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Tese de Doutorado

Efeitos da dispersão e da extinção na distribuição de mamíferos entre regiões e hábitats

André Luís Luza

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Sul como um dos pré-requisitos para obtenção do título de Doutor em Ciências – ênfase em Ecologia

Orientador: Profa. Dra. Sandra Maria Hartz
Co-orientador: Prof. Dr. Leandro da Silva Duarte

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RESUMO

Os distintos padrões de distribuição e diversidade de espécies surgindo de comparações entre regiões e hábitats resultam de um complexo balanço entre dispersões, especiações e extinções. A relevância da perspectiva ‘entre regiões e hábitats’ deve-se ao fato de o limite ecológico entre regiões ou entre hábitats ser caracterizado por uma mudança nas condições abióticas e na estrutura da vegetação. Dependendo do grau de mudança em condições abióticas e na estrutura da vegetação, os limites ecológicos podem causar extinções ou impedir a dispersão de linhagens entre regiões e de espécies e indivíduos entre manchas de hábitat. O principal objetivo da tese foi entender como características das espécies e dos hábitats influenciam na força dos processos de dispersão e de extinção em escala regional e local. No primeiro capítulo avaliei se a distribuição de espécies e linhagens de mamíferos de diferentes guildas tróficas é limitada ao tipo de hábitat ancestral (i.e., se extinções seriam mais fortes entre hábitats ambientalmente contrastantes do que entre hábitats ambientalmente similares). Observei que, para a maioria das guildas tróficas, a distribuição das espécies não se limitou ao hábitat ancestral. No segundo capítulo avaliei a variação geográfica na expectativa de que extinções seriam mais fracas em comunidades de pequenos mamíferos ocupando hábitats modificados com estrutura similar ao hábitat pristino. Encontrei que a alta similaridade estrutural nem sempre garante baixas taxas de extinção, uma vez que a força da extinção varia geograficamente pela ação de processos históricos e evolutivos. No terceiro capítulo pretendi definir a força de extinções e de imigrações em resposta às modificações no hábitat. Para isto, comparei a riqueza, diversidade funcional e composição observada em comunidades de hábitats pristinos e modificados com a riqueza, diversidade funcional e composição que seriam esperadas pela estrutura do conjunto (*pool*) regional de espécies. Resultados demostraram que comunidades de pequenos mamíferos de diversos tipos de hábitats modificados parecem estar sob fraca extinção e dispersão. No quarto capítulo obtive registros de três espécies de roedores ao longo de um ano em campos sujeitos a diferentes níveis de pastejo por bovinos. Estes dados revelaram maior probabilidade de ocupação em campos não pastejados para duas das três espécies analisadas. Em suma, dependendo da escala de observação, constatei que processos históricos, evolutivos e antropogênicos podem ‘desequilibrar a balança’ para maior extinção ou dispersão, que por sua vez influenciam na extensão espacial de distribuição das espécies e na estrutura das comunidades e populações.

Palavras chave: aninhamento; Antropoceno; beta-diversidade; conjunto probabilístico de espécies; conversão de hábitats; fragmentação de hábitats; imigração; modelos hierárquicos; perdas e ganhos de espécies.

ABSTRACT

The different patterns of species distribution and diversity that may arise from comparisons between regions and habitats result from a complex balance between dispersals, speciations and extinctions. The relevance of the 'between-region and between-habitat' perspectives is that the ecological boundary delimiting regions and habitats are characterized by changes in the abiotic conditions and vegetation structure. Depending on the degree of change in abiotic conditions and vegetation structure, we may observe extinctions or environmentally bound dispersals across regions or habitat patches. The main objective of my dissertation was to understand the influence of species and habitat characteristics on the strength of extinction and dispersal processes. In the first chapter I evaluated whether the distribution of mammalian dietary guild species and lineages is bound by the ancestral habitat (i.e. if extinctions should be stronger between environmentally dissimilar than similar habitats). I found that, for most of the mammal dietary guild, the distribution was not bound by the ancestral habitat. In the second chapter I evaluated the geographic variation in the expectation that extinctions are weaker in small mammal communities from human-modified habitats with vegetation structure that is similar to the pristine habitats. I found that high similarity in vegetation structure does not always guarantee low extinction rates in human-modified habitats, because the extinction strength varies geographically due to influence of historical and evolutionary processes. In the third chapter I aimed to define the strength of extinctions and immigrations front to human-mediated modifications in the habitat. To do so, I compared the species richness, composition and functional diversity of pristine and human-modified habitats with the richness, composition and functional diversity expected given the structure of the regional species pool. I found that small mammal communities from several types of human-modified habitats seem to be under both weak extinction and immigrations. In the fourth chapter I estimated the probability of occupation of three rodent species in grasslands subjected to different intensities of cattle grazing. The data revealed highest probability of occupation in ungrazed grasslands for two of the three rodent species. In sum, depending on the scale historical, evolutionary and anthropogenic processes can ‘unbalance the balance’ to higher extinction or dispersal, which in turn might influence the spatial extent of species range and the structure of communities and populations.

Keywords: Anthropocene; beta-diversity; immigration; habitat conversion; habitat fragmentation; hierarchical models; nestedness; probabilistic species pools; species losses and gains.

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INTRODUÇÃO GERAL

Os distintos padrões de diversidade de espécies surgindo de comparações entre regiões e hábitats resultam de um complexo balanço entre dispersão, extinção, deriva e especiação (Graham et al., 2012; Cavender-Bares et al., 2009; Wiens & Donoghue, 2004). Limites ecológicos (*ecological boundaries*), também conhecidos como ecótonos (*ecotones*), ecoclinas (*ecoclines*) ou bordas (*edges*) (van der Maarel, 1990; Strayer et al., 2003; Cadenasso et al., 2003) são barreiras semi-permeáveis que delimitam regiões e manchas de hábitat e que regulam a força da dispersão, extinção, deriva e especiação (Wiens et al., 1985; Hansen et al., 1988; Cadenasso et al., 2003; Strayer et al., 2003; Ries et al., 2004; Fonseca & Joner, 2007). Limites ecológicos são caracterizados por mudanças em condições abióticas e na estrutura física dos hábitats, e podem ser identificados em diferentes escalas espaciais (Ries et al., 2004; Hansen et al., 1988). Por exemplo, podemos analisar se o limite entre biomas é impermeável a dispersão de linhagens (Wiens & Donoghue, 2004), ou se o limite entre manchas de habitats vizinhos é impermeável a dispersão de espécies e de indivíduos (Wiens et al., 1985; Hansen et al., 1988; Cadenasso et al., 2003; Ries et al., 2004). A permeabilidade varia em função de características do próprio limite ecológico (ex. largura, sinuosidade, contraste) (Cadenasso et al., 2003; Strayer et al., 2003) e de atributos das espécies em questão (ex. potencial dispersivo, especificidades no uso do hábitat e de recursos) (Hansen et al., 1998; Ries et al., 2004). Assim, um limite pouco óbvio pode ser suficientemente impermeável à dispersão de uma espécie pouco móvel e especializada a um determinado recurso (Wiens et al., 1985; Hansen et al., 1988; Cadenasso et al., 2003; Ries et al., 2004). O principal objetivo da tese foi entender como características das espécies e dos hábitats influenciam na força dos processos de dispersão e de extinção em escala regional e local.

O foco dado aos processos de extinção e dispersão deve-se ao fato que estes ocorrem em escalas espaciais e temporais muito mais finas do que a especiação e deriva e, portanto, são parâmetros mais sensíveis a mudanças abruptas na estrutura dos habitats. No primeiro capítulo, considerei todas as espécies de mamíferos do planeta porque o objetivo foi determinar se a distribuição de diferentes guildas tróficas de mamíferos (Kissling et al., 2014) seria delimitada pelo tipo de hábitat ancestral (bioma florestal ou aberto [e.g. campo, savana]). Para os demais capítulos, analisei os padrões de distribuição de pequenos mamíferos não-voadores entre hábitats prístinos e modificados por ações antropogênicas. O foco dado aos pequenos mamíferos (ordens Afrosoricida, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Peramelemorphia e Rodentia) deve-se ao fato destes pertencerem a um único nível trófico (onívoros) (Kissling et al., 2014), possuírem baixo potencial dispersivo (Withmee & Orme, 2013; Pacifi et al., 2013), terem protocolos amostrais estabelecidos (Bovendorp et al., 2017) e serem frequentemente considerados como indicadores do efeito de ações antropogênicas sobre a biodiversidade (Laurance, 1994; Pfeifer et al., 2017).

O estudo dos processos gerando os padrões de distribuição de espécies ao longo de limites ecológicos tem mais de um século de história, com raízes em estudos procurando determinar a natureza das comunidades ecológicas (Clements, 1916; Gleason, 1926). Por um lado, uma comunidade poderia ser um superorganismo e, portanto, uma unidade impermeável (“fechada”) a imigrações de espécies de outras comunidades (Clements, 1916). Em contraste, uma comunidade poderia ser permeável (“aberta”) e composta por espécies que compartilham tolerâncias ao ambiente; portanto, estaria sujeita a imigrações de espécies de outras comunidades (Gleason, 1926; Ricklefs, 2008). Embora existam comunidades extremamente fechadas à colonização, a maioria das comunidades estão sujeitas a imigrações (Leibold et al., 2004; Logue et al., 2011), sejam estas imigrações resultando de dinâmicas naturais dos habitats (e.g., migrações em resposta ao clima; de Vivo & Carmignotto, 2004) ou atividades antropogênicas (e.g., imigrações após desmatamento; Dornelas et al., 2014; McGill et al., 2015).

Dinâmicas climáticas naturais e atividades antropogênicas alteram a localização, qualidade e área das manchas de habitat e de seus limites ecológicos, que por sua vez resultam na expansão ou contração da distribuição das espécies por alterarem a predominância da dispersão e extinção (de Vivo & Carmignotto, 2004; Ewers & Didham, 2006; Fisher & Lindemeyer, 2007; Sandel et al., 2011). Por exemplo, variações na precipitação e temperatura desde o último máximo glacial (± 20.000 anos atrás) até os dias atuais têm moldado a ocorrência de biomas florestais, campos e de seus limites ecológicos em paisagens de diversas regiões do mundo (de Vivo & Carmignotto, 2004; Bond & Parr, 2010; Parr et al., 2014). Climas quentes e úmidos têm promovido a expansão da biota florestal a despeito da contração da biota típica de regiões campestres, enquanto que climas frios e secos têm promovido a expansão da biota campestre a despeito da contração da biota florestal (de Vivo & Carmignotto, 2004; Bond & Parr, 2010; Parr et al., 2014). Enquanto que alterações significativas na distribuição de habitats e de seus limites ecológicos devido ao clima ocorrem ao longo de vários séculos, tais alterações tendem a ocorrer muito mais rapidamente pela ação antropogênica (Jackson & Sax, 2010; Parr et al., 2014). A expansão e intensificação descontrolada da agricultura, principalmente em regiões com florestas tropicais e subtropicais, têm fomentado o estudo da distribuição de espécies ao longo de limites ecológicos produzidos pelo homem (Laurance, 1994; Prevedello & Vieira, 2010; Laurance et al., 2014; Pfeifer et al., 2017). Neste contexto, o estudo de limites ecológicos tem relevância para predizer invasões biológicas e compreender o efeito da conversão de habitats e das mudanças climáticas para a estrutura das comunidades e populações (McGill et al., 2015; Davidson et al., 2017; Pfeifer et al., 2017).

Para quantificar a especiação, deriva, dispersão e extinção, podemos: 1) reconstruir a distribuição ancestral das espécies de interesse diretamente em filogenias e comparar com o padrão de distribuição atual (através de ferramentas da macroevolução e filogeografia; Ree & Smith 2008), ou 2) analisar a variação temporal e espacial na estrutura de comunidades e populações (através de métodos da macroecologia, ecologia de comunidades e populações; Mackenzie et al., 2005; Dobrovolski et al., 2012; Holt et al., 2013; Penone et al., 2016). Embora existam abordagens permitindo unir macroevolução e macroecologia (Fritz et al., 2013; Lawing et al., 2017), estas são geralmente focadas em espécies, guildas ou linhagens particulares (e não em comunidades) e necessitam de informações sobre fósseis e sua biologia (ex. uso do habitat), que são de difícil obtenção para muitos grupos faunísticos. Nesta tese, utilizei métodos da macroecologia e ecologia de comunidades (i.e., análise da beta-diversidade e filo beta-diversidade entre comunidades [Almeida-Neto et al., 2008; Baselga, 2010; Melo et al., 2014], a análise do pool regional de espécies das comunidades [*probabilistic species pool*, Karger et al., 2016]) e métodos da ecologia de populações (modelos de ocupação de sítios, Mackenzie et al., 2005) para determinar o efeito dos processos de dispersão e extinção para a distribuição de mamíferos.

É bem estabelecido que dois diferentes fenômenos, substituição de espécies (*turnover*) e aninhamento (*nestedness*), podem resultar em variações na composição e riqueza entre sítios (i.e., beta-diversidade; Almeida-Neto et al., 2008; Baselga, 2012, 2010). Distinguir o efeito de cada fenômeno é essencial desde que eles são causados por diferentes processos ecológicos e históricos (Baselga, 2012, 2010). Uma completa substituição de espécies ocorre quando dois sítios não compartilham espécies devido as preferências de nicho das espécies, enquanto que um completo aninhamento ocorre quando um sítio pobre em espécies é um subconjunto aninhado de um sítio rico em espécies devido ao processo de perda de espécies (Patterson & Atmar, 1988; Almeida-Neto et al., 2008; Baselga, 2010). Construí um exemplo simples para demonstrar o efeito da especiação, extinção e dispersão (Figura 1). A especiação, um processo cujo efeito é mais evidente em escalas regionais (Baselga, 2010), resulta no aumento da dissimilaridade composicional entre sítios devido à substituição de espécies e linhagens entre comunidades (Figura 1A). No exemplo, percebe-se que cada hábitat (A e B) possui um conjunto exclusivo de espécies e, em larga extensão, de linhagens (a substituição de linhagens nunca vai ser completa já que todas as espécies possuem uma ancestralidade comum; Melo et al., 2014).

Determinar a predominância da extinção e dispersão é o principal interesse desta tese. O cenário de extinção (Figura 1B) foi propositalmente ajustado para demonstrar dois importantes aspectos do aninhamento: 1) a perda de espécies tende a causar diferenças em riqueza e diversidade filogenética entre sítios (o hábitat B é mais pobre do que A, se somarmos o número de espécies e os comprimentos dos ramos da filogenia conectando as espécies), e 2) em amplas escalas, podemos ter aninhamento filogenético mesmo quando os sítios não compartilham nenhuma espécie (na filogenia da Figura 1, o triângulo retângulo é filogeneticamente aparentado ao triângulo; portanto B é um subconjunto aninhado de A) (Graham & Fine, 2008; Melo et al., 2014). Finalmente, na figura 1, nos exemplos de especiação e extinção, os habitats A e B não compartilham espécies (i.e., havia uma completa substituição de táxons). Com a dispersão de uma espécie, os hábitats tornaram-se mais similares em composição, resultando no aumento do aninhamento e diminuição na substituição de táxons (Figura 1C). Portanto, extinção e dispersão são os processos que diminuem as diferenças de diversidade (Figura 1B) e aumentam a similaridade composicional entre regiões ou habitats (Figura 1C) (Graham & Fine, 2008; Baselga, 2012, 2010).

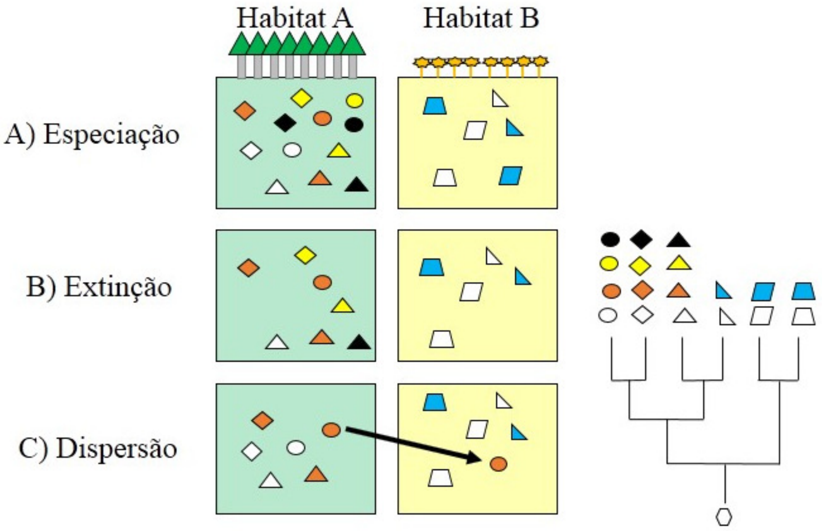

Figura 1: Exemplo demonstrando o efeito dos processos de especiação, extinção e dispersão para a estrutura de comunidades de dois habitats ambientalmente distintos (Habitat A e B). Baseado em Graham & Fine (2008). As diferentes formas geométricas "povoando" os diferentes hábitats (quadrados) representam diferentes espécies. A seta representa um evento de dispersão. A filogenia representa o grau de parentesco entre espécies.

No primeiro capítulo desta tese, que está formatado de acordo com as normas do periódico *Journal of Animal Ecology*, busco entender se as mudanças na distribuição (*distribution dynamics*) de espécies de mamíferos são limitadas ao hábitat ancestral. Mudanças na distribuição das espécies tem uma relação direta com dois mecanismos evolutivos relacionados às mudanças no nicho (*niche dynamics*): estase de nicho (*niche stasis*) ou mudança de nicho (*niche shifts*) (Pearman et al., 2008). Podemos esperar que a distribuição de uma dada espécie tenha permanecido estável ao longo do tempo devido à conservação do nicho ancestral (*niche stasis*) (Wiens & Graham, 2005; Pearman et al., 2008). Neste caso, a especiação acumula espécies dentro de um hábitat similar ao habitat ancestral (habitat A, figura 1B), dispersões ocorrem predominantemente entre habitats similares ao habitat ancestral, e dispersões para habitats dissimilares resultam em elevadas taxas de extinção (habitat B, Figura 1B). Desta forma, habitats que são ambientalmente distintos podem ser um subconjunto aninhado de hábitats similares ao ancestral (Pearman et al., 2008). Em contraste, podemos esperar que a distribuição de uma espécie tenha mudado ao longo do tempo, desde que dispersões são possíveis já que o nicho não mais se limita ao nicho ancestral (*niche shifts*) (Figura 1C) (Pearman et al., 2008; Benton, 2010). Mudanças no nicho pode ocorrer pelo desaparecimento do hábitat ancestral ou pela necessidade de explorar recursos de hábitats distintos (Benton, 2010). Desta forma, habitats que são ambientalmente distintos tornam-se similares em riqueza, e nenhum padrão de aninhamento é esperado (Figura 1A). A hipótese principal foi de que uma distribuição estável e estase do nicho produziriam aninhamento para guildas de mamíferos que demandam de recursos habitat-específicos (e.g., herbívoros pastadores [“*grazers*”] dependem de gramíneas campestres, frugívoros dependem de frutos suculentos encontrados em florestas; Kissling et al., 2014), enquanto que mudanças na distribuição e no nicho não produziriam aninhamento para guildas de onívoros que consomem recursos de diferentes habitats (Bofarull et al., 2008; Cantalapiedra et al., 2011).

Construí uma base de dados de ocorrência de pequenos mamíferos não-voadores em habitats prístinos e modificados por ações antropogênicas (material suplementar do Capítulo 2) para as análises dos capítulos 2 e 3, onde busco entender como a extinção e a dispersão determinam os padrões de riqueza e composição de espécies e atributos em comunidades de pequenos mamíferos de habitats prístinos e modificados por atividades antropogênicas. A modificação de habitats prístinos cria limites ecológicos artificiais entre manchas de habitat, promovendo a extinção de algumas espécies a despeito da imigração de outras (Ewers & Didham, 2006; Fischer & Lindemeyer, 2007; McGill et al., 2015). Habitats modificados tendem a perder espécies raras e habitat-especialistas, com reprodução lenta, dieta específica e com maior porte (Ewers & Didham, 2006; Fischer & Lindemeyer, 2007); no entanto, espécies generalistas, com reprodução rápida, dieta generalista e com menor porte ainda permanecem em habitats modificados (i.e., espécies remanescentes no habitat B). Assim, muitas espécies que ocorriam no habitat prístino não mais ocorrem no habitat modificado, principalmente se este difere consideravelmente em estrutura da vegetação quando comparado ao habitat não modificado (Ewers & Didham, 2006; Prevedello & Vieira, 2010). Neste sentido, habitats modificados e ambientalmente diferentes do ambiente prístino tendem a possuir um subconjunto aninhado da composição de espécies de habitats prístinos (Patterson & Atmar, 2000, 1986). Embora esta expectativa possa facilitar a gestão da paisagem para a conservação de espécies (ou seja, a implantação de florestas plantadas tem maior efetividade para a conservação de espécies florestais do que a implantação de lavouras, Ruffel et al., 2017), devemos considerar que as taxas de extinção e dispersão variam geograficamente (Dobrovolski et al., 2012; Holt et al., 2013; Penone et al., 2016). Determinar o quanto a variação geográfica e a similaridade estrutural entre habitats influenciam no aninhamento observado em comunidades de pequenos mamíferos não-voadores foi o objetivo do capítulo 2, que está formatado de acordo com as normas do periódico *Biological Conservation*.

O principal objetivo do capítulo 3, que está formatado de acordo com as normas do periódico *Conservation Biology*, foi distinguir extinções locais de dispersões, através da análise do conjunto regional de espécies de comunidades de pequenos mamíferos não-voadores de hábitats prístinos e modificados pelo homem. O conjunto regional de espécies (*regional species pool*) de um sítio inclui todas as espécies que podem potencialmente compor a comunidade daquele sítio dado o potencial de dispersão das espécies e as condições ambientais da localidade (Karger et al. 2015, 2016). Alterações antropogênicas alteram a estrutura do hábitat do sítio e podem 'reorganizar' as comunidades, seja pela extinção local de espécies como pela imigração de espécies que não ocorriam antes da modificação no hábitat (Filloy et al., 2010; Jackson & Sax, 2010; Corbelli et al., 2015; McGill et al., 2015). Desta forma, podemos determinar a força de extinções e imigrações por comparar a riqueza, diversidade funcional e composição observada nas comunidades de hábitats prístinos e modificados e a riqueza, diversidade funcional e composição esperadas dadas as propriedades do pool regional de espécies (Karger et al. 2015, 2016). Para exemplificar, considere que espécies florestais extintas localmente, devido à conversão de uma floresta para uma lavoura, são substituídas por espécies características de áreas abertas (ex. campos, savanas) dadas as características da vegetação e do tipo de recurso presente em lavouras (Filloy et al., 2010; Corbelli et al., 2015). Este balanço entre extinções e imigrações pode anular as diferenças de riqueza entre o habitat modificado e o prístino (considere a figura 1C, onde a dispersão de uma espécie tornou os hábitats igualmente ricos em espécies), mas pode consideravelmente alterar a composição de espécies e a diversidade funcional (Vellend et al., 2013; Dornelas et al., 2014). Desta forma, é imprescindível analisar as variações na composição de espécies e atributos para distinguir extinções de dispersões (Jackson & Sax 2010; McGill et al., 2015).

Uma comunidade é o conjunto de populações de espécies que coexistem no espaço e no tempo. Embora uma comunidade possua propriedades emergentes diferentes das propriedades das populações individuais que a compõem (Begon et al., 2005), parâmetros populacionais como ocupação e densidade são a base para compreender muitos fenômenos observados em escalas mais amplas (Debinski & Holt, 2000; Mackenzie et al., 2005; Ricklefs et al., 2008). Por exemplo, a probabilidade de ocupação de um sítio por uma espécie tem relação direta com seu tamanho populacional (Mackenzie et al., 2005). Populações grandes, que tem crescimento populacional positivo em sítios de alta qualidade (Habitat A, figura 1), fornecem indivíduos para habitats de baixa qualidade através da dispersão (Habitat B, Figura 1) (dinâmicas fonte-sumidouro [*source-sink dynamics*; Pulliam, 1988]). Alterações no hábitat podem influenciar a probabilidade de ocupação e o tamanho das populações. Por exemplo, o pastejo por ungulados altera a estrutura da vegetação e tende a diminuir a qualidade dos hábitats para a fauna, podendo provocar extinções locais (Luza et al., 2016). No capítulo 4 da tese, que está formatado de acordo com as normas do periódico *Perspectives in Ecology and Conservation*, procuro definir a probabilidade de ocupação de três espécies de roedores em campos sujeitos a diferentes regimes de pastejo por ungulados domésticos. Avaliar parâmetros populacionais é relevante para definir boas práticas para o manejo e conservação da diversidade nos níveis de populações, comunidades e ecossistemas (Tschnartke et al., 2012). Finalmente, os estudos incluídos nesta tese buscaram contribuir para o conhecimento do efeito dos processos de extinção e de dispersão para a estrutura de comunidades e populações em diferentes escalas espaciais.

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CAPÍTULO 1

Title: Mammal guild distribution dynamics between forest and open habitats

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Abstract

1. Distribution dynamics involves two evolutionary mechanisms linked to niche changes: niche stasis and shifts. Niche stasis should result in stable distribution and nested assemblages due to the high extinction rates in and unsuccessful dispersals into environmentally dissimilar habitats. Niche shifts should result in distribution shifts due to the low extinction rates in and successful dispersals into environmentally dissimilar habitats.

2. We evaluated whether the distribution dynamics of mammalian guilds are bound by the ancestral habitat. We hypothesized that the type of guild should influence the dominant mechanism and direction of distribution dynamics between open and forest ecoregions. We expected dynamics consistent with niche stasis for resource-specialized

guilds (carnivores, frugivores, grazers, mixed-feeders and granivores). We expected dynamics consistent with niche shifts for browsers and omnivore guilds.

3. We estimated nestedness in the distribution of 13 mammalian guilds between open and forest ecoregions within realms. We attributed each ecoregion to the respective habitat type and realm and rearranged the occurrence matrices to identify the mechanism and direction of the distribution dynamics. For each guild and matrix rearrangement, we used taxonomic and phylogenetic nestedness to identify, for example, if open-habitat mammals are a nested subset of forest mammals. We used matrix randomization and the resulting standardized effect sizes to compare the strength of nestedness among guilds and matrix rearrangements.

4. Standardized effect sizes indicate that, for most of guilds, the observed nestedness was higher than expected by random chance in both forest-to-open and open-to-forest directions. Nestedness analysis revealed that niche shifts are generalized across the mammalian guilds, since we found that niche shifts resulted in nestedness in a direction different from that expected given the ancestral habitat. We found evidence for niche stasis only for granivores and two omnivore guilds.

5. Nestedness identified that most of dispersals into environmentally dissimilar habitats resulted in successful occupations and diversifications due to niche shifts. Therefore, both forest-to-open and open-to-forest directions of distribution dynamics occurred during the history of occupation and diversification of the species composing the mammalian dietary guilds.

Keywords: beta diversity components, ecological biogeography, macroecological sources and sinks, nested subsets, phylo beta-diversity, taxa sharing, trophic specialization.

Introduction

The extant species tend to occupy habitats that are similar to the ancestral habitat (Davies, & Buckley, 2011; Crisp et al., 2009; Martinez-Meyer, Townsend Peterson, & Hargrove, 2004). In fact, dispersals following geological and climatic events seems to be more common in habitats that are environmentally similar to those previously occupied by the species, which might not change the type of habitat and the set of conditions and resources preferred by the species (Crisp et al., 2009; Martinez-Meyer, Townsend Peterson, & Hargrove, 2004). However, we still lack an understanding of how the use of resources by the species influences the direction of dispersal and extinction processes. Geological and climatic events alter the location and type of habitats and resources on which animals depend, which may cause changes in the extinction and dispersal probabilities (Fortelius et al., 2014; Price, Hopkins, Smith, & Roth, 2012), favoring higher levels of diversity for some guilds while depreciating levels in others (Damuth & Janis, 2011; de Vivo & Carmignotto, 2004; Fortelius et al., 2014; Ortiz-Jaureguizar & Cladera, 2006).

Low dispersal and high extinction rates in environmentally dissimilar habitats are caused by low fitness due to ancestral niche conservatism (red arrows; Fig. 1) (niche stasis *sense* Perman, Guisan, Broennimann, & Randin, 2008). In this context, the distribution of a species should embrace a unique type of habitat over time, because a high fitness is only ensured by the conditions and resources present in a habitat similar to the ancestral habitat (black arrows; Fig. 1) (Perman, Guisan, Broennimann, & Randin, 2008). In contrast, high dispersal and low extinction rates in both environmentally similar and dissimilar habitats are expected with the release from ancestral niche conservatism, which might occur due to changes in the distribution of preferred resources and habitats (niche shifts *sense* Perman, Guisan, Broennimann, &

Randin, 2008). Niche shifts might promote dispersal and diversification in a new habitat with a different set of conditions and resources when compared to the ancestral habitat (purple arrows, Fig. 1) (Benton, 2010; Perman, Guisan, Broennimann, & Randin, 2008). Thus, niche shifts should produce nestedness in a direction different from that expected given the ancestral habitat.

We used taxonomic and phylogenetic nestedness (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Melo, Cianciaruso, & Almeida-Neto, 2014) to analyze whether the distribution of extant mammalian guilds is bound by the ancestral habitat (Kissling et al., 2014). In its classic definition, nestedness is characterized by a site, impoverished by extinctions, which is therefore comprised of a nested subset of species and lineages from biologically richer source sites (Patterson & Atmar, 1986). We used nestedness assuming that both distribution and feeding habits of extant species and lineages have signals of past dynamics of extinctions and dispersals across habitats and regions (Cantalapiedra, Hernández-Fernández, & Morales, 2011; Cantalapiedra et al., 2014a; Damuth & Janis, 2011; Fortelius et al., 2014; Svenning, Fløjgaard, & Baselga, 2011) and that, independently of the mammalian orders composing a given guild, the ancestral would be an species preferring the same resource as the extant species.

We hypothesized that the distribution of the species composing the mammalian dietary guilds (Table 1) should show evidence of different mechanisms (niche stasis and shifts) and directions (forest-to-open and open-to-forest) of mammal distribution dynamics (Fig. 1). For each guild, we considered different directions in order to identify whether either open or forest ecoregions could be a source of species and lineages (Fig. 1; see Fig. S1.1 in Supporting Information). We considered biogeographic realms in the nestedness analysis because a biogeographic effect may either strengthen or weaken nestedness (examples in Fig. S1.1). We tested four hypotheses:

Hypothesis 1 - Niche stasis for frugivores: Niche stasis should result in taxonomically and phylogenetically nested assemblages when dispersals are either environmentally bound or prevented by environmental unsuitability (red and black arrows, Fig. 1) (Crisp et al., 2009; Martinez-Meyer, Townsend Peterson, & Hargrove, 2004; Svenning, Fløjgaard, & Baselga, 2011). Thus, we expected taxonomic and phylogenetic nestedness higher than expected by random chance only in the forest-to-open direction for frugivores. Open ecoregions are not expected to be a source of frugivores to forests, because the strict affinities of frugivores for forest resources might prevent their dispersal and diversification in open habitats (Davies, Purvis, Gittleman, 2009; Davies, & Buckley, 2011).

Hypothesis 2 - Niche stasis for carnivores and herbivore guilds (except browsers): We expected carnivore guilds, grazers, granivores, mixed-feeders of forest ecoregions more taxonomically and phylogenetically nested in open ecoregions than expected by random chance only in the open-to-forest direction due to niche stasis (Fig. 1). Forests are not expected to be a source of carnivore and herbivore species (except browsers, Hypothesis 4) to open-habitat ecoregions. These guilds had their origin and diversification with the rise of grassy biomes during the arid and cold Oligocene-Miocene transition (Damuth & Janis, 2011; Fortelius et al., 2014; MacFadden, 1997, 2006; Pires, Silvestro, & Quental, 2015), which suggest dependence on resources of open habitats.

Hypothesis 3 - Niche shifts for omnivore guilds: Niche shifts should result in low extinction and successful occupation rates in several habitat types after dispersals, resulting in non-directional (nestedness in both forest-to-open and open-to-forest) and random nestedness due to the lack of differences of composition and diversity between habitats (purple arrows, Fig. 1) (Graham & Fine, 2008; Melo, Cianciaruso, & Almeida-Neto, 2014). Thus, we expected non-directional and random taxonomic and phylogenetic nestedness for omnivore guilds as a result of niche shifts (Fig. 1). Omnivores rely on resources from many habitats (Bofarull, Royo, Hernández-Fernández, Ortiz-Jaureguizar, & Morales, 2008; Cantalapiedra, Hernández-Fernández, & Morales, 2011), which suggests low extinction rates after dispersals as they might be able to switch their diets and distributions under resource scarcity (Bofarull, Royo, Hernández-Fernández, Ortiz-Jaureguizar, & Morales, 2008; Davies, Purvis, & Gittleman, 2009; Price, Hopkins, Smith, & Roth, 2012).

Hypothesis 4 - Niche shifts for browsers: Niche shifts should result in phylogenetically nested assemblages when successful dispersers of a particular lineage diversify in a new habitat type (Fig. 1) (Graham & Fine, 2008; Melo, Cianciaruso, & Almeida-Neto, 2014). Thus, taxonomic nestedness should be random while phylogenetic nestedness should be higher than expected by random chance in both forest-to-open and open-to-forest directions for browsers, which may be caused by niche shifts and diversification of an open-habitat herbivore lineage in forests (Cantalapiedra et al., 2014; Cantalapiedra, Hernández-Fernández, & Morales, 2014) (Fig. 1).

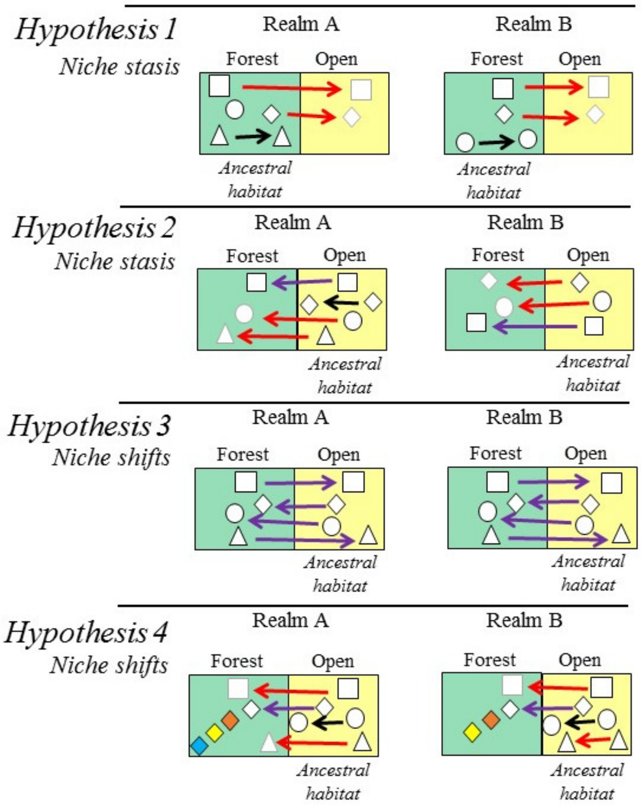

Fig. 1: Schematic representation of the hypotheses. Different mechanisms (either niche shifts or stasis) and directions of dynamics (either forest to open or open to forest) were expected for different mammalian guilds. The mechanism and direction may change across the biogeographic realms, because two realms (e.g., Realms A and B) can differ in taxonomic and phylogenetic diversity. Ancestral habitat in each hypothesis was defined according to the literature. Black arrows: environmentally bound dispersals; red arrows and symbols with gray lines: dispersals followed by extinctions; purple arrows and symbols with black lines: dispersals not followed by extinctions. The different symbols represent different species; symbols with same shape but different colors indicate phylogenetically related species.

Table1: Mammal dietary guilds (in lowercase) we analyzed in the study. For each guild we constructed an occurrence matrix, rearranged the rows (ecoregions) according to habitat type and realm and inferred dispersal and extinction processes using taxonomic and phylogenetic nestedness.

TROPHIC LEVEL/Dietary guild	**Feeding habit**	**Number of species (% of total)**	**Main orders (no. species)**	**Number of ecoregions (no. islands)**	**Matrix fill (%)**
NON-VOLANT MAMMALS OF THE WORLD	All mammals except Chiroptera	3,708 (100%)	Rodentia (2023), Eulipotyphla (390), Primates (323)	798 (81)	2.02
HERBIVORES	All mammal species that consume herbaceous, woody and leaf material, as well as fruits and seeds as their primary, secondary or occasional resource. These species do not feed on animals	1,476 (40%)	Rodentia (912), Cetartiodactyla (192), Primates (158)	749 (43)	1.89
Grazers	Herbivores that feed only on the leaves of herbaceous plants; they do not eat the leaves of woody plants	297 (8%)	Rodentia (168), Cetartiodactyla (60), Diprotodontia (42)	688 (24)	1.77
Browsers	Herbivores that feed strictly on the leaves of woody plants	358 (10%)	Rodentia (143), Cetartiodactyla (102), Primates (49)	727 (34)	2.26
Mixed-feeders	Herbivores that feed on the leaves of herbaceous and woody plants	241 (6%)	Rodentia (119), Cetartiodactyla (76), Lagomorpha (30)	700 (28)	2.54
Granivores	Species that strictly feed on plant seeds, and not fruits	167 (5%)	Rodentia (161) Cetartiodactyla (4) Peramelemorphia (1)	579 (8)	2.24
Frugivores	Species that strictly feed on plant fruits, and not seeds	276 (7%)	Rodentia (133), Primates (54), Diprotodontia (37)	607 (23)	1.87
CARNIVORES	All mammal species that use vertebrates and invertebrates as their primary, secondary or occasional resource. These species do not feed on plants	715 (19%)	Eulipotyphla (342), Carnivora (125), Rodentia (86)	740 (37)	2.76
Vertebrate-eaters	Carnivores that feed only on other vertebrates, and not on invertebrates	61 (2%)	Carnivora (51) Rodentia (4) Dasyuromorphia (3)	667 (22)	9.58

	Invertebrate-eaters	Carnivores that feed only on invertebrates, and not on vertebrates (also known as insectivores)	237 (6%)	Eulipotyphla (78), Rodentia (66), Afrosoricida (35)	688 (20)	2.11
OMNIVORES		All mammals that use both plant and animal material as primary, secondary or tertiary food items	1,506 (41%)	Rodentia (1018), Primates (154), Carnivora (104	791 (77)	2.04
†	Vertebrate- and seed-eaters	Omnivores that feed on vertebrates and seeds, but not on invertebrates or fruits	5 (0.13%)	Rodentia (5)	45 (1)	21.78
	Vertebrate- and fruit-eaters	Omnivores that feed on vertebrates and fruits, but not on invertebrates or seeds	35 (1%)	Cetartiodactyla (14), Carnivora (10), Rodentia (9)	491 (12)	6.93
†	Vertebrate- and fruit/seed-eaters	Omnivores that feed on vertebrates, fruits and seeds, but not on invertebrates	3 (0.08%)	Rodentia (2), Carnivora (1)	46 (0)	33.33
	Invertebrate- and fruit-eaters	Omnivores that feed on invertebrates and fruits, but not vertebrates or seeds	152 (4%)	Rodentia (58), Primates (42), Didelphimorphia (27)	405 (10)	3.12
	Invertebrate- and seed-eaters	Omnivores that feed on invertebrates and seeds, but not on vertebrates or fruits	176 (5%)	Rodentia (171) Primates (2) Eulipotyphla (1)	562 (9)	2.31
	Invertebrate- and fruit/seed-eaters	Omnivores that feed on invertebrates, fruits and seeds, but not on vertebrates	258 (7%)	Rodentia (222), Primates (20), Scadentia (14)	723 (54)	2.13
	Vertebrate/invertebrate- and seed-eaters	Omnivores that feed on vertebrates, invertebrates and seeds, but not on fruits	68 (2%)	Rodentia (42), Eulipotyphla (26)	704 (55)	3.21
	Vertebrate/invertebrate- and fruit-eaters	Omnivores that feed on vertebrates, invertebrates and fruits, but not on seeds	180 (5%)	Carnivora (64), Primates (52), Rodentia (23)	691 (19)	3.57

†Not analyzed due to low number of species.

Materials and Methods

Mammal distribution and feeding habits

We used the 814 World Wildlife Foundation ecoregions (Olson et al., 2001) as units to define mammal occurrence. Within their design, ecoregions consider the regional species pool, represent biogeographically and climatically homogeneous areas, capture large environmental heterogeneity at a global scale, differ in area and are objectively classified according to habitat type and biogeographic realm (Olson et al., 2001; Fritz, Bininda-Emonds, & Purvis, 2009).

Distribution polygons for 5,286 mammal species were taken from the IUCN (2014) and mapped over ecoregions using the spatial join function in ESRI ArcMap 10.2.2. A mammal species was considered to occur in a given ecoregion if the distribution polygon intercepted the limits of the ecoregion; all mammal species coexisting within the limits of an ecoregion composed an assemblage. From the 5,286 mammal species with distribution data, 593 were excluded because of the lack of information about their feeding habit or phylogeny. From the remaining 4,693 species (≈ 89% of the total of species) we removed bat species (985 species), because high dispersal ability should lead to high nestedness between adjacent regions (Peixoto, Braga, Cianciaruso, Diniz-Filho, & Brito, 2014). In total, the occurrence of 3,708 non-volant mammal species was recorded across 798 ecoregions. These were progressively filtered to obtain occurrence matrices for dietary guilds (Table 1), since guilds represent resource and habitat affinities better than trophic levels do (Kissling et al., 2014; Smith et al., 2016). We used a comprehensive mammalian diet database (MammalDIET v1.0; Kissling et al., 2014), which provided highly detailed information about mammalian feeding habits.

Factors defining ecoregion type

We extracted information on the habitat type (two levels, either forest or open) and the biogeographic realm of each ecoregion (eight levels: Afrotropic, Antarctica, Australasia, Indomalayan, Nearctic, Neotropic, Oceania and Palearctic [see Tables S1.1and S1.2 in Appendix S1]). The distinction between forest and open habitats reflects broad differences in vegetation structure and type of available niches and resources (Fortelius et al., 2014; Faurby & Svenning, 2015). Realms represent particular evolutionary units formed by long-term isolation of species (Penone et al., 2016) and where asymmetric adaptive radiations take place (Cantalapiedra, Hernández-Fernández, & Morales, 2014; Pires, Silvestro, & Quental, 2015). Ecoregions belonging to forest, woodland and mangrove biomes were considered forest habitats, while ecoregions belonging to grassland, shrubland, desert, savanna, inland-water and the rock and ice biomes were considered as open habitats (as in Faurby & Svenning, 2015).

Quantifying taxonomic and phylogenetic nestedness between ecoregions

We quantified differences in guild richness and composition between ecoregions, which should be the product of niche stasis and shifts, using taxonomic and phylogenetic nestedness. We fractionated the tree-based nestedness index TreeNODF (Melo, Cianciaruso, & Almeida-Neto, 2014) into phyloNODF, which quantifies the shared evolutionary history between rich and poor sites by accounting for branch lengths connecting coexistent species (i.e. phylogenetic diversity [PD]), and into S.Fraction, which quantifies the shared species composition between rich and poor regions and is equivalent to the classic nestedness metric of paired overlap and decreasing fill (NODF; Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). NODF and phyloNODF have two independent components: 1) site nestedness, based on differences in taxonomic and phylogenetic diversity between sites ($\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$), and 2) species nestedness, based on frequency differences between species ($\mathrm{NODF}_{\mathrm{species}}$ and $\mathrm{phyloNODF}_{\mathrm{species}}$; Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Melo, Cianciaruso, & Almeida-Neto, 2014). Since we were interested in the distribution dynamics between habitats, we used $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ to test our hypotheses. To calculate $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$, we analyzed occurrence matrices for each dietary guild (Table 1) together with a dated phylogeny of 5,020 mammal species (Fritz, Bininda-Emonds, & Purvis, 2009).

The pairwise basis and the sensitivity to matrix rearrangement makes $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ useful indexes to evaluate whether the distribution of extant mammalian guilds is bound by the habitat (Fig. S1.1). Nestedness will be greater than zero when the first site is taxonomically and phylogenetically more diverse than the second site in most of the pairwise comparisons and when most of incidences overlap between the columns; otherwise, $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ will be zero (Fig. S1.1). Such properties allowed us to test the different mechanisms and directions of distribution dynamics (Fig. 1). In practice, we can test if environmentally bound dynamics due to niche stasis results in a higher diversity of frugivores always being found in forest ecoregions when compared to open ecoregions (i.e., forest-to-open but not the *inverse* open-to-forest; Fig. S1.1). This is achieved by always setting the forest ecoregions in the upper rows of the guild occurrence matrix, because NODF and phyloNODF are designed to measure decreases in diversity from the upper (forest ecoregions) rows to the lower (open ecoregions) rows of the occurrence matrix (Fig. S1.1).

Considering the effects of biogeography and habitat type

We considered the effects of habitat because taxonomic and phylogenetic diversity of the mammal guilds differed between habitats (Tables S1.1 and S1.2). In addition, we consider biogeography because 1) taxonomic and phylogenetic diversity of the mammal guilds differed between realms (Tables S1.1 and S1.2); 2) ecoregions from different realms lack shared species; and 3) biogeography may result in distribution patterns consistent with niche stasis in one realm but not in others, which may weaken nestedness by nullifying the differences in diversity between habitats (the Realms A and B are equally rich in Fig. 1, hypothesis 3) or strengthen nestedness by decreasing taxonomic and phylogenetic diversity in poorer realms (forest ecoregions are nested on open ecoregions in Realm A and B, despite realm B having less species; Fig. 1, in hypothesis 2). We considered the effects of habitat and biogeography by rearranging the rows (ecoregions) of each guild matrix. Since any arbitrary site rearrangement affects the nestedness values, we additionally rearranged ecoregions, across all matrix rearrangements, by decreasing area within each habitat. We used the following matrix rearrangements:

Open-to-forest: Within each realm, the largest and richest open ecoregion is located at the upper row of the matrix and is followed by successively smaller and poorer open ecoregions. These are followed by the largest and richest forest ecoregion, which is successively followed by smaller and poorer forest ecoregions. The order of realms was defined according to realm richness and phylogenetic diversity (see Tables S1.1 and S1.2).

Forest-to-open: Within each realm, the largest and richest forest ecoregion is located at the upper row of the matrix and is followed by successively smaller and poorer forest ecoregions. These are followed by the largest and richest open ecoregion, which is successively followed by smaller and poorer open ecoregions. The order of realms was defined according to realm richness and phylogenetic diversity (see Tables S1.1 and S1.2).

Hypotheses testing

We compared the observed $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ for each guild with random index values generated by randomizing the matrix rows (500 randomizations of the 'permRows' algorithm) to evaluate if nestendess was higher or lower nestedness than expected by random chance. PermRows changes the position of ecoregions across the matrix but does not change the species frequency (Ulrich, Almeida-Neto, & Gotelli, 2009; Melo, Cianciaruso, & Almeida-Neto, 2014), which is appropriate when purposely rearranging the matrix structure according to predefined factors (Melo, Cianciaruso, & Almeida-Neto, 2014), as in the present case (Fig. S1.1). By disassembling the matrix structure we were able to define how much the observed nestedness, produced by a rearrangement, deviated from the nestedness produced by a random rearrangement; non-significant nestedness means lack of difference between the observed and random nestedness. The observed NODF and phyloNODF were compared to the random NODF and phyloNODF by calculating the standardized effect size (SES).

To test our four hypotheses (Fig. 1), we compared the magnitude of SES values between guilds and rearrangements, because SES for taxonomic and phylogenetic nestedness are insensitive to changes in the size and shape of the matrix (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Melo, Cianciaruso, & Almeida-Neto, 2014). Standardized effect size indicates how much the observed nestedness deviates positively ($\mathrm{SES} \geq 2$) or negatively ($\mathrm{SES} \leq 2$) from the random expectation at the 5% error level (two-tailed test) (Ulrich, Almeida-Neto, & Gotelli, 2009). Thus, the higher the SES for a given rearrangement, the greater the differences in taxonomic and phylogenetic diversity along that rearrangement when comparing to other rearrangements (Ulrich, Almeida-Neto, & Gotelli, 2009). Counts of the random index values above or below the observed index value represented P-values (Ulrich, Almeida-Neto, & Gotelli, 2009). In total, we analyzed nestedness for 26 occurrence matrices (two rearrangements for each of the 13 guilds; Table 1). We performed the nestedness analyses using the ‘treeNodfTest’ function implemented in the ‘CommEcol’ package (R v3.4.0, R Core Team 2017). To efficiently analyze the nestedness index for large matrices (see Table 1), we applied the ‘treeNodfTest’ function within functions to parallelize computations using a cluster (‘parallel’ package; R v3.4.0, R Core Team, 2017).

Results

When comparing the SES values between guilds and rearrangements, we found weak support for the initial hypotheses. Standardized effect sizes indicate that, for most of the guilds, the observed nestedness was higher than expected by random chance in both forest-to-open and open-to-forest directions. Thus, results revealed much more evidence of niche shifts than niche stasis (Fig. 2a, b). When considering taxonomic nestedness, we observed niche stasis only for granivores, omnivores feeding on invertebrates and seeds, and omnivores feeding on vertebrates and fruits (Fig. 2a). For granivores and omnivores feeding on invertebrates and seeds, we observed higher nestedness than expected in the open-to-forest but random nestedness in the forest-to-open direction; for omnivores feeding on vertebrates and fruits we observed the inverse pattern (Fig. 2a). We did not observe niche stasis when considering phylogenetic nestedness (Fig. 2b). Finally, it is interesting to observe the different magnitudes of SES for taxonomic nestedness between the open-to-forest and forest-to-open directions, which may be due to an ancestral habitat effect (Fig. 2a). We did not observe different magnitudes of SES when considering phylogenetic nestedness (Fig. 2b).

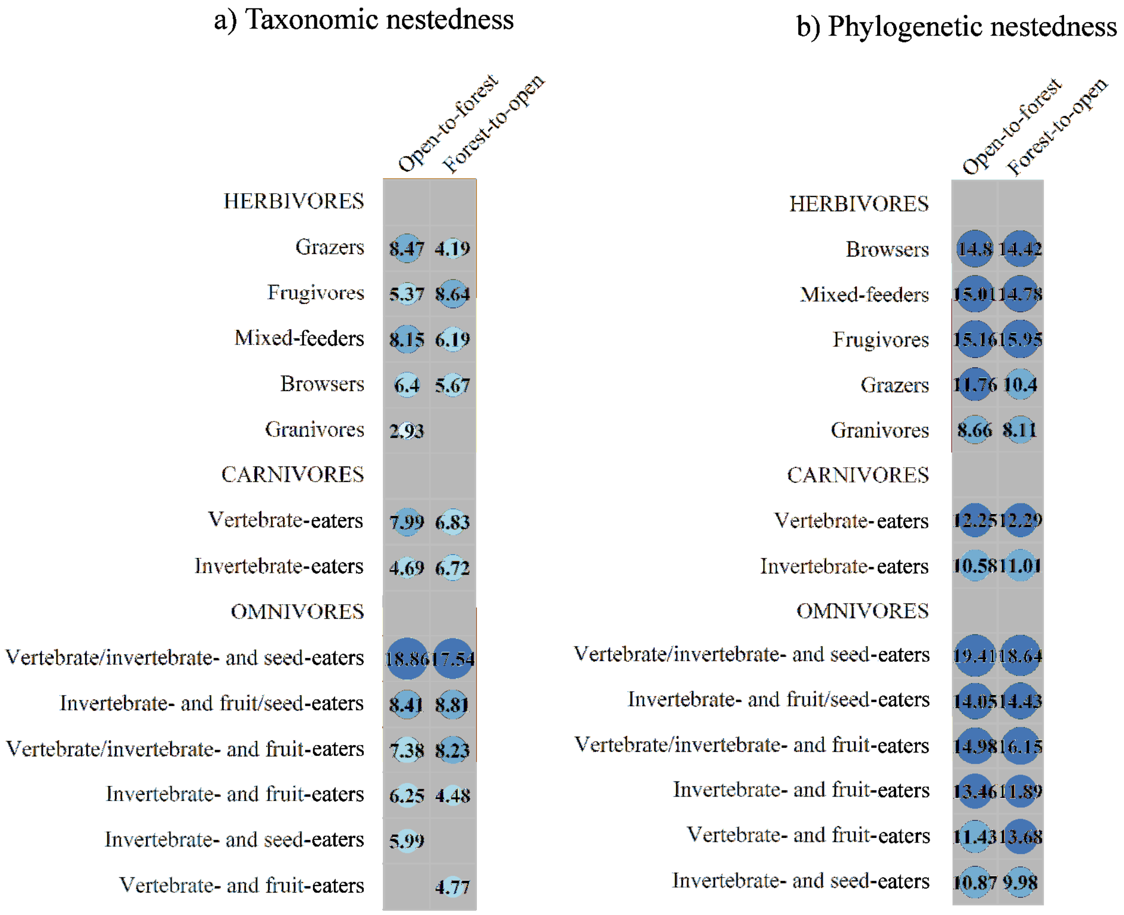

Fig. 2: Standardized effect size (SES) values for each ecoregion rearrangement for (a) taxonomic and (b) phylogenetic nestedness. For clarity we included the guilds in their respective trophic level. Values show how much observed $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ are higher (darker and larger circles) than random nestedness. The absence of a circle indicates that the observed $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$ do not differ from the random $\mathrm{NODF}_{\mathrm{sites}}$ and $\mathrm{phyloNODF}_{\mathrm{sites}}$.

Discussion

The distribution of species and lineages between habitats is controlled by the tendency of the species niche to be either stable or shift over time (Martinez-Meyer, Townsend Peterson, & Hargrove, 2004; Perman, Guisan, Broennimann, & Randin, 2008). Here, we used taxonomic and phylogenetic nestedness to find evidences of different mechanisms (niche stasis and shifts) and directions (forest-to-open and open-to-forest) of mammal distribution dynamics between forest and open ecoregions. Overall, we evidenced patterns of taxonomic and phylogenetic nestedness consistent with niche shifts for most of the dietary guilds.

We expected niche stasis for guilds depending on resources from a specific habitat (e.g. grazers, frugivores) due to a low fitness (low per capita survival and reproductive output) when dispersing toward an environmentally dissimilar habitat (Martinez-Meyer, Townsend Peterson, & Hargrove, 2004; Perman, Guisan, Broennimann, & Randin, 2008). We evidenced non-random taxonomic nestedness for granivores, omnivores feeding on invertebrates and seeds and omnivores feeding on vertebrates and fruits only in one direction, which indicates that the distribution of seed-eating mammals is environmentally bound. Open ecoregions were sources of seed-eating mammal species to forest ecoregions. Seed-eating mammals, such as the Heteromyidae and Dipodidae rodents, have unique morphological adaptations (e.g. bipedal ricochetal locomotion) to feed on small seeds from extremely open, seasonal and arid habitats (Kelt et al., 1996; Kelt, 1999). In contrast, forest ecoregions were sources of species of vertebrate and fruit-eating omnivore species to open ecoregions. Most of the species included in this omnivore guild belong to the *Cephalophus* (Cetartiodactyla) and *Hylomyscus* (Rodentia) genus, which are confined to dense Afrotropic forests. Finally, niche stasis for granivores, omnivores feeding on invertebrates and seeds and omnivores feeding on vertebrates and fruits indicates that, in few cases, moving into habitats that are similar to the ancestral habitat increases the species survival and reproductive output during range expansions (Perman, Guisan, Broennimann, & Randin, 2008).

Niche shifts due to low extinction rates in and successful dispersals into a dissimilar habitat should result in non-directional nestedness for omnivore guilds due to the absence of differences in taxonomic and phylogenetic diversity between ecoregions (Bofarull, Royo, Hernández-Fernández, Ortiz-Jaureguizar, & Morales, 2008; Davies, Purvis, & Gittleman, 2009; Price, Hopkins, Smith, & Roth, 2012). We observed evidences of niche shifts for most of the mammalian dietary guilds, since we found non-random nestedness in a direction different from that expected given the ancestral habitat. It is interesting to note the different magnitudes of SES between the open-to-forest and forest-to-open directions for the taxonomic nestedness. For instance, the difference in richness in the open-to-forest direction was twice-higher than forest-to-open for grazers, mixed-feeder herbivores and vertebrate-eater carnivores (Fig. 2a), in accordance with the origin of herbivores and carnivores in open ecosystems during the Oligocene-Miocene (Cantalapiedra et al., 2014; Cantalapiedra, Hernández-Fernández, & Morales, 2014; Pires, Silvestro, & Quental, 2015). In contrast, richness difference was 1.5 higher in the forest-to-open than open-to-forest direction for frugivores, in accordance with the origin of frugivores in forest habitats (MacFadden, 2006; Kissling et al., 2014).

The lack of phylogenetic nestedness differences between open to-forest and forest-to-open directions indicates that the species composing the mammalian guilds have expanded their distributions toward a habitat different from the ancestral habitat many times, which resulted in diversification (Benton, 2010). For example, forest

Boselaphini bovids are phylogenetically related to open-habitat species which expanded their distribution to forests during periods of forest expansion (Bibi, 2007). The posterior isolation due to forest contraction resulted in the evolution of morphological and behavioral adaptations to persist in forests (e.g., the decrease in body size, the decrease in the degree of hypsodonty and the emergence of solitary behavior) (Bibi, 2007; Damuth & Janis, 2011; Fortelius et al., 2014). Nonetheless, the lack of phylogenetic nestedness may result from the use of dietary guild as unity of analysis, which include species from different mammal orders with very different evolutionary histories. Thus, one of our assumptions (independently of the mammalian orders composing a given guild, the ancestral would be a species preferring the same resource as the extant species) may not hold. An analysis using monophyletic groups may be more appropriate to test distribution dynamics between forest and open ecoregions over time.

The analyses with mammalian guilds indicate that the compsumption of habitat-specific food items did not result in high extinction rates and unsuccessful dispersals in an environmentally dissimilar habitat. Nestedness identified that most of dispersals into environmentally dissimilar habitats resulted in successful occupations and diversifications due to niche shifts. Therefore, both forest-to-open and open-to-forest directions of distribution dynamics occurred during the history of occupation and diversification of the species composing the mammalian dietary guilds. Data on fossil distribution, diet and habitat affinities would be helpful to quantify the rate of extinction following dispersals to environmentally dissimilar habitats. Defining situations in which either niche stasis or shifts occur may improve our understanding of the processes shaping species and lineage distributions over space.

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Authors' contributions

ALL, LDSD and SMH conceived the ideas and designed methodology; ALL collected and analyzed the data; ALL, LDSD and SMH wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

The original trait database of Kissling et al., (2014) is available in the Dryad Repository (http://doi.org/10.5061/dryad.6cd0v). The mammal phylogeny of Fritz, Bininda-Emonds, and Purvis (2009) is available in: DOI: 10.1111/j.1461-0248.2009.01307.x. The mammal range maps are available in IUCN red list website (http://www.iucnredlist.org/), and the ecoregions from Olson et al., (2001) in the WWF website (https://www.worldwildlife.org/biomes).

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Supporting Information

Figure S1.1: The expected structure of the occurrence matrix according to our hypotheses. Rearrangements were expected to produce different degrees of taxonomic and phylogenetic nestedness, because nestedness indexes (NODF and phyloNODF) are sensitive to differences in composition and diversity between pairs of ecoregions. Here, we exemplify that a biogeography effect may weaken nestedness by decrease the differences of richness and composition overlap between pairs of rows and columns of an occurrence matrix (left-side matrices of hypothesis 2 and 4 are less nested than the right-side matrices). The different symbols represent different species; symbols with same shape but different colors indicate phylogenetically related species. obsNODF= Observed taxonomic NODF; obsPHYLO= observed phylogenetic NODF; rndNODF= random taxonomic NODF; rndPHYLO= random phylogenetic nestedness; SES= standardized effect sizes for NODF and phyloNODF. Random indexes were generated by matrix randomization.

Table S1.1: Ecoregion mean species richness ± SD by habitat type and biogeographic realm. We used these criteria plus the ecoregion area to rearrange ecoregions. Details of feeding habits in Table 1.

Table S1.2: Ecoregion mean phylogenetic diversity ±SD by habitat type and biogeographic realm. We used these criteria plus the ecoregion area to rearrange ecoregions. Details of feeding habits in Table 1.

Table S1.3: $\text{NODF}_{\text{sites}}$ (%) for mammal dietary guilds. Null Mean, Standardized Effect Size (SES) and significance values were generated by 500 randomizations of the "permRows" algorithm. Mean ± SD of $\mathrm{NODF}_{\mathrm{sites}}$ values for each dietary guild was calculated across the four matrix rearrangements. In **bold** we showed the rearrangement yielding the strongest nestedness values.

Table S1.4: $\mathrm{PhyloNODF}_{\mathrm{sites}}$ (%) for mammal dietary guilds. Null Mean, Standardized Effect Size (SES) and significance values were generated by 500 randomizations of the 'permRows' algorithm. Mean ± SD of $\mathrm{phyloNODF}_{\mathrm{sites}}$ values for each dietary guild was calculated across the four matrix rearrangements. In **bold** we show the rearrangement yielding the strongest nestedness values.

CAPÍTULO 2

Title: Broad-scale assessment of nestedness between pristine and human-modified habitats

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Abstract

Human-modified habitats that have similar vegetation structure to pristine habitats may be more amenable to animal persistence, but a global assessment of this expectation is lacking. We assessed nestedness in non-volant small mammal assemblages from pristine and human-modified habitats of 52 ecoregions, nine biomes and five realms. We expected least structurally similar human-modified habitats, in comparison with pristine habitats, should be composed by a nested subset of species from richer sites, and that such pattern should differ across realms. We obtained data on small mammal composition in pristine and human-modified habitats by combining an existing database (PREDICTS, 22 studies) with a new database based on peer-reviewed papers (158 held/1 054 total). The combined database included 180 studies, 499 mammal species and 1 052 sites. Pristine habitats consisted of grasslands and forests, and human-modified habitats of open crop fields/clear-cuts, anthropogenic edges and tree-plantations. We built occurrence matrices for all possible comparisons of pristine vs. human-modified habitats within ecoregions, and calculated multi-site nestedness. To determine the most important factor explaining multi-site nestedness, we analyzed several linear mixed models containing habitat comparisons and interaction terms between habitat comparisons, biomes and realms. We found weak, to no, relationship between nestedness and vegetation structure in human-modified habitats. Instead we found geographic variation in the patterns of nestedness between regions. Habitat conversion seems more important for forest than for grassland assemblages, and temperate-biome assemblages seem less susceptible to habitat alterations than tropical ones. Biogeographic variation in nestedness should be considered in conservation planning.

Key words: Anthropocene, biogeography effect, beta-diversity components, beta-diversity partitioning, fragmentation, non-volant small mammal database.

Highlights:

1. New database on small mammal composition in pristine and human-modified habitats
2. Inconsistent relationship between nestedness and habitat similarity across regions
3. Habitat conversion influenced forest mammals more than grassland mammals
4. Temperate biome assemblages appear to be less susceptible to land-use change
5. Region-specific conservation planning may help conserve small mammal species

1. Introduction

The alarming global rate of habitat conversion, fostered by technological advances and increasing food and timber demands, challenges the maintenance of viable animal populations (Newbold et al., 2016, 2015; Laurance et al., 2014; Hoekstra et al., 2005). Habitat fragmentation and conversion often cause an ordered process of species extinction and assemblage disaggregation, resulting in a pattern where impoverished assemblages from human-modified habitats are a nested subset of richer assemblages that occur in pristine habitats (Baselga, 2010; Patterson and Atmar, 2000, 1986). Species that are rare (Patterson and Atmar, 2000), habitat-specialists (Santos-Filho et al., 2016; Hurst et al., 2014), large bodied (Galetti et al., 2015), or have slow-reproduction (Flynn et al., 2009), or occupy a high-trophic level (Ewers and Didham

2006; Laurance, 1994), are more susceptible to decreased remnant area and increased isolation common in human-modified landscapes.

Some local studies have found that human-modified habitats with similar vegetation to pristine habitats host many native species (Corbelli et al., 2015; Martin et al., 2012; Passamani and Fernandez, 2011; Prevedelo and Vieira, 2010; Fonseca et al., 2009), because changes in abiotic conditions and vegetation heterogeneity are minimal (Prevedelo and Vieira, 2010; Fischer and Lindemeyer, 2007). However, this result is not consistent across studies (Ewers and Didham, 2006; Debinski and Holt, 2000) and high numbers of native species are lost even when human-modified habitats have similar vegetation structure to pristine habitats (Newbold et al., 2016, 2015; Yue et al., 2015; Barlow et al., 2007). The discrepancy among these local studies may be caused by site- or region-specific differences in species richness and composition (Penone et al., 2016; Holt et al., 2013; Dobrovolski et al., 2012) indicating that a broad-scale analysis is necessary to establish the consistency of the relationship between vegetation structure and species losses. Here, we present a broad-scale analysis to assess how biodiversity decreases along pristine-to-human-modified habitats.

Biogeographic history, climatic conditions and gradients of water and energy availability are broad-scale factors that alter the type and suitability of habitats across regions (Hawkins et al., 2003; Olson et al., 2001). These factors generate the uneven distribution of species within and between regions (Penone et al., 2016; Holt et al., 2013) and produce a natural change in species composition over time and space (Magurran, 2016). Thus, we might expect a geographical variation in how species respond to habitat conversion. For instance, species from regions composed by a mosaic of native grasslands and forest habitats may be less susceptible to habitat conversion and show weaker nestedness in human-modified habitats than species from regions composed by a single vegetation type (Lindell et al., 2007). Strategies for biodiversity conservation may therefore be region specific if the relationship between species losses and vegetation similarity is inconsistent across regions.

We assessed the degree of nestedness in the composition of non-volant small mammal assemblages from pristine and human-modified habitats in 52 ecoregions, nine biomes and five realms. We evaluated non-volant small mammals because they have a wide range of dietary and morphological adaptations allowing them to occupy human-modified habitats (Martin et al., 2012; Medan et al., 2011; Flynn et al., 2009). We assembled a database on the small mammal composition in pristine forests and grasslands and in three human-modified habitats: tree plantations, edges and open crop fields/clear-cuts. We computed nestedness between forest vs. human-modified habitats and grassland vs. human-modified habitats across biomes and realms. If habitat modification results in nestedness then we would expect that least structurally similar habitats would be more nested. However, given the variation in environmental conditions and history across biomes and realms, nestedness patterns might also vary geographically. Nestedness should vary between habitats across realms, because Australasia, the Neotropics and Nearctic might have more forest-adapted fauna in their current species pool than the Afrotropics and Palearctic, which have more open- and mosaic-adapted species (Malhi et al., 2016; Smith et al., 2016; de Vivo and Carmignotto, 2004). Therefore, we expected that tree plantations should be a nested subset of species from pristine forests for Australasia, the Neotropics and Nearctic but not for the Afrotropics and Palearctic. We also expected that open crop fields/clear-cuts should be a nested subset of species from pristine grasslands for the Afrotropics and Palearctic but not for Australasia, the Nearctic and Neotropics.

2. Methods

2.1 Obtaining the data

We used a database based on bibliographic searches (Luza et al., unpublished data; Appendix A1) and the PREDICTS database (Hudson et al., 2017) to obtain data on small mammal assemblage composition in pristine and human-modified habitats (see Appendix A2). The bibliographic search database provides a total of 220 of the 1 054 reviewed studies used several trapping techniques to sample non-carnivore, non-strictly forest (e.g. Primates, Dermoptera) species with an averaged body mass ≤ 5kg (references in Appendix A3). From the 220 studies, we removed those that imprecisely defined sampled habitat ("NA" entries for "Habitat" descriptor), sampling effort (trap/nights, ("NA" entries for "Effort_by_habitat" descriptor) or did not use one of the three classical techniques for small mammal sampling (live-, snap- and pitfall-traps). Sampling techniques such as camera-traps, transects, tracking tunnels, owl-pellet and scat analysis were only considered if they supplemented one of the three standard trap types. We removed Xenarthra, Monotremata, Macroscelidea, Pholidota because they represented a small number of species, and unidentified species.

Using the PREDICTS database (Hudson et al., 2017), we added information on assemblage composition in forest, grassland, tree plantation and crop fields/clear-cut habitats by matching the two databases according to descriptors containing similar information (study, site designation, longitude and latitude, sampling method, habitat type, species identity and incidence; see Appendix A2). Similar to the bibliographic search database, we removed from PREDICTS those studies that did not use one of the three classical techniques for small mammal sampling. Our combined database: 1) included fine-scale information on small mammal composition in paired human-modified and pristine habitats, 2) included information acquired through similar sampling techniques, and 3) clearly differentiated artificial pastures from pristine grasslands and savannas (Table A2.1) (Veldman et al., 2015; Parr et al., 2014).

Forest and grassland fragments, continuous remnants and advanced secondary-regeneration were considered pristine habitats, because composition and richness differences between these habitats are minimal (Newbold et al., 2015). We considered managed forests as pristine when the authors provided enough information about logging regimes to judge that they were only minimally disturbed (e.g. Ransome et al., 2009; Bayne and Hobson, 1998). Grasslands and savannas with native vegetation were considered as pristine habitats even if they were grazed by domesticated animals (Veldman et al., 2015). An edge was considered the boundary between the pristine and human-modified habitats. Species composition at edges was generally quantified with traps paralleling the sharp border between two habitats, mostly between forest and human-modified habitats (e.g. Santos-Filho et al., 2016; Ransome et al., 2009; Bayne and Hobson, 1998). We considered tree plantations those tree monocultures planted in grasslands and cleared forests. We considered clear-cuts, crop fields and young-secondary vegetation as open habitats. Since PREDICTS characterizes both grasslands and forest as primary vegetation, we refined this designation using the study description field ‘Habitat_as_described’ (see Hudson et al., 2017). If this entry was empty, we used PREDICTS broad classification of biome to differentiate forests from grasslands.

2.2 Data analysis

We assessed nestedness between all possible comparisons of pristine and human-modified habitats within the world ecoregions (Olson et al., 2001). Ecoregions are biogeographically and climatically homogeneous areas that capture environmental heterogeneity at broad scales and are considered to host distinct ecological communities

(Olson et al., 2001). We built occurrence matrices for each ecoregion to constrain the geographic extent used in site comparisons (i.e., to avoid calculating nestedness among sites from Amazon and Chilean forests which lack shared species). Each matrix within an ecoregion was our basic unit for nestedness analysis. Each ecoregion had up eight matrices of habitat comparisons: four matrices of forest and human-modified habitat comparisons (forests vs. forests, forests vs. edges, forests vs. open, forests vs. tree plantations), and four matrices for grassland and human-modified habitat comparisons (grasslands vs. grasslands, grasslands vs. edges, grasslands vs. open, grasslands vs. tree plantations). We analyzed nestedness in matrices containing ≥ 3 sites and ≥ 4 species to obtain multi-site comparisons and to avoid nestedness values close to 0 for very small matrices. We did not include data for the Indomalayan realm because it only had four habitat comparisons (Table A2.2).

For each matrix of habitat comparisons, we partitioned the multi-site Sorensen index and used the component referring to the dissimilarity due to nestedness ($\beta_{NES,}$ Baselga, 2010). Dissimilarity due to nestedness quantifies the total dissimilarity among sites caused by the process of ordered loss of species (Baselga, 2012, 2010; Patterson and Atmar, 1986). Species loss may nullify dissimilarity in species composition between pristine and the human-modified habitats when habitat conversion causes the loss of rare and endemic species but not of dominant and generalist species (Patterson and Atmar, 2000). By comparing the composition of species occurring in the species richer sites with those present in the poorer sites, the nestedness component of beta-diversity permits evaluation of the effect of habitat conversion on the loss of rare and endemic species (Baselga, 2010; Patterson and Atmar, 2000) and the potential of human-modified habitats to conserve regional diversity (Socolar et al., 2016). Dissimilarity due to nestedness represents an index proportional to the total number of species being considered in the multi-site comparisons, because partitioning removes the effect of differences in richness for beta diversity components (Baselga, 2012, 2010). Dissimilarity due to nestedness (β_{NES}) will be equal to one when the sites share all their species (no compositional difference), and zero when no species is shared (complete species replacement; Baselga, 2010).

We evaluated variation in dissimilarity due to nestedness (β_{NES}) using Linear Mixed Models (LMM; Bates, 2010) because the log of β_{NES} was normally distributed. LMM are hierarchical models where the response variables can be modeled as a function of fixed factors describing biological processes, while accounting for random factors related to data collection and sampling (Bates, 2010). In the case of multi-site Sorensen index, the number of sites in each matrix can be considered a random factor affecting the index values (Baselga, 2012, 2010). To evaluate this effect, we first correlated β_{NES} with the number of sites. Given the low but significant negative correlation ($r= -0.22$, $p < 0.001$), we ran a preliminary LMM analysis including the number of sites as random effect and habitat comparison, ecoregion, and interaction terms between biome x habitat, realm x habitat, realm x biome as fixed factors. Preliminary LMM analysis showed no variance in β_{NES} explained by the number of sites. In addition, preliminary LMM showed that ecoregions explained the largest amount of the variance in β_{NES} but standard deviations of ecoregion mean nestedness was very wide or could not be calculated, because many of the ecoregions had less than two nestedness values (i.e., 26 ecoregions had multi-site nestedness values only for two comparisons of pristine vs. modified habitat [e.g., forest vs. open and forest vs. edge]). Thus, ecoregions were treated as a random factor in our LMM analyses.

Since the number of nestedness measurements was much higher for forest vs. human-modified habitats (118 values) than for grassland vs. human-modified habitats

(33 values), we evaluated if the number of nestedness measurements could alter the results. We conducted a random sampling of 33 values of nestedness across the 118 values for forest vs. human-modified habitat comparisons within the realms. Thus, the number of nestedness values for forest vs. human-modified habitat comparisons was the same as grassland vs. human-modified habitat comparisons within each realm. We repeated the random sampling procedure 100 times and conducted 100 different LMM and model selection analyses. We conducted a particular sampling using the function ‘sample’ and repeated 100 times using the function ‘replicate’ (‘base’ package, R Core Team, 2017). We reported the marginal and conditional pseudo-R^2 values averaged across the 100 LMM analysis and the counting of the times that each model appeared as the best-ranked model across the 100 LMM analysis (see Results).

Our final set of models, built to test if the degree of nestedness is influenced by region and habitat modification, considered β_{NES} as response variable and different covariates as fixed factors. We built candidate models where: 1) nestedness varied according to habitat irrespective of the region (i.e., the independent effect of habitat comparison on β_{NES}), 2) nestedness varied according to both habitat and biome, where nestedness should differ when comparing similar habitats from different biomes (i.e., the effect biome x habitat comparison interaction on β_{NES}), 3) nestedness varied according to both habitat and realm, where nestedness should differ when comparing similar habitats from different realms (i.e., the effect of realm x habitat comparison interaction on β_{NES}), and 4) nestedness varied according to both biome and realm, where nestedness should differ when comparing similar biomes from different realms (i.e., the effect of realm x biome interaction on β_{NES}). For these analyses, we removed all interaction terms represented only by one matrix.

We selected the best model among the candidate models using Akaike Information Criterion for small samples sizes (AICc) (Burnham and Anderson, 2002). We ranked the best models according to their differences in AICc (ΔAICc) and their relative weight. We considered the model (s) with substantial empirical support those with ΔAICc ≤ 2 (Burnham and Anderson, 2002). The best-ranked model was readjusted by removing high leverage points (according to Cook's Distance), calculating the exponent of log βsne and removing the intercept to obtain the estimated mean of βsne (Crawley, 2007). Posteriorly, we calculated mean differences and confidence intervals for the levels of the fixed factor explaining the largest variance of βsne (Kuznetsova et al., 2017). We used Satterthwaite's approximation to estimate denominator degrees of freedom and p-values for the Linear Mixed Models (Kuznetsova et al., 2017). We calculated conditional and marginal pseudo-R^2 values for LMM (Nakagawa and Schielzeth, 2013) to obtain the relative contribution of fixed and random effects to nestedness degree. We partitioned the multi-site Sorensen using the package 'betapart', ran LMM using package 'lme4' and selected models using package 'MuMIn'. We identified high leverage points using package 'influence.ME' and calculated mean differences and confidence intervals using the package 'lmerTest'. All analyses were conducted in R v3.4.0 (R Development Core Team, 2017).

3. Results

Our final database includes 180 studies. Of these, 158 were obtained from Luza et al. (unpublished data) and 22 from PREDICTS (PREDICTS include 25 suitable studies on small mammal composition, but three of them were already included in Luza et al. database [see the complete list of data sources in Appendix A3]). Our combined database had few grassland sites in Australasia, Indomalayan and east Palearctic (Figure

1). Most sites were in the Neotropics and Nearctic (Figure 1, Table A2.1) and in tropical and temperate forest biomes (Table A2.2).

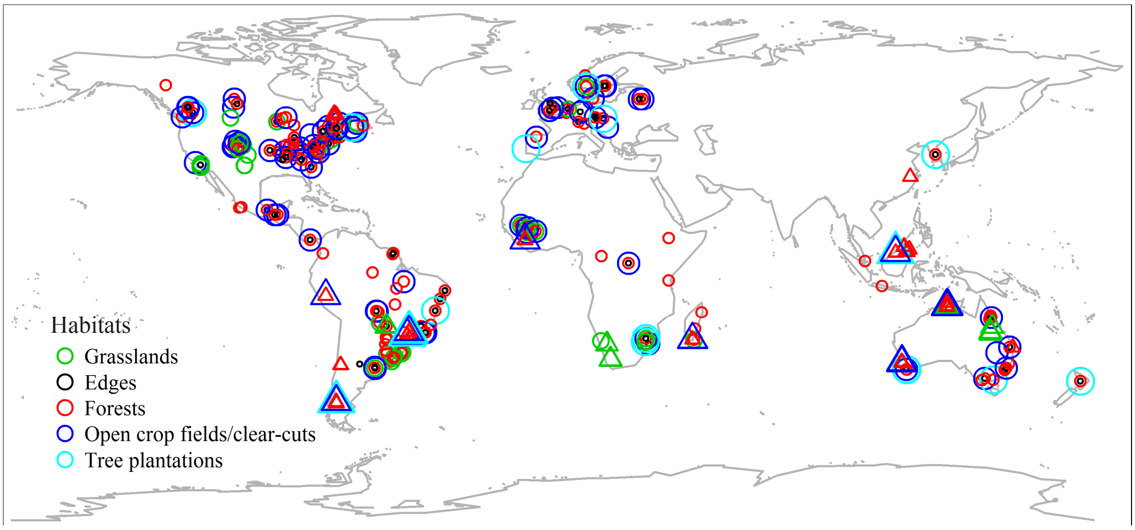

Figure 1: Global distribution of habitats in the combined database. Our combined database includes information from the Luza et al. (circles) and PREDICTS database (triangles).

Overall, we obtained composition data for 499 small mammal species from eight orders (Diprotodontia, Eulipotyphla, Rodentia, Didelphimorphia, Afrosoricida, Dasyuromorphia, Lagomorpha and Peramelemorphia) in 1 052 sites (Figure 1, Table A2.1). After removing ecoregions with few species and sites, the dataset included measurements of nestedness for 151 matrices (118 for forests vs. human-modified habitats, and 33 for grasslands vs. human-modified habitats) in 52 ecoregions, nine biomes and five realms. Matrices had, on average ± sd, 13.37 ± 18.52 sites (range= 3-110 sites) and 14.30 ± 7.51 species range 4-35 species), for forest vs. human-modified habitat comparison. Matrices had, on average ± sd, 10.88 ± 10.66 sites (range 3-40) and 13.97 ± 6.24 species (range 4-27) for grassland vs. human-modified habitat comparison.

Our analyses of dissimilarity due to nestedness between pristine and human-modified habitats within the ecoregions showed that habitat comparison was the covariate included in the most plausible model for nestedness between forest and human-modified habitats, although it explained only a very small portion of total variation in nestedness (≈ 1%, Table 1). Habitat comparison appeared as the most plausible model (ΔAICc ≤ 2) in 64 of the 100 LMM analysis (Table 2). This model showed that dissimilarity due to nestedness between forests and open crop fields/clear-cuts was significantly higher than nestedness between forest sites (Figure 2A); the difference between crop fields/clear-cuts and tree plantations was marginally significant. Since the first model explained a small portion of total variance, we also explored the results for the second model (realm x biome interaction) in which fixed factor explained more than 40% of total variation in nestedness (Table 1). Realm x biome interaction appeared as the second most plausible model in most of the 100 LMM analysis (Table 2). We found higher nestedness in Nearctic Boreal Forest and Taiga than in Tropical and Subtropical Moist Broadleaf Forests from the Afrotropics and Neotropics, and in Tropical and Subtropical Grasslands, Savannas and Shrublands from the Neotropics (Figure 2B).

The model containing the interaction between realm and biome had the best explanatory power for nestedness between grassland and human-modified habitats (Table 1). The habitat comparison model explained minor variation in nestedness (≈ 3%) and was not included among the best ranked models (ΔAICc < 2; Table 1). Nestedness was significantly higher for Neotropic Temperate Grasslands, Savannas and Shrublands compared to Neotropic Tropical Grasslands, Savannas and Shrublands (Figure 3).

Table 1: Model-ranking table for the linear mixed models. Models were ranked according ΔAICc and weight. Marginal (R^2m) and conditional (R^2c) pseudo-R^2 values refers to the contribution of fixed and fixed + random effects, respectively, to explain variation in nestedness degree (β_{NES}).

Comparison/ Model	Int (Mean β_{NES})	df	logLik	AICc	ΔAICc	Weight	R^2m	R^2c
Forest vs. human-modified habitat								
β_{NES} ~ habitat comparison + (1|ecoregion)	0.137	6	-97.072	206.9	0	0.995	0.008	0.830
β_{NES} ~ realm x biome interaction + (1|ecoregion)	0.144	20	-84.06	217.4	10.41	0.005	0.411	0.813
Grassland vs. human-modified habitat								
β_{NES} ~ realm x biome interaction + (1|ecoregion)	0.188	10	-10.174	51.9	0	0.828	0.672	0.672
β_{NES} ~ habitat comparison + (1|ecoregion)	0.155	6	-19.712	55.1	3.15	0.172	0.028	0.731

Table 2: Results for 100 LMM analysis of forest vs. human-modified habitat comparisons. We used the same number of nestedness values as in grassland vs. human-modified habitat comparisons (33 values) in each one of the 100 LMM analysis.

Model	Times as the most plausible model †	Times as the second most plausible model	Marginal pseudo-R^2 ‡	Conditional pseudo-R^2 ‡
β_{NES} ~ habitat comparison + (1|ecoregion)				
	64	31	0.03 ± 0.03	0.91 ± 0.14
β_{NES} ~ biome x habitat comparison interaction + (1|ecoregion)				
	15	10	0.44 ± 0.14	0.98 ± 0.04
β_{NES} ~ realm x habitat comparison interaction + (1|ecoregion)				
	23	24	0.26 ± 0.12	0.95 ± 0.12
β_{NES} ~ realm x biome interaction + (1|ecoregion)				
	0	35	0.47 ± 0.12	0.88 ± 0.15

† Counting of times that the model appeared as the best-ranked model (ΔAICc ≤ 2).

‡ Pseudo-R^2 values averaged across 100 LMM analysis.

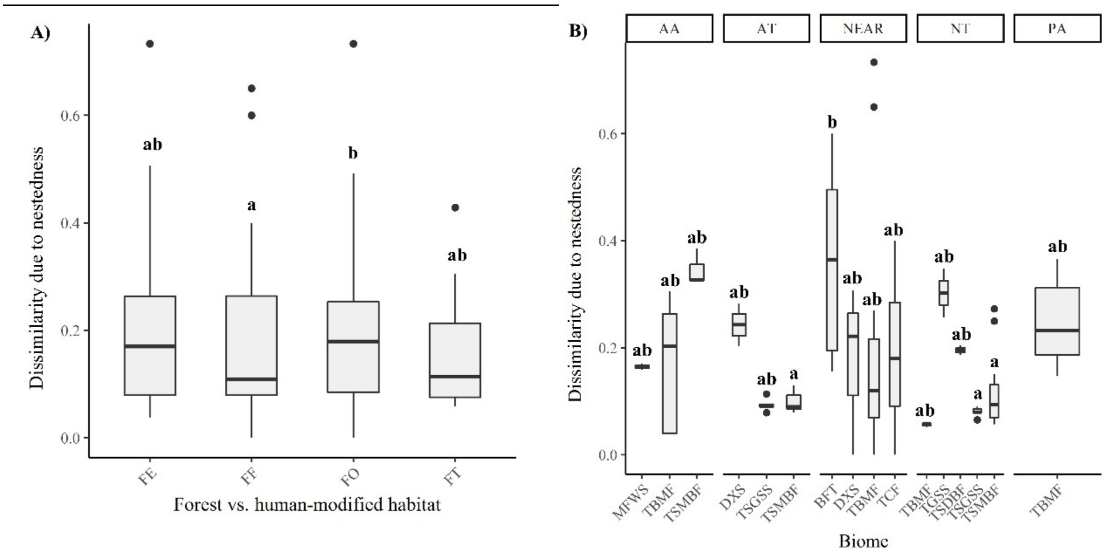

Figure 2: Mean, 1st and 3rd quartiles of nestedness between (A) forests and human-modified habitats and (B) between biomes across realms. Significant differences (different letters) were considered when $p \leq 0.05$. Points are outliers. Habitats: F= forest, E= edge, O= open, T= tree plantation. Realms: AT= Afrotropics, NEAR= Nearctic, NT= Neotropics, PA= Palearctic. Biomes: BFT= Boreal Forests and Taiga, DXS= Desert and Xeric Shrublands, MFWS= Mediterranean Forests, Woodlands and Shrublands, TBMF= Temperate Broadleaf and Mixed Forests, TCF= Temperate Coniferous Forests, TGSS= Temperate Grasslands, Savannas and Shrublands, TSBMF= Tropical and Subtropical Moist Broadleaf Forests, TSDBF= Tropical and Subtropical Deciduous Broadleaf Forests, TSGSS= Tropical and Subtropical Grasslands, Savannas and Shrublands.

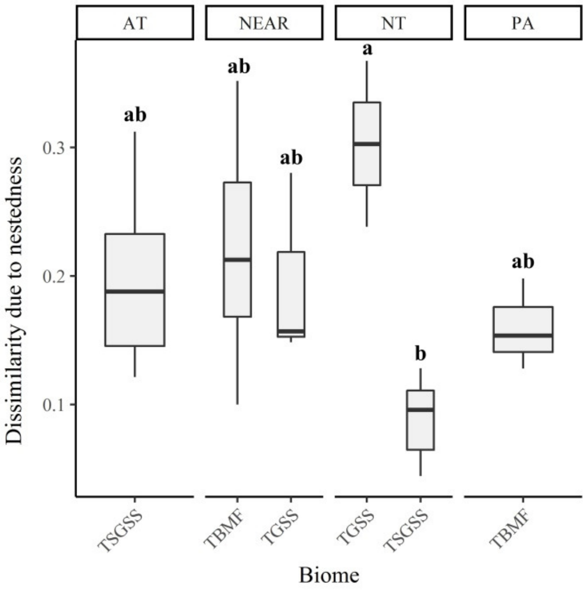

Figure 3: Mean, 1st and 3rd quartiles of nestedness between biomes across realms. Significant differences (different letters) were considered when $p \leq 0.05$. Realms: AT= Afrotropics, NEAR= Nearctic, NT= Neotropics, PA= Palearctic. Biomes: MFWS= Mediterranean Forests, Woodlands and Shrublands, TSGSS= Tropical and Subtropical Grasslands, Savannas and Shrublands, TBMF= Temperate Broadleaf and Mixed Forests, TGSS= Temperate Grasslands, Savannas and Shrublands, TSDBF= Tropical and Subtropical Deciduous Broadleaf Forests.

4. Discussion

Human-modified habitats are intensively managed to provide ecological services such as the production of food, fuel, timber and fiber (Laurance et al., 2014; Perrings et al., 2012; Flynn et al., 2009). These habitats often differ in vegetation structure when compared to native vegetation (Fischer and Lindemeyer, 2007; Ewers and Didham, 2006). In our global analysis of small mammal assemblage nestedness between pristine and human-modified habitats with different vegetation structure, we found weak, to no, relationship between nestedness and the vegetation structure of human-modified habitats. Instead, we found strong geographic variation in the patterns of nestedness between regions, which may explain previous disparate results (Tscharntke et al., 2012; Fischer and Lindemeyer, 2007; Ewers and Didham, 2006; Debinski and Holt, 2000). Biogeographic and historical factors influenced how species respond to habitat alteration, highlighting that region specific actions may be more fruitful for conservation planning than actions based on habitat similarity.

The effect of habitat conversion appeared to be more important for forest mammals than for grassland mammals (Sodhi et al., 2007). The subtle effect of habitat for forest mammals indicated that nestedness is higher between forests and open crop fields/clear-cuts than between forest habitats. Thus, different forest sites have higher compositional differences (i.e., higher turnover) than forests and open crop fields/clear-cuts, because a subset of generalist forest species persist in human-modified habitats with open structure (Passamani and Fernandez, 2011; Ransome et al., 2009). Similar results by Panzacchi et al., (2010) showed that habitat simplification due to clear-cutting and agriculture favored species that occur in both forests and fields at the expense of primarily forest-dwellers. This weak habitat effect was not apparent for grassland assemblages, perhaps because human-modified habitats provides supplementary or complementary resources to many small mammal species from grasslands and savannas (e.g. Martin et al., 2012; Bilenca et al., 2007; Johnson et al., 2002). For example, small mammal assemblages from Afrotropic grasslands might be resistant to afforestation, since no difference in composition was observed between native grasslands and tree plantations (Johnson et al., 2002). In the Neotropic temperate grasslands, borders of native grasslands surrounding crop fields were preferentially used by small mammals likely because they provide suitable sites for reproduction and shelter. In addition, many of species occurring in grassland borders exploit human-modified habitats during periods of high crop cover and resource availability (Bilenca et al., 2007). The lack of nestedness in grasslands may also be result of mammal evolution in grasslands experiencing natural disturbances such as burning, grazing by large herbivores and drought (Parr et al., 2014; Bond and Parr, 2010; de Vivo and Carmignotto, 2004).

We found geographical variation in how species respond to habitat conversion, where the composition of small mammal assemblages in temperate biomes was more nested than assemblages in tropical biomes. A globally and taxonomically (from bacteria to mammals) comprehensive meta-analysis on beta-diversity components also detected a pattern where nestedness increased toward temperate and polar regions (Soininen et al., 2018). Temperate-biome assemblages may be less susceptible to species losses due to land use change than tropical ones, because variation in species composition is lower in temperate regions (Tscharntke et al., 2012; Lindell et al., 2007; Sodhi et al., 2007). Past glaciation and climate seasonality likely influenced richness and distribution of species by causing more extinctions of small-ranged and rare species in temperate and seasonal regions (Dobrovolski et al., 2012; Davies and Buckley, 2011; Jansson, 2003; Hawkins et al., 2003). Widespread and generalist species, which currently dominate the assemblages from temperate and seasonal regions, were less affected by the historical extinctions (Dobrovolski et al., 2012; Davies and Buckley, 2011; Jansson, 2003). In contrast, climate stability allowing the persistence of a high number of rare, small-ranged and endemic species in the sites from Afrotropic and Neotropic Tropical Forests and Savannas, might explain the lower nestedness but higher turnover when compared to sites from Nearctic Boreal Forests and Neotropic Temperate Grasslands (Dobrovolski et al., 2012; Davies and Buckley, 2011; Jansson, 2003). Therefore, even in the absence of human impacts, assemblages located in temperate regions tend to show higher nestedness than assemblages from tropical regions (Soininen et al., 2018; Socolar et al., 2016).

Gaps in our combined database indicate regions where local studies on habitat conversion effects should be conducted. Most of our data were from tropical and temperate forest biomes (72% of total) and, within these biomes, we had more information for forests (49% of total) than for other habitats. Clear-cuts are particularly well sampled in Nearctic and contributed to most of the mammal composition data in open-habitats of temperate regions (e.g. Ransome et al., 2009; Bayne and Hobson, 1998), while crop fields are mainly studied in tropical biomes from the Neotropics and Australasia (e.g., Medan et al., 2011; Bilenca et al., 2007; Woinarski et al., 2009). We lack data for most human-modified habitats in the Indo-Malayan realm, a highly biodiverse region under accelerated forest clearing to oil-palm plantations (Yue et al., 2015; Laurance et al., 2014). Tree plantations were the least represented habitat in our database, likely because afforestation has expanded only recently in the Neotropics and Afrotropics (Veldman et al., 2015), and few studies have evaluated its effect on savanna and grassland biodiversity (e.g., Martin et al., 2012; Johnson et al., 2002). Finally, our database is underrepresented in native grasslands and savannas from Palearctic, Afrotropics and Neotropics. The research bias present in our database indicates that biomes of grasslands and savannas are understudied, resulting from the misinterpretation that habitat fragmentation is a tropical- and forest-specific problem (Veldman et al., 2015; Parr et al., 2014; Hoekstra et al., 2005).

5. Conclusions

Biogeographic variation in nestedness, which characterizes an ordered process of species extinction and assemblage disaggregation, should be considered in conservation planning. In temperate regions, improving the quality of human-modified habitats using low-yielding and wildlife-friendly practices for croplands and forestry (land-sharing) may conserve small mammals because site composition is more nested and has a large portion of the regional species pool (Socolar et al., 2016; Sodhi et al., 2007). In addition, creating large reserves in species-rich temperate regions may ensure the conservation of much of the regional species pool (Socolar et al., 2016; Baselga, 2010). In tropical regions, conservation must prioritize the conservation of native habitats because species composition changes from site to site (Dobrovolski et al., 2012; Baselga, 2010). Creating small reserves of grassland and forest habitats, restoring degraded habitats and corridors of native vegetation, and setting aside native habitats nearby crop fields and tree plantation may help conserve mammal species in tropical regions (Socolar et al., 2016; Laurance et al., 2014; Flynn et al., 2009; Rosenzweig, 2003). Future research should test across-taxa consistency in nestedness between pristine and human-modified habitats, since the geographic variation in nestedness appears to be a general trend for terrestrial plant and animal assemblages.

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Appendices

Appendix A1: Description of the database based on bibliographic searches.

Appendix A2: Obtaining the data and defining the basic sampling unit for nestedness analysis.

Appendix A3: List of 180 data sources included in the present manuscript.

CAPÍTULO 3

Running head: **Winners and losers of habitat conversion**

Title: **Inferring the strength of extinctions and immigrations in non-volant small mammal communities from human-modified habitats**

Keywords: Anthropocene, biodiversity trends, dark diversity, dispersal-extinction balance, fragmentation, mammal dispersion, regional species pool.

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Article Impact Statement: Small mammal communities from human-modified habitats host as much of the pool richness, functional diversity and composition as pristine habitats.

Inferring the strength of extinctions and immigrations in non-volant small mammal communities from human-modified habitats

Abstract: Differentiating local extinctions from immigrations is relevant because we may not find local biodiversity losses due to land-use change when extinctions are counterbalanced by immigrations. We evaluated whether communities in pristine (forests and grasslands) and human-modified habitats (forest edges, grassland edges, tree plantations, clear-cuts and crop fields) differed in richness, functional diversity and species and functional composition as expected given differential strength of extinction and immigration processes using a probabilistic pool approach. We obtained data on non-volant small mammal composition in pristine and habitat communities from two recently compiled databases. To build a probabilistic species pool with the probabilities of species occurrence in the local communities, we used annual rates of species dispersal from trait databases and probabilities of species persistence given the environment from species distribution modelling. We used linear regressions with generalized least squares to test whether pristine-habitat communities have more diversity of the pool than human-modified habitat communities. The response variables were the local community richness, functional diversity, composition and functional diversity of forest, grassland and human-modified habitat species relative to the probabilistic pool diversity. We found that human-modified habitats (except grassland edges) host similar pool richness and functional diversity as pristine habitats; functional diversity was lower in tree plantations, clear-cuts and crop fields than in forests. Composition analyses suggested that forest edges and grassland edges host less forest species of the pool than other habitats. Furthermore, the functional diversity of forest species was lower in grasslands, grassland edges and crop fields. Human-modified habitats host as many grassland species as pristine habitats, and forests host more human-modified habitat species than clear-cuts; human-modified habitats host similar functional diversity of grassland and human-modified habitat species as pristine habitats. Results showed that small mammal communities in human-modified habitats are under both weak extinction and immigration, an indicative of community resistance to land-use changes. However, the local extinction of few specialist species might not be compensated by the immigration of functionally similar species.

Introduction

The composition of local communities results from the sorting of species from the regional species pool (Karger et al. 2016; Lessard et al. 2016). The sorting is mediated by species-specific dispersal ability and site-specific environmental suitability, which influence the probability of species reaching and surviving in a given location, respectively (Belmaker & Jetz 2013; Karger et al. 2016; Lessard et al. 2016). Human activities can alter the environmental suitability of sites and may trigger the re-assembly of communities and ecosystems through local extinctions and immigrations (Dornelas et al. 2014, McGill et al. 2015; Newbold et al. 2015, 2016; Isbell et al. 2017). Human-modified landscapes are often mosaics of pristine-habitat patches embedded in human-modified habitats and likely vary in their suitability for different species (Umetsu et al. 2008; Prevedevello & Vieira 2010). The extinction of some pristine-habitat species, often termed ‘losers’, can release resources and provide opportunity for generalist and invasive species from other habitats and regions (termed ‘winners’) to immigrate into human-modified habitats (Jackson & Sax 2010; McGill et al. 2015). Differentiating local extinctions in from immigrations into human-modified habitats is important because we may not find an effect of land-use change on local species richness and functional diversity when local extinctions are counterbalanced by immigrations, yet we may be losing species and ecological functions characteristic of pristine habitats (Vellend et al. 2013, 2017; Dornelas et al. 2014; McGill et al. 2015). Here, we were interested in the processes of extinction and immigration because they occur in shorter temporal and finer spatial scales than speciation and genetic drift. Thus, extinction and immigration may be more sensitive to anthropogenic activities than speciation and genetic drift.

Evaluating species (e.g., richness, composition) and functional (e.g., functional distance between coexisting species, functional distance according to composition) diversity of a local community considering the diversity of its regional species pool is one way to distinguish local extinctions from immigrations (Magurran 2016; Lewis et al. 2017). In particular, a probabilistic species pool incorporates a probabilistic perspective to the concept of regional species pool (Karger et al. 2016; Lessard et al.

2016). The probabilistic species pool provides a null expectation, and potentially also a historical baseline, for comparing the observed species and functional diversity of a local community to that we would expect given the probabilistic species and functional diversity of the regional species pool (Karger et al. 2016). The species in the regional pool have a certain probability of overcoming dispersal barriers, persisting to the regional environment and belonging to a given local community (Belmaker & Jetz 2013; Karger et al. 2016; Lessard et al. 2016). Therefore, local communities might be composed of many specialized and functionally unique species, which have high probability to persist to the local environment (Belmaker & Jetz 2013; Lessard et al. 2016). Since these specialized species should be frequent in pristine forests and grasslands due to weak extinction and immigration rates (Gibson et al. 2011; Newbold et al. 2015, 2016; but see Barlow et al. 2016), the communities from pristine habitats should be more diverse than communities from human-modified habitats. However, such specialized and functionally unique species may become the 'losers' and be replaced by the 'winners' due to modifications in the quality, size, density and connectivity of habitat patches (Umetsu et al. 2008; Flynn et al. 2009; Corbelli et al., 2015; Dornelas et al. 2014). Here, we infer the strength of extinctions and immigrations using the probabilistic pool approach to calculate a community completeness index (Pärtel et al. 2013; Lewis et al. 2017) (see $p^{i}\Psi$ and $p^{i}\Psi_{C}$, Box 1) and test whether communities in pristine (forests and grasslands) and human-modified habitats (forest edges, grassland edges, tree plantations, clear-cuts and crop fields) differ in species richness and functional diversity and in species and functional composition (Fig. 1).

A community under both weak local extinctions and immigrations in a human-modified habitat should have similar species richness, functional diversity and composition relative to the regional species pool as a pristine habitat community (Fig.

1A) (Debinski & Holt 2000; McGill et al. 2015). A community under strong extinction and weak immigration in a human-modified habitat should have lower species richness and functional diversity and impoverished species and functional composition relative to the pool than a pristine habitat community (i.e., Fig. 1B) (Debinski & Holt 2000; McGill et al. 2015). In this case, the human-modified habitat has a small proportion of the regional species and functional pool and, since only few pristine-habitat species tolerating habitat modifications can persist in the modified habitat, many ecological functions are lost. Habitat modification may also substantially increase species richness and functional diversity and alter the species and functional composition when weak extinction is overcompensated by strong immigration, which may result in a new community comprised of many 'winners' that were absent before habitat conversion (Jackson & Sax 2010; Dornelas et al. 2014; McGill et al. 2015). In this case, a largest proportion of the pool should be present in the human-modified habitat (i.e., Fig. 1C). Finally, a community under both strong local extinction and immigration in a human-modified habitat should have the same richness and functional diversity relative to the pool as a pristine habitat community (Debinski & Holt 2000; Jackson & Sax 2010; McGill et al. 2015). However, the species and functional composition of the human-modified habitat community should be substantially altered because many 'winners' with distinct habitat preferences should thrive in the human-modified habitat (Fig. 1D).

Non-volant small mammals, which comprise species belonging to the Afrosoricida, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Peramelemorphia and Rodentia mammalian orders, are a suitable group for our analyses. They are conspicuous inhabitants of pristine grasslands and forests and of several types of human-modified habitats due to morphological and behavioral adaptations to the environment (Flynn et al. 2009; Medan et al. 2011). They are relatively well sampled across the globe and have been used as a model group to test the effect of land-use changes on biodiversity (e.g. Kingston & Morris 2000; Umetsu et al. 2008; Pardini et al. 2009, 2010; Pfeifer et al. 2017). Thus, data on small mammal occurrence is useful to the application of a regional perspective to the study of the animal community re-assembly due to human-mediated habitat modifications, which is still lacking. We expected that, relative to the regional species pool, A) communities from human-modified habitats would have lower species richness and functional diversity than pristine forests and grasslands; B) communities from forest-like human-modified habitats (tree plantations and forest edges) would have fewer of the species and functions of forest species than pristine forests but more than grasslands and open human-modified habitats (grassland edges, crop fields, clear-cuts); C) communities from open human-modified habitats would have fewer of the species and functions of grassland species than pristine grasslands but more than forest-like human-modified habitats; and, D) communities from pristine forests and grasslands would have fewer of the species and functions of human-modified habitat species than human-modified habitats.

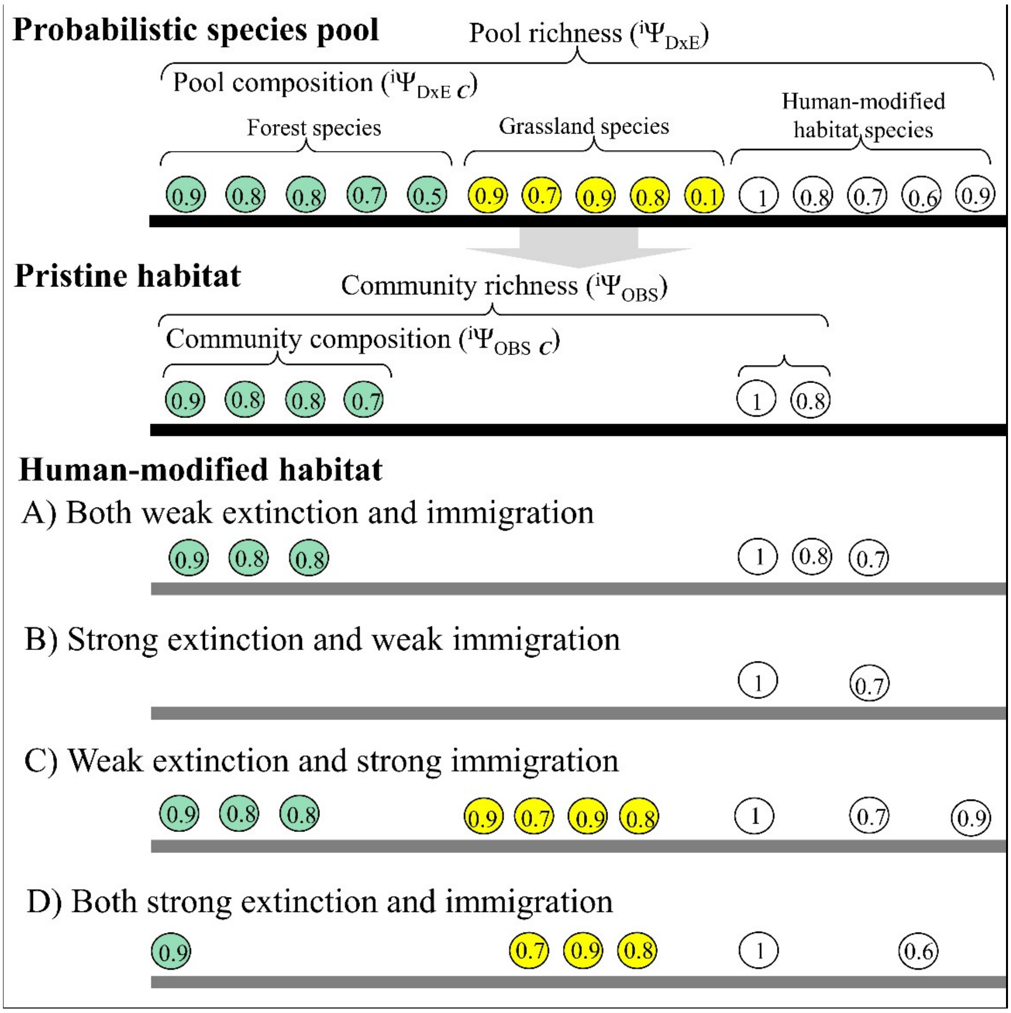

Figure 1: The effect of the local extinction-immigration balance (scenarios A to D) on the structure of human-modified habitat communities. Here, we compared local community richness, functional diversity, species and functional composition relative to the probabilistic pool diversity to differentiate extinctions from immigrations (see Box 1 for concepts and formulas). The values inside the circles depict the probability of species dispersal and persistence as defined by the probabilistic species pool approach. The circle colors depict the habitat preferences of the species.

Box 1: Concepts and formulas

Dispersal distance over time (*kt*): the ability a species has to disperse away from its known range during a given period. We used the natal dispersal distances (data from Whitmee & Orme 2013) and generation length (data from Pacifi et al. 2013) to obtain the annual dispersal ability of the species. We modified the parameter *kt* in the *Sensitivity analyses*.

Dispersal-based species pool: A species pool delineated according to species-specific dispersal abilities. The dispersal-based species pool contains the probabilities of species dispersal beyond their known range over 40 years. The species dispersal probability (D_n) was defined as $D_n = 1 - \prod_{n=1}^{N} \quad (1 - e^{-kt\,n}\ )$, where the exponent of the species dispersal rate *k* over the period *t* defines the ability to reach *n* to *N* cells (Karger et al. 2016). We defined *t* as 40 years to match the start of the “Green revolution” period, from which the species tolerating modifications in the habitat should start to thrive in human-modified landscapes (Laurance et al. 2014).

Environment-based species pool: A species pool delineated according to site-specific environmental suitability. The environment-based pool contains the probabilities of species persistence given the climate suitability (data from Karger et al. 2017).

Probabilistic species pool: A species pool delineated according to species-specific dispersal abilities and site-specific environmental suitability. The probabilistic species pool was obtained using the formula ${}^{i}\Psi = \sum_{s=1}^{S} \prod_{x=1}^{n} Pxs$, where we multiplied the independent probabilities generated by *x* to *n* filters defining the pool; in our case, the two filters were dispersal (D) and environment (E). The probabilistic pool (${}^{i}\Psi_{DxE}$) contains the probabilities of species occurrence in the local communities weighted by species-specific dispersal ability and site-specific environmental suitability.

Local community: The set of species coexisting in a pristine (forest, grassland and natural edges) or human-modified (forest edge, grassland edge, tree plantation, clear-cut, crop field) habitats. Data on community composition were obtained from Luza et al. (unpublished data) and Hudson et al. (2017). The richness and composition of a local community was probabilistic, because we replaced the presences by the respective probabilities of species dispersal and persistence, as defined by the probabilistic pool approach.

Local community richness (functional diversity) ($^{i}\Psi_{OBS}$): the community richness was defined as $^{i}\Psi_{\mathrm{OBS}} = \sum_{s=1}^{S} Ps$, where we summed the probabilities Ps from s=1 to S species found in a local community (i.e. the sum of the height of all bars with black circles, Fig. 2); the probabilities were extracted from the probabilistic species pool. The functional diversity of a local community was the mean functional distance between coexisting species.

Pool richness (functional diversity) ($^{i}\Psi_{DxE}$): The total richness (functional diversity) in the pool of a local community. Pool richness was defined as $^{i}\Psi_{\mathrm{DxE}} = \sum_{s=1}^{S} Ps$, where we summed up the probabilities P from s=1 to the S species belonging to the pool (i.e. the sum of the height of all bars with black, white and red circles, Fig. 2). The functional diversity of the pool of a local community was the mean functional distance between all species in the pool.

Local community richness (functional diversity) relative to the pool richness (functional diversity) ($p^{i}\Psi$): we obtained the proportion of species (functions) of the regional pool which is found in a local community by dividing $^{i}\Psi_{\mathrm{OBS}}$ by $^{i}\Psi_{\mathrm{DxE}}$. The index $p^{i}\Psi$ is similar to the community completeness index (Pärtel et al. 2013; Lewis et al. 2017), which measures the proportion of the species (functions) of the regional pool which is found in a local community.

Local community composition (functional composition) ($^{i}\Psi_{OBS\ C}$): the community composition was defined as $^{i}\Psi_{OBS\ C} = \sum_{s=1}^{S} Ps\ \boldsymbol{C}$, where we summed the probabilities Ps from s=1 to S preferring the habitat $\boldsymbol{C}$ (i.e. the sum of the height of green bars with black squares, Fig. 2); the probabilities were extracted from the probabilistic species pool. $\boldsymbol{C}$ can be forest, grassland or human-modified habitat species. The functional composition of a local community was the mean functional distance between the species preferring the habitat $\boldsymbol{C}$.

Pool species composition (functional composition) ($^{i}\Psi_{DxE\ C}$): The total number of species in the pool of a local community preferring a given habitat $\boldsymbol{C}$; $\boldsymbol{C}$ can be forest, grassland or human-modified habitat species. The pool composition was defined as $^{i}\Psi_{DxE\ C} = \sum_{s=1}^{S} Ps\ \boldsymbol{C}$ where we summed up the probabilities P from s=1 to the S species belonging to the pool preferring the habitat $\boldsymbol{C}$ (i.e. the sum of the height of all green bars, Fig. 2). The functional composition of the pool was the mean functional distance between the species of the pool preferring the habitat $\boldsymbol{C}$.

Local community species (functional) composition relative to the species (functional) composition of the pool ($p^{i}\Psi_{C}$): we analyzed the proportion of forest ($p^{i}\Psi_{forest}$), grassland ($p^{i}\Psi_{grassland}$) and human-modified habitats ($p^{i}\Psi_{human\text{-}modified}$) species and functions of the regional pool which is found in a local community by dividing $^{i}\Psi_{OBS\ C}$ by $^{i}\Psi_{DxE\ C}$. $\boldsymbol{C}$ can be forest, grassland or human-modified habitat species.

Methods

Delineating the probabilistic species pool

We used the probabilistic species pool approach (data for the step 1, Fig. 2) as a null probabilistic expectation to differentiate extinctions in from immigrations into human-modified habitats. The probabilistic species pool is a combination of a dispersal-based pool and an environment-based pool (Karger et al. 2016). Because the species pool is probabilistic, thresholds to define occurrences of ‘losers’ and ‘winners’ are not required. Instead, each species found in the pool have a probability $^{i}\Psi$ to occur in the local communities (Karger et al. 2016). Here, we explored four properties of the probabilistic species pool: 1) richness, which includes the sum of $^{i}\Psi$ across all species composing the pool; 2) composition, which includes the sum of $^{i}\Psi$ across all species sharing a habitat preference; 3) functional diversity, which includes the mean functional distance between species with $^{i}\Psi$ greater than zero; and 4) functional composition, which includes the mean functional distance between species with $^{i}\Psi$ greater than zero and sharing a habitat preference (Box 1, Fig. 1). Below we describe the steps used to delineate each pool.

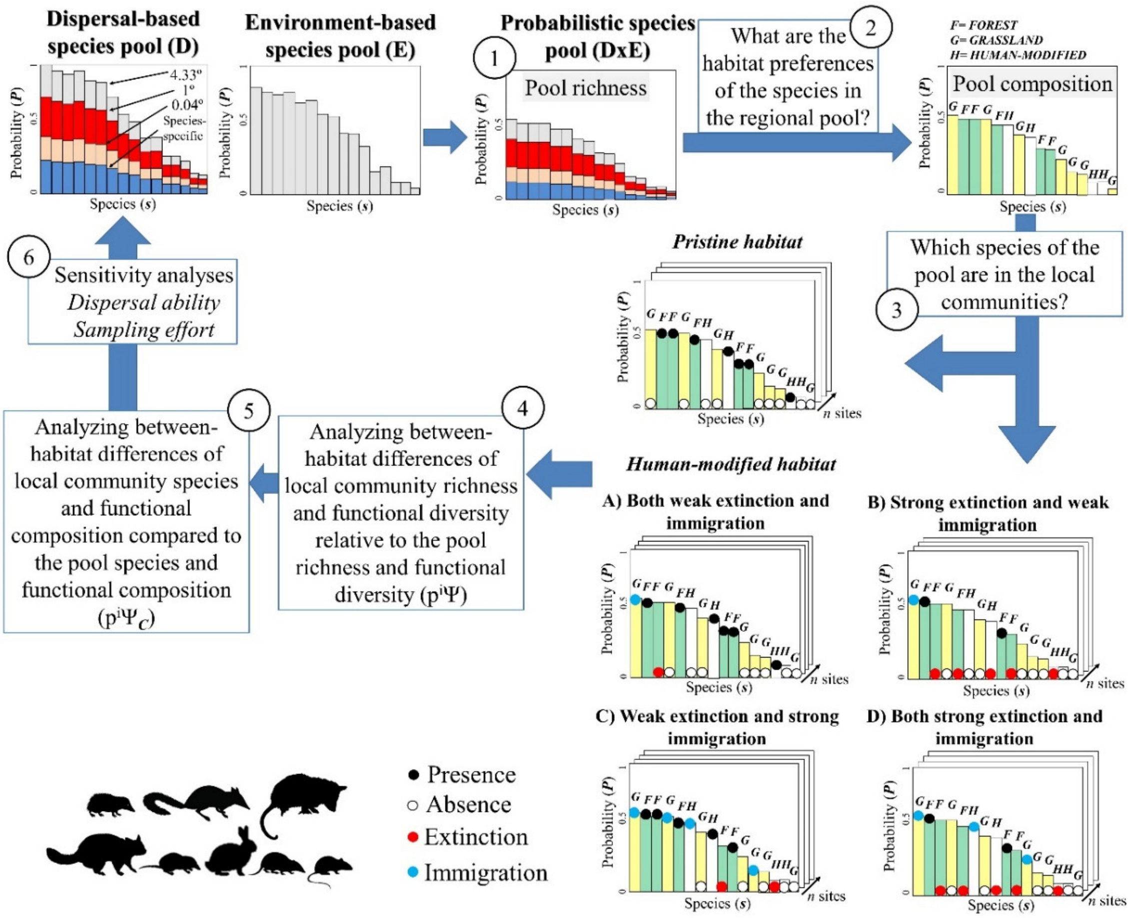

Figure 2: Framework for analyzing the local community diversity relative to the pool diversity. The steps were: 1) delineate a probabilistic species pool by weigh the probabilities of species occurrence (the height of the histogram bars) by dispersal and environment; 2) define the habitat preferences of the species in the pool (different bar colors and letters over the bars); 3) extract the probability of occurrence for all species recorded in the local communities (only the black circles [presences]) to obtain the probabilistic composition of the communities; 4) analyze species richness and functional diversity of the communities; 5) analyze species and functional composition of the communities; and 6) evaluate the sensitivity of the results to differential dispersal abilities to delineating the pool (different bar colors in the dispersal-based and probabilistic pools) and differential sampling effort to including sites in the analyses (*n* sites). Absences are due to dispersal limitation and environmental unsuitability.

Extinctions involve the loss of pristine-habitat species due to habitat conversion, whereas immigrations involve the arriving of species which were not present before the conversion of the habitat. Mammal silhouettes: top- Afrosoricida, Dasyuromorphia and Didelphimorphia; bottom- Diprotodontia, Eulipotyphla, Lagomorpha, Peramelemorphia and Rodentia.

The dispersal based-species pool

Data on species dispersal abilities are required to obtain the probability that each species will reach to the local communities (Karger et al. 2016). Dispersal ability limits the colonization of the species into all environmentally suitable sites (e.g., Amazonian forest species could occur in Indo-Malayan forests in the absence of dispersal limitation). Thus, the dispersal of species over time may change the composition of the pool of a local community (Karger et al. 2016; Lessard et al. 2016).

We used published data on natal dispersal distances (Whitmee & Orme 2013) and generation length (Pacifi et al. 2013) to calculate an annual rate of dispersal distance for small mammal species, which was the baseline to obtain the species-specific dispersal rate. The natal dispersal distance, which characterizes the movements of an individual from its birth until first reproduction, was obtained for 187 individuals (including males, females or both) of 49 small mammal species (≤ 5 kg, six orders [Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha and Rodentia]). We used the generation length, which characterizes the age at which an individual achieves half of its total reproductive output (Pacifi et al. 2013), as a period for the dispersal events. To our knowledge, generation length represents the most accurate estimate of the period during which an individual has higher probability to disperse.

Values of natal dispersal were lacking for many species; therefore, we used a non-parametric random forest algorithm (Stekhoven & Buehlmann 2012) to impute missing natal dispersal data for 3,030 species (from a total of 3,079 with generation length data). Before the imputing, we transformed the natal dispersal distances (originally in meters, miles or kilometers) into meters, and generation length (originally in days) into years. We ran the missForest function (‘missForest’ package [Stekhoven & Buehlmann 2012] in R [R Core Team 2017]) setting the maximum number of iterations and random forest trees to 100; the random forest algorithm stopped in the fourth iteration (i.e., the iteration in which the difference between the newly imputed data and the previous one starts to increase considerably) (Stekhoven & Buehlmann 2012). Since missForest is a method for imputing of missing data in multidimensional matrices, we included the adult body mass into the matrix for data imputing analysis. Adult body mass also was used to evaluate the consistency in the estimates of natal dispersal distances after data imputing (Figure S1 in the Supplementary Material). Estimates of imputing errors for natal dispersal distances were acceptable (normalized root mean squared error NRMSE= 0.096), given the large amount of missing values in the dataset. The positive and significant linear correlation between natal dispersal distance and body mass was preserved (Figure S1). We divided the natal dispersal distances (in meters) by generation length (in years) to obtain an annual rate of dispersal distance. The averaged rate across the 3,079 species was 129.41 ± 238.93 meters/year, ranging from 11.23 (*Dipodomys spectabilis*) to 11,989 meters/year (*Sciurus niger*). The averaged values are close to the scale at which small mammal species respond to the variation in landscape structure (133 and 533 meters [Umetsu et al. 2008; Bowman et al. 2002]).

We used the annual rate of dispersal distance for the 1,044 species for which we have the probabilities of occurrence weighted by the environment (see below the *The* *environment-based species pool*) to obtain the species-specific dispersal abilities over time (*kt*, Box 1) (Fig. S2). We defined a 40-year period for the dispersal events, because the dispersals promoted by habitat modifications should have started with the expansion and intensification of agriculture and forestry at the end of the sixties and the beginning of the seventies (the “Green Revolution” period; Laurance et al. 2014). We first transformed the meters annually dispersed by the species into kilometers and then into lat-long degrees (km potentially dispersed in 40 years/110 km), in order to obtain the species dispersal abilities in the same scale as the range maps (International Union for Conservation of Nature [IUCN 2017]). The range maps were transformed into raster with latitude-longitude projection and 2-degree cell resolution. Raster files were processed using functions implemented in the package ‘raster’ in R (R Core Team 2017). According to our data, the average dispersal ability of non-volant small mammal species is 0.04 ± 0.14 lat-long degrees over 40 years (min= 0.0041° [*Dipodomys spectabilis*], max= 4.33° [*Sciurus niger*]). Only four species had the ability to disperse more than 1 lat-long degree (*Brachylagus idahoensis*, *Didelphis virginiana*, *Lepus europaeus* and *Sciurus niger*). We highlight that the dispersal ability we measured here is always positive, constant and linear over time. Thus, it does not represent possible range contractions, long-distance and non-linear dispersals. We built the dispersal-based species pool using the ‘disppool’ function, in the ‘probpool’ package in R (Koenig et al. 2018).

The environment-based species pool

Delineating a probabilistic species pool requires site-specific environmental suitability (Karger et al. 2016). We obtained a general prediction of the probability of species occurrence given the climate using species distribution modelling (Guisan & Thuiller 2005). Climate data was taken from CHELSA (Karger et al. 2017). The data consist of a monthly temperature and precipitation climatology for the years 1979–2013 (Karger et al. 2017). We used mean annual temperature, standard deviation of annual temperature in a 0.5-degree grid cell, mean annual precipitation, and standard deviation of annual precipitation in a 0.5-degree grid cell as predictors. These variables are related to physiological tolerances of the species because they directly affect the probability of species persistence in a local site and alter the richness and composition of small mammal communities (Dambros et al., 2015; Maestri et al. 2016). We used generalized linear models (GLMs), generalized additive models (GAMs), and random forests as species distribution models with the same set of predictors. As presence data, we used the IUCN range maps on a 0.5-degree grid cell size (IUCN 2017). Absences were weighted, so that the sum of the absences equals the sum of the presences. We used a 10-fold cross validation of the models and calculated the AUC, Kappa, and TSS scores. Since the performance of the different models was similar (Table S1), we conducted further analyses using the predictions of the GLMs (Fig. S3). The model output included a continuous prediction of the probability of species occurrence (varying from 0 to 1) given the climate of the cells.

Although IUCN (2017) hosts range maps for most of the terrestrial mammals, the quality of such data are still inadequate to properly model the climate envelope for all mammal species. Thus, the number of species included in the environmental-based pool was limited to the set of species for which we could obtain at least general predictions of occurrence probability (1,044 non-volant small mammal species).

The probabilistic species pool

We built the probabilistic species pool for each community using the ‘probpool’ function from the ‘probpool’ R package (Koenig et al. 2018). The probabilistic species pool includes the probability of occurrence of small mammal species weighted by species-specific dispersal abilities and site-specific environment suitability (Box 1, Fig. S4). Newly discovered species missing in the IUCN database, as well species with inadequate distributional knowledge to obtain at least general occurrence predictions according to climate, were lacking in our pool. Thus, many species present in local communities were not in the pool of 1,044 species (Table 1). Species recorded in the local communities but lacking in the pool were manually imputed into the pool; we defined the probability value of 1 for the added species. We delineated the probabilistic species pool at 2-degree grid cell size due to computation difficulties. Thus, the extent of the pool of a community was 2-degree grid cell size.

Table 1: Number of sites by habitat according to different sampling efforts (trap/nights).

Habitat	50 trap/nights	100 trap/nights	500 trap/nights	1,000 trap/nights
Natural edge	4	4	3	1 [a]
Forest	300	297	244	172
Grassland	96	94	62	26
Forest edge	84	83	75	60
Grassland edge	25	23	22	16
Tree plantation	34	34	30	26
Clear-cut	98	98	55	38
Crop field	71	68	48	35
Total of sites	712	701	539	374
Mean ± SD sampling effort by habitat	6,324 ± 11,526	6,395 ± 11,571	7,358 ± 12,184	9,198 ± 13,195
Total of species in the local communities	464	456	440	400
Total number of species recorded in the local communities but lacking in the pool [b]	115	111	106	96
Total of species in the pool [c]	1,159	1,155	1,150	1,140

[a] Level removed from the GLS analyses with sampling threshold ≥ 1,000 trap/nights.

[b] The number of species manually imputed into the pool. Such species were recorded in the local communities but were not among the pool of 1,044 species having occurrence probability given the climate.

[c] The total number of species in the pool comprises the sum of 1,044 species and the number of species imputed into the pool.

Defining habitat preferences of the species composing the pool

We used the IUCN Habitats Classification Scheme API v3.1 (IUCN 2017) to obtain the habitat preferences for each of the 1,159 species (data for the step 2, Fig. 2). The most important habitat(s) for a species is defined according to a standardized list of habitat types (IUCN 2017; see Table S2). The species habitat preference may indicate different probabilities of extinction in or immigration into the pristine and human-modified habitats (Belmaker & Jetz 2013; Karger et al. 2016). To obtain the preferred habitat, we used the function ‘rl_habitats’ implemented in ‘rredlist’ package v0.4.0 in R (Chamberlain 2017). We used forest, grassland and human-modified habitat preferences to differentiate forest-specialists and grassland-specialists from edge, generalists, matrix-tolerant and gap-crossing species (Metzger et al. 2009; Pardini et al. 2009). We did not include the preferences for marine, lagoon, cave, other and unknown habitats. Among the 1,159 species, we found 724 species preferring forests-F, 799 grasslands-G and 430 human-modified habitats-H (represented by colors in and letters over the bars of local community histograms, Fig. 2). Few of the 1,159 species did not have information on habitat preferences. For these, we used information from phylogenetically related species (*Deltamys araucaria*= *D. kempi*; *Cerradomys vivoi*= *C. subflavus*; *Scapteromys meridionalis*= *S. tumidus*; *Ctenomys sericeus*= *Ctenomys coyhaiquensis*).

Data of local community composition

We used a recently compiled database (Luza et al. unpublished data) and the PREDICTS database (Hudson et al. 2017) to obtain data of small mammal community composition in pristine and human-modified habitats (data for step 3, Fig. 2). Both databases include fine-scale information on small mammal composition in mostly paired human-modified and pristine habitats, included information acquired through similar sampling techniques, and clearly differentiated the biodiversity of artificial pastures from the biodiversity of pristine grasslands and savannas (Parr et al. 2014; Veldman et al. 2015). Forest and grassland fragments, minimally disturbed managed forests, continuous remnants and advanced secondary-regeneration were considered as pristine habitats, because differences in composition and richness between these habitats are minimal and they best reflect the pristine structure of the natural habitats (Newbold et al. 2015). Grasslands and savannas with native vegetation were considered as pristine habitats even if they were grazed by domesticated ungulates (see Parr et al. 2014; Veldman et al. 2015). An edge was considered the boundary between habitats. We differentiated natural edges (between forests and grasslands) from forest edges (artificial edges between a forest and a human-modified habitat) and grassland edges (artificial edge between a grassland and a human-modified habitat). Natural edges were excluded from the analysis using sites sampled with ≥ 1,000 sampling effort due to the small number of samples (Table 1). We considered tree monocultures planted in grasslands and cleared forests as tree plantations. We considered clear-cuts and young-secondary vegetation as clear-cuts, and agriculture fields (soybean, hayfields, maize tillage, sugarcane, among others) as crop fields. According to the papers in the combined database, 85% of the sites were inserted in fragmented landscapes, whereas only 15% in landscapes of continuous forests and grasslands. The presence of a species in a given habitat was replaced by the respective probability of occurrence weighted by species dispersal ability and site environmental suitability (Fig. 1). Thus, the local community composition is probabilistic.

Analyzing richness and functional diversity of a local community relative to the pool

We obtained the species $p^{i}\Psi$ by dividing the sum of probabilities across all species found in a local community (${}^{i}\Psi_{OBS}$) by the sum of probabilities across all species included in the pool of a community (${}^{i}\Psi_{DXE}$) (Box 1). We obtained the functional $p^{i}\Psi$ by dividing the mean functional distance between all species found in a local community (${}^{i}\Psi_{OBS}$) by the mean functional distance between all species in the pool of a community (${}^{i}\Psi_{DXE}$). We calculated the functional distance between species (Gower distance applied on standardized trait values) using diet (the percentage of invertebrates, fruits and seeds included in the diet), activity period (either nocturnal or not) and foraging strata (arboreal, terrestrial, fossorial) obtained from the Elton traits v1.0 database (Wilman et al. 2014). These traits are acknowledged as important indicators of species ecological functions and niche partitioning abilities (Wilman et al. 2014). The linear correlation between the traits was always lower than 0.5. Trait standardization and Gower distance were calculated using 'decostand' and 'vegdist' functions of the 'vegan' package in R (R Core Team 2017).

We used linear regression analysis with generalized least squares (GLS) to evaluate if communities from human-modified habitats had smaller richness and functional diversity than pristine forests and grasslands ($p^{i}\Psi$) (step 4, Fig. 2). We used the log-transformed $p^{i}\Psi$ as response variable since it was normally distributed.

Analyzing species and functional composition of a local community relative to the pool

Using the information on habitat preferences for all species composing the local communities and pool (step 2, Fig. 2), we obtained the species $p^{i}\Psi_{forest}$ by dividing the sum of probabilities across all species found in a site preferring forests ($\Psi^{i}_{OBS\ forest}$) by the sum of probabilities across all species in the pool preferring the forest habitat ($\Psi^{i}_{DXE\ forest}$) (Box 1). We did this same procedure for species preferring grasslands ($p^{i}\Psi_{grassland}$) and human-modified habitats ($p^{i}\Psi_{human\text{-}modified}$). We then used $p^{i}\Psi_{forest}$ as response variable in a GLS analysis to test if communities from forest-like human-modified habitats (tree plantations and forest edges) had less of the forest species of the pool than pristine forests but more than grasslands and open-like human-modified habitats (grassland edges, crop fields, clear-cuts). We used $p^{i}\Psi_{grassland}$ in a GLS analysis to test if communities from open-like human-modified habitats had less of the grassland species of the pool than pristine grasslands but more than forest-like human-modified habitats. Finally, we used $p^{i}\Psi_{human\text{-}modified}$ in a GLS analysis to test if communities from pristine forests and grasslands had less of the human-modified habitat species of the pool than human-modified habitats (step 5, Fig. 2). We used the log-transformed $p^{i}\Psi_{forest}$, $p^{i}\Psi_{grassland}$ and $p^{i}\Psi_{human\text{-}modified}$ as the response variables because they were normally distributed.

We obtained the functional $p^{i}\Psi_{forest}$, $p^{i}\Psi_{grassland}$ and $p^{i}\Psi_{human\text{-}modified}$ dividing the mean functional distance across all forest, grassland and human-modified habitat species coexisting in a local community by the mean functional distance across all species of the pool with forest, grassland and human-modified habitat preferences. We used the same traits and analyses as in the functional $p^{i}\Psi$.

Generalized least squares

Generalized least squares allows for a proper estimation of standard errors and associated p-values when spatial dependence is present in the model errors (Pinheiro & Bates 2000). Such dependence was observed in species and functional $p^i\Psi$, log $p^i\Psi_{forest}$, log $p^i\Psi_{grassland}$ and log $p^i\Psi_{human\text{-}modified}$ (Moran I between 0.2 and 0.6, P< 0.01 across all analyses we ran). We used the Euclidean distances between lat-long site coordinates as the position variable in the within-group correlation structure of the GLS analysis. The range of the correlation parameter ρ was set to 1 and no nugget effect was defined (Pinheiro & Bates 2000). The range estimated by the model indicates the spatial distance at which the semi-variogram measuring spatial dependence first equals to 1; thus, the lower the ρ value the higher the spatial dependence between nearby sites (Pinheiro & Bates 2000). We adjusted the position of repeated coordinates by adding 0.01 degrees (1.1 km) to the latitude and longitude values, because Luza et al. (unpublished data) repeated coordinates when the authors of the papers provided only a general geographic location for the sampled habitats. To define the correlation structure that best fits to the data, we used ΔAIC and model weight to compare several models including different correlation structures (Exponential, Linear, Gaussian, Linear, Spherical and Ratio). Since, the exponential correlation structure best fitted to the data across all correlation structures we analyzed, we adjusted all GLS models with the exponential correlation structure. We reported the *F*-statistic values for the GLS analysis. *F*-statistics is the ratio between the explained and the unexplained variation; the higher the F-statistic the greater the effect of habitat on the community richness, functional diversity and species and functional composition.

We used plots of normalized residuals and qqplots to evaluate the adequacy of the GLS model (Pinheiro & Bates 2000). We removed outliers and highly influential points (high leverage according to Cook's distance) viewed in the diagnostic plots to achieve a normal distribution for the model errors. An effect of the habitat type was considered significant when $P < 0.05$. When observing such effect, we used contrast analysis (TukeyHSD Test) to identify differences in mean log $p^i\Psi$, $p^i\Psi_{forest}$, $p^i\Psi_{grassland}$ and $p^i\Psi_{human\text{-}modified}$ between pairs of habitats. We used the function 'lm.morantest' ('spdep' package) to evaluate spatial dependence in model residuals. We used the function 'model.sel' ('MuMIn' package) to the model selection procedure. We used functions of the package 'nlme' and 'stats' packages to calculate GLS regressions and TukeyHSD analyses. All analyses were conducted in R (R Core Team, 2017).

Sensitivity analyses

Sampling effort: We explored if the results of GLS and TukeyHSD analyses would be sensitive to different thresholds of sampling effort for site inclusion (50, 100, 500 and 1,000 trap/nights; Table 1), because effort may influence the observed diversity of a local community. We used 1,000 trap/nights as the maximum threshold because the effect of sampling effort on log $p^i\Psi$, log $p^i\Psi_{forest}$, log $p^i\Psi_{grassland}$ and log $p^i\Psi_{human\text{-}modified}$ was weaker ($R^2_{ad} \approx 0.04$; $P < 0.001$) than for sites sampled with 50, 100 and 500 trap/nights ($R^2_{ad} \approx 0.10$, $P < 0.001$).

Dispersal ability: We explored if the results of GLS and TukeyHSD analyses would be sensitive to the different values of dispersal ability used to delineate the probabilistic species pool, because we lack knowledge about the dispersal abilities of non-volant small mammal species. We delineated probabilistic species pools using species-specific dispersal abilities, 0.04° (the mean dispersal ability we found), 1° and

4.33° (the maximum dispersal ability we found, see *Dispersal-based species pool*) (Fig. 2, Table 2).

Table 2: Pool richness according to different dispersal abilities over 40 years (parameter kt).

Dispersal ability	50 trap/nights	100 trap/nights	500 trap/nights	1,000 trap/nights
Species-specific	23.21 ± 8.94	23.12 ± 8.95	23.82 ± 8.40	24.19 ± 7.94
Mean (0.04°)	23.10 ± 8.94	23.02 ± 8.95	23.70 ± 8.40	24.10 ± 7.93
One degree	24.78 ± 9.59	24.71 ± 9.60	25.56 ± 9.05	26.04 ± 8.54
Maximum (4.33°)	41.90 ± 19.60	41.78 ± 19.39	43.30 ± 18.09	44.30 ± 17.63
Local community richness	4.71 ± 3.09	4.58 ± 3.50	5.14 ± 3.77	5.73 ± 4.21

Results

Using a threshold of 50 trap/nights for site exclusion, our data included the presence of 464 species in 712 sites; the number of sites halved when the effort threshold was ≥ 1,000 trap/nights (Table 1). Average community richness by habitat varied from 4.6 to 5.7 species according to the different thresholds of sampling effort (Table 2). Pool richness varied when specifying different dispersal abilities over time (*kt*) (Table 2). Using species-specific *kt*, average pool richness was 23.21 ± 8.94 species; similar values were found when *kt* was 0.04° and 1° (Table 2). Pool richness almost doubled when *kt* was 4.33° (Table 2).

Analyses showed similar effects of habitat type on log $p^{i}\Psi$, $p^{i}\Psi_{forest}$, $p^{i}\Psi_{grassland}$ and $p^{i}\Psi_{human\text{-}modified}$ across the different values of *kt* (rows of the Tables 3 and 4). However, the analyses showed that the GLS results varied considerably across the different thresholds of sampling effort (columns of the Tables 3 and 4). Therefore, we reported the results of species-specific dispersal abilities and sites sampled with ≥ 1,000 trap/nights. Spatial autocorrelation was weak in all models (estimated range ρ varied from 001 to 0.05).

The effect of habitat type on community richness showed that pristine forests had greater species $p^i\Psi$ than grassland edges (Fig. 3a). The habitat effect on the composition of forest species showed that all habitats had more forest species ($p^i\Psi_{forest}$) than grassland edges; in addition, pristine forests had more forest species than grasslands, grassland edges and forest edges (Fig. 3b). Although GLS identified a significant habitat effect on $p^i\Psi_{grassland}$ (Table 3), we did not detect between-habitat differences in $p^i\Psi_{grassland}$ in the contrast analysis (Fig. 3c). Finally, we found that pristine forests had greater $p^i\Psi_{human\text{-}modified}$ than clear-cuts (Fig. 3d).

Table 3: F-statistic for GLS analyses showing the effect of habitat type on local community richness and composition relative to the pool richness ($p^i\Psi$) and composition ($p^i\Psi_{forest}$, $p^i\Psi_{grassland}$ and $p^i\Psi_{human\text{-}modified}$).

Community descriptor	Sampling effort threshold (trap/nights) [a]			
Dispersal ability (*kt*)	50	100	500	1,000
Community species richness (log $p^i\Psi$)				
Species-specific	6.09***	0.9	0.7	3.69**
Mean	6.08***	1	0.6	3.70**
One degree	6.18***	1	0.7	3.62**
Maximum	6.59***	1.5	0.7	9.24***
Community species composition				
Forest species (log $p^i\Psi_{forest}$)				
Species-specific	11.43***	7.6***	18.5***	9.58***
Mean	11.39***	7.7***	18.5***	9.57***
One degree	11.60***	7.5***	19.6***	9.50***
Maximum	12.36***	8.2***	28.3***	8.67***
Grassland species (log $p^i\Psi_{grassland}$)				
Species-specific	2.11*	0.9	2.5*	2.72*
Mean	2.11*	0.9	2.5*	2.72*
One degree	2.17*	0.9	2.5*	2.71*
Maximum	2.30*	1.1	2.7*	0.75
Human-modified habitat species (log $p^i\Psi_{human\text{-}modified}$)				
Species-specific	3.41**	0.7	1	3.89**
Mean	3.41**	0.7	1	3.89**
One degree	3.41**	0.7	1	3.87**
Maximum	3.61**	0.9	1	4.39**

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

[a] We used different thresholds of sampling effort to define the site inclusion in data analysis and different dispersal abilities over time (*kt*) to delineate the probabilistic species pools.

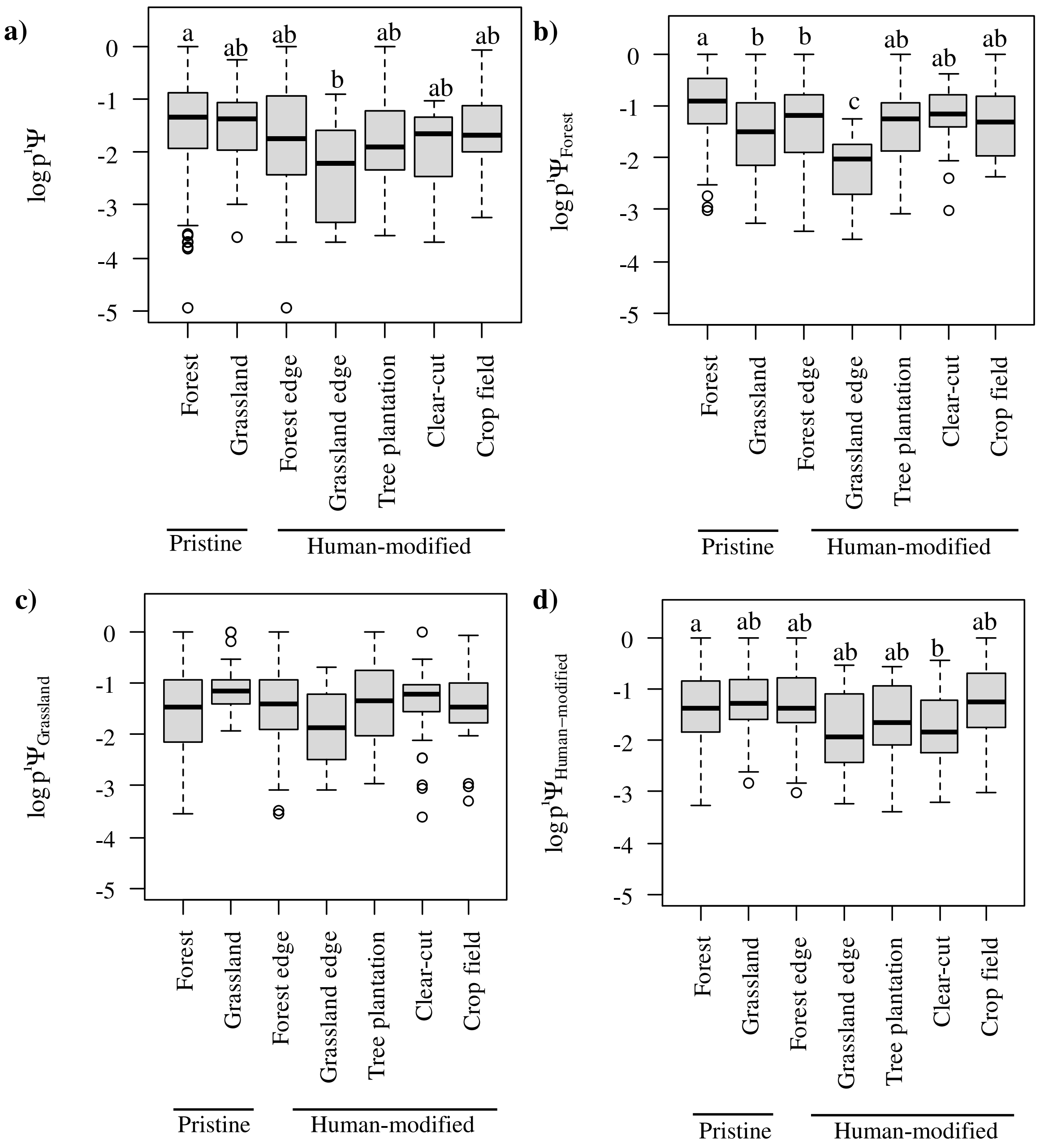

Figure 3: Between-habitat differences in local community richness relative to the pool richness ($p^i\Psi = {}^i\Psi_{OBS}/{}^i\Psi_{DxE}$*) (**a**) and local community composition relative to the pool composition* $p^i\Psi_C = {}^i\Psi_{OBS\,C}/{}^i\Psi_{DxE\,C}$*, where **C** can be a forest (**b**), grassland (**c**) or human-modified habitat species (**d**). Results for species-specific dispersal ability over time (kt) and habitats sampled with ≥ 1,000 trap/nights. Zero in the log scale indicates one in the original scale of* $p^i\Psi$*. Horizontal bars are mean values, and boxes are 1st and 3rd quartiles. Points are outliers, which were removed from the GLS and TukeyHSD analyses. Mean values followed by the same letters are not significantly different*

($p > 0.05$). The absence of letters in ***c****) indicates the lack of between-habitat differences in local-regional richness.*

The analyses of the effect of habitat type on community functional diversity showed that pristine forests had a larger proportion of the functional diversity of the pool than tree plantations, clear-cuts and crop fields (Fig. 4a). Functional diversity of forest species was higher in pristine forests than in pristine grasslands, grassland edges and crop fields (Fig. 4b). We did not observe between-habitat differences in functional diversity when considering the composition of grassland (Fig. 4c) and human-modified habitat species (Fig. 4d).

Table 4: F-statistic for GLS analyses showing the effect of habitat type on local community functional diversity and composition relative to the pool functional diversity ($p^i\Psi$) and composition ($p^i\Psi_{forest}$, $p^i\Psi_{grassland}$ and $p^i\Psi_{human\text{-}modified}$).

Community descriptor	Sampling effort threshold (trap/nights) [a]			
Dispersal ability (*kt*)	50	100	500	1,000
Community functional diversity (log $p^i\Psi$)				
Species-specific	19.3***	6.8***	17.2***	7***
Mean	19***	6.7***	19.2***	6.5***
One degree	18***	8***	4***	9***
Maximum	18***	6***	6***	9***
Community functional composition				
Forest species (log $p^i\Psi_{forest}$)				
Species-specific	23.7***	7.6***	49.3***	5.6***
Mean	23.1***	3.7**	43.7***	5.5***
One degree	25***	11***	9***	6***
Maximum	25***	14***	12***	10***
Grassland species (log $p^i\Psi_{grassland}$)				
Species-specific	13.3***	2.1*	2.3*	0.4
Mean	13.2***	2 *	2.3*	0.3
One degree	14***	2*	2*	0.3
Maximum	12***	2*	2*	0.3
Human-modified habitat species (log $p^i\Psi_{human\text{-}modified}$)				
Species-specific	12.7***	1.1	0.8	2.1*
Mean	12.8***	0.9	0.9	1.8
One degree	11***	1.8	1	2*
Maximum	10***	3*	1	2*

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

[a] We used different thresholds of sampling effort to define the site inclusion in data analysis and different dispersal abilities over time (*kt*) to delineate the probabilistic species pools.

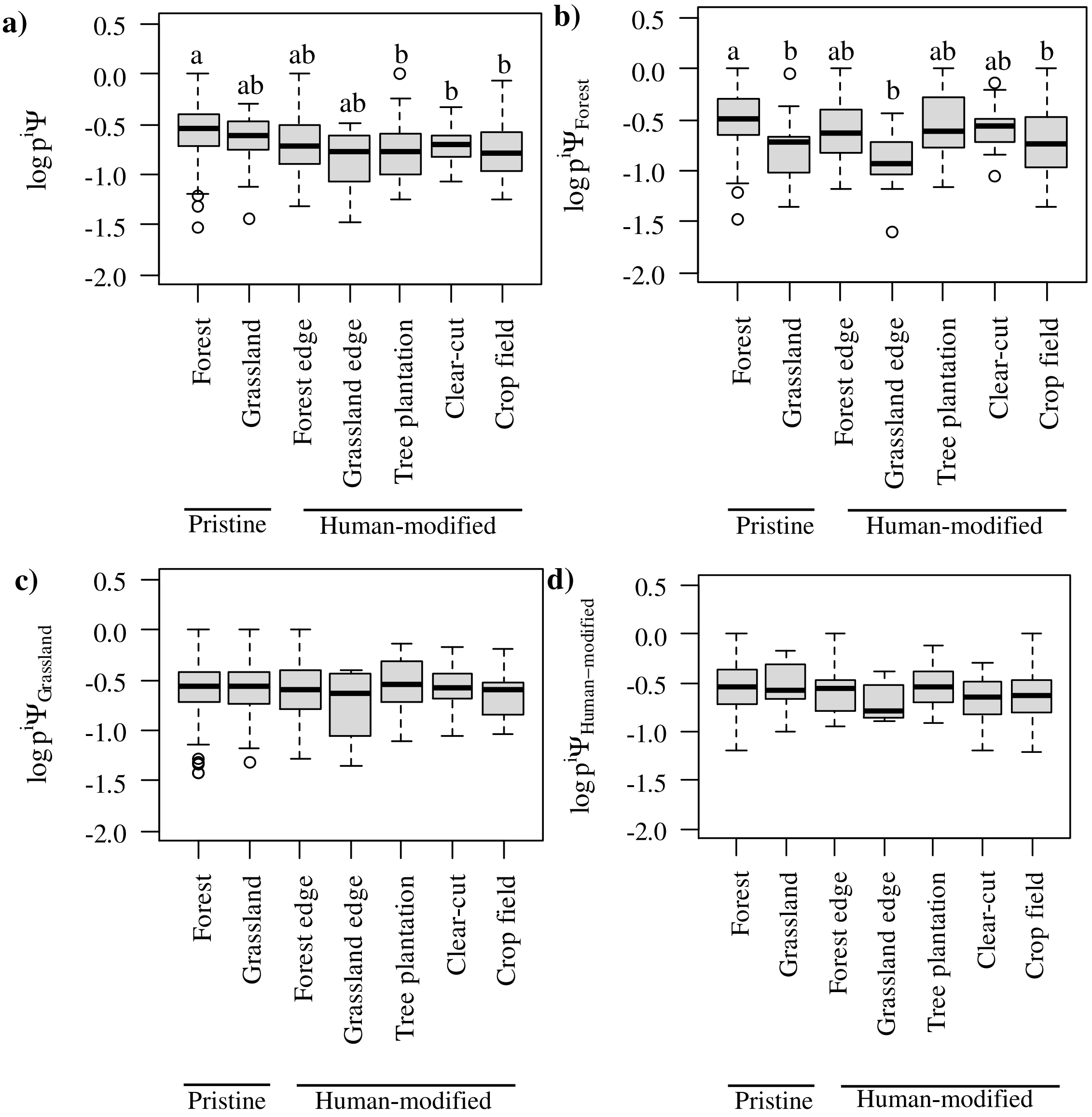

*Figure 4: Between-habitat differences in local community functional diversity relative to the pool functional diversity ($p^{i}\Psi = {}^{i}\Psi_{OBS}/{}^{i}\Psi_{DxE}$) (**a**) and local community functional composition relative to the pool functional composition $p^{i}\Psi_{C} = {}^{i}\Psi_{OBS\,C}/{}^{i}\Psi_{DxE\,C}$ where **C** can be forest (**b**), grassland (**c**) or human-modified habitat species (**d**). Results for species-specific dispersal ability over time (kt) and habitats sampled with ≥ 1,000 trap/nights. Zero in the log scale indicates one in the original scale of $p^{i}\Psi$. Horizontal bars are mean values, and boxes are 1st and 3rd quartiles. Points are outliers, which were removed from the GLS and TukeyHSD analyses. Mean values followed by the*

same letters are not significantly different ($p > 0.05$). The absence of letters in ***c)*** *and* ***d)*** *indicates the lack of between-habitat differences in local-regional richness.*

Discussion

The balance between local extinctions and immigrations may produce new communities with altered diversity as compared to the pristine habitat communities and the regional species pool (Jackson & Sax 2010; McGill et al. 2015). Our data on small mammal occurrence in pristine and human-modified habitats showed that small mammal communities from several types of human-modified habitats were as complete (i.e. held most of regional pool species and functional diversity) as pristine habitat communities. Some studies show that small mammal communities of secondary forests, forest edges and tree plantations (e.g., shaded-cocoa plantations, *Eucalyptus* and *Pinus* plantations) have similar richness to pristine forests (e.g., Barlow et al. 2007; Fonseca et al. 2009; Pardini et al. 2009). Functional diversity analyses showed that tree-plantations, crop fields and clear-cut cannot preserve the functional diversity of the regional pool. These results (except for grassland edges) suggest that either strong or weak extinction and immigration may be occurring in the human-modified habitat communities (Jackson & Sax 2010).

The local extinction of rare, habitat-specialist and functionally unique species can be counterbalanced by the immigration of ‘winner’ species (Vellend et al. 2013, 2017; Dornelas et al., 2014). We can differentiate weak from strong extinction and immigration by analyzing the species and functional composition of the local communities relative to the pool composition (Jackson & Sax 2010; McGill et al., 2015). By a deeper look in the habitat preferences of the species composing the local communities and pool, we observed that 1) human-modified habitats held as many grassland species and functions of the pool as pristine habitats, 2) grassland edges held less forest species and functions than other pristine and human-modified habitats, 3) forest edges and pristine grasslands held less forest species of the pool than pristine forests, 4) pristine grasslands, grassland edges and crop fields held less functions of forest species than pristine forests and 5) clear-cuts held less human-modified habitat species of the pool than pristine forests.

The occurrence of grassland species across several types of human-modified habitats might be due to the presence of supplementary and complementary resources to grassland mammals in the human-modified habitats (Johnson et al. 2002; Bilenca et al. 2007; Tscharntke et al. 2012). Further, the small mammal evolution in grasslands experiencing natural disturbance regimes (burning, grazing by large herbivores) may increase the species tolerance to habitat alterations (Bond & Parr 2010; Parr et al. 2014). Perhaps considering the habitat affinities of the species within different biomes (tropical vs. temperate grasslands; e.g., Lindell et al. 2007) would allow further inferences about the influence of land-use change on species and functional composition of grassland mammal communities. Grassland edges occur in a spatial context where grassy biomes dominate the landscapes and in a biotic context where the pool held species adapted to natural disturbances (Parr et al. 2014; Veldman et al. 2015); such aspect was evidenced according to each time smaller number of forest species and functions from pristine grasslands to grassland edges. Although linear habitats such as grassland edges might be a refuge for grassland small mammals (Bilenca et al. 2007; Sullivan et al. 2012), the smaller richness and functional diversity of grassland edge communities we registered here was due to the strong extinction and weak immigration of forest species in the grassland edges.

We showed that forest-specialist species (but not their functions) were lost at high rates along forest edges. Forest edges had less forest species of the pool than forests, although the forest edges had as much functional diversity of forest species as pristine forests. In a global meta-analysis about the effects of forest edges on vertebrates, Pfeifer et al. (2017) showed that edges negatively influenced the incidence and abundance of forest-specialist species. In fact, the more sensitive a species is to the creation and presence of edges, the less area the species can use across the fragmented landscape (Ries et al. 2004; Pfeifer et al. 2017). Our results support the idea that forest edges might not be suitable to the persistence of forest specialists, although it might be suitable for some functionally similar species. We observed that crop fields held as many forest species as pristine forests; however, crop fields held less functional diversity of forest species of the pool. Thus, crop fields might not maintain a significant portion of the functions of forest species due to the unsuitable habitat for functionally unique forest species. Finally, the larger number of human-modified habitat species in forests than in clear-cuts indicates that species with affinities to human-modified habitats are, in essence, a subset of forest species with generalist habits (edge-tolerant, matrix-tolerant and gap-crossing species) (Umetsu et al. 2008; Metzger et al. 2009; Pardini et al. 2009). Overall, the analyses of species and functional diversity highlighted the irreplaceability of pristine forests to maintain forest specialists and functionally unique species in the regional pool (Barlow et al. 2007; Gibson et al. 2011; Newbold et al. 2016, 2015).

Our results were less sensitive to dispersal ability to delineate the probabilistic species pool than to differential sampling effort to site inclusion. When dispersal ability was the highest (4.33°, ≈ 476 km over 40 years), we generally perceived more between-habitat differences in $p^i\Psi$ and $p^i\Psi_C$ than when dispersal ability was species-specific, mean (0.04º) and 1º. However, the results using 4.33º dispersal ability seem improbable for most of the non-volant small mammal species, given their very limited dispersal ability. We observed that the different thresholds of sampling effort we imposed considerably influenced the results. Here, we presented the most robust results for those communities sampled with large sampling effort, established trapping procedures (mostly pitfall- and live-trapping) and temporally replicated sampling campaigns. Such sampling configuration might be more effective to recording rare species and detecting movements of individuals between habitat types. Finally, our maps of the dispersal-based, environment-based and probabilistic species pools (Figs. S2 to S4) nearly resemble the global maps of mammal richness and composition (e.g. Kissling et al. 2014), which indicates that our results for species and functional $p^{i}\Psi$ and $p^{i}\Psi_{C}$ may not change by using the complete set of small mammal species of the world.

Although our results showed that small mammal communities are under weak local extinction and immigration –mainly if we consider species richness, we must consider other factors before concluding that the small mammal communities are resistant to land-use changes and that a significant proportion of the small mammal biodiversity can be preserved in human-modified habitats. For example, we could not evaluate if weak extinction and immigration would be a result of high amount of pristine habitat surrounding the sites (Pardini et al. 2010), since such information is difficult to obtain from the published papers. Furthermore, pristine forests and grasslands may not be at a ‘pristine’ state, because anthropogenic activities (e.g., hunting, livestock) can decrease the quality of pristine habitats for the species (Barlow et al. 2016). An another aspect is that incidence may not be the best indicator of species performance front to anthropogenic influences (Tscharntke et al. 2012; McGill et al. 2015; Isbell et al. 2017). The databases that we used here (Hudson et al. 2017; Luza et al. unpublished data) allow analysis of abundance while accounting for sampling particularities. Other important aspect is that species have delayed response to habitat modifications, which results in extinction debts (Johnson et al. 2002; Metzger et al. 2009). The evaluation of extinction debts demands the knowledge of the time since habitat conversion, which is hardly known by the researchers. Finally, different taxa tend to show different responses to human modifications on habitat (Barlow et al. 2007; Metzger et al. 2009; Pardini et al. 2009; Gibson et al. 2011). For example, plant communities from regions subjected to low human influence are more complete relative to the regional pool than regions with high human influence (Ronk et al. 2015). Researchers interested in the effects of human activities on biodiversity should consider other taxa in order to obtain a broader picture of the biodiversity trends in human-modified landscapes.

The consequences of human-mediated modifications on the habitat depend not only on how many species are lost or gained, but also on the identity and functions of the species that increase or decrease in frequency (Isbell et al. 2017; Lewis et al. 2017). Inconsistent response of the local communities to anthropogenic activities have heathen debates on global vs. local declines in biodiversity, since global biodiversity declines are not accompanied by local declines (see Gonzalez et al. 2016, Vellend et al. 2017, Cardinale et al. 2018). We showed that non-volant small mammal communities from human-modified habitats are under both weak local extinction and immigration. However, unique ecological functions are being lost even under weak local extinction and immigration, since the extinction of few specialist species might not be compensated by the immigration of functionally similar species.

Summary

Anthropogenic activities may ‘unbalance the balance’ to strong local extinction or immigration, which in turn influence the structure of ecological communities. The regional pool of species that could potentially reach and survive in a local community can be used to detect whether a community is under both weak extinction and immigration, which may result in a human-modified habitat community with similar richness, functional diversity and composition when compared to a pristine habitat community. Our results showed that small mammal communities are under both weak local extinction and immigration and they might be resistant to land-use change – although the few extinct species might not be replaced by functionally similar species.

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Supplementary material

Figure S1: Linear relationship between small mammal adult body mass and natal dispersal distance (m/yr= meters per year) in the original (187 entries, 49 species) and in the imputed dataset (187 entries, 49 species + 3,030 species).

Figure S2: The dispersal-based pool delineated according to the different dispersal abilities of species over 40 years (k). Upper maps: k defined species-specific and mean. Bottom maps: k defined as 1º and 4.33º (maximum dispersal ability). Map resolution: 2-degree grid cell size.

Figure S3: The environmental-based species pool. Predictions were based on Generalized Linear Models. Map resolution: 2-degree grid cell size.

Table S1: Results showing the statistics used to test the predictive performance of the models.

Figure S4: The probabilistic species pool delineated according to site-specific environmental suitability and species-specific dispersal ability. We showed maps for four values of dispersal ability (k) over 40 years: UPPER: species-specific dispersal and mean dispersal value (0.04º); BOTTOM: 1º and maximum dispersal value (4.33º). Map resolution: 2-degree grid cell size.

Table S2: Habitat types characterizing the habitat preferences of the 1,159 non-volant small mammal species included in the probabilistic species pool.

CAPÍTULO 4

Rodent occupancy in grassland paddocks subjected to different grazing intensities in South Brazil

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Abstract

Livestock is promoting the global collapse of mammal populations. The discovery of the best management practices that reconcile conservation with production is urgently needed. We evaluated the effect of cattle grazing on the occupation of three rodent species (*Akodon azarae*, *Oligoryzomys flavescens* and *Oxymycterus nasutus*). We collected habitat covariates and sampled rodents, using live traps and tracking tunnels, in 20 paddocks subjected to different grazing pressures, from two research stations, across four seasons. We applied single-season occupancy modeling to determine whether rodent detection and occupation varied as a function of the covariates describing sampling occasions and grazing intensity. We ran sensitivity analyses to evaluate the effect of the differential sampling effort we applied across research stations. All species had higher detection probabilities during the winter. *Oxymycterus nasutus* showed a higher detection probability under tall vegetation. *Akodon azarae* reached a higher occupation probability in ungrazed areas, although it also had a low probability of occupation in highly grazed paddocks. *Oligoryzomys flavescens* occupation seemed constant across the grazing gradient. *Oxymycterus nasutus* reached a higher occupation probability in ungrazed areas. Decreasing stocking rates and maintaining ungrazed areas might compose the best management practices for small mammal conservation in the grasslands of Southern Brazil.

Keywords: beef production; cattle raising; detectability; land sparing; non-volant small mammals; Pampa biome.

Introduction

The biomass of humans and their livestock far outweighs the biomass of extant or extinct mammals (Smith et al., 2016). Around 26 % of the Earth’s surface is dedicated to livestock farming (Ripple et al., 2014; Robinson et al., 2014), resulting in habitat conversion, overgrazing, soil erosion, high water wastage, high disease transmission risk and high emissions of greenhouse gases (Ripple et al., 2014, 2015; Phalan et al., 2016). Alteration of habitats for livestock is promoting the collapse of mammal populations globally (Ripple et al., 2015), and finding systems and practices that reconcile conservation with production are urgently needed (Phalan et al., 2016). Beef production in naturally growing pastures seems more environment-friendly than other alternatives (e.g., feedlots), as the adaptations of grassland plants and animals suggests coevolution with ungulates (Overbeck *et al*., 2007; Bond and Parr, 2010). This implies that grazing does not affect (Fig. 1A) and may even favor wildlife (Fig. 1B, dotted line). Here, we are concerned with the population-scale processes underlying the negative relationship between livestock grazing and the diversity of mammal communities in the Pampa biome (Pedó et al., 2010; Luza et al., 2016a), which might invalidate the neutral and positive responses of rodents to grazing (Fig. 1A and B, continuous line).

Grazing by large ungulates can directly (food competition, shelter/nest trampling) or indirectly (vegetation foraging) influence small mammals (Keesing, 1998; Matlack et al., 2001). Ungulate foraging and trampling alters vegetation density, height and cover, as well as the formation and maintenance of litter cover and soil permeability (Matlack et al., 2001; Fox et al., 2003). While overgrazing promotes the growth of disturbance-tolerant plants (rhizomatous and stoloniferous) and the consumption of disturbance-intolerant plants, low/no grazing promotes the accumulation of flammable biomass and the growth of tussocks, shrubs and trees, which cover rhizomatous and stoloniferous plants (Duarte et al., 2006; Overbeck et al., 2007). Grassland habitat structure varies seasonally, because vegetation growth is slower during the winter, which influences cattle density (Nabinger et al., 2009; Trindade et al., 2012) and probably affects the occurrence of rodents (Pedó et al., 2010; Vieira and Paise, 2011). Experimentally manipulating the horizontal (e.g., distance between vegetation patches) and vertical (e.g., height) structure of the vegetation provides a valuable opportunity to evaluate the effect of changes in grassland structure on both beef production and wildlife (Nabinger et al., 2009; Trindade et al., 2012).

Tussock grasses, shrubs and trees assure the high abundance and resilience of small mammal populations in grasslands and grassland-forest ecotones (e.g., Pedó et al., 2010; Luza et al., 2016a). Grazing might exert a negative effect on animal populations when management regimes misuse environmental carrying capacities, potentially subjecting specialist and lightweight species requiring tall/dense vegetation to high mortality and low recruitment rates (Keesing, 1998; Moenting and Morris, 2006). Small mammals requiring tall/dense vegetation are able to colonize a disturbed area that has been abandoned (Fox et al., 2003). In contrast, only opportunist and non-resident species occupy continuously and intensively grazed habitats (Fox et al., 2003). Overgrazing is becoming increasingly common in South Brazilian landscapes, because the government and economy demands the intensification of beef production in grassland remnants, which are becoming smaller and more isolated due to their conversion into crop fields and tree plantations (Carvalho and Batello, 2009; Azpiroz et al., 2012). Thus, an analysis of the occupancy of rodent species with different life histories, in grasslands which are subjected to different grazing intensities, may aid the formulation of the best management practices for the South Brazilian grasslands.

We aimed to evaluate the relationship between cattle grazing and paddock occupancy by three rodent species (Fig. 1). Rodents are conspicuous inhabitants of grasslands and human-modified habitats due to their morphological and behavioral adaptations to diverse environmental conditions (Vieira and Paise, 2011; Sponchiado et al., 2012; Luza et al., 2016a). Studied species consist of the insectivores-omnivores Azara's grass mouse (*Akodon azarae* [Fischer 1829]) and long-nosed hocicudo (*Oxymycterus nasutus* [Waterhouse 1837]), and the herbivore-granivore yellow pygmy rice rat (*Oligoryzomys flavescens* [Waterhouse 1837]). To evaluate rodent occupancy we took the possibility of imperfect detection into account, because a species can be undetected even when occupying a given site (MacKenzie et al., 2002; Guillera-Arroita, 2017).

We expected that the scansorial and bipedal *Oligoryzomys flavescens* would not be influenced by the grazing gradient (Fig. 1A), because the species is extremely agile and able to exploit exposed habitats (Taraborelli et al., 2003). Conversely, we expected that the semi-fossorial *Oxymycterus nasutus* should have both the highest detection in tall grasslands and the narrowest distribution across the grazing gradient (Fig. 1D- dotted line), because it is the less-vagile and has the largest body of the studied species. We expected unimodal detection and occupation probabilities for the cursorial *Akodon azarae* (Fig. 1C- continuous line), with its activity concentrated in areas of moderate grazing intensity due to both the high availability of green leaves and insects and its small body size which allows it to move under a thin litter layer (Bilenca and Kravetz, 1998).

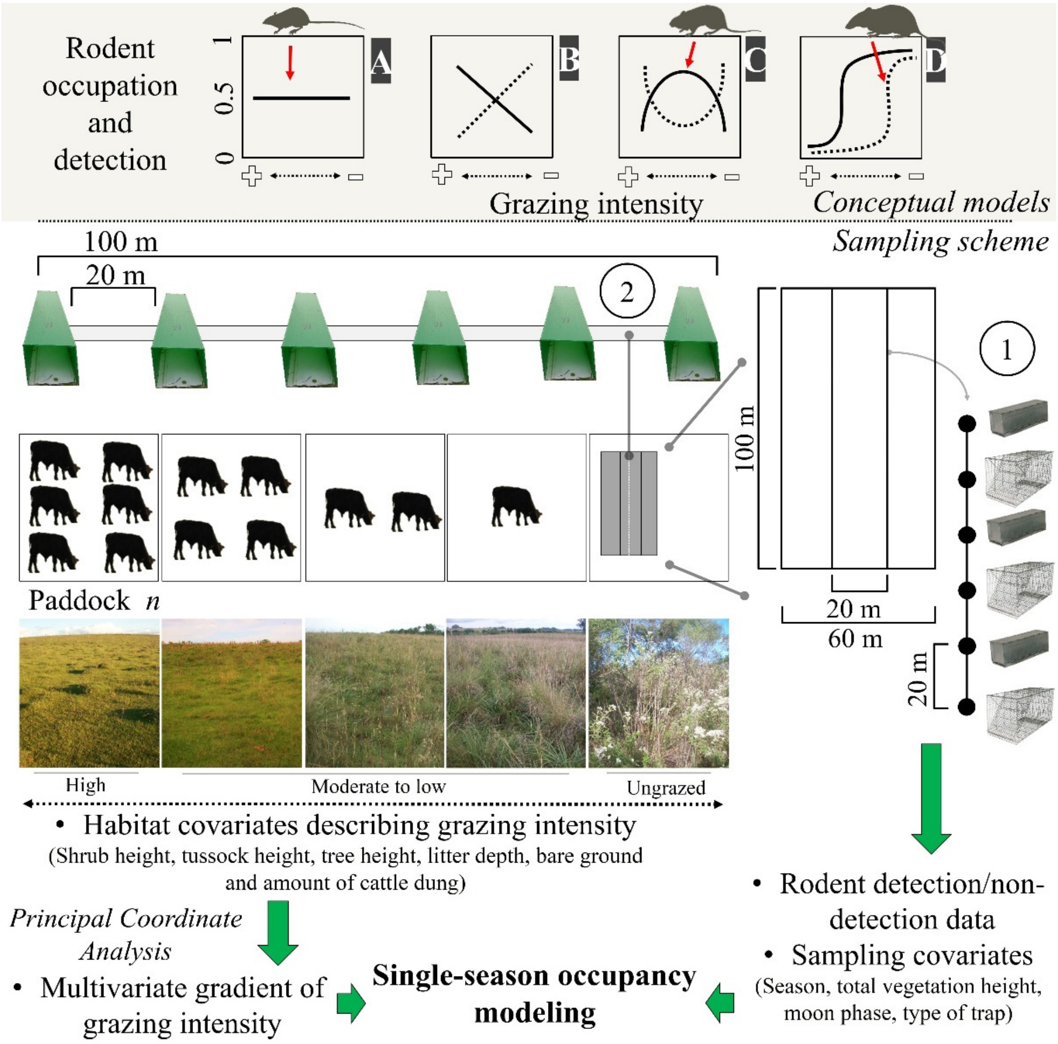


Fig. 1: Conceptual models (upper) and sampling scheme (lower) used in the study. Continuous or dotted lines in the conceptual models describe neutral (A), positive/negative linear (B), unimodal/bimodal (C) and logistic (D) relationships between rodent occupation/detection and grazing intensity. We sampled rodents using: 1) live trap grids and 2) tracking tunnel transects. We set grids and transects in ten paddocks subjected to different grazing intensities in each research station. We measured habitat covariates at each trapping point and sampling covariates for each sampling day, and related them to rodent detection using single-season occupancy modeling. Pictures show the variation in habitat structure across the gradient of grazing intensity (Pictures: A. L. Luza).

Material and methods

Study areas

We conducted the study from March 2016 to February 2017 on 16 grazed and 4 ungrazed paddocks located in two research stations within the Pampa biome in South Brazil. In Bagé, the eight grazed and two ungrazed paddocks were located in an experimental grassland (31.301170ºS, 53.950588ºW) of ≈ 300 hectares belonging to the Brazilian Agricultural Research Corporation (EMBRAPA). In Eldorado do Sul, the eight grazed and two ungrazed paddocks were located in an experimental grassland (30.103136ºS, 51.684382ºW) of ≈ 80 ha belonging to the Universidade Federal do Rio Grande do Sul (EEA). As the use of high stocking rates (i.e., keeping a high density of cattle within an area) is a widespread practice on South Brazilian farms (Carvalho and Batello, 2009), we chose these stations because they included the few sites where grazing manipulation has allowed the development of vegetation patches under several grazing levels, including ungrazed areas. Mean temperature throughout the study was 17.93± 5.83 ºC, with a mean precipitation of 0.85± 5.65 mm/day (Fig. S1.1).

Study species

The studied species predominantly occur in open-habitats and are among the most abundant species in the South Brazilian grasslands (Pedó et al., 2010; Vieira and Paise, 2011; Sponchiado et al., 2012; Luza et al., 2016a). *Akodon azarae* (mean± sd adult weight of 30.16 ± 9.02 g., according to our data) is a cursorial, opportunist and competitively aggressive species that occurs mainly in grasslands but uses crop fields when they provide high resource availability (Bilenca and Kravetz, 1998; Bilenca et al., 2007; Fraschina et al., 2009). *Oligoryzomys flavescens* (18.90 ± 6.48 g.) is able to exploit low-cover habitats due to its ability to efficiently flee from predators by suddenly changing its direction (Taraborelli et al., 2003). *Oxymycterus nasutus* (61.79 ± 16.72 g.) is the largest of the study species and seems the most sensitive to changes in habitat structure, since it notably avoids habitats with low vegetation cover (Pedó et al., 2010; Luza et al., 2016a). Other species that could be detected in the study areas include *Reithrodon typicus*, *Ctenomys torquatus*, *Calomys laucha*, *Cavia aperea* and *Scapteromys aquaticus*.

Non-volant small mammal sampling

A trapping campaign was conducted in each season (from autumn 2016 to summer 2017, Fig. S1.1) at both research stations. At each station we placed ten grids of Sherman (25 × 8 × 9 cm) and Tomahawk (47 x 17,5 x 15 cm) traps in the center of ten paddocks subjected to different grazing intensities (Fig. 1; further details in Appendix S1). Grids were distanced at least 100 m from each other and covered ≈ 80 hectares in EMBRAPA and ≈ 100 hectares in EEA. Each grid had 12 Sherman and 12 Tomahawk traps alternatingly placed at 6 points spaced 20 m apart along four transects (Fig. 1). Traps were left for five days in each paddock, which was considered sufficient for rapid population assessments (Fraschina et al., 2009; Vieira and Paise, 2011). Traps were revisited twice a day (morning and afternoon) to capture diurnal individuals and to avoid potential rodent mortality due to adverse weather conditions and predation. Total live-trapping effort was 4,800 trap/nights in EMBRAPA and 1,200 trap/nights in EEA (only one live-trapping campaign, see below); net live-trapping effort (i.e., discounting the unavailable traps) was 4,967 trap/nights.

We placed one transect of tracking tunnels (50 x 10 x 10 cm) within each grid (Fig. 1). We placed tunnels 20 m apart and monitored them across two nights per season. We reset the paper sheet and the ink of the tracking tunnels if rainfall occurred during the first night of sampling. Total tracking tunnel effort was 480 tunnel/nights. Since the autumn live-trapping campaign in EEA yielded no captures, any further live-trapping effort would unlikely have resulted in enough captures to make a difference in the models. Therefore, we only used tunnels to monitor paddocks in this site.

We took morphological measurements and ear tissue samples of all captured individuals and marked them with ear tags (~7mm). To acquire a reference footprint collection (Palma and Gurgel-Goncalves, 2007), we placed live-trapped individuals in a box with a paper sheet and ink to collect their footprints. We released trapped individuals at the point of capture. We baited traps with strong-smelling bait composed of bananas, peanuts, sardines, cod-liver oil, vanilla essence and corn meal. We identified footprints through geometric morphometrics (Palma and Gurgel-Goncalves, 2007) (Appendix S2, Table S2.1, Figures S2.1 - S2.4). Finally, we measured habitat covariates at each trap/tunnel point to characterize the vegetation of the paddocks (Figure 1; Tables S1.1 and S1.2). Permanova and Betadisper analyses of habitat covariates revealed between-paddock differences in habitat structure (Appendix S1), where highly grazed and ungrazed paddocks composed the two extremes of the grazing gradient (Fig. S1.2; Table S1.3).

Data analysis

We examined the relationship between rodent occupancy and grazing intensity using hierarchical single-season occupancy modeling (MacKenzie et al., 2002). Hierarchical models involve Bernoulli regressions to model the probability of site occupation (ψ) and species detection (p); ψ is the expected occupation state value of the site z after accounting for p. The probability that a site is occupied by a species is ψ, and the probability that it is unoccupied by the species is 1 – ψ. When a species is not occupying a site the species cannot be detected ($p = 0$), but when a species is present at a site the species is detected with probability $p > 0$. Some species are imperfectly detected due to differential trap type, abiotic conditions such as the season, and biologic aspects that alter the species activity, for example predator avoidance (MacKenzie et al., 2002; Guillera-Arroita, 2017).

We obtained the final detection data by combining the data obtained from the sequence of five days of live trapping per season and adding the data from the one additional day of tunnel tracking (the day in which we removed the tunnels). Overall, matrices for each rodent species contained 20 paddocks and 24 sampling occasions (days) in EMBRAPA (20 days [all seasons] plus 4 tunnel tracking days [all seasons]), and 9 sampling occasions in EEA (five live trapping days [only autumn] plus four tunnel tracking days [all seasons]). We accommodated the lack of live-trapping sampling in EEA by setting the detections to NA (MacKenzie et al., 2002). We used single-season occupancy modeling as the assumptions of site-closure to colonization and independence among sites seemed plausible for our single-year sampling (MacKenzie et al., 2003). We checked the sensitivity of the results using the complete dataset, which contained data obtained from sites sampled with different sampling efforts, by analyzing the 24 sampling occasions of the EMBRAPA site (Appendix S3).

We constructed an *a priori* set of candidate models to evaluate whether grazing intensity affects the occupation probability (Table S1.4). The models also composed concurrent hypotheses to assess whether season, total vegetation height (including linear, quadratic and cubic terms to represent the conceptual models of Fig. 1), the interaction and additive effect of season and total vegetation height, trap type (the use of live-traps or tracking tunnels) and the moon phase influences the probability of detection. Our data did not allow the inclusion of a site effect in the models because the low number of species records in the EEA site caused perfect model separation. The sample size of 20 paddocks prevented the testing of several interaction terms. To avoid wasting degrees of freedom when estimating the parameters for categorical covariates, we used the paddock centroid extracted from the Principal Coordinate Analysis as the occupation covariate in the candidate models (Appendices S1 and S3). Paddock centroid represents the point that minimizes the among-season differences in habitat characteristics within a given paddock (Anderson, 2006), and is a good representation of the between-paddock variation in grazing intensity.

We used the Akaike Information Criteria, corrected for small sample sizes (AICc), to select the models that presented the most detection and occupation information while using the fewest parameters (Burnham and Anderson, 2002). AICc weights (*w*) indicate the empirical support for each model, relative to others in the candidate set. We considered that models with Delta AICc > 4 units had low support (Burnham and Anderson, 2002). We estimated model parameters using maximum likelihood, and the goodness-of-fit of the best models was estimated through parametric bootstrapping (Fiske and Chandler, 2011). The same tests were used in the sensitivity analyses (Appendix S3). Analyses were conducted using functions implemented in ‘vegan’, ‘MuMIn’ and ‘unmarked’ R packages (R Core Team, 2017).

Results

A net effort of 4,967 trap/nights resulted in the capture of 88 individuals of the three study species. A net effort of 480 tunnel/nights yielded 57 detections of the three study species (Table S1.5). *Akodon azarae*, *Oligoryzomys flavescens* and *Oxymycterus nasutus* were detected in both research stations, although in EEA they were only found in ungrazed areas (Table S1.5). We detected *Akodon azarae* and *Oxymycterus nasutus* in all seasons, while *Oligoryzomys flavescens* was not found in the spring. We recorded 55 recaptures of 30 different individuals (Table S1.5); most recaptures occurred within the same season (n=52), with only three recaptures taking place in different seasons. Twenty-five recaptures occurred in the same trap that caught the individual the first time, 20 occurred within 20 m. of the trap responsible for their first capture and 16 occurred within 40 m. Only four recaptures occurred in traps 60 m. away from the trap that caught the individual for the first time. We recorded only one movement between grids (one *Akodon azarae* individual moving more than 150 m. between traps), which should not influence the results because it was not a new detection of the species. We recorded 13 afternoon captures during winter, one in autumn, one in spring and one in the summer.

Rodent detection and paddock occupation

Parametric bootstrapping showed that all of the best-ranked models fit the data well. Either season or season and total vegetation height were the detection covariates used in the best-ranked models for the three rodents (Table 1; complete results in Tables S1.6, S1.7 and S1.8). Detection of the three species was at least three times higher in the winter than in the non-winter months (Tables 2, S3.3, S3.5 and S3.7). Using EMBRAPA data, we found that season explained the detection of *Akodon azarae* and *Oligoryzomys flavescens* (Tables S3.2 and S3.4). Season and total vegetation height were the detection covariates used in the best-ranked models of *Oxymycterus nasutus* (Table 1 and S3.6). The highest detection probabilities of *Oxymycterus nasutus* were found in the winter months and under tall vegetation (Table 2; Table S3.7).

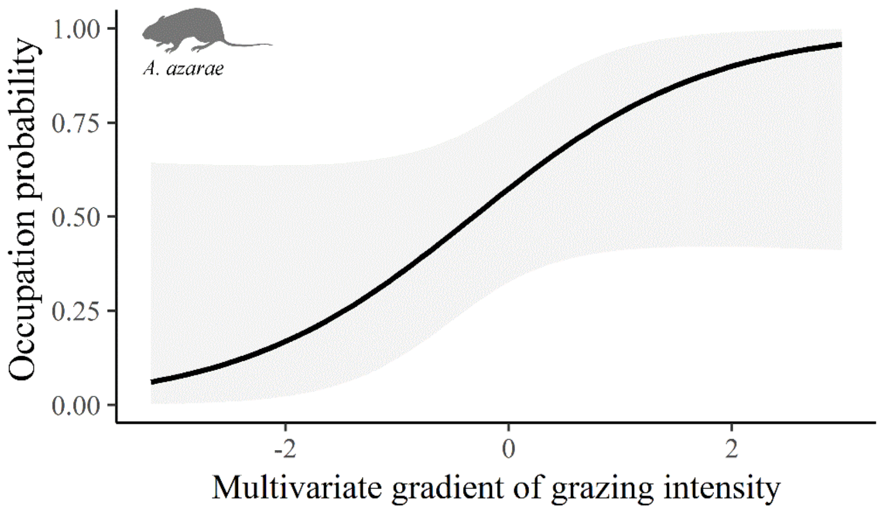
The gradient of grazing intensity (paddock centroid, Fig. S1.2) was included among the most plausible models for the three species (Table 1). Although the occupation estimates had a low precision, the model predictions showed a negative relationship between the probability of paddock occupation and grazing intensity (Fig. 2). *Akodon azarae* had the broadest distribution across the grazing intensity gradient, with a probability of occupancy of 0.05 in intensively grazed grasslands; using only the EMBRAPA data, the probability that the species occupied moderately grazed paddocks was 0.55. *Oligoryzomys flavescens* had both a subtly narrower distribution than *Akodon azarae* did, and it had occupation probabilities greater than 0.5 in paddocks subjected to moderate-low grazing intensities (Fig. 2); using the EMBRAPA data, the probability of occupation of *Oligoryzomys flavescens* was constant across the grazing gradient (Table S3.4). *Oxymycterus nasutus* showed the narrowest distribution across the grazing gradient, with its highest occupation occurring in ungrazed areas; this result was consistent using both the complete and the EMBRAPA datasets (Tables S1.8 and S3.6).

Table 1: Model-selection table with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S1.2).

Species	**df**	**LogLik**	**AICc**	**Delta AICc**	**Weight**
Akodon azarae					
p(Season) ψ (PCO1)	4	-128.49	267.60	0.00	0.55
p(Season+total height) ψ (PCO1)	5	-127.44	269.20	1.52	0.26
p(Season) ψ (.)	3	-131.14	269.80	2.14	0.19
p(Total height^3) ψ (PCO1^3)	4	-152.87	316.40	48.77	0.00
Oligoryzomys flavescens					
p(Season) ψ (PCO1)	4	-81.06	172.80	0.00	0.74
p(Season+total height) ψ (PCO1)	5	-80.92	176.10	3.34	0.14
p(Season) ψ (.)	3	-84.43	176.40	3.57	0.12
p(Season:total height^3) ψ (PCO1^3)	5	-91.48	197.20	24.45	0.00
Oxymycterus nasutus					
p(Season) ψ (PCO1)	4	-66.66	144.00	0.00	0.45
p(Season) ψ (.)	3	-68.59	144.70	0.69	0.32
p(Season+total height) ψ (PCO1)	5	-66.33	147.00	2.96	0.10
p(.) ψ (PCO1)	3	-70.71	148.90	4.93	0.04

Table 2: Estimates of detection probability given as a function of the sampling occasion covariates.

Linear combination (logit scale)	Detection probability	Confidence interval 2.5%	97.5%	Season	Total vegetation height (cm)
Azara's grass mouse (*Akodon azarae*)					
-1.67	0.16	0.05	0.38	Non-winter	4
-1.93	0.13	0.06	0.26		42
-2.20	0.10	0.05	0.18		104.3
-2.73	0.06	0.03	0.13		166
-3.00	0.05	0.02	0.13		228
-3.24	0.04	0.01	0.13		284
1.38	0.80	0.49	0.94	Winter	4
1.12	0.75	0.51	0.90		42
0.85	0.70	0.52	0.83		104.3
0.32	0.58	0.45	0.70		166
0.05	0.51	0.34	0.68		228
-0.19	0.45	0.24	0.69		284
Yellow pigmy rice rat (*Oligoryzomys flavescens*)					
-2.00	0.12	0.03	0.40	Non-winter	4
-2.13	0.11	0.03	0.29		42
-2.27	0.09	0.04	0.21		104.3
-2.53	0.07	0.03	0.19		166
-2.66	0.07	0.02	0.22		228
-2.78	0.06	0.01	0.27		284
0.02	0.51	0.13	0.88	Winter	4
-0.11	0.47	0.17	0.80		42
-0.24	0.44	0.22	0.69		104.3
-0.51	0.38	0.25	0.52		166
-0.64	0.35	0.19	0.55		228
-0.76	0.32	0.12	0.61		284
Long-nosed hocicudo (*Oxymycterus nasutus*)					
-2.01	0.12	0.02	0.45	Non-winter	4
-1.79	0.14	0.04	0.40		42
-1.57	0.17	0.07	0.38		104.3
-1.14	0.24	0.10	0.49		166
-0.92	0.29	0.09	0.62		228
-0.73	0.33	0.07	0.75		284
-1.24	0.22	0.03	0.71	Winter	4
-1.03	0.26	0.06	0.66		42
-0.81	0.31	0.12	0.60		104.3
-0.37	0.41	0.25	0.59		166
-0.16	0.46	0.25	0.69		228
0.04	0.51	0.22	0.79		284



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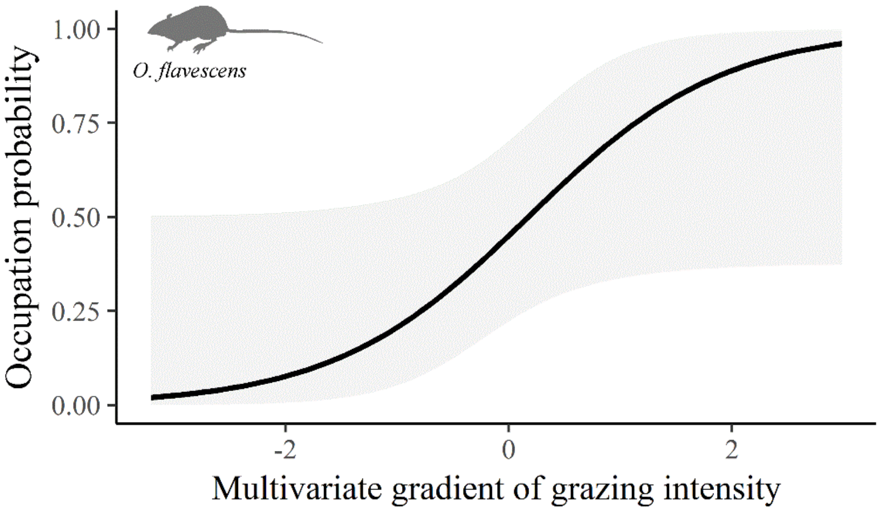

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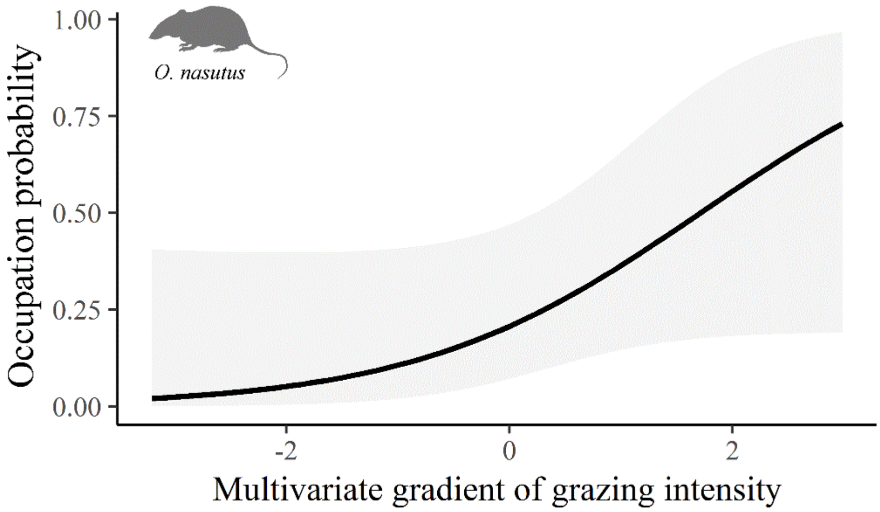

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Fig. 2: Occupation probability as a function of the gradient of grazing intensity. Values of the multivariate gradient of grazing intensity were extracted from Axis 1 of the Principal Coordinate Analysis (Fig. S1.2). The lowest negative values indicate the highest grazing intensities, whereas the highest positive values indicate the absence of grazing.

Discussion

Livestock contributes to the food security of almost a billion people, but its effects on wildlife and world climate deserves attention as cattle biomass and the amount of land dedicated to livestock farming exceeds any other land use (Ripple et al., 2014; Robinson et al., 2014; Phalan et al., 2016). We evaluated rodent detection and occupation in grasslands hosting species thought to be resilient to grazing (Overbeck et al., 2007; Bond and Parr, 2010). Since we used different sampling procedures and efforts, we used both hierarchical occupancy modeling and sensitivity analyses to estimate rodent occupation. Overall, rodent detection was influenced by season and total vegetation height, whereas rodent occupation was negatively influenced by the increased intensity of cattle grazing.

Grassland structure varies seasonally (Trindade et al., 2012), influencing cattle management and rodent detectability. Grassland managers generally decrease the stocking rates in winter because vegetation grows slowly due to the lower photoperiod and colder weather; thus, the production of seeds and green leaves decreases considerably (Trindade et al., 2012; Nabinger et al., 2009). To meet their minimum energetic requirements rodents overlap and shorten their activity periods during winter, in response to food shortage, low photoperiod and cold nights, heavy and constant rain, and low activity of predators (Fraschina et al., 2009; Vieira and Paise, 2011; Maestri and Marinho, 2014). These factors may increase bait attractiveness and detectability in the winter (Vieira and Paise, 2011). Correspondingly, the probability of detection of the three rodent species was higher in the winter. *Oxymycterus nasutus*, the less vagile of the species, had a higher probability of detection during winter months in tall grasslands. The detection probability of *Akodon azarae* and *Oligoryzomys flavescens* was more dependent on season than on vegetation height. Thus, decreasing stocking rates in the winter may be a good management practice since rodents are subjected to low food availability and high climatic stresses.

Ungulate foraging and trampling influence rodent habitats by altering the vegetation density, height and cover, as well as the formation and maintenance of litter cover and soil permeability (Matlack et al., 2001; Fox et al., 2003). Species not influenced by cattle grazing prosper in human-modified landscapes, while intolerant and less-vagile species may be restricted to fewer sites with a low or absent grazing intensity (Medan et al., 2011; Azpiroz et al., 2012; Luza et al., 2014). Occupancy models showed that cattle grazing did not influence the occupation of *Oligoryzomys flavescens*, which is due to the ability of this bipedal species to exploit habitats with different degrees of vegetation cover (Taraborelli et al., 2003; Luza et al., 2016a). In contrast, occupancy models showed that the probability of occupation of *Akodon azarae* and *Oxymycterus nasutus* increased with decreasing grazing intensity. Paddocks with dense and heterogeneous vegetation, composed of tussock grasses, tall shrubs and scattered trees, ensure safe foraging for plant leaves, seeds and invertebrates below and inside the layers of dense vegetation (Moenting and Morris, 2006). Although *Akodon azarae* is considered an opportunistic species (Bilenca et al., 2007), its preferred conditions and resources are found in ungrazed grasslands. *Oxymycterus nasutus* had the narrowest distribution along the grazing gradient and was the species most sensitive to grazing. This could be due to its large body size, low vagility and semi-fossorial nature (Pedó et al., 2010; Luza et al., 2016a). Ungrazed areas might provide favorable habitats and support larger rodent populations (Keesing, 1998). For example, Keesing (1998) found that ungrazed savannas harbored an herbivorous rodent with a density twice that of grazed areas. Thus, populations of many species that are in need of conservation rely on ungrazed areas for reproduction and shelter (Pedó et al., 2010; Azpiroz et al., 2012; Luza et al., 2016b).

The differences we found in the sensitivity analyses by comparing the complete dataset (both EMBRAPA and EEA sites) with the EMBRAPA dataset of *Oligoryzomys flavescens* can be explained by the species occurrence only in the ungrazed areas of EEA. The failure to obtain any detection of the studied species in the grazed areas of EEA might be due to factors such as the high degree of grassland conversion into tree plantations and crop fields in the surrounding landscape. This is a more probable explanation than the difference in species detections being due to differential sampling techniques and effort, because we did not 1) record more detections in autumn when we used both tracking tunnels and live-traps, 2) record more detections in tunnels when obtaining a higher live-trapping success in EMBRAPA (Table S1.5) and 3) find that the model considering the effect of trap type was among the best-ranked models for the three species (see Results). Despite the high uncertainty in the estimates of occupation probability, resulting from the low number of species detections, we showed that the occupation of *Akodon azarae* and *Oxymycterus nasutus* increased with a decreasing grazing intensity.

Our results support the idea that the main problem related to livestock is overgrazing, which occurs when too many cattle continuously graze in the same area. Increasing the number of cows in an area is erroneously used in South Brazilian grasslands to increase beef production (Carvalho and Batello, 2009), which has a negative effect on rodents that are sensitive to changes in habitat structure. We advocate for spare ungrazed areas, with the simultaneous decrease of the stocking rate to avoid overgrazing in grasslands used for beef production. We determine that this constitutes the best management strategy for conserving large rodent populations in the grassy landscapes of South Brazil. Low-intensity management that considers the carrying capacity of a grassland (i.e., potential grass growth) is the most productive strategy regarding beef production for these grasslands (Nabinger et al., 2009; Trindade et al., 2012), and may provide the minimal habitat requirements for rodent occurrence. Therefore, the land sparing approach, which embraces both the maintenance of ungrazed habitats while intensifying beef production in the remaining landscape (Phalan *et al.*, 2016), could be an alternative for South Brazilian grassy landscapes if beef production respects the carrying capacity of grasslands.

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Data statement

Data can be requested directly from the corresponding author.

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Supporting information:

Appendix S1: Research station management and analyses of the effect of grazing on habitat structure.

Figure S1.1: Temperature (ºC) and maximum precipitation (mm.) during the course of the study. Each point shows the mean daily temperature (ºC), and point size represents the maximum daily rainfall (mm) (from 2015-12-01 to 2017-03-15). Data was obtained from the Brazilian National Institute of Meteorology (INMET; http://www.inmet.gov.br/portal/). The horizontal line segments indicate the periods of rodent sampling in each season.

Figure S1.2: Principal Coordinate Analysis plot showing the between-season and between-paddock variation in habitat. Variation captured by the two first ordination axes is included within the axes labels. Convex hulls delimit paddock groups according to their grazing intensity; the lines inside each convex hull link the paddock centroid with the habitat of each season. We used the continuous value of the paddock centroid as the quantitative measurement of the grazing intensity. Black circles indicate centroids from EEA (Eldorado do Sul, RS) paddocks, and white circles indicate centroids from EMBRAPA (Bagé, RS) paddocks.

Table S1.1: Habitat covariates collected at trapping points distributed across grazing paddocks from two livestock research stations in the Pampa biome, Brazil. A point refers to one Sherman, one tomahawk or one tracking tunnel. For the data analysis, covariates were averaged by paddock. Covariates marked with * had low or moderate correlation and were used to extract the multivariate gradient of grazing intensity (Fig S1.2).

Table S1.2: Habitat covariates by grazing paddock. * Grazing intensity was derived from the paddock's position along the disturbance gradient (Fig. S1.2). We present the total number of live-trap captures and recaptures per species in each paddock. Detections derived from tracking tunnels are presented in ***bold*** and ***italic***.

Table S1.3: Correlations between habitat covariates and the axes of the Principal Coordinate Analysis (Fig. S1.2).

Table S1.4: Candidate models potentially explaining rodent detection (p) and site occupation (ψ).

Table S1.5: Sampling effort and number of detections presented according to species, site, trap type and season. In Eldorado do Sul (EEA), we sampled from winter 2016 to summer 2017 using tracking tunnels only. Within parenthesis, we present the number of recaptures for live-trap sampling. In **bold**, we present the number of tracking tunnels with detections.

Table S1.6: AICc ranking of all candidate models for Azara's grass mouse (*Akodon azarae*).

Table S1.7: AICc ranking of all candidate models for the yellow pigmy rice rat (*Oligoryzomys flavescens*).

Table S1.8: AICc ranking of all candidate models for the long-nosed hocicudo (*Oxymycterus nasutus*).

Appendix S2: Footprint morphometrics.

Table S2.1: Accuracy (%) of the classification of the footprints in the reference collection. We collected the footprints after measuring and weighing rodents trapped in live-traps (Tomahawk and Sherman).

Fig. S2.1: Shape variation (upper) and footprint size distribution (in cm, bottom) for the left foot of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (346 footprints), whereas black points compose the consensus shape.

Fig. S2.2: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the right foot of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (325 footprints), whereas black points compose the consensus shape.

Fig. S2.3: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the left hand of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (355 footprints), whereas black points compose the consensus shape.

Fig. S2.4: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the right hand of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (310 footprints), whereas black points compose the consensus shape.

Appendix S3: Sensitivity analyses using the EMBRAPA data.

Fig. S3.1: Principal coordinate analysis plot showing the between-season and between-paddock variation in habitat structure. Variation captured by the two first ordination axes is included within the axes labels. Convex hulls delimit paddock groups according to their grazing intensity; the lines inside each convex hull link the paddock centroid with the habitat of each season. We used the continuous value of the paddock centroid as the quantitative measurement of the grazing intensity. Data was collected from EMBRAPA (Bagé, RS).

Fig. S3.2: Occupation probability (ψ) of *Akodon azarae*, given as a function of the gradient of grazing intensity. Values of the multivariate gradient of grazing intensity were extracted from Axis 1 of the Principal Coordinate Analysis (Fig. S2.1). The lowest negative values indicate the highest grazing intensities, whereas the highest positive values indicate the absence of grazing.

Fig. S3.3: Occupation probability (ψ) of *Oxymycterus nasutus*, given as a function of the gradient of grazing intensity. Values of the multivariate gradient of grazing intensity were extracted from Axis 1 of the Principal Coordinate Analysis (Fig. S2.1). The lowest negative values indicate the highest grazing intensities, whereas the highest positive values indicate the absence of grazing.

Table S3.1: Correlations between habitat covariates and the axes of the Principal Coordinate Analysis (Fig S2.1).

Table S3.2: Model-selection table for *Akodon azarae*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1=

gradient of grazing intensity (Fig. S2.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Table S3.3: Estimates of the detection probabilities of *Akodon azarae*, given as a function of the sampling occasion covariates.

Table S3.4: Model-selection table for *Oligoryzomys flavescens*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S2.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Table S3.5: Estimates of the detection probabilities (p) of *Oligoryzomys flavescens*, given as a function of the sampling occasion covariates.

Table S3.6: Model-selection table for *Oxymycterus nasutus*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S2.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Table S3.7: Estimates of the detection probabilities (p) of *Oxymycterus nasutus*, given as a function of the sampling occasion covariates.

CONSIDERAÇÕES FINAIS

A habilidade das espécies em seguir expansões ou retrações no hábitat (sejam estas causadas por dinâmicas climáticas ou por atividades antropogênicas) depende tanto da velocidade em que o hábitat muda quanto do potencial dispersivo das espécies em superar limites ecológicos e adversidades ambientais (Isbell et al., 2017; Davidson et al., 2017; Sandel et al., 2011; Prevedello & Vieira, 2010; Umetsu et al., 2008; Debinski & Holt, 2000). Geralmente, espécies com elevada especificidade a um determinado hábitat e recurso tem menor capacidade de dispersão e maior propensão à extinção quando os hábitats mudam (Cantalapiedra et al., 2011; Sandel et al., 2011; Bofarull et al., 2008). Utilizando análises de aninhamento (*nestedness*), um componente da diversidade β que caracteriza a perda ordenada de espécies entre sítios e regiões (Baselga, 2010; Almeida-Neto et al., 2008), observei que a distribuição de somente três de 13 guildas analisadas é limitada ao hábitat ancestral, sugerindo que um elevado *fitness* (baixas taxas de mortalidade e altas taxas de reprodução) é alcançado independentemente da similaridade entre o hábitat ancestral e o novo hábitat ocupado. Esta capacidade de mudança de nicho (*niche shifts*, Perman et al., 2008) pelas espécies de mamíferos pode indicar baixas taxas de extinção com a mudança no hábitat devido a alterações climáticas, embora análises mais profundas são necessárias para elucidar propriamente o efeito das mudanças climáticas (e.g., Davidson et al., 2017).

Processos de extinção regional e global de espécies (diversidade ɣ) podem ser explicados não somente pela extinção local de espécies (i.e., diminuição da diversidade α) mas também pela perda das diferenças na composição de espécies entre sítios (i.e., diminuição da diversidade β geralmente culminando com o aumento da contribuição do componente de aninhamento) (Isbell et al., 2017; Socolar et al., 2016; McGill et al., 2015). Observamos uma variação regional no processo de extinção de espécies através da análise da composição de comunidades de pequenos mamíferos não-voadores em hábitats prístinos e modificados por ações antropogênicas (capítulo 2). O componente de aninhamento foi maior para as comunidades de biomas temperados do que para as comunidades tropicais, e maior entre florestas e hábitats modificados do que entre campos e hábitats modificados. A estabilidade climática de regiões tropicais ao longo do tempo geológico parece ter favorecido o acúmulo de diversidade em regiões tropicais, principalmente devido às baixas taxas de extinção de espécies; em contraste, extinções e recolonizações parecem ser eventos comuns em regiões temperadas (Soininen et al., 2018; Dobrovolski et al., 2012; Jansson, 2003). Já o maior aninhamento observado entre florestas e lavouras/clareiras (*crop fields/clear-cuts*) parece resultar da severa simplificação do hábitat culminando na extinção de espécies florestais raras em lavouras e clareiras (McGill et al., 2015; Tschnartke et al., 2012; Ewers & Didham, 2006).

As análises da composição de comunidades de pequenos mamíferos não-voadores em hábitats modificados por ações antropogênicas sugerem extinções na escala regional (capítulo 2) praticamente sem extinções locais e mudanças na composição de espécies relativo aos hábitats prístinos e ao esperado pelo conjunto regional de espécies (capítulo 3). De fato, esta é uma das várias respostas da biodiversidade que podem ser evidenciadas em escala local (McGill et al. 2015). Por exemplo, Pardini e colaboradores (2010), Fonseca e colaboradores (2009) e Barlow e colaboradores (2007) observaram que florestas primárias (*old-growth forests*), florestas secundárias e florestas plantadas não diferiram em riqueza de espécies de pequenos mamíferos; no entanto, perceberam um processo de diminuição na diversidade β entre hábitats devido à imigração de espécies florestais generalistas nos diferentes tipos de hábitats modificados. Assim, há um certo grau de inconsistência nas tendências da biodiversidade observadas em escalas locais, principalmente devido às dificuldades de diferenciar extinções de imigrações. Debates tem surgido sobre como propriamente diferenciar as extinções de imigrações em escala local e se avaliações da biodiversidade na escala local deveriam ser consideradas para o planejamento de conservação de espécies e de serviços ecossistêmicos (veja, por exemplo, Cardinale et al., 2018; Vellend et al., 2017; Gonzalez et al., 2016).

A extinção regional de espécies nem sempre é acompanhada por extinções locais justamente pelo balanço entre extinções e imigrações (McGill et al., 2015; Jackson & Sax, 2010). A alternativa que utilizei para diferenciar extinções de imigrações foi considerar a ‘diversidade obscura’ de espécies (“*dark diversity*”) (Lewis et al., 2017; Pärtel et al., 2013); a outra alternativa seria o acompanhamento das variações na riqueza e composição de comunidades ao longo do tempo (*time-series analysis*; Cardinale et al., 2018; Vellend et al., 2017, 2013; Dornelas et al., 2014). A diversidade obscura de espécies contida no pool regional de espécies inclui o conjunto de espécies com probabilidade diferencial de chegar e sobreviver nas comunidades, mas que já não ocorrem nestas devido a interações bióticas ou distúrbios antropogênicos (Lewis et al., 2017; Karger et al., 2016; Pärtel et al., 2013). A comparação da diversidade de espécies e de funções de comunidades de hábitats pristinos e modificados em relação ao que seria esperado pelo conjunto regional de espécies indicou baixas taxas de extinção e imigração. No entanto, a perda de poucas espécies resultou em diminuição da diversidade funcional em alguns hábitats modificados (bordas de campos, lavouras). Em geral, as comunidades de hábitats modificados pareceram ser resistentes a modificações no hábitat, já que parecem ser tão ‘completas’ e capazes de manter a riqueza e composição regional quanto as comunidades de hábitats prístinos. Um aspecto importante a se considerar é que espécie pode estar presente em um hábitat mesmo fadada à extinção; assim, sua presença não garante um bom status de conservação (Isbell et al., 2017; McGill et al., 2015; Jackson & Sax, 2010). Um outro fato a se considerar é a sensibilidade dos táxons às modificações no hábitat. A ausência de extinções locais pode ser transitória devido à atrasada resposta dos pequenos mamíferos às modificações no hábitat (Metzger et al., 2010; Johnson et al., 2002). Assim, débitos de extinção podem se acumular ao longo do tempo (Isbell et al., 2017; Jackson & Sax, 2010). Considerar outros mamíferos, como aqueles pertencendo às guildas cuja distribuição foi fortemente limitada ao hábitat ancestral (granívoros), pode revelar respostas mais claras sobre a influência de atividades antropogênicas sobre a biodiversidade.

Um importante pressuposto para as análises comparando hábitats prístinos e modificados (capítulos 2 e 3) foi que comunidades dos campos e florestas prístinas estariam sujeitas à baixas taxas de extinção; portanto, estes hábitats prístinos resguardariam a diversidade ‘original’ de espécies e funções ‘do o conjunto regional de espécies. No entanto, isto nem é sempre o caso, como constatei no último capítulo desta tese. Incêndios, caçadas, pastejo por ungulados domésticos, corte ilegal de árvores, abertura de estradas e a drenagem de banhados são algumas fontes de degradação que influenciam na qualidade dos hábitats prístinos para a fauna e flora (Barlow et al., 2016, 2007; Luza et al., 2016, 2014; Azpiroz et al., 2012; Gibson et al., 2011). Por exemplo, Barlow e colaboradores (2016) estimaram que distúrbios dentro das florestas reduziram severamente (41-61%) a qualidade esperada das florestas primárias para a conservação de plantas, aves e besouros de uma região da Amazônia. Gibson e colaboradores (2011) realizaram uma meta-análise do valor de diversos tipos de hábitats modificados para a conservação de espécies florestais; constataram que nenhum hábitat contribui tanto para a conservação de espécies florestais quanto as florestas prístinas sob mínima influência antropogênica. Para ecossistemas campestres, diversas evidências sugerem que campos sob altos níveis de perturbação (intensamente pastejados e frequentemente queimados) tem pouco valor para a conservação de vertebrados e plantas lenhosas (Carlucci et al., 2016; Luza et al., 2016, 2014; Azpiroz et al., 2012; Andersen et al., 2012; mas veja Overbeck et al., 2016; Parr et al., 2014; Pillar & Vélez, 2010; Bond & Parr, 2010). Avaliar o papel de ecossistemas campestres para a conservação da biodiversidade é relevante uma vez que queimadas e o pastejo por ungulados têm sido considerados elementos indispensáveis à diversidade de plantas e animais em ecossistemas campestres (Pillar & Vélez, 2010; Overbeck et al., 2007).

Para avaliar a estrutura de populações de mamíferos em hábitats prístinos sujeitos à influência antropogênica, registramos a ocorrência de três espécies de roedores durante um ano em campos sob diferentes níveis de pastejo por bovinos. As análises revelaram que a espécie de roedor com maior massa corporal e menor capacidade de dispersão (*Oxymycterus nasutus*) dentre as espécies avaliadas teve maior probabilidade de ocupação em hábitats não pastejados. Portanto, a supressão de áreas não pastejadas possivelmente provocaria a extinção local de *O. nasutus* mesmo em campos prístinos; outras espécies dependendo de vegetação campestre alta e densa também poderiam ter o mesmo destino (Luza et al. 2016; Pedó et al. 2010). Desde que ambientes pastejados dominam as paisagens campestres do sul do Brasil (Carlucci et al., 2016; Luza et al., 2016, 2014), manter hábitats pristinos livres da influência antropogênica é indispensável para a conservação de populações de mamíferos e de outros organismos (Barlow et al., 2016, 2007; Luza et al. 2016, 2014; Gibson et al., 2011).

O principal objetivo da tese foi contribuir para o conhecimento de como características das espécies e dos hábitats influenciam na força dos processos de dispersão e de extinção em escala regional e local. Para tanto, utilizamos ferramentas da macroecologia e ecologia de comunidades (diversidade β, conjuntos probabilísticos de espécies) e ecologia de populações (modelos hierárquicos de ocupação e detecção). Em suma, dependendo da escala de observação, encontramos que processos históricos, evolutivos e antropogênicos podem 'desequilibrar a balança' para maior extinção ou dispersão, que por sua vez influencia na extensão espacial de distribuição das espécies e na estrutura das comunidades e populações. Perspectivas futuras incluem a avaliação do tempo necessário para o pagamento de débitos de extinção e como podemos frear este processo. Além disto, análises com grupos de mamíferos mais dependentes de tipos específicos de hábitats e recursos (e.g., granívoros) podem demonstrar mais claramente o efeito da influência antropogênica sobre a biodiversidade. Finalmente, ecossistemas campestres ainda são pouco conhecidos do ponto de vista científico (e.g., Vorontsova et al., 2016) e muito negligenciados pela agenda conservacionista (Veldman et al. 2015; Parr et al., 2014; Overbeck et al., 2007; Hoekstra et al., 2005). Embora os dados analisados nos capítulos desta tese considerem muitos sítios campestres de diversas partes do planeta, uma meta-análise em escala global se faz necessária para avaliar o valor de ecossistemas campestres sob diferentes níveis de distúrbios para a conservação de sua flora e fauna específicas.

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MATERIAL SUPLEMENTAR

CAPÍTULO 1

Mammal guild distribution dynamics between forest and open habitats

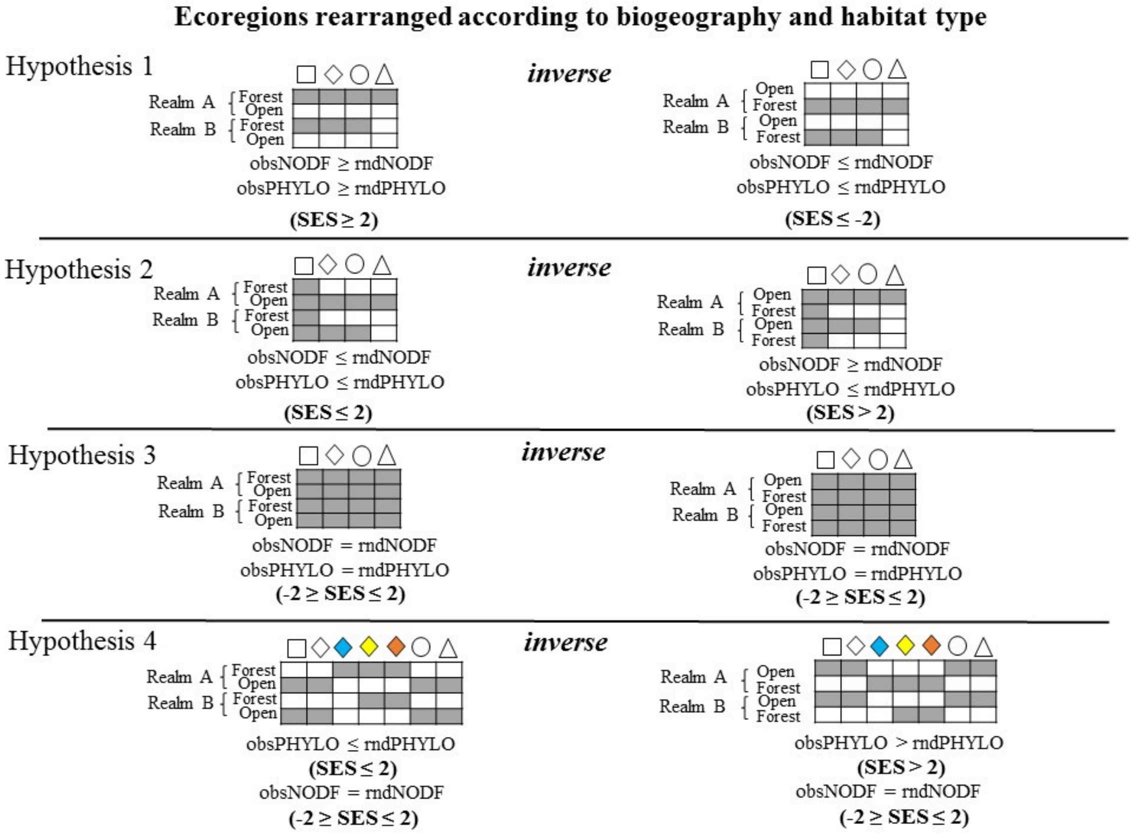

Figure S1.1: The expected structure of the occurrence matrix according to our hypotheses. Rearrangements were expected to produce different degrees of taxonomic and phylogenetic nestedness, because nestedness indexes (NODF and phyloNODF) are sensitive to differences in composition and diversity between pairs of ecoregions. Here, we exemplify that a biogeography effect may weaken nestedness by decrease the differences of richness and composition overlap between pairs of rows and columns of an occurrence matrix (left-side matrices of hypothesis 2 and 4 are less nested than the right-side matrices). The different symbols represent different species; symbols with same shape but different colors indicate phylogenetically related species. obsNODF= Observed taxonomic NODF; obsPHYLO= observed phylogenetic NODF; rndNODF=

random taxonomic NODF; rndPHYLO= random phylogenetic nestedness; SES= standardized effect sizes for NODF and phyloNODF. Random indexes were generated by matrix randomization.

Table S1.1: Ecoregion mean species richness ± SD by habitat type and biogeographic realm. We used these criteria plus the ecoregion area to rearrange ecoregions. Details of feeding habits in Table 1.

	HABITAT TYPE		BIOGEOGRAPHIC REALM							
TROPHIC LEVEL/Dietary guild	FOREST	OPEN	AFROTROPIC	ANTARCTICA	AUSTRALASIA	INDO-MALAYAN	NEARCTIC	NEOTROPIC	OCEANIA	PALEARCTIC
HERBIVORES										
Grazers	5.27 ± 3.82	7.78 ± 5.64	11.85 ± 6.69	0 ± 0	4.97 ± 3.93	3.55 ± 2.42	6.17 ± 2.86	5.03 ± 3.62	0 ± 0	6.20 ± 4.15
Browsers	7.42 ± 4.78	9.19 ± 6.82	15.88 ± 7.52	0 ± 0	3.6 ± 3.13	6.06 ± 4.50	8.12 ± 3.62	6.54 ± 3.05	1 ± 0	8.0 ± 4.44
Mixed-feeders	7.05 ± 4.74	5.56 ± 3.89	10.83 ± 4.61	0 ± 0	2.64 ± 1.35	5.69 ± 4.17	6.18 ± 3.03	3.60 ± 2.43	1 ± 0	7.26 ± 4.06
Granivores	3.57 ± 2.25	4 ± 2.88	2.64 ± 1.81	0 ± 0	1.69 ± 0.78	1.49 ± 0.85	3.96 ± 1.63	3.60 ± 1.92	0 ± 0	5.25 ± 3.10
Frugivores	5.97 ± 5.39	3.74 ± 3.68	6.11 ± 3.3	0 ± 0	7 ± 9.60	7 ± 3.65	1.76 ± 0.96	7.13 ± 4.59	0 ± 0	1.53 ± 0.78
CARNIVORES										
Vertebrate-eaters	5.61 ± 2.67	6.25 ± 2.57	5.45 ± 2.13	0 ± 0	2.26 ± 1.21	6.08 ± 3.25	5.38 ± 1.93	5.93 ± 1.23	0 ± 0	6.52 ± 3.30
Invertebrate- eaters	4.97 ± 2.86	5.05 ± 3.25	6.88 ± 4.07	0 ± 0	4.6 ± 2.44	3.74 ± 2.52	3.00 ± 1.42	6.04 ± 2.63	0 ± 0	4.94 ± 2.63
OMNIVORES										
Vertebrate- and fruit-eaters	2.49 ± 2.07	2.31 ± 1.99	5.01 ± 3.83	0 ± 0	1 ± 0	1.12 ± 0.33	1.35 ± 0.53	2.77 ± 0.94	0 ± 0	1.77 ± 0.75
Invertebrate- and fruit-eaters	4.93 ± 4.16	4.38 ± 4.35	7.33 ± 4.67	0 ± 0	2.67 $ 2.58	3.74 ± 3.22	1.21 ± 0.43	5.56 ± 4.11	0 ± 0	1.04 ± 0.19
Invertebrate- and seed-eaters	3.15 ± 2.60	5.51 ± 4.38	7.17 ± 4.68	0 ± 0	3.97 ± 2.25	2.12 ± 1.49	5.42 ± 3.51	2.91 ± 2.23	0 ± 0	2.95 ± 2.93
Invertebrate- and fruit/seed-eaters	6.04 ± 6.48	4.49 ± 3.96	5.478 ± 3.57	0 ± 0	3.67 ± 3.56	12.69 ± 8.71	3.29 ± 1.89	3.38 ± 2.78	1.45 ± 0.60	5.48 ± 5.44
Vertebrate/invertebrate- and seed-eaters	2.31 ± 2.13	1.95 ± 1.74	3.27 ± 2.27	1 ± 0	1 ± 0	4.48 ± 2.44	1.01 ± 0.11	1.06 ± 0.24	1 ± 0	2.28 ± 1.82
Vertebrate/invertebrate- and fruit-eaters	6.87 ± 4.59	5.70 ± 3.72	8.62 ± 3.04	0 ± 0	2.18 ± 1.74	9.71 ± 4.86	4.02 ± 1.72	9.00 ± 4.35	0 ± 0	3.63 ± 1.99

Table S1.2: Ecoregion mean phylogenetic diversity ±SD by habitat type and biogeographic realm. We used these criteria plus the ecoregion area to rearrange ecoregions. Details of feeding habits in Table 1.

	HABITAT TYPE		BIOGEOGRAPHIC REALM							
TROPHIC LEVEL/Dietary guild	FOREST	OPEN	AFROTROPIC	ANTARCTICA	AUSTRALASIA	INDO-MALAYAN	NEARCTIC	NEOTROPIC	OCEANIA	PALEARCTIC
HERBIVORES										
Grazers	335.94 ± 145.93	417.35 ± 300.32	571.84 ± 207.36	0 ± 0	233.81 ± 104.32	284.78 ± 122.78	348.08 ± 106.47	324.02 ± 128.01	0 ± 0	396.82 ± 162.45
Browsers	449.22 ± 176.47	490.71 ± 217.17	702.85 ± 232.28	0 ± 0	304.79 ± 115.40	362.68 ± 177.07	499.44 ± 125.41	477.95 ± 148.43	147.10 ± 0	426.68 ± 129.35
Mixed-feeders	343.65 ± 135.65	405.52 ± 169.55	592.97 ± 168.83	0 ± 0	259.96 ± 98.77	326.59 ± 142.88	340.82 ± 79.44	289.01 ± 81.39	147.10 ± 0	391.90 ± 113.31
Granivores	255.39 ± 88.43	269.77 ± 105.89	201.06 ± 79.26	0 ± 0	208.73 ± 72.95	171.22 ± 47.90	286.05 ± 77.29	282.68 ± 82.95	0 ± 0	293.84 ± 104.23
Frugivores	409.35 ± 239.37	293.67 ± 184.59	425.08 ± 175.08	0 ± 0	338.15 ± 235.42	501.91 ± 186.70	165.05 ± 34.19	499.25 ± 239.73	0 ± 0	173.13 ± 50.08
CARNIVORES										
Vertebrate- eaters	297.26 ± 79.43	307.52 ± 80.89	285.35 ± 85.52	0 ± 0	235.08 ± 78.93	307.26 ± 86.08	288.69 ± 36.43	263.63 ± 60.39	0 ± 0	348.27 ± 79.45
Invertebrate- eaters	385.97 ± 149.04	381.81 ± 159.63	478.95 ± 173.08	0 ± 0	415.65 ± 101.80	352.67 ± 163.39	269.57 ± 77.60	458.06 ± 144.54	0 ± 0	335.78 ± 115.74
OMNIVORES										
Vertebrate- and fruit-eaters	144.04 ± 55.05	132.77 ± 47.68	179.23 ± 62.57	0 ± 0	96.20 ± 0	103.81 ± 20.91	113.74 ± 26.09	180.63 ± 48.83	0 ± 0	108.66 ± 18.69
Invertebrate- and fruit-eaters	352.25 ± 182.60	307.12 ± 191.46	416.87 ± 192.82	0 ± 0	213.24 ± 71.82	280.08 ± 113.62	178.62 ± 62.64	417.68 ± 189.65	0 ± 0	150.59 ± 17.68
Invertebrate- and seed-eaters	227.02 ± 92.40	279.28 ± 115.29	307.58 ± 101.34	0 ± 0	237.66 ± 85.60	197.10 ± 60.50	322.41 ± 131.31	208.25 ± 81.08	0 ± 0	216.91 ± 82.19
Invertebrate- and fruit/seed- eaters	282.64 ± 151.49	261.00 ± 107.43	286.33 ± 83.48	0 ± 0	181.88 ± 50.21	431.26 ± 188.35	263.88 ± 74.62	224.07 ± 95.05	151.34 ± 5.35	280.44 ± 136.80
Vertebrate/invertebrate- and seed- eaters	132.58 ± 65.78	118.98 ± 49.76	146.81 ± 63.31	96.20 ± 0	96.20 ± 0	181.02 ± 75.21	97.31 ± 10.31	101.94 ± 22.88	96.20 ± 0	135.66 ± 70.45
Vertebrate/invertebrate- and fruit- eaters	411.66 ± 197.27	362.28 ± 161.04	489.58 ± 121.46	0 ± 0	184.59 ± 82.28	500.75 ± 227.55	274.46 ± 72.91	540.10 ± 154.12	0 ± 0	272.63 ± 77.63

Table S1.3: $\text{NODF}_{\text{sites}}$ (%) for mammal dietary guilds. Null Mean, Standardized Effect Size (SES) and significance values were generated by 500 randomizations of the “permRows” algorithm. Mean ± SD of $\text{NODF}_{\text{sites}}$ values for each dietary guild was calculated across the four matrix rearrangements. In **bold** we showed the rearrangement yielding the strongest nestedness values.

	Biogeography and habitat effect						
TROPHIC LEVEL/	Open-to-forest			Forest-to-open			Mean ± sd
Dietary guild	S.Fraction	Null Mean	SES	S.Fraction	Null Mean	SES	
HERBIVORES							
Grazers	4.01	3.16	**8.47****	3.60	3.16	4.19**	3.76 ± 0.28
Browsers	5.17	4.36	**6.40****	5.12	4.37	5.67**	5.00 ± 0.17
Mixed-feeders	6.83	5.48	**8.15****	6.51	5.47	6.19**	6.28 ± 0.50
Granivores	4.21	3.76	**2.93****	3.96	3.74	1.43	4.07 ± 0.19
Frugivores	3.73	3.14	5.37**	4.12	3.15	**8.64****	3.76 ± 3.76
CARNIVORES							
Vertebrate- eaters	13.05	10.54	**7.99****	12.74	10.56	6.83**	12.28 ± 0.78
Invertebrate- eaters	4.51	3.91	4.69**	4.79	3.91	**6.72****	4.56 ± 0.24
OMNIVORES							
Vertebrate- and fruit- eaters	6.93	6.87	0.18	8.40	6.86	**4.77****	7.79 ± 0.91
Invertebrate- and fruit- eaters	4.28	3.30	**6.25****	3.98	3.28	4.48**	3.85 ± 0.42
Invertebrate- and seed- eaters	3.33	2.68	**5.99****	2.70	2.69	0.09	2.99 ± 0.39
Invertebrate- and fruit/seed- eaters	9.74	7.40	8.41**	9.77	7.38	**8.81****	9.26 ± 0.58
Vertebrate/invertebrate- and seed- eaters	42.37	24.39	**18.86****	41.67	24.34	17.54**	34.94 ± 8.28
Vertebrate/invertebrate- and fruit- eaters	12.13	9.89	7.38**	12.43	9.87	**8.23****	11.28 ± 1.24

Significance intervals: 0.001 – 0.01 ‘**’; 0.01 – 0.05‘*’; 0.05 – 0.1 ‘.’; 0.1 – 1 ‘’

Table S1.4: PhyloNODF$_{sites}$ (%) for mammal dietary guilds. Null Mean, Standardized Effect Size (SES) and significance values were generated by 500 randomizations of the ‘permRows’ algorithm. Mean ± SD of phyloNODF$_{sites}$ values for each dietary guild was calculated across the four matrix rearrangements. In **bold** we show the rearrangement yielding the strongest nestedness values.

	Biogeography and habitat effect						
TROPHIC LEVEL/	Open-to-forest			Forest-to-open			Mean ± sd
Dietary guild	phyloNODF	Null Mean	SES	phyloNODF	Null Mean	SES	
HERBIVORES							
Grazers	34.42	25.64	**11.76****	33.49	25.68	10.40**	31.59± 3.89
Browsers	35.92	25.89	**14.80****	36.23	25.92	14.42**	33.96± 4.12
Mixed-feeders	41.89	29.65	**15.01****	41.49	29.71	14.78**	37.02± 5.89
Granivores	36.61	28.89	**8.66****	35.92	28.81	8.11**	33.09± 3.71
Frugivores	34.7	23.97	15.16**	35.69	24.01	**15.95****	29.91± 6.74
CARNIVORES							
Vertebrate- eaters	47.51	35.82	12.25**	47.67	35.89	**12.29****	43.49± 4.81
Invertebrate- eaters	27.47	21.26	10.58**	28.06	21.21	**11.01****	25.23± 2.98
OMNIVORES							
Vertebrate- and fruit- eaters	34.29	24.02	11.43**	35.65	24	**13.68****	30.05± 5.97
Invertebrate- and fruit- eaters	27.54	18.34	**13.46****	26.59	18.32	11.89**	23.26± 4.63
Invertebrate- and seed- eaters	39.68	29.05	**10.87****	38.52	29.11	9.98**	34.32± 6.68
Invertebrate- and fruit/seed- eaters	45.59	32.55	14.05**	45.52	32.51	**14.43****	41.28± 4.94
Vertebrate/invertebrate- and seed- eaters	52.54	31.54	**19.41****	51.72	31.48	18.64**	43.80± 9.73
Vertebrate/invertebrate- and fruit- eaters	39.78	27.77	14.98**	40.41	27.71	**16.15****	34.00± 7.18

Significance intervals: 0.001 – 0.01 ‘**’; 0.01 – 0.05‘*’; 0.05 – 0.1 ‘.’; 0.1 – 1 ‘’

CAPÍTULO 2

Broad-scale assessment of nestedness between pristine and human-modified habitats

Appendix A1: Description of the database based on bibliographic searches.

Title: A global database on non-volant small mammal composition in pristine in human-modified habitats

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Abstract

Non-volant small mammals, which include small-bodied representatives from several mammal orders, have been used as a model group to test the effects of habitat conversion and edge creation on biodiversity. Small mammals occupy a large variety of habitat types and vegetation strata, and have varied lifestyles and diets. They include species with slow- (European Hare *Lepus europaeus*) to fast-life history species (Etruscan shrew *Suncus etruscus*) and very specialized (e.g. Atlantic bamboo rat, *Kannabateomys amblyonyx*) to very generalist habits and diets (e.g. house mouse *Mus musculus*, the only terrestrial mammals present in Antarctica). There are no databases with global coverage focusing on small mammal composition in pristine and human-modified habitats, and including neglected pristine habitats (e.g. grasslands and savannas). Here, we searched peer-reviewed papers in primary literature to synthesize almost half century (1973-2017) of research on small mammal diversity in pristine forests, grasslands and their natural edges, and in five types of human-modified habitats (anthropogenic forest edges, anthropogenic grassland edges, crop fields, clear-cuts and tree plantations). The complete database includes information from 220 peer-reviewed papers. We obtained data for 568 species (including 29 unidentified) in 462 sites distributed in 101 ecoregions, 12 biomes and six realms. We also obtained the abundance values at the habitat scale for most of recorded species. We hope that our database will be useful for researchers interested in local- to broad-scale patterns of alpha- and beta-diversity in pristine and human-modified habitats.

Keywords: habitat conversion, fragmentation, Didelphimorphia, Eulipothyphla, Rodentia, non-volant small mammal sampling.

Specifications Table

Subject area	*Biology*
More specific subject area	*Ecology*
Type of data	*Table*
How data was acquired	*Bibliographic searches*
Data format	*Raw*
Experimental factors	*We obtained the composition and abundance of non-volant small mammal species in pristine and human-modified habitats. We also obtained information on the sampling design and effort and the geographic location of the sampled habitats.*
Experimental features	*Bibliographic searches in primary literature*
Data source location	*Global coverage*
Data accessibility	*Data is available with this article.*

Value of the data

1. New and geographically replicated database with focus on small mammal composition in paired pristine and human-modified habitats;
2. Database included the composition and abundance of non-volant small mammal species (eight mammalian orders) measured with different sampling techniques and efforts;
3. Pristine and human-modified can be compared because the dataset includes fine-scale information on small mammal composition, abundance and sampling procedures;
4. Database clearly differentiated artificial pastures from pristine grasslands and savannas;

5. Researchers interested in the analysis of specific regions, habitat types, sampling techniques and taxonomic groups can easily extract information from our database.

Data

We searched peer-reviewed papers in primary literature to synthesize almost half century (1973-2017) of research on small mammal diversity in pristine forests, grasslands and their natural edges, and in five types of human-modified habitats (anthropogenic forest edges, anthropogenic grassland edges, crop fields, clear-cuts and tree plantations) (Table 1).

The data sources were (see complete references in **References**): Adams and Geis [1], Archibald et al. [2], Ardente et al. [3], Ascensão et al. [4], Bachmann et al. [5], Barlow et al. [6], Bayne and Hobson [7], Bayne and Hobson [8], Bekele [9], Bennet [10], Bernardo et al. [11], Bilenca et al. [12], Birkedal et al. [13], Blouin-Demers and Weatherhead [14], Bock et al. [15], Bolger et al. [16], Borges et al. [17], Bowers and Dooley Jr. [18], Bowers et al. [19], Brady et al. [20], Briggs [21], Brodie et al. [22], Busch and Kravetz [23], Busch and Kravetz [24], Cain III et al. [25], Carfagno et al. [26], Carrilho et al. [27], Cerboncini et al. [28], Chalfoun et al.[29], Christianini and Galetti [30], Constantine et al. [31], Cooney et al. [32], Craig et al. [33], Cramer and Willig [34], Cramer and Willig [35], Croonquist and Brooks [36], Darveau et al. [37], Braga et al. [38], De Jonge and Dienske [39], De La Sancha [40], De Lima and Gascon [41], De Villafañe et al. [42], Decher [43], Degraaf [44], Degraaf et al. [45], del-Val et al. [46], Di Napoli & Cáceres [47], Diersing and Severinghaus [48], Dunstan and Fox [49], Elgueta et al. [50], Escudero et al. [51], Estrada et al. [52], Ewacha et al. [53], Fenske-Crawford and Niemi [54], Fischer et al. [55], Fortin and Doucet [56], Fraschina et al. [57], Fredebaugh et al. [58], Friend [59], Garmendia et al. [60], Germain et al. [61], Glitzner and Gossow [62], Godoi et al. [63], Goguen et al. [64], Goldingay and Whelan [65], Goodman and Thorstrom [66], Goosem and Marsh [67], Goosem [68], Goosem et al. [69], Goosem [70], Granjos and Duplantier [71], Green and Catterall [72], Greenwood and Dawson [73], Grushecky et al. [74], Hadley and Wilson [75], Hanson et al. [76], Hansson [77], Hansson [78], Hansson [79], Hansson [80], Hansson [81], Harding et al. [82], Hargis et al. [83], Harrington et al. [84], Hastings et al. [85], Hernandez [86], Heske [87], Hoobs et al. [88], Hodara and Busch [89], Hopkins and Kennedy [90], Hurst et al. [91], Hutchison and Rodgers [92], Jefferies et al. [93], Jenks et al.[94], Johnson and Karels [95], Johnson et al. [96], Jones and Lindquist [97], Jung and Powell [98], Kasper et al. [99], Kays and DeWan [100], Keinath and Hayward [101], Kellner et al. [102], Kelt [103], King et al. [104], King et al. [105], Kinston and Morris [106], Klausen et al. [107], Klein and Cameron [108], Klenner and Sullivan [109], Knight and Fox [110], Kollman and Buschor [111], Kristan III et al. [112], Lacerda et al. [113], Laidlaw et al. [114], Lambert et al. [115], Larivière and Messier [116], Laurance [117], Lee and Rhim [118], Lehtonen et al. [119], Leimgruber et al. [120], Leon et al. [121], Lindemann et al. [122], Lomolino and Smith [123], López-Barrera et al. [124], Lukyanova [125], Luza et al. [126], Maier and Degraaf [127], Malcolm and Ray [128], Malick et al. [129], Manson and Stiles [130], Manson et al.

[131], Mauffrey et al. [132], Mazerolle et al. [133], Medellin and Equihua [134], Melo et al. [135], Mendes-Oliveira et al. [136], Menzel et al. [137], Mongo et al. [138], Moore and Swihart [139], Mugerwa et al. [140], Murphy et al. [141], Nocera and Dawe [142], Nupp and Swihart [143], Osbourne et al. [144], Osunkoya [145], Pagels et al. [146], Panzacchi et al. [147], Pardini [148], Paschoal et al. [149], Pascoe et al. [150], Pasitschniak-Arts and Messier [151], Passamani and Fernandez [152], Pavey et al. [153], Pedersen et al. [154], Persons and Eason [155], Pinto et al. [156], Pires and Cademartori [157], Pires et al. [158], Purger et al. [159], Purger et al. [160], Püttker et al. [161], Radtke and Wilson [162], Ramanamanjato and Ganzhorn [163], Ramesh et al. [164], Ransome et al. [165], Renfrew et al. [166], Rhim and Lee [167], Rhim et al. [168], Ribeiro et al. [169], Řičánková et al. [170], Rose et al. [171], Rovero et al. [172], Sálek et al. [173], Sálek et al. [174], Santos-Filho et al. [175], Santos-Filho et al. [176], Santos-Filho et al. [177], Schlesser et al. [178], Schlinkert et al. [179], Schnell et al. [180], Sekgororoane and Dilworth [181], Shore et al. [182], Sidorovich et al. [183], Silva [184], Sinclair et al. [185], Smith [186], Sodhi et al. [187], Srbek-Araujo and Chiarello [188], Stanley [189], Stepankova and Vohralik [190], Stephens et al. [191], Stephenson [192], Sterner et al. [193], Stevens and Husband [194], Storm and Choate [195], Suarez et al. [196], Suchomel et al. [197], Sullivan et al. [198], Sunde et al, [199], Suzán et al. [200], Svobodová et al. [201], Tattersall et al. [202], Terwilliger and Pastor [203], Thoisy et al. [204], Thompson III et al. [205], Thornton et al. [206], Thorstrom et al. [207], Tomback et al. [208], Haegen et al. [209], Vargas-Salinas and López-Aranda [210], Vernes and Dennis [211], Walters [212], Weirich et al. [213], Wilson et al. [214], Wittenberg [215], Wolcott et al. [216], Yatsiuk et al. [217], Youngentob et al. [218], Yue et al.[219], Zub et al. [220].

Most of the suitable papers were designed to evaluate the habitat preferences of small mammal species and to compare differences in community richness and composition between pristine and human-modified habitats [Refs. 1, 2, 3, 4, 6, 8, 12, 15, 16, 18, 19, 20, 21, 27, 28, 31, 33, 34, 35, 36, 37, 38, 39, 40, 41, 43, 47, 48, 49, 51, 55, 56, 59, 62, 63, 64, 65, 67, 68, 69, 70, 71, 72, 75, 77, 78, 80, 81, 82, 84, 87, 88, 89, 90, 91, 92, 93, 95, 96, 102, 103, 104, 106, 109, 112, 114, 115, 117, 118, 119, 122, 125, 126, 128, 129, 132, 133, 134, 136, 137, 138, 139, 141, 143, 144, 146, 147, 148, 151, 152, 158, 165, 168, 169, 174, 175, 176, 177, 178, 179, 181, 182, 183, 184, 191, 192, 194, 195, 197, 198, 202, 206, 210, 212, 214, 216, 218, 219]. We considered as suitable the papers assessing the effect of habitat conversion and edges on medium and large-sized mammals that provided information on the distribution of mammals weighing ≤ 5 kg [Refs. 11, 17, 22, 50, 60, 94, 99, 100, 113, 140, 149, 157, 164, 167, 172, 188]. We also considered suitable some papers assessing the effect of habitat conversion and edges to prey availability [Refs. 14, 26, 66, 73, 83, 86, 116, 150, 153, 154, 173, 199, 201, 207, 211, 215, 217, 220], predation of nests [Refs. 7, 25, 29, 44, 45, 52, 54, 76, 105, 107, 120, 127, 159, 160, 166, 185, 186, 187, 189, 205, 209], predation of saplings, fruits, seeds and invertebrates [Refs. 13, 30, 46, 61, 74, 79, 85, 111, 124, 130, 131, 135, 145, 156, 162, 193, 203, 208], small mammal populations (when presenting information of coexisting species [Refs. 9, 10, 23, 24, 32, 42, 53, 57, 97, 98, 101, 108, 110, 121, 123, 142, 155, 161, 163, 170, 171, 180, 190] and to increased epidemiological threats linked to the abundance of mammalian vectors [Refs. 5, 58, 196, 200, 204, 213]. The composition of non-volant small mammal assemblages in each habitat was generally obtained using trapping grids or transects (see Pearson & Ruggiero [221]) in discrete habitats (e.g. one grid or transect in the forest interior, one in the grassland interior, and one in the human modified-habitat [e.g. 33, 189]) or across habitats (e.g. grid or transect from forest interior until grassland interior [e.g. 126,176]). References 221 to 224 were used to better describe the data and not contributed to the present database.

Table 1: Number of sampling units (habitats) by biogeographic realm.

	Afrotropics	Australasia	Indo-Malay	Nearctic	Neotropics	Palearctic	Total
Pristine habitats							
Forest	40	37	6	109	89	30	311
Grassland	16	0	0	59	21	6	102
Natural edge	1	0	0	2	0	1	4
Human-modified habitats							
Forest edge	4	14	0	39	16	24	97
Grassland edge	1	2	0	8	10	6	27
Clear-cut	1	3	0	44	1	9	58
Crop field	13	7	0	27	18	15	80
Tree plantation	4	6	1	4	2	17	34
Total	80	69	7	292	157	108	713

Experimental Design, Materials and Methods

We used a bibliographic search to obtain data on small mammal assemblage composition in pristine and human-modified habitats. We searched peer-reviewed papers in SCOPUS and ISI Web of Knowledge, according to indexed title, abstract, keywords and topics, using two sets of key words: 1) mammal* AND edge* AND forest*, and 2) mammal* AND edge* AND grassland* OR crop* OR field* (Table 2). The first set of key words returned few papers about native grasslands (Table 2). To better represent grasslands and their edges, we performed the second search (Table 2). In total, we performed six bibliographic searches but considered five, as one of them provided no suitable papers (Table 2). A total of 220 of the 1 054 reviewed papers used several trapping techniques to sample non-carnivore, non-strictly forest (e.g. Primates, Dermoptera) species with an averaged body mass ≤ 5kg (Table 2). The database has a global coverage, with most of sites located in the Neotropics and Nearctic (Figure 1, Table 1). Temporal information on assemblage composition was summarized since we were mainly interested in spatial patterns of species distribution across pristine and human-modified habitats. Thus, the absence of a species in a given site was considered presence if that species was recorded in that site in other sampling occasion.

In few cases, insufficient details prevented a precise definition of assemblage composition in a given habitat. In that case, we first contacted authors to obtain information omitted in the published papers (see Acknowledgements for the list of authors). If no detail was provided by the contacted authors, we set this entry as undefined (“NA”) (see Table 3). In just one case (Hutchison and Rodgers [92]) we checked information provided by thesis because we were not able to assess the published paper. We repeated the values of the lat-long geographical coordinates (generally the locality coordinates) when the authors of the reviewed papers not provided the specific location of the sampled habitats.

Forest and grassland fragments, continuous remnants and advanced secondary-regeneration were considered pristine habitats, because composition and richness differences between these habitats are minimal [222]. We considered managed forests as pristine when the authors provided enough information about logging regimes to judge that they were only minimally disturbed [8,165]. Grasslands and savannas with native vegetation were considered as pristine habitats even if they were grazed by domesticated animals [126, 223]. An edge was considered the boundary between the pristine and human-modified habitats. Species composition at edges was generally quantified with traps paralleling the sharp border between two habitats, mostly between forest and human-modified habitats [8,165,175,176]. We considered tree plantations those tree monocultures planted in grasslands and cleared forests. We considered clear-cuts, crop fields and young-secondary vegetation as open habitats.

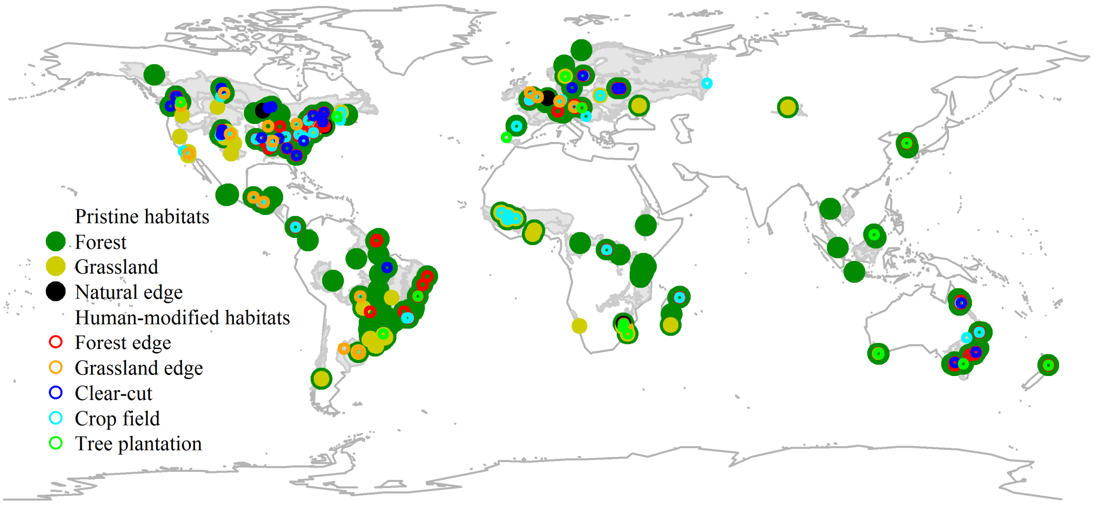

Figure 1: Global distribution of the sampled habitats. We present the world ecoregions (Olson et al. [224]) in the background (gray color).

We obtained abundance measurements from relative abundances, captures per trapping effort, total number of individuals and averaged abundance (e.g., averaged at habitat scale, average abundance estimates from occupancy models). Frequency of occurrence was extracted from those papers using sampling techniques that do not allow differentiating individuals (e.g., tracking tunnels, camera-traps). Species abundance obtained over many sampling occasions was summed up to obtain a unique abundance value by habitat. When precise abundance information in tables or text was lacking, we interpreted figures (except ordination diagrams) and axes values to obtain abundance values. We set abundance as undefined ("NA" entry) when authors presented total summed abundance by site instead by habitat (Table 3). For papers providing averaged abundance <1, we set this values to a minimum of 1.

Many authors provided abundances based on captures per trapping effort (CPTE; generally, 100 or 1,000 traps) but did not state if CPTE was calculated from either total sampling effort or habitat sampling effort. In such cases, we divided the total sampling effort by the number of sampled habitats to obtain a value of sampling effort by habitat. We then multiplied this value with the CPTE of each species to obtain the species abundance by habitat. Sampling effort for scat analysis (owl pellet analysis, scat content) was total number of analyzed samples; sampling effort for walking/car/ski track techniques was the total travelled distance. We summed up sampling efforts for those sites sampled with several sampling methods. Site abundance varied from one to 5,256 individuals (299.13 ± 556.43). The most abundant species are *Myodes gapperi* (N= 8,627), *Peromyscus maniculatus* (N= 7,837), *Microtus pennsylvanicus* (N= 7,613) and *Myodes glareolus* (N= 6,040).

Table 2: Number of papers in each bibliographic search.

Database	Search order	Search topics (date of the last update)	Total number of papers (% already included in the previous search)	Suitable peer-reviewed papers
Scopus	1º	_mammal_* AND _edge_* AND _forest_* (2017/26/07)	506	131
	2º	_mammal_* AND _edge_* AND _grassland_* OR _crop_* OR _field_* (2017/26/07)	364 (34%)	28
Isi Web of Science	3º	_mammal_* AND _edge_* AND _forest_* (2017/08/08)	609 (60%)	52
	4º	_mammal_* AND _edge_* AND _grassland_* OR _crop_* OR _field_* (2017/08/08)	3 082 493 † (-)	-
	5º	_mammal_* AND _edge_* AND _grassland_* OR _cropfield_* (2017/09/08)	124 (48%)	9
Scopus	6º	_mammal_* AND _edge_* AND _grassland_* OR _cropfield_* (2017/09/08)	63 (100%)	0
Total number of papers			1 054	220

† Not considered due to large number of health science papers.

Table 3: Description table.

Descriptor	**Type of variable (descriptor)**	**Levels of categorical and binary descriptors** **Unit of continuous descriptors**	**Characterization of levels**
SCOPUS_search	Categorical	Five levels: Forest Open Forest/open ForestWEB GrasslandWEB	Descriptor characterizing in which bibliographic search a given paper was found: SCOPUS searches: Forest (keywords: mammal* AND edge* AND forest*); Open (keywords: mammal* and edge* and grassland* or crop* or field*); Forest/open: peer-reviewed papers found in both searches. WEB OF SCIENCE searches: ForestWEB (keywords: mammal* AND edge* AND forest*); GrasslandWEB (keywords: mammal* and edge* and grassland* or crop* or field*)
Reference	Categorical	220 data sources (peer-reviewed papers)	The citation of a suitable paper. Complete references in **References** below this table.
Region	Categorical	210 levels	Information on major region and country where a given site was sampled.
Site	Categorical	126 levels	Sites (localities) sampled within a region. We named *unique* those papers including only one site, or those papers for which it was not possible to define different sites. We named the sites as *uniqueA*, *uniqueB* (and so on) for those papers clearly including more than one site but which were not named by the authors. Otherwise, sites were named with the designation provided by the authors.
n_year	Categorical	11 levels: two_season_snapshot many_years mon_snapshot mon_snapshot_year	The number of years that a given site was sampled. two_year_snapshot: discrete snapshots (quick sampling) performed in two or more years but in similar seasons (i.e., at least one temporal replication); many years: continuous sampling for many years (apparently without discrete snapshots);

		NA one_year snapshot two_season_snapshot two_seasons two_snapshots two_year_snapshot	mon_snapshot: discrete snapshots in sequential months but total sampling did not cover one year; mon_snapshot_year: seasonal sampling where monthly discrete snapshots were conducted during more than one year; NA: undefined one_year: continuous sampling for at maximum one year snapshot: one discrete sampling in the time, without temporal replication; two_season_snapshot: discrete snapshots performed in two or more seasons in the same year; two_seasons: sampling was performed continuously during two or three seasons. Sampling did not cover one year; two_snapshots: more than one discrete snapshot was conducted in the same season;
snapshot	Categorical	Three levels: 1; 0; NA	Description if sampling was temporally replicated (1) or not (one discrete snapshot, 0). NA: undefined.
season_trap	Categorical	19 levels	The season (s) in which the sampling was conducted. Depending on the “n_year” descriptor, “season_trap” descriptor may describe just one season (we provide the name of the season) or all seasons (many_year_seasons). Further, the number of seasons depends on the region where a fieldwork was conducted (subtropical regions: autumn, winter, spring, summer; tropical regions: dry and wet seasons). NA: undefined.
one_season	Categorical	Three levels: 1; 0; NA	If sampling was conducted in one (1) or more seasons (0). NA: undefined.
effort_by_habitat	Continuous	Number of traps per night by habitat	Depending on the sampling method, sampling effort can be in trap/nights, number of analyzed scats, kilometers or hours travelled in transects. NA: undefined.
type_trap	Categorical	76 levels	Combinations of trap types used to the sampling of small mammal species, embracing: box-like traps: sherman, wooded chmela, longworth, BTTm, triptrap, and elliott live-traps;

			snap-like traps: Victor snap, spring traps, Museum snap, fenn trap, mouse and rat snap traps; wire meshed traps: tomahawk, wire cage, mascot, ugglan, havahart; traces: methods to register tracks and bits (artificial eggs, hairtubes, sandplots, trackplates, snowtracks, tracking tunnels, transects, visual insights, sandplots); pitfall traps: buckets connected or not by drift-fences; scats: species presence in owl-pellets, dogscats, catpreys; cameratrap: camera-traps (pictures, videos); NA: undefined
box-like	Categorical	Three levels: 1; 0; NA	Mammal sampling using sherman, wooded chmela, longworth, BTTm, triptrap, and Elliott live-traps (1) or not (0). NA: undefined.
snap-like	Categorical	Three levels: 1; 0; NA	Mammal sampling using Victor snap-traps, spring snap-traps, Museum snap-traps, fenn snap-traps, mouse and rat snap-traps (1) or not (0). NA: undefined.
wire_meshed	Categorical	Three levels: 1; 0; NA	Mammal sampling using tomahawk, wire cage, mascot, ugglan and havahart wire-traps (1) or not (0). NA: undefined.
traces	Categorical	Three levels: 1; 0; NA	Mammal sampling using artificial eggs, hairtubes, sandplots, trackplates, snowtracks, tracking tunnels, transects, visual insights, sandplots (1) or not (0). NA: undefined.
pitfall	Categorical	Three levels: 1; 0; NA	Mammal sampling using plastic buckets connected or not by drift-fences (1) or not (0). NA: undefined.
scats	Categorical	Three levels: 1; 0; NA	Mammal sampling by analyzing prey remains in owl-pellets, regurgitations or scats (1) or not (0). NA: undefined.
camera	Categorical	Three levels: 1; 0; NA	Mammal sampling using camera-traps (1) or not (0). NA: undefined.
Lat_orig	Continuous	Several types	Original latitude values provided by the authors
Long_orig	Continuous	Several types	Original longitude values provided by authors
Lat	Continuous	Decimal degrees	Latitude value in degrees after checking the location of sites

Long	Continuous	Decimal degrees	Longitude value in degrees after checking the location of sites
Species	Categorical	568 species (including 29 non-identified species)	Binomial name (or genus plus ‘sp.’ when the species was not identified) following Wilson & Reeder 2005 (also applied by IUCN assessment and Catalogue of Life).
Order	Categorical	12 levels	The mammal orders
Habitat	Categorical	Six levels	Habitat where species were registered (see main text for details) Edge – habitat edges Forest – pristine forests Grassland – pristine grasslands NA – undefined Open – anthropogenic habitats with open vegetation structure Tree_plantation – tree plantations
Clearcut	Binary	Two levels: 1 and 0	If habitat is a clear-cutting (1) or not (0). In the case of 0, habitat is a crop field (e.g. soybean field, hayfield, artificial pasture).
forest_edge	Binary	Two levels: 1 and 0	If edge is bordering a forest (1) or grassland (0)
GF_edge	Binary	Two levels: 1 and 0	Natural edge between pristine grasslands and forests (1); anthropogenic edge (0)
fragm	Categorical	Three levels: 1; 0; NA	Sampling was conducted in fragments of forests or grasslands (1) or it was conducted in continuous patches (e.g., conservation unities) (0). NA: undefined.
Abundance	Continuous	Continuous value	Number of individuals of a given species. NA: undefined.
Presence	Binary	Two levels: 1 and NA	Species presence (1) or undefined (NA).

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Appendix A2: Obtaining the data and defining the basic sampling unit for nestedness analysis.

1. Obtaining data on species composition in pristine and human-modified habitats

We used a new database (Luza et al., unpublished data) and the PREDICTS database (Hudson et al., 2017) to obtain data for conduct the nestedness analysis. Both are taxonomically and spatially comprehensive databases that shares many descriptors. Both databases are formatted as data-frames (i.e., studies and localities in the rows; site and species descriptors in the columns). We obtained a combined data-frame of databases by matching descriptors relevant for building maps, defining species composition and extracting environmental and biogeographic information of sampled sites. Descriptors of the unpublished database (Luza et al., unpublished data) were “Reference”, “Region”, “Site”, “Longitude”, “Latitude”, “Trap_type”, “Effort_by_habitat”, “Habitat”, “Species”, “Order” and “Presence”. Descriptors of PREDICTS were “Reference”, “Site_name”, “SSB”, “Longitude”, “Latitude”, “Sampling_method”, “Sampling_effort”, “Habitat_as_described”, “Best_guess_binomial”, “Order” and “Measurement”. The descriptor “Measurement”, which also contain abundances, was transformed in presences. “Best_guess_binomial” refers to the species taxonomic identity according the Catalogue of Life (http://www.catalogueoflife.org/), which matches with our taxonomic classification (International Union for Conservation of Nature, IUCN).

2. Defining the basic sampling unit for nestedness analysis

We combined the descriptors ‘Reference’, ‘Site’, ‘Subsite’ and ‘Habitat’ (‘Reference’, ‘Site_name’, ‘SSB’ and ‘Habitat_as_described’ in the case of PREDICTS) to obtain our basic sampling unity for analysis. Thus, each sampling unity represents one habitat type sampled in one site in a given region and study. For example, if a given study provided information for species composition in one forest and one anthropogenic edge, it had two sampling unities. The combination of sites and habitats resulted in a total of 598 sampling unities for Luza et al. and 454 for PREDICTS (Tables A2.1 and A2.2). The large number of sites in PREDICTS database - even though it considered fewer studies - arises from the fact that PREDICTS includes the raw information on sampling effort (at day, month or year scale; see “Sample_date_resolution” in PREDICTS data-frame) by site. Such detailed information, which in the case of PREDICTS was obtained directly from data compilers and authors, generally is omitted from published peer-reviewed papers.

Table A2.1: Number of sites in the combined database by realm and habitat. In parenthesis we present the number of sites obtained from PREDICTS database (Hudson et al., 2017).

Realm	Forest	Grassland	Edge	Open	Tree plantation	Total
Afrotropics	25 (18)	13 (18)	4 (-)	12 (17)	3 (-)	110
Australasia	30 (84)	- (53)	12 (-)	8 (47)	6 (-)	240
Indo-Malayan †	3 (25)	-	-	- (2)	- (1)	31
Nearctic	100 (87)	57 (-)	40 (-)	63 (-)	4 (-)	351
Neotropics	74 (36)	16 (5)	22 (-)	18 (13)	1 (34)	219
Palearctic	19 (14)	3 (-)	28 (-)	20 (-)	17 (-)	101
Total	515	165	106	200	66	1 052

†Not analyzed due to the low number of habitat comparisons.

Table A2.2: Number of sites in the combined database by realm and terrestrial biome.

Realm	Biome	Bibliographic search	PREDICTS
Australasia	Mediterranean Forests, Woodlands and Scrub	9	48
	Temperate Broadleaf and Mixed Forests	24	44
	Temperate Grasslands, Savannas and Shrublands	3	-
	Tropical and Subtropical Grasslands, Savannas and Shrublands	8	92
	Tropical and Subtropical Moist Broadleaf Forests	12	
Afrotropics	Deserts and Xeric Shrublands	1	29
	Montane Grasslands and Shrublands	1	-
	Tropical and Subtropical Grasslands, Savannas and Shrublands	35	-
	Tropical and Subtropical Moist Broadleaf Forests	20	24
Indo-Malayan	Montane Grasslands and Shrublands	-	3
	Tropical and Subtropical Moist Broadleaf Forests	3	25
Nearctic	Boreal Forests/Taiga	43	87
	Deserts and Xeric Shrublands	9	-
	Mediterranean Forests, Woodlands and Scrub	41	-
	Temperate Broadleaf and Mixed Forests	101	-
	Temperate Conifer Forests	42	-
	Temperate Grasslands, Savannas and Shrublands	28	-
Neotropics	Temperate Broadleaf and Mixed Forests	-	38
	Temperate Grasslands, Savannas and Shrublands	18	-
	Tropical and Subtropical Coniferous Forests	3	-
	Tropical and Subtropical Dry Broadleaf Forests	21	-
	Tropical and Subtropical Grasslands, Savannas and Shrublands	16	47
	Tropical and Subtropical Moist Broadleaf Forests	73	3
Palearctic	Boreal Forests/Taiga	1	-
	Mediterranean Forests, Woodlands and Scrub	3	-
	Temperate Broadleaf and Mixed Forests	80	14
	Temperate Conifer Forests	3	-
	Total	598	454

3. References

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Appendix A3: List of the 180 data sources included in the present manuscript

1. Data sources of Luza et al. (unpublished data) (158 studies):

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CAPÍTULO 3

Supplementary material

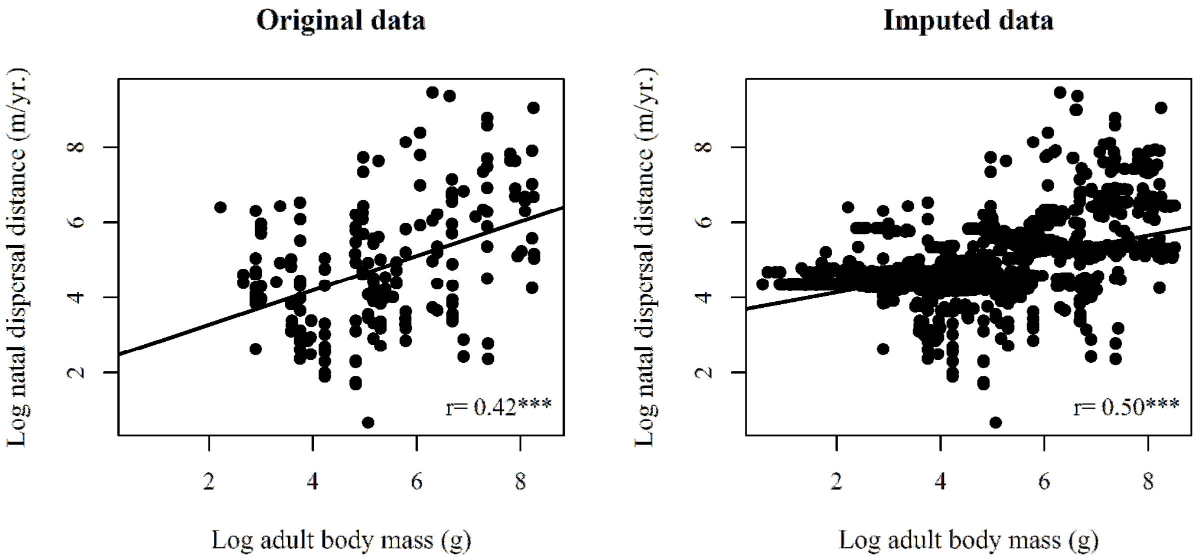

Figure S1: Linear relationship between small mammal adult body mass and natal dispersal distance (m/yr= meters per year) in the original (187 entries, 49 species) and in the imputed dataset (187 entries, 49 species + 3,030 species).

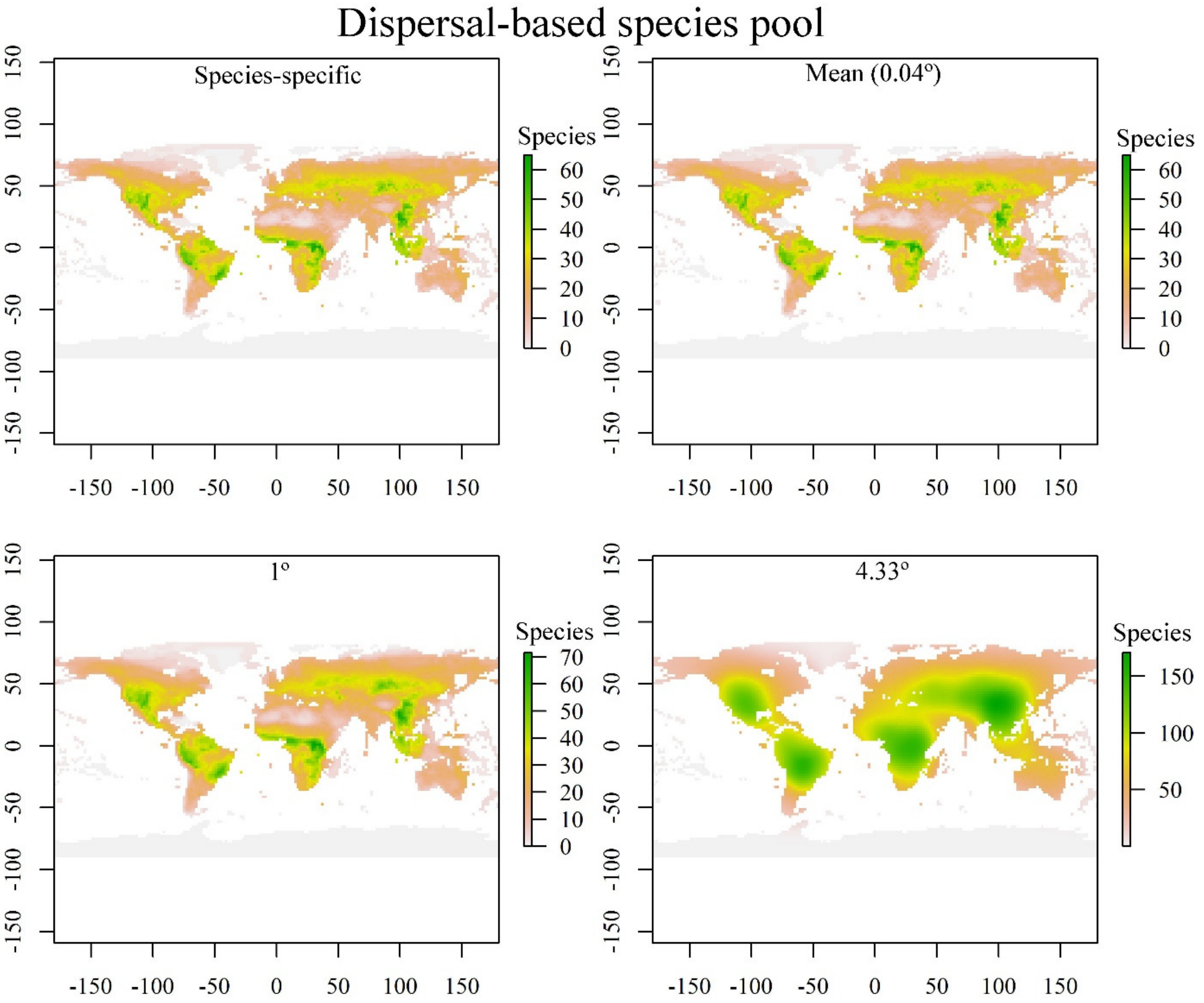

Figure S2: The dispersal-based pool delineated according to the different dispersal abilities of species over 40 years (k). Upper maps: k defined species-specific and mean. Bottom maps: k defined as 1º and 4.33º (maximum dispersal ability). Map resolution: 2-degree grid cell size.

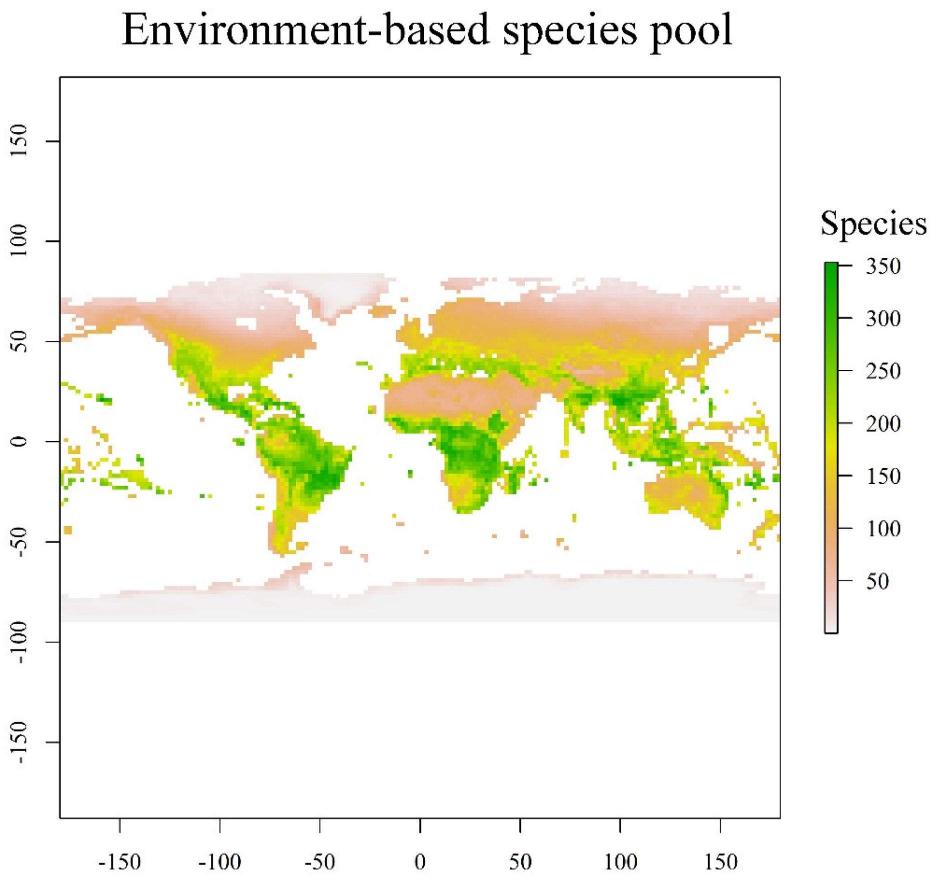

Figure S3: The environmental-based species pool. Predictions were based on Generalized Linear Models. Map resolution: 2-degree grid cell size.

Table S1: Results showing the statistics used to test the predictive performance of the models.

Model	AUC	TSS	Kappa
Generalized linear models			
Range	0.602 - 0.996	0.174 - 0.968	0.012 - 0.909
Mean ± sd	0.912 ± 0.055	0.741 ± 0.115	0.459 ± 0.181
Generalized additive models			
Range	0.640 - 0.994	0.237 - 0.963	0.0180 - 0.900
Mean ± sd	0.922 ± 0.047	0.752 ± 0.107	0.472 ± 0.179
Random forest			
Range	0.692 - 0.995	0.268 - 0.950	0.022 - 0.891
Mean ± sd	0.924 ± 0.045	0.729 ± 0.105	0.496 ± 0.185

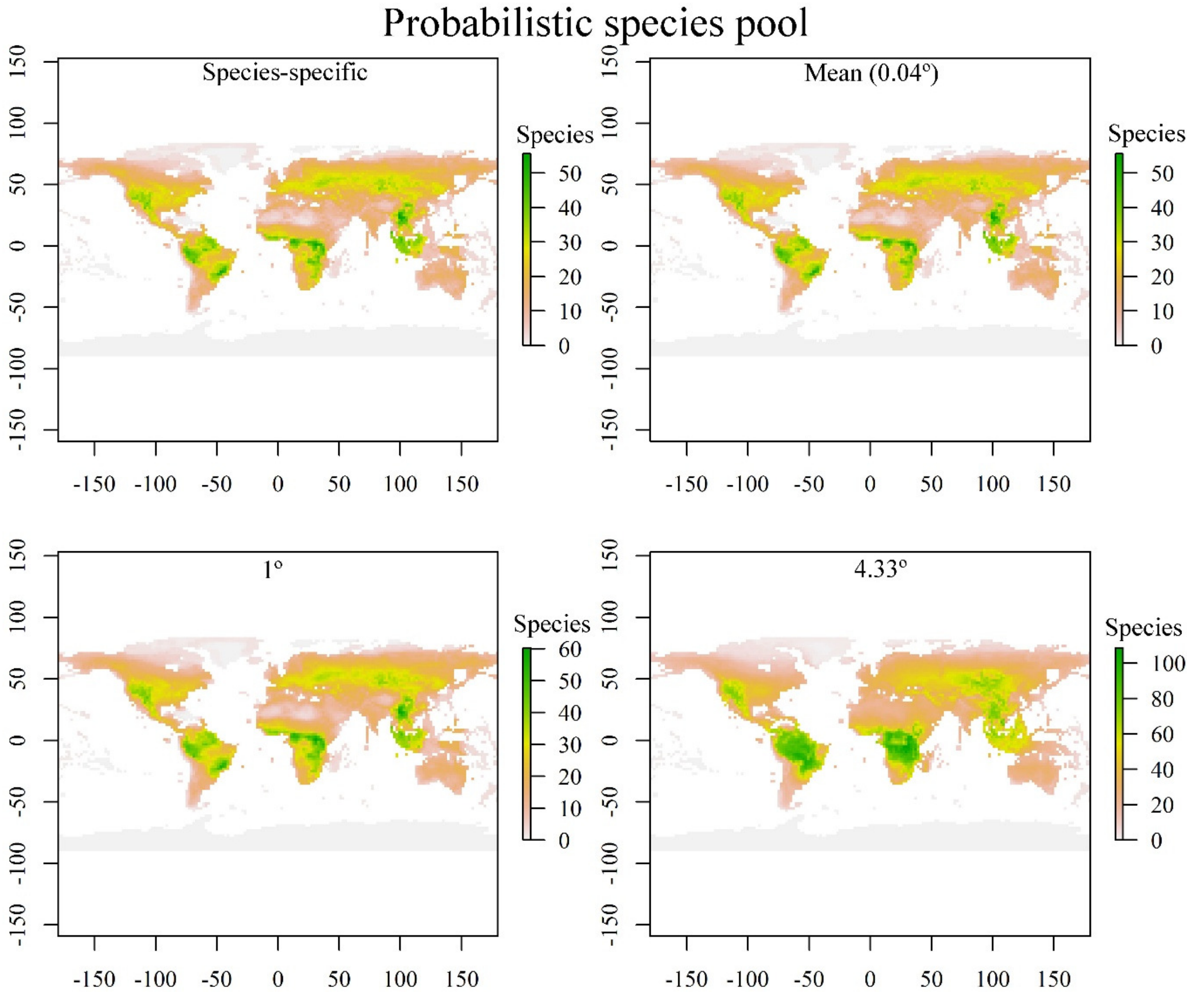

Figure S4: The probabilistic species pool delineated according to site-specific environmental suitability and species-specific dispersal ability. We showed maps for four values of dispersal ability (k) over 40 years: UPPER: species-specific dispersal and mean dispersal value (0.04º); BOTTOM: 1º and maximum dispersal value (4.33º). Map resolution: 2-degree grid cell size.

Table S2: Habitat types characterizing the habitat preferences of the 1,159 non-volant small mammal species included in the probabilistic species pool.

Forest (724)	**Grassland (799 species)**	**Human-modified (430 species)**
Forest - Boreal	Grassland - Subantarctic	Artificial/Aquatic - Aquaculture Ponds
Forest - Subantarctic	Grassland - Subarctic	Artificial/Aquatic - Canals and Drainage Channels, Ditches
Forest - Subarctic	Grassland - Subtropical/Tropical Dry	Artificial/Aquatic - Excavations (open)
Forest - Subtropical/Tropical Dry	Grassland - Subtropical/Tropical High Altitude	Artificial/Aquatic - Irrigated Land (includes irrigation channels)
Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	Grassland - Subtropical/Tropical Seasonally Wet/Flooded	Artificial/Aquatic - Ponds (below 8ha)
Forest - Subtropical/Tropical Moist Lowland	Grassland - Temperate	Artificial/Aquatic - Salt Exploitation Sites
Forest - Subtropical/Tropical Moist Montane	Grassland - Tundra	Artificial/Aquatic - Seasonally Flooded Agricultural Land
Forest - Subtropical/Tropical Swamp	Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	Artificial/Aquatic - Wastewater Treatment Areas
Forest - Temperate	Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	Artificial/Aquatic - Water Storage Areas (over 8ha)
	Wetlands (inland) - Freshwater Springs and Oases	Artificial/Terrestrial - Arable Land
	Wetlands (inland) - Geothermal Wetlands	Artificial/Terrestrial - Pastureland
	Wetlands (inland) - Karst and Other Subterranean Hydrological Systems (inland)	Artificial/Terrestrial - Plantations
	Wetlands (inland) - Permanent Freshwater Lakes (over 8ha)	Artificial/Terrestrial - Rural Gardens
	Wetlands (inland) - Permanent Freshwater Marshes/Pools (under 8ha)	Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest
	Wetlands (inland) - Permanent Inland Deltas	Artificial/Terrestrial - Urban Areas
	Wetlands (inland) - Permanent Rivers/Streams/Creeks (includes waterfalls)	Introduced vegetation
	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes	
	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Marshes/Pools	

Wetlands (inland) - Seasonal/Intermittent Freshwater Lakes (over 8ha)
Wetlands (inland) - Seasonal/Intermittent Freshwater Marshes/Pools (under 8ha)
Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Lakes and Flats
Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Marshes/Pools
Wetlands (inland) - Seasonal/Intermittent/Irregular Rivers/Streams/Creeks
Wetlands (inland) - Shrub Dominated Wetlands
Wetlands (inland) - Tundra Wetlands (incl. pools and temporary waters from snowmelt)
Rocky areas (eg. inland cliffs, mountain peaks)
Shrubland - Mediterranean-type Shrubby Vegetation
Shrubland - Subantarctic
Shrubland - Subarctic
Shrubland - Subtropical/Tropical Dry
Shrubland - Subtropical/Tropical High Altitude
Shrubland - Subtropical/Tropical Moist
Shrubland - Temperate
Savanna - Dry
Savanna - Moist
Desert - Cold
Desert - Hot
Desert - Temperate

CAPÍTULO 4

Rodent occupancy in grassland paddocks subjected to different grazing intensities in South Brazil

Appendix S1: Research station management and analyses of the effect of grazing on habitat structure.

In the research stations where the study took place, grazing intensity is manipulated to experimentally evaluate the production of beef from the cattle breeds of Aberdeen Angus and Brangus-Ibagé (Nabinger et al., 2009; Trindade et al., 2012). Researchers from EEA manage grasslands according to daily forage allowances (i.e., the amount of forage available on a daily basis for cattle in relation to their live weight) and adjust the stocking rate according to potential pasture growth (i.e., paddocks support less cattle in winter because vegetation growth is slower). Each EEA paddock with continuous grazing occupied ≈ 5 hectares. The highest forage allowance is 16%, meaning that around 16 kg of dry matter is available daily per 100 kg of live weight (Nabinger et al., 2009; Trindade et al., 2012). Moderate forage allowance is 8-12%, while the lowest allowance is 4% (i.e., overgrazing where many animals eat a small quantity of food) (Nabinger et al., 2009; Trindade et al., 2012).

EMBRAPA paddocks have 5-70 ha under continuous grazing. The lowest food allowance is 6-8% in EMBRAPA (as seen in Fig. S1.2), which occurs around cattle troughs and in thin soils. EMBRAPA researchers mow the vegetation in the spring and autumn to remove dry and senescent biomass which accumulated during growth periods, as well as to increase the regrowth of palatable leaves (Nabinger et al., 2009). In both sites, researchers maintain ungrazed areas (for 6 years in EMBRAPA and 11 years in EEA). Cattle only access the ungrazed areas and forest patches to forage and find shelter during harsh weather (Nabinger et al., 2009; Frank et al., 2012). The climate was similar between the two research stations (Fig. S1.1). The presence of trees is very rare outside ungrazed areas at EEA, while solitary trees and forest patches are scattered throughout EMBRAPA (as perceived in Table S1.2). Neither site is managed using burning.

We performed multivariate analysis to explore habitat differences within (Test for Homogeneity of Multivariate Dispersion, Betadisper; Anderson, 2006) and between (Multivariate Analysis of Variance, Permanova; Legendre and Legendre, 2012) paddocks. We did not use trap distance to the nearest tussock, shrub and tree (Table S1.1) in any analysis, because they were inversely correlated with tussock, shrub and tree height. First, we explored habitat data through Principal Coordinate Analysis (PCO), based on Euclidean distance between standardized covariates (Legendre and Legendre, 2012). The position of paddocks along the grazing gradient revealed three groups with low overlap (high, moderate/low, ungrazed; Table S1.2; Fig. S1.2). Groups were then used to test habitat differences within (seasonal variation) and between paddocks (spatial variation) through Betadisper and Permanova (999 permutations) tests. Permutations were used to generate random F-statistic values. P-values were derived by counting the number of times that random F-statistic values were higher than the observed F-statistic values (Legendre and Legendre, 2012). Since we measured the covariates for each trap in EMBRAPA (24 points/paddock) and in each tunnel in EEA (6 points/paddock), we also ran analyses controlling for differences in the number of points by restricting permutations with a ‘site’ block factor. We did not find any differences in the results when considering the blocking factor ‘site’ in the multivariate analyses. We performed a post-hoc contrast analysis with Bonferroni correction of P-values to test for pairwise differences in habitat within and between the three grazing intensities.

Results for these analyses revealed significant within-paddock differences in vegetation structure and heterogeneity over the seasons (Betadisper's F= 8.27, $P \leq 0.012$), with the contrast analysis revealing that paddocks under moderate/low grazing intensities are seasonally less variable than ungrazed paddocks ($P < 0.001$) (Fig. S1.2). These results were also evidenced by the habitat data collected only from the tracking tunnel points (Betadisper's F= 11.13, $P \leq 0.001$). As observed in the field, seasonal changes in the habitat structure in ungrazed areas resulted from the rapid and ephemeral appearance of shrub and tree saplings, which might have promoted changes in microhabitat characteristics over very short time scales. Furthermore, the increase in stature and in green leaf production during the reproduction of rosette (*Eryngium horridum*) and tussock species (e.g., *Aristida laevis*, *Saccharum angustifolium*) in the spring and summer largely contributed to the changes in vegetation structure in grazed paddocks (Table S1.2).

Vegetation structure also varied between paddocks, with highly grazed paddocks and ungrazed areas representing the extreme end-points of the disturbance gradient (Fig. S1.2; Permanova's F= 20.36; R^2= 0.35; $P\leq 0.001$). Post-hoc contrast analysis revealed that the habitat provided by ungrazed areas differed significantly from the habitat of low/moderately and highly grazed paddocks, and that the habitat provided by low/moderately grazed paddocks significantly differed from those under intense grazing (Bonferroni adjusted P-values= 0.003). The results were similar when using the habitat data from tracking tunnel points (Permanova's F= 18.21; R^2= 0.32; $P\leq 0.001$). In the Principal Coordinate Analysis (Fig. S1.2), high positive scores for axis I reveals increases for litter depth and the height of trees, shrubs and tussock grasses, while the high negative scores for axis I indicates increases in the amount of cattle dung (Table

S1.3). The axis 2 revealed a within-paddock gradient for the ungrazed areas, characterizing differences in the amount of bare ground and tree height (Table S1.3).

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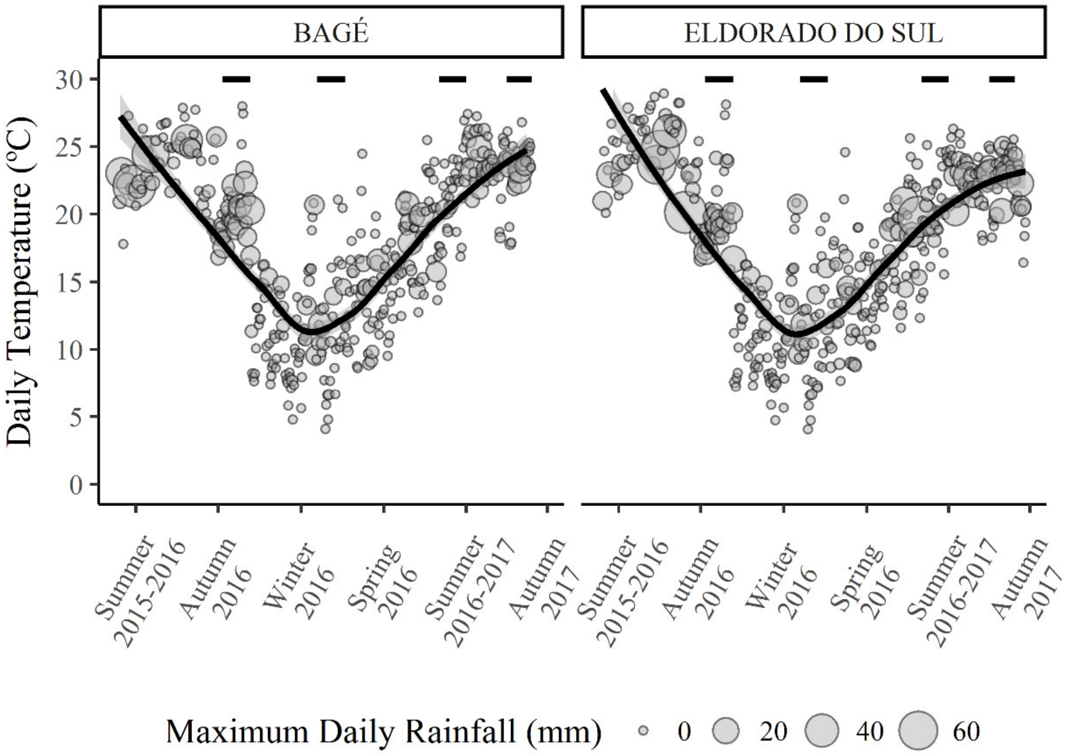

Figure S1.1: Temperature (ºC) and maximum precipitation (mm.) during the course of the study. Each point shows the mean daily temperature (ºC), and point size represents the maximum daily rainfall (mm) (from 2015-12-01 to 2017-03-15). Data was obtained from the Brazilian National Institute of Meteorology (INMET; http://www.inmet.gov.br/portal/). The horizontal line segments indicate the periods of rodent sampling in each season.

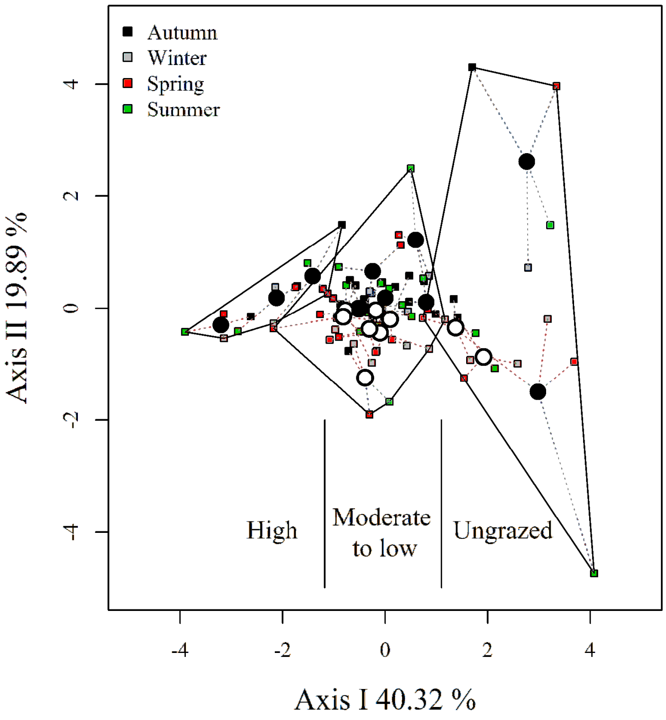

Figure S1.2: Principal Coordinate Analysis plot showing the between-season and between-paddock variation in habitat. Variation captured by the two first ordination axes is included within the axes labels. Convex hulls delimit paddock groups according to their grazing intensity; the lines inside each convex hull link the paddock centroid with the habitat of each season. We used the continuous value of the paddock centroid as the quantitative measurement of the grazing intensity. Black circles indicate centroids from EEA (Eldorado do Sul, RS) paddocks, and white circles indicate centroids from EMBRAPA (Bagé, RS) paddocks.

Table S1.1: Habitat covariates collected at trapping points distributed across grazing paddocks from two livestock research stations in the Pampa biome, Brazil. A point refers to one Sherman, one tomahawk or one tracking tunnel. For the data analysis, covariates were averaged by paddock. Covariates marked with * had low or moderate correlation and were used to extract the multivariate gradient of grazing intensity (Fig S1.2).

Variable (unity)
Site covariates
Vegetation composition and height (cm)
Herbaceous height (cm): The amount of a graduated pole touching herbaceous plants, which included the leaves and reproductive structures of prostrated species (*Paspalum notatum*, *Paspalum dilatatum*, *Axonopus affinis*, *Axonopus argentinum*, *Dichondra sericea*, *Andropogon lateralis*) that generally occur under high grazing intensity.
Tussock height (cm) *: The amount of a graduated pole touching tussock species, which form a dense canopy of dry biomass above the ground. The maximum tussock height was reached when leaves were mostly erect (i.e., no dense structure). The main tussock species were *Saccharum angustifolium*, *Paspalum quadrifarium*, *Stipa* spp., *Aristida jubata*, *Aristida laevis*, *Andropogon lateralis* and the exotic plant *Eragrostis plana* (which form a dense cover very near to the soil). Rosette species (*Eringyum horridum*, *E. pandanifolium*) were regarded as tussocks because these plants form a dense above-ground structure.
Shrub height (cm) *: The amount of a graduated pole touching the stems, leaves and branches of shrubs (e.g., *Baccharis dracuncunifolia*, *Heterotalamus alienus*, *Heterothalamus rupestris*, *Baccharis trimera*, *Achyrocline alata*, *Eupatorium buniifolium*, *Senecio brasiliensis*).
Tree height (cm) *: The amount of a graduated pole touching the stems, leaves and branches of trees (e.g., *Schinus polygamus*, *Quilaja brasiliensis*, *Lithrea brasiliensis*, *Zanthoxylum rhoifolium*).
Litter depth (cm) *

The depth of litter (senescent leaves and stems) at a given point.

*Bare ground * and cattle dung* (%) *

The amount of bare ground and cattle dung at a given point, measured using a 1 m^2 plot divided into 100 subplots.

Distance to nearest tussock, shrub, and tree (meters)

Distance between a given point and the nearest tussock, shrub and tree.

Slope (degrees)

The slope at a given point. Vegetation composition and structure differ according to slope and relief.

Sampling-occasion covariates

Total vegetation height (cm): the total height reached by the vegetation, regardless of type (herbs, tussocks, shrubs or trees), measured using a graduated pole. This covariate represents the total vegetation over a given trapping point in a given season.

Moon phases: trapping occurred under full moon (1) or not (0)

Season: winter (1) or not (0)

Type of trap: tracking tunnel (1) or live-trap (0)

Table S1.2: Habitat covariates by grazing paddock. * Grazing intensity was derived from the paddock's position along the disturbance gradient (Fig. S1.2). We present the total number of live-trap captures and recaptures per species in each paddock. Detections derived from tracking tunnels are presented in ***bold* and *italic***.

Site	Grazing intensity*	*Akodon azarae*	*Oligoryzomys flavescens*	*Oxymycterus nasutus*	Total height (cm)	Herbaceous height (cm)	Shrub height (cm)	Tree height (cm)	Tussock height (cm)	Litter depth (cm)	Bare ground (%)	Cattle dung (%)	Distance to nearest tussock (m)	Distance to nearest shrub (m)	Distance to nearest tree (m)	Slope (°)
EMBRAPA	NO	7	7	14	189.33±11.12	2.59±1.99	62.08±9.06	24.28±15.23	38.35±10.58	1.78±0.24	0±0	0±0	0.04±0.05	0.25±0.14	3.06±0.4	8.14±0.96
EMBRAPA		8	15	15	166.38±10.45	3.58±2.71	66.42±12.22	9.6±9.38	36.28±6.89	1.61±0.41	0.01±0.01	0.01±0.01	0.16±0.11	0.22±0.14	4.72±0.58	5.1±0.98
EEA		***2***	***2***	0	237.62±81.5	1.33±1.97	101.29±69.26	52.5±73.09	35.67±9.08	2.02±0.38	0.01±0.01	0±0	0±0	0.23±0.12	2.89±1.67	4.38±2.23
EEA		***1***	***1***	***1***	206.24±58.09	0.42±0.83	120.54±72.13	1.25±2.5	39.32±8.41	1.49±0.38	0.08±0.05	0±0	0.05±0.09	0.26±0.17	3.92±2.19	12.76±2.54
EMBRAPA	LOW TO INTERMEDIARY	3	0	0	91.5±35.43	2.56±1.1	15.15±6.3	0±0	23.46±8.79	0.96±0.11	0.01±0.01	0.02±0.02	0.11±0.1	0.71±0.38	79.51±17.99	4.97±1.06
EMBRAPA		6	1	0	102.97±27.25	1.22±0.56	11.99±5.5	1.56±3.12	36.11±10.21	1.07±0.28	0.01±0.01	0.03±0.02	0.04±0.05	1.31±0.48	18.6±2.05	3.56±0.51
EMBRAPA		25	***1***	0	92.85±21	2.09±0.78	11.69±4.24	6.47±6.42	25.97±8.23	1.32±0.51	0±0	0.02±0.01	0.16±0.12	1.27±0.99	24.95±3.2	4.52±0.62
EMBRAPA		9	0	0	77.38±10.65	2.94±1.41	12.77±9.33	0±0	21.22±5.17	1.49±0.39	0.01±0	0.03±0.02	0.24±0.37	0.68±0.58	19.68±0.81	6.46±0.69
EMBRAPA		6	1	3	97.39±32.74	4.46±2.33	23.98±4.74	3.65±4.76	21.88±9.7	1.58±0.28	0.02±0.01	0.03±0.02	0.21±0.11	0.25±0.13	10.71±1.18	8.08±1.99
EMBRAPA		0	0	0	77.79±19.06	4.55±1.88	25.58±8.44	8.2±9.74	12.24±4.64	0.86±0.28	0.01±0.01	0.02±0.01	0.68±0.26	0.07±0.05	7.89±0.61	8.66±1.6
EMBRAPA		7	5	1	83.21±15.31	4.16±2.49	13.73±6.4	1.93±1.29	20.9±8.09	1.01±0.34	0.01±0.01	0.03±0.02	0.47±0.56	1.17±0.74	13.78±0.95	7.05±0.79
EMBRAPA		1	9	0	123.04±20.95	6.85±2.76	16.59±5.23	39.52±19.06	12.98±3.85	1.08±0.06	0.01±0.01	0.03±0	1.2±0.51	0.27±0.1	10.35±0.85	7.94±0.71
EEA		0	0	0	86.25±16.38	4.62±5.46	17.83±7.06	0±0	34.46±6.58	0.57±0.25	0.01±0.01	0.01±0.02	0±0	0.88±0.59	96.67±6.67	5.21±1.66
EEA		0	0	0	106.12±21.25	0±0	6.5±7.52	0±0	43.5±6.25	0.86±0.45	0.03±0.02	0±0	0±0	25.87±49.42	100±0	7.29±1.67
EEA		0	0	0	106.12±20.72	0.42±0.83	12.04±2.15	0±0	42.67±3.05	1.25±0.32	0±0	0±0	0±0	0.73±0.22	73.12±34.6	8.25±2.03
EEA		0	0	0	107.54±14.3	0±0	2.42±4.83	0±0	41.58±3.6	0.92±0.33	0±0.01	0.02±0.02	0±0	27.29±48.5	100±0	1.62±1.01
EEA		0	0	0	74.88±14.88	3.83±2.16	28.08±18.63	3.25±6.5	25.21±12.75	0.77±0.29	0±0.01	0.02±0	0.25±0.31	0.51±0.37	100±0	5.54±1.44
EEA	HIGH	0	0	0	60.17±20.36	4±1.97	3.21±6.42	0±0	17.79±8.08	0.31±0.19	0.02±0.01	0.02±0.02	0.17±0.2	8.95±12.95	100±0	6.71±2.1
EEA		0	0	0	7.96±5.07	5.79±1.38	2.46±4.92	0±0	0±0	0.38±0.11	0.01±0.01	0.03±0.03	49.17±14.17	12.11±7.59	100±0	3.62±1.86
EEA		0	0	0	6.73±3.31	3.1±2.07	1.79±3.58	0±0	0±0	0.22±0.06	0.01±0.01	0.07±0.02	33.38±19.51	6.99±3.7	100±0	4.03±1.55

Table S1.3: Correlations between habitat covariates and the axes of the Principal Coordinate Analysis (Fig. S1.2).

	PCO 1 (40.32%)	PCO 2 (19.89%)
Shrub height	0.72	0.03
Tree height	0.40	-0.66
Tussock height	0.73	0.17
Litter depth	0.79	-0.32
Bare ground	0.25	0.74
Cattle dung	-0.75	-0.25

Table S1.4: Candidate models potentially explaining rodent detection (p) and site occupation (ψ).

Model	Number of parameters
p(.) ψ (.)	2
p(.) ψ (PCO1)	3
p(Season) ψ (.)	3
p(Total height) ψ (.)	3
p(Season) ψ (PCO1)	4
p(Moon) ψ (PCO1)	4
p(Trap) ψ (PCO1)	4
p(Total height) ψ (PCO1)	4
p(Total height^2) ψ (PCO1^2)	4
p(Total height^3) ψ (PCO1^3)	4
p(Season+total height) ψ (PCO1)	5
p(Season:total height) ψ (PCO1)	5
p(Season: total height^2) ψ (PCO1^2)	5
p(Season: total height^3) ψ (PCO1^3)	5

Table S1.5: Sampling effort and number of detections presented according to species, site, trap type and season. In Eldorado do Sul (EEA), we sampled from winter 2016 to summer 2017 using tracking tunnels only. Within parenthesis, we present the number of recaptures for live-trap sampling. In **bold**, we present the number of tracking tunnels with detections.

	Live-trap†/ **tunnel** effort	*Akodon azarae*	*Oligoryzomys flavescens*	*Oxymycterus nasutus*	TOTAL
BAGÉ (EMBRAPA)	4,239	39 (33)	28 (10)	21 (12)	88 (55)
	240	**34**	**11**	**5**	**50**
Autumn 2016	1,104	10 (5)	1	2	13 (5)
	60	**5**	**1**	**2**	**8**
Winter 2016	1,065	23 (27)	24 (7)	12 (8)	59 (42)
	60	**26**	**9**	**1**	**36**
Spring 2016	1,031	5 (1)	0	1	6 (1)
	60	0	0	0	0
Summer 2017	1,039	1	3 (3)	6 (4)	10 (7)
	60	**3**	**1**	**2**	**6**
ELDORADO DO SUL (EEA)	728	0	0	0	0
	240	**3**	**3**	**1**	**7**
Autumn 2016	728	0	0	0	0
	60	0	**1**	**1**	**2**
Winter 2016	-	-	**-**	-	-
	60	**2**	**2**	0	**4**
Spring 2016	-	-	-	-	-
	60	0	0	0	0
Summer 2017	-	**-**	-	-	-
	60	**1**	0	0	**1**
TOTAL (Live-traps)	4,967	39 (33)	28 (10)	21 (12)	88 (55)
TOTAL (Tracking tunnels)	**480**	**37**	**14**	**6**	**57**

† Net sampling effort (trap/nights) for live traps, calculated by discounting the number of unavailable traps (armed and unbaited, disarmed and baited/unbaited or switched) from the total sampling effort. The total sampling effort calculated per site and season was: 24 traps x 10 paddocks x 5 nights = 1,200 trap/nights. Since we only conducted live-trap sampling in EEA in the autumn, the total effort in this site was 1,200

trap/nights. Since we conducted live-trap sampling in EMBRAPA across the four seasons, the total sampling effort for this site was 4,800 trap/nights.

Table S1.6: AICc ranking of all candidate models for Azara's grass mouse (*Akodon azarae*). p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S1.2). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	df	LogLik	AICc	Delta AICc	Weight
p(Season) ψ (PCO1)	**4**	**-128.487**	**267.6**	**0**	**0.552**
p(Season+total height) ψ (PCO1)	**5**	**-127.435**	**269.2**	**1.52**	**0.259**
p(Season) ψ (.)	**3**	**-131.138**	**269.8**	**2.14**	**0.19**
p(Total height^3) ψ (PCO1^3)	4	-152.873	316.4	48.77	0
p(Season: total height^3) ψ (PCO1^3)	5	-151.749	317.8	50.14	0
p(Season: total height^2) ψ (PCO1^2)	5	-153.491	321.3	53.63	0
p(.) ψ (PCO1)	3	-157.317	322.1	54.49	0
p(Season:total height) ψ (PCO1)	5	-154.703	323.7	56.05	0
p(Trap) ψ (PCO1)	4	-156.531	323.7	56.09	0
p(Moon) ψ (PCO1)	4	-156.615	323.9	56.26	0
p(Total height) ψ (PCO1)	4	-156.953	324.6	56.93	0
p(.) ψ (.)	2	-159.967	324.6	57	0
p(Total height^2) ψ (PCO1^2)	4	-157.087	324.8	57.2	0
p(Total height) ψ (.)	3	-159.606	326.7	59.07	0

Table S1.7: AICc ranking of all candidate models for the yellow pigmy rice rat (*Oligoryzomys flavescens*). p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S1.2). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	df	LogLik	AICc	Delta AICc	Weight
p(Season) ψ (PCO1)	**4**	**-81.06**	**172.8**	**0**	**0.737**
p(Season+total height) ψ (PCO1)	**5**	**-80.921**	**176.1**	**3.34**	**0.139**
p(Season) ψ (.)	**3**	**-84.429**	**176.4**	**3.57**	**0.124**
p(Season:total height^3) ψ (PCO1^3)	5	-91.476	197.2	24.45	0
p(Total height^3) ψ (PCO1^3)	4	-94.445	199.6	26.77	0
p(Season:total height) ψ (PCO1)	5	-93.297	200.9	28.09	0
p(Trap) ψ (PCO1)	4	-95.242	201.2	28.36	0
p(Season: total height^2) ψ (PCO1^2)	5	-93.654	201.6	28.81	0
p(.) ψ (PCO1)	3	-97.183	201.9	29.08	0
p(Moon) ψ (PCO1)	4	-97.048	204.8	31.98	0
p(Total height) ψ (PCO1)	4	-97.183	205	32.24	0

p(.) ψ (.)	2	-100.53	205.8	32.98	0
p(Total height) ψ (.)	3	-100.526	208.6	35.76	0
p(Total height^2) ψ (PCO1^2)	4	-99.129	208.9	36.14	0

Table S1.8: AICc ranking of all candidate models for the long-nosed hocicudo (*Oxymycterus nasutus*). p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S1.2). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	**df**	**LogLik**	**AICc**	**Delta AICc**	**Weight**
p(Season) ψ (PCO1)	**4**	**-66.661**	**144**	**0**	**0.448**
p(Season) ψ (.)	**3**	**-68.588**	**144.7**	**0.69**	**0.317**
p(Season+total height) ψ (PCO1)	**5**	**-66.333**	**147**	**2.96**	**0.102**
p(.) ψ (PCO1)	3	-70.709	148.9	4.93	0.038
p(.) ψ (.)	2	-72.637	150	5.99	0.022
p(Total height^3) ψ (PCO1^3)	4	-70.048	150.8	6.77	0.015
p(Trap) ψ (PCO1)	4	-70.14	150.9	6.96	0.014
p(Total height) ψ (PCO1)	4	-70.233	151.1	7.14	0.013
p(Moon) ψ (PCO1)	4	-70.382	151.4	7.44	0.011
p(Total height) ψ (.)	3	-72.118	151.7	7.75	0.009
p(Season:total height) ψ (PCO1)	5	-69.172	152.6	8.64	0.006
p(Season: total height^3) ψ (PCO1^3)	5	-70.11	154.5	10.52	0.002
p(Total height^2) ψ (PCO1^2)	4	-72.265	155.2	11.21	0.002
p(Season: total height^2) ψ (PCO1^2)	5	-71.563	157.4	13.42	0.001

Appendix S2: Footprint morphometrics

We based the identification of free-ranging individuals on a reference footprint collection of the live-trapped individuals. We scanned papers with footprints at 600 dpi resolution and analyzed them in TPSDIG v.2.30 (Rohlf, 2015). Landmarks were set in toe and central pads of right hand and foot (see van Apeldoorn et al., 1993; Palma and Gurgel-Gonçalves, 2007). Whenever possible, we used at least three footprints from each individual paper to improve consistency in footprint classification. We estimated the location of missing landmarks in the reference collection using available information from the toes and pads of the respective species, while missing landmarks for free-ranging individuals were based in toes and pads of the complete reference collection (Table S2.1). In both cases, we applied the "TPS" method for missing landmarks, which adjust a thin-plate spline to interpolate missing landmarks from individuals presenting all landmarks (Gunz et al., 2009; Adams et al., 2016). For identification of footprints from free-ranging individuals, we overlapped tunnel samples with the reference collection (Table S2.1). We created new variables describing footprint shape after correcting for non-shape differences through Generalized Procrustes Analysis (GPA), which involves the translation, scaling and rotation of a footprint to decrease distances among corresponding landmarks (Rohlf and Slice, 1990). We used the GPA corrected landmark-coordinates for projecting, in a shape space, the footprints of free ranging plus reference individuals, and then performed the classification using Canonical Variate Analysis (CVA). *A priori* defined groups in CVA consisted of the respective species (for those footprints in the reference collection) and the tracking tunnel point (for free-ranging individuals). CVA provided the probability that the footprint from a given free-ranging individual belongs to either one of the pre-defined species groups or their own group (i.e. unidentifiable) (Lawing and Polly, 2010). We tested accuracy on free-ranging individual classification between species groups through Canonical Variate Analysis (CVA) based in 1,000 permutations and the robust ‘mve’ covariance estimation method. We calculated the ratio between the counting of correct and incorrect footprint classification of the reference collection to define classification accuracy (see Table S2.1 below). We measured size variation by considering the perimeter embracing the peripheral landmarks. We merged identification for right/left hands and feet to define species detection/non-detection in a given paddock. We performed the morphometric analyses with functions implemented in geomorph and Morpho packages in R (R Development Core Team, 2017).

We compared CVA scores among species and observed that the three rodent species differed in hand and foot shapes (Procrustes ANOVA; 999 permutations; $P \leq 0.05$). Furthermore, the size of hands and feet of the yellow pigmy rice rat (*Oligoryzomys flavescens*) were found to be larger than those of the other two species (Fig. S2.1, S2.2, S2.3, S2.4). The toes of the hands and feet of the yellow pigmy rice rat are farther from the central pads than those of the long-nosed hocicudo (*Oxymycterus nasutus*) and Azara’s grass mouse (*Akodon azarae*). Conversely, the toes of long-nosed hocicudo are closer to central pads than those of the other species, which confers an adaptation to a semi-fossorial mode of life. The hand and foot morphology of Azara’s grass mouse was found to be intermediate in size and shape relative to the two other species.

Table S2.1: Accuracy (%) of the classification of the footprints in the reference collection. We collected the footprints after measuring and weighing rodents trapped in live-traps (Tomahawk and Sherman).

Limb (number of footprints)	Azara's grass mouse	Yellow pigmy rice rat	Long-nosed hocicudo	Kappa statistic	Overall accuracy (%)
Hand					
Right (310)	93.30	99.08	76.40	0.88	92.60
Left (355)	96.64	99.09	89.58	0.93	95.49
Foot					
Right (325)	90.91	82.64	85.29	0.79	86.60
Left (346)	89.67	83.93	87.34	0.80	87.28

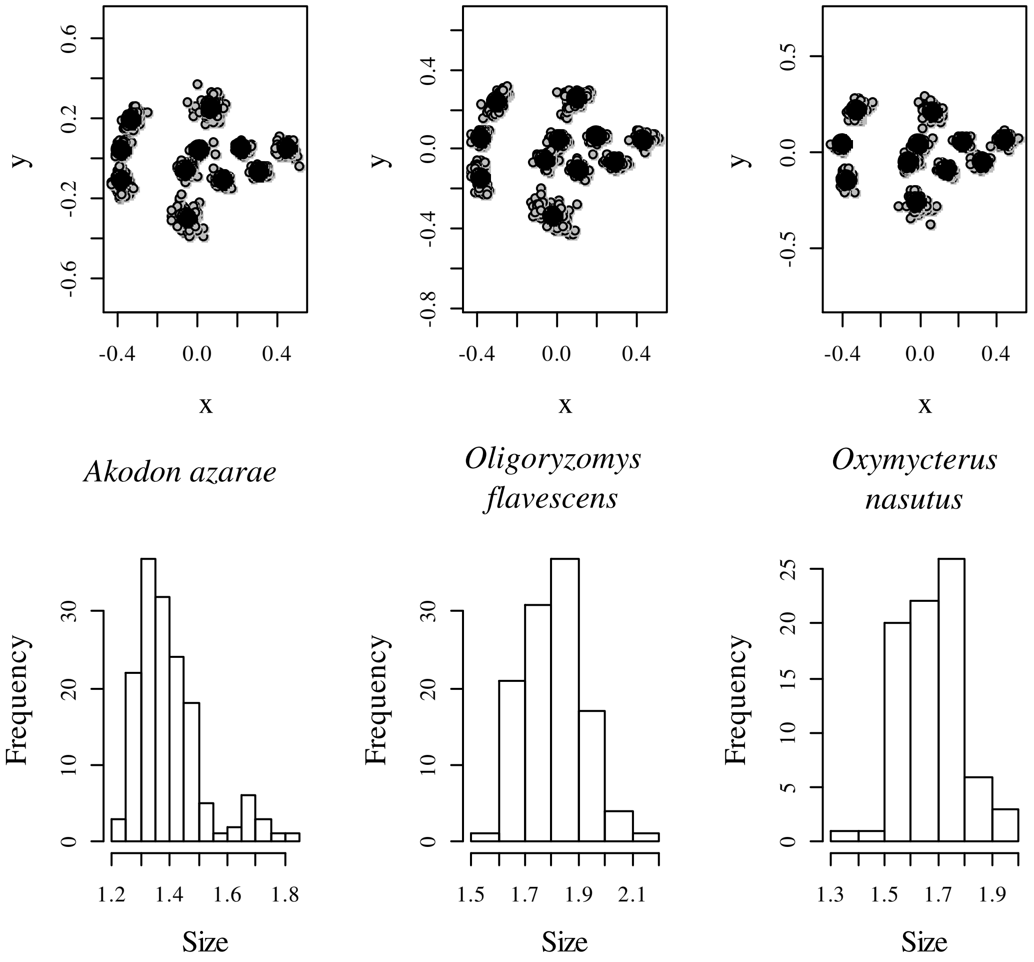

Fig. S2.1: Shape variation (upper) and footprint size distribution (in cm, bottom) for the left foot of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (346 footprints), whereas black points compose the consensus shape.

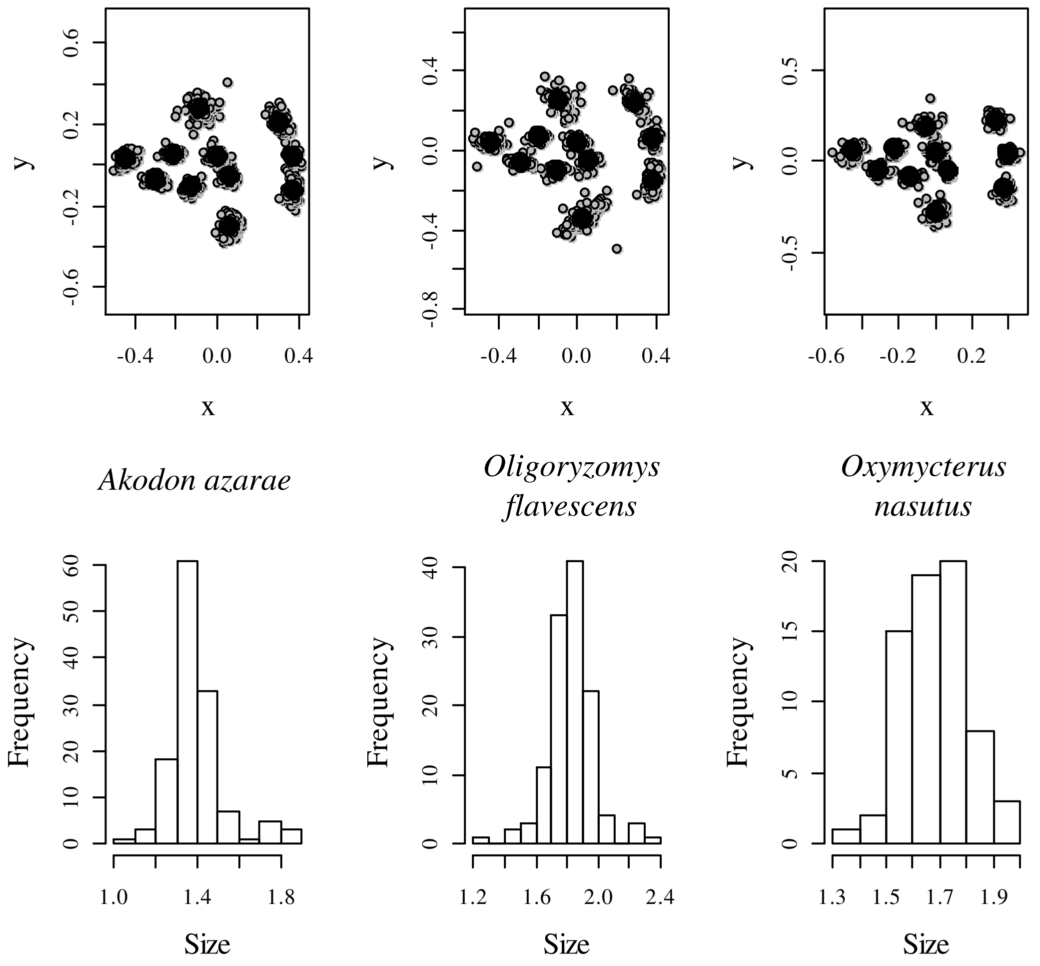

Fig. S2.2: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the right foot of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (325 footprints), whereas black points compose the consensus shape.

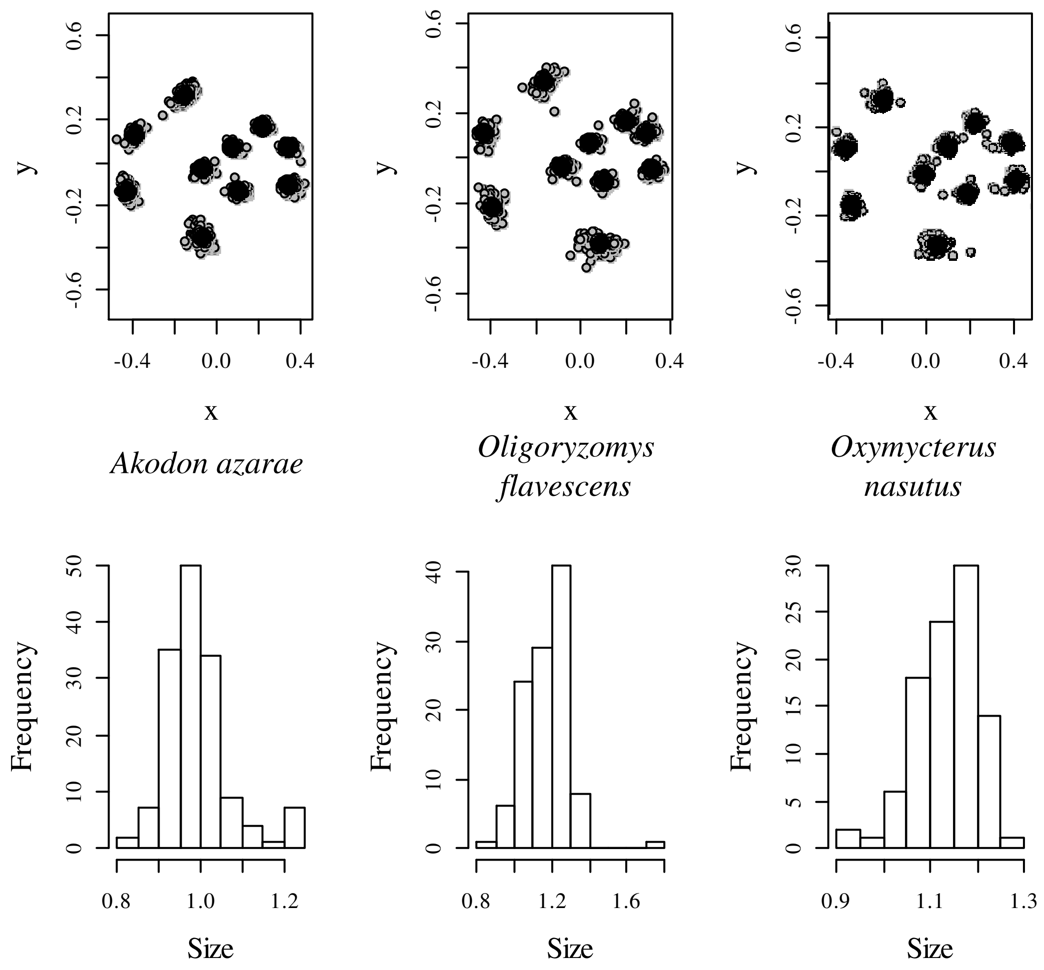

Fig. S2.3: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the left hand of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (355 footprints), whereas black points compose the consensus shape.

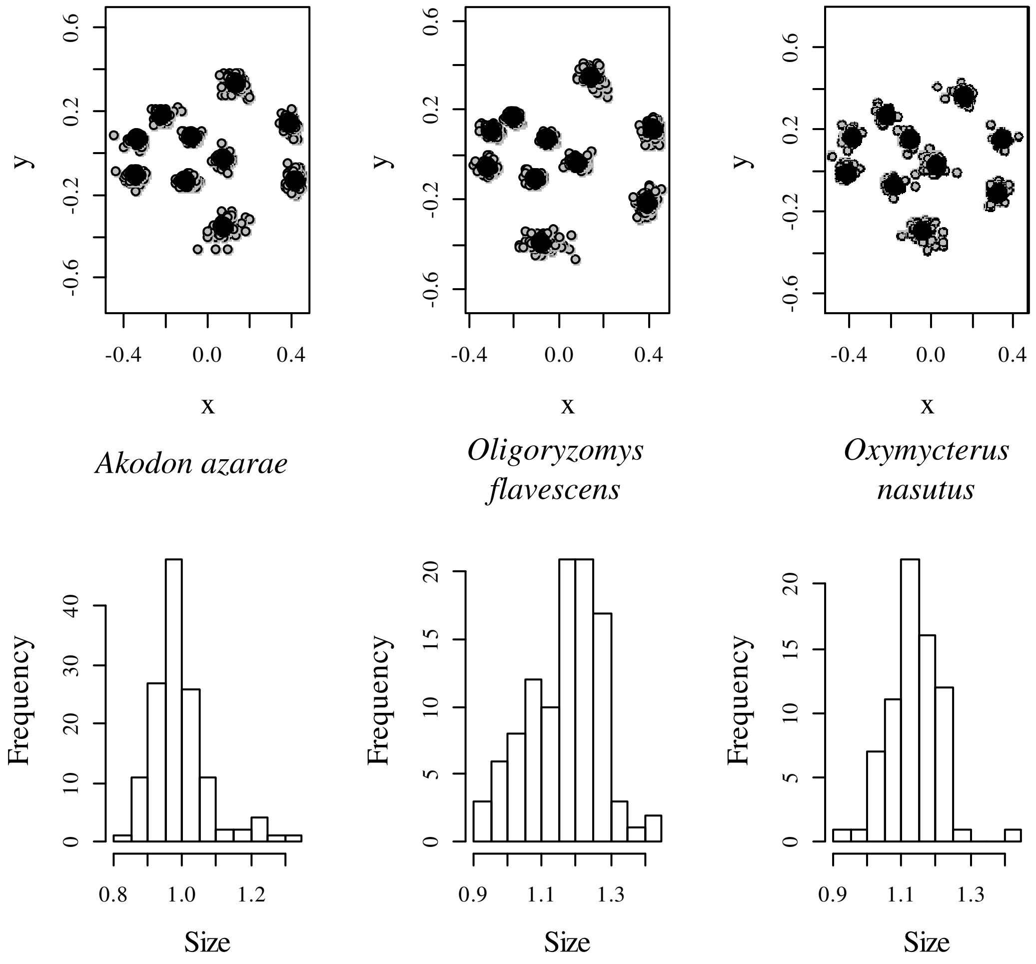

Fig. S2.4: Distribution of variation in footprint shape (upper) and size (in cm, bottom) for the right hand of the three studied rodent species. The gray points are landmarks for each individual in the reference collection (310 footprints), whereas black points compose the consensus shape.

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Appendix S3: Sensitivity analyses using EMBRAPA data.

We re-ran the analyses using the data from the EMBRAPA locality, collected from rodents sampled in ten grazing paddocks across one year, using both tunnels and live traps. We evaluated the between-paddock (spatial) and within-paddock (seasonal) variation in habitat structure using Permanova and Betadisper (Test for Homogeneity of Multivariate Dispersions) tests, respectively. P-values were generated through randomizations (similarly to the analyses using EEA and EMBRAPA data; Appendix S1). We used the habitat covariates as response variables and grazing level as the predictor variable; we blocked randomizations according to the type of trap (live-traps or tracking tunnel) we used.

The Permanova analysis we ran showed between-paddock variations in habitat structure ($F= 17.57$, $R^2= 0.31$, $P\leq 0.001$). However, the Betadisper analysis did not identify within-paddock (seasonal) variation in habitat structure ($F= 0.08$, $P=0.908$). We observed pairwise differences in the habitat characteristics between all combinations of ungrazed, lowly and moderately grazed paddocks (Bonferroni adjusted $P= 0.003$), although the lowly and moderately grazed paddocks had a similar habitat according to the principal coordinate analysis (Fig. S3.1). The habitat of ungrazed paddocks was characterized by a deeper layer of litter and taller tussocks, shrubs and trees (Table S3.1). Paddocks subjected to low to moderate grazing intensities were characterized by a higher percentage of both bare ground and cattle dung in a square meter (Table S3.1).

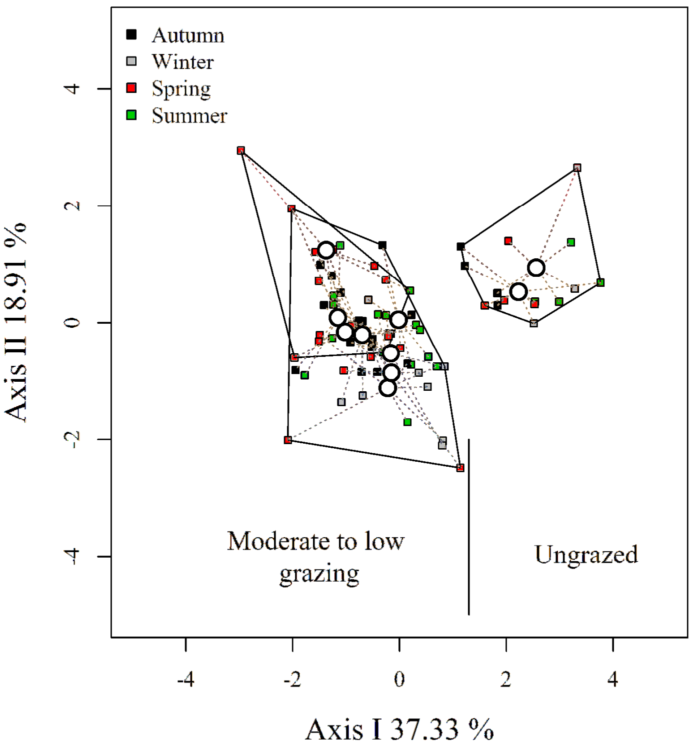

Fig. S3.1: Principal coordinate analysis plot showing the between-season and between-paddock variation in the habitat structure. Variation captured by the two first ordination axes is included within the axes labels. Convex hulls delimit paddock groups according to their grazing intensity; the lines inside each convex hull link the paddock centroid with the habitat of each season. We used the continuous value of the paddock centroid as the quantitative measurement of the grazing intensity. Data was collected from EMBRAPA (Bagé, RS).

Table S3.1: Correlations between habitat covariates and the axes of the Principal Coordinate Analysis (Fig S3.1).

	Pcoa1 (37.33%)	Pcoa2 (18.91%)
Shrub height	0.82	0.29
Tree height	0.46	0.29
Tussock height	0.72	-0.3
Litter depth	0.73	-0.17
Bare ground	-0.41	0.69
Cattle dung	-0.39	-0.62

The results of the single-season occupancy models run using the EMBRAPA data showed that, for *Akodon azarae,* the models that were more strongly supported included season as the covariate explaining the probability of detection (Table S3.1). The probability of detection was higher in the winter than in the non-winter months (Table S3.3). The probability of occupation increased with decreasing grazing intensity, although the confidence intervals were very wide (Fig S3.2).

Table S3.2: Model-selection table for *Akodon azarae*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S3.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	**df**	**LogLik**	**AICc**	**Delta AICc**	**Weight**
p(Season) ψ (.)	**3**	**-100.294**	**210.6**	**0**	**0.875**
p(Season) ψ (PCO1)	**4**	**-99.263**	**214.5**	**3.94**	**0.122**
p(Season+total height) ψ (PCO1)	5	-98.338	221.7	11.09	0.003
p(Trap) ψ (PCO1)	4	-116.29	248.6	37.99	0
p(.) ψ (.)	2	-122.456	250.6	40.04	0
p(Season: total height^2) ψ (PCO1^2)	5	-113.173	251.3	40.76	0
p(.) ψ (PCO1)	3	-121.431	252.9	42.27	0
p(Moon) ψ (PCO1)	4	-118.765	253.5	42.94	0
p(Total height) ψ (.)	3	-121.892	253.8	43.2	0
p(Total height^3) ψ (PCO1^3)	4	-120.816	257.6	47.04	0
p(Total height) ψ (PCO1)	4	-120.879	257.8	47.17	0
p(Total height^2) ψ (PCO1^2)	4	-121.42	258.8	48.25	0
p(Season: total height^3) ψ (PCO1^3)	5	-118.431	261.9	51.27	0
p(Season:total height) ψ (PCO1)	5	-120.012	265	54.44	0

Table S3.3: Estimates of the detection probabilities (p) of *Akodon azarae*, given as a function of the sampling occasion covariates.

Season	Detection probability	Standard Error	Linear combination (logit scale)
Non-winter	0.088	0.029	-2.335
Winter	0.592	0.067	0.374

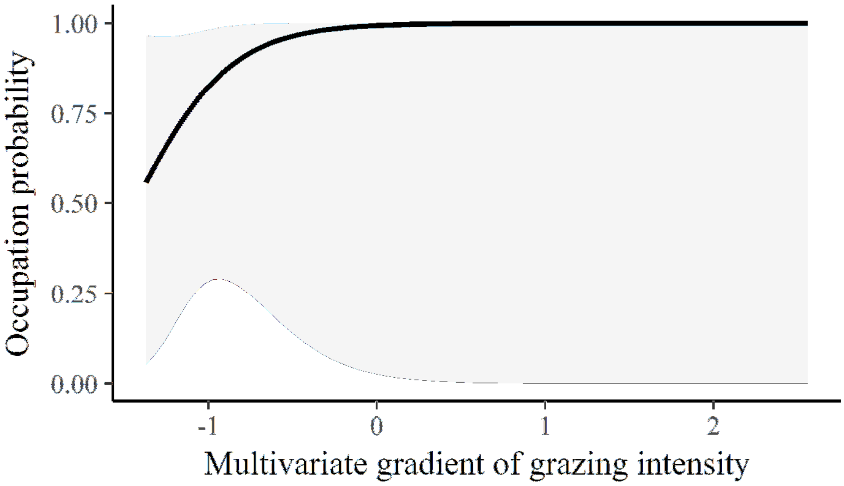

Fig. S3.2: Occupation probability (ψ) of *Akodon azarae*, given as a function of the gradient of grazing intensity. Values of the multivariate gradient of grazing intensity were extracted from Axis 1 of the Principal Coordinate Analysis (Fig. S3.1). The lowest negative values indicate the highest grazing intensities, whereas the highest positive values indicate the absence of grazing.

The results of the single-season occupancy models run using the EMBRAPA data showed that, for *Oligoryzomys flavescens,* the models that were more strongly supported included season as the covariate explaining the probability of detection (Table S3.4). The probability of detection was higher in the winter than in the non-winter months (Table S3.5). The probability of occupation was constant across the gradient of grazing intensity (Table S3.4).

Table S3.4: Model-selection table for *Oligoryzomys flavescens*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S3.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	**df**	**LogLik**	**AICc**	**Delta AICc**	**Weight**
p(Season) ψ (.)	**3**	**-59.933**	**129.9**	**0**	**0.906**
p(Season) ψ (PCO1)	4	-59.259	134.5	4.65	0.088
p(Season+total height) ψ (PCO1)	5	-57.463	139.9	10.06	0.006
p(.) ψ (.)	2	-71.533	148.8	18.91	0
p(Total height) ψ (.)	3	-70.015	150	20.16	0
p(.) ψ (PCO1)	3	-70.866	151.7	21.87	0
p(Total height^2) ψ (PCO1^2)	4	-68.975	154	24.08	0
p(Total height) ψ (PCO1)	4	-69.422	154.8	24.98	0
p(Total height^3) ψ (PCO1^3)	4	-69.699	155.4	25.53	0
p(Season: total height^2) ψ (PCO1^2)	5	-66.158	157.3	27.45	0
p(Trap) ψ (PCO1)	4	-70.675	157.3	27.48	0
p(Season:total height) ψ (PCO1)	5	-68.213	161.4	31.56	0
p(Season: total height^3) ψ (PCO1^3)	5	-68.718	162.4	32.57	0
p(Moon) ψ (PCO1)	4	-118.765	253.5	123.66	0

Table S3.5: Estimates of the detection probabilities (p) of *Oligoryzomys flavescens*, given as a function of the sampling occasion covariates.

Season	Detection probability	Standard Error	Linear combination (logit scale)
Non-winter	0.0914	0.0413	-2.297
Winter	0.441	0.084	-0.237

The results of the single-season occupancy models run using the EMBRAPA data showed that, for *Oxymycterus nasutus,* the models with the stronger support included season and total vegetation height as the covariates explaining the probability of detection (Table S3.6). The probability of detection was higher in the winter than in the non-winter months (Table S3.7), and it was also higher in areas with taller vegetation (Table S3.7). The probability of occupation increased with decreasing grazing intensity, although the confidence intervals were very wide (Fig S3.3).

Table S3.6: Model-selection table for *Oxymycterus nasutus*, with candidate models ranked according to their AICc. p = detection probability; ψ = occupation probability. PCO1= gradient of grazing intensity (Fig. S3.1). The models with stronger support are those with Delta AICc ≤ 4 (in **bold**).

Model	**df**	**LogLik**	**AICc**	**Delta AICc**	**Weight**
p(Total height) ψ (.)	**3**	**-55.178**	**120.4**	**0**	**0.316**
p(Season+total height) ψ (PCO1)	**5**	**-47.871**	**120.7**	**0.38**	**0.261**
p(Season) ψ (.)	**3**	**-55.804**	**121.6**	**1.25**	**0.169**
p(Total height) ψ (PCO1)	**4**	**-53.269**	**122.5**	**2.18**	**0.106**
p(Season) ψ (PCO1)	**4**	**-53.779**	**123.6**	**3.2**	**0.064**
p(Total height^3) ψ (PCO1^3)	4	-54.627	125.3	4.9	0.027
p(Total height^2) ψ (PCO1^2)	4	-55.042	126.1	5.73	0.018
p(.) ψ (.)	2	-60.71	127.1	6.78	0.011
p(.) ψ (PCO1)	3	-58.686	127.4	7.02	0.009
p(Season:total height) ψ (PCO1)	5	-51.234	127.5	7.11	0.009
p(Season: total height^3) ψ (PCO1^3)	5	-51.81	128.6	8.26	0.005
p(Season: total height^2) ψ (PCO1^2)	5	-51.978	129	8.6	0.004
p(Moon) ψ (PCO1)	4	-58.412	132.8	12.47	0.001
p(Trap) ψ (PCO1)	4	-58.494	133	12.63	0.001

Table S3.7: Estimates of the detection probabilities (p) of *Oxymycterus nasutus*, given as a function of the sampling occasion covariates.

Detection probability	Standard Error	Linear combination (logit scale)	Season	Total vegetation height (cm)
0.0117	0.0132	-4.438	Non-winter	4
0.0272	0.0241	-3.575		42
0.0622	0.0415	-2.713		104.3
0.2712	0.1153	-0.988		166
0.4685	0.176	-0.126		228
0.657	0.1992	0.65		284
0.0411	0.0457	-3.149	Winter	4
0.0922	0.0759	-2.287		42
0.1939	0.1062	-1.425		104.3
0.5744	0.1159	0.3		166
0.7617	0.1071	1.162		228
0.8742	0.085	1.938		284

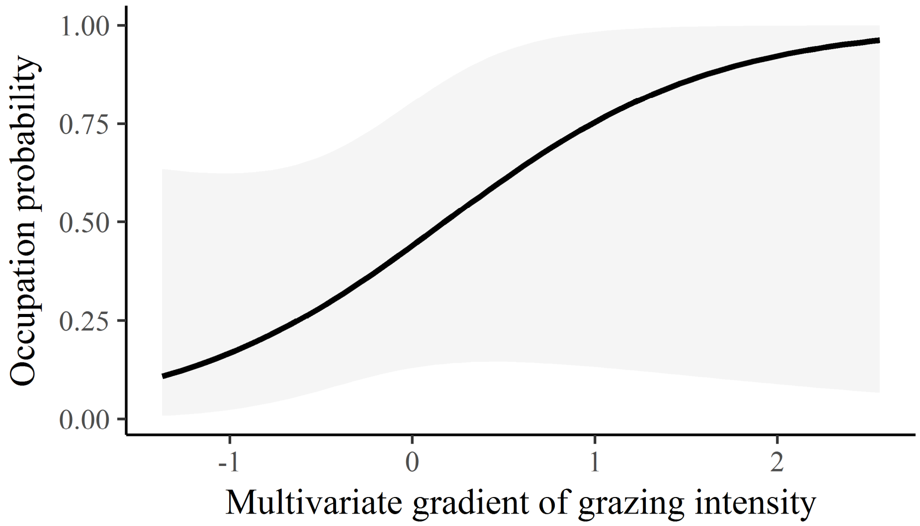

Fig. S3.3: Occupation probability (ψ) of *Oxymycterus nasutus* as a function of the gradient of grazing intensity. Values of the multivariate gradient of grazing intensity were extracted from Axis 1 of the Principal Coordinate Analysis (Fig. S3.1). The lowest negative values indicate the highest grazing intensities, whereas the highest positive values indicate the absence of grazing.