corroborated by the trade-off between reproduction and size in some mammal species (see Fisher and Blomberg 2011, for Australian marsupials; and Bergallo and Magnusson 1999, for *N. squamipes*). In this case, individuals tend to directly allocate energy for reproduction instead of increase body mass. Furthermore, our results for *E. russatus* and *S. angouya* match with the competition hypothesis, provided that they increase size with increasing resources (García-Mendoza et al. 2018) and that such rodents are often the most abundant small-mammal species in the Atlantic Forest (Pardini et al. 2005). Therefore, while the most common rodent species increase size in resource-rich places, marsupials decrease it, in a possible character displacement that can be related to feeding overlap between these clades (Galletti et al. 2016). In the case of *N. squamipes*, this species is semiaquatic and because of that it should not compete with other cricetid rodents like *E. russatus* and *S. angouya*. Thus, other unknown physical condition could be responsible for determining the size decrease observed in *N. squamipes* in resource-rich areas, besides the hypothesis of greater allocation in reproduction rather than in increasing size (Bergallo and Magnusson 1999).

In the present study we found support to the converse of Bergmann's rule at the population level for four marsupial species, as well as support for Bergmann's rule for two rodent species. Knowing that ecogeographical patterns of traits at community level will not necessarily reflect population-level patterns (Dunham et al. 2013), our study does not support the findings of Maestri et al. (2016) for the rodent community level provided that only marsupials increase size with increasing temperatures. Our results shed light in the role of temperature and specially the role of resources to unravel body mass clines of different taxonomic clades. Precipitation, meaning environmental resources, is the most important predictor for size variation in the small mammals in our study, however it shows an unexpected trend: size decreasing in more resource-rich sites. Overall, Atlantic-Forest small mammals just partially follow the common ecogeographical rules (Bergmann's and Resource rules, as *E. russatus* and *S. angouya* do). Therefore, an opposite ecogeographic pattern is seen when comparing marsupials and rodents, and thus the mechanisms explaining their size variations are complex and can be related to the overall differences between these two clades like physiology (Sánchez-Villagra 2013).

Further researches should focus on other mechanisms other than those correlated with common predictor variables (e.g. temperature, precipitation, NPP) used in ecogeographical studies, such as the influence of physiology, population density, competition, character displacement, and predation on body size variation of small mammals.

5 | DECLARATIONS

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Conflicts of interest/Competing interests: Not applicable

Availability of data and material: Data are available in the supplementary material

Code availability: Not applicable

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7 | TABLES

Table 1. Marsupial and rodent species (separated by sexes when there was sexual size dimorphism) with number of specimens (N), mean body mass (Mean; in grams), standard deviation (SD), and minimum and maximum (Min–Max) body mass.

Marsupials	N	Mean	SD	Min–Max
Didelphini				
Philander quica	77	296	118	125 – 700
Marmosini				
Marmosa paraguayana females	43	78	34	26 – 165
Marmosa paraguayana males	64	91	39	15 – 180
Thylamyni				
Gracilinanus microtarsus females	61	22	8	12 – 48
Gracilinanus microtarsus males	88	26	11	12 – 53
Marmosops incanus	187	60	21	38 –135
Rodents				
Akodontini				
Thaptomys nigrita females	77	18	5	7–34
Thaptomys nigrita males	142	20	5	7–49
Oryzomyini				
Euryoryzomys russatus	158	76	21	34–128
Nectomys squamipes females	54	188	72	72–410
Nectomys squamipes males	67	220	72	97–406
Sooretamys angouya	81	94	30	36–158

Table 2. Summary results of the ecogeographic patterns of the study species. The symbols "+" mean adherence to the rule (for Bergmann: negative association of latitude and/or temperature with body mass; for Resource: positive association of precipitation and/or NPP with body mass) and "-" the opposite (for Bergmann: positive association of latitude and/or temperature with body mass; for Resource: negative association of precipitation and/or NPP with body mass). When blank, the species do not show a significant pattern (P > 0.05).

Tribe	Species	Bergmann's rule	Resource rule
Didelphini	*Philander quica*	-	-
Marmosini	*Marmosa paraguayana* females	-	-
	Marmosa paraguayana males	-	-
Thylamyni	*Gracilinanus microtarsus* females		
	Gracilinanus microtarsus males		-
	Marmosops incanus	-	-
Akodontini	*Thaptomys nigrita* female		
	Thaptomys nigrita male		+
Oryzomyni	*Euryoryzomys russatus*	+	+
	Nectomys squamipes females		-
	Nectomys squamipes males		
	Sooretamys angouya	+	+

8 | FIGURE CAPTION

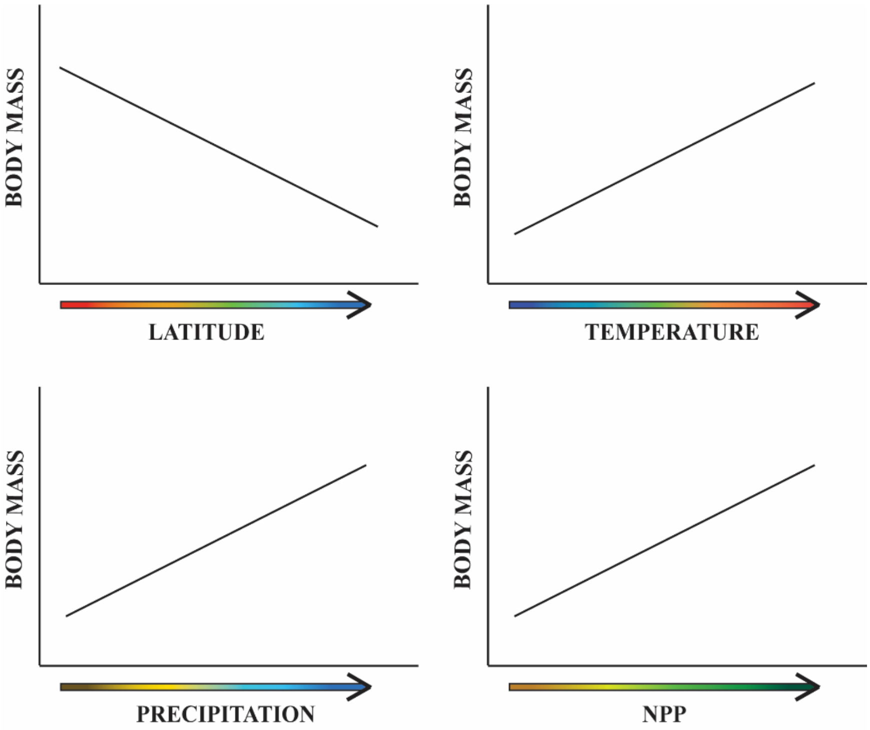

Fig 1 Hypothesis illustration of body mass responses to four predictor variables, encompassing two major ecogeographical rules (Bergmann's = latitude and temperature; Resource = precipitation and net primary productivity (NPP))

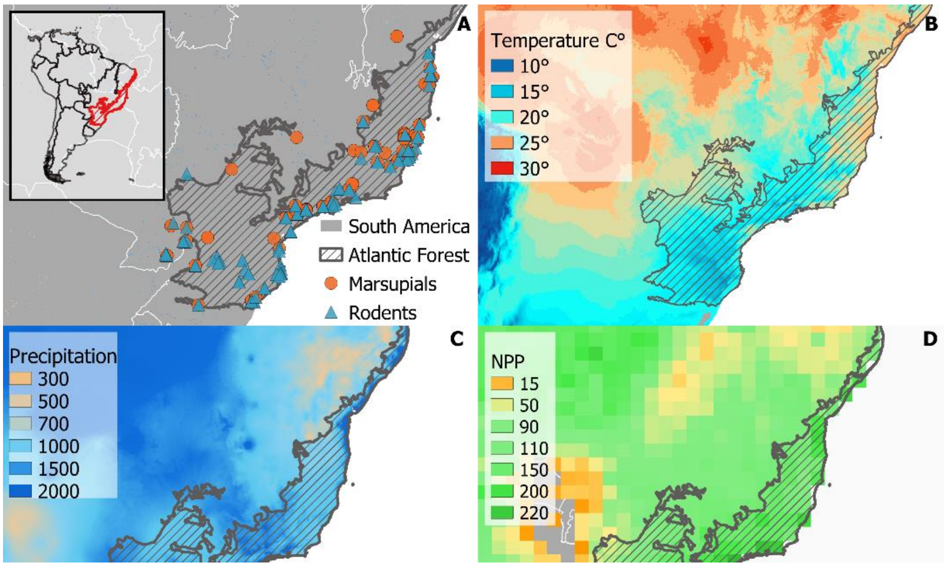

Fig 2 Representation of the study area with the small mammal samples used in the present study (A); and the environmental variables: mean annual temperature (B); precipitation (C); and net primary productivity (D)

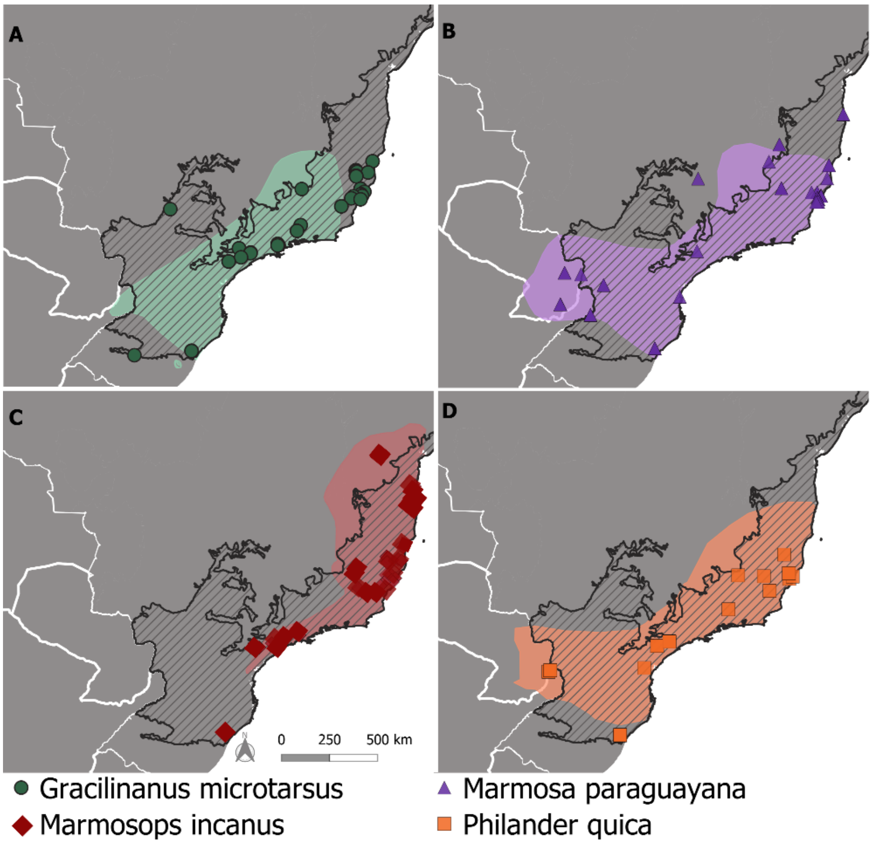

Fig 3 Maps with the samples used for each Marsupial species and the distribution according to the International Union for Conservation of Nature (IUCN); *Gracilinanus microtarsus* (A); *Marmosa paraguayana* (B); *Marmosops incanus* (C); *Philander quica* (D)

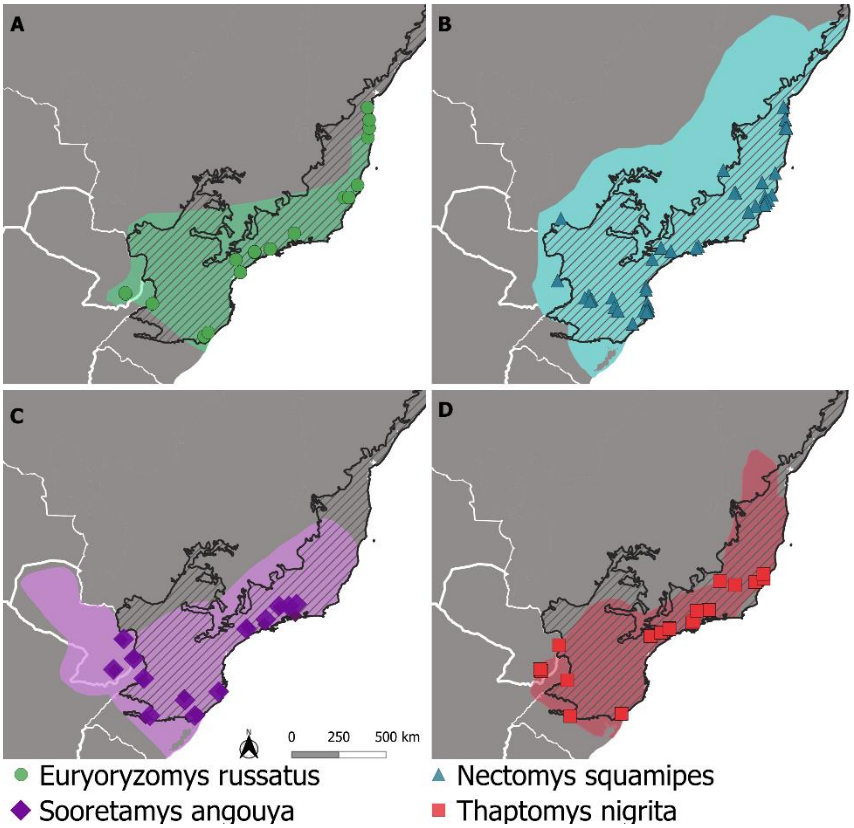

Fig 4 Maps with the samples used for each Rodent species and the distribution according to the International Union for Conservation of Nature (IUCN); *Euryoryzomys russatus* (A); *Nectomys squamipes* (B); *Sooretamys angouya* (C); *Thaptomys nigrita* (D)

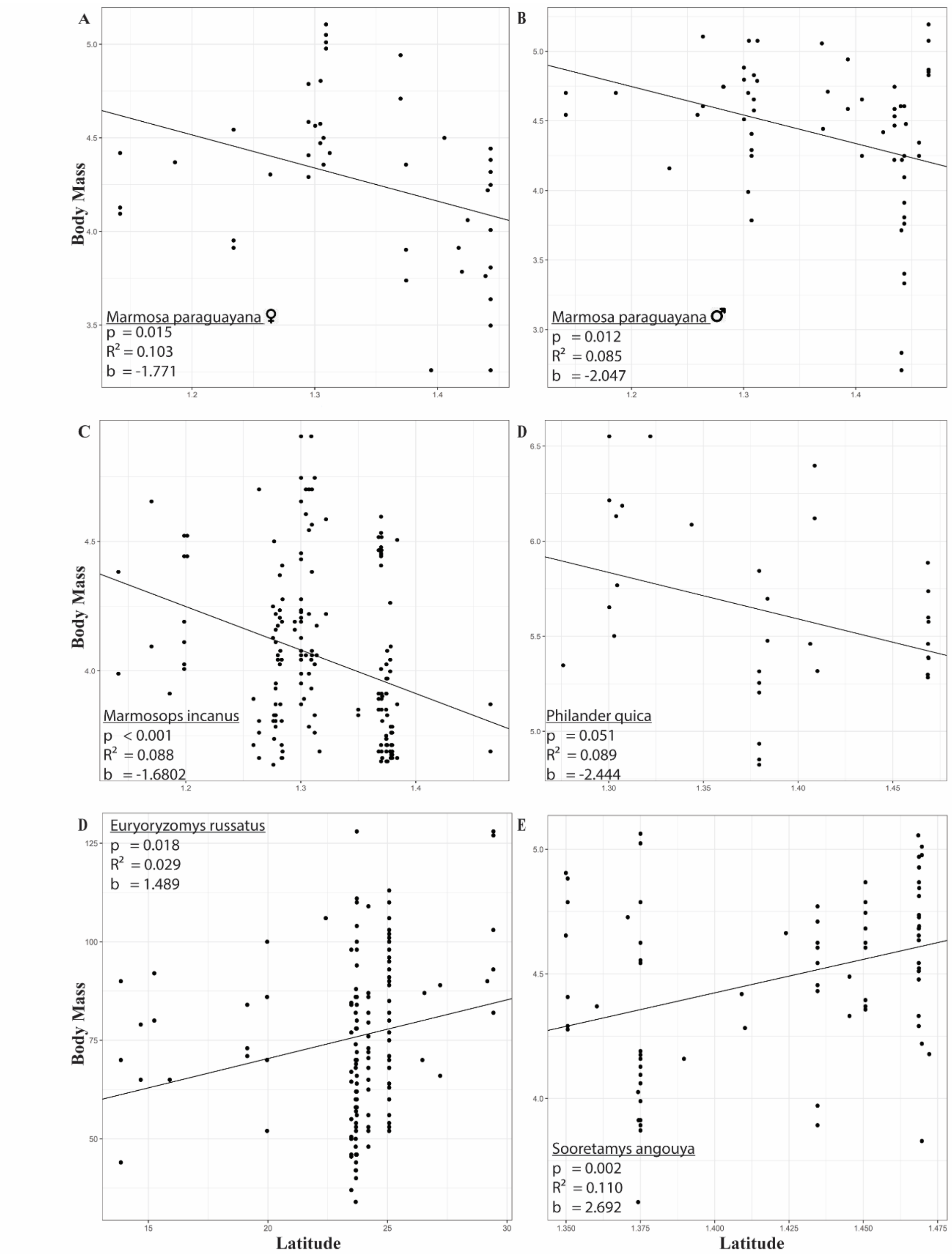

Fig 5 Linear regression models of body size and latitude for the species that showed significant patterns. Species names as well as P, R² and slope (b) values are shown in each graphic

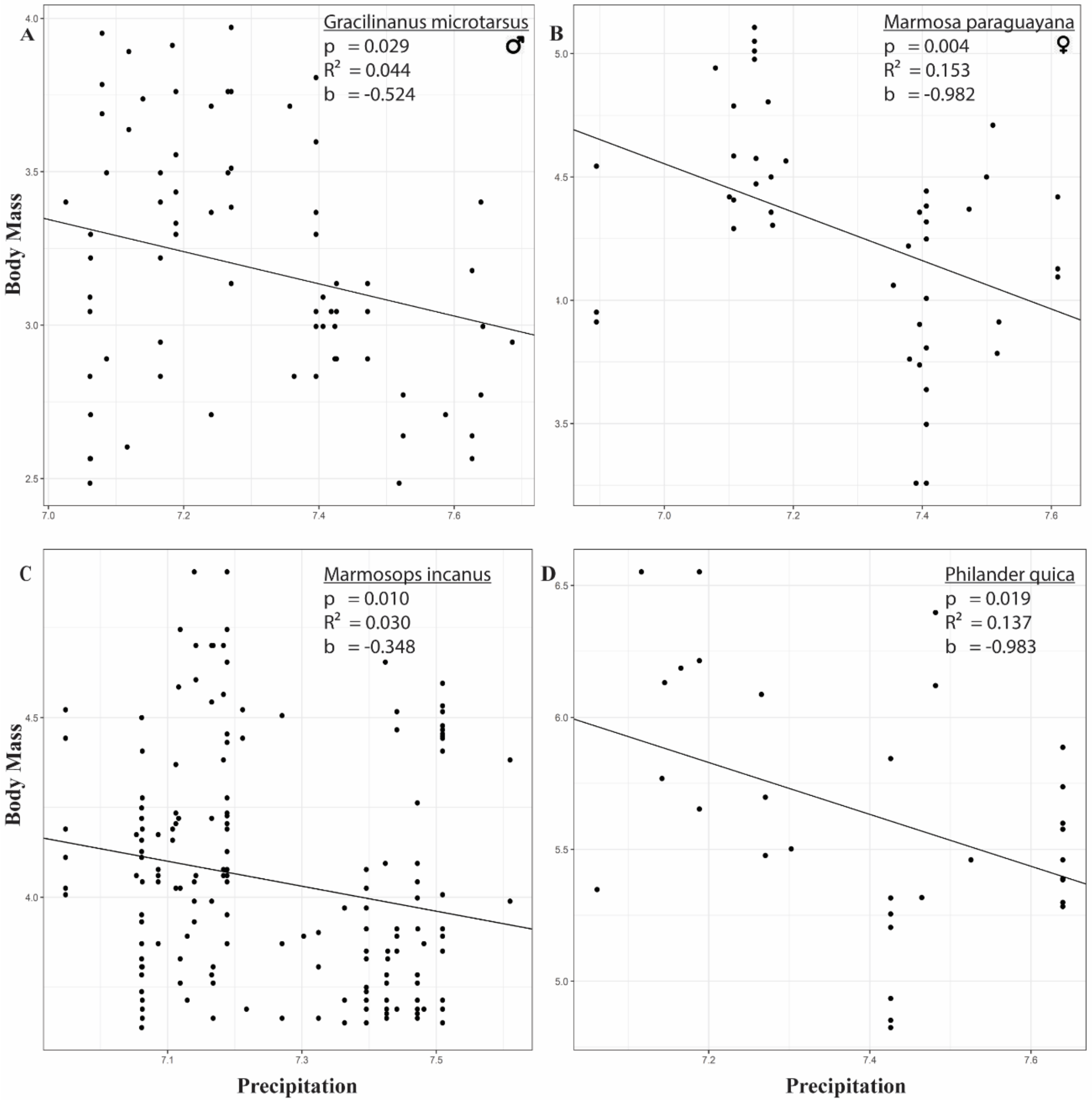

Fig 6 Linear regression models of body size and annual precipitation for the marsupial species that showed significant patterns. Species names as well as P, R² and slope (b) values are shown in each graphic

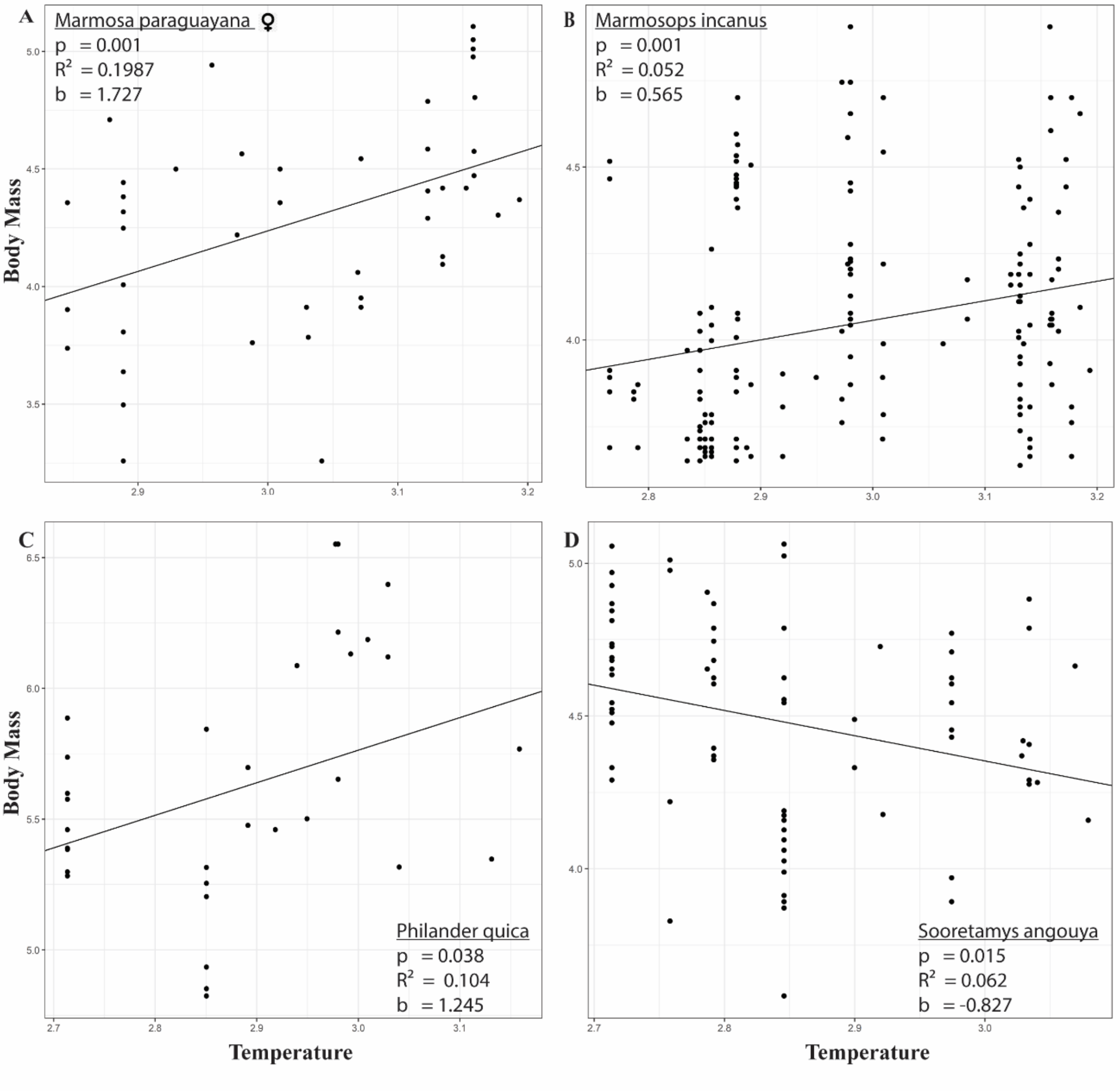

Fig 7 Linear regression models of body size and annual mean temperature for the species that showed significant patterns. Species names as well as P, R^2 and slope (b) values are shown in each graphic

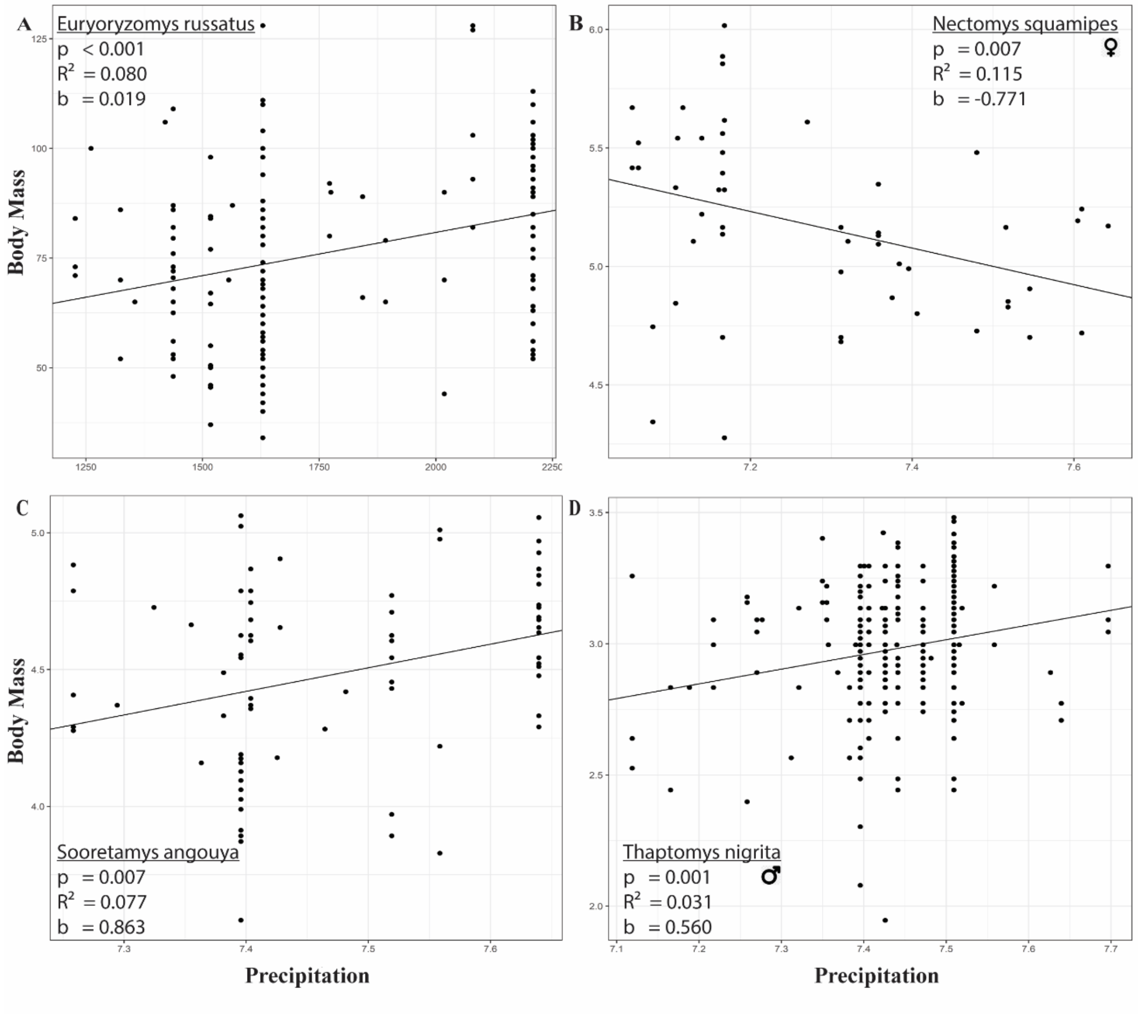

Fig 8 Linear regression models of body size and annual precipitation for the rodent species that showed significant patterns. Species names as well as P, R² and slope (b) values are shown in each graphic

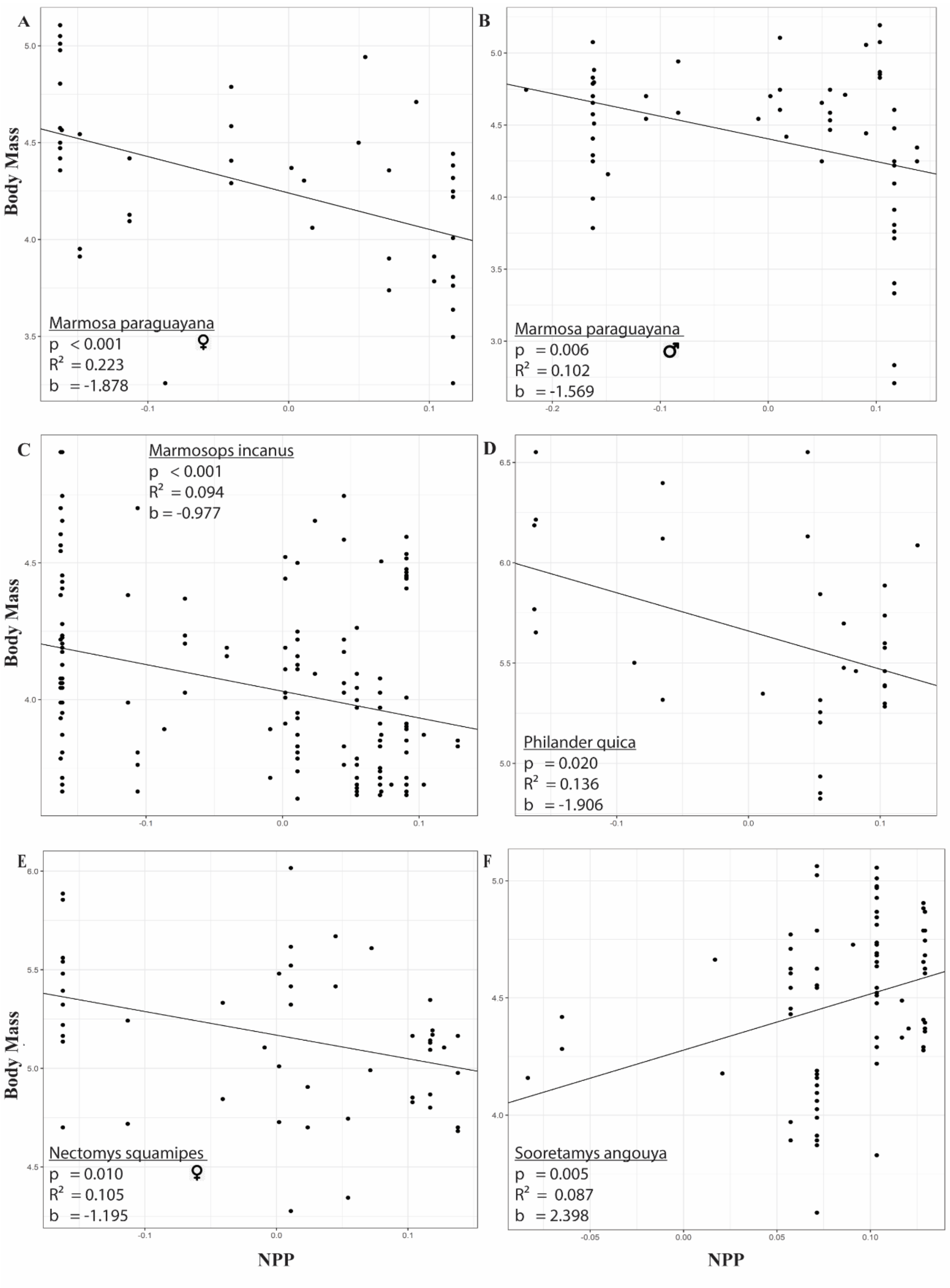

Fig 9 Linear regression models of body size and net primary production for the species that showed significant patterns. Species names as well as P, R² and slope (b) values are shown in each graphic