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Escola Superior de Agricultura “Luiz de Queiroz”
Centro de Ecologia Nuclear na Agricultura

Efeitos da conversão de floresta tropical em usos antrópicos da terra sobre a diversidade de serpentes

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Tese apresentada para obtenção do Título de Doutora em Ciências. Área de concentração: Ecologia Aplicada

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Onde há uma vontade, há um caminho.
Provérbio popular

Sumário

RESUMO

Efeitos da conversão de floresta tropical em usos antrópicos da terra sobre a diversidade de serpentes

A conversão de habitats naturais em usos antrópicos da terra é considerada uma das principais causas da perda de espécies. No entanto, seus efeitos sobre a diversidade de serpentes ainda são pouco conhecidos, inclusive em ecossistemas megadiversos, como as florestas tropicais. Nesta tese buscamos entender como os distintos componentes da diversidade (i.e., diversidade de espécies, funcional e filogenética) de serpentes respondem à conversão de habitats, considerando tanto os efeitos de processos locais como no nível da paisagem. Investigamos também como a paisagem seleciona distintamente as espécies de serpentes por seus traços e quais são os traços selecionados, bem como as implicações dessa seleção para o funcionamento e a resiliência dos ecossistemas estudados. Para isso, coletamos dados de comunidades de serpentes em uma área fragmentada de Mata Atlântica composta por diferentes usos da terra (silvicultura e pasto). Identificamos que a perda de cobertura florestal leva a perda de todos os aspectos da diversidade de serpentes, porém em diferentes escalas espaciais. A diversidade de espécies aumentou com a proporção de floresta e o nível de fragmentação da paisagem, enquanto a diversidade funcional aumentou com a quantidade de floresta na paisagem. Da mesma forma, a diversidade filogenética aumentou com a proporção de floresta e, inesperadamente, também aumentou com a proporção de silvicultura em escala local, indicando que espécies de serpentes com restrição de movimento e/ou especialistas no uso do habitat podem ser evolutivamente distantes. Logo, estratégias de conservação devem considerar múltiplas escalas espaciais para conservar distintos componentes da diversidade de serpentes. Além disso, também identificamos que a configuração espacial do habitat e o tipo de uso da terra são os principais fatores influenciando a distribuição dos traços funcionais de serpentes nas paisagens estudadas. A distância entre as manchas de fragmentos florestais selecionou distintamente as espécies de serpentes com base em seu tamanho corporal e no grau de especialização de dieta, enquanto o tipo de uso da terra selecionou as espécies por seu modo de forrageio. Essa organização das comunidades de serpentes mediada pela paisagem resultou em potencial perda de funcionamento e resiliência dos ecossistemas associados a comunidades dominadas por espécies generalistas. Porque os traços funcionais selecionados (i.e., tamanho corporal, dieta e modo de forrageio) pela paisagem apresentam formas de medir padronizadas, propomos que sejam considerados como marcadores funcionais em outros estudos que visem entender a resposta das serpentes aos distúrbios ambientais. Sendo assim, concluímos que a quantidade de floresta e a proximidade entre os fragmentos florestais são dois fatores fundamentais para conservar os distintos componentes da diversidade de serpentes, para manter a paisagem conectada para as diferentes espécies e para possibilitar a manutenção dos processos ecossistêmicos em mosaicos de floresta tropical e usos da terra. Em termos práticos, isso ressalta a importância da manutenção das reservas legais e das áreas de proteção permanente em propriedades privadas, sobretudo se formarem corredores ecológicos, contribuindo para garantir a persistência das diferentes espécies de serpentes e dos processos ecossistêmicos.

Palavras-chave: Serpentes; Diversidade; Ecologia da paisagem; Mata Atlântica; Conservação

ABSTRACT

Effects of tropical forest conversion into anthropic land uses on snake diversity

Natural habitat conversion into anthropic land uses is considered the main cause of species loss. Nonetheless, its effects on snake diversity are still poorly understood, including in megadiverse ecosystems such as tropical forests. In this thesis we aim to understand how distinct components of snake diversity (i.e., species, functional and phylogenetic) respond to habitat conversion, considering both the effects of local and landscape processes. We also investigated how landscapes distinctly select snake species by their traits and which traits are selected, as well as the implications of this selection for ecosystem functioning and resilience. For this, we collected data of snake communities in a fragmented area of Mata Atlântica composed of different land uses (silviculture and pasture). We identified that loss of forest cover induced loss of all diversity components, although at different spatial scales. Species diversity increased with the proportion of forest cover and the number of forest patches in the landscape. Similarly, phylogenetic diversity increased with the proportion of forest cover and, unexpectedly, with the proportion of silviculture at the local scale, indicating that snake species with movement restriction and/or habitat specialist are evolutionarily distant. Thus, conservation strategies should consider multiple spatial scales in order to conserve distinct components of snake diversity. Moreover, we also identified that spatial configuration of forest and land use types are the main factors influencing the distribution of snake functional traits in the studied landscapes. The distance among forest patches distinctly selected snake species based on their body size and diet specialization, whereas the type of land use selected snakes by their foraging mode. This organization of snake communities mediated by landscape resulted in potential loss of functioning and resilience of the ecosystems associated with communities dominated by generalist species. Because functional traits (i.e., body size, diet specialization and foraging mode) selected by landscape present standardized ways of measuring, we propose they are considered as functional markers in other studies that aim to understand snake response to environmental disturbances. Therefore, we concluded that forest proportion and proximity among forest patches are two fundamental factors to conserve the distinct components of snake diversity, to allow forest connection for different snake species and to enable the maintenance of ecosystem processes in mosaics of tropical forest and land uses. In practical terms, this highlights the importance of the maintenance of legal reserves and areas of permanent protection in private properties, especially if they form ecological corridors, contributing to ensure the persistence of different snake species and ecosystem processes.

Keywords: Snakes; Diversity; Landscape ecology; Atlantic Forest; Conservation

1. INTRODUÇÃO GERAL

A expansão das atividades antrópicas em áreas de ecossistemas naturais é uma das principais causas do declínio global na biodiversidade (Cowie et al., 2022). Estima-se que cerca de 50% da cobertura terrestre já foi convertida em usos antrópicos (Millennium Ecosystem Assessment, 2005), transformando áreas contínuas de habitat em paisagens fragmentadas. A resposta das espécies a essas mudanças depende dos requerimentos ecológicos, da tolerância aos usos antrópicos da terra (i.e., matrizes) e da capacidade de dispersão de cada espécie, sendo, portanto, uma resposta espécie-específica. Os distúrbios nos habitats remanescentes podem gerar mudanças ambientais capazes de reestruturar a composição e abundância de espécies em comunidades ecológicas (Barros et al., 2002; Alroy, 2017). Por outro lado, as matrizes podem apresentar condições favoráveis para o estabelecimento de espécies generalistas ou mesmo espécies invasoras, mas as mesmas condições podem ser desfavoráveis para especialistas de habitat (Díaz et al., 1994; Carrara et al., 2015). Entender como a conversão de habitats influencia a resposta das espécies e a organização das comunidades ecológicas tornou-se fundamental para conservar a maior biodiversidade possível, sobretudo diante de um cenário em que a pressão antrópica sobre ambientes naturais tende a se manter (Johnson et al., 2017; Taubert et al., 2018).

Múltiplos fatores podem influenciar a diversidade em mosaicos de habitats naturais e antropizados. A perda da quantidade de habitat nativo é o fator negativo mais evidente (Pimm et al., 2014), tendo em vista que o tamanho das populações e o número de espécies diminuem quanto menor for a área de habitat nativo disponível, tal como previsto pela relação espécie-área (Arrhenius, 1921; Gleason, 1922). Porém, habitats nativos podem sofrer degradação em qualidade, como observado nas áreas de borda dos remanescentes florestais. A borda dos fragmentos pode diferir em estrutura de habitat ou em condições ambientais (e.g., microclima) em relação ao núcleo desses fragmentos, resultando em variação na composição de espécies e/ou no número de indivíduos (i.e., abundância), também conhecido como efeito de borda (Murcia, 1995; Harper et al., 2005; Filgueiras et al., 2016). A composição da matriz é outro fator importante. Apesar dos estudos de fragmentação de habitats serem baseados na teoria de biogeografia de ilhas que considera que a matriz é inóspita e homogênea, os tipos de matriz se apresentam como diferentes ambientes que podem variar no grau de hostilidade para as espécies, podendo ou não ser um novo tipo de habitat para as mesmas (Haila, 2002; Kupfer et al., 2006). Desse modo, os distintos elementos que compõem a paisagem podem influenciar os padrões de co-ocorrência de espécies em comunidades ecológicas.

Além disso, os diferentes tipos de matriz e a configuração espacial do habitat podem influenciar a movimentação das espécies e ser determinantes para reorganizar a diversidade em paisagens fragmentadas (Taylor et al., 1993; Fahrig, 2007). Matrizes que apresentam maior similaridade aos habitats nativos das espécies tendem a ser mais amigáveis, sendo mais permeáveis para a movimentação das espécies entre manchas de habitat, enquanto as matrizes com alto contraste em relação aos habitats naturais, tendem a ser mais hostis ou impermeáveis para as espécies (Laurance, 2008; Prevedello & Vieira, 2010). Por outro lado, a distância entre os fragmentos de habitat, por exemplo, pode influenciar a movimentação das espécies entre fragmentos (Thomas et al., 2001; Goodwin & Fahrig, 2002). Espécies com maior habilidade de dispersão podem alcançar e se beneficiar do uso de recursos em outros remanescentes, enquanto as espécies com mobilidade reduzida podem não conseguir e sofrer o efeito do isolamento de suas populações (Ricketts, 2001; Fahrig, 2007). A configuração espacial do habitat e a tolerância das espécies aos tipos de matriz são, portanto, fatores que podem moderar a distribuição das espécies nas paisagens, modificando os padrões de composição de espécies e abundância em comunidades locais (Villard & Metzger, 2014). Assim, tanto os elementos que compõem a paisagem como a configuração espacial deles (i.e., a estrutura da paisagem) poderiam atuar como filtros ambientais, selecionando distintamente a forma como as espécies de um pool regional se distribuem em comunidades locais, processo também conhecido como (des) montagem de comunidades (Tscharntke, Tylianakis, et al., 2012; Duflot et al., 2014; Negoita et al., 2016).

A montagem de comunidades usualmente acontece em múltiplas escalas espaciais, podendo ser influenciada também por processos em escala local (i.e., nos arredores das unidades amostrais) (Ricklefs, 2004). Processos dependentes de densidade (e.g., mecanismos de coexistência de espécies e interações ecológicas) podem definir os padrões de co-ocorrência de espécies observados numa localidade, assim como a dispersão também pode definir padrões de distribuição de espécies (Fukami, 2010; HilleRisLambers et al., 2012). Sendo assim, a dispersão, os processos locais e aqueles que ocorrem no nível da paisagem podem atuar em conjunto ou com predominância de algum deles na organização de comunidades ecológicas. Ao identificar a contribuição de cada escala espacial é possível compreender de forma mais assertiva quais processos atuam sobre o sistema de estudo (Levin, 1992; Chave 2013), o que pode ajudar a definir a escala espacial na qual os esforços de conservação devem ser direcionados.

A abordagem que integra diferentes componentes da diversidade tem sido eficiente para esclarecer os fatores envolvidos na (des) organização de comunidades ecológicas em múltiplas escalas espaciais (Webb et al., 2002; Weiher et al., 2011; Mouquet et al., 2012; Rader et al., 2014). Além da diversidade de espécies, a conversão dos habitats naturais pode afetar outros aspectos da diversidade, como o filogenético e o funcional. A diversidade filogenética permite acessar a história evolutiva compartilhada pelas espécies (Faith, 1992), enquanto a diversidade funcional representa a diversidade de características que influenciam o papel das espécies no funcionamento e resiliência dos ecossistemas (Petchey & Gaston, 2006). Para acessar as consequências das mudanças de habitat para as linhagens e suas relações de parentesco e para o funcionamento de ecossistemas é necessário incorporar as estimativas de diversidade filogenética e funcional (Flynn et al., 2009; Frishkoff et al., 2014; Cisneros et al., 2015). De fato, são esses componentes que permitem detectar a ocorrência de filtros ambientais (i.e., perda não aleatória de espécies), sinalizando se as espécies perdidas são evolutivamente próximas e/ou ecologicamente semelhantes (Webb, 2000; Webb et al., 2002). Cabe ressaltar ainda que se espécies funcionalmente redundantes forem perdidas, essa perda pode não ter efeitos no funcionamento do ecossistema (Naeem, 1998; Yachi & Loreau, 2002). Ao contrário, se espécies com características únicas são perdidas pode haver perda de resiliência e funcionamento ecossistêmico (Fonseca & Ganade, 2001). Portanto, os efeitos das mudanças dos habitats das espécies podem ser melhor compreendidos quando avaliados por diferentes aspectos da diversidade.

Os efeitos da conversão de habitats sobre a diversidade de serpentes ainda são pouco conhecidos (Gardner et al., 2007; Doherty et al., 2020), sobretudo em relação aos processos que atuam no nível da paisagem. No geral, são mais estudados os efeitos sobre cada espécie, investigando como ela se move e/ou seleciona habitats em paisagem fragmentada (Carfagno & Weatherhead, 2006; Wisler et al., 2008; DiLeo et al., 2010; Miller et al., 2012; Nordberg et al., 2021). Quando os efeitos são estudados sobre as taxocenoses de serpentes, o delineamento mais frequentemente utilizado é o da perspectiva do fragmento. Essa perspectiva avalia os parâmetros de diversidade em relação às características do fragmento estudado, como tamanho, tipo ou qualidade do habitat (McGarigal & Cushman, 2002). Estudos desse tipo realizados com taxocenoses de serpentes demonstraram redução da diversidade de espécies na matriz quando comparada ao fragmento de vegetação nativa (Mott et al., 2010; Kurz et al., 2014) ou quando relacionada ao tamanho do fragmento, encontrando menor diversidade no fragmento de menor tamanho, como esperado pela relação espécie-área (Kjoss & Litvaitis, 2001). No entanto, as serpentes exploram recursos em diferentes microhabitats do ambiente nativo (Marques, 1998; Martins & Oliveira, 1998) e é provável que elas se movimentem pela paisagem para usar recursos em diferentes remanescentes de habitat ou mesmo da matriz. Para considerar tanto os efeitos dos diferentes tipos de ambientes que as serpentes podem usar, como os efeitos da movimentação das espécies por esses ambientes é necessário adotar a perspectiva da paisagem (i.e., as variáveis preditoras são associadas a características da paisagem, como proporção de habitat nativo e de matriz, número de fragmentos de habitat, área da borda dos fragmentos, dentre outros) ao invés da perspectiva do fragmento (McGarigal & Cushman, 2002; Arroyo-Rodríguez & Fahrig, 2014). Essa mudança de perspectiva pode ajudar a compreender com maior precisão como os processos da paisagem afetam a diversidade de serpentes e, consequentemente, delinear estratégias que auxiliem na conservação de espécies e na manutenção do funcionamento ecossistêmico em paisagens fragmentadas.

O objetivo geral desta tese é entender os efeitos da conversão de habitats sobre a diversidade de espécies, funcional e filogenética de serpentes, considerando tanto a influência da escala local como a do nível da paisagem. Para isso, coletamos dados de comunidades de serpentes em uma área fragmentada de Mata Atlântica composta por matrizes mistas (silvicultura e pasto). No primeiro capítulo, testamos se processos nas distintas escalas espaciais atuam sobre os distintos componentes da diversidade de serpentes, identificando quais os fatores envolvidos, e testamos se as matrizes atuam como filtros ambientais para as serpentes. Posteriormente, no segundo capítulo, testamos como a paisagem seleciona distintamente as espécies de serpentes por seus traços e quais são os traços selecionados, bem como as implicações dessa seleção para o funcionamento e a resiliência daqueles ecossistemas.

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2. MULTI-SCALE EFFECTS OF HABITAT CHANGES ON DIVERSITY OF RAIN FOREST SNAKES

Gabriella Leal-Santos, Leandro Riverberi Tambosi, Sandrine Pavoine, Marcio Martins

Abstract

Native habitat conversion into anthropic land uses is the main threat to biodiversity and can affect it at different spatial scales. However, habitat changes effects on snake diversity are largely unknown. Here, we used a multi-model inference approach to evaluate the effects of local and landscape composition (percentage of forest cover, silviculture and pasture) and habitat fragmentation (number of forest patches and total edge) on species, functional and phylogenetic diversity of snake communities in tropical fragmented landscapes. Also, we tested if anthropic land uses acted as environmental filters for snakes. Species and functional diversity mainly responded to the landscape elements: species richness, abundance, and functional diversity decreased with deforestation. In addition, species richness and abundance increased with the proportion of forest and the number of patches in the landscape. In contrast, phylogenetic diversity was mostly driven by the local habitat composition and richness-free phylogenetic diversity increased not only with the proportion of forest but also with the proportion of silviculture. Although habitat types did not filter entire clades and functional groups, each species tended to have a cooccuring species with similar traits (at landscape level) and a close relative (at both levels) in impacted habitats while, in contrast, the coocurrence of close relatives and functionally similar species was avoided in the native forest. Our findings indicate that snake responses to habitat changes occur at multiple scales and highlight the importance of conserving native forest to maintain multiple components of biodiversity. Strategies for conserving snake diversity in tropical fragmented landscapes should thus consider management practices at both local and landscape scales.

Keywords: Snakes; Landscape ecology; Fragmented landscapes; Snake conservation, Species, functional and phylogenetic diversity; Atlantic Forest; Spatial scales

2.1. Introduction

The increasing anthropic pressure over tropical forests has converted continuous areas of habitat in mosaics where forest remnants are interspersed with anthropic land uses (e.g., exotic forest plantations, farmlands), being named human-modified tropical landscapes (HMTL) (Laurance et al., 2014). The set of human-modified areas in a landscape is hereafter referred to as matrix. The forest remnants and the matrices thus from the HMTL. Species response to anthropic land use may rely on both landscape composition (i.e., proportion of forest and land use types) and habitat fragmentation. Landscapes with greater amount of native habitat usually provide more resources for species, supporting high diversity (Watling et al., 2020). Fragmentation tends to reduce habitat and resource availability for species that cannot move within the matrix, but it can benefit habitat generalist species, leading to distinct effects on populations size and species persistence in these mosaics (Fahrig, 2003; Hodgson et al., 2011; Hanski, 2015; Jambhekar & Isvaran, 2022). However, local patterns of biodiversity are frequently shaped by multi-scale spatial processes and local-scale changes of species habitat also affect biodiversity (Avila-Cabadilla et al., 2012). Therefore, local diversity in such HMTLs can be a cumulative outcome of the effects of local-scale and landscape-level factors.

Beyond species diversity (SD), measures of diversity now consider the total amount of evolutionary history belonging to a set of taxa (i.e., phylogenetic diversity, PD; Faith, 1992) along with the diversity of ecological traits that represent the species roles in an ecosystem (i.e., functional diversity, FD; Tilman, 2001). FD provides a mechanistic link between species ecological traits and ecosystem functioning (Díaz & Cabido, 2001), while PD represents the long-term evolutionary potential of a taxon to respond to environmental changes (Faith, 1992). These components can be affected by land use changes beyond changes in SD alone (Flynn et al., 2009; Uchida et al., 2019). Altogether, phylogenetic and functional diversities allow identifying whether a matrix acts as an environmental filter by selecting species ecologically similar and/or evolutionarily close (Frishkoff et al., 2014; Rader et al., 2014). A multifaceted approach of diversity thus contributes to elucidate how anthropogenic activities can drive ecological and evolutionary processes in such land mosaics.

Effects of native habitat conversion into anthropic land uses are well documented for several endothermic terrestrial vertebrates (Pardini, 2004; Banks-Leite et al., 2014; Carrara et al., 2015), but studies investigating its effects on snakes are still rare (e.g., Kjoss & Litvaitis, 2001). Part of this scarcity of studies can be attributed to the fact that snakes often present cryptic habits (Boback et al., 2020), without any behavior that facilitates their finding in nature, such as vocalization or breeding aggregation (except for few species) (Gibbons et al., 2000). Additionally, their populations tend to present small densities (Parker & Plummer, 1987; Dorcas & Wilson, 2009). Because these characteristics make sampling difficult, it is understandable that snakes are less studied than birds and mammals (Doherty et al., 2020) or that they are considered in a more inclusive group, such as reptiles or herpetofauna, in studies focused on understanding the consequences of habitat changes (Greenberg et al., 1994; Kurz et al., 2014; McAlpine et al., 2015). Nonetheless, as habitat is a species-specific attribute, the species response to habitat changes tends to be different among snake species (Wiens et al., 2002) and between them and other ectothermic species. Thus, such inclusive groupings may generate misleading implications for conservation (Gibbons et al., 2000).

Conversion of native habitats into disturbed habitats may affect snakes for different reasons. Snake assemblages are strongly structured by the type of vegetation cover, presenting clearly distinct diversity patterns between forest and non-forest areas along latitudinal gradients (Cavalheri et al., 2015). At the local scale, vertically heterogeneous habitats are required by arboreal and semi-arboreal snakes, while horizontal habitat heterogeneity offers a diverse set of microhabitats used by terrestrial, fossorial and cryptozoic species (Marques, 1998; Martins & Oliveira, 1998). Nevertheless, matrices often present a simplified and homogeneous habitat structure (Foley et al., 2005) and may not meet the habitat requirements of many snake species. Also, microclimatic conditions in matrices tend to differ from natural habitat conditions influencing species sorting in land mosaics (Hanski, 2011; Hodgson et al., 2011; Williams & Newbold, 2020). For instance, high temperatures in altered habitats could favor only warm-adapted reptile species (Frishkoff et al., 2015). Lastly, prey types found in matrices may not meet the requirements of diet specialists (Ryall & Fahrig, 2006) and exposure to predators can vary among distinct matrix types (Mönkkönen et al., 2007; DeCesare et al., 2014), which can directly affect snake interactions with other species and their persistence in matrices. Nonetheless, matrix environments are not completely inhospitable to species and the degree of permeability and the use of resources in such environments are species-specific (Perfecto & Vandermeer, 2008).

Here we assessed the effects of habitat changes on snake diversity at local and landscape scales in a fragmented area of Atlantic Forest, which matrix is composed predominantly by silviculture (monocultures of exotic *Eucalyptus* sp. and *Pinus* sp.), followed by cattle pasture. The Atlantic Forest is a megadiverse biome (Joly et al., 2014) that harbors a high diversity of snakes, with approximately 30% of the snake species that occur in Brazil, most of them endemic to this biome (Barbo et al., 2021). Part of this diversity is found in unprotected areas with increasing anthropic activities. It is thus important to identify which factors threaten and which, inversely, contribute to the maintenance of rain forest snakes in fragmented landscapes (Ribeiro et al., 2011). For this, we determined the relative effects of local and landscape composition (i.e., percentage of forest cover and matrix composition) and habitat fragmentation (i.e., number of forest patches and the total length of forest edges) on species, functional and phylogenetic diversity of snakes. We identified at which spatial scale habitat changes most affect each component of diversity. Additionally, we tested whether silviculture and pasture act as environmental filters for rain forest snakes, therefore negatively affecting snake diversity.

2.2. Material and Methods

2.2.1. Study area

This study was conducted in Monte Verde, southern Minas Gerais state in Brazil (Fig. 1). The region is mountainous, with altitudes ranging between 1.250 m and 1.600 m above sea level and has a subtropical climate with two well-defined seasons: warm and wet from October to March and cold and dry from April to September (Meireles et al., 2014). The study area was once continuously covered by Atlantic Forest, a highly diverse and endangered tropical forest (Myers et al., 2000; Joly et al., 2014). However, nowadays it is an agroforestry mosaic with mixed high-montane rain forest interspersed predominantly with silviculture (*Eucalyptus* sp. and *Pinus* sp.), but also with pastures and a few human settlements. The mature forest is the native vegetation with the largest cover consisting of tall trees up to 20 m high at the canopy, harboring a well-structured understory, with eventual emergent individuals of *Araucaria angustifolia*, and a shrub-herbaceous stratum (Meireles et al., 2014).

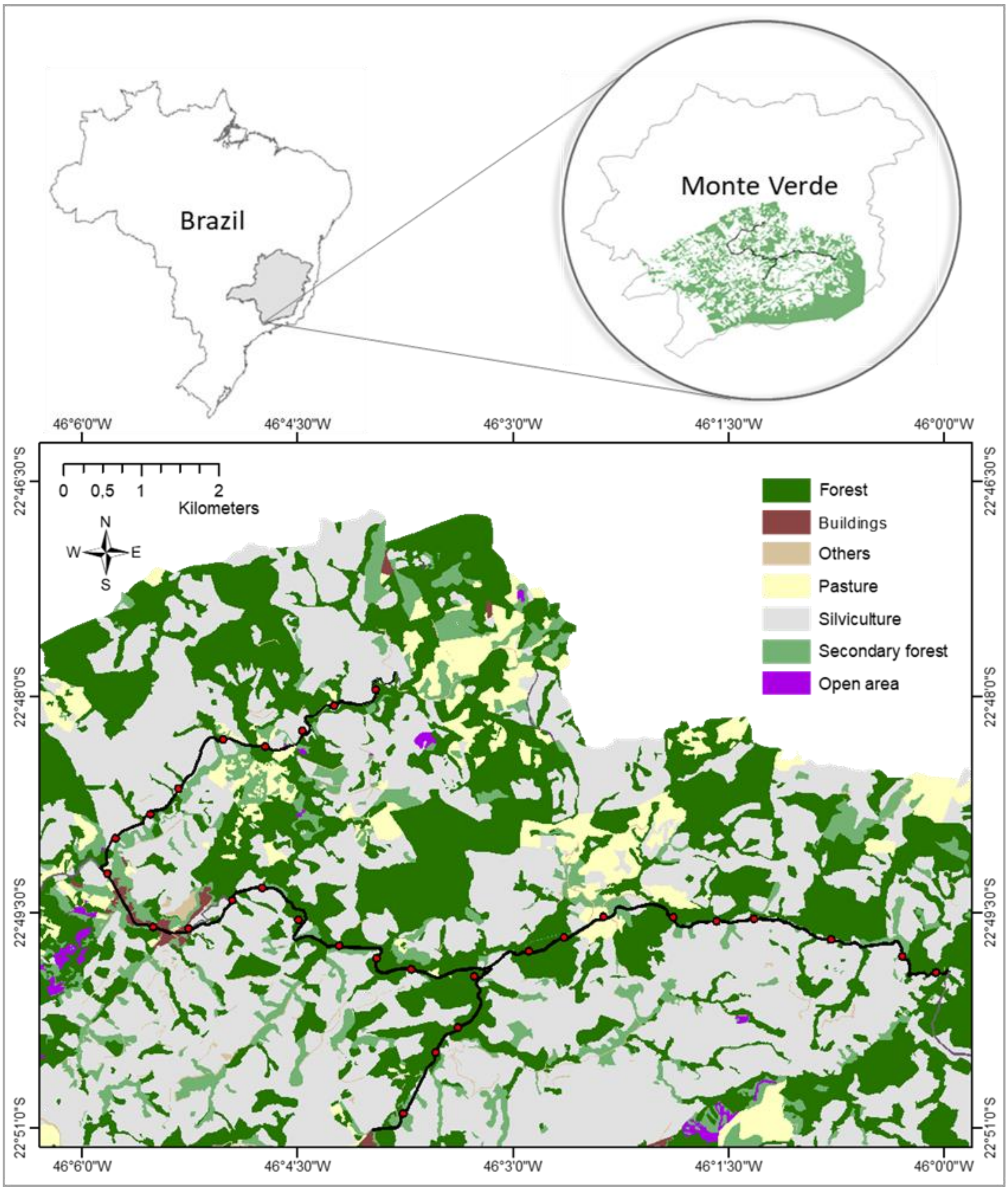

Figure 1. Location of Monte Verde district in Minas Gerais state (gray area in Brazil) and land cover of the study area. The black line represents the sampling road and the red points indicate the center of landscapes used to analyze local communities.

2.2.2. Snake data

Snake samplings were carried out from January to March, and from October to December of 2019 and 2020, excluding March of 2020. The main sampling method was time constrained search by car (TCSC, Fitch, 1987), performed for 8 hours and 30 minutes per day during 10-11 days per month, totaling 935 hours of sampling by car. In order to increase the number of individuals captured, we intensified the sampling effort in each site (Dorcas &

Wilson, 2009). To do this, in each sampling day, the TCSC was done in the same unpaved and low traffic road, (approximately 22 km long) travelled slowly by car (20-30 km/h) (Sawaya et al., 2008) at least twice in the morning and at night of each sampling day, in a way that each road segment was sampled on average 60 times per month. The sampling effort in this method was standardized and it represents the total number of hours spent at each segment of road, which includes the average number of times that each segment was travelled. Because of the high effort spent to find an individual snake (approximately 9 h), we also gathered observations made by local citizens in the same road during the months of sampling period, who provided either specimens or photographs. Regardless of the sampling method used, geographical coordinates were collected for each individual snake found, and the taxonomic identification was confirmed at the herpetological collection of Butantan Institute. Snakes were collected in compliance with Brazilian environmental regulations under the Sisbio license 59947-1, issued by the Chico Mendes Institute for Biodiversity (ICMBio).

Snake functional traits were selected based on previous knowledge of their ecology and natural history (Gibbons & Semlitsch, 1987; Mushinsky, 1987; Greene, 1997; Shine & Wall, 2007). They are related to their ecological functions in the ecosystem and also indicate how they may be affected by habitat changes (i.e., effect and response traits; Violle et al., 2007). The functional traits used were: diet, body size, daily activity, microhabitat use, habitat use, foraging mode and reproductive mode. These traits are linked to snake trophic web position and individual fitness. Each trait measurement was taken from each individual collected. Diet information was gathered mainly by dissection of the snake's gut, being complemented with literature data. Detailed information about snake functional traits is provided in the appendix A. Phylogenetic information was obtained from the most recently published phylogeny (Zaher et al., 2019), which was pruned to obtain a phylogenetic tree including only species from the local communities.

2.2.3. Landscape and local scales

In order to find the spatial scale in which the landscape elements has the strongest effect on snake communities, the so-called scale of effect (Jackson & Fahrig, 2012), we measured the amount of forest within multiple buffers surrounding a focal site (Brennan et al., 2002). The use of space by each species was used as a proxy to delineate possible landscape spatial scales (Jackson & Fahrig, 2015). For this, we considered two aspects of species dispersal abilities, body size and mobility, because some snake species may have large bodies, but are sedentary (Doherty & Driscoll, 2018; Todd & Nowakowski, 2021). We thus built circular buffers around ten focal sites with 600 m, 1000 m and 1400 m in diameter. Only ten sites were chosen to ensure they are distant enough from each other, avoiding overlapping landscapes and spatial dependence (Fig.S1, appendix B). We analyzed data using a Generalized Linear Model (GLM) with Poisson distribution to verify at which scale the ecological response (i.e. species richness and abundance) is best predicted by the total amount of habitat in the landscape (Zuur et al., 2009a). The scale with the lowest Akaike's information criterion corrected for small samples (AICc) was 600 m, hereafter referred to as landscape scale. As for the local scale, we considered 50 m radius around each local community (see below).

2.2.4. Study design

The entire road used for snake sampling (Fig. 1) was analyzed at local and landscape scales, but in order to measure environmental and biodiversity variables, the road was subdivided into focal landscapes. To do so, we worked with hexagonal grid cells with radius length similar to the landscape radius previously tested (i.e., 300 m). The segments of road inside a grid cell constitute a sampling unit. The center of each sampling unit was used as a reference point to build circular buffers that represent focal landscape, from where landscape variables were measured. Meanwhile, 50 m buffers were built from either side of the segments of the roads to measure local variables (Fig. S2, appendix B). We used data from 30 sampling units for species diversity analysis (Fig. S3, appendix B) and 22 sampling units for the functional and phylogenetic components of diversity since we removed landscape with less than 2 species (details for sampling size differences are shown in "Species, phylogenetic and functional diversity" section).

2.2.5. Landcover and predictor variables

We mapped the landcover at the study area using satellite images of 1 m resolution and available images at Google Earth, and this mapping was subsequently validated in the field. In this high-resolution map, local and landscape compositions of land use and land cover were calculated as the percentage of native forest (mature, secondary and in initial state), silviculture (plantations of exotic *Eucalyptus* sp. and *Pinus* sp.) and pasture. These three classes cover more than 85 % of the studied landscapes. Landscape fragmentation was measured by number of patches and total edge of native forest. Both local and landscape variables analyzed present a wide range of predictor variables (Table S1, appendix B). To increase the chance to detect an effect of the predictor variables and to avoid a biased selection of factors that may have the strongest influence on biodiversity parameters (Eigenbrod et al., 2011; Pasher et al., 2013), we discarded variables with small variation (e.g., buildings and open area) along the road. Local and landscape measures were calculated using the software ArcGIS (version 10.7) and FRAGSTATS (version 4.2).

2.2.6. Species, phylogenetic and functional diversity

Species diversity was described by species richness and abundance in each sampling unity. Detection probabilities of species at each site were estimated and low detection probabilities were found across the sampling units (< 0.2; Table S2, appendix B). As the absence of species may also occur due to anthropogenic activities, we chose to keep local communities even with no individuals found (n = 3). We used two complementary metrics to describe the phylogenetic structure of local communities (Mazel et al., 2016). Phylogenetic diversity (PD) was measured using Faith's index (Faith, 1992) that represents the total amount of evolutionary history in the assemblage. It can be seen as the richness in "independent evolutionary history" (Nee & May, 1997) or as the richness in "evolutionary units" (Pavoine, 2016) observed in the assemblage. The phylogenetic patterns of relatedness were measured by the mean pairwise phylogenetic distance (MPD) between the species in the assemblage (Webb, 2000; Webb et al., 2002). Contrary to PD, MPD does not express a richness but the divergence between the species. While PD always increases by adding a species to an assemblage, MDP may decrease if the added species is a close relative to one or several species in the assemblage. PD and MPD thus express distinct aspects of the diversity in the phylogenetic characteristics of an assemblage.

Four species in the study area are not present in the phylogenetic tree used here (Zaher et al., 2019), and to include them in our analysis, we ran simulations to consider different placements for each species at the base node of their genera. To do so, we used SUNPLIN (https://bioinfo.inf.ufg.br/sunplin/) to generate 1000 phylogenetic trees including these species in distinct positions or with different branch lengths (Figure S4, appendix B). Then, we calculated PD and MPD for each tree. The mean value of these metrics allowed us to work with the phylogenetic uncertainty of these insertions and their values were used in the statistical analysis.

The functional diversity (FD) measurements used here are similar to those of the phylogenetic metrics, but they are based on functional dendrograms. We used Petchey's index (Petchey & Gaston, 2002) to measure FD and the equivalent of MPD to quantify functional relatedness among species (FMPD). As the selected functional traits are variables that present different statistical nature (e.g. categorical, quantitative, proportional), we built the functional dendrogram based on a distance matrix of the Gower's index extended to deal with these types of variables, as proposed by Pavoine and collaborators (2009), and we used UPGMA as clustering algorithm.

Functional and phylogenetic measurements were correlated with species richness confirmed by Pearson correlation test and, in order to remove this confounding effect, we used null models (Gotelli & Graves, 1996). We built null communities by fixing species richness and abundance in each assemblage while randomizing species composition. These null models created new values for PD and FD. This procedure was repeated 999 times, providing a null distribution. For the phylogenetic metrics, we repeated this process for each of the 1000 trees, generated by SUNPLIN. Afterwards, we standardized these metrics by calculating an effect size (ES_PD and ES_FD) which indicates the number of standard deviations an observation is from the mean of the null distribution (Gotelli & McCabe, 2002). The same approach was used with MPD measures (ES_MPD and ES_FMPD) which are appropriate to detect patterns of phylogenetic or functional convergence/divergence different from a null scenario. Therefore, it allows to identify environmental filter occurrence (i.e., functional/phylogenetic clustering; Webb et al., 2002). As the standardized effect sizes (SES) for phylogenetic and functional variables did not follow normal distribution, we used probit-transformed p values as effect sizes (ES; Botta-Dukát, 2018) because using SES (Gotelli & McCabe, 2002) for these variables would cause misleading results (Botta-Dukát, 2018). Positive and negative values of ES indicates whether the amount of diversity (PD or FD) is above or below their expected value given the species richness of a community in a scenario where the species composition of assemblages is random. In complement, all effect sizes of PD, FD, MPD or FMPD indicate overdispersion when they are positive, and clustering when they are negative (Botta-Dukát, 2018). However, ES_PD and ES_FD indicate terminal overdispersion or clustering (Mazel et al., 2016): the fact for a species in a community to miss (overdispersion) or have (clustering) a closely related (for ES_PD) or functionally-similar (for ES_FD) co-occurring species. In contrast, ES_MPD and ES_FMPD indicate basal overdispersion or clustering (Mazel et al., 2016): the co-occurrence (for overdispersion) or the absence (for clustering) in the community of a variety of large lineages (for ES_MPD) or functional groups (for ES_FMPD) present in the region. Communities with no individuals or only one are meaningless for effect size measures. We thus considered only those with at least two species (n=22) for ES analyses. We checked that ES values of each metric were not correlated with species richness using Pearson correlation tests.

2.2.7. Statistical analysis

In order to explore how land use and land cover affect diversity at local and landscape scales we used a model selection approach, considering each scale separately. GLMs with negative binomial distribution were used to analyze species richness and abundance. We used Linear Models (LM) to analyze functional and phylogenetic metrics (i.e., PD, FD, ES_PD, ES_FD, ES_MPD and ES_FMPD) since they present normal distribution confirmed by Shapiro-Wilk test.

To avoid collinearity problems between the predictor variables in multivariate models, we estimated variance inflation factor (VIF). In general, VIF $\geq$ 4,0 indicates possible collinearity (Kutner et al., 2005) and variables with such values were not included together in the same model. Instead, these variables were included in different models (see Table S3, appendix B) which were subsequently compared. This procedure allowed testing all the predictor variables.

We used a multi-model inference approach to identify the model with the most empirical support (Burnham & Anderson, 2002). The models were ranked from the best to the worst based on the AICc. The set of models with ΔAICc $\leq$ 2 compared with the best model, were considered to have equivalently strong empirical support and similar plausibility (Burnham & Anderson, 2002). The residuals of each selected model were checked for normality, homoscedasticity, independence and overdispersion. Only the models that met those criteria were considered in the results. Deviance and R^2 were used to estimate the variation explained by the selected GLMs and LMs, respectively (Zuur et al., 2009a). To test whether landscape or local scale has the strongest influence on diversity components, the selected models for each response variable were compared between scales using the AICc selection procedure. The variation in the standardized sampling effort and in the data collected by citizens could influence the number of individuals found along the road (Gardner et al., 2007), then they were incorporated into the models as covariates.

Considering the proximity between the sampling units and the overlapping landscapes (maximum overlap was 27%) in our study design, we checked for spatial dependence of the residuals in each model (i.e., from the full model to the selected one) for each response variable using a variogram. Spatial dependence was detected in the selected models for species richness and abundance. In order to deal with spatial dependence, we built generalized least squares models (GLS) composed of the selected variables and different types of spatial correlation structure (e.g., exponential, Gaussian, linear, rational, spherical. (Zuur et al., 2009b) in each model. Since abundance variable did not follow normal distribution, generalized estimation equations (GEE) were used in a way similar to that described for GLS, in order to include a dependence structure in abundance models (Zuur et al., 2009a). Additionally, we also used null models to test the presence of spatial correlation and overdispersion of the residuals in the selected GLMs using the DHARMa package. All analysis were conducted in R 4.1.1 (R Core Team, 2020) and R packages used are listed in the appendix B.

2.3. Results

2.3.1. Land-use effects on species, phylogenetic and functional diversity

Our analyses showed that the variation in species richness and abundance of snakes along the road was best explained by both the amount of native forest and the number of forest patches at the landscape scale, being both positively related to diversity (Fig. 2; Table S4, appendix B). Similarly, at the local scale, native forest was positively related to species diversity, while silviculture presented a negative effect (Fig. S5; Table S4, appendix B). However, in the comparison of spatial scales only the landscape models were selected (Table 1).

Table 1. Best models for landscape and local scale used in the spatial scale comparison. ΔAICc values ≤ 2 indicate the spatial scales with the strongest effect on diversity components.

	Spatial Scale	Selected model	ΔAICc	(a) Deviance	(a) R^2
Species diversity	**Landscape**	**Richness ~ Native forest + (b) NP**	**0**	46.40826	-
	Local	Richness ~ Native forest	6,8	28.26815	-
	Landscape	**Abundance ~ Native forest + NP**	**0**	45.91019	-
	Local	Abundance ~ Native forest	6,7	19.1126	-
PD	**Local**	**(c) ES_PD ~ Native forest + Silviculture**	**0**	-	0.5327
	Landscape	ES_PD ~ Native forest	6,9	-	0.207
	Local	(d) ES_MPD ~ Null	0	-	0
	Landscape	ES_MPD ~ Null	0	-	0
FD	**Landscape**	**(c) ES_FD ~ Native forest**	**0**	-	0.1882
	Local	ES_FD ~ Null	2,9	-	0
	Local	(d) ES_FMPD ~ Null	0	-	0
	Landscape	ES_FMPD ~ Null	0	-	0

(a) Deviance values are presented for GLMs and R^2 values for LMs.
(b) NP = number of forest patches.
(c) ES_PD or ES_FD = effect size of phylogenetic or functional diversities.
(d) ES_MPD or ES_FMPD = effect size of phylogenetic or functional mean pairwise distance.

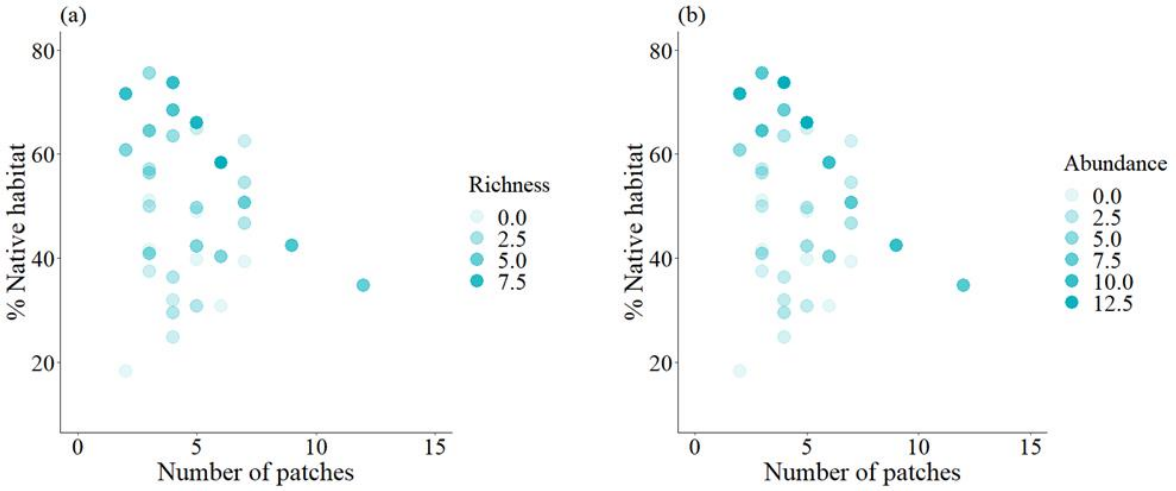

Figure 2. Relationship between selected predictor variables at the landscape scale and predicted values of snake species richness (a) and abundance (b) of local communities. Legend indicates that light colors represent the lower predicted values, while dark colors represent the higher values of each response variable.

Snake standardized phylogenetic diversity (ES_PD) was mainly driven by the total amount of native habitat and of silviculture at the local scale (Fig. 3a; Table S4, appendix B), which was the scale with the strongest effect on ES_PD (Table 1), while the total amount of native habitat was the selected landscape predictor (Fig. S6; Table S4, appendix B). In both cases, ES_PD increased from negative (terminal phylogenetic clustering) to positive (terminal phylogenetic overdispersion) with the amount of native habitat. However, patterns of basal phylogenetic clustering or overdispersion were not detected as MPD distribution in our case study was not different, at both spatial scales, from the null model (ES_MPD tending to zero value; Table S4, appendix B).

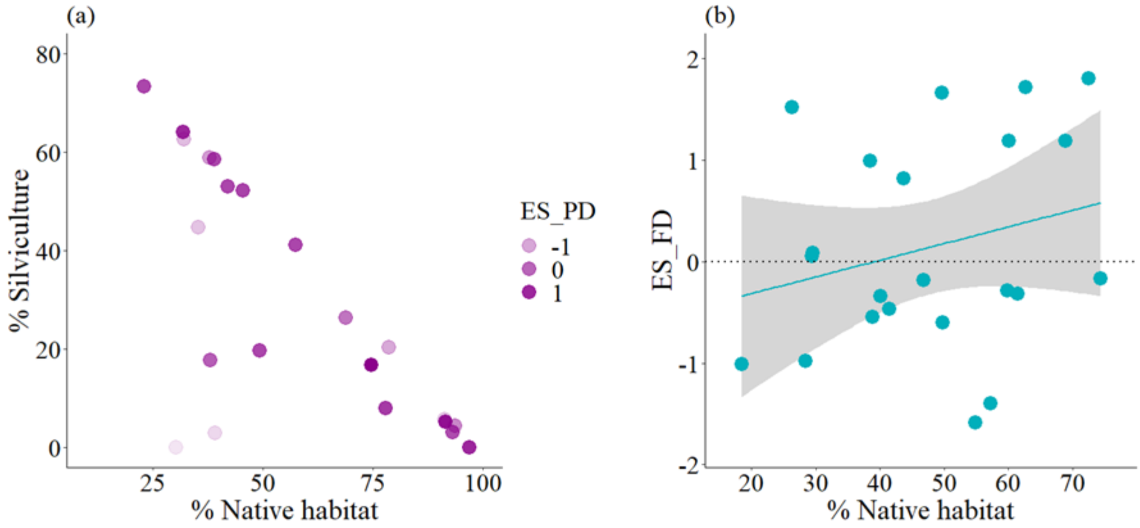

Figure 3. Relationship between selected predictor variables and predicted effect sizes values of phylogenetic diversity (ES_PD) at the local scale (a) and of functional diversity (ES_FD) at the landscape scale (b). Predicted values of ES_PD in (a) are represented by light color for negative values, intermediate color for values equal or close to zero and dark color for positive values. Note the positive ES_PD values in areas with high percentages of silviculture and native habitat (a).

The amount of native forest at the landscape scale was the only identified factor influencing (increasing) the snake functional diversity expected given the species richness of a community (ES_FD) in this land mosaic (Fig. 3b; Table S4, appendix B). ES_FD increased from negative (terminal functional clustering) to positive (terminal functional overdispersion) with the amount of native habitat. However, compared to ES_PD, it did so at the landscape level only. Similarly to phylogenetic components, no patterns of basal functional clustering or overdispersion were detected at both spatial scales (Table 1; Table S4, appendix B).

2.4. Discussion

In this study, different effects of habitat changes were observed on snake diversity, depending on the component of diversity considered and on the spatial scale. Overall, the patterns we observed (Mazel et al., 2016) revealed that a decrease in forest cover led to species richness and abundance decline and to a decline of functional and phylogenetic diversity both via species loss and an increase of functional and phylogenetic redundancy (low minimum functional distance between a species and its co-occurring species and low phylogenetic distance between a species and its closest relative). However, they also revealed that these trends depended on the spatial scale considered (local versus landscape level) and that the impact of silviculture is actually more complex on phylogenetic diversity than on the other components of diversity (species richness, abundance and functional diversity). First, the measured elements of landscape composition and fragmentation drove species diversity, with the amount of native forest and the number of forest patches positively influencing species richness and abundance. Second, the main effects on phylogenetic diversity were observed at the local scale, with ES_PD increasing with larger forest area, and also, contrary to our expectations, increasing with silviculture. Lastly, only landscape scale had effects on functional diversity, with the amount of native forest increasing ES_FD. When taken together, these results suggest that snake response to habitat changes in HMTLs occurs at multiple spatial scales.

Snake response to anthropogenic changes in their habitats was found to rely mostly on the total amount of native habitat and the number of forest patches, with larger areas of native habitat harboring more individuals and species even when the number of patches increased. The positive effect of the latter suggests that habitat fragmentation in the landscape may have contributed to mitigate the expected negative effects of habitat loss (Villard & Metzger, 2014). An increase in number of habitat patches can reduce isolation among them, may facilitate biological fluxes (Fahrig, 2013; Watling et al., 2020) and can act as refuge sites during silviculture harvest periods. Indeed, the remaining forest cover is relatively large in the studied landscapes (some reach up to 40% of forest cover) and this may favor individual inter-patch movements, making landscapes functionally connected and contributing to maintain those populations (Wiens et al., 2002; Ewers & Didham, 2006; Villard & Metzger, 2014). Besides, the increase in forest patches can provide different microhabitat types for species (Fahrig, 2013), thus favoring snake diversity.

The movement of species with high dispersal capacity and unique functional traits may explain the increase in the observed functional diversity at the landscape level (Figure S7, SM-

2) and similarly in the standardized FD (ES_FD). We found that FD increased when the total amount of native habitat was high, as expected, showing the importance of large native areas for the maintenance of species with different ecological strategies. Although fragmentation has not affected ES_FD, its positive effects on snake species diversity suggests that the movements of generalist species among habitat patches can influence the snake traits distribution across the landscape. Such inter-patch movements may change the dominance of traits in communities (Leal et al., 2012; Magnago et al., 2014) and alter ecosystem functioning in land cover mosaics (Morris, 2010), even when habitat fragmentation does not influence functional richness (Magnago et al., 2014; Suárez-Castro et al., 2020). But understanding how fragmentation modulates snake traits distribution across landscapes still remains a knowledge gap.

Regarding patterns of species relatedness (MPD), neither basal clustering nor overdispersion was observed for functional and phylogenetic components, being both better explained by a random pattern. This finding suggests that random species dispersion among local communities was more relevant to explain the presence of large lineages and functional groups than the effects of land cover composition and fragmentation. Elements that influence species permeability in fragmented landscapes, such as habitat and matrix configuration (Perfecto & Vandermeer, 2008; Bauder et al., 2020), may thus have an important role to explain snake diversity patterns in these landscapes (Villard & Metzger, 2014).

In contrast, functional-link and phylogenetic-relatedness trees revealed switch from terminal clustering to overdispersion for functional and phylogenetic components as a function of forest cover. When removing the effect of species diversity on PD, we found positive effects of forest cover and silviculture at the local scale, which was the most relevant scale to explain patterns of ES_PD. Positive effects of forest amount on PD were expected because larger areas of habitat support more species (Connor & McCoy, 2015) and PD tends to increase with an increasing number of species from different genera (Rodrigues & Gaston, 2002). Indeed, observed PD increased as the amount of forest increased (Figure S8, SM-2). The fact that it similarly influenced ES_PD shows that the increase in phylogenetic diversity with forest amount is not solely due to an increase in species richness. Contrary to our expectations, silviculture also showed positive effects on ES_PD when associated with native habitats, suggesting that the generalist snakes that use silviculture have distant relatedness (e.g., *Atractus zebrinus*, *Bothrops jararaca* and *Mussurana quimi*). Furthermore, the fact that ES_PD is more structured at the local level than at the landscape level may be related to the low dispersal ability of some habitat specialists (e.g., *Taeniophallus affinis* and *Thamnodynastes nattereri*) belonging to distinct lineages.

Altogether our results showed that anthropic land uses can distinctly affect the components of snake diversity. We showed that an increase in the proportion of the matrix compared with that of native forest leads to a loss of the species and functional components of diversity. Snake species richness and abundance were first affected by the loss of forest and within the matrix they were particularly affected by silviculture, as shown in Table S4 and Figure S4. The loss in phylogenetic diversity driven by the loss in species richness in silviculture areas could be partially compensated by the fact that co-occurring species are phylogenetically distant. However, there was no such compensation for functional diversity, since the decrease in functional diversity with deforestation was more drastic than that of phylogenetic diversity; this was all the more true with deforestation for silviculture (Fig. S7) and may result in loss of ecosystem functioning (Díaz & Cabido, 2001).

2.4.1. Implications for conservation

Our study showed that snake response to habitat changes occurred at multiple spatial scales, with landscape elements mediating species and functional diversity, while phylogenetic diversity was influenced by local scale. This suggests that strategies for conserving the distinct components of snake diversity in HMTLs should consider management practices both at local and landscape scales (Gonthier et al., 2014). Moreover, snake dispersal in landscape seems to be the main factor explaining the pattern of functional and phylogenetic relatedness, suggesting that habitat configuration may have an important role on the spatial distribution of snakes in these landscapes and, consequently, on functional and phylogenetic structure of snake assemblages. Thus, beyond the effects of habitat loss and fragmentation, landscape configuration may also affect snake diversity patterns, being important its inclusion in further studies at the landscape level.

Practices of the silvicultural management, such as insecticide use and periodic timber harvesting, may modify the suitability of silviculture plantation as a habitat for species and tend to influence species presence and their movement in these landscapes (Kupfer et al., 2006). Hence, further studies that investigate how species respond to these management practices and at which growth stage silviculture plantations become a suitable habitat for generalist species can improve our understanding about the effects of this matrix type on snake diversity. Nevertheless, the increased snake species diversity observed in landscapes with the highest native habitat arranged in more patches suggests that the mosaic configuration of silviculture plantations and forest patches is a more sustainable type of management than keeping large and continuous areas of silviculture plantations. In addition, our findings show that species, functional and phylogenetic components of snake diversity increased when the proportion of native habitat was high, therefore highlighting the importance of the maintenance of native vegetation areas in private properties (e.g., Area of Permanent Protection and Legal Reserves in Brazilian environmental policy), in order to ensure species persistence and the provision of ecosystem services in fragmented landscapes (Metzger et al., 2019).

Finally, our study supports the idea that an integrated approach of different components of diversity and a multi-scale analysis are required to accurately assess how snakes respond to habitat changes in human-dominated tropical landscapes.

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3. HABITAT CONFIGURATION MEDIATES COMMUNITY (DIS) ASSEMBLY OF RAIN FOREST SNAKES

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Abstract

Habitat modifications induced by anthropic land-use changes are considered major drivers of ongoing biodiversity loss. However, for some understudied organisms, such as snakes, there is still a lack of information about how they are affected by land use changes. We tested if and how the structure of subtropical fragmented landscapes selected snake traits, moderating the community assembly process. In addition, when tropical forests lose species, it is often assumed that other species similar in function will prevent a decline in ecosystem functioning. To test this insurance hypothesis, we assessed the influence of landscape elements on species diversity and on the level of functional redundancy of snake communities in such landscapes. Landscape structure was described by the proportion of forest, exotic silviculture plantation and pasture, the number of forest patches and the mean distance among forest patches, whereas the snake traits tested were related to habitat use, diet and dispersal ability. We identified that body size, diet specialization and foraging mode were the snake traits selected by landscape components. Small species and diet specialists were dominant when distance among forest patches was the smallest, and as the distance increased the snake communities became composed of larger species and generalist in diet. The increase in silviculture areas also favored diet generalists. Moreover, landscapes with a high proportion of pasture favored species with active hunting mode, while ‘sit-and-wait’ ambush species seem to prefer to cross silviculture instead of pasture. We also found that both species diversity and functional redundancy decreased when forest patches became distant from each other. Hence, snake species lost cannot be replaced by functionally redundant species in these landscapes. Our findings thus provide information about the varying susceptibilities of snake species, showing which trait states are found in species able to cross silviculture and pasture and which ones made species vulnerable in fragmented landscapes. We highlight the importance of habitat connectivity to maintain species diversity and ecosystem functioning in silvicultural landscapes.

Keywords: Snakes, Fragmented landscapes, Habitat configuration, Functional trait selection, Community assembly, Functional composition, Functional redundancy

3.1. Introduction

The ongoing anthropic pressure on tropical forests has turned urgent the need to assess its impacts on biodiversity and ecosystem functioning (Edwards et al., 2019), especially for groups whose effects of habitat changes are still poorly understood, such as snakes (Bonnet et al., 2002; Doherty et al., 2020). Patterns of species composition in forested landscapes may be influenced by the amount of land cover types (landscape composition) and their spatial arrangement (landscape configuration) (Wiens, 2002). Landscapes with intermediate cover of native vegetation (e.g., 40% - 50% of forest cover) tend to be richest in species, while habitat simplification often observed in the matrix (i.e., in the area surrounding remnant native vegetation) tends to negatively affect most species (Frishkoff & Karp, 2019; Gardiner et al., 2018). In addition, native habitat and matrix configuration can directly affect species movements across the landscape, influencing the connectivity among habitat patches (Tulloch et al., 2016; Villard & Metzger, 2014) and also how the landscape species pool become accessible to the local communities (Resetarits et al., 2005; Tscharntke, Clough, et al., 2012). Understanding how landscape structure participates in this community assembly process, distinctly selecting snakes by their traits, can provide valuable insights about how snakes respond to environmental changes. Besides, the effects of diversity on ecosystem processes are attributed to functional traits (Díaz & Cabido, 2001), allowing to assess the possible consequences of snake trait selection to the ecosystem functioning.

As snakes are understudied in comparison to other organisms, the challenge that still remains is to identify the snake traits that respond to environmental changes and also have significant effects on ecosystems, considering the assumption that their traits would scale up to ecosystem functioning (Chapin et al., 2000; Lavorel & Garnier, 2002). A helpful approach to this purpose is the measure of functional composition based on the dominance of single traits, the ‘community-weighted mean’ trait values (CWMs, Garnier et al., 2004). This measure considers the biomass ratio hypothesis (Grime, 1998), which establishes that the link between traits and their properties in the ecosystems is related to the contribution of the species’ biomass in the community. Thus, the dominant species are the main contributors to the functioning of ecosystems, since their traits are more abundant or frequent in the functional composition of communities (Garnier et al., 2004; Mokany et al., 2008). Based on this, when variation in landscape elements filters out certain trait states, it results in changes of dominant species in communities and can be detected as shifts in the functional composition of each trait (Sande et al., 2016; Strahan et al., 2016). Hence, the CWMs values selected by landscape factors may help us to identify the patterns of trait selection in snakes (or dominance of the trait state), its possible effects on ecosystem functioning and the landscape influence on community organization.

Species distribution mediated by landscape may also have effects on the resilience of ecosystem processes (Oliver et al., 2015). According to the insurance hypothesis, increasing biodiversity ensures the maintenance of ecosystem functioning in the face of environmental changes (Naeem, 1998; Walker, 1992). This insurance occurs because different species perform equivalent functions, and this functional redundancy at the community-level can prevent a decline in ecosystem processes and services (Yachi & Loreau, 1999). Therefore, the selection of functionally redundant species may ensure ecosystem functioning (Fonseca & Ganade, 2001) in fragmented landscapes, but when particular functions are lost with species erosion, it may impair ecosystem resilience (Naeem et al., 2012).

Considering that species with the ability to use a wide range of resources and reach scattered habitat patches have a greater chance of survival in fragmented landscapes (Farneda et al., 2015; Rand & Tscharntke, 2007), we expect that snakes with larger size, habitat and/or diet generalists are selected by the increase in matrix area or in inter-patch distance in forested landscapes. Differently from large endothermic predators that are often affected by habitat loss (Newbold et al., 2020), the increase in matrix environments may benefit the largest snake species. It is expected because beyond body size being related to metabolic rates (Nagy, 2005) and being used to infer dispersal capacity (Jenkins et al., 2007), it also reflects surface-to-mass ratio of heat exchange with the environment (Lillywhite, 2014). Larger snakes have a smaller surface-to-mass ratio, gaining heat from the environment more slowly than small snakes (Blackburn et al., 1999; Lillywhite, 2014). As human land uses have substantially higher surfaces temperature than nearby tropical rain forests (Senior et al., 2017), larger snakes tend to be less harmed by increased temperatures in the matrix than small species. Besides, other ecological aspects of snakes may be distinctly selected by forest conversion into matrix environments, for instance their foraging modes, microhabitat use and daily activity. Identifying which traits turn snakes vulnerable to or able to persist in modified landscapes may contribute to the design and monitoring of conservation strategies for snakes.

As proxies for particular ecosystem processes, functional traits are not restricted to a set of species and may be compared across ecoregions, through standardized methodologies to measure traits (Weiher et al., 1999). Thus, by considering snake traits with some degree of standardization in the measurement, it may be possible to identify among the snake traits those that respond to land use, which may thus be used as functional markers to predict snake response to environmental changes in other localities with different environmental gradients or land uses (Vandewalle et al., 2010).

Here, we tested if and how elements of landscape composition and configuration moderated the selection of snake functional traits, influencing the community assembly process and the viability of ecosystem functioning associated with these communities. We selected landscapes predominantly composed by tropical forest, exotic silviculture plantation and cattle pasture in a fragmented area of Atlantic Forest, an important biodiversity hotspot that shelters a large number of snake species (Barbo et al., 2021; Ribeiro et al., 2011). We investigated the landscape effects on traits related to habitat use, diet and dispersal. For doing so, in each community, we assessed the CWM values of each trait, species diversity and the level of functional redundancy. The relation between functional redundancy and species diversity was assessed to detect the occurrence of 'insurance effects'. We found which snake traits were selected and its consequences for ecosystem resilience by testing the effect of landscape structure (i.e., percentage of native forest, silviculture and pasture, number of forest patches and mean distance among forest patches) on CWM values of each trait, functional redundancy and species diversity.

3.2. Material and Methods

3.2.1. Study area

The study area is located in Monte Verde, a mountainous region in southern Minas Gerais state in Brazil (Figure 1a), with altitude varying from 1.250 m to 1.600 m above sea level. Its climate is subtropical with cold and dry months during autumn and winter and warm and wet months during spring and summer (Meireles et al., 2014). Monte Verde was once a continuous tract of Atlantic Forest, which is considered a biodiversity hotspot (Myers et al., 2000) due to its high concentration of endemic species and habitat loss. Nowadays, native forest fragments in Monte Verde are interspersed mainly with exotic silviculture plantations (*Eucalyptus* sp. and *Pinus* sp.), pastures and a few human settlements. Native forest is composed of different successional stages, from the initial and intermediate to mature forest, being the latter the largest cover of native vegetation. It consists of tall trees up to 20 m high at the canopy, harboring a well-structured understory, with eventual emergent individuals of *Araucaria angustifolia*, and a shrub-herbaceous stratum (Meireles et al., 2014).

3.2.2. Landscape data

We selected 22 landscapes along a gradient of native forest, silviculture plantations and pastures (Figure 1b, maximum overlapping area between landscapes = 23 %). Landscape scale for snake species in Monte Verde was previously detected (see first chapter), representing the area within a 600 m diameter buffer around the center of each sampling site. Inside each landscape, we quantified landscape composition as the percentage of native forest, silviculture plantations and pasture, and landscape configuration as the number of forest patches and mean distance among forest patches, which is a measure that summarizes how far the native fragments are from each other, separated by matrix environment. These measures were quantified using the softwares ArcGis (version 10.7), Fragstat (version 4.2) and R (version 4.1.1).

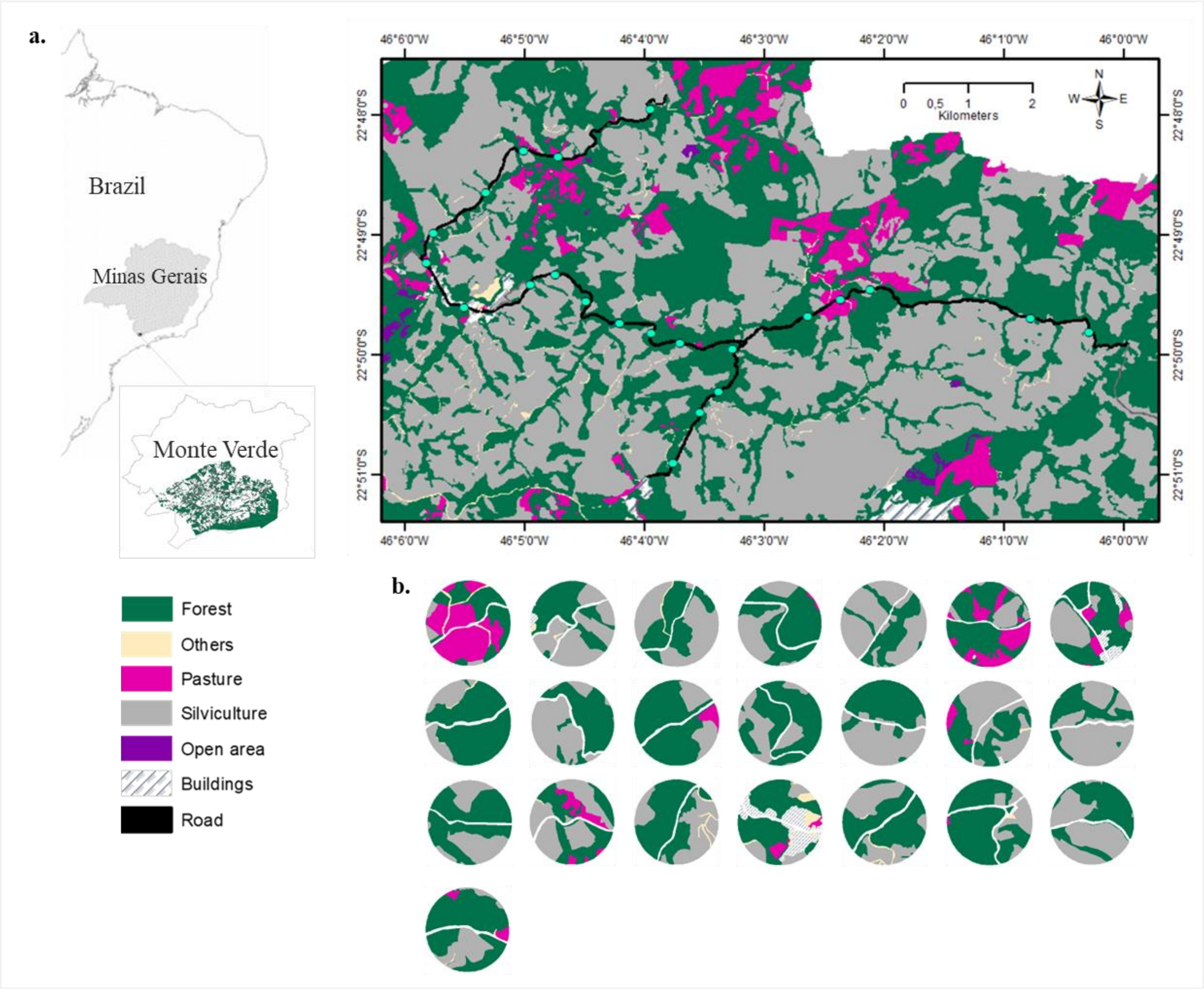

Figure 4. The location of Monte Verde district in Minas Gerais state, Brazil, and land cover of the study area. The road used to sample snakes is shown in black and the light green points indicate the center of the studied landscapes used to analyze snake local communities. **b.** Spatial structure of the 600-meter diameter landscapes studied in Monte Verde.

3.2.3. Snake data

The main snake sampling method was time constrained search by car (Fitch, 1987). Snake sampling was carried out in the morning and at night, from January to March, and from October to December 2019 and 2020, except for March 2020. The same unpaved and low traffic road, approximately 22 km long, was travelled by approximately 8 h and 30 min per day, during 10-11 days per month. The sampling effort was high, being each road segment sampled on average 60 times per month. Snake captured or photographed by local people in the same road during the sampling period were also used in this study. Regardless of the sampling method used, geographical coordinates were collected for each individual snake found, and the taxonomic identification of specimens was confirmed at the herpetological collection of Butantan Institute.

The snake functional traits used in this study were: substrate use, daily activity, foraging mode, body size (total length), diet and habitat specialization (Table 1 and Table S1, appendix C). Trait information was gathered by measuring and examining captured snakes in the field and in the literature (Tables S2 and S3, appendix C). These traits were selected considering that landscape can influence species sorting due to their differences in dispersal, resource use and habitat requirements in space and time (Batáry et al., 2007; Carrara et al., 2015). Substrate use, daily activity and habitat specialization are traits related to habitat use, while diet specialization is related to feeding preference and snake position in food web. Foraging mode and body size are both related to dispersal abilities, but body size is also related to predator position in food webs, as intermediate or top predator (Schmitz, 2008). Substrate use and daily activity described the main microhabitat used and period of activity of the species, respectively. Species with active individuals in both periods were classified as ‘both’. Habitat specialization considered the number of non-native habitat types where individuals of each species were found. Species found only in native habitat were classified as ‘specialist’, in few habitat types (e.g., 2-3 types, native or non-native) were classified as ‘intermediate’, and those found in many habitat types (e.g., ≥ 4, native or non-native) were classified as ‘generalists’. Diet specialization was classified in four categories based on the main food items of the species diet. ‘Super specialists’ were those species that eat only one type of prey, ‘specialists’ were those that feed predominantly of one prey type but occasionally can eat another prey type, ‘generalist’ were those that eat 3 prey types and ‘super generalists’ those that eat more than 4 prey types. Detailed information about habitat and prey types is provided in Table S3. Literature used in addition to field information to define trait states are provided in the appendix C (Table S2).

Table 2. Description of the snake functional traits used in this study.

Snake functional trait	Data type	States
Substrate use	Ordinal	1 = terrestrial; 2 = fossorial; 3 = semi-arboreal
Daily activity	Ordinal	1 = diurnal; 2 = both; 3 = nocturnal
Foraging mode	Ordinal	1 = sit-and-wait; 2 = active
Body size	Quantitative	Millimetres
Diet specialization	Ordinal	1 = super generalist; 2 = generalist; 3 = specialist; 4 = super specialist
Habitat specialization	Ordinal	1 = generalist; 2 = intermediate; 3 = specialist

3.2.4. Community data

We previously assessed detection probability of each species in the sampling sites as proposed by MacKenzie et al. (2002) by considering the possibility of a species go undetected even when it is present in the site. Low values of detection probability were found for snake species present in our community data (see Leal-Santos et al., in prep.). We thus calculated functional measures considering presence/absence species data. Functional composition for each trait was assessed by the community-weighted mean values (CWMs) (Garnier et al., 2004) and functional redundancy was calculated as proposed by Ricotta et al. (2016), which can be interpreted as the average functional ordinariness of a species in a community, since presence/absence data was used (Ricotta et al., 2016). Explanation about why Ricotta et al. (2016) measure of functional redundancy is still valid with presence/absence data is provided in the appendix. These two measures assess the ecological role of species indirectly via their functional traits. The functional redundancy assumes that species with similar traits are likely to support similar functions (Ricotta et al., 2016), while CWM represents the most dominant trait state in the community. Information about the statistical types of traits is provided in Table 1. Beyond functional measures, species richness of each community was also considered.

3.2.5. Statistical analysis

We used linear models to test the effects of the landscape variables on each CWM value, functional redundancy and Simpson index. Thus, each CWM value was analyzed separately. Also, a linear model was used to compare functional redundancy with species richness.

We estimated the variance inflation factor (VIF) in order to avoid collinearity among predictor variables in multivariate models. Those variables with VIF values ≥ 4,0 were not included together in the same model (Kutner et al., 2005). Instead, these variables were included in different models which were subsequently compared. To do so, a multi-model inference approach was adopted to identify which components of the landscape structure select the CWM values and to identify how landscape acted on functional redundancy of snakes and species diversity (Burnham & Anderson, 2002). Akaike's information criterion corrected for small samples (AICc) was used to select the models that best fit the data, being considered equally plausible those models with a difference in ΔAICc ≤ 2,0 (Burnham & Anderson, 2002). Also, the existing relation between functional redundancy and Simpson index of species diversity was assessed by linear regression, further compared with null model (Gotelli & Graves, 1996).

Before the analysis, the 22 landscapes were tested for spatial correlation using a Mantel correlogram and no spatial effect was detected, but we included Moran eigenvectors in all models as covariables to deal with a possible effect of the spatial proximity on predictor or response variables. The spatial filtering approach selects the single eigenvectors that most influence spatial dependence in residuals, removing spatial dependence from linear models (Griffith & Peres-Neto, 2006). Posteriorly, the residuals of each selected model were checked for normality, homoscedasticity, independence and overdispersion (Zuur et al., 2009a). Independence of the residuals was checked also with variograms and with Moran's I test. Only the models that followed these criteria were considered in the results. It is worth mentioning that no leverage effect was detected in any selected model. In addition, the variation in the standardized sampling effort and in the data collected by local people could influence the number of individuals found along the road (Gardner et al., 2007). To test if they indeed had an effect on each response variable, we compared models with their inclusion as covariables with models without them and the latter option was selected.

3.3. Results

The snake functional traits selected by landscape were body size, diet specialization and foraging mode; and the distance among forest patches was the common variable selecting these traits (Figure 5 and Table 2). Substrate use, daily activity and habitat specialization were not selected by the landscape variables used in this study, presenting no difference from a random distribution.

The increase in distance among forest patches favored the snake species from medium to largest body size and those that eat some or many different food items, while smaller species with a specialized diet benefited from the greater proximity between forest fragments (Figure 5). Besides, the highest silviculture proportion also favored those snake species with a broader diet (Table 2).

Active foraging mode is benefited by a slight decrease in distance among forest patches, but the increase in pasture area has a stronger effect on it (see slope values in Table 2). Thus, the active foraging mode is dominant in communities whose landscapes have closer forest patches, but also when the proportion of pasture areas increased, even if the distance among patches increased. On the other hand, sit-and-wait species are not dominant in landscapes with high proportions of pasture or short distance among patches.

Functional redundancy and species richness were also selected by the distance among forest patches. Both reduced with increasing distance between forest fragments and also with increasing silviculture proportion for species richness only (Figure 6 a and b). As expected, species richness increased as the amount of forest increased (Table 2) and functional redundancy increased with increasing species richness (Figure 6 c).

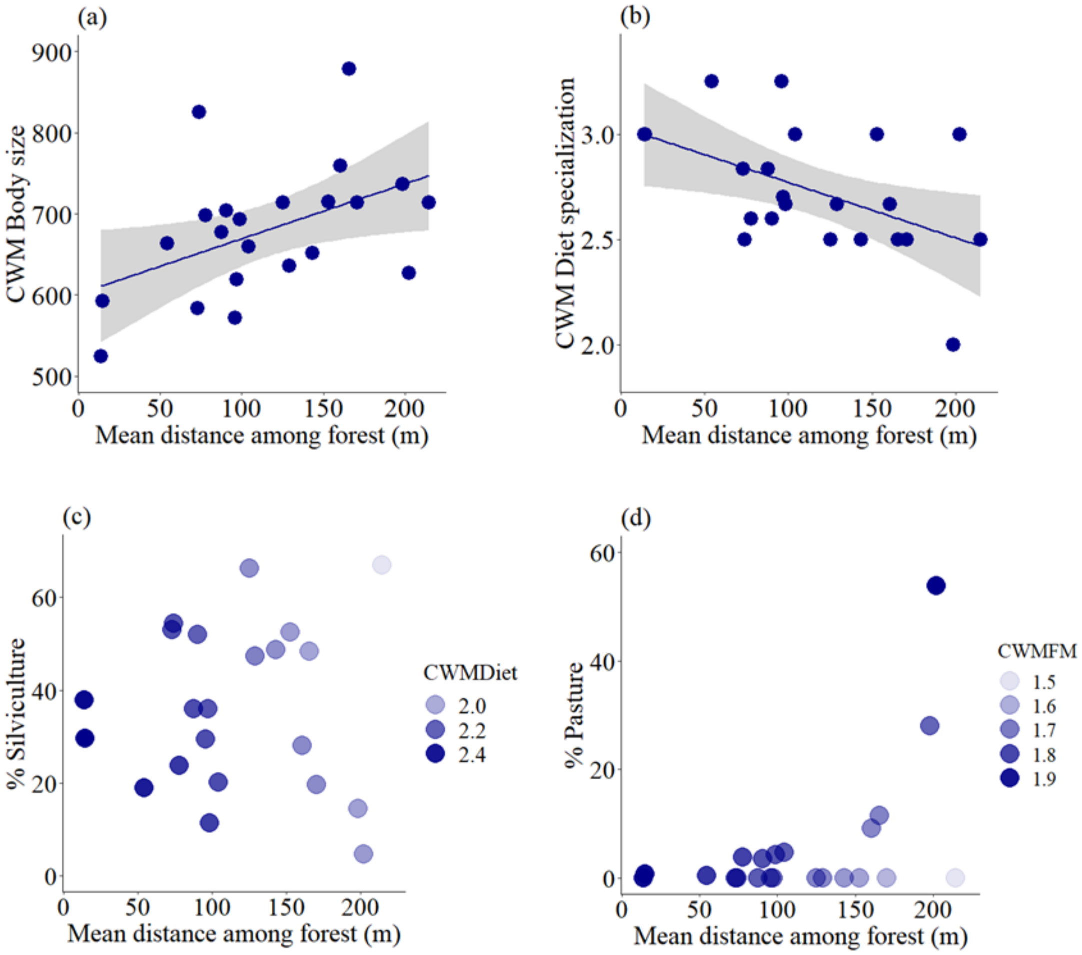

Figure 5. Relationship between the selected landscape variable(s) with the predicted CWM values of body size (a), diet specialization (b and c) and foraging mode (c). Legend in (c) indicates the predicted CWM values of diet specialization and in (d) of foraging mode (CWMFM). The range of ordinal traits was described in Table 1.

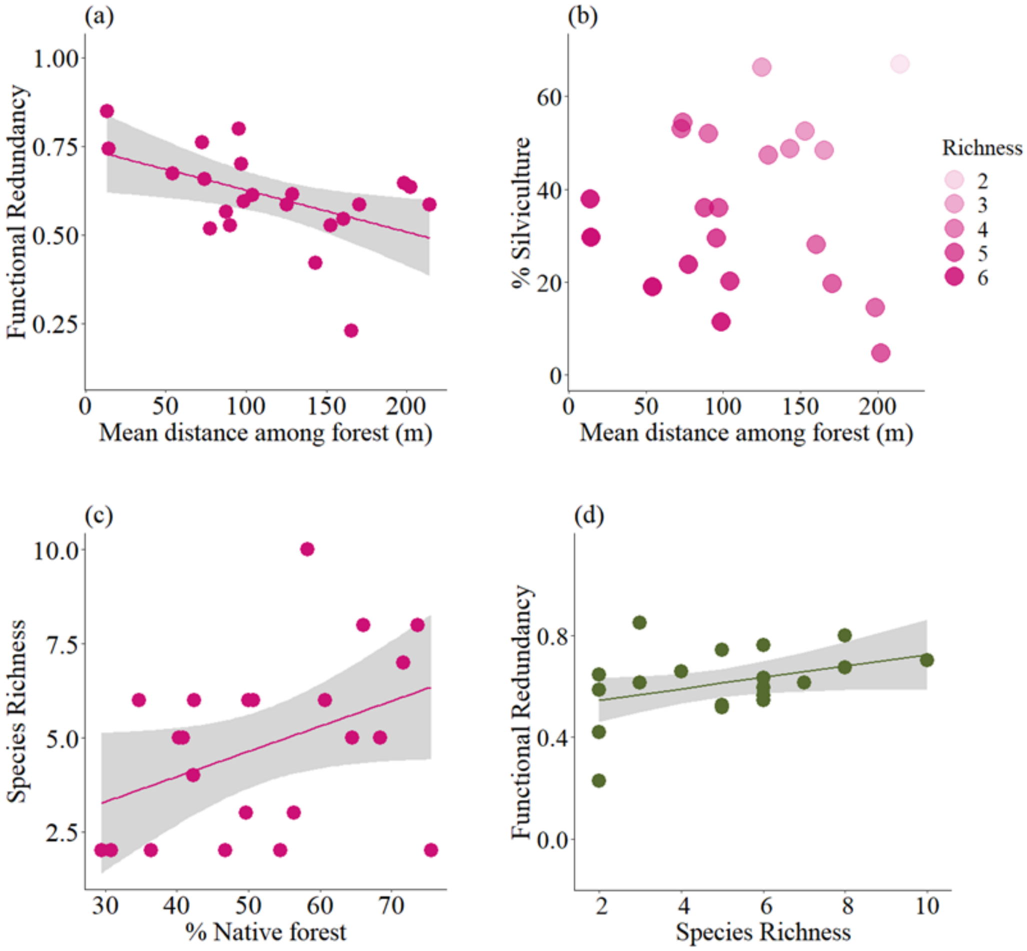

Figure 6. Relationship between functional redundancy (a) and species richness (b and c) with the selected landscape variables and between functional redundancy and species richness (d).

Table 3. Details on selected models for each response variable.

Selected model	**Intercept**	**(1) Slopes**	**ΔAIC**	**Adj. R square**
CWM Body size ~ (2) Mean distance	601.38	0.7	0	0.3787
CWM Diet ~ Mean distance	2.73	-0.1478	0	0.3153
CWM Diet ~ Mean distance + % Silviculture	2.73	-0.1473; Silvic. = -0.068	1.6	0.3228
CWM Foraging ~ Mean distance + % Pasture	1.95	-0.002; Pasture = 0.0076	0	0.3019
Functional Redundancy ~ Mean distance	0.744	-0.06604	0	0.2165
Species richness ~ Mean distance + % Silviculture	4.7727	-0.90; Silvic. = -0.899	0	0.2274
Species richness ~ % Native forest	4.7727	0.9421	0.9	0.1219
Functional Redundancy ~ Species richness	0.5016	0.0224	0	0.1390

(1) Slopes are given for each explanatory variation in the same order as they are entered in the model

(2) Mean distance = Mean distance among forest patches

3.4. Discussion

Our results showed that total length, diet specialization and foraging mode were the snake traits selected by landscape structure, with forest configuration being a common factor mediating the distribution of these traits in the studied landscapes. Shifts in composition of body size in communities were influenced by the distance among forest patches that, together with the proportion of silviculture and pasture, also acted on composition of diet specialization and foraging mode, respectively. Besides, our results confirmed that functional redundancy increases with species richness, supporting the idea that the ‘insurance effect’ occurs in the snake communities studied. However, functional redundancy and species richness decreased in landscapes with greater distance among forest patches and also increased silviculture. The ecosystem's vulnerability to future disturbances thus increases in these fragmented and modified landscapes.

Different habitat configurations selected the states of snake traits distinctly, pointing out the scenarios that are favorable for or threaten the persistence of different snake species. In landscapes where the distance among forest patches was greater (mean distance = 200 m), the snake communities became composed of species presenting larger body size and are diet generalists (i.e., feeding on a few or many different prey items). This means that the snake species able to cross the matrix types and reach distant habitat patches are the largest ones of the study area, with improved dispersal ability, a broader resource use and most likely tolerant to the temperatures of the matrix environment (Lillywhite, 2014). Nonetheless, it is worth mentioning that diet specialists which are habitat generalists (e.g., *Crotalus durissus* and *Atractus zebrinus*) were found in these landscapes with distant forest patches, but they were not dominant in the community. Another important consideration is that although these landscapes have selected larger species, their offspring and juvenile individuals are smaller, and it is reasonable to consider that the adult instead of the juveniles were the selected individuals of these species. However, an intraspecific functional approach would be more appropriate to confirm if the selection by distant forest patches acted on an intraspecific level (Grass et al., 2021), despite knowing the difficulties to obtain a representative sample of snakes in nature. On the other hand, we found that the most dominant traits of the snake communities when the distance among forest patches was the smallest (i.e., < 50 m) were small size and narrow diet. This suggests that main matrix types (silviculture and pasture) are not permeable to these species that show a strong tendency to stay in the same forest patches or do interpatch movements only in really short distances, therefore being trait states that belong to snakes habitat specialists.

A species with restricted movements in fragmented landscapes usually have its persistence threatened. Indeed, the movement of individuals from different populations among habitat patches occupied by the species make gene flow possible, increasing phenotypic diversity in the face of environmental changes (Hanski, 2011; Hanski & Gaggiotti, 2004). Limiting movements thus tends to limit phenotypic diversity. Because the smallest snake species tend to stay in the forest patch due to their reduced mobility or intolerance to matrix environments, gene flow can be disrupted and the long-term viability of these local populations could be compromised by inbreeding and random fixation of deleterious mutations, for example (Lande, 1998; Manel et al., 2003; Saccheri et al., 1998). However, forest restoration could reverse this scenario, restoring structural connectivity for these species. The form of stepping stones seems appropriate for this (Manning et al., 2006; Uezu et al., 2008), especially if the restored patches allow connection to larger patches because species richness and abundance increased in these landscapes when forest cover was high and distributed in more patches (first chapter). To improve conservation planning, circuit theory could be applied (Dickson et al., 2019) and the distances found here could be used as a starting point for models of isolation by resistance, which allow to find different possible pathways to connect populations by dispersal (McRae et al., 2008). This could provide a more accurate way to set the distribution of restored patches in order to connect these populations, contributing to the maintenance of the smallest species, as well as their ecosystem functions and providing services in these fragmented landscapes.

We also found that matrix composition mediated species traits distribution, but its effect was observed only when associated with habitat configuration. The more isolated the patches became and the proportion of silviculture increased in the landscapes, the more species with a broader diet became predominant in snake communities (Table 2). This result confirmed what was mentioned above, that the movement across silviculture to reach distant patches was done mainly by species with a broader or generalist diet.

Moreover, snake species that are active foragers were dominant in the communities when the distance among forest patches in the landscape was shorter, but as the proportion of pasture have the strongest effect on this trait, the active foragers were dominant also in landscapes with larger pasture areas, even if distance among patches became larger. Considering this finding with the previous ones, we found that snake communities were predominantly composed of small species, diet specialists and active foragers when the distance among patches was shorter. In addition, we found that when snake species are larger, those who are active foragers were able to cross areas with a high proportion of pasture. Active foraging snakes often have a broader use of space (Fraga et al., 2017) and an environment with simplified habitat, like pasture, may have facilitated the inter-patch movement in longer distances of these larger species. Conversely, 'sit-and-wait' species were not favored by pasture areas, but were able to cross the matrix and reach distant forest patches (> 150 m, see Figure 2c). As ambush hunters, they stay for some time in a tight coil waiting for the prey to pass (Mushinsky, 1987), but in pasture areas this behavior would enhance their exposure to predators and the risk of overheating during the day (Huey, 1991; Lillywhite, 2014). Because in this study there are only three 'sit-and-wait' species that reach larger size (i.e., *Bothrops jararaca*, *Bothrops neuwiedi*, and *Crotalus durissus*), the same result also suggest that these ambush species prefer to cross, or even use as habitat, the silviculture matrix instead of pasture. This indicates therefore that even when snakes are habitat generalists, their movement throughout the landscape tends to differ between cover and non-covered matrix types due to their foraging mode. Thus, matrix configuration could also mediate snake distribution in these landscapes.

The snake traits selected by landscape structure have the advantage of presenting a standardized procedure of measurement (e.g., Cundall et al., 2016; Fitch, 1987), making their comparison possible among studies, and they were identified using functional metrics that has been effective to detect the response to environmental changes of different organisms (e.g., Mueller et al., 2016). Hence, our findings suggest that the selected functional traits (body size, diet specialization and foraging mode) can be used as functional markers in future studies to evaluate snake response to environmental changes in different localities (Vandewalle et al., 2010). On the other hand, we found that landscape elements had no effect on the distribution of habitat specialization, daily activity or substrate use. The absence of effect on habitat specialization, although unexpected, may be because the proportion of habitat available, as native or matrix types, is large enough in the landscapes (i.e., native: 29-75 %, silviculture: 4-67 %, pasture: 0-53 %) to fail to select species distinctly by their habitat requirements. Similarly, if the required prey is active at day and night, snake species would not be selected by their daily activities. Besides, the snake species found in this study do not use exclusively one type of substrate in the environment (e.g., Hartmann et al., 2009), thus this trait may not have been selected because the species are not strictly arboreal, aquatic or fossorial, using the ground eventually in their movements inside the forest or matrix. Although the studied landscapes have not mediated these traits, we still recommend their inclusion in further studies, considering that they describe important aspects of habitat preferences and may prove useful to understand snake response in other scenarios of habitat loss and fragmentation.

As landscape moderated the selection of functionally important traits for the ecosystem, the absence of these traits or species in generalist-dominated snake communities may directly affect ecosystem functioning. For instance, the loss of trophic guilds, as the snake species that feed exclusively on frogs, shows a loss of trophic interaction that may affect food web structure and stability (Balvanera et al., 2006; Melián & Bascompte, 2002; Putten et al., 2004). In contrast, body size and foraging mode are important traits for the quantitative aspect of the food web, linked to the fluxes of matter and energy along trophic interactions (Barnes et al., 2018). Predator body size influences consumption rate and prey size (Jonsson et al., 2005; Séguin et al., 2014) and is a key trait for snake position in the food web, as intermediate or top predators, which indicates different effects on regulation of the lower trophic levels (Gauzens et al., 2016; Vance-Chalcraft et al., 2007). Similarly, active and ambush hunters differ in how they act in top-down control of ecosystems (Luttbeg et al., 2020; Schmitz, 2008). The selection of these traits by forest configuration can therefore affect both the structure and stability of food webs and the fluxes of matter and energy (Barnes et al., 2018), but further studies based on trophic interactions at the snake community level could better assess the effects of this non-random species loss on ecosystem functioning.

At last, we found that functional redundancy increased with high snake species richness and both measures were driven by forest configuration and richness was also driven by the proportion of silviculture or native forest. More diverse communities in species that perform similar functions (i.e., high functional redundancy) were found in landscapes with high proximity among forest patches, ensuring thus that the functions provided by these communities to the ecosystem can be maintained even in the face of environmental fluctuations (Hooper et al., 2005; Naeem, 1998). However, when the distance among forest patches increased, being filled by silviculture plantations (which increase in proportion as distance increases), the smallest and diet specialist snake species were not able to reach distant patches or tolerate silviculture environment, causing species loss that was followed by a decrease in functional redundancy. This showed how important these vulnerable species can be for ecosystem resilience and how their loss in generalist-dominated snake communities can imperil the maintenance of ecosystem processes and services.

In conclusion, our study demonstrated that forest configuration and matrix composition at the landscape-level acted on the (dis)assembly process of snake communities, selecting snakes differently according to their body size, diet specialization and foraging mode. These traits can thus be considered as functional markers to understand snake community responses to land uses. We have also shown that proximity among forest patches was the main factor influencing snake distribution in the studied landscapes, changing community functional trait composition, patterns of species diversity and ecosystem resilience. Communities found in landscapes with closer forest patches were predominantly composed of small-sized and diet specialist snakes and were more diverse in species performing similar functions, potentially making these ecosystems more resilient to environmental changes. As the distance among forest patches increased, communities became composed of larger snakes with broader diets, showing lower species diversity and functional redundancy, which indicates that ecosystems associated with generalist-dominated snake communities are more vulnerable to disturbances. Moreover, the snake species that are able to cross the matrix (i.e., habitat generalists) were also selected by their traits. Active hunters were dominant in landscapes with a high proportion of pasture, while ‘sit-and-wait’ ambush species seemed to prefer to cross silviculture instead of pasture. Our findings thus provided information about the varying susceptibilities of snake species in fragmented landscapes, showing which traits are found in species able to cross different matrix types and which traits made species vulnerable to silvicultural landscapes. Finally, we highlight the importance of restoring habitat connectivity in Monte Verde landscapes in order to avoid the loss of species and contribute to maintain or enhance ecosystem functioning in the face of environmental disturbances.

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4. CONCLUSÃO GERAL

Os estudos apresentados nesta tese mostraram que a conversão de florestas tropicais em usos antrópicos da terra afeta distintamente os componentes da diversidade de serpentes e em diferentes escalas espaciais. A diversidade de espécies aumentou com a proporção de floresta e o nível de fragmentação da paisagem, enquanto a diversidade funcional aumentou com a quantidade de floresta na paisagem. Isso indica que paisagens florestais fragmentadas que apresentam maiores quantidades de habitat nativo são capazes de manter maiores populações de serpentes e de manter espécies com características funcionais únicas. O efeito positivo da fragmentação indica que as espécies poderiam se beneficiar da utilização de recursos em diferentes fragmentos florestais na paisagem, logo sugerindo que existe movimentação das espécies de serpentes entre os fragmentos remanescentes. Por outro lado, o resultado referente à diversidade filogenética indica que há restrição de movimento para algumas espécies, já que a escala local teve maior influência sobre este componente da diversidade. Assim como os outros componentes, a diversidade filogenética aumentou com a proporção de floresta e, inesperadamente, também aumentou com a proporção de silvicultura, indicando que espécies de serpentes com restrição de movimento e/ou especialistas no uso do habitat podem ser evolutivamente distantes. Então, a perda de diversidade filogenética devido à perda em riqueza de espécies em áreas de silvicultura poderia ser parcialmente compensada pelo fato de que as espécies que co-ocorrem são filogeneticamente distantes. Logo, estratégias de conservação devem considerar múltiplas escalas espaciais para conservar distintos componentes da diversidade de serpentes.

Nossos estudos também mostraram que a configuração espacial do habitat é o principal fator influenciando a distribuição dos traços funcionais de serpentes nas paisagens estudadas. As espécies de serpentes foram selecionadas distintamente de acordo com a distância entre os fragmentos florestais. Espécies com tamanho maior e generalistas em dieta eram predominantes nas comunidades em que os fragmentos eram mais distantes entre si (200 m), enquanto espécies menores e especialistas em dieta eram mais frequentes quando a distância entre fragmentos era menor (50 m), mostrando que existem diferentes cenários de conectividade de habitat para as espécies de serpentes e um provável efeito de isolamento sobre as espécies menores e especialistas. Tais características sinalizam, portanto, quais espécies de serpentes florestais tendem a ser mais vulneráveis em paisagens fragmentadas. Além disso, as comunidades com predomínio de serpentes maiores e generalistas apresentaram menor redundância funcional, indicando que a mudança em composição de espécies de serpentes ocasionada pelos diferentes cenários de configuração do habitat pode ser acompanhada de uma potencial perda de funcionamento e resiliência dos ecossistemas. Quando esses resultados são considerados em conjunto com os anteriores concluímos que a quantidade de floresta e a proximidade entre os fragmentos florestais são dois fatores fundamentais para conservar os distintos componentes da diversidade de serpentes, para manter a paisagem conectada para as diferentes espécies e para possibilitar a manutenção dos processos ecossistêmicos em mosaicos de floresta tropical e usos da terra. Em termos práticos, isso ressalta a importância da manutenção das reservas legais e das áreas de proteção permanente em propriedades privadas, sobretudo se formarem corredores ecológicos, contribuindo para garantir a persistência das diferentes espécies de serpentes e dos processos ecossistêmicos.

Embora a configuração do habitat nativo na paisagem tenha sido o principal filtro ambiental selecionando distintamente os traços das espécies de serpentes, também verificamos que áreas com maior proporção de pasto selecionam as espécies de serpentes de acordo com o seu modo de forrageio. As espécies generalistas que atravessam maiores distâncias (200 m) para alcançar outro fragmento de floresta preferem se movimentar pela silvicultura quando caçam por emboscada (senta-e-espera) mas, quando caçam a presa ativamente, preferem se deslocar pelo pasto. Isso mostra que a configuração espacial da matriz também pode influenciar a movimentação das serpentes na paisagem. Logo, esse resultado sugere que o ambiente de pasto é ainda mais hostil para serpentes florestais do que o ambiente da silvicultura. Outro resultado importante é a identificação do tamanho corporal, especialização em dieta e modo de forrageio como marcadores funcionais das serpentes, ou seja, como traços funcionais que podem ser utilizados em outros estudos que visem entender a resposta das serpentes às perturbações ambientais. Por fim, cabe ressaltar a importância de se utilizar uma abordagem integrada dos diferentes componentes da diversidade e uma análise que considere múltiplas escalas espaciais para obter maior compreensão de como as serpentes respondem às mudanças de habitat em paisagens tropicais fragmentadas.

APPENDIX A.

Snakes are predators and their ecological functions in ecosystems are related to food web structure and dynamics (Gravel et al., 2016). They can act as both predator and prey and, depending on their body sizes, can become top-predators. Snake traits used here are related to their position in food webs and/or their individual fitness (e.g., growth and survival), as described in Table S1.

Snake body measurements were taken in the field from live individuals or immediately after being euthanized, and are expressed in millimeters. Information about other traits was obtained from field observations at the moment of the snake encounter. Habitat use describes individuals found in native and non-native habitat. Diet describes the main food items of the species.

The quantitative trait (body size) was expressed as mean values. Species with individuals found both by day and at night were classified as 'both' and those found using different types of substrates were classified as 'multiple'. Snake trait used in this work was provided in Table S2.

Table S1: Trait information.

Trait	How was it measured?	Type of trait	Ecological function related to the trait	Type of variable
Body size	Total body length	Response; effect	Food web position; ecological performance	Quantitative
Diet	Main food items	Response; effect	Food web position	Fuzzy
Daily activity	Diurnal/nocturnal/both	Effect	Food web position	Nominal
Substrate use	Terrestrial/fossorial/semi-arboreal/semi-aquatic/multiple	Response; effect	Food web position	Nominal
Foraging mode	Active/sit-and-wait	Response; effect	Food web position; ecological performance	Nominal
Habitat use	Native/non-native	Response; effect	Food web position	Fuzzy
Reproductive mode	Oviparous/viviparous	Effect	Ecological performance; food web position	Nominal

Table S2: Trait data. Columns 6-7 refers to habitat use and columns 9-18 refers to diet.

Species	Microhabitat	Daily activity	Reproductive mode	Foraging mode	Number of individuals	Ind. in matrix	Total length	Earthworm	Myriapod	Frog	Lizard	Bird	Small mammal	Snakes	Amphisbaenian	Slug	Fish
Atractus zebrinus	fosorrial	nocturnal	oviparous	active	28	8	435	1	0	0	0	0	0	0	0	0	0
Bothrops jararaca	semi-arboreal	both	viviparous	sit-and-wait	53	15	869	0	1	1	1	1	1	0	0	0	0
Bothrops neuwiedi	terrestrial	both	viviparous	sit-and-wait	3	2	557	0	0	0	0	0	1	0	0	0	0
Chironius bicarinatus	semi-arboreal	diurnal	oviparous	active	17	5	1152	0	0	1	0	0	0	0	0	0	0
Echinanthera cephalostriata	terrestrial	diurnal	oviparous	active	15	2	558	0	0	1	0	0	0	0	0	0	0
Erythrolamprus aesculapii	terrestrial	diurnal	oviparous	active	1	1	822	0	0	0	0	0	0	1	0	0	0
Mussurana montana	terrestrial	nocturnal	oviparous	active	17	1	604	0	0	0	1	0	0	1	0	0	0
Mussurana quimi	terrestrial	nocturnal	oviparous	active	7	4	530	0	0	0	1	0	1	1	0	0	0
Oxyrhopus clathratus	terrestrial	nocturnal	oviparous	active	11	2	535	0	0	0	1	1	1	0	0	0	0
Philodryas olfersii	semi-arboreal	diurnal	oviparous	active	1	1	1055	0	0	1	1	1	1	1	0	0	0
Philodryas patagoniensis	terrestrial	diurnal	oviparous	active	3	3	1167	0	1	1	1	1	1	1	1	0	0
Taeniophallus affinis	terrestrial	diurnal	oviparous	active	1	0	498	0	0	1	1	0	1	0	0	0	0
Taeniophallus persimilis	terrestrial	diurnal	oviparous	active	3	0	417	0	0	1	0	0	0	0	0	0	0
Thamnodynastes nattereri	terrestrial	nocturnal	viviparous	active	8	0	569	0	0	1	0	0	0	0	0	0	0
Thamnodynastes strigatus	multiple	nocturnal	viviparous	active	70	16	445	0	0	1	1	0	1	1	0	0	1
Tomodon dorsatus	terrestrial	diurnal	viviparous	active	22	4	590	0	0	0	0	0	0	0	0	1	0

APPENDIX B.

This appendix provides detailed information about: (1) Spatial scales and measures taken in each one; (2) study design; (3) species addition in the phylogenetic tree; and (4) statistical analysis. Also, we provide graphs of the selected models at the spatial scale with the weakest effect on biodiversity variables.

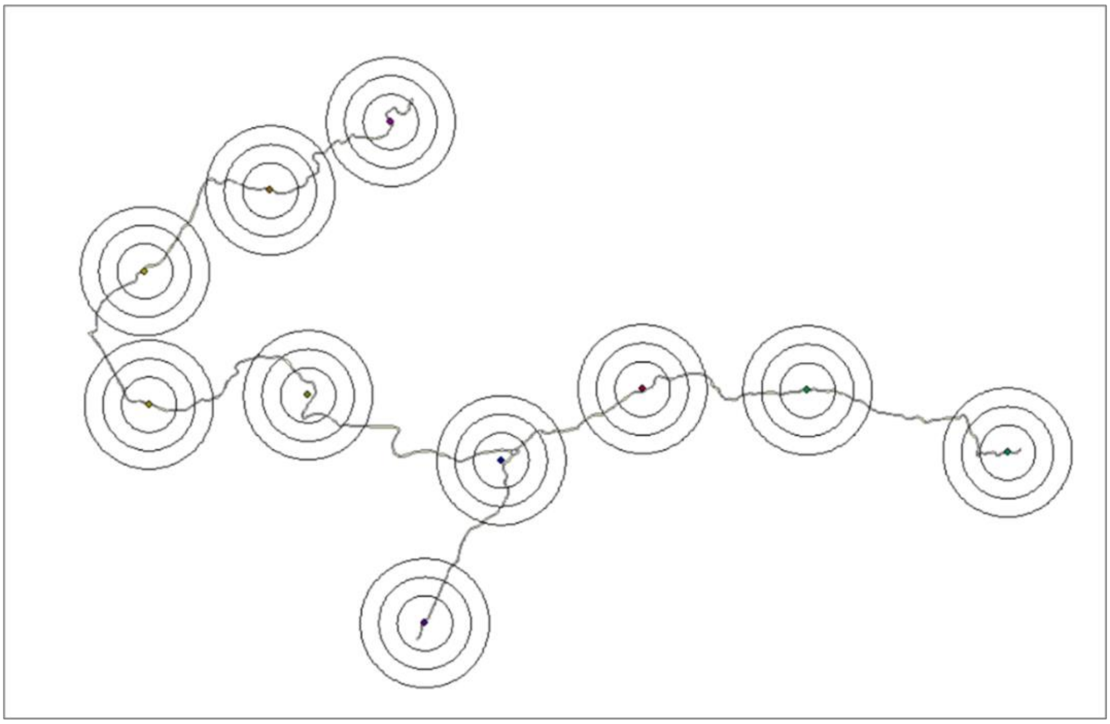

Figure S1: Multiscale design to find the scale of effect. Circular buffers with 600 m, 1000 m and 1400 m
in diameter were built around the center of ten sampling units in the study area.

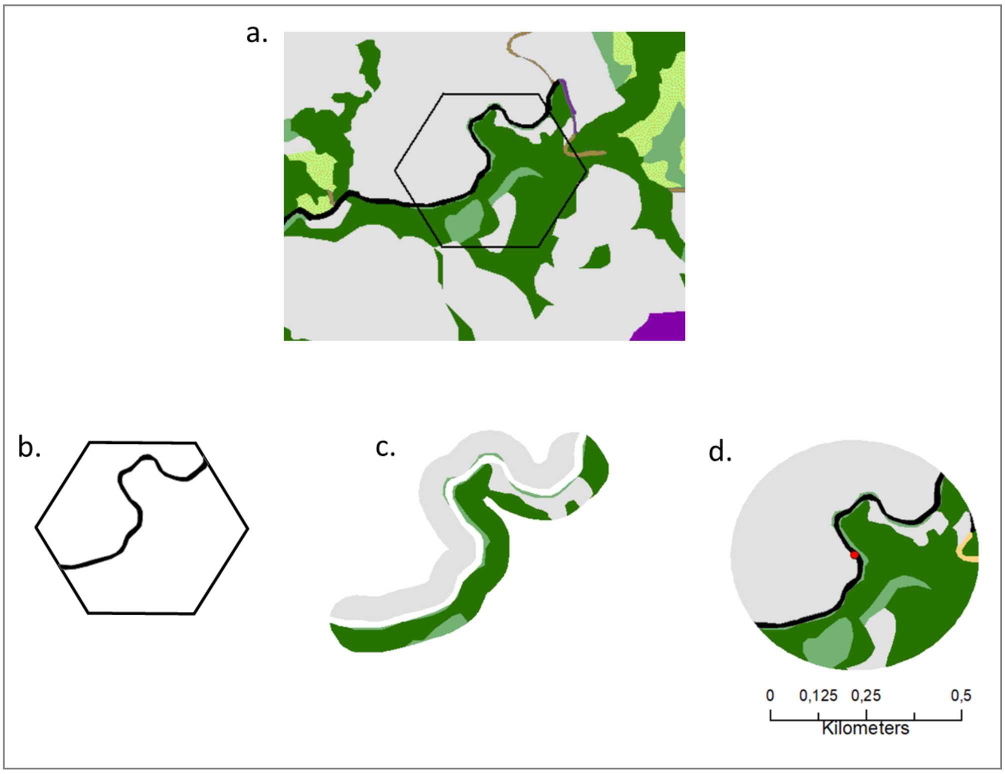

Figure S2: Sampling units and local and landscape scales in the study design. (a) A hexagonal grid cell overlapping a portion of the road (wide black line) to illustrate how the entire road was subdivided into segments. (b) The segment inside this grid cell is a sample unit. (c) Local scale: a buffer with 50 m radius around a sampling unit. (d) Landscape scale: a buffer with 300 m radius around the central point of a sampling unit.

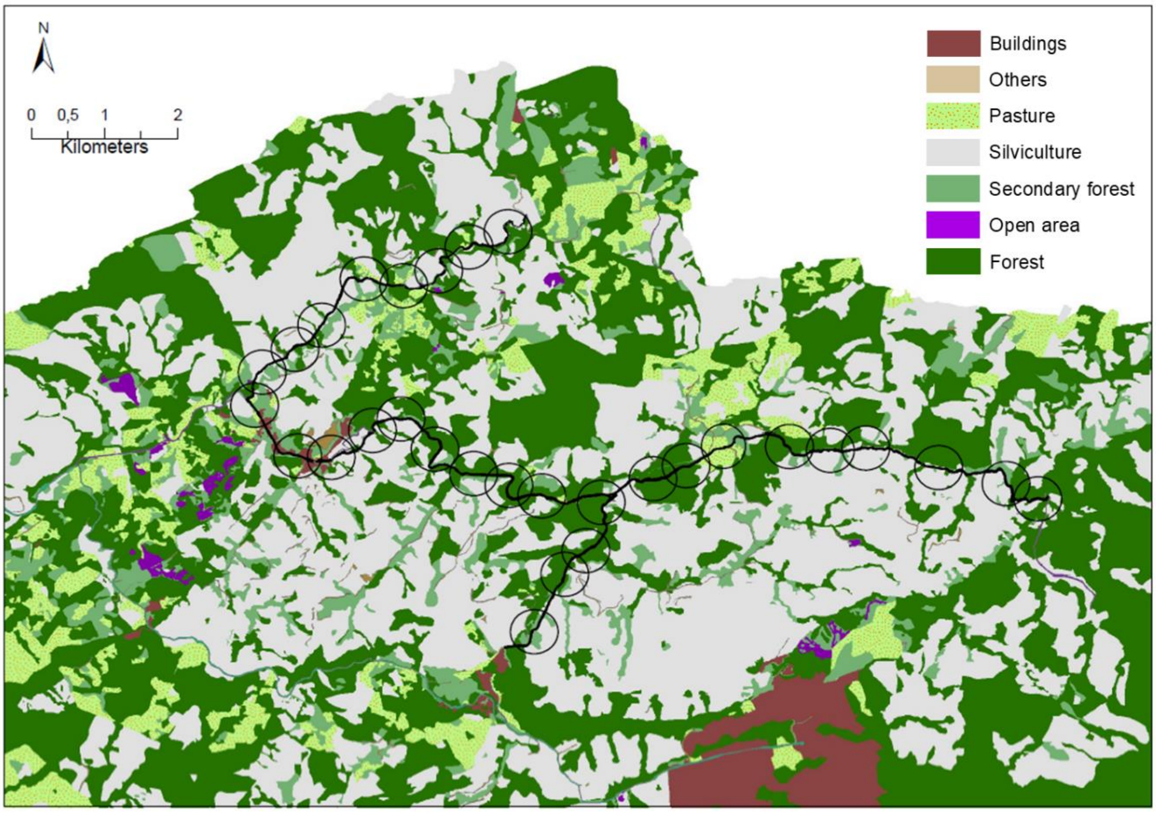

Figure S3: Focal landscapes used in the species diversity analyses (n=30, maximum overlapping = 27%).

Table S1: Range of predictor variables.

Spatial scale	% Native forest	% Silviculture	% Pasture	NP	TE	Response variable
Local	9 - 96	0 - 73	0 - 52	-	-	richness / abundance
Landscape	24 - 75	4 - 67	0 - 53	2 - 12	2201 - 5743	richness / abundance
Local	23 - 97	0 - 73	0 - 52	-	-	functional and phylogenetic variables
Landscape	29 - 75	4 - 67	0 - 53	2 - 12	2201 - 5743	

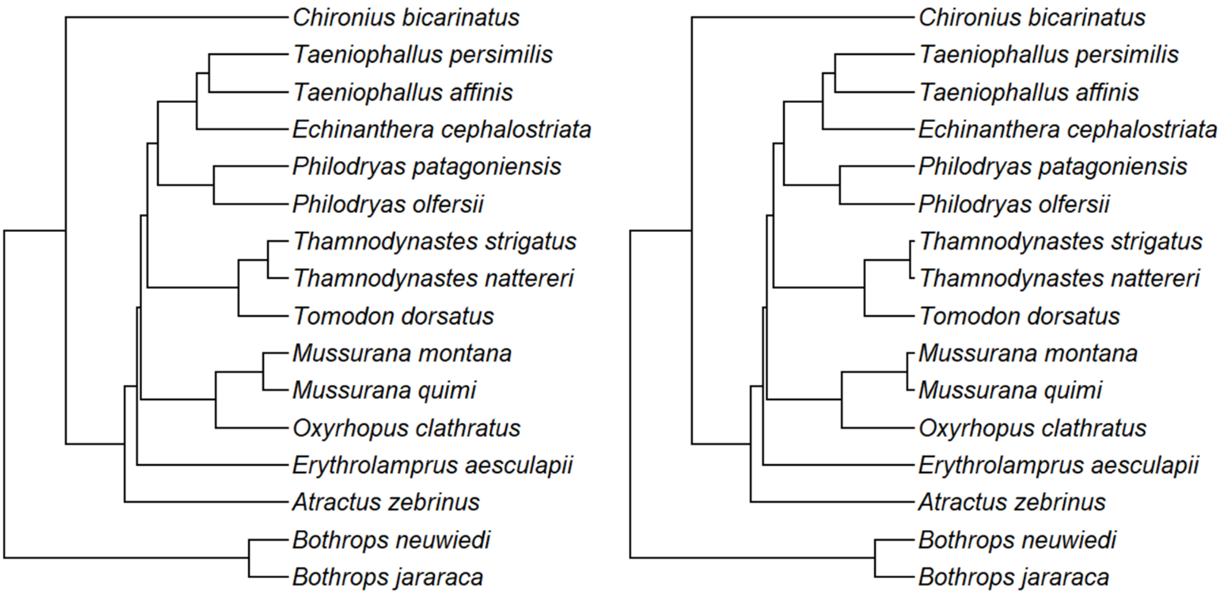

Figure S4: Two phylogenetic trees picked up from the 1000 generated in the random procedure of species addition illustrate the different branch lengths of the species added. *Taeniophallus persimilis*, *Thamnodynastes nattereri*, *Mussurana montana* and *Echinanthera cephalostriata* were added at the base node of their genera or tribe.

The probability of detecting a particular species given it is present at the site was calculated using the model for estimating the site occupancy probability proposed by MacKenzie and collaborators (2002). Input data described species presence at each site in each month of surveying. Due to the low occurrence of some species similar in morphology, thus also similar in visual detection, we grouped these species by genus or tribe in the input data. Further, we identified if landscape variables influenced estimates occupancy of each species or genus or tribe at each site. For this, each landscape variable was individually included as a covariate in the model, being five models with additional parameters and the null model. Model selection was based on AICc criterion. The best fitted model was that with ΔAICc ≤ 2.0. All models were run in the program Presence (version 2.13.18) using a single season model. We found that the amount of native habitat and the number of forest patches individually had the strongest influence on most species, with the latter better explaining the occupancy estimates of *Thamnodynastes nattereri*, *Thamnodynastes strigatus* and *Tomodon dorsatus*. Meanwhile, total edge was the single variable influencing the occupancy of *Chironius bicarinatus*.

Table S2: Lowest and highest value of detection probability estimated for each species or genus or tribe, with respective standard errors. Atractus = *A. zebrinus*; Bothrops = *Bothrops jararaca* + *B. neuwiedi*; Chironius = *C. bicarinatus*; Echinantherini tribe = *Echinanthera cepahlostriata* + *Taeniophallus assimilis* + *T. persimilis*; Pseudoboini tribe = *Mussurana montana* + *M. quimi* + *Oxyrhopus clathratus*; Thamnodynastes = *T. strigatus* + *T. nattereri*; Tomodon = *T. dorsatus.*

	Estimate (min.)	Std. Error	Estimate (max.)	Std. Error (max.)
Atractus	0.0296	0.0141	0.1105	0.0413
Bothrops	0.0617	0.0235	0.1600	0.0459
Chironius	0.0116	0.0117	0.0648	0.0377
Echinantherini	0.0036	0.0035	0.0944	0.0281
Pseudoboini	0.0354	0.0156	0.1856	0.0702
Thamnodynastes	0.0371	0.0242	0.1320	0.0445
Tomodon	0.0163	0.0145	0.0750	0.0598

R packages

The following R packages were used in this study: *ade4, ape, bbmle, car, clue, DHARMa, geepack, geiger, gstat, MASS, MuMIn, nlme, phangorn, picante, sp, stats* and *VGAM.*

Table S3: Models built at landscape and local scales for species richness. Similar models were built for abundance, ES_PD, ES_FD, ES_FMPD and ES_MPD.

Spatial scale	Models built
Landscape	Richness ~ Native + Pasture + NP + TE
	Richness ~ Native + Pasture + NP
	Richness ~ Native + NP
	Richness ~ Native
	Richness ~ Silviculture + Pasture + NP + TE
	Richness ~ Silviculture + Pasture + NP
	Richness ~ Silviculture + Pasture
	Richness ~ Silviculture
	Richness ~ Pasture
Null model	Richness ~ 1
Local	Richness ~ Native + Silviculture + Pasture
	Richness ~ Native + Pasture
	Richness ~ Native
	Richness ~ Silviculture
	Richness ~ Pasture

Table S4: Selected models for each diversity component at the landscape and local scales, considering ΔAICc ≤ 2.0. The table shows values of intercept, slope, deviance, r-squared and the residuals tests for overdispersion and spatial correlation in GLMs. NP = number of forest patches.

	Spatial scale	Selected model	Intercept	Slope		AICc	(a) Deviance	(a) R^2
Species diversity	Landscape	Richness ~ Native + (b) NP	2.86775	Native: 1.508767	NP: 1.217623	124.9726	46.40826	-
		Abundance ~ Native + NP	3.887293	Native: 1.752904	NP: 1.308824	153.4549	45.91019	-
	Local	Richness ~ Native	3.067159	1.160267	-	131.7573	28.26815	-
		Richness ~ Silviculture	3.070711	-0.8811967	-	132.1964	27.2817	-
		Abundance ~ Native	4.390073	1.259551	-	160.1078	19.1126	-
		Abundance ~ Silviculture	4.408258	-0.8167067	-	160.5957	17.88704	-
Functional diversity	Landscape	(c) ES_FD ~ Native	0.1429	0.4073	-	66.99719	-	0.1882
		(d) ES_FMPD ~ Null	-	-	-	-	-	-
	Local	ES_FD ~ Null model	-	-	-	-	-	-
		ES_FMPD ~ Null	-	-	-	-	-	-
Phylogenetic diversity	Landscape	ES_PD ~ Native	-0.07443	0.42662	-	67.17616	-	0.207
		ES_MPD: Null model	-	-	-	-	-	-
	Local	ES_PD ~ Native + Silviculture	-0.07443	Native: 0.97730	Silvic: 0.77555	60.3401	-	0.5327
		ES_MPD: Null model	-	-	-	-	-	-

(a) Deviance values are presented for GLMs and R^2 values for LMs.

(b) NP = number of forest patches.

(c) ES_PD or ES_FD = effect size of phylogenetic or functional diversities.

(d) ES_MPD or ES_FMPD = effect size of (functional) mean pairwise distance.

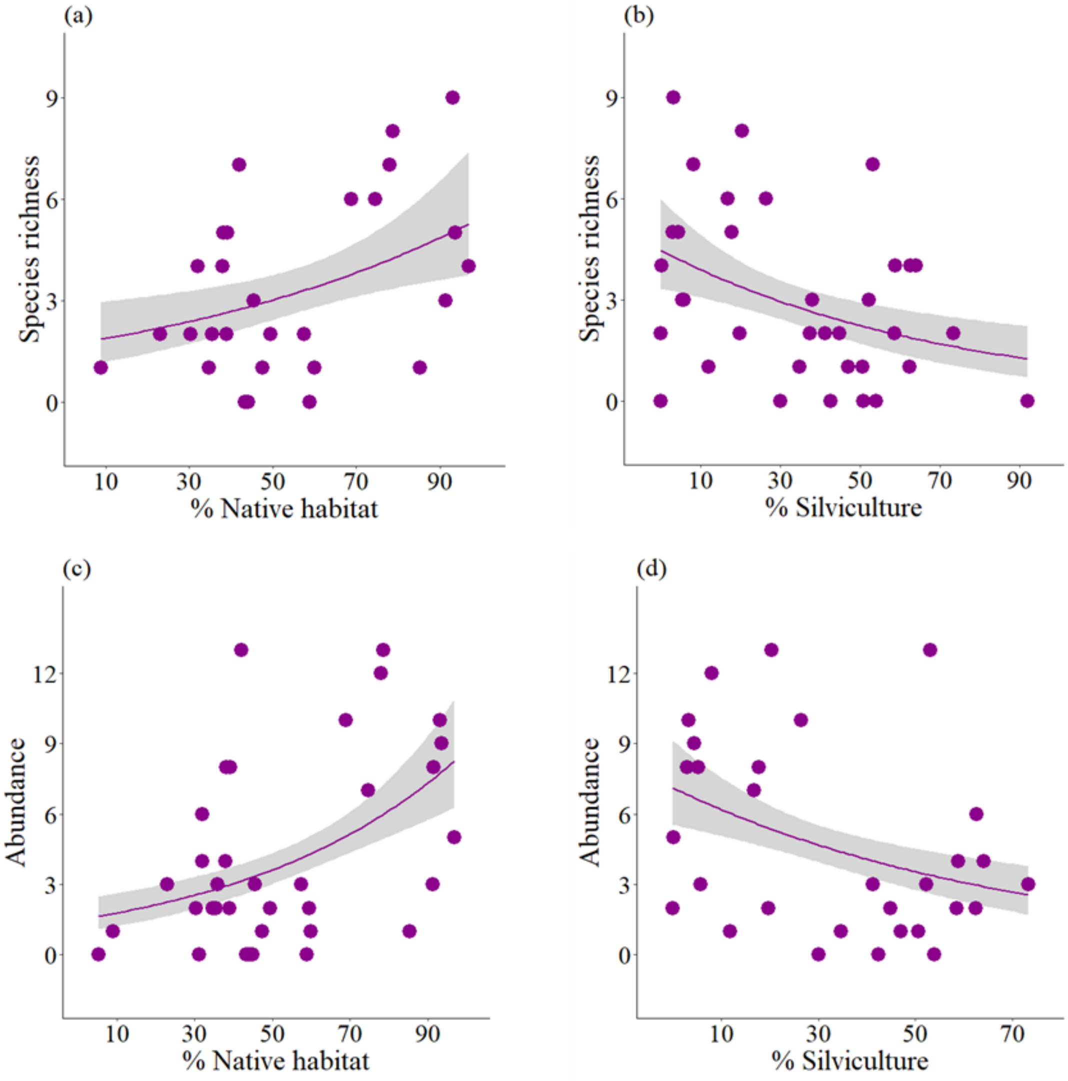

Figure S5: Relationship between selected predictor variables and predicted values of snake species richness and abundance at the local scale.

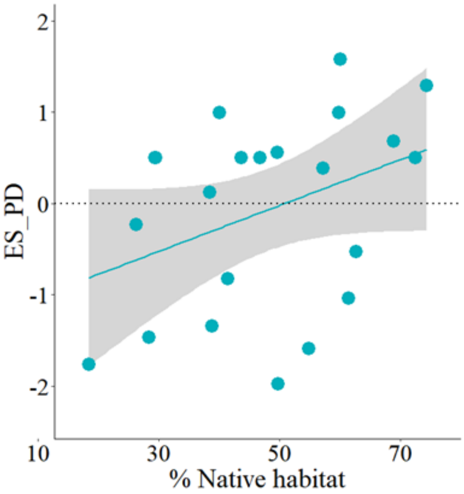

Figure S6: Relationship between selected predictor variable and predicted values of ES_PD at the landscape scale.

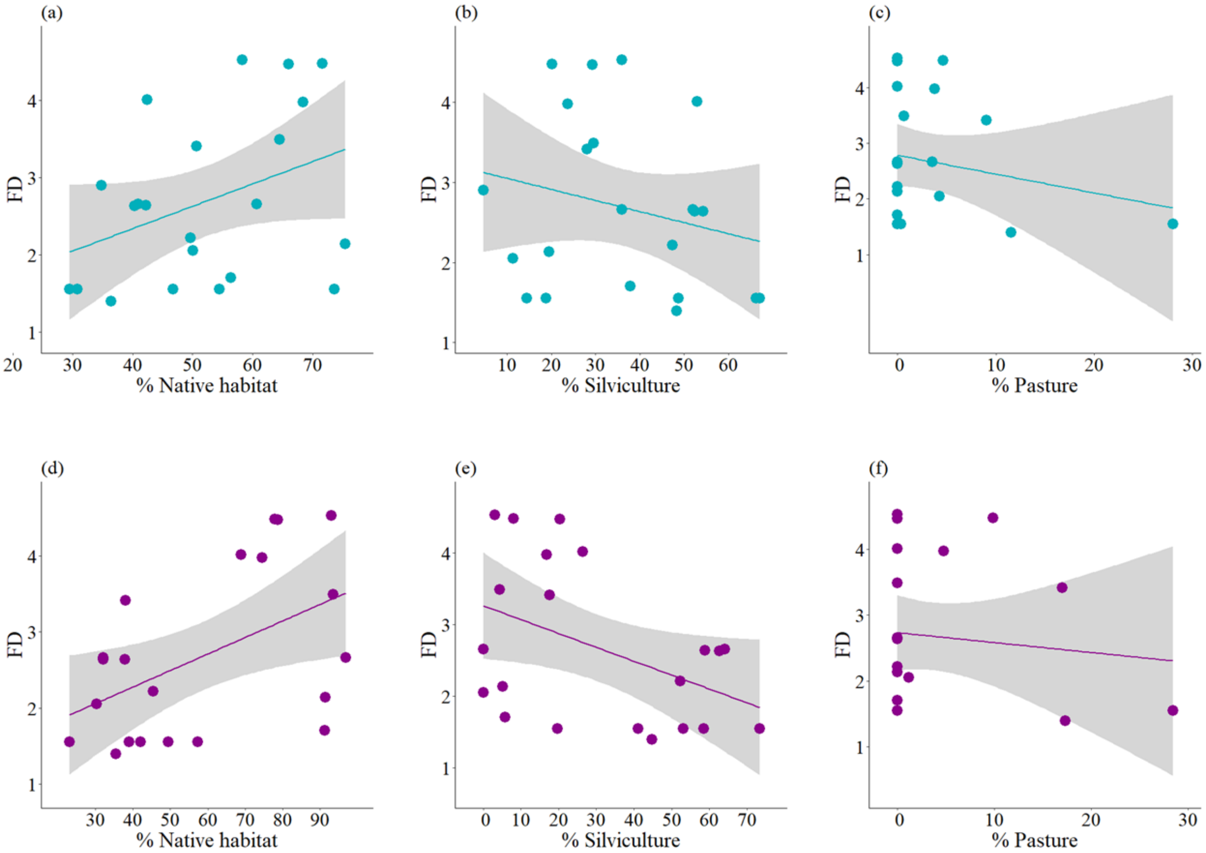

Figure S7: Relationship between raw FD and % of native habitat, silviculture and pasture at the landscape level (a, b, c) and at the local scale (d, e, f).

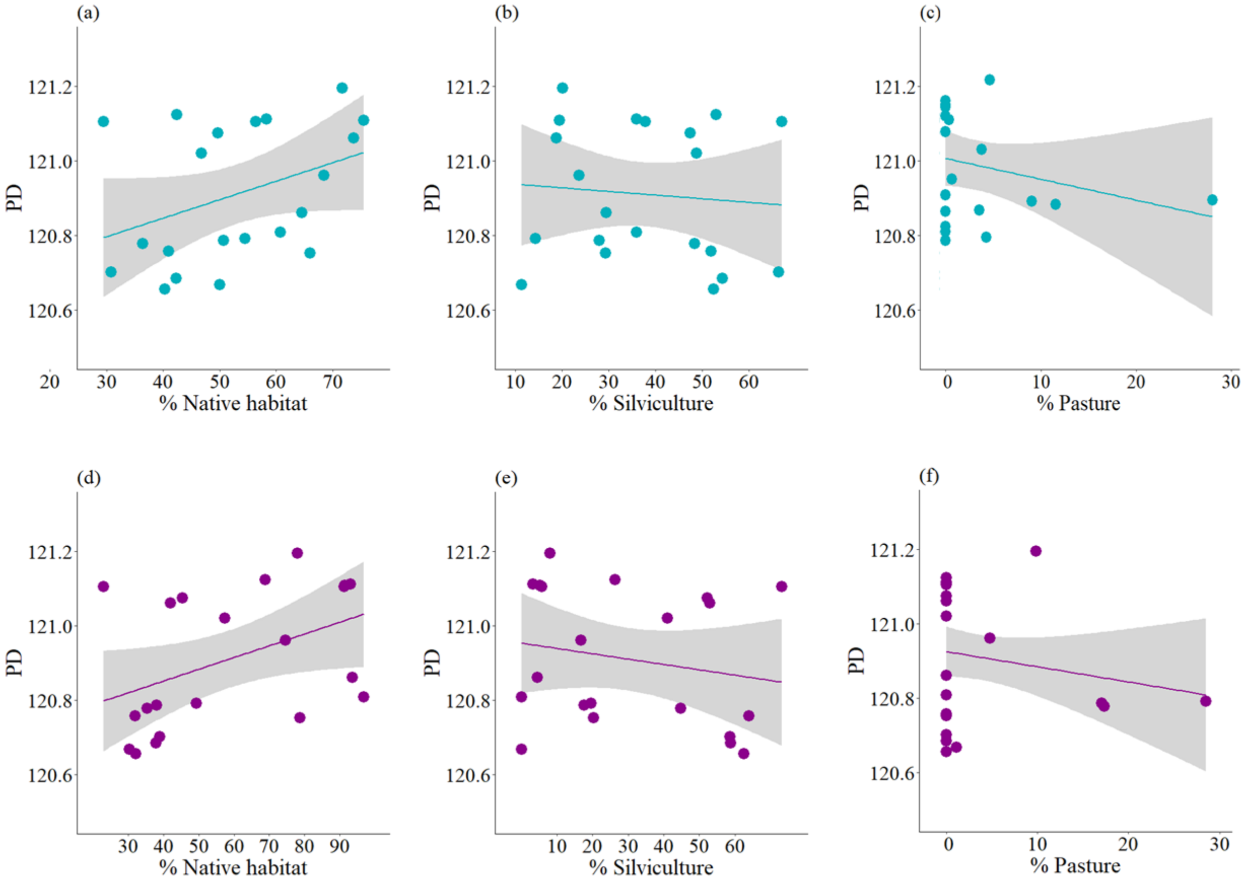

Figure S8: Relationship between raw PD and % of native habitat, silviculture and pasture at the landscape level (a, b, c) and at the local scale (d, e, f).

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APPENDIX C.

- **Snake data**

All snake trait measurements were based on data collected in this work and on literature data, except total length measures that are exclusively from this work. To obtain information in literature about snake habitat use, we considered field information of studies that recorded the number of individuals of each species found in each habitat type (native and distinct non-native types). For diet specialization, we considered the studies with diet information based on gastrointestinal contents and/or regurgitated prey, with confirmation of the identity of prey types. Diet information considered the main feeding items of the diet of species, not considering items rarely consumed by a species as its diet component. Literature used for habitat and diet specialization is provided in Table S1, for daily activity and substrate use we used the Marques et al. (2019) and for foraging mode, the data provided by Glaudas et al. (2019).

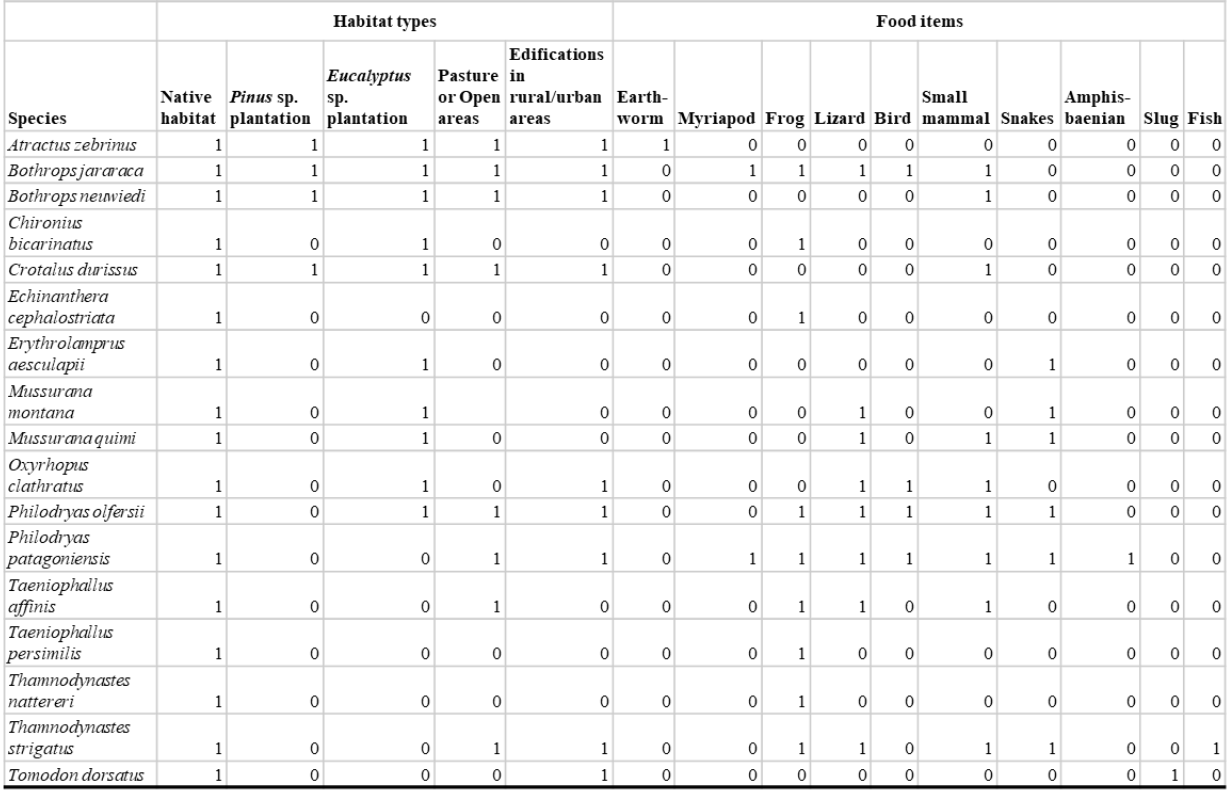
Table S1: Snake trait data.

Species	**Habitat specialization**	**Diet specialization**	**Substrate use**	**Daily activity**	**Foraging mode**	**Mean total length**
Atractus zebrinus	3	1	2	2	2	435
Bothrops jararaca	3	3	3	3	1	869
Bothrops neuwiedi	3	1	1	3	1	557
Chironius bicarinatus	2	1	3	1	2	1152
Crotalus durissus	3	1	1	2	1	967
Echinanthera cephalostriata	1	1	1	1	2	558
Erythrolamprus aesculapii	2	1	1	1	2	822
Mussurana montana	2	2	1	2	2	604
Mussurana quimi	2	2	1	2	2	530
Oxyrhopus clathratus	2	2	1	2	2	535
Philodryas olfersii	3	3	3	1	2	1055
Philodryas patagoniensis	2	3	1	1	2	1167
Taeniophallus affinis	2	3	1	1	2	498
Taeniophallus persimilis	1	1	1	1	2	417
Thamnodynastes cf. *nattereri*	1	1	1	2	2	569
Thamnodynastes strigatus	2	3	1	2	2	445
Tomodon dorsatus	2	1	1	1	2	590

Table S2: References of habitat and diet information used to classify these snake traits as levels of specialization.

Species	**References for habitat use**	**References for diet**
Atractus zebrinus	This work; Menezes et al., 2018	This work; Marques et al., 2019
Bothrops jararaca	This work; Cardoso, 2011	This work; Martins et al., 2002
Bothrops neuwiedi	This work; Cardoso, 2011	This work; Martins et al., 2002
Chironius bicarinatus	This work; Sazima & Haddad, 1992	This work; Rodrigues, 2007
Crotalus durissus	This work; Cardoso, 2011	This work; Sant'Anna & Abe, 2007
Echinanthera cephalostriata	This work; Pontes et al., 2009	This work; Gomes, 2012
Erythrolamprus aesculapii	This work; Sazima & Abe, 1991	This work; Marques & Puorto, 1994; Lopes & Vaz-Silva, 2012
Mussurana montana	This work; Menezes et al., 2018	This work; Hartmann et al., 2009; Gaiarsa et al., 2013
Mussurana quimi	This work	This work; Gaiarsa et al., 2013
Oxyrhopus clathratus	This work; Cardoso, 2011	This work; Marques & Sazima, 2004
Philodryas olfersii	This work; Sazima & Haddad, 1992; Hamdan et al., 2013	Machado-Filho, 2015
Philodryas patagoniensis	This work; Cardoso, 2011	This work; Marques & Hartmann, 2005; Pontes, 2007
Taeniophallus affinis	This work; Sazima & Haddad, 1992	Gomes, 2012
Taeniophallus persimilis	This work	Gomes, 2012
Thamnodynastes cf. *nattereri*	This work	This work; Marques et al., 2019
Thamnodynastes strigatus	This work; Cardoso, 2011	This work; Bernarde et al., 2000; Ruffato et al., 2003
Tomodon dorsatus	This work; Cardoso, 2011	This work; Sazima et al., 2005

Table S3: Information used to classify the level of habitat and diet specialization of the snake species.



	Habitat types					**Food items**									
Species	**Native habitat**	***Pinus* sp. plantation**	***Eucalyptus* sp. plantation**	**Pasture or Open areas**	**Edifications in rural/urban areas**	**Earth-worm**	**Myriapod**	**Frog**	**Lizard**	**Bird**	**Small mammal**	**Snakes**	**Amphis-baenian**	**Slug**	**Fish**
Atractus zebrinus	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Bothrops jararaca	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0
Bothrops neuwiedi	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0
Chironius bicarinatus	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Crotalus durissus	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0
Echinanthera cephalostriata	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Erythrolamprus aesculapii	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Mussurana montana	1	0	1		0	0	0	0	1	0	0	1	0	0	0
Mussurana quimi	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0
Oxyrhopus clathratus	1	0	1	0	1	0	0	0	1	1	1	0	0	0	0
Philodryas olfersii	1	0	1	1	1	0	0	1	1	1	1	1	0	0	0
Philodryas patagoniensis	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0
Taeniophallus affinis	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0
Taeniophallus persimilis	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thamnodynastes nattereri	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thamnodynastes strigatus	1	0	0	1	1	0	0	1	1	0	1	1	0	0	1
Tomodon dorsatus	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0

- **Measure of functional redundancy with presence/absence data**

Hereafter note that it should be specified that the functional distances (d_{ij}) between species are bounded between 0 and 1.

When species abundances are considered, Ricotta et al. (2016) suggested

FR = 1 - Q/D (Eq. 1)

with Q the quadratic entropy and D the Simpson index, as a measure of functional redundancy. In absence of abundance, considering that species weights are even and equal to 1/S, with S the observed number of species, Eq. 1 reduces to

$$\mathrm{FR}_{\mathrm{PA}} = \frac{\sum_{i=1}^{S}\left(\frac{1}{S-1}\sum_{j=1, j\neq i}^{S} s_{ij}\right)}{S} \qquad \text{(Eq. 2)}$$

with s_{ij} being the similarity between species i and j calculated as $s_{ij} = 1 - d_{ij}$, where d_{ij} are the dissimilarities between species i and j. $o_i = \frac{1}{S-1}\sum_{j=1, j\neq i}^{S} s_{ij}$ is the average functional similarity between species i and all others. o_i can be viewed as the functional ordinariness of species i in its community. $\mathrm{FR}_{\mathrm{PA}}$ thus is the average functional ordinariness of a species in a community. As such, it can be used as a measure of functional redundancy.

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