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## Temporal dynamics of small mammals in Eucalyptus plantations in Southeast Brazil



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### ABSTRACT

The presence of small terrestrial mammals along the commercial cycle of *Eucalyptus* plantations indicates that silvicultural landscapes can be considered as their habitat. In the present study we evaluated the temporal variation of small terrestrial mammals for more than 10 generations during the first commercial cycle of *Eucalyptus* in Southeast Brazil. During this period we carried out forty-four monthly campaigns, totaling 10,560 bucket.nights in pitfall traps. Thirteen species (four marsupials and nine rodents) were collected in the *Eucalyptus* plantations, seven of which (*Akodon montensis*, *Calomys tener*, *Crytonanus agricolai*, *Gracilinanus microtarsus*, *Necomys lasiurus*, *Oligoryzomys flavescens*, and *Oligoryzomys nigripes*) persisted for the entire study period. In general, they have an explosive population growth during the first two years of collection followed by a decline in all environments, and an apparent regrowth trend in the fourth year for some species with a trend in dominant species from Cerrado to forest dwellers. Marsupials exhibited a similar trend, but slower and later. The spatio-temporal patterns of variation detected in this study strongly suggest that for most of the remaining species of small rodents and marsupials, silvicultural landscapes have distinct habitats including the *Eucalyptus* plantations. This means that they should be evaluated in terms of its habitat quality not only its permeability. The perception of the *Eucalyptus* plantations as habitat should stimulate the development of wildlife-friendly management techniques, which improve their carrying capacity, food web complexity and biological diversity without compromising their primeval mission of biological production.

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## 1. Introduction

Agricultural landscapes support a relevant part of biodiversity despite its numerous negative impacts (Verdade et al., 2014a, 2016). Although fundamental, conservation units (e.g., National Parks, Biological Reserves, etc.) would not be able to provide integral conservation to wild species of fauna and flora even if they worked perfectly, which they do not, even in developed countries (Kroner et al., 2019; Naughton-Treves and Holland, 2019). On the other hand, wild varieties and races of domesticated species of plants and animals, which depend on wild places to be conserved, are among the most threatened taxa of the world (McGowan et al., 2019). Agriculture *lato sensu* depends on them to respond to new pathogens and parasites as well as to environmental changes. Therefore, wildlife depends on agricultural landscapes to be fully conserved, whereas agriculture depends on the wilderness to be effectively sustainable (Verdade et al., 2014a).

However, the distribution of land between agriculture (i.e. biological production) and biodiversity (i.e. biological conservation) has been controversial with some advocating for intensive agriculture apart from conservation areas, whereas others propose conservation areas interspersed in less intensive agricultural landscapes. The former approach has been called “land-sparing”, whereas the latter has been called “land-sharing” (Green et al., 2005). Actually, the geometric difference between them is a matter of scale. For instance, local land-sparing properties may be interspersed on a land-sharing landscape or region (Kremen, 2015). In addition, local ecological history (*sensu* Balée, 2014) may have resulted in one or another system for historical and circumstantial reasons, not strictly for technical purposes. For instance, in USA the Land Act established in 1820 resulted in predominantly land-sparing landscapes during the post-European colonization towards the West (Gordon, 2002). On the other hand, in Brazil the Forest Code (established in 1934 and actualized many times since then) determined that each property must keep a certain percentage of native vegetation (primarily forests), which resulted in a land-sharing public policy (Metzger et al., 2010). To be effective, such approach depends on the assumption of agricultural landscapes multifunctionality (Martinelli et al., 2010), in which they keep biological production as their primary mission, and biological conservation as their secondary – yet fundamental – mission (Verdade et al., 2014a).

Forestry is possibly one of the most advanced agro-industrial sectors in Brazil in terms of environmental certification, predominantly led by the Forest Stewardship Council (FSC, Araujo et al., 2009). After a fast and strong period of deforestation in the former Atlantic Forest, *Eucalyptus* trees have been introduced in Southeast Brazil in the late 1800s to provide charcoal to an increasing industry, and prevent an even more massive destruction of the Atlantic Forest (Dean, 1996). After an intensive and successful program of plant breeding, adapted varieties of *Eucalyptus* currently cover approximately 5 million ha (Embrapa, 2020), and produce paper, cellulose and pulp for national and international market, and charcoal for local consumption.

The commercial expansion of *Eucalyptus* plantations in Southeast Brazil was carried out since the 1970's predominantly over former pastures (Lisboa and Prado, 2019). Under such circumstances, approximately 70% of the original medium to large species of terrestrial mammals (Dotta and Verdade, 2007, 2011; Timo et al., 2015), 60% of the species of birds (Penteado et al., 2016), and a relevant diversity of amphibians (Lopes et al., 2016) and stream fish (Gerhard and Verdade, 2016) can still be found in silvicultural landscapes dominated by *Eucalyptus* plantations in Southeast Brazil.

Small terrestrial mammals are among the group that lost more species under such land use, with only approximately 20% of the original species remaining (Gheiler-Costa et al., 2012; Martin et al., 2012). However, small terrestrial mammals are the basis of the food web in agricultural/silvicultural landscapes in Southeast Brazil (Verdade et al., 2011), supporting the original mesopredators (e.g., canids and small to middle-sized felids) (Murray and Gardner, 1997; Juarez and Marinho-Filho, 2002; Wang, 2007; Dotta and Verdade, 2009). Such novel – and likely simpler – food web can lead to new selective pressures on both prey and predators (Rosalino et al., 2013, 2014).

In general, sampling processes occur at small term, ecological processes at medium term, and evolutionary processes at long term (Preston, 1960). However, most biodiversity studies are short to medium term, but with time as a dimension simply smashed for the sake of simplicity (Magnusson and Mourão, 2005). This can be particularly problematic in agricultural/silvicultural landscapes, where the plantation can have a commercial cycle of years or even decades (e.g., FAO, 2020). In such circumstances, temporal heterogeneity can be as relevant a driver of biodiversity patterns as spatial heterogeneity (e.g., Holt, 2008; Verdade et al., 2006; Timo et al., 2015).

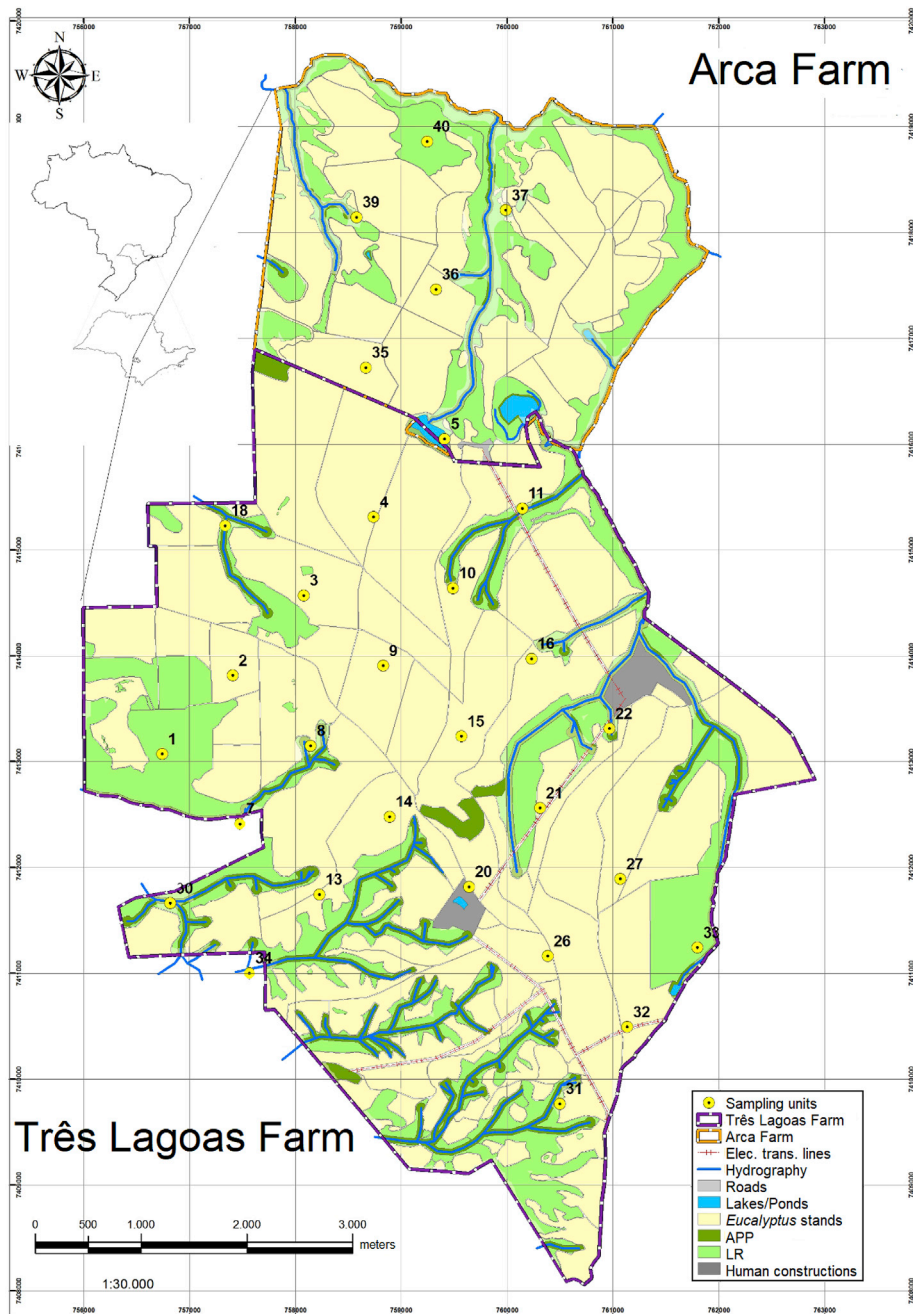
The presence of small terrestrial mammals along the commercial cycle of *Eucalyptus* plantations would indicate that silvicultural landscapes can be considered as their habitat, since the present study covers more than 10 generations time, i.e., two to three generations per year (Strong and Johnson, 1965; Pacifici et al., 2013). We therefore consider the occurrence of terrestrial small mammals at the *Eucalyptus* plantations along generations as evidence that it is habitat for those species. In such context we established the following null hypotheses: (i) *Eucalyptus* plantations do not support resident populations of small terrestrial mammals along its commercial cycle (six to seven years); and (ii) there is no variation in the pattern of intra- or inter-specific temporal dynamics between the *Eucalyptus* plantations and other silvicultural landscape environments.

## 2. Study area

This study was carried out at farms Três Lagoas (3242 ha; 23°22'0" – 23°20'41"S/48°28'0" – 48°27'57"W) and Arca (1123 ha; 23°20'0" – 23°18'5"S/48°27'30" – 48°28'20"W), in Angatuba municipality, located in Alto Paranapanema water basin, São Paulo State, Southeast Brazil (Fig. 1). The native vegetation of the study area is formed by a transitional zone between semi-deciduous Atlantic Forest and Cerrado, which was almost completely replaced by coffee and cotton plantation

between 1870 and 1930. After the great economic crash of 1929 and the consequent decline of the local agriculture, native vegetation recovered to a second growth vegetation which, by its turn, was deforested in the 1970s, in order to implant exotic pasture for livestock production (Lisboa and Prado, 2019).

Between August 2006 and November 2007, 2224 ha of the exotic pasture in Fazenda Três Lagoas were converted into *Eucalyptus* plantations, and the remaining area was abandoned for natural revegetation forming legal conservation areas (896 ha), according to the Brazilian Environmental Law. A similar process occurred a little later in Fazenda Arca (September 2007–May 2008), resulting in 722 ha of *Eucalyptus* plantations and 361 ha of legal protection areas. Then, from August 2006 to May 2008 in both farms combined 2946 ha of *Eucalyptus* plantations have been established and 1257 ha have been preserved as Areas of Permanent Protection (APP) and Legal Reserve (LR), according to the Brazilian Forest Code (Metzger et al., 2010).



**Fig. 1.** Study area. Fazenda Arca and Fazenda Três Lagoas, Angatuba municipality, state of São Paulo, Brazil.

*Eucalyptus* stands were composed by *Eucalyptus urophila*, *E. grandis* and its hybrid *E. urograndis*, and sparsed native trees (*Copaifera langsdorffii*, *Gochnatia polymorpha*, *Machaerium villosum*, *Pera obovata*, *Pterogyne nitens*, *Tabebuia alba*) which were kept during the deforestation in the 1970s as well as in the *Eucalyptus* plantation in 2006–2008. The APP and LR were composed by second growth fragments of riparian forest (dominated by *Calophyllum brasiliense*, *Gymnanthes concolor*, *Nectandra megapota mica*, *Sorocea bonplandii*, *Bauhinia* sp., *Croton floribundus* and *Piptocarpha gonoacantha*), Cerrado *strictu sensu* (dominated by *Anadenanthera falcata*, *Caryocar brasiliensis*, *Dimorphandra mollis*, *Stryphnodendron adstringens* and *Roupala brasiliensis*), “cerradão” (dominated by *Xylopia brasiliensis*, *Miconia chatacea*, *Tapirira guianensis*, *Amaioua guianensis*, *Siparuna guianensis*, *Persea pyrifolia*, *C. langsdorffii*, *P. obovata*, *M. villosum*), and patches of abandoned pasture (composed by Asteraceae, Fabaceae, Melastomataceae, Solanaceae and Verbeceae species, *Pteridium aquilium* and African grass *Urochloa* spp.) (Athayde et al., 2015) (Fig. 2).

According to Köppen, the region climate is subtropical with mean temperature ranging from 17 °C to 22 °C along the year. During the whole study period (from August 2007 to August 2011) the mean temperature was 20.5 °C, whereas the average monthly cumulative rain varied between 113 mm and 152.65 mm (Source: Itatinga Forestry Science Experimental Station – Escola Superior de Agricultura “Luiz de Queiroz”, Universidade de São Paulo).

### 3. Methodology

#### 3.1. Sampling methodology

The sampling design used in this study is an adaptation of the Biodiversity Research Program (PPBio) methodology, which is based on a grid design, with each grid nodule separated 1 km from each other. This sampling protocol consists of 30 sampling units encompassing the three landscape components: native vegetation patches (N = 7; 17.6% of the study area; 550ha), abandoned exotic pasture (N = 5; 11.1%; 346ha) and *Eucalyptus* plantations (N = 18; 67.7%; 2220ha), varying from zero to approximately 900m from the plantation border.

The sampling comprised three distinct stages during the first cycle of the local *Eucalyptus* plantation. The first stage (from August 2007 to July 2009) corresponds to the early-cycle, whereas second (from August 2009 to August 2010) and third stages (from January 2011 to August 2011) correspond to mid-cycle of the *Eucalyptus* plantation. During these periods we carried out forty-four monthly campaigns with two nights per campaign in 30 sampling units with four buckets per sampling unit (Y-shaped with four 100 L buckets, one in the end each 15 m branch and one in the middle), totaling 10,560 bucket.nights (6336 in *Eucalyptus* plantations, 2464 in native vegetation and 1760 in abandoned pastures). The buckets were completely buried and connected to each other by a plastic net 80 cm high and buried 10 cm deep. All buckets had small holes, to allow rain drainage, a water container and a piece of Styrofoam to prevent animals' dehydration and drowning, respectively. Traps were active for two consecutive nights and checked every morning. Captured animals were identified to the species level, measured, weighted, sexed and marked with microchips and then released at the capture site (as described in Martin et al., 2012).

#### 3.2. Analytical methodology

Capture success was considered the number of individuals captured divided by the sampling effort (per environment and total) in percentage. Species abundance counts were analyzed using generalized linear mixed Poisson models, including a different smoothing function over time per species and landscape environment combination, the natural logarithm of the number of samples as an offset term, and an observation-level random effect to account for overdispersion (Demétrio et al., 2014), using the lme4 package (Bates et al., 2015). We used B-spline basis functions with three degrees of freedom for the smoothers to capture the nonlinear behavior over time. Species that presented very sparse counts and no clear temporal trend were excluded from the analysis. We tested differences between curves using likelihood-ratio (LR) tests for nested models and assessed goodness-of-fit using half-normal plots with simulation envelopes, using the hnp package (Moral et al., 2017).



Fig. 2. Environments found in the silvicultural landscape of the present study (A. *Eucalyptus* plantations; B. Abandoned pastures; C. Native vegetation).

We then obtained the predicted abundances from the fitted models for each individual species at each landscape environment and computed the Pearson correlation coefficient matrices and compared with the ones obtained using the raw data. Finally, we performed a principal components analysis and generated a biplot to check for possible evidence suggesting that species move from one environment to the other during the ageing of the *Eucalyptus* plantation.

All analyses were carried out using R software (R Core Team, 2018) and all plots produced using the ggplot2 package (Wickham, 2016). All code and data are made available as Suppl. Material.

#### 4. Results

A total of 2267 individuals from 16 species (11 rodents and five marsupials) were collected. The overall sampling success was 21.5%, varying between 1.1% and 1.7% (respectively at abandoned pastures and *Eucalyptus* plantation) for marsupials, and between 14% and 35.3% (respectively for *Eucalyptus* plantation and abandoned pastures) for rodents (Table 1). Only three species (*Oligoryzomys flavescens*, *O. nigripes* and *Calomys tener*) represented 77.6% (1760/2267) of all captures (Fig. 3). Recaptures varied from 9% at first stage to 0.9% at the second and 0.7% at the third stage.

*Eucalyptus* plantations respond for most of the variation in the first principal component, whereas the pasture does so for the second at PCA (Fig. 4). However, there is no evidence suggesting that species move from one environment to the other during the ageing of the *Eucalyptus* plantation. In addition, *G. microtarsus* is the most negatively associated species with *C. tener* and *C. agricolai*, which informs an asynchronous dynamic across all environments (Fig. 5). Finally, there is a positive association between *N. lasiurus*, *C. tener* and *O. flavescens*, and between *A. montensis* and *O. nigripes*, suggesting a synchronous dynamic within these two groupings.

Nine species (*Didelphis albiventris*, *D. aurita*, *Juliomys pictipes*, *Oxymycterus* sp., *Rattus rattus*, *Nectomys squamipes*, *Cerradomys subflavus*, *Cavia aperea* and *Monodelphis kunsii*) presented a low number of individuals (49) along the study period (Fig. 3) without a clear temporal pattern. Hence, these species were not included in the modelling (see Suppl. Materials for the full dataset). Thirteen species (four marsupials and nine rodents) were collected in the *Eucalyptus* plantations, seven of which (*Akodon montensis*, *Calomys tener*, *Cryptonanus agricolai*, *Gracilinanus microtarsus*, *Necomys lasiurus*, *Oligoryzomys flavescens*, and *Oligoryzomys nigripes*) persisted for the entire study period (see Suppl. Materials). Therefore, we reject our first null hypothesis that the *Eucalyptus* plantations do not support resident populations of small mammals.

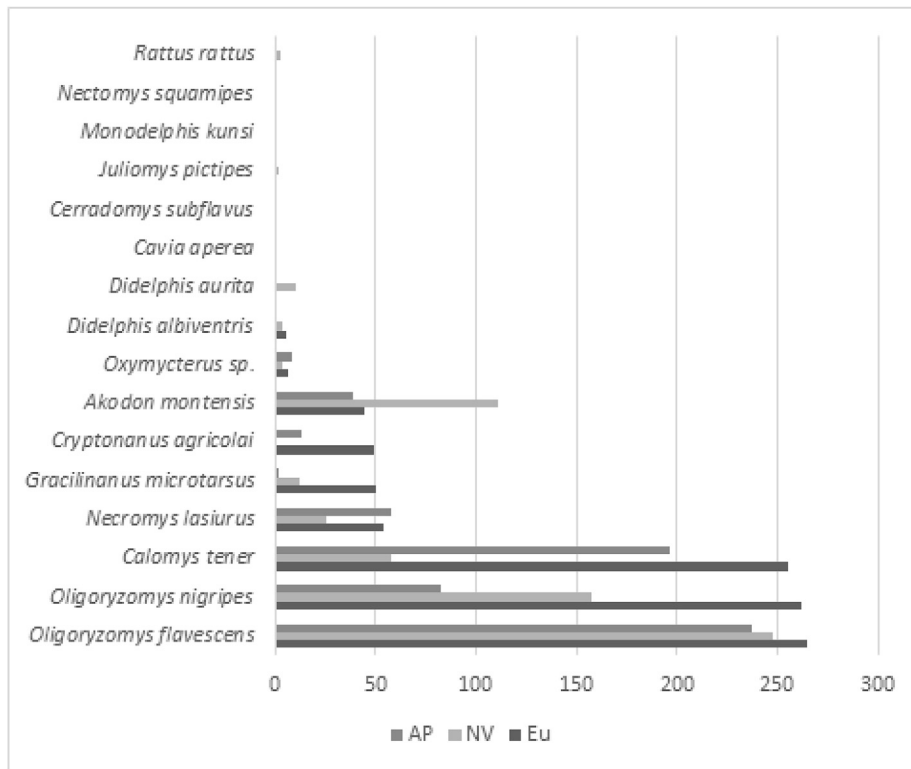
In general, there was an explosive population growth during the first two years of collection followed by a decline in all environments, and an apparent regrowth trend in the fourth year for some species. Some of the rodents presented a dramatic early growth while marsupials exhibited a similar trend, but slower and later. Within the rodents, the predominant species are *O. flavescens*, *C. tener*, *O. nigripes*, and *A. montensis*. *Necomys lasiurus* is also relatively abundant in native vegetation and pasture, with the same population trend, but smaller growth (Fig. 4).

There were differences between the temporal patterns for the species within each of the environments (Table 2a). Looking in isolation into each species, *C. agricolai*, *A. montensis* and *O. nigripes* exhibited different temporal patterns in each

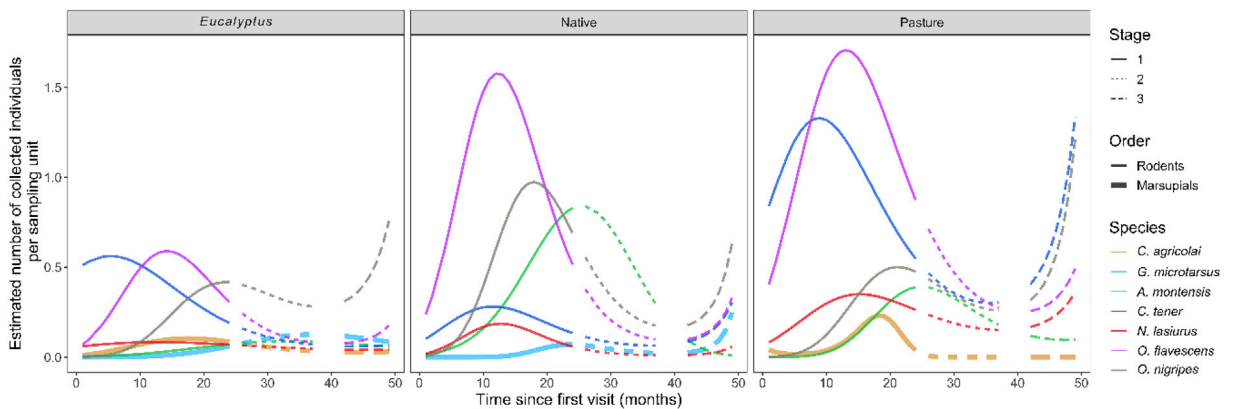
**Table 1**

Total number of collected marsupial and rodent species per environment, and total marginal counts. Sampling units: *Eucalyptus* plantations (N = 18), native vegetation (N = 7) and abandoned pasture (N = 5).

Order	Species	<i>Eucalyptus</i>	Native vegetation	Pasture	Total
Marsupialia	<i>Cryptonanus agricolai</i>	49	1	13	63
	<i>Didelphis albiventris</i>	5	4	0	9
	<i>Didelphis aurita</i>	1	10	0	11
	<i>Gracilinanus microtarsus</i>	50	12	2	64
	<i>Monodelphis kunsii</i>	0	0	1	1
	Total	105	27	16	148
	No. of captures/No. of sampling units	5.8	3.9	3.9	4.9
	Sampling success (%)	1.7	1.1	0.9	1.4
Rodentia	<i>Akodon montensis</i>	44	111	39	194
	<i>Calomys tener</i>	255	58	196	509
	<i>Cavia aperea</i>	1	0	0	1
	<i>Cerradomys subflavus</i>	1	0	1	2
	<i>Juliomys pictipes</i>	1	2	0	3
	<i>Necomys lasiurus</i>	54	25	58	137
	<i>Nectomys squamipes</i>	0	1	0	1
	<i>Oligoryzomys flavescens</i>	265	248	237	750
	<i>Oligoryzomys nigripes</i>	262	157	82	501
	<i>Oxymycterus</i> sp.	6	4	8	18
	<i>Rattus rattus</i>	0	3	0	3
	Total	889	609	621	2119
		No. of captures/No. of sampling units	49.4	87	124.2
	Sampling success (%)	14	24.7	35.3	20.1



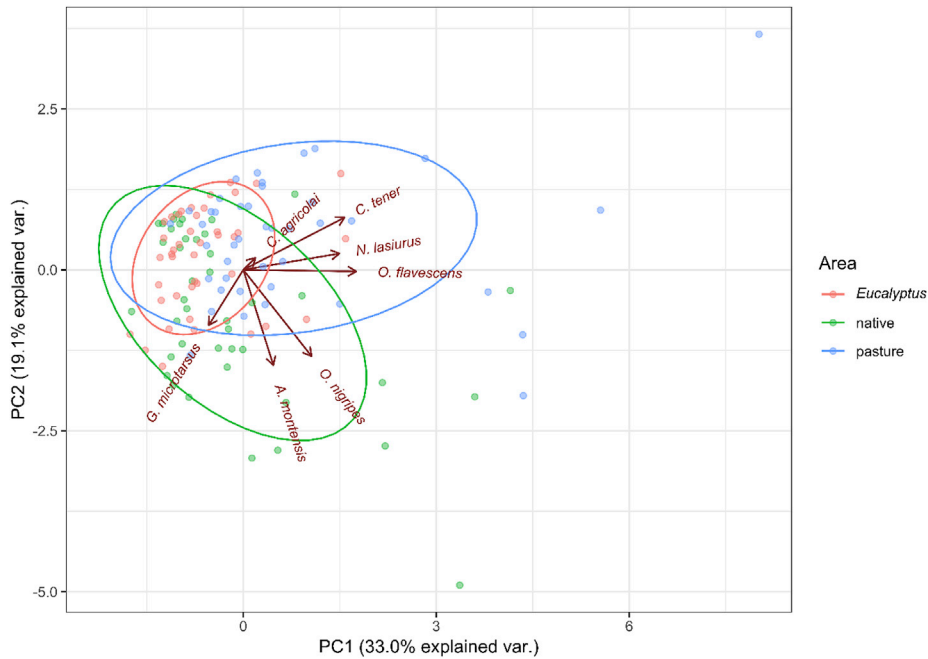
**Fig. 3.** Predicted number of collected individuals per sample for the rodent and marsupial species data over time in each environment. Each species is plotted with a different color, the thicker lines represent marsupial species, and each sampling stage is represented with a different line type (stage 1: continuous, stage 2: dotted, stage 3: dashed).



**Fig. 4.** Biplot of the principal component analysis of the species count data per environment. The three stages have been described at sampling methodology session.

environment (Table 2b). Therefore, we also reject our second null hypothesis. Moreover, *C. tener*, *N. lasiurus* and *O. flavescens* presented the same temporal patterns, but different abundances in each environment, while *G. microtarsus* presented both the same temporal pattern and abundance in all environments (Table 2b).

When comparing the relationship between the species' predicted abundances in different environments, we observed that while in *Eucalyptus* plantation the *O. nigripes*'s population growth was delayed when compared to *N. lasiurus* and *C. tener*, in native vegetation these patterns are synchronized (Fig. 6, bottom panels). We also observed a similar pattern change when looking at these relationships for the pasture environment. Other relationships are weaker, i.e., patterns are changing from synchronous to asynchronous (and vice-versa) when the environment changes (Fig. 6, bottom panels). Therefore, there is an



**Fig. 5.** Barplots of the total number of specimens collected for each species in each environment throughout the entire sampling period. AP: Abandoned pastures; NV: Native vegetation; Eu: *Eucalyptus* plantations (x-axis: No. of captured individuals; y-axis: species of small mammals).

**Table 2**

Likelihood-ratio (LR) test statistics, associated number of degrees of freedom and p-values for assessing the effects of (a) time, species, and their interaction within each of the three environments (*Eucalyptus*, native vegetation and pasture), and (b) time, area, and their interaction within each of the seven species of rodents and marsupials whose spatio-temporal patterns were analyzed (*C. agricolai*, *G. microtarsus*, *A. montensis*, *C. tener*, *N. lasiurus*, *O. flavescens*, and *O. nigripes*).

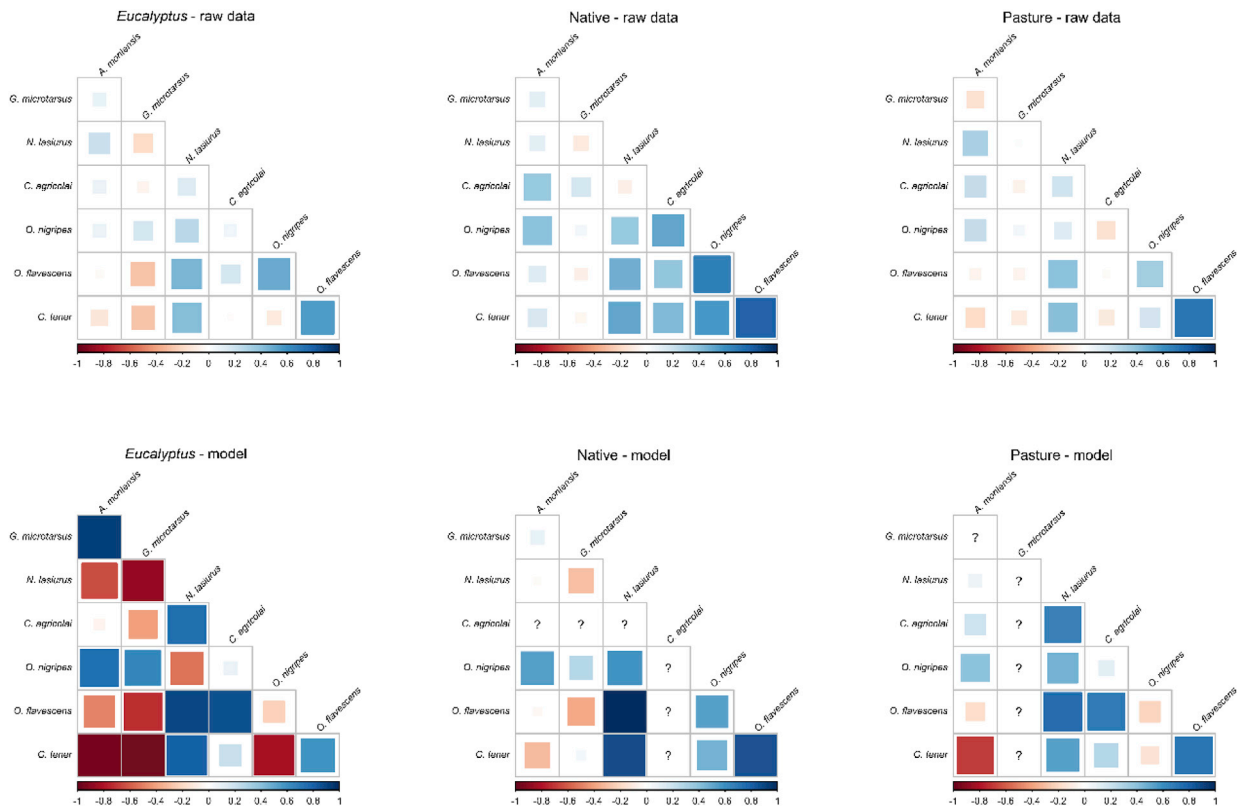
(a) Effect	Area		
	<i>Eucalyptus</i>	Native vegetation	Pasture
Time x Species	LR = 117.41, d.f. = 18, p < 0.0001*	LR = 81.05, d.f. = 18, p < 0.0001*	LR = 66.91, d.f. = 18, p < 0.0001*
Species	LR = 90.95, d.f. = 6, p < 0.0001*	LR = 153.6, d.f. = 6, p < 0.0001*	LR = 167.80, d.f. = 6, p < 0.0001*
Time	LR = 13.29, d.f. = 3, p = 0.0040*	LR = 44.05, d.f. = 3, p < 0.0001*	LR = 22.40, d.f. = 3, p < 0.0001*
(b) Species	Area		
	Effect Time x Area	Area	Time
<i>C. agricolai</i>	LR = 9.26, d.f. = 3, p = 0.0260*	LR = 0.55, d.f. = 1, p = 0.4581	LR = 15.11, d.f. = 3, p = 0.0017*
<i>G. microtarsus</i>	LR = 5.14, d.f. = 3, p = 0.1615	LR = 1.50, d.f. = 1, p = 0.2202	LR = 30.56, d.f. = 3, p < 0.0001*
<i>A. montensis</i>	LR = 18.12, d.f. = 6, p = 0.0059*	LR = 21.46, d.f. = 2, p < 0.0001*	LR = 54.74, d.f. = 3, p < 0.0001*
<i>C. tener</i>	LR = 10.23, d.f. = 6, p = 0.1153	LR = 43.79, d.f. = 2, p < 0.0001*	LR = 37.47, d.f. = 3, p < 0.0001*
<i>N. lasiurus</i>	LR = 6.57, d.f. = 6, p = 0.3623	LR = 23.31, d.f. = 2, p < 0.0001*	LR = 10.12, d.f. = 3, p = 0.0176*
<i>O. flavescens</i>	LR = 3.68, d.f. = 6, p = 0.7198	LR = 24.61, d.f. = 2, p < 0.0001*	LR = 66.28, d.f. = 3, p < 0.0001*
<i>O. nigripes</i>	LR = 13.13, d.f. = 6, p = 0.0410*	LR = 2.74, d.f. = 2, p = 0.2537	LR = 59.12, d.f. = 3, p < 0.0001*

effect of the environment in the synchronicity of the population dynamics of these species, which also rejects our second null hypothesis.

Last but not least, along the study period there was no edge effect for the species that used the *Eucalyptus* plantations, at least for the spatial scale used (i.e.,  $\leq 1$  km from the plantation edge) (Regression equations:  $r^2_{\text{adj}} < 0.1$ ,  $p > 0.1$ ,  $df = 17$  for the whole study period). This pattern suggest that such species use indeed *Eucalyptus* plantations as residents.

## 5. Discussion

Most of the species detected on this study (approx. 81%, 13/16) have been found in the *Eucalyptus* plantations. A bit more than half of that (approx. 54%, 7/13) persisted for the whole study period, which comprises most of the first commercial cycle of *Eucalyptus* plantations. Therefore, they can be considered as residents of the silvicultural landscape, including *Eucalyptus* plantations, for more than 10 generations.



**Fig. 6.** Correlation matrices for the observed (top panels) and predicted (bottom panels) spatio-temporal species abundances in each of the three environments. There are no correlation for the abundance predictions for *C. agricolai* and *G. microtarsus* in native vegetation and pasture, respectively (represented as “?” in the plots), since the individual counts for these species in these areas are very sparse and present no clear temporal pattern (total number of collected individuals = 3).

Sampling success was much higher for rodents (14–35.3%) than for marsupials (0.9–1.7%), which is compatible with their relative abundance in silvicultural landscapes of Southeast Brazil, where small rodents are considerably more abundant (e.g., Gheler-Costa et al., 2012). However, the present sampling success of these rodents are higher than comparable studies (e.g., Umetsu et al., 2006). In pitfall trapping this is likely related to high densities and/or high dispersion as no baits are used. The higher capture rate at the early cycle than later suggest the dispersion (possibly higher following land use change) may be relevant. By hypothesis, a further decrease in sampling success and recapture rate may be related to a decrease in abundance as *Eucalyptus* trees grow.

The most abundant species (*O. nigripes*, *O. flavescens* and *C. tener*) are generalist small rodents from Cerrado and the ecotone between it and the Atlantic Forest (Eisenberg and Redford, 1999; Weksler and Bonvicino, 2005). They appear to have been adapting to land use change in Southeast Brazil (Vieira and Marinho-Filho, 1998), which have been occurring in the last Century: second-growth forest (from 1930's to 1970's) to pasture of exotic grass (from 1970's to 2000's) to *Eucalyptus* plantations (since 2000).

Species abundance data are very noisy, and it is difficult to see the main changes in the relationships between them in different environments (Fig. 4, top panels; Suppl. Materials). However, the fitted models generated predicted species abundances that are useful to uncover the underlying temporal patterns, thus revealing a plausible true signal of the ecological processes driving the changes in abundance. However, asynchrony among these species suggest that they likely differ in terms of resource use along the production cycle of *Eucalyptus* plantations and the concomitant revegetation process occurring in abandoned pastures (i.e., after livestock exclusion due to *Eucalyptus* implantation).

Difference in overall abundance and its temporal variation between small rodents and marsupials may be related to differences in their life strategy. Small marsupials invest significantly more energy in parental care than rodents (Hopson, 1973). In addition, their slower growth rate and less investment in progeny make them k-selected species, whereas the fast growth and higher investment in reproduction make the small rodents r-selected species (Pianka, 1970; Engen and Sæther, 2017).

In small rodents the likely key process for such asynchrony is a possible combination between the relatively lower spatial heterogeneity but higher temporal heterogeneity of *Eucalyptus* plantations in relation to the remnant native vegetation and



abandoned pastures. Such spatial-temporal variation in agricultural/silvicultural landscapes might be mostly related to the distinct pulses of biomass production (and extraction) between productive and non-productive areas (Holt, 2008).

These rodents are relevant prey for Neotropical mesopredators, which possibly explains their diversity in agricultural/silvicultural landscapes (Verdade et al., 2011). However, they are also potential pests for agriculture (Fischer and Schroder, 2014) and host for emerging infectious diseases (Gheler-Costa et al., 2013). Therefore, their role on the human modified environments should be pursued. In such context, the complexity of their trophic process should be evaluated in future studies as an ecological indicator of the conservation value of agricultural/silvicultural landscapes (Verdade et al., 2014a). Remote sensing estimates of biomass might possibly allow its use as a proxy of small rodents' diversity in regional scale. In addition, the relatively low cost of diet analyses based on traditional triage (Klare et al., 2011) and DNA analyses (Pompanon et al., 2012) might allow its use as an index of biocomplexity in local scale (e.g., a conservation unit).

The spatial-temporal patterns of variation detected on this study strongly suggest that for most of the remaining species of small rodents and marsupials, silvicultural landscapes present distinct habitats including the *Eucalyptus* plantations during their commercial cycle. However, these habitats vary not only in space but also in time, in especial the *Eucalyptus* plantations themselves due to the trees' fast growth. At the beginning, *Eucalyptus* trees are still relatively small, which gives the plantation an open habitat characteristic. During this period, the Cerrado species of small rodents (i.e., *O. flavescens* and *Calomys tener*, according to Talamoni et al., 2008) are dominant. However, as the *Eucalyptus* trees grow *O. nigripes* replaces them as the dominant species. *O. nigripes*, is predominantly a forest dweller (Machado et al., 2013). Thus, it can benefit from both the fast growth of *Eucalyptus* trees and the revegetation process of the native vegetation, faster in the forest than in Cerrado areas (Athayde et al., 2016).

By the point of view of the ecology and conservation of small mammals *Eucalyptus* plantations in southeast Brazil should be evaluated in terms of habitat quality not only permeability (e.g., Wiens, 1996; Driscoll, 2005; Estavillo et al., 2013; Boesing et al., 2018). However, the abundance decrease suggested by the decrease in captures and recaptures of small mammals suggest that such habitat quality decreases along the first commercial cycle of *Eucalyptus* plantations. On one hand, this adds a bit more uncertainties to the concept of habitat itself (Hall et al., 1997; Mitchell, 2005). On the other hand, it gives us the chance to measure (i.e., quantify) the resources that determine its quality to the resident species (Morrison et al., 1992; Garshelis, 2000; Anderson and Gutzwiller, 2005), like the small rodents of the present study. In such context, it may be tempting – and tricky! – to estimate its carrying capacity for them or other species in real world (Robinson, 1989: 49–50; Caughley and Sinclair, 1994: 117–118; Chapman and Byron, 2018). However, their role in local food web suggest that future studies should explore these conceptual and applied uncertainties in order to better understand and manage multifunctional agricultural/silvicultural landscapes (Hurst et al., 2014).

The possible relationship between agricultural/silvicultural management techniques (e.g., Gheler-Costa et al., 2013) as well as intensification and land use change (e.g., Verdade et al., 2015) should be prioritized in future studies. In addition, the distinct temporal heterogeneity of biomass pulse (e.g., Holt, 2008) between the *Eucalyptus* plantations and the native vegetation might mimic a feast-famine process in small mammals and their predators in agricultural/silvicultural landscapes, which should be considered also by future studies on both biological production and conservation (Verdade et al., 2014b).

Last but not least, the perception of *Eucalyptus* plantations as habitat of some species like explicitly suggested by the present results and previous studies (e.g., Millan et al., 2015; Timo et al., 2015) should stimulate the development of wildlife-friendly management techniques. Such techniques might allow improvement of agricultural/silvicultural habitats (including the plantations themselves) quality and the consequent enhance on their carrying capacity, food web complexity and biological diversity without compromising their primeval mission of biological production.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01217>.

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