

**UNIVERSIDADE ESTADUAL DE SANTA CRUZ**

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**THE RELATIVE ROLE OF FOREST STRUCTURE AND LANDSCAPE SCALE  
INFLUENCING PATTERNS OF BAT AND BIRD ASSEMBLAGES IN  
ANTHROPOGENIC LANDSCAPES IN SOUTHERN BAHIA, BRAZIL**

**ILHÉUS – BAHIA**

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Orientadora: Deborah Maria de Faria

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## REVISÃO DA LITERATURA

### RESUMO

Os padrões de diversidade são determinados por processos que ocorrem em escalas espaciais distintas. Na escala da paisagem, a composição e configuração dos remanescentes florestais e da matriz são os principais determinantes dos padrões de diversidade. A estrutura da vegetação da matriz afeta a permeabilidade e define a intensidade de processos como efeito de borda e alterações na composição de espécies. De maneira geral, em paisagens com mais de 50% de hábitat a composição é determinante da diversidade, sendo a perda de hábitat o principal processo regulador das populações locais. Enquanto efeitos da configuração seriam mais evidentes quando o total de hábitat na paisagem fosse inferior a 30%. Entretanto, Martensen et al. (2012) encontraram efeitos da configuração para aves florestais em paisagens com 30-50 % de hábitat. Algumas espécies florestais são capazes de utilizar a matriz, mas a maioria desenvolveu especializações a micro habitats, micro climas e a recursos mais disponíveis em florestas maduras e prístinas, demandando uma área mínima para persistir na paisagem. Por outro lado, espécies generalistas de hábitat são, em geral, beneficiadas pela perda de habitat e fragmentação em detrimento das espécies florestais. Existem evidências de que a presença e composição de espécies de aves são mais influenciadas pela estrutura da vegetação, conectividade, tamanho do fragmento, e até que a importância do tamanho do fragmento e da conectividade depende do montante de hábitat na paisagem. O caso dos morcegos não é diferente, há trabalhos demonstrando que a diferença nas taxas de captura, riqueza e diversidade de morcegos estão relacionadas ao tamanho dos fragmentos, a estrutura local da vegetação, ao montante de hábitat na paisagem e a conectividade. Portanto, o padrão de distribuição dos organismos vai depender não só das características estruturais do ambiente e do montante de hábitat na paisagem, mas também dos requerimentos ambientais de cada táxon. A área de estudo deste trabalho, a região de Una, Bahia, Brasil, é um dos maiores remanescentes contínuos de floresta atlântica do nordeste, formado por um mosaico de ambientes estruturalmente complexos. A matriz de Una foi tida como permeável a maioria das espécies de aves e morcegos, porém, a heterogeneidade dos ambientes e suas diferentes estruturas de vegetação, promoveram mudanças na composição das espécies. Houve um incremento local de espécies generalistas, mas sem perdas de espécies florestais, demonstrando um forte efeito local. Entretanto, o efeito da cobertura florestal na paisagem e a interação desse efeito com descritores locais da estrutura da vegetação ainda permanece desconhecido. Nesse contexto, o presente estudo objetiva investigar o papel de processos operando em diferentes escalas espaciais na determinação dos padrões de riqueza e abundância de morcegos e aves a na região de Una. Especificamente, esperamos (1) que haja efeito da estrutura da vegetação, como descritor da escala local, sobre aves e morcegos, pois isso já foi descrito, (2) esperamos que não haja efeito da cobertura florestal na escala da paisagem, (3) esperamos encontrar respostas distintas entre os grupos biológicos, devido a diferenças na capacidade de locomoção, e também (4) dentro de cada grupo, entre espécies previamente classificadas como generalistas e florestais devido aos requerimentos ambientais de cada.

Palavras-chave: Escala espacial. Espécies generalistas. Espécies florestais. Matriz. Região de Una.



## LITERATURE REVIEW

### ABSTRACT

The diversity patterns are determined by processes occurring at different spatial scales. At the landscape scale, composition and configuration of the remaining forest and the matrix are the main determinants of the patterns of diversity. The vegetation structure affects the permeability of the matrix and defines the intensity of processes such as edge effect and changes in species composition. In general, in landscapes with more than 50 % of remaining habitat the composition is critical for diversity and habitat loss is the primary regulatory process of local populations. While the effects of the configuration would be more evident when the total habitat in the landscape is less than 30 %. However, Martensen et al. (2012) found effects of configuration for forest birds in landscapes with 30-50 % of habitat. Some forest species are able to use the matrix, but most developed specializations to microhabitats, microclimates and to resources more available in mature and pristine forests, requiring a minimum area to persist in the landscape. On the other hand, habitat generalist species are generally benefited by habitat loss and fragmentation in detriment of forest species. There are evidences that the presence and composition of bird species are more influenced by vegetation structure, connectivity, fragment size, and that to the importance of fragment size and connectivity depends on the amount of habitat in the landscape. The case of bats is not different, there are studies showing that the difference in catch rates and diversity of bats are related to fragment size, local vegetation structure, the amount of habitat in the landscape, and connectivity. Therefore, the pattern of distribution of organisms will depend not only on the structural characteristics of the environment and the amount of habitat in the landscape, but also to the environmental requirements of each taxon. The study area of this work, the region of Una, Bahia, Brazil, is one of the largest remaining continuous forest of northeastern Atlantic forest, formed by a mosaic of structurally complex environments. The matrix of Una is permeable to most species of birds and bats, however, the heterogeneity of the environments and their different vegetation structures, promoted changes in species composition. There was an increment of local generalist species, but without loss of forest species, demonstrating a strong local effect. However, the effect of forest cover in the landscape and the interaction of this effect with local descriptors of vegetation structure remains unknown. In this context, this study aims to investigate the role of processes operating at different spatial scales in determining patterns of species richness and abundance of bats and birds in the Una region. Specifically, we expect (1) to find an effect of vegetation structure, as a descriptor of local scale, on birds and bats, as this has already been described, (2) we expect no effect of forest cover at the landscape scale, (3) we expect to find different responses among biological groups, due to differences in flying abilities, and also (4) within each group, between species previously classified as habitat generalists and forest specialists due to environmental requirements of each.

Keywords: Spatial scale. Generalist species. Forest species. Matrix. Una region.

## 1 REVISÃO DA LITERATURA

Os padrões de diversidade são determinados por diferentes processos que ocorrem em escalas espaciais distintas (FORMAN, 1995; GASTON; BLACKBURN, 2000; WIENS; MOSS, 2005). A escala espacial está associada a dimensão espacial de um fenômeno (WU; JONES; LI, 2006) mas é definida de acordo com a espécie em estudo e, por isso, o olhar sobre a paisagem deve ser feito a partir desta espécie, de maneira a refletir seus requerimentos ecológicos (METZGER, 2001). Segundo Metzger (2001, p.4) a paisagem pode ser definida como “um mosaico heterogêneo formado por unidades interativas, sendo esta heterogeneidade existente para pelo menos um fator, segundo um observador e numa determinada escala de percepção”.

Na escala da paisagem, a composição e configuração dos remanescentes florestais e dos ambientes modificados são os principais determinantes dos padrões de diversidade (ANDREN, 1994; FAHRIG, 2003; PARDINI et al., 2010). A composição refere-se ao número e a quantidade dos diferentes tipos de ambiente que são parte da paisagem, i.e., quanto da paisagem é composto por um ambiente específico e em quantas manchas ele está distribuído (MacGARIGAL; CUSHMAN; ENE, 2012). Em paisagens antropizadas, costuma-se diferenciar ambientes nativos remanescentes daqueles que claramente sofreram modificações ou foram implementados pelo homem. Este conjunto de ambientes antropizados que envolvem os remanescentes florestais é conhecido como matriz (GASCON et al., 1999) e tem um papel importante na determinação dos padrões de diversidade existentes nas paisagens, principalmente por afetar a permeabilidade destas últimas à biota. Matrizes compostas por ambientes localmente complexos promovem mais heterogeneidade a paisagem, favorecem o intercâmbio de indivíduos entre remanescentes florestais e conferem mais conectividade a paisagem do que matrizes menos complexas, como pastagens (GASCON et al., 1999; TSCHARNTKE et al., 2005). Da mesma forma, a estrutura da vegetação da matriz também define a intensidade de outros processos como efeito de borda e alterações na composição de espécies (LAURANCE et al., 2002). Por exemplo, na Colômbia, Numa, Verdú e Sánchez-Palomino (2005) compararam a riqueza e composição de espécies de morcegos em fragmentos florestais e matrizes de plantações sombreadas e não sombreadas de café, e encontraram que as plantações sombreadas apresentam uma composição de espécies mais semelhante aos remanescentes florestais do que as plantações não sombreadas. Já Pineda et al. (2005) encontraram a mesma riqueza e composição de espécies de morcego em plantações sombreadas de café e fragmentos florestais no México. De maneira similar, na

região cacauzeira do sul da Bahia, Brasil, paisagens com matrizes de plantações sombreadas de cacau e florestas secundárias, demonstraram capacidade de manter alta riqueza de aves, morcegos (FARIA, 2006; FARIA et al., 2006), samambaias, lagartos, pequenos mamíferos e borboletas (PARDINI et al., 2009), entretanto, houve um incremento de espécies generalistas em detrimento das espécies florestais nas bordas de florestas e ambientes da matriz (FARIA et al., 2006; PARDINI et al., 2009).

A capacidade de exploração da paisagem pelos organismos também depende da configuração dos ambientes que a compõem, ou seja, do arranjo espacial e da forma destes ambientes (PRIST; MICHALSKI; METZGER, 2012). A fragmentação de hábitat, i.e. processo de subdivisão do hábitat na paisagem, é independente da perda de hábitat *per se* e afeta a biota devido a alteração resultante nos padrões originais de configuração espacial dos hábitats na paisagem (FAHRIG, 2003). Remanescentes florestais próximos entre si conferem mais conectividade a paisagem do que remanescentes distantes entre si, enquanto a forma dos fragmentos mostra a relação entre área - perímetro, traduzindo a quantidade de área nuclear e intensidade do efeito de borda com influências amplamente discutidas na literatura (ver LAURANCE et al., 2002; LAURANCE et al., 2007; PARDINI et al., 2009; PRIST; MICHALSKI; METZGER, 2012).

A importância relativa da composição e configuração dos hábitats na paisagem sobre a determinação dos padrões de diversidade pode variar. Estima-se que em paisagens com mais de 50% de hábitat nativo remanescente a composição seja a principal característica determinante da diversidade na paisagem, sendo a perda de hábitat o principal processo afetando as populações locais (ANDRÉN, 1994). Efeitos da configuração dos hábitats remanescentes parecem ser mais evidentes quando o total de hábitat remanescente na paisagem é inferior a 30%, sugerindo, portanto, que a fragmentação seria o principal processo agindo sobre os organismos (ANDRÉN 1994; FAHRIG 2003; PARDINI et al. 2010). Martensen et al. (2012), entretanto, encontraram efeitos da configuração para aves florestais em paisagens com 30-50 % de hábitat remanescente, demonstrando que os efeitos da perda e fragmentação de habitat variam entre organismos a depender de seus requerimentos ambientais e ecológicos. Na revisão feita por Fahrig (2003) a autora aponta que a perda de hábitat tem efeitos mais severos sobre a biota do que a fragmentação *per se*, afetando direta e negativamente a (1) riqueza espécies, a (2) abundância e (3) distribuição de populações e a (4) diversidade genética. Já os efeitos da fragmentação parecem ser mais idiossincráticos, com estudos mostrando impactos tanto positivos quanto negativos a depender do contexto da

paisagem e da espécie ou grupo alvo (BOSCOLO; METZGER, 2009; FAHRIG, 2003; WILLIG et al., 2007).

Muitas espécies são restritas a ambientes específicos e demandam uma área mínima para persistir na paisagem. Este é o caso da maioria das espécies florestais, que desenvolveram especializações a micro habitats, micro climas e a recursos mais disponíveis em florestas maduras e prístinas, sendo pouco resistentes a perturbações (DEVELEY; PERES, 2000; LAURANCE, 2004; WALTHER, 2002). Entretanto, apesar de dependerem das florestas, algumas espécies florestais também são capazes de utilizar a matriz (ANTONGIOVANNI; METZGER, 2005; FARIA et al., 2006; PARDINI et al., 2009). Por outro lado, espécies mais generalistas no uso do hábitat são capazes de utilizar diferentes ambientes presentes na matriz, sendo em geral, beneficiadas pela redução do tamanho dos remanescentes florestais e pela ruptura de áreas antes contínuas em detrimento das espécies florestais (LAURANCE et al., 2002; LAW; DICKMAN, 1998; PARDINI et al., 2009).

Diferenças na resposta dos organismos a perda e fragmentação de hábitat podem ser explicadas pela variação na resposta destes últimos frente as modificações na qualidade dos ambientes resultantes destes dois processos, ou seja, modificações que afetam a escala local. Por definição hábitat é o conjunto de ambientes capazes de serem explorados por uma dada espécie, sendo um conceito espécie - específico (FISCHER; LINDENMAYER, 2007), e por isso, espécies distintas respondem de maneira variada a diferentes tipos de alteração no hábitat. O hábitat é comumente descrito pelas comunidades de plantas que determinam as características estruturais do ambiente (TEWS et al., 2004). Algumas medidas como distribuição do diâmetro das árvores, e distribuição vertical da folhagem (GARDEN et al., 2007; McELHINNY et al., 2005; THIOLLAY, 1997), são importantes descritores utilizados para avaliar a complexidade e heterogeneidade de ambientes florestais, bem como a adequabilidade destes para as espécies (FARIA et al., 2009; TEWS et al., 2004). De fato, alterações gerais dos padrões locais de heterogeneidade e complexidade estrutural dos habitats muitas vezes exercem maior influencia na adequação destes últimos para as espécies do que sua composição *per se* (MacARTHUR; MacARTHUR, 1961), principalmente em paisagens com poucos remanescentes florestais originais (UEZU; METZGER, 2011). A diversidade local, portanto, pode ser influenciada por processos locais reguladores de sobrevivência e reprodução, associados a condições bióticas e abióticas dentro das manchas (MacARTHUR; LEVINS, 1964; SHURIN; ALLEN, 2001) e por fatores medidos em escalas mais amplas, como a diversidade do conjunto regional de espécies, o tipo de uso da terra (CROME; RICHARDS, 1988; PATRIQUIN; BARCLAY, 2003; HEMP, 2005; WILLIG et al., 2007), e

processos ecológicos operando em escalas maiores (DeFRIES et al, 2010; FORMAN, 1995). O movimento dos indivíduos entre manchas (DUNNING; DANIELSON; PULLIAM, 1992; HANSKI; GILPIN, 1997) influencia na persistência de populações pela disponibilidade e uso de recursos (DUNNING; DANIELSON; PULLIAM, 1992; WIENS, 1989) e pela colonização e recolonização de manchas (LEVINS, 1970; BROWN; KODRICK-BROWN, 1977). Desta forma, a distribuição e abundância das espécies dependem do balanço entre processos em escalas espaciais distintas (LAWTON, 1999; RICKLEFS, 1987) o que dificulta a previsão da ocorrência destas últimas a partir de um conjunto de informações limitado a uma única escala (PETERS et al., 2004; SCHOOLEY; BRANCH, 2007).

Espécies e grandes grupos biológicos apresentam ampla variação de respostas tanto aos processos que ocorrem em escalas espaciais distintas, quanto a tipos variados de alterações antrópicas nestas diferentes escalas (LAW; DICKMAN, 1998; LAURANCE et al., 2001; LAURANCE et al., 2002; TSCHARNTKE et al., 2005; PINTO; KEITT, 2008; DeFRIES et al., 2009). No entanto espera-se que grupos ecológicos com características semelhantes respondam de maneira similar a estas alterações operando em diferentes escalas. Aves e morcegos, por exemplo, estão entre os vertebrados com maior riqueza local de espécies, com grande papel na funcionalidade ecológica dos sistemas ecológicos, principalmente nas florestas tropicais onde são importantes vetores para a dispersão de sementes, polinização e controle de populações de insetos (HAILA, 1985; FINDLEY, 1993; FLEMING, 1993; GORRESEN; WILLIG, 2004; WIENS, 1989; WILLIG et al., 2007). Da mesma forma, a riqueza de ambos é intimamente ligada à presença e complexidade estrutural das florestas (ESTRADA; COATES-ESTRADA, 2002; LEMAÍTRE et al. 2012) e por serem capazes de voar, tem maior vagilidade se comparados a outros grupos de vertebrados terrestres, sendo plausível esperar que sejam influenciados por escalas espaciais distintas. Existem evidências de que a presença e composição de espécies de aves são mais influenciadas pela estrutura da vegetação (ALEIXO, 1999; KHANAPOSHTANI et al., 2012, 2013), conectividade (BOSCOLO; METZGER, 2011; UEZU; METZGER; VIELLIARD, 2005), tamanho do fragmento (UEZU; METZGER; VIELLIARD, 2005) e que a importância do tamanho do fragmento e da conectividade, dependem do montante de hábitat remanescente na paisagem (BETTS et al., 2006). Corroborando com essa variedade de respostas, Banks-Leite, Ewers e Metzger (2013) testaram a influência da escala local, i.e. estrutura da vegetação, escala do fragmento, i.e. tamanho e forma dos fragmentos florestais, e da cobertura florestal na escala da paisagem em aves de sub-bosque, e encontraram que no nível da comunidade a qualidade do hábitat na escala local foi o melhor descritor, enquanto no nível

das espécies as respostas foram tão variáveis que não foi possível encontrar um padrão geral. O caso dos morcegos não é diferente, há trabalhos que demonstram que a diferença nas taxas de captura, riqueza e diversidade de morcegos estão relacionadas ao tamanho dos fragmentos (COSSON; PONS; MASSON, 1999), a estrutura local da vegetação (AVILA-CABADILLA et al., 2009; FENTON et al., 1992; FARIA et al., 2006; NUMA; VERDÚ; SÁNCHEZ-PALOMINO., 2005; PINEDA et al., 2005), ao montante de hábitat na paisagem (GORRESEN; WILLIG; STRAUSS, 2005; PINTO; KEITT, 2008) e a conectividade (HENRY; PONS; COSSON, 2007).

A área de estudo do presente trabalho, a região de Una, sul da Bahia, Brasil, é um dos maiores remanescentes contínuos de floresta atlântica do nordeste, formado por um mosaico de ambientes, sendo grande parte florestas maduras (49%), seguida por áreas abertas (27%), florestas secundárias (15%), cabrucas (4%) e seringais (2%) (PARDINI, 2004). Vários grupos biológicos, incluindo aves e morcegos, já foram estudados nesta região na tentativa de entender sua capacidade de retenção da biodiversidade visto que a partir de uma perspectiva teórica, i.e. alta proporção de florestas maduras parcialmente envoltas por uma matriz estruturalmente complexa, ela apresenta um contexto favorável (FARIA; SOARES-SANTOS; SAMPAIO, 2006; FARIA et al., 2006, 2007; PARDINI et al., 2009). Tanto para aves quanto para morcegos a matriz é tida como permeável a maioria das espécies, já que não foram encontradas diferenças na riqueza e composição de espécies entre fragmentos florestais de tamanhos diferentes, porém houveram mudanças na composição de espécies a depender do ambientes amostrado na matriz (PARDINI et al., 2009). Estes estudos explicam a variação do uso dos ambientes pelos organismos pela estrutura da vegetação, que reflete a qualidade do ambiente para cada taxon, demonstrando que existe um efeito da escala local (PARDINI et al., 2009). Nesse contexto, o presente estudo objetiva investigar o papel de processos operando em diferentes escalas espaciais na determinação dos padrões de riqueza e abundância de morcegos e aves a na região de Una. Especificamente, esperamos (1) que haja efeito da estrutura da vegetação, como descritor da escala local, sobre aves e morcegos, pois isso já foi descrito na literatura, (2) esperamos que não haja efeito da cobertura florestal na escala da paisagem ou que ocorra apenas sobre a abundância e riqueza das espécies florestais devido a maior exigência ambiental deste grupo e a elevada quantidade de cobertura florestal na área, e por fim (3) esperamos encontrar respostas distintas entre os grupos biológicos, devido a diferenças na capacidade de locomoção, e também (4) dentro de cada grupo, entre espécies previamente classificadas como generalistas e florestais devido aos requerimentos ambientais de cada uma.

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## **THE RELATIVE ROLE OF FOREST STRUCTURE AND LANDSCAPE SCALE INFLUENCING PATTERNS OF BAT AND BIRD ASSEMBLAGES IN ANTHROPOGENIC LANDSCAPES IN SOUTHERN BAHIA, BRAZIL**

### **ABSTRACT**

Habitat loss is an important anthropogenic process influencing the patterns of biodiversity distribution. Currently, most of the remaining landscapes are mosaics of different land uses, where anthropogenic pressure alters their ability to maintain biodiversity. Local and landscape scale conditions and ecological requirements of species, define the potential of organisms to persist in these landscapes. Therefore, I studied the relative effects of vegetation structure and forest cover at the landscape scale on birds and bats in a mosaic landscape in Una region, Bahia, Brazil, particularly testing for interactive effects. Besides the comparison between taxa, I also tested these latter effects on species previously classified as forest dependent and generalists, using richness and abundance as response variables. I discussed the issue of scale by testing the effect of forest cover on five possible landscape scales, using an information theoretic approach. Different from expected, bat and bird assemblages were influenced by both scales, but responses were different between groups and assemblages of forest dependent and generalist species. The variation in richness and abundance of birds was largely explained by the interactive effect between local and landscape descriptors, while bats showed a less clear pattern of interactive response. Generalist species of bats and birds were benefited by the heterogeneity of environments that comprise the landscape, presenting high species richness and abundance. However, generalist birds showed a greater capacity to use the matrix in relation to generalist bats, fact associated to differences in flight strategy between groups. Both generalist assemblages responded to forest cover in various landscape scales, preventing us to identify a single scale of influence. As expected, forest birds were more demanding about the local quality of the environment, being poorly represented in the matrix, and to high forest cover in large spatial scales. These results suggest different conservation strategies for each assembly. While generalists do not seem to demand management efforts in Una, the conservation of forest birds is a most urgent priority, since they require large tracts of continuous forest across the landscape. Also, my results indicate that for some the remaining forest in the study area is not ideal. Most of the area under study is protected by the Una Biological Reserve and Una Wildlife refuge, but as reported in other conservation units, the forests harboring these species are still under anthropogenic pressure. Therefore, effective management for forest birds should focus in enhancing the inspection of these protected areas, and in stimulating the creation of privately owned reserves, especially in mature forest remnants adjacent to the existing protected areas of Una region.

*Keywords:* Habitat loss. Forest dependent species. Habitat generalist species. Information theoretic approach. Interaction.

## 2.1 INTRODUCTION

Habitat loss is an important anthropogenic process influencing the current patterns of biodiversity distribution, particularly species abundance and richness (PIMM; RAVEN, 2000; TSCHARNTKE et al., 2005). Most of the remaining landscapes are now mosaics of habitat patches embedded in a matrix with different land uses where anthropogenic pressure alters the ability of such landscapes to retain biodiversity by removing habitat cover and by simplifying or altering the remaining habitat (see TSCHARNTKE et al. 2005). The reduction of native vegetation has direct impacts on the viability of populations through changes in area requirements (LINDENMAYER et al., 2008), reducing the connectivity (GASCON et al., 1999; MEYER; KALKO, 2008; PRIST et al. 2012; UEZU; METZGER, 2011), the species source pool and species complementarity (TSCHARNTKE et al., 2005). Likewise, the simplification of habitat patches drives local changes in vegetation structure (FARIA et al., 2009), consequently reducing the available species-specific habitat requirements (KHANAPOSHTANI et al., 2013), jeopardizing exchanges among local systems (TSCHARNTKE et al., 2005) and changing species composition (PARDINI et al., 2010).

The influences of habitat loss and fragmentation over biodiversity are hard to disentangle as both are scale and context-dependent. Andrén (1994), in a study of simulated landscapes, proposed a fragmentation threshold starting at <30% of original habitat in the landscape, from which the remnants would be isolated or poorly connected and therefore, the fragments per se would be crucial in maintain biodiversity, i.e. the processes occurring in the local scale would be more important in determining biodiversity patterns. Andrén (1994) also predicts that in landscapes with high amounts of forest cover (e.g. over 50%) the short distance between remnants would allow organisms to move throughout the whole landscape, i.e. the processes occurring in the landscape scale would be more important in determining biodiversity patterns. According, Pardini et al. (2010) empirically demonstrated the existence of the 30% threshold for non-volant small mammals, while Martensen et al. (2012) found understory birds were influenced by fragmentation in landscapes with 30-50% of remaining habitat. Such differences between empirical studies were attributed to the distinct ecological requirements of both taxonomic groups (MARTENSEN et al., 2012) and highlights the variety of effects that habitat loss and fragmentation may exert on organisms. Another issue is that theoretical models neglect the matrix role in buffering the effects of habitat reduction and

fragmentation, which may allow populations to persist in fragmented landscapes (TSCHARNTKE et al., 2005).

The study of landscape cover impacts automatically implies in scale-dependence, and the relative importance of processes operating in local or landscape scales will change with the total amount of forest cover in the landscape, which statistically implies an interaction between landscape and local descriptors. As organisms perceive the landscape differently, we are still establishing the scales at which habitat amount might influence them (FAHRIG, 2003; TSCHARNTKE et al., 2005), contributing to the actual debate about the relative importance of local and landscape scales mainly due to the implications of this information for conservation planning. For example, Gorresen, Willig and Strauss (2005) found habitat amount was a significant predictor of bat abundance and assemblage structure in scales above 3 km in radius. While Boscolo and Metzger (2009) searched for the optimum landscape scale to predict the occurrence of three bird species and found each one to be strongly correlated to a particular spatial scale, which was related to variation in species area requirements due to dietary needs. Likewise, there are various studies demonstrating that forest specialists and habitat generalists give different answers to the question of the relative importance of landscape and local effects and to the scale at which landscape effects operate (BETTS et al., 2006; BOSCOLO; METZGER, 2011; PARDINI et al., 2009; PINTO; KEITT, 2008). Local variables found to be important include the vertical profile (GARDEN et al., 2007; THIOLLAY, 1997) and the diameter distribution of trees (MCELHINNY et al., 2005), descriptors of the forest structure used to assess the complexity and the heterogeneity of environments, and determining intra-habitat mobility of animals (GARDEN et al., 2007) with many studies demonstrating their influence over biological groups (ACKER et al., 1998; BREARLEY et al., 2004; LOEB; O'KEEFE, 2006; PACIENCIA; PRADO 2005; PARDINI et al., 2009). For example, in original or disturbed environments, low vegetation clutter, forest gaps and openings are known to provide suitable commuting and foraging habitat for bats (KUSCH et al., 2004; LAW; CHIDEL, 2002; LOEB; O'KEEFE, 2006), while for birds changes in the original forest structure due to logging were related to a significant decrease in avian richness, abundance, diversity (KHANAPOSHTANI et al., 2013; THIOLLAY, 1997) and species composition (ALEIXO, 1999), because differently from bats, many bird species are restricted to specific vertical strata inside the forest (WALTHER, 2002).

The most important structural parameters for the maintenance of animal communities are likely to be different for each taxonomic group (FARIA et al., 2009), but some factors may have a key function and affect groups or species that share ecological similarities



(GARDEN et al., 2007), like bats and birds. Both groups encompass most vertebrate species in Neotropical forests in the local scale, because of their trophic diversity are crucial for the functioning of tropical ecosystems (e.g. HAILA, 1985; FINDLEY 1993; WIENS, 1989) and as both are able to fly, which in general confers more mobility, are likely to be influenced by a range of spatial scales. Therefore, we studied the relative impacts of local and landscape descriptors on bird and bat fauna in mosaic landscape, characterized by high amounts of forest cover (>65%), particularly testing for interactive effects. We expect (1) to find an effect of vegetation structure, as a descriptor of the local scale, on birds and bats, as this has already been described (FARIA, 2006; PARDINI et al., 2009), (2) we expect no effect of forest cover at the landscape scale, (3) we expect to find different responses among biological groups, due to differences in flying abilities, and also (4) within each group, between species previously classified as habitat generalists and forest specialists due to different environmental requirements of each. We addressed the question of scale by testing the possible effects of the forest cover in five landscape scales, using an information theoretic approach. This study was performed in one of the Earth's major biodiversity hotspots where a mosaic landscape exists and is under continuing pressure, and where the conservation management implications of the answers to these questions have major importance in the preservation of biodiversity.

## 2.2 METHODS

### 2.2.1 Study area

The area under study comprises approximately 15,000 ha of a forest mosaic in different successional stages (FARIA et al. 2009). The region harbors one of the largest amounts of Atlantic Forest of Northeast Brazil, including two continuous conservation units, the Una Biological Reserve (REBIO Una) and Una Wildlife Refuge (REVIS Una), that together encompass nearly 42,000 ha of protected areas (see Figure 1). Nearly 50% of the studied landscape is dominated by mature forest fragments, 27% of pasture, 15% by early secondary forests, 6% by shade cacao plantations and 2% by rubber tree plantations (PARDINI, 2004). Most of the shade cacao plantation is under *cabruca*, a traditional system in which cacao shrubs (*Theobroma cacao*) are grown under the shadow of a few native canopy trees. Despite the intense fragmentation process in this landscape, most forest tracts

are not completely isolated, and the matrix remains permeable for most species (PARDINI et al., 2009).

The original vegetation is classified as tropical lowland rainforest (OLIVEIRA-FILHO; FONTES, 2000) and harbors tall vegetation, characterized by a stratification in lower, canopy and emergent layers, and abundant in epiphytes, ferns, bromeliads and lianas (THOMAS et al., 1998). Mean annual temperature is 24° C and rainfall averages 1.500 mm/year (MORI et al. 1983).

### 2.2.2 Sites selection and sampling design

This study is part of a multitaxonomic inventory, the RestaUna Project, carried out from September 1997 to August 2000 at Una Biological Reserve and surrounding areas, located in the municipality of Una and Ilhéus, Bahia, Brazil (Figure 1) (PARDINI et al., 2009). Bats and birds were surveyed in five different forest categories that comprised the bulk of the forest mosaic, namely edges and interiors of large (>1,000 ha) and small (< 100 ha) mature forests fragments and interiors of secondary forests (FARIA et al. 2009). But in the present work mature forests, secondary forests and *cabruças* were pooled together into a single landcover class named forest cover (FC).

### 2.2.3 Species sampling

The sampling sites were distributed along three spatially separated blocks of 5583 ha ( $\pm$  362 ha), each block (I, II, III) encompassing 10 sites, totaling 30 sampling sites (Figure 2). In each sampling site were established two parallel 200 x 2 m plots where the vertical forest structure was estimated (FARIA et al., 2009). In each site, bats were equally sampled on four non-consecutive nights using eight 2.5 m high ground mist nets of length, covering a nightly a sampling area of 165 m<sup>2</sup> for 5 h after sunset (FARIA, 2006). Because ground mist nets are a selective sampling method (KUNZ; KURTA, 1988) findings were restricted to understorey phyllostomid bats.

Birds were monitored by point count surveys, establishing three points located 100 m apart along each 200 m transect (FARIA et al., 2007). All points were sampled at five hourly intervals starting at sunrise. Nocturnal birds were not included in the dataset (FARIA et al., 2007). Points sampled in the same time interval were 200 m apart. Each point was

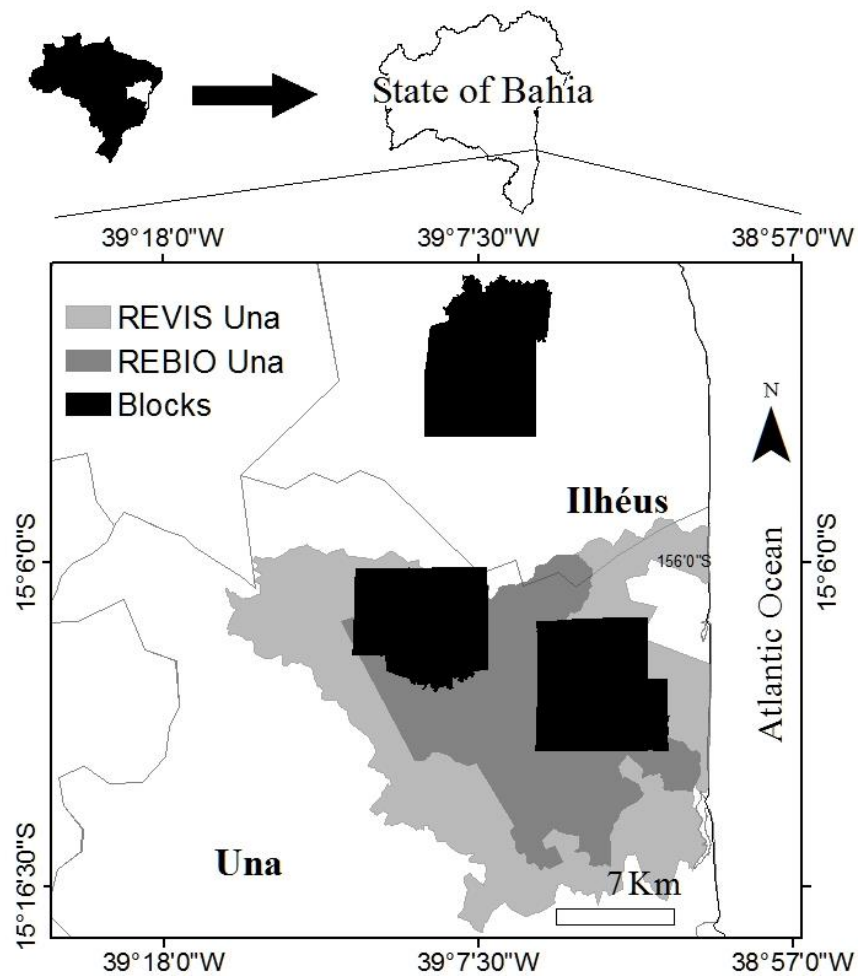


Figure 1 - Map of Brazil, highlighting the state of Bahia and inside the framework the region of Una. In the same region the sampling blocks and the protected areas of Una Biological Reserve (REBIO Una) and Una Wildlife Refuge (REVIS Una).

sampled for 15 minutes, and all birds sighted or heard in a 30 m fixed-radius were recorded (FARIA et al., 2007). Each transect was sampled over a period of 7–12 days.

#### 2.2.4 Local and landscape metrics

We used vertical and horizontal vegetation profiling to generate metrics of local patch quality (table 1). Foliage profile - a descriptor of forest vertical structure - was assessed following Malcolm (1995), by estimating the interval occupied by foliage in eight forest vertical strata (v) in 24 points in each sampling transect: 0-1 m; 1-5 m; 5-10 m; 10-15 m; 15-20 m; 20-25 m; 25-30 m and 30-35 m (FARIA et al. 2009). We used the mean interval of points with contact in each stratum for the analysis. As horizontal descriptors we used the

diameter at breast height (d.b.h.) of each woody tree measured along a two parallel 200 x 2 m plots located in each sampling site. Each individual was assigned to the following d.b.h. classes: 5-10 cm, 10-15 cm, 15-25 cm, 25-35 cm and > 35 cm (FARIA et al. 2009).

We then derived additional synthetic variables to describe hypothetical differences between local habitats impacted by human disturbance. More mature forest often has distinct vertical gaps such as a relatively low vegetation cover at 5m above ground level (compared to denser cover near ground level and at 10m (FARIA et al. 2009). We therefore summed the cover at 0 to 1 m and 5 to 10 m, and created the variable G1R to represent the ratio between this quantity and the cover at 1-5m (PEKIN et al., 2012). Differentially-affected habitat patches can also differ in the number of vertical strata and in the presence or absence of the uppermost vertical strata (MCELHINNY et al., 2005). We therefore created the metrics S and CLCu described in Table 1 (PEKIN et al., 2012). Differences in local patch quality can also be captured in statistics of horizontal structure such as the standard deviation of diameter at breast height (sddbh) (MCELHINNY et al., 2005), and so we further calculated it by using the d.b.h. of each measured woody tree (Table 1).

The landscape metric corresponds to the amount of forest cover (FC), and was calculated from a landcover map, produced by stereoscopy interpretation from a set of 1:10,000 aerial photographs taken in 1997 together with ground truthing, where the identification of the main habitats that comprise Una region were included (FARIA et al. 2009). We measured the FC at five concentric circles around each sampling site (henceforth landscape scale), with radius varying in 200 m intervals from 200 – 1,000 m (Figure 3). Forest cover in each of the landscape scales was calculated using Patch Analyst 5 extension (ELKIE, P.; REMPEL, R.; CARR, 1999) for ArcGIS software version 9.3.1 (ENVIRONMENTAL SYSTEMS RESEARCH, 2009).

#### 2.2.5 Classification of species

For birds we adopted a previous classification in which species assemblages were separated in forest specialists or generalists according to the level of species dependence of forested habitats (see PARDINI et al. 2009). For bats, due to the scarcity of gleaning animalivorous species (e.g. forest dependent) we restrict our findings to generalist species.

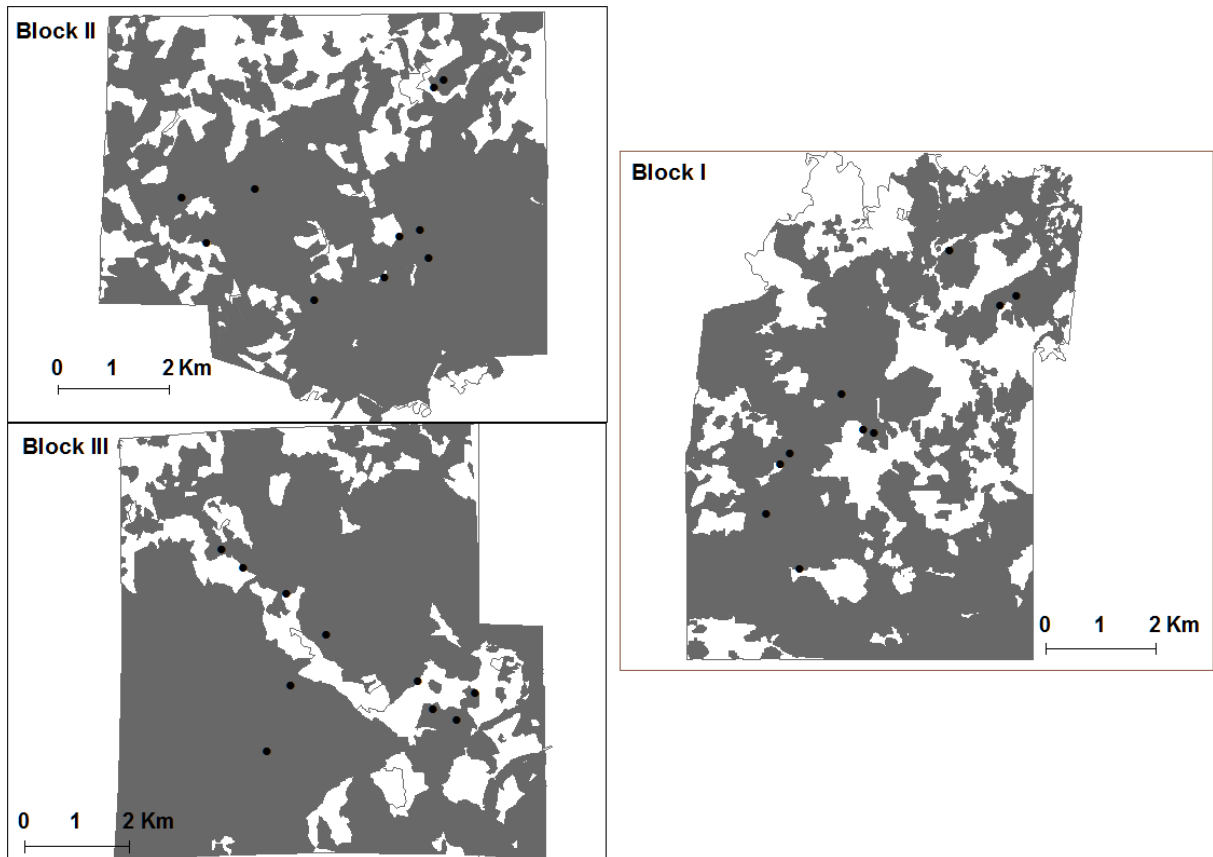


Figure 2 - Sampling blocks (II, I and III) in Una region demonstrating the forest cover (dark grey), open areas (white) and the location of the sampling sites (black spots) (modified after Pardini (2004)).

Table 1 - Metrics used to characterize the local scale and the equations used to calculate them

Metrics	Atributes	Description
Sddbh	$\sigma = \sqrt{E[(X - \mu)^2]}$	Standard deviation of the diameter at breast height
S	$n_s$	The number of different vertical strata in each site (strata defined as the number of our vertical height categories in which cover was greater than the tenth percentile of cover from the pooled sample.
G1R	$(v_{0-1} + v_{5-10}) / v_{1-5}$	Vertical gap ratio at approximately 1-5 m with higher values showing greater gap definition
CLCu	$v_{1-10} / (v_{1-10} + v_{10-20})$	Foliage cover of lower canopy relative to upper canopy, a measurement that reflects the level of complexity and development of mid-story trees, with lower values meaning a less developed understory ( $v_{1-10}$ ) relatively to canopy layer ( $v_{10-20}$ )

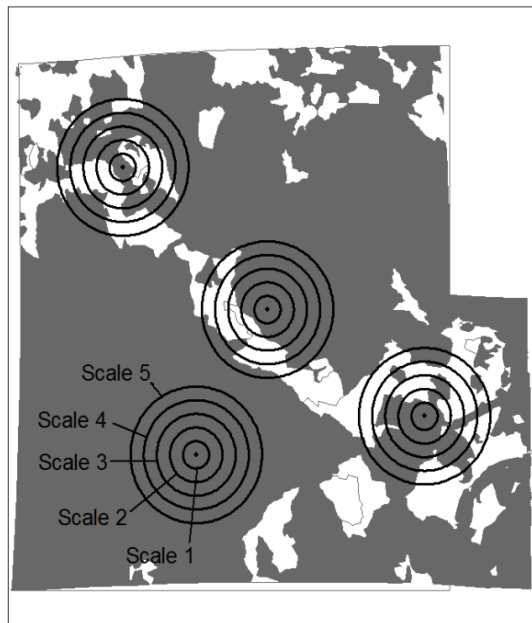


Figure 3 - Schematic illustration of the general approach used to measure FC amount. For each site, they were measured at increasingly larger scales (200 a 1000 m).

### 2.2.6 The statistical models

We performed a standardization procedure prior the analyses among the independent variables by subtracting each observation by the mean of the variable and dividing by the standard deviation. We tested the effects of local and landscapes variables separately on (a) abundance and (b) richness of forest (i) habitat specialist birds, (ii) habitat generalist birds and (iii) habitat generalist bats, a total of six separate broader-scale analyses. Within that broad analytical framework, we tested for improvements in model fit generated by varying the individual patch structure metric, and by varying the scale at which forest cover was measured. Specifically, the models were run at five possible landscape scales, 200 m to 1000 m radius at 200 m intervals. We converted observed richness to estimated total richness using the Chao1 statistic. Individual descriptors of local patch structure could potentially be strongly correlated, both with each other and with forest cover, creating collinearity problems in regression analyses (DORMANN et al., 2007). Sample size was 30, suggesting that models including several terms in a multivariate framework might have limited power. We therefore limited all models to testing a maximum of a single local metric, forest cover and an interaction, optionally including a block effect. We reduced problems with collinearity by excluding from analysis any local variable with a correlation of  $\geq 0.7$  with the forest cover variable at the scale being tested (DORMANN et al., 2007). Nevertheless, collinearity

between forest cover and local patch variables also suggests that an observed landscape effect might simply be an artifact, in which an apparent landscape effect could be better explained by a local effect with which landscape forest cover happens to be strongly correlated. Indeed, initial exploration of the correlation structure between variables suggests that this was likely to be a potential problem. We therefore tested further models in which the forest cover term was sequentially replaced by all local patch descriptors that had a correlation of  $\geq 0.7$  with forest cover at the scale tested (Appendix).

Each sub-analysis therefore considered one local patch structure metric and forest cover at one scale, and tested separately for four possibilities: (1) Dependent variable explained only by local patch structure; (2) Dependent variable explained only by forest cover; (3) Dependent variable explained by both local patch structure and forest cover; (4) Dependent variable explained by local patch structure and forest cover in interaction. A further four options tested the importance of a block effect in addition to these basic patterns.

The procedures described imply a large number of possible models, so we tested models in an automated program that used an information theoretic framework (BURNHAM, KENNETH; ANDERSON, 2002), script created by A. Waldron and available on request from the author) and compared model fit on the basis of the second order Akaike Information Criterion (AICc) to avoid the problems of multiple comparisons in a hypothesis testing approach (BURNHAM; KENNETH; ANDERSON, 2002). We considered all models with delta AICc  $< 2$  as equally plausible (BURNHAM; KENNETH; ANDERSON, 2002) and used model weights between the same local descriptors to verify which effect is stronger, the additive, interactive or the single scale model. We performed Generalized Linear Models (GLMs) with negative binomial errors, chosen in preference to Poisson error structures to minimize problems associated with overdispersion in an automated framework (ZUUR et al., 2009). Best-fitting models were further examined using diagnostic plots, including plots comparing fitted models to observed data and semiovariograms to examine possible non-independence of errors due to spatial autocorrelation (CRESSIE, 1993). Analyses were run using the R package (R CORE TEAM, 2013), and the packages Vegan (Oksanen et al. 2013), MuMIn (Barton, 2013), geoR (Ribeiro Jr and Diggle 2001), MASS (RIPLEY et al., 2013) and nlme (Pinheiro et al. 2013) respectively to calculate the Chao index, to calculate Akaike values, to create semivariograms and to perform negative binomial GLMs.

## 2.3 RESULTS

We recorded 19 species of generalist bats from 1,241 captures, nearly 80% of the captures comprised only three common species, *Carollia perspicillata* (33.68%), *Rhinophylla pumilio* (34.17%) and *Artibeus obscurus* (10.41%). For birds we found 8,590 registers and 192 species, broken down into forest dependent (35 species, 1,821 individuals) and generalist species (157 species, 6,769 individuals). Forest dependent birds are mostly represented by canopy and understory frugivorous and insectivorous species, with three species (*Drymophila squamata* (20%), *Herpsilochmus pileatus* (11%) and *Pyriglena leucoptera* (10.54%), comprising 42 % of the registers). Both forest dependent and generalist birds are mostly represented by insectivorous and frugivorous species. The forest cover presented small variation (Mean = 72.1% / Sd = 6.01%), always representing more than 66% of the environment in all landscape scales.

### 2.3.1 Model selection

#### 2.3.1.1 Abundance of generalist bats

Bat abundance was influenced by larger spatial scales, 800 m and 1000 m, with six possible models explaining these relationships: two interactive, three additive and one for the local scale only (Table 2). In interactive models, higher foliage density in the upper strata (15-20m) was associated with higher bat abundance, but the strength of this effect increased as landscape-level forest cover decreased (Figure 4a). Forest cover has minimal effects on abundance in habitats where upper strata have low or zero density (low values of v15-20) (Figure 4b), but strongly negative effects where the upper strata are well represented (Figures 4a;b). The other interactive model included the level of clutter in the understorey vegetation (CLCu, see Table 2). Lack of clutter in the understorey (low values CLCu) increased abundance when FC was low (Figures 4c;d), but the strength of this effect declined to near-zero as the amount of FC in the landscape increased to maximum levels (e.g.v15-20 and CLCu) (Figures 4a;b;c;d).



Table 2 - Combinations of variables best explaining the abundance and richness of generalist bats (ABAT and RBAT, respectively) and birds (ABGBD and RGBD, respectively) and the abundance and richness of forest dependent birds (ABFBD and RFBD, respectively):

	Block	Coef Local	Coef Land	I	AICc	$\Delta_i$	$w_i$	Local	scale	Land
ABAT	NA	0.2154246	-0.2342406	NA	252.35	0.12	0.48	v15-20	1000	FC
	NA	0.2194103	-0.1813554	NA	253.29	1.07	0.41	v15-20	800	FC
	NA	-0.216754	-0.2398491	0.201	253.31	1.09	0.42	CL_Cu	1000	FC
	NA	0.2118278	-0.2423065	-0.11	253.83	1.61	0.23	v15-20	1000	FC
	NA	0.2228577	NA	NA	254.08	1.85	0.69	v15-20	200	FC
	NA	-0.206435	-0.2177152	NA	254.14	1.92	0.28	CL_Cu	1000	FC
RBAT	NA	0.2279493	-0.0965025	-0.47	134.85	0.00	0.94	G1R	400	FC
	NA	0.3266919	NA	NA	135.03	0.17	0.58	Sddbh	200	FC
	NA	0.3046168	-0.1991989	NA	135.03	0.18	0.39	Sddbh	1000	FC
	NA	0.2534571	-0.1493743	-0.15	135.91	1.06	0.28	Sddbh	400	FC
	NA	0.3049831	-0.1369915	NA	135.94	1.08	0.31	Sddbh	800	FC
	NA	0.3029238	-0.0944179	NA	136.37	1.51	0.22	Sddbh	400	FC
	NA	0.307164	-0.1003748	NA	136.38	1.53	0.26	Sddbh	600	FC
	NA	0.2733987	-0.2228745	-0.13	136.74	1.89	0.16	Sddbh	1000	FC
ABGBD	NA	-0.265205	-0.2794783	-0.21	305.28	0.00	0.89	v20-25	200	FC
RGBD	NA	0.095185	-0.011821	0.117	244.97	0.00	0.76	v1-5	400	FC
	NA	0.1047706	-0.0104354	0.13	245.63	0.66	0.80	v1-5	600	FC
ABFBD	+	0.1690771	0.1997934	0.127	290.92	0.00	0.89	Sddbh	200	FC
RFBD	NA	0.1325578	0.2199959	0.167	193.57	0.00	0.52	v20-25	800	FC
	NA	0.1382721	0.2103099	0.145	195.04	1.48	0.34	v20-25	1000	FC
	NA	0.1380264	0.1931002	NA	195.09	1.52	0.33	v20-25	1000	FC
	NA	0.1343635	0.162124	NA	195.42	1.85	0.21	v20-25	800	FC

+ = Block included in the model; Coef Local = coefficient of the local metric; Coef Land= Coefficient of the landscape metric; I = Coefficient of the interaction when present;  $\Delta_i$ = Delta AICc;  $w_i$  = correspondent weights for models with the same local descriptors; Local = local metrics and Land = landscape metric; and NA= Not available.

### 2.3.1.2 Richness of generalist bats

Similar to the abundance, the strength of the effect of local descriptors on richness is weak or even negative when habitats are immersed in landscapes with high amounts of FC, but the strength of this effect increases with decreasing FC until it becomes strongly positive

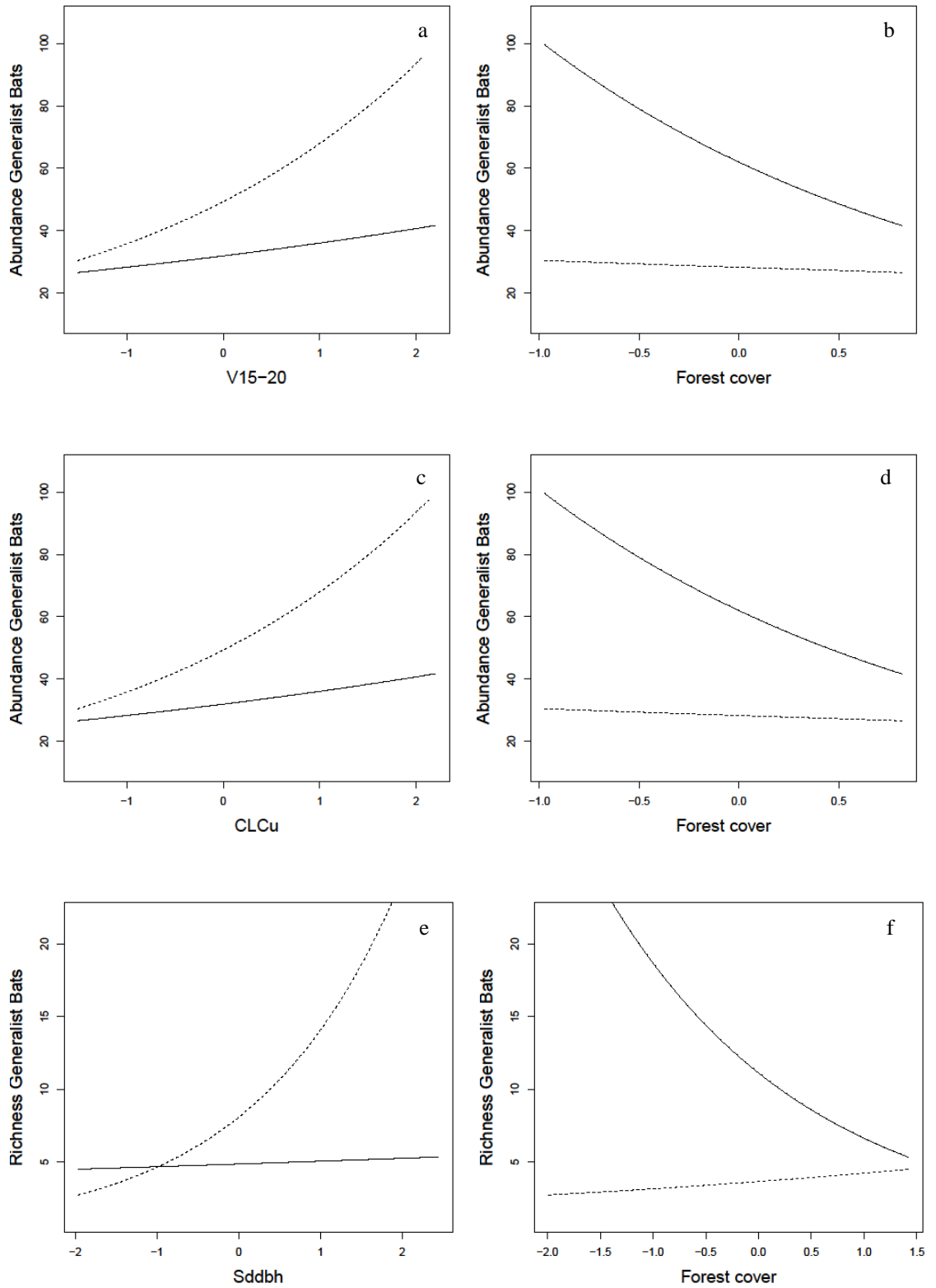


Figure 4 - Interaction plots for predicted values for abundance and richness of generalist bats in two scenarios; (a,c,e) the local scale: Solid line = maximum values of forest cover; dotted line = minimum values of forest cover; and (b,d,f) the landscape scale: Solid line = maximum values of the local predictor; dotted line = minimum values of local predictor.

in largely open landscapes. For bats, habitat quality appears to be related to high values of sddbh or the presence of vegetation gap at 1-5 m (G1R), as the pattern of both interactions is similar we only present the results of sddbh. The richness of generalist bats is higher in habitats with gaps of foliage along an understory stratum, or with a high variance in tree sizes (high values of G1R or sddbh), but the strength of this effect increased as landscape-level FC decreased (Figures 4e;f). As the quality of the landscape becomes more similar to the habitat quality, local bat richness gradually drops (Figure 4f). This community descriptor responded to scales above 400 m, had 8 possible models: 5 additives, 2 interactive and 1 showed a local effect only, than all possibilities are statistically supported (Table 2).

#### 2.3.1.3 Abundance of generalist birds

The abundance of birds responded to canopy cover (v20-25) and forest cover in the 200 m scale (Table 2). Bird abundance is high when canopy cover is also high (high values of v20-25) and the strength of this effect is increased with decreasing FC in a landscape scale (Figure 5a), if FC is increased abundance is sharply reduced (Figure 5b). In habitats with low canopy cover (low values of v20-25) abundance can also be relatively high and the amount of FC in the landscape is largely irrelevant (Figure 5b).

#### 2.3.1.4 Richness of generalist birds

The richness of generalist birds responded to the interaction between v1-5 and FC in the 400 m and 600 m scales, the interaction doesn't change much with scale so the interpretation is similar (Table 2). Greater richness is related to habitats with high clutter in the understory (high values of v1-5) and the strength of this effect is increased in landscapes with intermediate to high amounts of FC (Figures 5e;f). However, richness can still be high in a better quality habitat (low values of v1-5) and this effect is increased in landscapes with low amounts of FC (Figures 5e;f).

#### 2.3.1.5 Abundance of forest dependent birds

Abundance of forest dependent birds responded to the interaction between sddbh and FC in the 200 m scale and presented a block effect (Table 2) correspondent to statistical

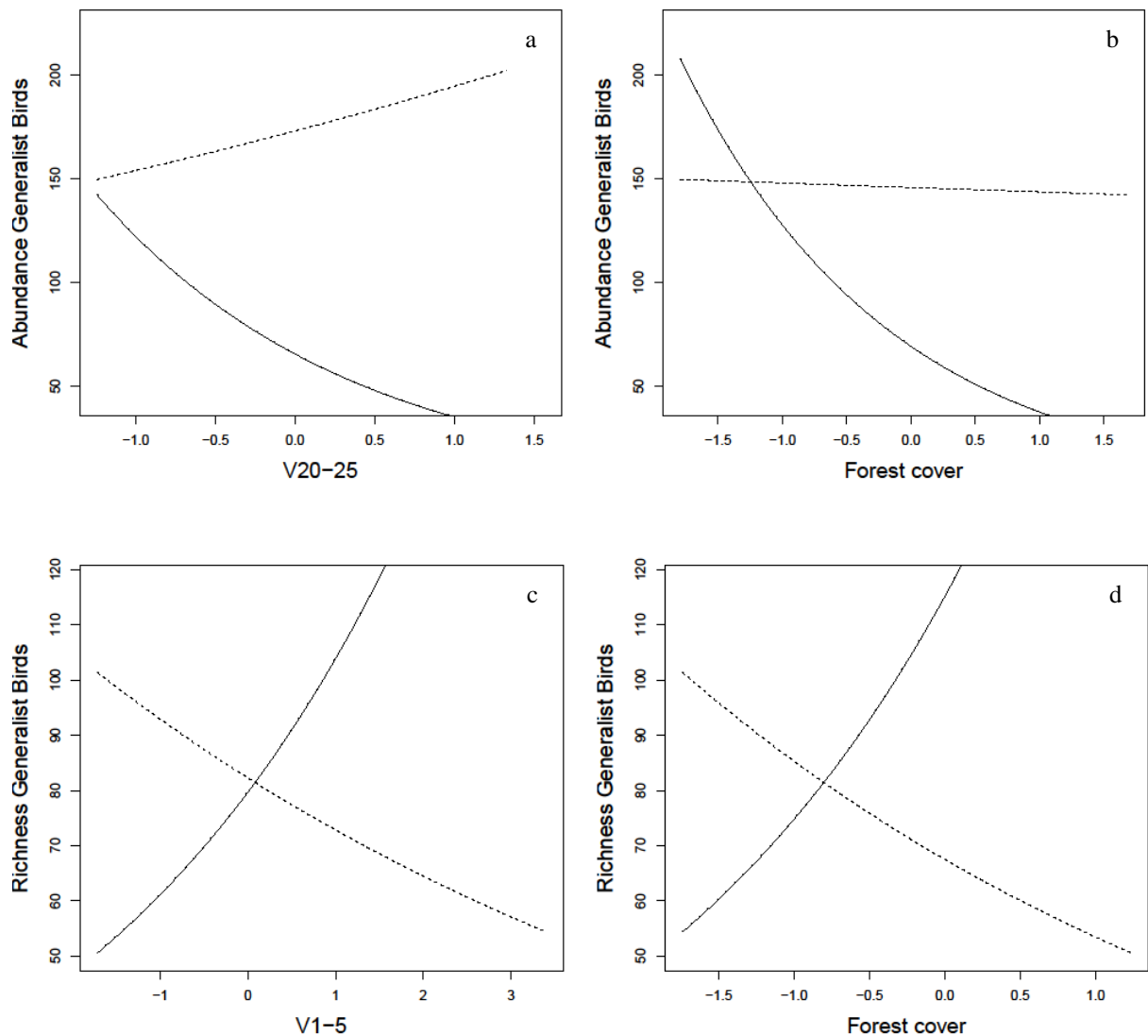


Figure 5 - Interaction plots for predicted values for abundance and richness of generalist birds in two scenarios; (a,c) the local scale: Solid line = maximum values of forest cover; dotted line = minimum values of forest cover; and (b,d) the landscape scale: Solid line = maximum values of the local predictor; dotted line = minimum values of local predictor.

differences in mean abundance between blocks. Abundance will be highest in habitats with a high variance of tree sizes (high values of sdbh) and the effect is increased when FC is high in the 200 m scale (Figure 6a;b). If the habitat has a more homogenous distribution of tree sizes (low values of sdbh) abundance is held low independent of the effect of forest cover in the 200 m landscape (Figure 6b). Similarly, if FC is low abundance is held low and local quality effect (high or low values of sdbh) doesn't change this pattern (Figure 6a).

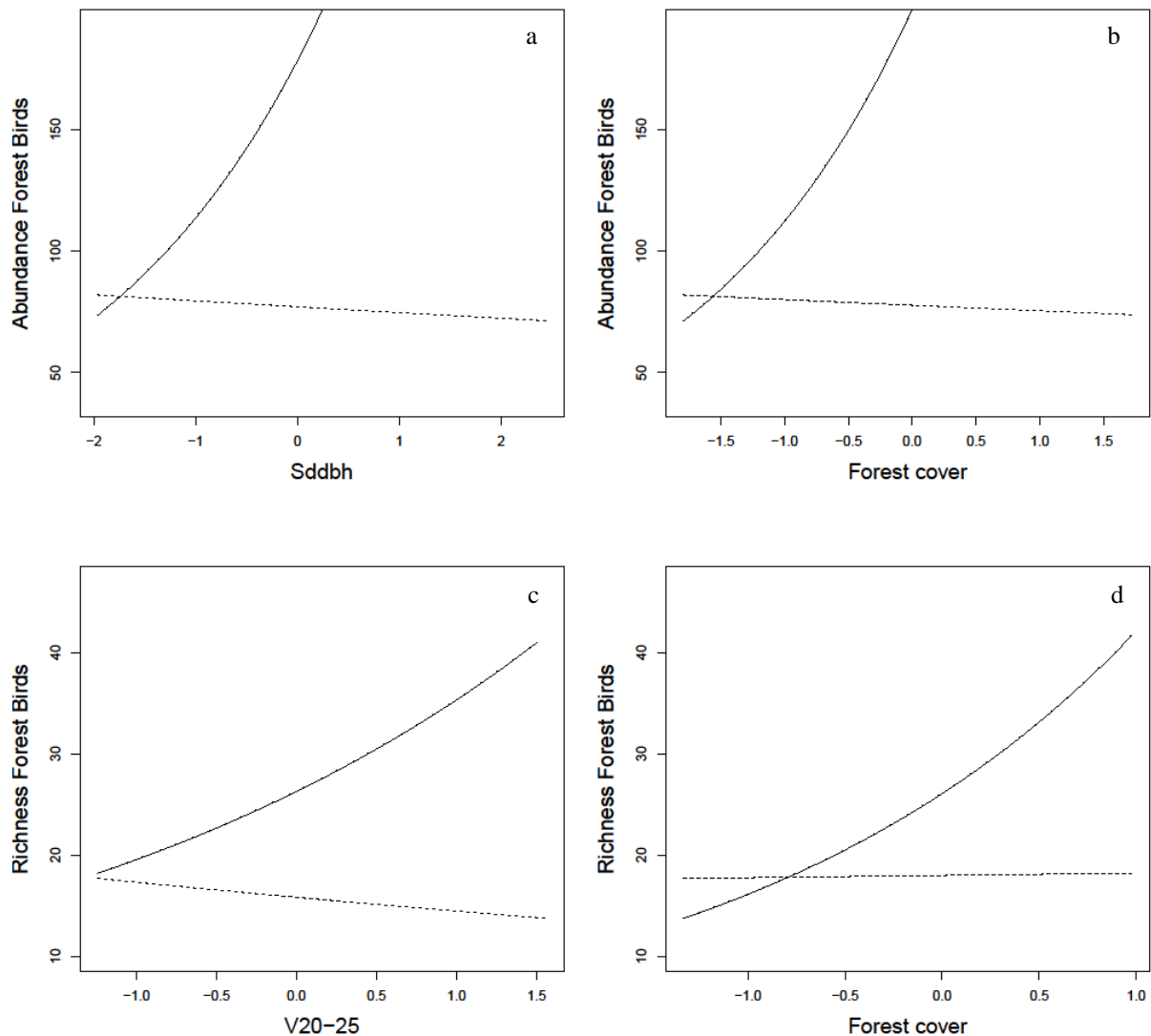


Figure 6 - Interaction plots for predicted values for abundance and richness of forest dependent birds in two scenarios; (a,c) the local scale: Solid line = maximum values of forest cover; dotted line = minimum values of forest cover; and (b,d) the landscape scale: Solid line = maximum values of the local predictor; dotted line = minimum values of local predictor.

### 2.3.1.6 Richness of forest dependent birds

The richness of forest dependent birds responded to v20-25 and FC in the 800 m and 1000 m scales in both additive and interactive models (Table 2). The interaction interpretation showed that richness is always higher in habitats with high canopy cover (high values of v20-25) surrounded by high FC above 800 m (Figure 6c;d). If the habitat is surrounded by minimum values of FC in the landscape scale above 800 m the richness will be low and local effect doesn't change this pattern (Figure 9c). Similarly, if the habitat presents minimum

values of canopy cover (low values of v20-25), the strength of the effect of FC in the landscape is irrelevant and the richness will be held low and constant (Figure 6d).

### 2.3.2 Spatial autocorrelation (SAC)

The abundance of forest dependent birds presented a pattern in space, however, we did not find the traditional pattern of increasing model residuals similarity with decreasing distance that implies in type one errors (Cressie 1993) (Figure 6), therefore, we did not apply corrections for SAC. There may be incomplete independence between observations in forest dependent bird abundance models and parameter estimates may be biased as a result, with unclear impacts on the results of model selection.

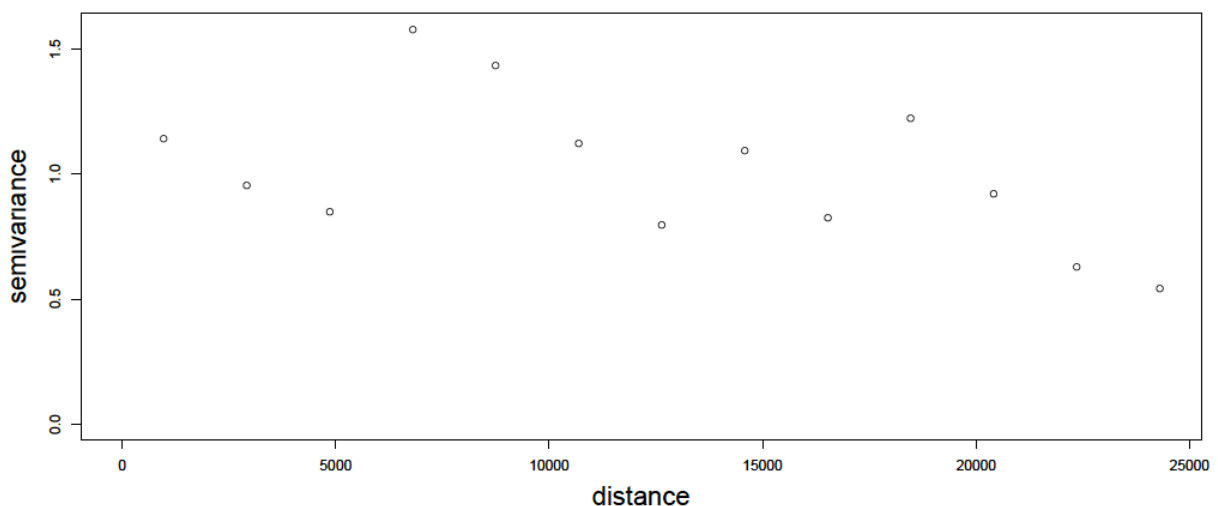


Figure 6 - Semivariogram of the abundance of forest dependent birds.

## 2.4 DISCUSSION

### 2.4.1 The relative impacts of forest structure and habitat amount on generalist species

As expected, we encountered a pervasive effect of the forest structure on the abundance and richness of generalist bats and birds in Una, corroborating previous studies in the same area (FARIA, 2006; FARIA; BAUMGARTEN, 2007; FARIA et al., 2006;

PARDINI et al., 2009) and worldwide (ALEIXO, 1999; AVILA-CABADILLA et al., 2009; GHADIRI KHANAPOSHTANI et al., 2013; KALKO; HANDLEY, 2001; WILLIG et al., 2007). However, we were able to identify which elements of the vegetation structure were more determinants to describe the patterns of abundance and richness of both groups.

For generalist bats, habitats with a well developed canopy layer (v15-20 m), less dense understory (low CLCu) and with the presence of thick trees (High sddb) are likely to present high values of local species richness and abundance, such as interiors of forest fragments and *cabruca*s. By contrast, secondary forests are mainly characterized by a single thick foliage stratum up to 10 m height (FARIA et al., 2009). For instance, while 90% of bat species were registered in *cabruca*s, including nearly all the forest-dependent gleaning bats, secondary forests were considered as suboptimal habitats due to the low species richness and virtually no captures of gleaning bats (FARIA, 2006). Although the three abundant bat species were ubiquitously reported among all sampling sites, their abundances markedly differed among habitat types (FARIA, 2006). These local features are consistent with important ecological requirements of bats, particularly related with flight. While a well developed canopy layer provide bats with food and shelter, including a protective cover from predators, a less developed understory may facilitated bat to maneuver during flight. Although bat species can markedly differ in their ability to explore different textures of habitat type, dense vegetation can impose an important physical barrier for bats limiting their movements through the habitat. This agree with studies in temperate and tropical regions (ERICKSON; WEST, 2003; KUSCH et al., 2004; LOEB; O'KEEFE, 2006; NUMA; VERDÚ; SÁNCHEZ-PALOMINO, 2005).

The variation in bat abundance is influenced by the fluctuation in capture frequency of only three frugivorous species, but local pattern of species richness incorporates more species that have different requirements, with local predictors more clearly related to habitat quality (high values of sddb) and the presence of gaps within the forest (G1R) being selected. The sddb is a measure of variation in tree size, and is considered an indicative of micro-habitat diversity within the environment (ACKER et al., 1998), while G1R reflects well defined gaps within the forest known to facilitate maneuver, providing suitable commuting and foraging habitat for bats (LOEB; O'KEEFE, 2006). While tropical bird communities present a vertical stratification (WALTHER, 2002) studies on bats point to an overall less clear pattern of vertical habitat partitioning. Habitat quality for a generalist bat might be simply translated to the presence of roosts and free space to fly within a forest environment.

The interactive effect of the forest cover and local variables in increasing bat abundance and richness was only observed in landscapes with low amounts of forest cover, this might explain the lower weights of these models in relation to the additive, and local scale models, since the studied landscapes are always represented by high amounts of forest cover. Despite the many plausible models, we suggest bat richness and abundance patterns are likely to be determinate by the local vegetation structure in detriment of the amount of forest cover in the landscape. Bats often use multiple, contrasting environments in order to match their ecological requirements (LAW; DICKMAN, 1998) and the increase in abundance and richness of generalist bats in Una was also related to more contrasting scenarios (e.g. mature forests and cabruças within landscapes with low forest cover). This contrast is greater in larger spatial scales and in the edges between forest types. Bat richness was associated to scales above 400 m while abundance was associated to larger spatial scales (800 to 1000 m). Although the home ranges of bats are poorly known, Gorresen et al. (2005) studied some bat species common to this work and found each species responded similarly to landscape characteristics at scales of 3 km to 5 km in radius. This might suggest that the processes influencing the most abundant generalist bats are operating in scales above the one we have worked, and if this is true, the encountered landscape scale of response might be underestimated.

Generalist birds, as well as generalist bats, are usually favored by contrasting scenarios but the interactive effect was the best to explain this pattern. Richness of generalist birds decrease with vegetation clutter (high values of v1-5) in habitats surrounded by minimum values of forest cover in intermediate scales, i.e. 400-600 m, perhaps because some generalist bird species, like generalist bats, may present difficulties to maneuver in these habitats or because there will be a lack of other forested habitats that could contribute to species able to use multiple habitats (LAW; DICKMAN, 1998). While in a landscape with high amounts of forest cover, which is the case of Una, a cluttered habitat is likely to be different from its surroundings and beta diversity at the interface might increase (LAW; DICKMAN, 1998). Una's landscape is a complex mosaic of different habitat physiognomies and their interfaces (e.g. edges) where previously linked to the main changes in animal assemblages composition favoring generalist species (PARDINI et al., 2009). Model results show generalists are benefit in habitats with high clutter in the understory or with a high canopy cover (high values of v20-25) both surrounded by low amounts of FC in a small scale (200 m). But the real scenario is of high amounts of FC in such a small scale, so generalists' abundance might be concentrated in forest edges and high clutter habitats such as secondary forests of Una.



Habitat generalist birds, in contrast to generalist bats, are able to use secondary forests and edges (PARDINI et al., 2009), habitats associated with high insect abundance (see LUNDE; HARESTAD, 1986; KALCOUNIS; BRIGHAM, 1995; GRINDAL; BRIGHAM, 1999) which are the prey of the bulk of generalist assembly. They also presented a smaller spatial scale of response to FC than bats, suggesting that small and intermediate scales of Una's landscapes may provide more resources or niches for this group, possibly because generalist birds are able to use secondary forests that bats cannot, so they fly less searching for resources. They also might benefit by less contrasting scenarios than bats, which might reflect the buffering effect of secondary forests in mature forests, and ecological constraints of the species that compose the generalist assemblage. Therefore, overall response for generalists shows their high capacity to explore different habitats with differing levels of disturbance (LAURANCE et al., 2002).

#### 2.4.2 The relative impacts of forest structure and habitat amount on forest species

Forest dependent birds, as expected, presented the most distinct response to changes in local and landscape characteristics. They are more abundant when local and small-scale landscape qualities are high, i.e. high values of sddbh and FC in 200m scale, respectively. Abundance patterns might be biased towards the most abundant species: *Pyriglena leucoptera*, *D. squamata* and *H. pileatus*. The territory size of *P. leucoptera* is estimated to be less than 2 ha (DUCA et al., 2006) and the species present a low capacity of gap-crossing between fragments (AWADE; BOSCOLO; METZGER, 2011). *Drymophila squamata* is widely distributed in the Atlantic forest (RAJÃO; CERQUEIRA, 2006) but like *H. pileatus* present little ecological information on the literature (WHITNEY et al., 2000). These birds were captured in all habitats of Una's mosaic, including edges (FARIA et al., 2006), features that might have contributed for their high abundance in Una. By contrast, for high richness they also need high quality habitats (high values of v20-25) and high forest cover in large spatial scales (>800 m). Highest richness levels are achieved only when high quality habitats are present in landscapes with high forest cover in large scales. In contrasting scenarios (e.g. high quality habitat x low FC in the landscape) richness of forest dependent birds is generally low. The forest birds from Una are mostly represented by canopy and understory frugivorous and insectivorous, with many endemic species to the Atlantic forest and under threat (Silveira and Straube 2008). Forest birds are known to present clear vertical stratification (WALTHER, 2002), being adapted to dark humid conditions of forest interiors (LAURANCE; STOUFFER;

LAURANCE, 2004), having little need to cross clearings or non-forested areas in their evolutionary history (GREENBERG, 1989) or to persist in habitats with harsher conditions such as edges (LAURANCE et al., 2004, 2002). So unwillingness to leave old-growth forests may be an intrinsic behavioral response of these assemblages (GREENBERG, 1989) reflecting constraints of morphology or behavior, as some species may be unable to use secondary growth areas (WINKLER; LEISLER, 1985). Develey and Peres (2000) found forest insectivorous species to have a more restricted diet, with many foraging through huge areas to guarantee the required intake of energy. Likewise, large frugivores also need large areas of suitable habitat to fulfill their ecological requirements (BUCHMANN et al., 2013). Therefore, the encountered pattern for richness of forest birds is reflecting the necessity of high quality habitats and large forest tracts to ensure the maintenance of the ecological requirements described above.

## **2.5 CONCLUSIONS AND CONSERVATION REMARKS**

The forest cover in the five landscape scales we've measured showed a decrease in the proportional representation of mature forests and an increase in disturbed habitats in larger spatial scales. However, because we did not discriminate among different habitat types while measuring FC in each landscape scale, the value of FC was relatively constant among them. Still, forest cover influenced bat and bird assemblages demonstrating that different taxonomic groups encompass a range of species-specific responses to habitat structure, loss (BUCHMANN et al., 2013; FAHRIG, 2003) and heterogeneity (TSCHARNTKE et al., 2005). Therefore, we than can draw five main conclusions on our study: (1) contrary to our expectations bat and bird assemblages were influenced by both local and landscape scales; (2) but as we expected the influence of local metrics and landscape scales varied within and between assemblages. (3) Generalist species presented a more similar pattern of influence to habitat loss than forest dependent species, benefiting by contrasting scenarios. (4) Birds typically respond to the interaction between landscape and local effects, while (5) generalist bats were influenced by both scales interactively, additively or mainly by the local scale.

The plasticity in habitat requirements presented by generalist bats and birds reduces their proneness of extinction making their conservation strategy distinct from forest dependent species. In Una region, where landscapes still hold a significant amount of forest remnants

and heterogeneous habitat types, we found abundant and rich assemblages of generalist bats and birds demonstrating they do not need large continuous forested areas, but in contrast to forest birds, are benefitted by the encountered pattern of habitat simplification and loss. However, differences in structural features among habitat types, and in different landscape contexts, affected differently both assemblages. We were not able to identify a single best scale of response for generalists, as a consequence of the many plausible scales in the model selection and probably to idiosyncrasies of the species included in this group. However, for bird species, we have found a strong interactive effect between local and landscape measures that might be considered in future modeling. Nevertheless, generalists do not seem to be in need of management in Una, they will be naturally rich and abundant if the mosaic remains as it is. Although generalist species are less vulnerable to habitat or landscape disturbances, it is important to not forget that they are all native taxa and might be responsible for the maintenance of important ecological services as soon as other species disappear in anthropogenic landscapes (TSCHARNTKE et al., 2005).

Conservation of forest dependent birds is more concerning since this group depends on high quality habitats and high amounts of forest cover throughout the whole landscape and our findings indicate that for some the remaining forest cover of the area studied is not ideal. Most of the area studied is under protection by the *Rebio Una* and *Revis Una*, but as reported in other conservation units the forests harboring these species are still under anthropogenic pressure. Therefore, effective management for forest species should focus in enhancing the inspection of these protected areas, and in creating privately owned reserves (RPPN), especially in mature forest remnants adjacent to existing protected areas of Una.

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## APPENDIX

Table of intervariable correlations among the local predictors and forest cover (FC).

	CLCu	S	Sddbh	V0-1	V1-5	V5-10	V10-15	V15-20	V20-25	V25-30	V30-35	G1R	FC
CLCu	1.00	-0.66	-0.73	0.20	0.57	0.50	-0.85	-0.92	-0.75	-0.61	-0.33	-0.21	0.04
S	-0.66	1.00	0.51	0.01	-0.07	-0.12	0.55	0.63	0.71	0.38	0.38	0.02	-0.19
sddbh	-0.73	0.51	1.00	0.04	-0.38	-0.36	0.63	0.65	0.48	0.64	0.15	0.18	-0.22
V0-1	0.20	0.01	0.04	1.00	0.52	0.26	-0.09	-0.12	-0.23	-0.04	-0.07	-0.14	0.05
V1-5	0.57	-0.07	-0.38	0.52	1.00	0.52	-0.29	-0.47	-0.43	-0.40	-0.35	-0.57	-0.11
V5-10	0.50	-0.12	-0.36	0.26	0.52	1.00	-0.19	-0.41	-0.44	-0.41	-0.12	0.34	0.01
V10-15	-0.85	0.55	0.63	-0.09	-0.29	-0.19	1.00	0.74	0.49	0.47	0.11	0.16	0.01
V15-20	-0.92	0.63	0.65	-0.12	-0.47	-0.41	0.74	1.00	0.81	0.56	0.40	0.20	-0.01
V20-25	-0.75	0.71	0.48	-0.23	-0.43	-0.44	0.49	0.81	1.00	0.51	0.49	0.06	-0.03
V25-30	-0.61	0.38	0.64	-0.04	-0.40	-0.41	0.47	0.56	0.51	1.00	0.42	0.07	-0.01
V30-35	-0.33	0.38	0.15	-0.07	-0.35	-0.12	0.11	0.40	0.49	0.42	1.00	0.28	0.13
G1R	-0.21	0.02	0.18	-0.14	-0.57	0.34	0.16	0.20	0.06	0.07	0.28	1.00	0.10
FC	0.04	-0.19	-0.22	0.05	-0.11	0.01	0.01	-0.01	-0.03	-0.01	0.13	0.10	1.00