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A simple graphical model of small mammal succession after fire in the Brazilian cerrado

Un modèle graphique simple de repeuplement par les petits mammifères du cerrado brésilen après brûlis

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Abstract

We studied the succession of small mammal species after fire in the cerrado (Neotropical savanna) of Central Brazil. Populations of small mammals were sampled with live-trapping techniques in a series of nine sites of different successional age, ranging from 1 to 26 years after fire. Ten species of small mammals were captured through all the seral stages of succession. Species richness ranged from two to seven species by seral stage. The species were arranged in different groups with respect to abundance along the succession: the first was composed of early successional species that peaked <2 years after fire (*Calomys callosus, C. tener, Thalpomys cerradensis, Mus musculus, Thylamys velutinus*); the second occurred or peaked 2–3 years after fire (*Necromys lasiurus*, *Gracilinanus* sp., *Oryzomys scotti*). *Gracilinanus agilis* peaked in the last seral stage. Species richness of small mammals showed an abrupt decrease from an average of four species immediately after fire to two species 5–26 years after the last fire. We propose a simple graphical model to explain the pattern of species richness of small mammals after fire in the cerrado. This model assumes that the occurrence of species of small mammals is determined by habitat selection behavior by each species along a habitat gradient. The habitat gradient is defined as the ratio of cover of herbaceous to woody vegetation. The replacement of species results from a trade-off in habitat requirements for the two habitat variables.

Keywords: Brazil; habitat selection; marsupials; model; rodent; savanna; species richness.

Résumé

Nous avons étudié le repeuplement par les petits mammifères du cerrado (Savane néotropicale) du Brésil Central après brûlis. Les animaux ont été piégés dans neuf sites variant par leur dernière date de brûlis (entre de 1 à 26 ans). Dix espèces de petits mammifères ont été capturées dans l'ensemble des sites. Cette richesse spécifique a variée de deux à sept; avec cinq espèces dans le site de 2 ans (*Calomys callosus, C. tener, Thalpomys cerradensis, Mus musculus, Thylamys velutinus*) et trois dans celui de 3 ans (*Necromys lasiurus*, *Gracilinanus* sp., *Oryzomys scotti*). L'espèce *Gracilinanus agilis* a été piégée dans la parcelle la plus ancienne. Le nombre de petits mammifères a décru en moyenne de quatre espèces immédiatement après le brûlis, puis de deux espèces entre 5 et 26 ans plus tard. Nous avons proposé un modèle graphique simple pour expliquer les patterns de la richesse spécifique après le feu dans le cerrado. Ce modèle suppose que la pression de selection dûe à l'habitat agit sur la la réapparition/reproduction des espèces de petits mammifères par un gradient de reconstitution du milieu ambiant (gradient ambiant). Ce gradient ambiant est défini comme le rapport entre la surface de couverture herbacée et la couverture ligneuse de la végétation. La reproduction/reconstitution des espèces résulte d'une relation inverse entre ces deux variables de l'habitat.

Mots cles: Brésil; marsupiaux; modèle; richesse spécifique; rongeurs; Savane; selection de l'habitat.

Introduction

Fire can profoundly alter the composition and structure of small mammal communities (Whelan 1995). The subsequent patterns of successional changes in small mammals show a strong dependence on both structural and floristic components of vegetation (Beck and Vogl 1972, Krefting and Ahlgren 1974, Atkeson and Johnson 1979, MacMahon 1981, Huntly and Inoue 1987). Fox (1982) compared previous successional models (e.g., Connell and Slayter 1977) against an observed pattern of small-mammal secondary succession after fire, but these models did not state the mechanisms by which all species enter and leave the succession. An alternative model (accommodation model) was proposed by Fox (1982), in which species responses are externally controlled by vegetational changes. This model also states that the regeneration time axis (*sensu* Grubb 1977) is an integrative long-term resource axis of different components of vegetational changes to which species of small mammals respond along the succession. This model is similar to the gradient-in-time model (Peet 1992), whereby species composition changes in response to environmental changes throughout succession. We can recognize two elements in these models: the first is an emphasis on control by external environmental factors; and the second is acknowledgment of the absence or weakness of species interactions.

The cerrado biome covers approximately 2.0 million km^2 in the Central Plateau of Brazil. The cerrado (the largest Neotropical savanna) has a prevailing xeromorphic vegetation mosaic of physiognomic forms, ranging from pure grassland to closed woodland. Fire is a frequent event in this vegetation mosaic, occurring approximately once every 2 years at the end of the dry season in August–October (Eiten 1972). Previous studies on the responses of small mammals to fire in the cerrado were conducted by Borchert and Hansen (1983), Gettinger and Ernest (1995), Vieira (1999), Vieira and Marinho-Filho (1998), Henriques et al. (2000) and Briani et al. (2004).

In this paper we offer a hypothesis to describe the species replacement sequence independent of species interactions along a post-fire succession. We derive a simple graphical model that predicts the pattern of small mammal richness after secondary fire succession in the cerrado. This hypothesis has two main elements: habitat species specialization and long-term changes in habitat quality, which we call the habitat gradient trajectory. According to this hypothesis, the occurrence of small mammal species results from habitat selection by small mammals along a habitat gradient trajectory. We use this simple hypothesis to describe the succession of small mammal species in a post-fire successional mosaic of the cerrado of central Brazil. First, we address questions concerning the secondary succession of small mammals in the cerrado. Second, we derive the graphical model and use it to explore the pattern of species richness during small mammal succession in nine cerrado sites.

Material and methods

The study area was located in the core of the cerrado biome at 15°57′ S and 47°53′ W, 15 km SW of Brasília (DF), in the Área de Proteção do Gama Cabeça de Veado, a multiple-use conservation unit. The climate of the area is markedly seasonal, with a dry season between May and August (<10% precipitation). The average annual temperature of 21.9°C is typical of a continental subtropical climate, and the mean annual rainfall is 1469 mm.

Data on small mammal succession were gathered in nine sites. Three sites were sampled in April 1997 during the wet season (1, 2 and 12 years after the last fire), and six different sites were sampled in both January 2000 (wet season) and August 2000 (dry season) (1, 2, 3, 6, 9 and 26 years after the last fire). All sites were located in cerrado (*sensu stricto*) physiognomy with the last fire occurrence between 1974 and 1999. The cerrado physiognomy includes structural forms with total woody plant cover ranging between 40% and 70%, with scattered trees and shrubs, canopy generally between 5 and 7 m, and a ground layer of grasses and herbs.

In each site, data on small mammals were collected in transects ranging in time since the last fire from 1 to 26 years, representing a temporal sequence of vegetation succession after fire. Capture stations were located at 10-m intervals along two parallel transects of 190 m (40 stations) in 1997 or one transect of 490 m (50 stations) in 2000. Sites were sampled during 4 days in 1997 and 5 days in 2000 in each season, totaling 160 trap nights for the 190-m transects and 500 trap nights for the 490-m transects. At each station, one Sherman live trap (23×9×8 cm^3), baited with a mixture of oatmeal, cornflour, canned sardines, banana and peanut butter, was set on the ground. Traps were checked early each morning. Captured animals were identified to species, marked by toe-clipping and released at the capture point.

We chose short-term trapping for this study because of the constraints imposed by large, widely dispersed study sites and the necessity of sampling all areas within a short time period. Despite criticism of this sampling method, a minimum trapping effort of 160 trap nights is sufficient to capture approximately 90% of the annual total number of species in cerrado physiognomy using the Jackknife estimate (R.P.B. Henriques, unpublished data). We believe that this capture effort provides a reliable estimate of species composition and species richness of the small mammal community in the area.

Results

A total of nine species of small mammals were captured in all the seral stages of succession: five native rodents (*Calomys callosus*, *Thalpomys cerradenis*, *Calomys tener*, *Necromys lasiurus*, *Oryzomys scotti*), one introduced rodent (*Mus musculus*) and three marsupials (*Thylamys velutinus*, *Gracilinanus agilis* and *Gracilinanus* sp.). The number of species ranged from two to seven in each seral stage (Figure 1). Species were arranged in three groups with respect to successional occurrence. The first group comprised early successional species that

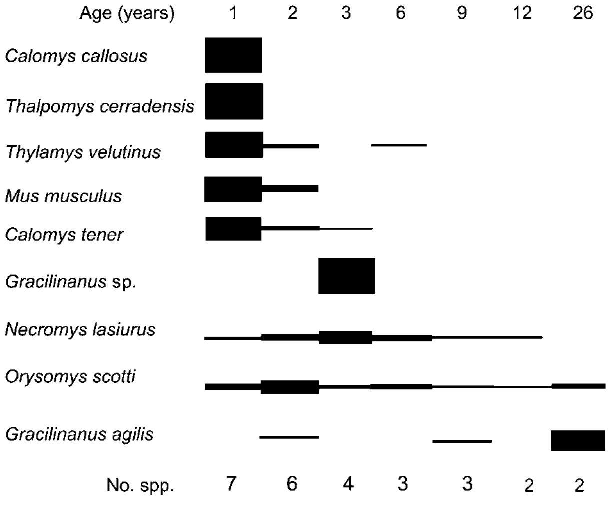

Figure 1 Small mammal succession after fire in the cerrado of central Brazil. The thickness of the line for each species is a measure of the relative abundance of the species in that year. The numbers of species recorded each year are shown at the bottom of the Figure.

occurred or peaked in abundance <2 years after fire. This group included *C. callosus, C. tener, T. cerradensis*, *M. musculus*, and *T. velutinus*. The second group comprised species that occurred or peaked in abundance 2–3 years after fire. This group included *Necromys lasiurus, Gracilinanus* sp. and *O. scotti*. This last species occurred in all seral stages. *Gracilinanus agilis* was recorded in some early seral stages, but peaked in the last stage.

The species richness along seral stages showed an abrupt decrease from an average of four during early seral stages (<2 years) in recently burned areas to two species after 5 years of fire protection and late seral stages more than 20 years after fire (Figure 2). Indeed, there was a significant exponential relation between time since the previous fire and species richness (r^2=0.60). The pattern of species richness was not a result of trap effort, and correlation between the number of species and trap effort was not significant (r_s=0.05; p=0.902; n=9). The decrease in species richness was associated with changes in the composition of the small mammal community.

Discussion

Small mammal succession

The number of species (n=9) recorded over the complete succession (Figure 1) was high compared to that recorded in post-fire succession in California and South Africa (Fox et al. 1985). The pattern of small mammal succession in the cerrado showed the replacement of three species (*C. callosus*, *T. cerradensis* and *Gracilinanus* sp.), with their occurrence only in specific seral stages. *N. lasiurus* occurred in six and *O. scotti* in seven seral stages, but with changes in abundance. This pattern differs from other studies in which most small mammal succession exhibits changes in abundance rather than replacement of species, as in the chaparral in California and heath in Australia (Fox 1982, 1990, Fox et al. 1985).

All the early successional species (*T. velutinus*, *C. callosus*, *C. tener*, *T. cerradensis* and *M. musculus*) have shown a large increase in population density after fire, suggesting that they could be fire- or disturbance-enhanced species (Vieira and Palma 1996, Vieira 1999, Henriques et al. 2000). *M. musculus* was indicated as a fire-prone species, occurring in the early stages of fire succession in forests and heath in Australia and North America (Fox 1982, 1990, Fox et al. 1985). The marsupial *G. agilis* was most abundant in late seral plots (>12 year of fire protection. Previous captures of this species were recorded in gallery forest (Henriques et al. 1997, Lacher and Alho 2001) or closed cerrado woodland protected from fire (Henriques et al. 1997, 2000, Mendonça 2003).

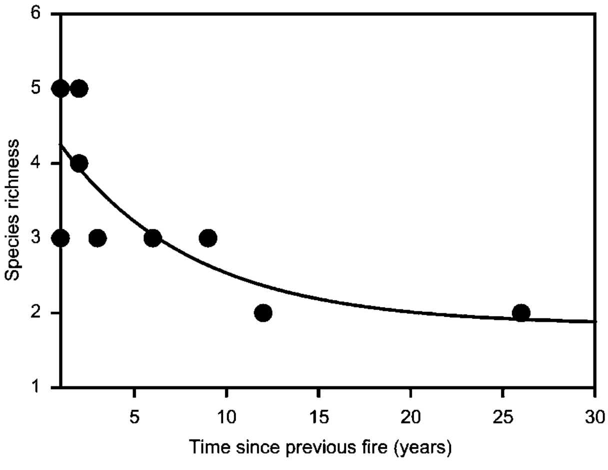

Figure 2 Variation of species richness in relation to time since previous fire in the cerrado of central Brazil. Regression equation: $y=1.83+2.77e^{-0.14t}$; r^2=0.60.

Different from other studies that showed a gradual increase in the abundance of small mammals during succession (Fox 1982, 1990, Bigalke and Willan 1984, Fox et al. 1985), the pattern observed in this study showed a sharp decline from maximum abundance in the early seral stages to a minimum in late seral stages. This result is consistent with the fact that grass ground cover shows a high increase immediately after fire (Meirelles and Henriques 1992). Over time, this cover decreases and shrub and tree cover increases after fire (Moreira 2000). In cerrado with >20 years after the last fire, grass ground cover is even more drastically reduced and a litter layer occurs on the ground, especially under trees and thick shrubs (R.P.B. Henriques personal observation). The initial colonists are terrestrial granivorous/folivores rodent species (Borchert and Hansen 1983, Briani 2001, Vieira 2002), which prefer areas with higher herbaceous cover and relatively low woody cover (Lacher et al. 1989, Henriques and Alho 1991, Henriques et al. 1997). The later successional stages include semi-arboreal and arboreal frugivorous/insectivorous species (Briani 2001, Vieira 2002, A.F. Mendonça personal communication). These results strongly indicate that the occurrence of small mammal species in specific seral stages along succession in the cerrado may be determined by habitat specialization.

The model

The habitat gradient was defined as the ratio of herbaceous (H, grass/forbs) to woody (W, shrub/tree) cover. The process of habitat selection by each species along the habitat gradient is illustrated in Figure 3A. Consider the case in which 13 different species differ in their habitat requirements and can be separated along a H/W habitat gradient. The point at which each species attains its greatest abundance along the habitat gradient is determined by its habitat requirements. Thus, species A is dominant at high H/W ratios because it prefers areas with higher H but lower W than species B. These species thus have a trade-off in their habitat requirements, so that a superior habitat for one species is inferior for another one. Throughout this paper, we assume that all of the species replacements have trade-offs such that the species are inversely ranked in their requirements for the two habitat variables. At all points along the gradient, H and W are superior habitats for some species. We also assume that each species uses the habitat gradient as if species were optimally foraging (Rapport 1971).

Burning in the cerrado promotes herbaceous cover, whereas fire exclusion promotes success of woody cover (Hoffmann 1999, Moreira 2000, Hoffmann and Moreira 2002). Therefore, succession after fire in the cerrado

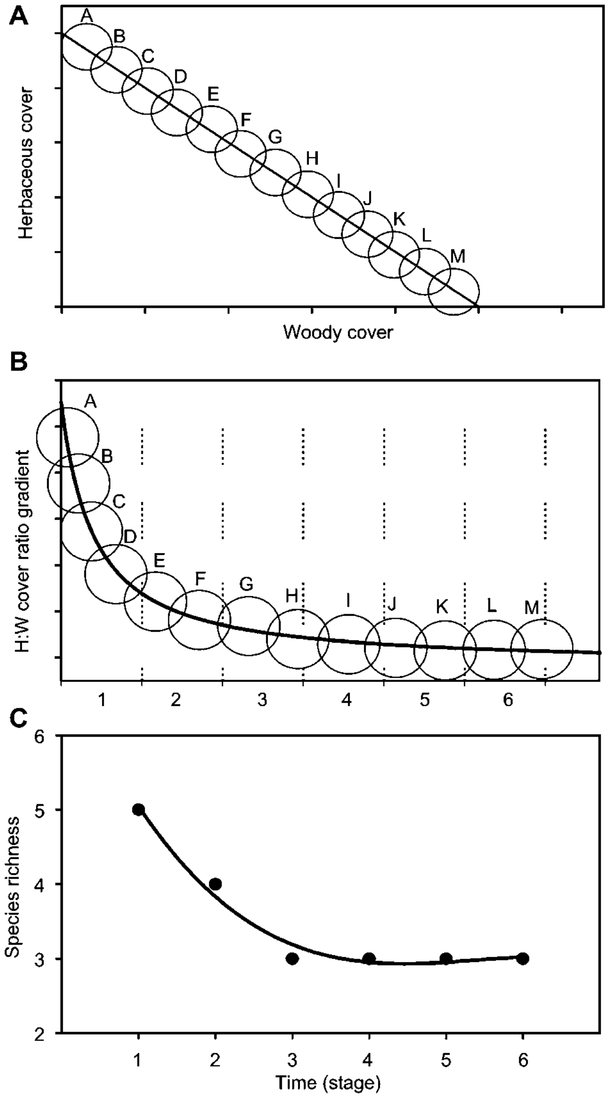

Figure 3 (A) Hypothetical distribution of 13 species (A–M) that differ in their habitat requirements for herbaceous and woody cover. (B) Occurrence of 13 species (A–M) with different habitat requirements along a habitat gradient trajectory during succession. (C) Pattern of species richness in succession of species shown in (B). The line was fitted by hand.

leads to an increase in woody cover and a corresponding decrease in herbaceous cover. The habitat gradient trajectory or H/W ratio over time is expected to be negatively correlated, which leads to successive replacement of one dominant species by another along the habitat gradient trajectory. The pattern of species replacement over time depends critically on how quickly the habitat gradient trajectory changes. Previous studies showed that initially after fire, the rate of increase in herbaceous cover is higher than for woody cover (Meirelles and Henriques 1992). In our model we assumed that the rate of change is higher in the initial stages of succession and decreases with time (Figure 3B). Determination of the number of small mammal species over time depends on how many species can coexist within a successional stage. For instance, for stage 1 in Figure 3B, the number of species would be 5. In stage 2, the number would be 4, and so on, which gives rise to the curve of species richness in Figure 3C. Thus, the hypothesis predicts that maximum species richness should occur in the initial stages of succession, where the rate of habitat gradient change is higher.

This prediction agrees well with the results presented here. This hypothesis also explains changes through space, such as separation of species along a habitat gradient in the cerrado (Mares et al. 1986, Henriques et al. 1997, Lacher and Alho 2001). Here we propose that differences in the herbaceous/woody cover ratio represent the major gradient axis along which habitat specialization of small mammals has differentiated in the cerrado, and that the secondary succession after fire may reflect these life history attributes.

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