Dental microwear texture analysis and diet in caviomorphs (Rodentia) from the Serra do Mar Atlantic forest (Brazil)

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Running Header: Dental microwear and diet in caviomorphs

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Abstract.

The Serra do Mar Atlantic forest (Brazil) shelters about 15different species of caviomorph rodents and thus represents a unique opportunity to explore resource partitioning. We studied 12 species with distinct diets using dental microwear texture analysis (DMTA). Our results revealed differences (complexity, textural fill volume, and heterogeneity of complexity) among species with different dietary preferences, and among taxa sharing the same primary dietary components but not those with similar secondary dietary preferences (heterogeneity of complexity). We found three main dietary tendencies characterized by distinct physical properties: consumers of young leaves had low complexity; bamboo specialists, fruit and seed eaters, and omnivorous species, had intermediate values for complexity; grass, leaf, and aquatic vegetation consumers, had highly complex dental microwear texture. Dietary preferences and body mass explained a major part of the resource partitioning that presumably enables coexistence of these species. DMTA was useful in assessing what foods contributed to resource partitioning in caviomorphs. Our database for extant caviomorph rodents is a prerequisite for interpretation of dental microwear texture of extinct caviomorph taxa, and thus for reconstructing their diets and better understanding the resource partitioning in paleocommunities and its role in the successful evolutionary history of this rodent group.

Key-words: ecology, microwear, resource partitioning, rodent, Serra do Mar

Resumen.

La Selva Atlántica de la Serra do Mar (Brasil) contiene aproximadamente 15 especies de roedores caviomorfos y por lo tanto representa un entorno único para explorar la partición de recursos. Estudiamos 12 especies con dietas distintas usando análisis de textura de microdesgaste dental (DMTA). Nuestros resultados revelaron diferencias (complejidad, volumen de relleno de la textura, y heterogeneidad de complejidad) entre especies con distintas preferencias dietarias, y entre taxones que comparten la misma preferencia dietaria primaria pero no la misma preferencia dietaria secundaria (heterogeneidad de complejidad). Destacaron tres tendencias dietarias principales, caracterizadas por sus distintas propiedades físicas: los consumidores de brotes y hojas blandas tienen baja complejidad; los especialistas en bambú, consumidores de frutos y semillas, y especies omnívoras tienen valores intermedios de complejidad; los consumidores de pastos, hojas y de vegetación acuática tienen texturas de microdesgaste dental sumamente complejas. Las preferencias dietarias y la masa corporal explican una parte importante de la partición de los recursos que presumiblemente permite la coexistencia de especies en la Mata Atlántica de la Serra do Mar. El DMTA es útil para evaluar que preferencias dietarias contribuyeron en la partición de los recursos en los caviomorfos. Nuestra base de datos sobre roedores caviomorfos actualmente existentes es un prerrequisito para la interpretación de la textura del microdesgaste dental en taxones de caviomorfos extintos y, por lo tanto para así reconstruir sus dietas y lograr una mejor comprensión de la partición de recursos en las paleocomunidades y su rol en la historia evolutiva exitosa de este grupo de roedores.

Palabras clave: ecología, microdesgaste, partición de recursos, roedor, Serra do Mar

INTRODUCTION

Rodents are the most diverse and speciose group of placental mammals (Wilson and Reeder 2005; Burgin et al. 2018). A large portion of placental diversity is comprised of hystricognathous rodents from South America: the caviomorphs (Caviomorpha Wood 1955).The fossil record for caviomorphs extends back to the late middle Eocene (Antoine et al. 2012; Boivin et al. 2017) and exhibits at least 40 million years of endemic evolution on the South American continent. During this period, several adaptive radiations contributed to the emergence and structuration of caviomorph communities that can be observed today (e.g., Boivin et al. 2019).Caviomorphs display great taxonomic diversity (four superfamilies and ten families; Lacher et al. 2016), and are found in diverse environments (Patton et al. 2015; Wilson et al. 2016). The diversity of ecological conditions encountered by this group is associated with a diversity of morphological adaptations. Indeed, caviomorphs vary in body size from about 100g to 65kg (Patton et al. 2015; Wilson et al. 2016), display distinct activity patterns and life modes (Patton et al. 2015; Wilson et al. 2016),and exhibit different locomotor behaviors (Wilson and Geiger 2015). This diversity of life history traits is reflected in differential exploitation of resources (see Townsend and Croft 2008, and references therein).Today, the greatest species richness of caviomorphs is observed in Amazonia and the Atlantic forest, where 12 to 19 species may co-occur (Upham and Patterson 2015). These sympatric species provide an opportunity to explore resource partitioning among rodents sharing a unique habitat.

Herbivory seems to be a common feeding strategy for caviomorphs, although consumption of insects is important in some species (Mares and Ojeda 1982; Henry 1999).Over the past four decades, dental microwear analysis has been applied to various extant mammals as a means to detect dietary variation among populations (Rensberger 1973; Walker et al. 1978;

Ramdarshan et al. 2011). It has been used in extinct species to infer diets (Covert and Kay 1981; Solounias et al. 1988; Merceron et al. 2004). The objective of this approach is to interpret scars produced during mastication on the enamel surface of the tooth. Abrasion of the enamel depends directly on physical properties of the food consumed (Calandra and Merceron 2016), although exogenous grit is another factor that may affect dental microwear formation (Silcox and Teaford 2002; Scott 2012; Karme et al. 2016). Although dental microwear has been shown to reflect mostly dietary habits, the degree to which the environment contributes to the signal is unclear (Sanson et al. 2007; Lucas et al. 2013). In rodents, differences have been found among populations from distinct environments, but those differences were ultimately explained by the availability of different food items rather than environmental exogenous grit (Burgman et al. 2016). While 2D microwear analysis has been performed on caviomorph rodents (Townsend and Croft 2008), no analysis has been performed at the community or assemblage level scale for caviomorphs as has been done for platyrrhine primates (Ramdarshan et al.2011) and ungulates (Merceron et al. 2014).

Dental microwear texture analysis (DMTA) is based on the automatic quantification of 3D surfaces through a scale sensitive fractal analysis (Ungar et al. 2003; Scott et al. 2005, 2006). It considerably reduces the intra- and inter-observer error(DeSantis et al. 2013)and has proven to be effective at detecting intra- and interspecific variation in diet for both extant and extinct species (Merceron et al. 2010, 2016a, 2018a; Percher et al. 2017; Berlioz et al. 2017, 2018; Blondel et al. 2018), including rodents (Belmaker 2018). Studies on captive animals have identified food properties producing dental microwear etiology (Ramdarshan et al. 2016, 2017; Merceron et al. 2016b, 2018b; Francisco et al. 2018; Teaford et al. 2018). The most important properties for microwear texture formation seem to be hardness, toughness, and abrasiveness (Calandra and Merceron 2016). A complex microwear texture is linked to food hardness, while the anisotropy of microwear texture (i.e., its orientation) generally relates to degree of toughness and abrasiveness (review by Ungar 2015). Heterogeneity of complexity is related to the diversity of food items that an individual consumes on a daily basis (Scott et al. 2012;Souron et al. 2015): species with a low diversity of consumed food are expected to have a lower heterogeneity than opportunistic species.

Few DMTA studies have been conducted on rodents (murids: Burgman et al. 2016; voles: Calandra et al. 2016; guinea pigs: Winkler et al. 2019). DMTA provides information about food properties, but the dietary interpretations depend on the studied taxon. Thus, it is important to establish a reference dataset for DMTA in caviomorphs. Here, we explore the dietary preferences of several sympatric species of caviomorph rodents from the Atlantic forest through DMTA. To test the dietary preferences across the 12 studied taxa, we clustered them into seven dietary categories based on their primary diet components. Specifically, we tested1)whether dental microwear textures differ among diets across caviomorph species; and 2) whether differences in dental microwear texture appear in taxa sharing the same primary diet. We focused on species sampled within the same ecoregion, hence did not analyze the effect of different environments on microwear texture. Because body mass is associated with ecological segregation among rodents (Bowers and Brown 1982), we analyzed resource exploitation in light of this factor. We established a comparative dataset of wild caviomorphs based on DMTA. Further, we explored interspecific segregation, assessed the importance of dietary preferences in an assemblage of wild caviomorphs, and determined if dental microwear texture can be used as a proxy for dietary preferences and food resource exploitation in extinct caviomorph taxa, and thus for describing past communities.

Materials and Methods

We studied specimens of 12 species in eight genera of wild caviomorph rodents from the Serra do Mar coastal forest ecoregion (World Wildlife Fund [WWF] for Nature *sensu* IBGE 1993; Olson et al. 2001) housed in the collection of the Museu Nacional do Universidad Federal do Rio de Janeiro (MN-UFRJ) in Brazil (Table 1; Appendix I). The Serra do Mar Atlantic forest (SDMAf), within the Atlantic forest biogeographic province (Cabrera and Willink 1973) on the southeastern coast of Brazil (Fig. 1), is recognized as a major biodiversity and endemism hotspot in South America (Myers et al. 2000; Galindo-Leal and Câmara 2003). The environment is composed mainly of moist forest with four strata of vegetation and trees reaching heights of 30m (Veloso et al. 1991). The SDMAf has a subtropical climate (Mantovani 1993). All specimens came from the states of Rio de Janeiro and Sao Paulo (Fig. 1) and were collected between 1916 and 2013.

We studied the Caviidae, *Cavia aperea* and *Hydrochoerus hydrochaeris*; *Dasyprocta leporina* (Dasyproctidae), *Coendou spinosus* (Erethizontidae); and the Echimyidae, *Euryzygomatomys spinosus*, *Kannabateomys amblyonyx*, *Trinomys dimidiatus*, *T. eliasi*, *T. gratiosus*, *T. iheringi*, *Phyllomys pattoni*, and *P. nigrispinus*. Ecological and dietary data were compiled from the literature, including field observations and ethological reports, fecal analyses, and stomach content of wild specimens. Some taxa, such as *Phyllomys nigrispinus* and *Trinomys eliasi*, are poorly known and complete dietary data are lacking. In these cases, we expected that DMTA would provide clues to the resources they consume. We recognized seven dietary categories based on the primary diet component: aquatic vegetation, bamboo, grass, fruit-seed, leaf, leaf-insect, and young leaf (for detailed descriptions of the dietary categories see Supplementary Data SD1). Ecological data, body mass estimates, as well as assigned dietary categories, and sources for each species, are summarized in Table 1.

We studied the first upper molar because it is diagnostic in rodents (Gomes Rodrigues et al. 2009; Firmat et al. 2010; Oliver et al. 2014). After cleaning teeth with acetone-soaked cotton swabs, dental impressions were made with a silicone material (polyvinyl siloxane ISO 4823, President Regular Body, Coltène-Whaledent Corporation). We studied primarily the mesiolingual aspect of the protocone (Fig. 2). However, if the protocone surface showed signs of alteration or presence of organic matter or glue, the mesiolingual part of the hypocone was studied because those facets are parallel to each other, are located on the same side of the occlusal surface, and share the same function during mastication(Butler 1980). Scans were made directly from the silicon molds with the "TRIDENT" Leica DCM8 white-light scanning confocal microscope (Leica Microsystems) with a 100× long-distance lens (Numerical Aperture = 0.90; working distance = 0.9 mm), housed at the PALEVOPRIM laboratory (Université de Poitiers).Scanning protocol, pre-treatment, and analysis on 50x50 scans, followed procedures described in Supplementary Data (SD2; Fig. 2A).

Scale Sensitive Fractal Analysis (SSFA; Scott et al. 2006) was performed on the selected enamel surface with the Toothfrax and Sfrax software programs (Surfract Corporation, Norwich, Vermont, USA) to quantify complexity (area scale of fractal complexity: Asfc), anisotropy (exact proportion of length scale anisotropy of relief: epLsar), heterogeneity of complexity (heterogeneity of the area scale of fractal complexity between sub-surfaces from a given surface: HAsfc), and textural fill volume (Tfv). HAsfc was calculated with four (HAsfc4), nine (HAsfc9) and 16 (HAsfc16) sub-surfaces (Supplementary Data SD3). Scott et al.(2006) described each of these variables in detail.

All statistical analyses were performed in R (R Development Core Team, 2018). A Box-Cox transformation (Box and Cox 1964) was used to assure normality for the parametric tests. Multivariate normality was evaluated with Mardia's test statistic (package "MVN" for R); univariate normality was assessed with the Shapiro-Wilk test. A MANOVA (MANOVA; package "Car" for R) was used to determine if dietary categories share a similar dental microwear pattern. Subsequently, a one-way ANOVA (package "Car") was used on each variable to test the hypothesis that different groups share similar dental microwear texture parameters. The *P*–value was adjusted following the B-Y method (Benjamini and Yekutieli 2001) in order to control the risk false discovery. In the first analysis we compared taxa across dietary categories for all samples. Next, we compared taxa within the "fruit-seed" category and taxa within the "leaf" category. If the overall ANOVA was significant, we used both Tukey's honestly significant difference test (HSD) and Fisher's least significant difference (LSD) pairwise tests to determine exactly where the differences were. We used both tests in an effort to balance risks of type I and type II errors (Cook and Farewell 1996). When the LSD test detected significant differences but the HSD did not, we considered the results to be marginally significant (Burgman et al. 2016). The same MANOVA, ANOVA, and a posteriori tests were performed following a Levene transformation of the data (see Plavcan and Cope 2001) to analyze the dispersion of sample values within and between diet categories.

RESULTS

Mean, median, and standard deviation, were calculated for each dental microwear texture parameter by species (Table 2). Both MANOVAs on Box-Cox transformed data ($d.f.=6$, $P<0.001$) and on Levene's transformed data ($d.f. = 6$, $P<0.005$) suggested differences in dental microwear texture depending on dietary categories.

Means of complexity (Asfc) and textural fill volume (Tfv) differed significantly between dietary groups (ANOVAs, Table 3A) but not between taxa within dietary groups (ANOVAs, Table 4A). Variance of textural fill volume (Tfv) differed significantly between taxa within "fruit-seed" eaters group (Table 4B). In addition, means of heterogeneity (HAsfc16) differed significantly between dietary groups (Table 3A) and also marginally (HAsfc9 and HAsfc16) between taxa within "fruit-seed" eaters group (Table 4A). The variance of heterogeneity differed significantly among dietary groups (HAsfc16; Table 3B) and between taxa within "fruit-seed" eaters group (HAsfc4; Table 4B). Anisotropy was not significantly different among dietary groups or taxa (Tables 2, 3, and 4). The results of the post-hoc tests indicate that complexity (Asfc) is the variable that differs most among groups (Table 5; Fig. 3A).

"Young leaf" eaters were characterized by significantly low complexity and lower values of textural fill volume (Figs. 3A and 3E) and were associated with significantly larger variances for textural fill volume compared to "aquatic vegetation" and "leaf-insect" eaters (Table 5B). "Bamboo" eaters had marginally higher complexity than "young leaf" eaters and were not different from "fruit-seed" eaters (Fig. 3). "Bamboo,""fruit-seed," and "leaf-insect" eaters had significantly lower complexity than those classified as "grass," "aquatic vegetation," and "leaf" eaters (Fig. 3A). "Leaf-insect" eaters had marginally higher textural fill volumes than "bamboo" and "fruit-seed" eaters (Figs. 3E and 4D). Among "fruit-seed" eaters, heterogeneity (HAsfc9 and HAsfc16) was marginally different between *Dasyprocta leporina* and three of the four species of the genus *Trinomys* (*T. dimidiatus*, *T. eliasi*, and *T. gratiosus*; Fig. 4C).The values of heterogeneity (HAsfc4) in *D. leporina* and *T.eliasi* samples were significantly more dispersed than those in *T. dimidiatus*, *T. gratiosus*, and *T. iheringi*."Grass,""aquatic vegetation," and "leaf" eaters, had higher complexities than taxa belonging to other dietary groups, and higher values of textural fill volume than "young leaf" eaters (Figs. 3A and 3E). They displayed important intragroup and intraspecific variability but did not differ among themselves (Fig. 5). "Aquatic vegetation,""grass," and "leaf-insect" eaters, displayed a marginally lower dispersion of textural fill volume values than "bamboo,""fruit-seed," and "young leaf" eaters."Aquatic vegetation" eaters had marginally higher textural fill volume than "bamboo" and "fruit-seed" eaters (Fig. 3E). "Grass" eaters displayed marginally higher textural fill volume than "bamboo" eaters (Fig. 3E). "Leaf" eaters had significantly higher heterogeneity (HAsfc16) than "young leaf" and "fruit-seed" eaters (Figs. 3C and 3D)."Leaf" eaters displayed more dispersed values of complexity and heterogeneity (HAsfc16) than other dietary groups, particularly "young leaf" eaters (Table 5B).

DISCUSSION

Dietary habits and dental microwear texture.—Complexity was responsible for most of the significant differences among diets followed by textural fill volume. We observed a trend of increasing complexity and texture fill volume from species eating young leaves or bamboo shoots, to species feeding on grasses and mature leaves (Figs.3A and 3E).The lowest complexity, lowest textural fill volume, and lowest heterogeneity of complexity, were observed for "young leaf" eaters represented by *Coendou spinosus* (Table 2; Fig. 3). Values for this species are consistent with its extremely specialized folivorous diet with preferences for young leaves of Fabaceae (Passamani 2009), dicotyledoneous plants with small amounts of biosilica (Piperno 1988), and very low values in lignified tissues. Our results are consistent with Ramdarshan et al. (2016) who found lower complexity for sheep fed only red clover fodder (Fabaceae) compared to sheep fed a mixture of red clover and barley.

Kannabateomys amblyonyx was the only bamboo specialist in the study (Olmos et al. 1993). It consumes the inner soft tissues of bamboo shoots after removing the hard and spiny outer sheet (Fabre et al. 2016). The soft inner part is the only portion processed by the molars, which could explain the low values of complexity. Unfortunately, we could only analyze three individuals of *K. amblyonyx*.

"Fruit-seed" consumers included five species: *Dasyprocta leporina* and the four species of *Trinomys* (Table 1). This group displayed microwear textures that can be explained by the diversity of elements composing typical frugivorous and granivorous diets (Fig. 4). These taxa displayed higher complexity than "young leaf" eaters but lower complexity than "grass,""aquatic vegetation," and "leaf" eaters (Fig. 3A). *Dasyprocta leporina* feeds mainly on seeds and fruit pulp available on the forest floor (Henry 1999; Jorge and Peres 2005). *Trinomys* and *Dasyprocta leporina* are among the main seed dispersers of palm species in the Atlantic rainforest of Brazil (Galetti et al. 2006; Donatti et al. 2009). They remove the exocarp using their incisors to extract the soft nutritious seeds inside (Henry 1999),which explains why this species does not have the expected complex enamel surface on their cheek teeth as expected for seed eating species (Scott et al. 2012; Ramdarshan et al. 2016).

Among "fruit-seed" eaters (Fig. 4C), the difference in heterogeneity of complexity between three of the four species of *Trinomys* and *Dasyprocta* might reflect the inclusion of insects in the diet of *Trinomys* (except for *T. iheringi*; Brito and Figueiredo 2003; Mello et al. 2015), whereas *Dasyprocta* complements its diet with leaves (Henry 1999; Jorge and Peres 2005).In contrast, *T. iheringi* had less heterogeneous microwear texture than the other species of *Trinomys*, which is consistent with the fact that this species does not include insects in its diet to the same extent as its sister species (Bergallo and Magnusson 1999).

Scott et al. (2012) proposed that higher heterogeneity values might reflect a more variable diet. Burgman et al. (2016) also had results consistent with this interpretation. Among the "fruit-seed" category in the present study, the more heterogeneous microwear textures were observed when the diets were more variable, including insects as an important secondary food. However, heterogeneous sampling among seasons, years, and environments, might also explain these inter-specific differences. The species of *Trinomys* are parapatric as they tend to have similar ecologies from one locality to another (Fabre et al. 2016). Our results confirm these assertions as there were no significant differences in their dental microwear texture (Fig. 4A-D). In the case of *Trinomys eliasi*, for which dietary preferences are poorly known, DMTA does not detect any differences with other species of *Trinomys*.

The microwear texture of “leaf-insect” eaters (*Euryzygomatomys spinosus*) is more complex than that of “young leaf” eaters but less complex than those of “aquatic vegetation” and “leaf” eaters. It differs from “bamboo” and “fruit-seed” eaters in having marginally higher values of textural fill volume (Table 5).The major components of the diet of *E. spinosus* (leaves and insects, Alho 1982; Patton et al. 2015) area secondary food for *D. leporina* (leaves) and *Trinomys* (insects). The values of heterogeneity of complexity of *E. spinosus* were similar to values observed for four species of *Trinomys*, but were marginally higher than values of heterogeneity observed for *D. leporina* (Fig. 4C). This seems to confirm a relationship between the presence of insects in the diet and a more heterogeneous microwear texture.

Dental microwear texture of grazing ruminants or equids is characterized by medium to high anisotropy and low to medium complexity due to a highly abrasive diet composed of tough but not hard elements (Scott 2012; Merceron et al. 2018). However, it is not what we observed for “grass” eaters among our rodent sample. Indeed, *C. aperea* displayed high values of complexity comparable with that of dicotyledon foragers in our sampled caviomorphs (Fig. 5A-B). *Cavia aperea* is described as a grass-eater inasmuch as it relies mainly on monocotyledons (Rood 1972; Guichón and Cassini 1998). Although *C. aperea* eats grass shoots and blades, it favors ears full of millimetric seeds (Lacher 2016). Ramdarshan et al. (2016) showed that sheep fed on clover with or without a supplement of seeds differ in dental microwear complexity, with the most complex enamel surface being recorded for sheep fed clover with 25% as dry matter weight of barley. Further, a controlled-food experiment on capuchin monkeys showed that even a single feeding event including hard objects has a significant effect on dental microwear (Teaford et al. 2018).Thus, the inclusion of small seeds in the diet of *C. aperea* likely results in high complexity on the enamel surface.

The diet of *H. hydrochaeris* is composed mainly of grasses and sedges (Mones and Ojasti 1986). It also feeds on bark and aquatic vegetation (Macdonald 1981),which may be related to the highly complex microwear texture measured (Fig. 5A-B). Both in *C. aperea* and *H. hydrochaeris*, the secondary dietary components (small seeds or bark) affect dental microwear.

The dental microwear texture for "leaf" eaters was complex (Fig. 5A-B). Moreover, the complexity and heterogeneity of complexity were variable between specimens. Both species of *Phyllomys* have a dicotyledon based folivorous diet (Emmons and Feer 1997).However, such highly complex and variable microwear texture clearly indicates that these two species do not feed only on leaves, but that their diet maybe more opportunistic and include significant amounts of hard food items such as hard seeds, insects or bark. Unfortunately, species of *Phyllomys* are difficult to observe, limiting our knowledge of their dietary habits (Leite 2003). *Phyllomys nigrispinus* does not display a microwear texture distinct from that recorded for *P. pattoni* (Fig. 5A-D) and it might be expected that *P. nigrispinus* has the same dietary preferences as *P. pattoni*, which could explain their tightly parapatric ranges (Leite and Loss 2015).

Resource partitioning and interspecific segregation.— The differential exploitation of resources facilitates the coexistence of species (Schoener 1974). For caviomorph rodents from the SDMAf, dietary preferences seem to play an important role in the ecological segregation, given the diversity of diets among the studied species (Table 1). DMTA detected differences in dietary habits among most caviomorph rodents except "aquatic vegetation,""grass," and "leaf," consumers, and between "fruit-seed" and "bamboo" consumers, which have diet differences that are not reflected by their microwear textures.

Because body mass also is related to ecological segregation (Bowers and Brown 1982; Robinson and Redford 1986; Morales and Giannini 2010), we consider sympatric caviomorphs of the SDMAf taking that factor into account. The "aquatic vegetation" consumer *H. hydrochaeris* (35-60kg), the "grass" eater *C. aperea* (400-700g) and the two species of "leaf" consumers of the genus *Phyllomys* (200-300g) have distinct diets that are not reflected by different microwear textures. However they occupy different body mass ranges and have different lifestyles (Table 1). The "fruit-seed" consumers and the "bamboo" consumer *K. amblyonyx* (400g) have similar microwear textures that do not reflect their different diets. They also differ in body mass (*K. amblyonyx* weighs about 400g; *D. leporina* weighs about1.5kg; the four species of *Trinomys* weigh about160 to 240g and display segregation in terms of habits (Table 1).

There is neither segregation by diet nor segregation by body mass between both species of *Phyllomys*, and among the parapatric species of *Trinomys*. In these cases, ecological segregation involves differences in microhabitat preferences (Vieira 2003). *Phyllomys pattoni* occupies a wider range of microhabitats than *P. nigrispinus* (Fabre et al. 2016). The four species of *Trinomys* are parapatric, which means that they show very similar ecological traits but do not occupy identical habitats. Indeed, *T. gratiosus* and *T. iheringi* are found above 600m in Rio de Janeiro and Sao Paulo states, respectively. *Trinomys dimidiatus* prefers relatively open interior climax lowland forests, while *T. eliasi* prefers coastal forests (Fabre et al. 2016).

Considerations of microwear in caviomorph rodents.—With 2D low-magnification microwear analyses, Townsend and Croft (2008: 738) concluded that differences in microwear patterns among caviomorph rodents were more subtle than those for ungulates (Solounias and Semprebon 2002) and primates (Godfrey et al. 2004). Our DMTA analysis of a geographically restricted sample performed at the species level showed that differences in dental microwear textures among caviomorph rodents (Figs. 3-5; Table 5) have similar ranges as those observed for ungulates (Scott 2012) or primates (Scott et al. 2012; Ungar et al. 2017).

The intraspecific microwear texture variation exhibited by caviomorphs makes the analysis and understanding of the interspecific variability more difficult. However, intraspecific variation was expected. Although caviomorphs are mainly leaf or fruit eaters, many of them include animal matter, bark, or seeds, in their diets and are more opportunistic than ruminants. Ramdarshan et al. (2016) showed that small hard objects scar the enamel surface to a greater extent than large ones. Thus, even a moderate percentage of insects or hard small seeds may generate variation in dental microwear, as we observed in *C. aperea* (Fig. 5) and *Trinomys* within the "fruit-seed" category (Fig. 4). As dental microwear records the last days or weeks of wear (Teaford and Oyen 1989; Schultz et al. 2013), it is sensitive to any change in diet. Thus, opportunistic behavior increases inter– and intra- taxon variability in microwear textures. Furthermore, the functional importance of incisors in food processing among rodents (e.g., in *Dasyprocta* and *Kannabateomys*) can modulate the role of cheek teeth in the fragmentation of food elements. Finally, a recent experimental study showed that the same plant may leave different microwear textures, depending on whether it is wet or dry (Winkler et al. 2019).A portion of the intraspecific variability of microwear texture complexity of both species of *Phyllomys* might be explained by such variations (Fig. 5).The exploration of intra-taxa seasonal variability among the genera *Coendou* and *Trinomys* of the SdMAf did not shed light on any significant differences (Supplementary Data SD4). However, as dental microwear texture is linked to the physical properties of the food, it means only that, in both cases, those physical properties remain the same throughout the year. Whether it is because the items consumed remain the same or because different items have analogous properties is unknown.

Part of the high apparent intraspecific variability may be artificial. The scanned surface was small due to the tooth and body size of the mammals studied here. Thus, the effect of a small hard or abrasive element affects a higher portion of this scanned area (50 µm × 50 µm) compared to larger surfaces usually considered for studies on primates or ungulates (200 µm × 200 µm; Martin et al. 2018; Merceron et al. 2018). This means that analysis on small surfaces for rodents or any other small mammal favors intra-specific variability (Ramdarshan et al. 2017). Furthermore, our geographically restricted and species-specific level study resulted in small sample sizes for some taxa, which may have resulted in some bias. Nonetheless, interspecific and inter-dietary group differences were more important than intraspecific variations in our sample (Table 5).

One limiting factor for interpreting DMTA results for caviomorphs is the lack of detailed published ethological and ecological data for members of the group. There are few detailed ethological analyses of caviomorphs compared to primates or ungulates (for primates see Napier and Napier 1967; Percher et al. 2017; for ungulates see Field 1972; Gebert and Verheyden-Tixier 2001). The detailed lists of consumed items that can be found for some species of ungulates or primates allow for a better interpretation of their dental microwear textures. Experimental settings (Ramdarshan et al. 2016; Teaford et al. 2018) and applied studies (Berlioz et al. 2018) have shown that secondary foods may affect dental microwear textures to a considerable extent, suggesting that poor dietary records for some South American rodents may explain the apparent discrepancy with tooth wear.

This study represents a first step in the use of the DMTA to generate proxies for studying the ecology of caviomorph rodents. Our data covers the main dietary preferences among extant caviomorph rodents, and is therefore a prerequisite for interpretation of dental microwear textures of extinct caviomorph taxa as a means of reconstructing and estimating their diets, and further our understanding of the resource partitioning in paleocommunities and its role in the successful evolutionary history of this rodent group.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Dietary preferences of each studied species from the Serra do Mar Atlantic forest (Brazil) compiled from the literature, and description of the seven dietary categories used in this study.

Supplementary Data SD2.— Details of the scanning, pre-treatment and analysis of50 x 50 scan procedures used to acquire the dental microwear surfaces studied in this work.

Supplementary Data SD3.—Studied specimens and their individual dental microwear textural parameters (seasons indicated as followed: dry season or winter time = d, wet season = w).

Supplementary Data SD4.—Summary of results and discussion of the impact of seasonality (wet season *versus* winter time) on the dental microwear texture of the specimens of the genera *Coendou* and *Trinomys* from the Serra do Mar Atlantic forest (Brazil).

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FIGURE LEGENDS

Figure 1. —Geographic location of the Serra do Mar coastal forest (as delineated by Olson et al. 2001 *sensu* IBGE 1993) situated in the Atlantic forest (eastern Brazil).Simplified distribution of the brazilian Atlantic forest inspired by Pinto and Grelle (2012).Brazilian states abbreviations: CE, Ceará; RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; PI, Piauí; BA, Bahia; GO, Goiás; MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; MS, Mato Grosso do Sul; SP, São Paulo; PR, Paraná; SC, Santa Catarina and RS, Rio Grande do Sul.

Figure 2.—Graphical representation of the acquisition process and measurement position of the chewing facet of the right upper first molar (M1) of *Coendou spinosus* (MN19327)and corresponding photosimulation and 3D representation of the studied surface (A).Photosimulations of obtained 3D surfaces for each dental morphotype (B). Drawings and photosimulations of (from left to right):*Cavia aperea* (MN24372), *Dasyprocta leporina* (MN6694), *Euryzygomatomys spinosus* (MN70164), *Phyllomys pattoni* (MN31566), *Hydrochoerus hydrochaeris* (MN73284), and *Kannabateomys amblyonyx* (MN6239). The light gray filling indicates the enamel layer. Arrows indicates mesio-lingual direction. Scale bar = 1 mm.

Figure 3.—Boxplots of microwear texture variables by dietary preferences. A, complexity (Asfc); B, anisotropy (epLsar); C, heterogeneity of complexity (HAsfc9); D, heterogeneity of complexity (HAsfc16); E, textural fill volume (Tfv). Dietary categories: Aq, “aquatic vegetation;”Ba, “bamboo;”FS, “fruit-seed;”Gr, “grass;”Le, “leaf;”LI, “leaf-insect;”YL, “young leaf.”

Figure 4.—Boxplots of microwear texture variables for “fruit-seed”(black) and “leaf-insect” (grey) eating species. A, complexity (Asfc); B, anisotropy (epLsar); C, heterogeneity of complexity (HAsfc16); D, textural fill volume (Tfv).When pairwise comparison showed significant differences between taxa, different letters indicates significant differences (Fisher’s LSD, $p<0.05$).

Figure 5. —Boxplots of microwear texture variables for “grass”(Gr), “aquatic vegetation”(Aq) and “leaf” eating (Le) species. A, complexity (Asfc); B, anisotropy (epLsar); C, heterogeneity of complexity (HAsfc9); D, textural fill volume (Tfv).

TABLES

Table 1.—Classification, ecology and sample size of caviomorph rodents used in this study. Life-styles: arboreal (A), semi-aquatic (SA), semi-fossorial (SF), and terrestrial (T). Body mass is expressed in grams. Asterisks indicate that body masses were not available in the catalog of the MN-UFRJ for the sampled specimens and were derived from Alvarez et al. (2017; supplementary material). Double asterisks indicate when body mass was available for only one specimen.

Taxa	Habitat	Lifestyle	Activity	Mean mass (sd)	Diet	Dietary group	References[a]
Caviidae							
Cavia apera Brazilian guinea pig	gallery forest, also found near cultivated areas	T	diurnal	552.2*	mainly grasses, including inflorescences and seeds	grass	1, 2, 3, 4, 5, 6, 7, 8
Hydrochoerus hydrochaeris Capybara	open area, close to water, along rivers and streams	SA	diurnal or nocturnal	51899*	grasses, sedges, aquatic vegetation, occasionally browse on shrubs	aquatic vegetation	3, 5, 7, 8, 9, 10, 11, 12
Dasyproctidae							
Dasyprocta leporina Red-rumped agouti	open forest, usually distant from both water and dense vegetation	T	diurnal	4136.7 (784)	primarily fruits and seeds, and nuts (scatter hoarder), and leaves as a fallback food	fruit-seed	7, 8, 13, 14, 15, 16
Erethizontidae							

Coendou spinosus Paraguayan hairy dwarf porcupine	humid tropical and subtropical forest, prefers primary forest	A	nocturnal	1435 (351)	young leaves of Fabaceae, Sapotaceae and Dilleniaceae, sprouts and flowers, ant pupae	youngleaf	2, 7, 8, 11, 17, 18, 19
Echimyidae							
Trinomys dimidiatus Rio de Janeiro spiny rat	relatively open interior climax evergreen rainforest	T	nocturnal	223.4 (12)	fruits, seeds, maybe insects	fruit-seed	7, 8, 20
Trinomys eliasi Elia's spiny rat	evergreen moist forest, dry land forest, most common in dense undergrowth	T	nocturnal	211.4 (32)	fruits, seeds, maybe insects	fruit-seed	7, 8, 21, 22
Trinomys gratiosus Gracile Atlantic spiny rat	evergreen forest with a lot of humidity and a dense overstory, above 600m	T	nocturnal	241.7 (46)	fruits, seeds, maybe insects	fruit-seed	7, 8, 23
Trinomys iheringi São Paulo spiny rat	evergreen forest with a lot of humidity, above 600m	T	nocturnal	162.4 (22)	fruits, seeds (scatter hoarder, Arecaceae), maybe insects	fruit-seed	7, 8, 24, 25, 26, 27
Euryzygomatomys spinosus Guiara	habitat generalist	SF	nocturnal	241.2 (17)	leaves and insects, sometimes bark, omnivorous	leaf-insect	2, 5, 7, 8, 28, 29, 30
Kannabateomys amblyonyx Atlantic bamboo rat	inland rainforest, wet gallery forest and bamboo patches	A	nocturnal or crepuscular	414.4 (43)	inner tissues of shoots of bamboo, after removal of outer hard and spiny sheet	bamboo	3, 5, 7, 8, 11, 31, 32, 33

Phyllomys pattoni Patton's Atlantic tree rat	evergreen rainforest, prefers primary forest and dense vegetation	A	nocturnal	226.9 (5)	folivorous diet, maybe more diverse than other arboreal Echimyidae	leaf	5, 6, 7, 8, 31
Phyllomys nigrispinus Black-spined Atlantic tree rat	coastal evergreen rainforest	A	nocturnal	325**	folivorous diet	leaf	5, 6, 7, 8, 31

[a]References:1) Rood 1972; 2) Redford and Eisenberg 1992; 3) Eisenberg and Redford 1999;4) Guichón and Cassini 1998; 5) Woods and Kilpatrick 2005; 6) Canevari and Vaccaro 2007; 7) Patton et al. 2015; 8) Wilson et al. 2016;9) Macdonald 1981; 10) Mones and Ojasti 1986; 11) Emmons and Feer 1997; 12) Quintana et al. 1998; 13) Smythe 1986; 14) Dubost 1988; 15) Henry 1999; 16) Jorge and Peres 2005; 17) Wilson and Reeder 2005; 18) Passamani 2009; 19) Caldara and Leite 2012; 20) Mello et al.2015; 21) Brito and Figueiredo 2003; 22) Roach and Naylor 2016; 23) Patterson 2016; 24) Bergallo 1994; 25) Bergallo 1995; 26) Bergallo and Magnusson 1999; 27) Donatti et al. 2009; 28) Alho 1982; 29) Gonçalves et al. 2007; 30) Catzeflis et al. 2008; 31) Emmons 1990; 32) Olmos 1992; 33) Olmos et al. 1993.

Table 2.—Descriptive statistics of dental microwear texture parameters for each taxon of the Serra do Mar Atlantic Forest ecoregion. Number of individuals per sample = n; $\bar{X}$ = mean; med = median; sd= standard deviation.

		Asfc			epLsar (x10^{-3})			HAsfc4			HAsfc9			HAsfc16			Tfv		
Taxa	n	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd
Cavia aperea	4	3.12	2.80	1.27	2.47	2.51	0.82	0.34	0.29	0.12	0.39	0.41	0.12	0.48	0.47	0.16	1334.38	1097.80	564.61
Coendou spinosus	18	0.37	0.33	0.17	4.12	3.62	2.25	0.29	0.30	0.12	0.35	0.37	0.12	0.37	0.34	0.11	100.76	22.83	172.70
Dasyprocta leporina	7	1.18	1.21	0.52	3.12	2.79	1.84	0.25	0.16	0.15	0.25	0.22	0.13	0.29	0.26	0.13	655.18	456.55	633.84
Euryzygomatomys spinosus	6	0.95	0.88	0.47	4.71	4.77	1.47	0.38	0.37	0.18	0.48	0.49	0.14	0.46	0.44	0.11	1736.28	1709.99	601.46
Hydrochoerus hydrochaeris	5	4.91	3.79	2.52	2.77	2.12	2.30	0.32	0.35	0.14	0.49	0.54	0.23	0.50	0.48	0.11	1801.30	1797.15	345.80
Kannabateomys amblyonyx	3	0.68	0.61	0.24	3.06	3.01	2.50	0.44	0.34	0.28	0.55	0.65	0.32	0.55	0.58	0.32	401.21	37.35	662.83
Phyllomys nigrispinus	5	5.04	5.91	2.53	2.68	2.61	0.57	0.54	0.45	0.26	1.02	0.66	0.83	1.28	1.51	0.70	2055.31	2689.50	1085.74
Phyllomys pattoni	6	4.04	3.92	2.81	3.31	3.52	1.76	0.41	0.36	0.23	0.53	0.47	0.29	0.53	0.48	0.24	697.97	317.51	1149.61
Trinomys dimidiatus	10	1.41	0.98	1.33	3.39	3.34	1.97	0.35	0.34	0.10	0.38	0.37	0.09	0.44	0.42	0.15	316.68	302.98	256.85
Trinomys eliasi	4	1.33	1.16	0.94	4.14	4.03	3.10	0.44	0.45	0.02	0.54	0.56	0.05	0.53	0.52	0.11	617.38	460.70	738.06
Trinomys gratiosus	8	0.88	0.83	0.39	4.91	5.39	2.44	0.34	0.30	0.16	0.46	0.40	0.25	0.52	0.38	0.34	849.81	747.08	788.58
Trinomys iheringi	7	1.10	1.06	0.62	3.48	3.40	2.12	0.29	0.28	0.08	0.36	0.34	0.10	0.37	0.35	0.09	499.84	149.42	706.34

Asfc: complexity; epLsar: anisotropy; HAsfc: heterogeneity of complexity calculated from 4, 9 and 16 subsurfaces respectively; Tfv: textural fill volume.

Table 3.—Results of the ANOVAs for dietary categories. A, on Box-Cox transformed data; B, on Levene transformed data. Adjusted *P*-values follow B-Y method (Benjamini and Yekutieli 2001).

Variables	Effect	df	SS	MS	*F*	P
(A)						
Asfc	Diet	6	54.02	9.00	25.78	<0.001
	Residuals	76	26.55	0.35		
epLsar ($x10^{-3}$)	Diet	6	9.82	1.64	1.01	0.427
	Residuals	76	123.58	1.63		
HAsfc4	Diet	6	0.77	0.13	1.57	0.493
	Residuals	76	6.18	0.08		
HAsfc9	Diet	6	3.97	0.66	2.57	0.093
	Residuals	76	19.57	0.26		
HAsfc16	Diet	6	5.91	0.99	3.08	0.046
	Residuals	76	24.29	0.32		
Tfv	Diet	6	2064.70	344.12	9.92	<0.001
	Residuals	76	2636.60	34.69		
(B)						
Asfc	Diet	6	0.94	0.16	3.61	0.033
	Residuals	76	3.30	0.04		
epLsar ($x10^{-3}$)	Diet	6	0.62	0.10	1.27	0.831
	Residuals	76	6.24	0.08		
HAsfc4	Diet	6	0.02	0.00	0.62	0.715
	Residuals	76	0.36	0.00		
HAsfc9	Diet	6	0.11	0.02	1.81	0.398
	Residuals	76	0.77	0.01		
HAsfc16	Diet	6	0.22	0.04	3.07	0.047
	Residuals	76	0.90	0.01		
Tfv	Diet	6	38.63	6.44	3.46	0.033
	Residuals	76	141.51	1.86		

Table 4. —Results of the ANOVAs for species within dietary categories. A, on Box-Cox transformed data; B, on Levene transformed data.

			Asfc		epLsar (x10^{-3})		HAsfc4		HAsfc9		HAsfc16		Tfv	
Subset	Effect	df	F	P	F	P	F	P	F	P	F	P	F	P
(A)														
“fruit-seed”	Taxa	4	0.25	0.91	0.65	0.63	2.56	0.06	3.74	<0.05	2.90	<0.05	0.46	0.76
“leaf”	Taxa	1	1.24	0.30	3.80	0.09	0.71	0.42	1.53	0.25	4.50	0.07	4.55	0.07
(B)														
“fruit-seed”	Taxa	4	0.75	0.57	0.40	0.81	7.60	<0.05	2.62	0.06	1.50	0.23	2.81	<0.05
“leaf”	Taxa	1	0.03	0.87	1.38	0.27	0.19	0.68	0.27	0.62	0.64	0.45	4.31	0.07

Table 5. —Posthoc pairwise comparisons between dietary categories. A, on Box-Cox transformed data; B, on Levene transformed data. Significance at $p < 0.05$ is indicated in regular font when both Tukey's HSD and Fisher's LSD tests are significant and in bold associated to an asterisk when only Fischer's LSD test is significant (marginal).

(A)	aquatic vegetation	bamboo	fruit-seed	grass	leaf	leaf-insect
bamboo	Asfc,Tfv					
fruit-seed	Asfc,Tfv					
grass		Asfc,**Tfv***	Asfc, **Tfv***			
leaf		Asfc, **Tfv***	Asfc, HAsfc16			
leaf-insect	Asfc	**Tfv***	Tfv	**Asfc***	Asfc	
young leaf	Asfc, Tfv	**Asfc***	Asfc, Tfv	Asfc, Tfv	Asfc, HAsfc16, Tfv	Asfc, Tfv

(B)	aquatic vegetation	bamboo	fruit-seed	grass	leaf	leaf-insect
bamboo	**Tfv***					
fruit-seed	**Tfv***					
grass		**Tfv***	**Tfv***			
leaf	**HAsfc16***	**Asfc***	**Asfc***, HAsfc16	**Asfc***, HAsfc16		
leaf-insect		**Tfv***	**Tfv***		**Asfc***, **HAsfc16***	
young leaf	Tfv			**Tfv***	Asfc, HAsfc16	Tfv

APPENDIX I

Appendix I. —List of all studied specimens with catalog numbers and locality of capture.

Collection	Catalog number	Taxon	Locality
MN-UFRJ	2236	*Cavia aperea*	Rio de Janeiro, Teresópolis
MN-UFRJ	6741	*Cavia aperea*	Rio de Janeiro, Teresópolis, Fazenda Guinle
MN-UFRJ	24369	*Cavia aperea*	Rio de Janeiro, Angra dos Reis, Praia Vermelha, Ilha Grande
MN-UFRJ	24372	*Cavia aperea*	Rio de Janeiro, Angra dos Reis, Praia Vermelha, Ilha Grande
MN-UFRJ	46517	*Coendou spinosus*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	46518	*Coendou spinosus*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	5514	*Coendou spinosus*	Rio de Janeiro, Mangaratiba, Fazenda da Lapa
MN-UFRJ	7260	*Coendou spinosus*	Rio de Janeiro, Teresópolis, Fazenda Carlos Guinle
MN-UFRJ	8239	*Coendou spinosus*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	8240	*Coendou spinosus*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	19327	*Coendou spinosus*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	59613	*Coendou spinosus*	Rio de Janeiro, Carmo, Fazenda Providência
MN-UFRJ	69896	*Coendou spinosus*	Rio de Janeiro, Petrópolis, Rodovia BR 040, km 66
MN-UFRJ	75317	*Coendou spinosus*	Rio de Janeiro, Piraí, Ribeirão das Lajes
MN-UFRJ	75961	*Coendou spinosus*	Rio de Janeiro, Sumidouro, Vale do Encanto
MN-UFRJ	30494	*Coendou spinosus*	Rio de Janeiro, Angra dos Reis, Enseada de Palmas, Ilha Grande
MN-UFRJ	74408	*Coendou spinosus*	Rio de Janeiro, Rio de Janeiro, Reserva do Grajaú
MN-UFRJ	79251	*Coendou spinosus*	Rio de Janeiro, Areal, Rodovia BR040, Km 37
MN-UFRJ	79284	*Coendou spinosus*	Rio de Janeiro, Areal, Rodovia BR040, Km 31
MN-UFRJ	79385	*Coendou spinosus*	Rio de Janeiro, Duque de Caxias, Rodovia BR 040, Km 93
MN-UFRJ	79561	*Coendou spinosus*	Rio de Janeiro, Petropolis, Rodovia BR040, Km 84
MN-UFRJ	79574	*Coendou spinosus*	Rio de Janeiro, Petropolis, Rodovia BR040, Km 80
MN-UFRJ	5652	*Dasyprocta leporina*	Rio de Janeiro, Paraty, Pedra Branca

MN-UFRJ	6694	*Dasyprocta leporina*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	6698	*Dasyprocta leporina*	Rio de Janeiro, Sahy
MN-UFRJ	7310	*Dasyprocta leporina*	Rio de Janeiro, Duque de Caxias
MN-UFRJ	7719	*Dasyprocta leporina*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	8481	*Dasyprocta leporina*	Rio de Janeiro, Serra dos Órgãos, Mantiqueira
MN-UFRJ	43195	*Dasyprocta leporina*	Rio de Janeiro, Colônia São Bento
MN-UFRJ	6779	*Euryzygomatomys spinosus*	Rio de Janeiro, Teresópolis, Fazenda Boa Fé
MN-UFRJ	24153	*Euryzygomatomys spinosus*	São Paulo, Salesópolis, Casa Grande
MN-UFRJ	24154	*Euryzygomatomys spinosus*	São Paulo, Salesópolis, Casa Grande
MN-UFRJ	70164	*Euryzygomatomys spinosus*	Rio de Janeiro, Comendador Levy Gasparian
MN-UFRJ	71933	*Euryzygomatomys spinosus*	Rio de Janeiro, Santa Maria Madalena, Parque Estadual do Desengano
MN-UFRJ	76464	*Euryzygomatomys spinosus*	Rio de Janeiro, Cachoeiras de Macacu, Fragmento 19
MN-UFRJ	7663	*Hydrochoerus hydrochaeris*	Rio de Janeiro, Paraty, Pedra Branca
MN-UFRJ	73284	*Hydrochoerus hydrochaeris*	Rio de Janeiro, Rio de Janeiro, Condomínio Alphaville, Barra da Tijuca
MN-UFRJ	73634	*Hydrochoerus hydrochaeris*	Rio de Janeiro, Cabo Frio, Praia Rasa, Área da Marinha
MN-UFRJ	75761	*Hydrochoerus hydrochaeris*	Rio de Janeiro, Rio de Janeiro, Restinga de Grumari, Recreio dos Bandeirantes
MN-UFRJ	79156	*Hydrochoerus hydrochaeris*	Rio de Janeiro, Três Rios, Rodovia BR040, km 13 sentido Juiz de Fora
MN-UFRJ	1956	*Kannabateomys amblyonyx*	Rio de Janeiro, Teresópolis, Varzea de Teresópolis
MN-UFRJ	6239	*Kannabateomys amblyonyx*	Rio de Janeiro, Teresópolis, Varzea de Teresópolis
MN-UFRJ	81356	*Kannabateomys amblyonyx*	Rio de Janeiro, Duque de Caxias, Rodovia BR040, km 102 sentido Juiz de Fora
MN-UFRJ	6440	*Phyllomys nigrispinus*	Rio de Janeiro, Teresópolis
MN-UFRJ	6441	*Phyllomys nigrispinus*	Rio de Janeiro, Teresópolis
MN-UFRJ	6442	*Phyllomys nigrispinus*	Rio de Janeiro, Teresópolis
MN-UFRJ	6443	*Phyllomys nigrispinus*	Rio de Janeiro, Teresópolis
MN-UFRJ	31562	*Phyllomys nigrispinus*	Rio de Janeiro, Angra dos Reis, Ilha Grande
MN-UFRJ	2239	*Phyllomys pattoni*	Rio de Janeiro, Casimiro de Abreu, Fazenda União
MN-UFRJ	2240	*Phyllomys pattoni*	Rio de Janeiro, Casimiro de Abreu, Fazenda União
MN-UFRJ	6449	*Phyllomys pattoni*	Rio de Janeiro, Niterói, São Francisco
MN-UFRJ	21508	*Phyllomys pattoni*	Rio de Janeiro, Santa Cruz, Estrada Rio-Petrópolis
MN-UFRJ	31566	*Phyllomys pattoni*	Rio de Janeiro, Angra dos Reis, Ilha Grande
MN-UFRJ	70175	*Phyllomys pattoni*	Rio de Janeiro, Casimiro de Abreu, Fazenda União

MN-UFRJ	1949	*Trinomys dimidiatus*	Rio de Janeiro, Angra dos Reis
MN-UFRJ	4944	*Trinomys dimidiatus*	Rio de Janeiro, Duque de Caxias, Barro Branco
MN-UFRJ	4946	*Trinomys dimidiatus*	Rio de Janeiro, Duque de Caxias, Barro Branco
MN-UFRJ	4947	*Trinomys dimidiatus*	Rio de Janeiro, Duque de Caxias, Barro Branco
MN-UFRJ	4948	*Trinomys dimidiatus*	Rio de Janeiro, Duque de Caxias, Barro Branco, Estrada União Indústria km 51
MN-UFRJ	4950	*Trinomys dimidiatus*	Rio de Janeiro, Duque de Caxias, Barro Branco
MN-UFRJ	60209	*Trinomys dimidiatus*	Rio de Janeiro, Itaguaí, Morro da Mazomba, próximo à sede
MN-UFRJ	67512	*Trinomys dimidiatus*	Rio de Janeiro, Guapimirim, Parque Nacional da Serra dos Órgãos - Vale do Rio Soberbo
MN-UFRJ	67513	*Trinomys dimidiatus*	Rio de Janeiro, Guapimirim, Parque Nacional da Serra dos Órgãos - Vale do Rio Soberbo
MN-UFRJ	81652	*Trinomys dimidiatus*	Rio de Janeiro, Rio de Janeiro, Parque Nacional da Tijuca
MN-UFRJ	26811	*Trinomys eliasi*	Rio de Janeiro, Maricá, Restinga de Maricá
MN-UFRJ	28806	*Trinomys eliasi*	Rio de Janeiro, Maricá, Restinga de Maricá
MN-UFRJ	28815	*Trinomys eliasi*	Rio de Janeiro, Maricá, Restinga de Maricá
MN-UFRJ	28932	*Trinomys eliasi*	Rio de Janeiro, Maricá, Restinga de Maricá
MN-UFRJ	31370	*Trinomys gratiosus*	Rio de Janeiro, Sumidouro, Fazenda São José da Serra, Serra do Paquequer
MN-UFRJ	33517	*Trinomys gratiosus*	Rio de Janeiro, Sumidouro
MN-UFRJ	43807	*Trinomys gratiosus*	Rio de Janeiro, Teresópolis, Fazenda Boa Fé
MN-UFRJ	61806	*Trinomys gratiosus*	Rio de Janeiro, Sumidouro, Porteira Verde
MN-UFRJ	75821	*Trinomys gratiosus*	Rio de Janeiro, Teresópolis, Waldemar
MN-UFRJ	75826	*Trinomys gratiosus*	Rio de Janeiro, Teresópolis, Fragmento 12
MN-UFRJ	75827	*Trinomys gratiosus*	Rio de Janeiro, Teresópolis, Fragmento 6
MN-UFRJ	75828	*Trinomys gratiosus*	Rio de Janeiro, Teresópolis, Fragmento 6
MN-UFRJ	6451	*Trinomys iheringi*	São Paulo, Ilha de São Sebastião
MN-UFRJ	24433	*Trinomys iheringi*	São Paulo, Ubatuba, Rio Praia Dura, Serra d'Água
MN-UFRJ	28800	*Trinomys iheringi*	São Paulo, Ubatuba, Rio Praia Dura, Serra d'Água
MN-UFRJ	43821	*Trinomys iheringi*	Rio de Janeiro, Teresópolis, Rio das Bengalas
MN-UFRJ	43829	*Trinomys iheringi*	São Paulo, Juréia
MN-UFRJ	54153	*Trinomys iheringi*	Rio de Janeiro, Teresópolis, Rio das Bengalas
MN-UFRJ	6453	*Trinomys iheringi*	São Paulo, Ilha de São Sebastião

Supplementary data 1: Detailed description of the seven dietary categories

We recognized seven dietary categories based on the primary diet component: aquatic vegetation, bamboo, grass, fruit-seed, leaf, leaf-insect, and young leaf (Table 1).

Because dental microwear texture reflects the physical and biomechanical properties of consumed items, we took the silica content of plants (when known) and the dietary specialization (when extreme) into account to better depict the spectrum of dietary habits of the sampled species. The broad dietary categories used in previous works that did not focus on microwear (e.g., Nowak 1991; Ojeda et al. 2015) were not adequate for the objectives of this study. The same is true for the categories used in Townsend and Croft(2008). Townsend and Croft (2008) worked at the generic level, including several data from individuals fed in captivity.

Our sample included some strictly folivorous taxa (*Phyllomys*) that feed on dicotyledons (Emmons and Feer 1997; Leite 2003; Wilson et al. 2016) that generally have lower silica content than monocotyledons (Hodson et al. 2005). Thus, we assigned these folivorous taxa to the category “leaf.” Townsend and Croft (2008) included both *Cavia aperea* and *Hydrochoerushydrochaeris* into the “grass-leaf”category. Furthermore, *C. aperea* prefers grasses that have high silica content (Rood 1972; Guichón and Cassini 1998) while *H. hydrochaeris*consumes a high proportion of sedges (Quintana et al. 1998) and sometimes browses on shrubs (Macdonald 1981; Mones and Ojasti 1986; Wilson et al. 2016) thatdiffer in biosilica content (Piperno 1988; Prychid et al. 2004). We therefore separated these speciesin two dietary categories: “grass”(*C. aperea*) and “aquatic vegetation”(*H. hydrochaeris*). According to Townsend and Croft (2008), the genus *Coendou* is a fruit-leaf eater.

However,the species studied here, *Coendou spinosus*, does not consume fruit and has been observed feeding on young leaves of six species of trees, mainly Fabaceae (Passamani 2009) with low silica content (Piperno 2006),and possibly some flowers and ant pupae (Redford and Eisenberg 1992). We assigned *C. spinosus*to the category "young leaf."Finally, *Dasyproctaleporina* is often categorized as a fruit-leaf consumer. Because it feeds on >80% fruit pulp and seeds (Dubost 1988; Henry 1999; Bongers et al. 2013), we considered this species as a "fruit-seed"eater, like the four species of *Trinomys* that also consume mainly fruit and seeds (Bergallo and Magnusson 1999; Brito and Figueiredo 2003; Mello et al. 2015; Patterson 2016; Roach and Naylor 2016). *Kannabateomysamblyonyx*is a bamboo specialist (Olmos et al. 1993) that consumes inner tissues of bamboo shoots after removing the outer hard sheet (Emmons 1990; Olmos 1992; Fabre et al. 2016). Because its diet is extremely specialized (a single genus of plant), we assigned this species to the "bamboo"category. *Euryzygomatomysspinosus*is omnivorous (Alho 1982) and includes a significant proportion of insects in its diet (Gonçalves et al. 2007; Catzeflis et al. 2008; Fabre et al. 2016). We assigned this species to a category of "leaf-insect"corresponding to its mixed diet including leaves as well as fruit, seeds, grasses, and insects.

Ecological data, assigned dietary categories and sources for each species are summarized in Table 1 of the main text.

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Supplementary data 2: Detail of the scanning, pre-treatment and analysis procedures for 50x50 scans used to acquire the dental microwear surfaces studied in this work.

The scanning process generated 1360 × 1024 point clouds with a vertical sampling of less than 0.002 µm and a lateral sampling (x, y) of 0.129 µm (175 × 132 µm). These scans were saved as ".plu"files by the LeicaScan software (Leica Microsystems). They were then pre-treated using Leica Map software (Mountain Technology, Leica Microsystems). After removing aberrant peaks with automatic operators including morphological filters (see Merceron et al. 2016 for details) and vertical inversion, a 50 × 50 µm area (the largest size of the studied surface for all species) was extracted. The 2nd order polynomial surface was subtracted to calculate the textural parameter on the microwear surface without the effects of the dental facet shape (Francisco et al. 2018). The surface was leveled and saved as a Digital Elevation Model (".sur") for Scale Sensitive Fractal Analysis(SSFA).

Because of the variety of patterns of enamel layers and sizes among the species (Fig.2B), the available enamel surface that could be compared across taxa was limited. Teeth of *Cavia aperea* have a narrow enamel layer;Winkler et al. (2019) selected a maximum 60 x 60 µm surface on that layer ("enamel band"*sensu* Winkler et al. 2019). However, *Kannabateomys amblyonyx* displays a narrower enamel layer than *C. aperea*. Therefore, the size of the largest area captured for *Kannabateomys amblyonyx* (i.e., 50 µm× 50 µm) defined the maximum size for all other species.

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Collection number	Taxon	Habitat	Diet	Season	Asfc	epLsar	HAsfc4	HAsfc9	HAsfc16	TFV
MN-2236	Cavia aperea	terrestrial	grass		2.87	0.0020	0.51	0.49	0.57	971.21
MN-24.372	Cavia aperea	terrestrial	grass		2.72	0.0016	0.26	0.25	0.33	1016.87
MN-24369	Cavia aperea	terrestrial	grass		1.97	0.0030	0.25	0.33	0.36	1178.73
MN-6741	Cavia aperea	terrestrial	grass		4.92	0.0033	0.32	0.49	0.65	2170.70
MN-19327	Coendou spinosus	arboreal	young leaf		0.12	0.0042	0.28	0.41	0.31	0
MN-30494	Coendou spinosus	arboreal	young leaf	w	0.47	0.0059	0.16	0.19	0.21	161.87
MN-46517	Coendou spinosus	arboreal	young leaf		0.20	0.0058	0.11	0.29	0.31	0
MN-46518	Coendou spinosus	arboreal	young leaf		0.33	0.0059	0.49	0.51	0.43	8.30
MN-5514	Coendou spinosus	arboreal	young leaf		0.42	0.0009	0.23	0.38	0.56	49.81
MN-59613	Coendou spinosus	arboreal	young leaf	w	0.25	0.0089	0.33	0.53	0.32	0
MN-69896	Coendou spinosus	arboreal	young leaf	d	0.15	0.0042	0.09	0.21	0.30	0
MN-7260	Coendou spinosus	arboreal	young leaf	d	0.26	0.0025	0.35	0.47	0.32	0
MN-74408	Coendou spinosus	arboreal	young leaf	d	0.56	0.0070	0.22	0.16	0.26	506.36
MN-75317	Coendou spinosus	arboreal	young leaf	w	0.33	0.0067	0.49	0.54	0.60	556.16
MN-75961	Coendou spinosus	arboreal	young leaf	d	0.54	0.0054	0.40	0.33	0.39	49.81
MN-79251	Coendou spinosus	arboreal	young leaf	d	0.32	0.0030	0.42	0.38	0.35	95.46
MN-79284	Coendou spinosus	arboreal	young leaf	w	0.17	0.0018	0.23	0.37	0.30	0
MN-79385	Coendou spinosus	arboreal	young leaf	d	0.43	0.0031	0.21	0.28	0.40	37.35
MN-79561	Coendou spinosus	arboreal	young leaf	d	0.66	0.0027	0.19	0.21	0.20	278.08
MN-79574	Coendou spinosus	arboreal	young leaf	w	0.70	0.0016	0.31	0.19	0.43	0
MN-8239	Coendou spinosus	arboreal	young leaf		0.30	0.0017	0.40	0.36	0.43	0
MN-8240	Coendou spinosus	arboreal	young leaf		0.51	0.0028	0.34	0.39	0.49	70.56
MN-43195	Dasyprocta leporina	terrestrial	fruit-seed		0.97	0.0032	0.16	0.11	0.16	24.90
MN-5652	Dasyprocta leporina	terrestrial	fruit-seed		0.73	0.0019	0.16	0.26	0.28	1303.25
MN-6694	Dasyprocta leporina	terrestrial	fruit-seed		1.21	0.0045	0.14	0.33	0.43	726.33
MN-6698	Dasyprocta leporina	terrestrial	fruit-seed		1.34	0.0027	0.15	0.15	0.15	332.04
MN-7310	Dasyprocta leporina	terrestrial	fruit-seed		2.08	0.0005	0.25	0.21	0.26	456.55
MN-7719	Dasyprocta leporina	terrestrial	fruit-seed		1.45	0.0062	0.30	0.22	0.22	1693.39
MN-8481	Dasyprocta leporina	terrestrial	fruit-seed		0.49	0.0028	0.56	0.50	0.50	49.81
MN-24153	Euryzygomatomys spinosus	semifossorial	leaf-insect		0.46	0.0044	0.57	0.60	0.64	1830.36
MN-24154	Euryzygomatomys spinosus	semifossorial	leaf-insect		0.65	0.0052	0.23	0.67	0.38	1589.63
MN-6779	Euryzygomatomys spinosus	semifossorial	leaf-insect		0.96	0.0023	0.48	0.46	0.47	1195.34
MN-70164	Euryzygomatomys spinosus	semifossorial	leaf-insect		0.87	0.0062	0.26	0.29	0.34	987.81

MN-71933	Euryzygomatomys spinosus	semifossorial	leaf-insect		1.83	0.0042	0.18	0.35	0.51	2295.21
MN-76464	Euryzygomatomys spinosus	semifossorial	leaf-insect		0.89	0.0061	0.55	0.51	0.41	2519.34
MN-73284	Hydrochoerus hydrochaeris	semi-aquatic	aquatic plant		3.15	0.0008	0.10	0.25	0.48	2361.62
MN-73634	Hydrochoerus hydrochaeris	semi-aquatic	aquatic plant		2.83	0.0005	0.38	0.54	0.69	1519.07
MN-75761	Hydrochoerus hydrochaeris	semi-aquatic	aquatic plant		8.87	0.0021	0.29	0.59	0.42	1510.77
MN-7663	Hydrochoerus hydrochaeris	semi-aquatic	aquatic plant		5.91	0.0050	0.35	0.28	0.42	1797.15
MN-79156	Hydrochoerus hydrochaeris	semi-aquatic	aquatic plant		3.79	0.0054	0.49	0.80	0.49	1817.91
MN-1956	Kannabateomys amblyonyx	arboreal	bamboo		0.61	0.0056	0.22	0.19	0.22	37.35
MN-6239	Kannabateomys amblyonyx	arboreal	bamboo		0.95	0.0030	0.76	0.80	0.85	1166.28
MN-81356	Kannabateomys amblyonyx	arboreal	bamboo		0.49	0.0006	0.34	0.65	0.58	0
MN-31562	Phyllomys nigrispinus	arboreal	leaf		1.44	0.0021	0.45	0.42	0.51	572.76
MN-6440	Phyllomys nigrispinus	arboreal	leaf		5.91	0.0022	0.48	0.99	1.51	2917.78
MN-6441	Phyllomys nigrispinus	arboreal	leaf		8.02	0.0032	0.33	0.58	1.65	2876.28
MN-6442	Phyllomys nigrispinus	arboreal	leaf		6.14	0.0034	1.00	2.45	2.13	2689.50
MN-6443	Phyllomys nigrispinus	arboreal	leaf		3.66	0.0026	0.44	0.66	0.61	1220.24
MN-21508	Phyllomys pattoni	arboreal	leaf		1.30	0.0050	0.35	0.30	0.37	327.89
MN-2239	Phyllomys pattoni	arboreal	leaf		3.52	0.0051	0.83	1.02	0.94	3029.84
MN-2240	Phyllomys pattoni	arboreal	leaf		6.15	0.0039	0.41	0.63	0.59	307.13
MN-31566	Phyllomys pattoni	arboreal	leaf		4.32	0.0031	0.16	0.29	0.33	340.34
MN-6449	Phyllomys pattoni	arboreal	leaf		0.79	0.0022	0.37	0.66	0.60	182.62
MN-70175	Phyllomys pattoni	arboreal	leaf		8.13	0.0005	0.33	0.31	0.33	0
MN-1949	Trinomys dimidiatus	terrestrial	fruit-seed		0.85	0.0015	0.50	0.46	0.45	390.14
MN-4944	Trinomys dimidiatus	terrestrial	fruit-seed	w	0.49	0.0038	0.25	0.35	0.34	83.01
MN-4946	Trinomys dimidiatus	terrestrial	fruit-seed	w	0.66	0.0034	0.43	0.31	0.42	444.10
MN-4947	Trinomys dimidiatus	terrestrial	fruit-seed	w	1.10	0.0004	0.36	0.55	0.78	307.13
MN-4948	Trinomys dimidiatus	terrestrial	fruit-seed	w	4.91	0.0019	0.31	0.27	0.26	95.46
MN-4950	Trinomys dimidiatus	terrestrial	fruit-seed	w	1.49	0.0055	0.32	0.33	0.31	796.89
MN-60209	Trinomys dimidiatus	terrestrial	fruit-seed	d	1.94	0.0032	0.37	0.43	0.39	298.83
MN-67512	Trinomys dimidiatus	terrestrial	fruit-seed	d	0.30	0.0021	0.21	0.28	0.42	0
MN-67513	Trinomys dimidiatus	terrestrial	fruit-seed	d	0.87	0.0063	0.22	0.39	0.44	120.36
MN-81652	Trinomys dimidiatus	terrestrial	fruit-seed		1.49	0.0057	0.48	0.43	0.58	630.87
MN-26811	Trinomys eliasi	terrestrial	fruit-seed	d	1.26	0.0026	0.44	0.47	0.41	49.81
MN-28806	Trinomys eliasi	terrestrial	fruit-seed	w	0.38	0.0077	0.42	0.56	0.66	0
MN-28815	Trinomys eliasi	terrestrial	fruit-seed	w	1.06	0.0055	0.46	0.57	0.48	871.60
MN-28932	Trinomys eliasi	terrestrial	fruit-seed	w	2.62	0.0007	0.45	0.56	0.57	1548.13

MN-31370	Trinomys gratiosus	terrestrial	fruit-seed	d	0.46	0.0062	0.22	0.20	0.21	0
MN-33517	Trinomys gratiosus	terrestrial	fruit-seed		0.92	0.0071	0.21	0.22	0.27	2191.45
MN-43807	Trinomys gratiosus	terrestrial	fruit-seed	w	1.52	0.0053	0.32	0.58	0.37	821.79
MN-61806	Trinomys gratiosus	terrestrial	fruit-seed	d	0.74	0.0055	0.69	0.87	0.96	1834.51
MN-75821	Trinomys gratiosus	terrestrial	fruit-seed	w	1.01	0.0032	0.43	0.42	0.52	58.11
MN-75826	Trinomys gratiosus	terrestrial	fruit-seed		0.55	0.0028	0.25	0.25	0.40	680.68
MN-75827	Trinomys gratiosus	terrestrial	fruit-seed		0.54	0.0082	0.28	0.39	0.34	398.45
MN-75828	Trinomys gratiosus	terrestrial	fruit-seed		1.33	0.0009	0.36	0.76	1.12	813.49
MN-24433	Trinomys iheringi	terrestrial	fruit-seed	d	0.48	0.0031	0.28	0.25	0.30	49.81
MN-28800	Trinomys iheringi	terrestrial	fruit-seed	d	2.27	0.0036	0.26	0.34	0.30	224.13
MN-43821	Trinomys iheringi	terrestrial	fruit-seed		0.43	0.0017	0.25	0.42	0.39	4.15
MN-43829	Trinomys iheringi	terrestrial	fruit-seed	w	1.18	0.0052	0.15	0.28	0.35	16.60
MN-54153	Trinomys iheringi	terrestrial	fruit-seed	d	1.06	0.0069	0.34	0.40	0.44	149.42
MN-6451	Trinomys iheringi	terrestrial	fruit-seed	w	1.31	0.0005	0.35	0.29	0.29	1552.28
MN-6453	Trinomys iheringi	terrestrial	fruit-seed	w	0.93	0.0034	0.39	0.52	0.54	1502.47

Supplementary data 4: Intrageneric effect of seasonality on dental microwear texture

Material - The Serra do Mar Atlantic forest (SDMAf) is subjected to a subtropical climate with annual rainfall ranging from 1400 mm to 4000 mm (Mantovani 1993). During winter, rainfall is regular but less abundant than during other seasons thereby generating some seasonality although winter is not a dry period. No data were available for the effect of rainfall variation on the flora of the SDMAf. Date of capture, when available, was used to test whether microwear textures showed seasonal intrageneric differences.

Statistics - We followed the same protocol as the main work to compare dental microwear textures between rainy and dry "seasons" within taxa. Only *Coendou spinosus* and the species within the genus *Trinomys* had sufficient numbers in both seasons to allow analysis. Thus, in each case (*Coendou* and *Trinomys* separately), MANOVAs were performed to assess differences across seasons both on Box-Cox transformed data and Levene's transformed data.

Results - Mean, median, and standard deviation of the mean were calculated for each dental microwear texture parameter by genus and season (Table SD4.1). The MANOVAs on Box-Cox transformed data (*Coendou*, df= 1, p value= 0.97; *Trinomys*, df= 1, p value= 0.92) and the MANOVAs on Levene's transformed data (*Coendou*, df= 1, p value= 0.46; *Trinomys*, df= 1, p value= 0.76) detected no significant differences among species captured in the wet season and those captured in winter (Fig. SD4.1).

Interpretation - Our assessment of the possible effects of "seasonality" on microwear texture of *Coendou* and *Trinomys* did not show significant differences, indicating that variations in diet throughout the year were not sufficient to generate differences in dental microwear textures (Table SD4.1; Fig. SD4.1). Dental microwear records short term (days or weeks) wear (Teaford and Oyen 1989; Schultz et al. 2013). Thus, significant differences in microwear textures would indicate clear differences in seasonal diets. However, the absence of significant differences in dental microwear does not mean the consumed items remain the same throughout the year. It suggests instead that the physical properties of the consumed items do not change from one season to another. There may be year-round availability of analogous items and selection by these species for items displaying the same physical properties. Besides, seasonality in the states of Rio de Janeiro and Sao Paulo is not strongly marked (Mantovani 1993) and its effect on the flora is unknown. In this context, it is not surprising that the seasonality did not heavily affect the studied species.

References

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Figures captions

Figure SD4.1. Boxplots of microwear texture variables for *Coendou* and *Trinomys* by season of capture (wet season in black and winter in grey). A, complexity (Asfc); B, anisotropy (epLsar); C, heterogeneity of complexity (HAsfc9); D, textural fill volume (Tfv).

Table SD4.1.—Descriptive statistics of dental microwear texture parameters for specimens of the genera *Coendou* and *Trinomys* captured in wet season and winter time (when data available). Number of individuals per sample = n; $\bar{X}$ = mean; med = median; sd = standard deviation.

Taxa	Season	n	Asfc			epLsar ($x10^{-3}$)			HAsfc4			HAsfc9			HAsfc16			Tfv		
			$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd	$\bar{X}$	med	sd
Coendou	wet	5	0.38	0.33	0.21	4.97	5.85	3.23	0.30	0.31	0.13	0.37	0.37	0.17	0.37	0.32	0.15	143.61	0	241.04
	winter time	7	0.42	0.43	0.18	3.99	3.07	1.67	0.27	0.22	0.13	0.29	0.28	0.11	0.32	0.32	0.07	138.15	49.81	188.47
Trinomys	wet	13	1.44	1.10	1.19	3.59	3.44	2.25	0.36	0.36	0.09	0.43	0.42	0.13	0.45	0.42	0.16	622.89	444.10	605.60
	winter time	9	1.04	0.87	0.68	4.39	3.63	1.83	0.34	0.28	0.15	0.40	0.39	0.20	0.43	0.41	0.21	302.98	120.36	583.15

Asfc: complexity; epLsar: anisotropy; HAsfc: heterogeneity of complexity calculated from 4, 9 and 16 subsurfaces, respectively; Tfv: textural fill volume.

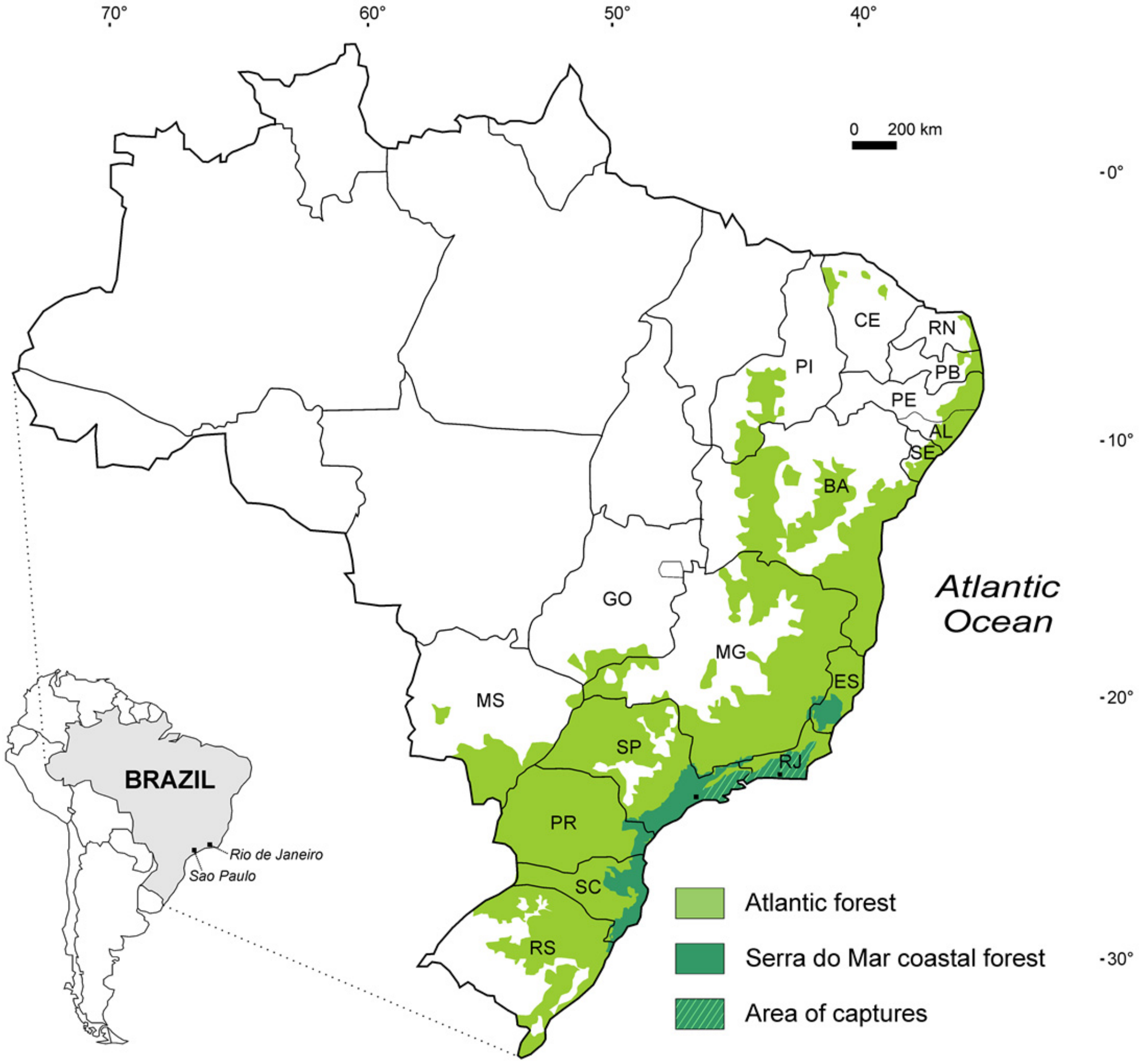

70°
60°
50°
40°
0 200 km
0°
10°
20°
30°
CE
RN
PI
PB
PE
AL
SE
BA
Atlantic Ocean
GO
MG
MS
ES
SP
RJ
PR
SC
RS
BRAZIL
Rio de Janeiro
Sao Paulo
Atlantic forest
Serra do Mar coastal forest
Area of captures

Figure 1

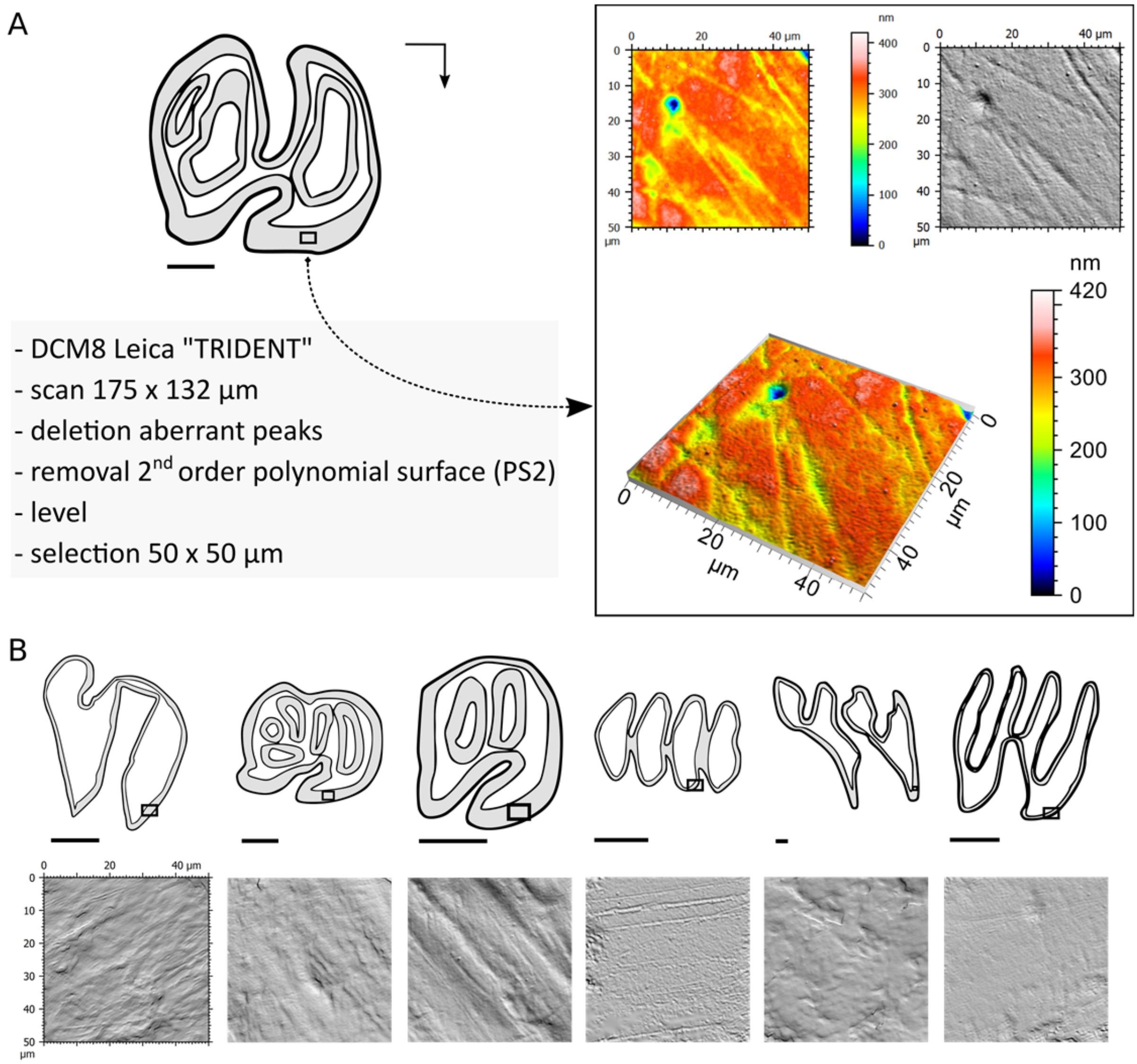

A
- DCM8 Leica "TRIDENT"
- scan 175 x 132 µm
- deletion aberrant peaks
- removal 2nd order polynomial surface (PS2)
- level
- selection 50 x 50 µm
nm
420
300
200
100
0
B

Figure 2

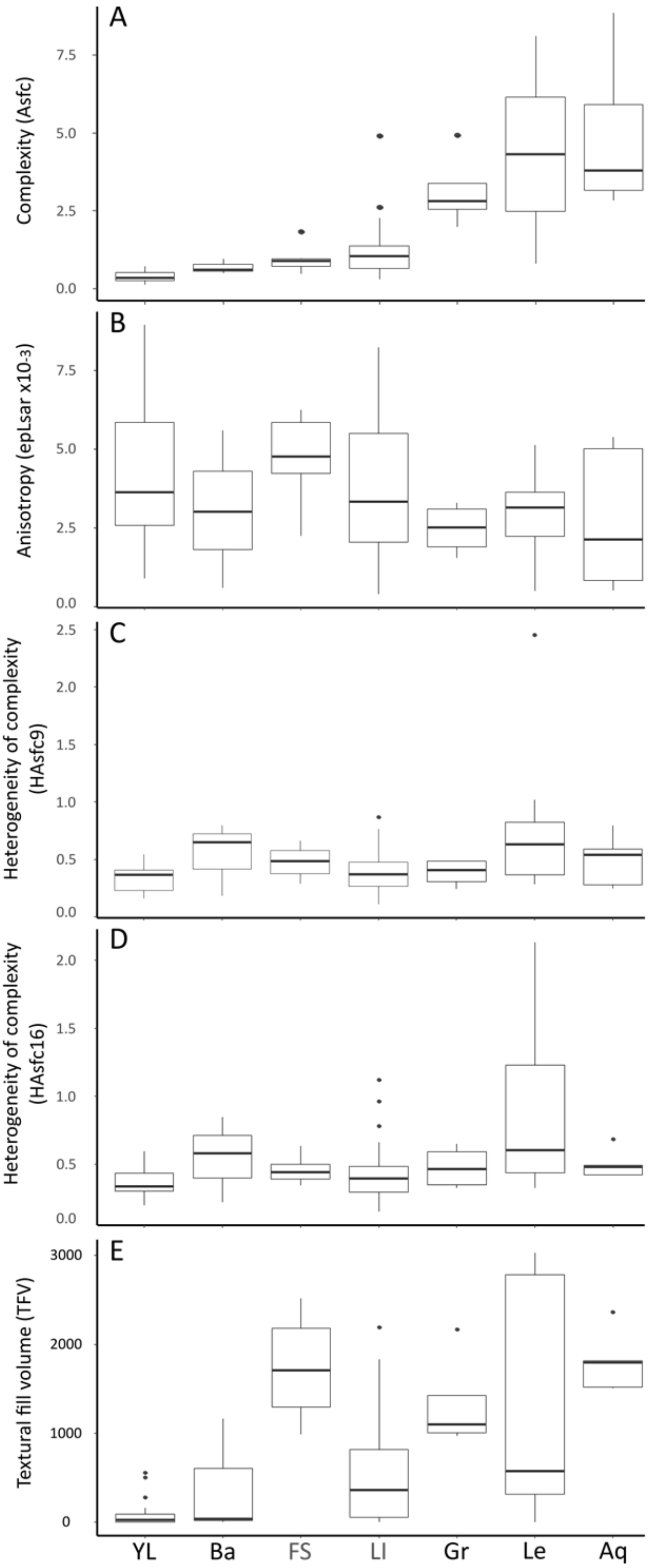
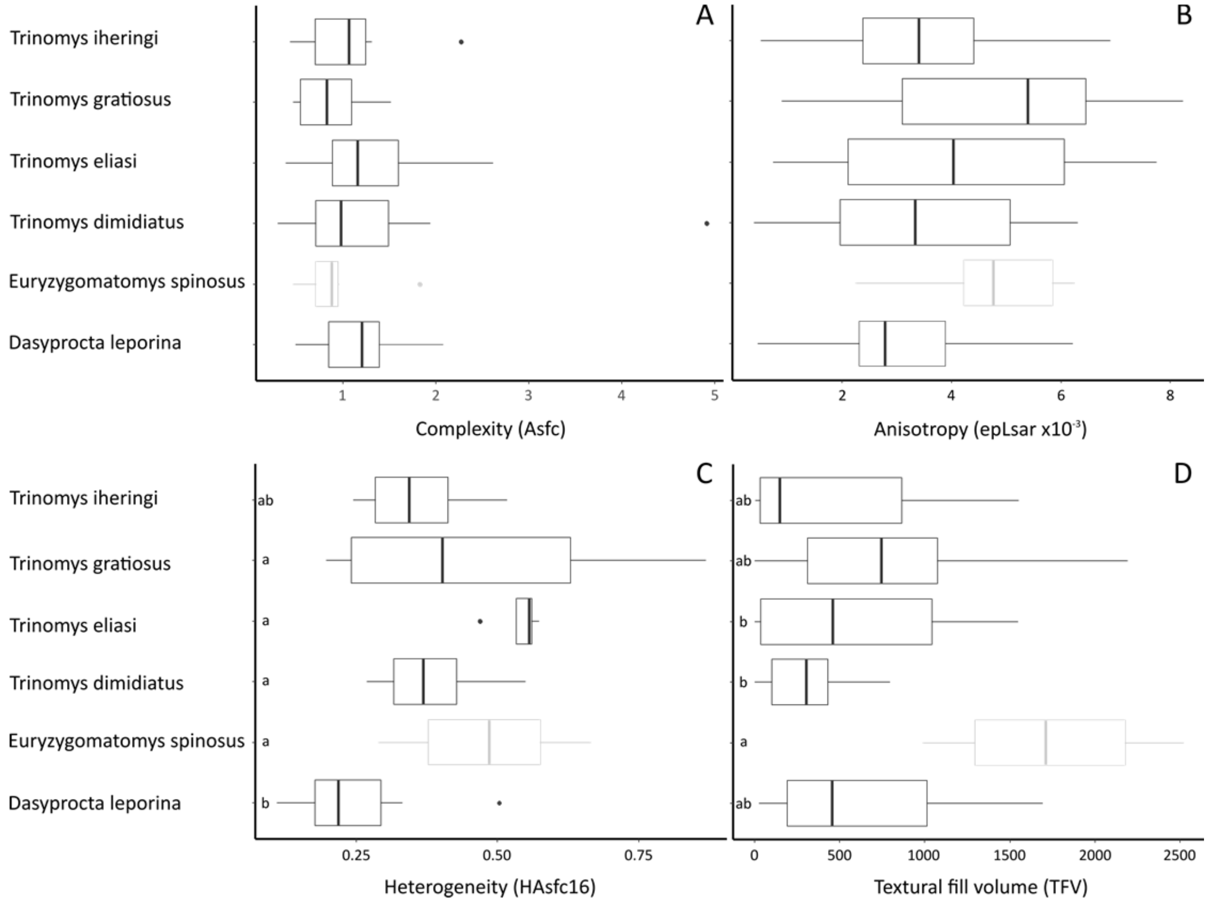

A
B
C
D
E
Complexity (Asfc)
Anisotropy (epLsar x10-3)
Heterogeneity of complexity (HAsfc9)
Heterogeneity of complexity (HAsfc16)
Textural fill volume (TFV)
0.0
2.5
5.0
7.5
0.0
0.5
1.0
1.5
2.0
2.5
0
1000
2000
3000
YL
Ba
FS
Ll
Gr
Le
Aq

Figure 3



A
B
C
D
Trinomys iheringi
Trinomys gratiosus
Trinomys eliasi
Trinomys dimidiatus
Euryzygomatomys spinosus
Dasyprocta leporina
Complexity (Asfc)
Anisotropy (epLsar x10-3)
Heterogeneity (HAsfc16)
Textural fill volume (TFV)

Figure 4

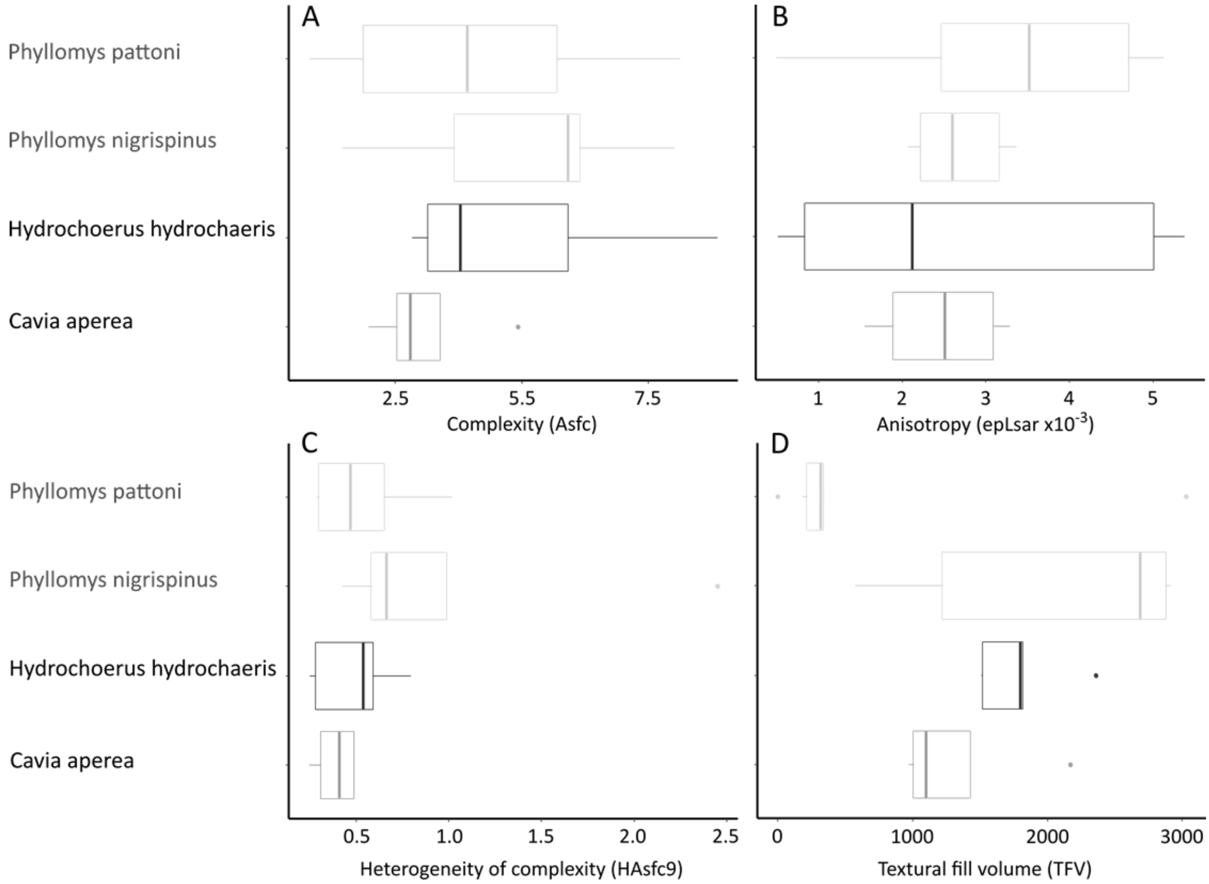

A
B
C
D
Phyllomys pattoni
Phyllomys nigrispinus
Hydrochoerus hydrochaeris
Cavia aperea
2.5
5.5
7.5
Complexity (Asfc)
1
2
3
4
5
Anisotropy (epLsar x10-3)
0.5
1.0
1.5
2.0
2.5
Heterogeneity of complexity (HAsfc9)
0
1000
2000
3000
Textural fill volume (TFV)

Figure 5