MURCIÉLAGOS EN PAISAJES FRAGMENTADOS: EL EFECTO MODULADOR DE LA MATRIZ SOBRE LA RESPUESTA A LA PÉRDIDA Y FRAGMENTACIÓN DEL HÁBITAT

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RESUMEN

La pérdida y transformación del hábitat, incluyendo la fragmentación del mismo, constituyen una de las principales amenazas a la biodiversidad. A pesar de la protección que ofrecen las áreas protegidas, dichas tierras no resultan suficientes para los propósitos de conservación. Por lo tanto, el destino de la biodiversidad también dependerá de la capacidad de las especies para sobrevivir en paisajes modificados por el hombre y de nuestra capacidad de gestión para ayudar a mitigar los impactos de la pérdida y fragmentación del hábitat sobre la biota nativa.

La intensidad de los efectos de la pérdida y fragmentación del hábitat sobre la riqueza y abundancia de especies puede, además, estar mediada por la estructura de la matriz circundante. Matrices con una estructura similar al hábitat original podrían proporcionar hábitats complementarios para las especies de bosque y de esta forma compensar los efectos de la pérdida de hábitat, respecto a matrices estructuralmente diferentes, que representarían hábitats inhóspitos para la biota original, reduciendo su riqueza y abundancia de especies. Por lo tanto, además de la conservación de grandes extensiones de bosque nativo, una mayor consideración debería ser otorgada al manejo de la complejidad estructural de la matriz, como otro objetivo importante para la conservación de la biodiversidad en paisajes fragmentados. Hasta la fecha, la mayor parte de las investigaciones en fragmentación provienen de estudios realizados en sistemas donde los parches de bosque remanente están rodeados por un solo tipo de matriz, sin analizar cómo los efectos de la pérdida y fragmentación del hábitat están modulados por la naturaleza de la matriz.

En este contexto, evalué el impacto de la pérdida de hábitat y fragmentación *per se* sobre los murciélagos y cómo sus efectos son mediados por la complejidad estructural de la matriz circundante en el paisaje. Para ello, evalué, en primer lugar el papel de las plantaciones de pino como hábitat de forrajeo para los murciélagos insectívoros analizando la riqueza de especies y los niveles de actividad en el bosque nativo, plantaciones de pino y villas pobladas en un paisaje fragmentado del centro de Chile (Capítulo 1). Segundo, analicé si el sotobosque, un factor clave para mejorar el valor de las plantaciones forestales para la conservación de la biodiversidad, disminuye el uso de este tipo de plantaciones por

los murciélagos como consecuencia del aumento del grado de desorden estructural dentro del hábitat (Capítulo 2). Finalmente, evalué cómo la pérdida de hábitat y la fragmentación *per se* de manera independiente, afectarían la abundancia relativa de murciélagos en paisajes agrícolas y forestales de Chile central y cómo dichos efectos varían en función del tipo de matriz (Capítulo 3).

La elevada abundancia relativa de murciélagos registrada en las plantaciones de pino respecto a otros hábitats como el bosque nativo, dan cuenta que las plantaciones forestales podrían constituir un hábitat alternativo para este grupo de mamíferos aumentando su capacidad para persistir en paisajes modificados por el hombre donde las plantaciones forestales son un componente importante. Asimismo, la abundancia relativa de murciélagos fue similar entre plantaciones con sotobosque y plantaciones sin sotobosque, lo que indica que sus niveles de actividad no se ven afectados por la presencia del sotobosque. En este sentido, las plantaciones con un sotobosque desarrollado representan un hábitat adecuado para los murciélagos a pesar del alto grado de desorden estructural. Por otro lado, la abundancia relativa de los murciélagos insectívoros en el centro de Chile estuvo fuertemente asociada con la pérdida de hábitat y con la fragmentación *per se* y estos efectos estuvieron modulados por la complejidad estructural de la matriz que rodea los parches de bosque. La abundancia relativa de murciélagos fue mayor en paisajes moderadamente fragmentados, indicando que paisajes con remanentes de bosque nativo distribuidos en un mayor número de parches rodeados por una matriz de bajo contraste podrían contribuir a la persistencia de los murciélagos en paisajes modificados amortiguando los efectos de la pérdida del hábitat. Los esfuerzos de manejo en paisajes fragmentados deberían entonces estar dirigidos a reducir el grado de contraste fragmento-matriz para mitigar los efectos de la pérdida de hábitat contribuyendo así a la conservación de la biodiversidad.

ABSTRACT

Habitat loss and fragmentation are one of the major causes of the current unprecedented rate of species extinction and biodiversity loss. Despite the protection conveyed by protected areas, these will not suffice for biodiversity conservation. Thus, the fate of biodiversity will also depend on the capacity of species to survive in human-modified landscapes and on our ability to manage such landscapes to help mitigate the impacts of forest fragmentation on wildlife species.

The intensity of the effects of habitat loss and fragmentation on biodiversity might be mitigated by the structure and quality of the landscape matrix. Structurally similar matrix to the original habitat could provide suitable habitats for forest species and thus compensate for habitat loss, more so than dissimilar structural matrix, which would be inhospitable for the original biota, reducing their species richness and abundance. Therefore, besides the conservation of large patches of native forest, more consideration has to be given to managing the complexity of the matrix, as another important objective of biodiversity conservation in forest landscapes. Currently, most fragmentation research stem from studies conducted on systems where remnants patches are surrounded by a single type of matrix without addressing how habitat loss and fragmentation effects are mediated by the nature of surrounding matrix.

In this context, I examined the impacts of forest loss and fragmentation *per se* on bats and how these effects are mediated by the structural complexity of the surrounding matrix in the landscape. First, I assessed the role of exotic pine plantations as foraging habitat for insectivorous bats by evaluating species richness and activity in native forest, pine plantations and human settlements in central Chile (Chapter 1). Second, I focused on a potential tradeoff that might emerge when enhancing habitat quality for terrestrial species might hamper the value of such a habitat for bats. I asked if understory, a key factor in enhancing the value of forestry plantations for biodiversity conservation, reduce the use of such plantations by bats as a result of the increase in the structural clutters within the habitat (Chapter 2). Finally, I examined how forest amount and fragmentation *per se* independently affect bat abundance in agricultural and plantation dominated landscapes of central Chile (Chapter 3).

The high activity levels of bats recorded in pine plantations compared to other habitats such as native forest suggested that forestry plantations might act as an alternative habitat for this group of mammals enhancing their capacity to persist in human-modified landscapes in which such production-oriented land-use are an important component. Bat activity was similar between plantations with well-developed understory and plantations without it, suggesting that their activity levels are not affected by the presence of developed undergrowth. Thus, plantations with a well-developed understory represented a suitable habitat for bats despite the higher degree of structural clutter. Relative abundance of insectivorous bats in central Chile was strongly associated with both forest loss and fragmentation *per se* and that these effects were modulated by the structural complexity of the matrix in which forest patches are embedded. The relative abundance of bats was higher in moderately fragmented forest, demonstrating that landscapes with native forest distributed in a larger number of patches surrounded by a low contrast matrix may support bat diversity and abundances with no negative consequence. This study represent the first attempt to examine the effects of landscape matrix on the response of bats to forest loss and fragmentation, providing evidence that low contrast matrices can mitigate the effects of forest loss. Management efforts in fragmented landscapes should aim in reducing the degree of fragment-matrix contrast to mitigate the strength of forest loss and thus the conservation of biodiversity.

General introduction

Deforestation is a major cause of the current unprecedented rate of species extinction and biodiversity loss (Wade et al. 2003). Globally, the area of forest decreases by some 15 million ha annually, mostly due to conversion into agricultural land and plantation forests (FAO 2011), resulting in widespread habitat loss and fragmentation (Wade et al. 2003). Despite the protection conveyed by protected areas, these will not suffice for biodiversity conservation. Thus, the fate of biodiversity will also depend on the capacity of species to survive in human-modified landscapes and on our ability to manage such landscapes to help mitigate the impacts of forest fragmentation on wildlife species (Chazdon et al. 2009). Consequently, the response of biodiversity to habitat loss and fragmentation is crucial for conservation biology (Fahrig 2003).

As a landscape-level process, habitat loss and fragmentation involves both a reduction in area (habitat loss) and the breaking apart of habitat remnants (fragmentation *per se*), two highly correlated processes that could trigger different ecological effects on biodiversity and therefore, should be considered separately for conservation purposes (Fahrig 2003). In fact, habitat loss have a greater impact on biodiversity compared to the effects of fragmentation *per se* to reduce species richness and abundance of several taxa (Cushman 2006; Ritchie et al. 2009; Cerezo et al. 2010). The effects of fragmentation *per se*, meanwhile, are generally much weaker and abundance and species richness can either increase or decrease in fragmented landscapes (Fahrig 2003).

The intensity of the effects of habitat loss and fragmentation on biodiversity might be mitigated by the structure and quality of the landscape matrix (Kupfer et al. 2006; Debinski 2006; Prevedello & Vieira 2009). An increased evidence suggest that matrix quality is determinant in species' responses to forest fragmentation (Gascon et al. 1999; Debinski 2006). The landscape matrix can contribute to biodiversity through supplementing species habitat or resources to the populations surviving in remnant habitats, allowing dispersal between isolated patches, thus increasing landscape connectivity, and buffering the effects of disturbance regimes (Kupfer et al. 2006). In contrast, some matrices may act as ecological traps for native species or as sources of invasive species that can spread into remnants (Gascon et al. 1999). Landscapes with structural similarity between matrix and patches of original habitat would allow more faunal movement, while a dissimilar structural matrix would impede much movement (Gascon et al. 1999). Therefore, besides the conservation of large patches of native forest, more consideration has to be given to managing the complexity of the matrix, as another important objective of biodiversity conservation in human-modified landscapes (Simonetti et al. 2012).

To date, most fragmentation research stem from studies conducted on systems where remnants patches are surrounded by a single type of matrix (e. g. either low-contrast or high fragment-matrix contrast) (McGarigal & McComb 1995; Ethier & Fahrig 2011; Thornton et al. 2011) without addressing how habitat loss and fragmentation effects are mediated by the nature of surrounding matrix (Debinski 2006). In this sense, rigorously comparing habitat loss and fragmentation effects between situations where one has patches surrounded by a low contrast matrix and those with high patch-matrix contrast will provide important guidance in the context of landscape management for the conservation of biodiversity.

As a forested habitat, forestry plantations could contribute to improve the quality of the matrix where native forest remnants are embedded, more so than alternative land uses such as intensive agriculture (Lindenmayer & Hobbs 2004). Forestry plantations could increase tree cover in fragmented landscapes, providing habitat for forest dwelling species (Gascon et al. 1999) increasing connectivity among forest fragments (Ferreras 2001; Renjifo 2001). Forestry plantations might represent a "soft" matrix for the biota inhabiting native forest patches, as exemplified by the willingness of some taxa to move through plantations particularly when it has a well developed understory (Estades et al. 2012). Enhancement of the understory in plantations might increase species richness and abundance, enhancing diversity of numerous taxa, including invertebrates, birds and non-flying mammals (Estades et al. 2012; Simonetti et al. 2013).

Bats are well-suited to examine habitat loss and fragmentation effects because they are highly mobile, and ecological diverse with a variety of feeding and roosting habitats (Adams & Pedersen 2013). Forests are a key habitat for bats throughout the world and many species depend on forest attributes that are reduced in fragmented forest (e.g. foliage and cavity of mature trees and snags, canopy cover, riparian habitat, etc.; Lacki et al. 2007). In landscape where native forest have been replaced by exotic forestry plantations, bats are able to use such lands for commuting, foraging and roosting (Borkin & Parsons 2010, 2011). Therefore, how bat species respond to the change in structure and land-use will influence their ability to survive in human-modified landscapes.

The structural characteristics or physical clutter of the habitat influence bats' choice of foraging habitat, avoiding to navigate through structurally complex environments (Kusch et al. 2004). Increased clutter is a primary reason for reduced bat activity in forested habitats (Tibbels & Kurta 2003; Webala et al. 2011). Undergrowth in forestry plantations might then be an acoustic clutter that could adversely affect the flight and foraging activities of bats within this habitats (Norberg & Rayner 1987). Therefore, while the presence of dense understory vegetation, might enhance forestry plantations as habitat for a suite of species, it might conflict with conditions required supporting bats.

Although bat abundance is supposed to be positively related to the amount of forest cover at the landscape level (Gorresen & Willig 2004; Farrow & Broders 2011), the effects of fragmentation *per se* is still unclear, though increases in bat abundance with increasing forest fragmentation are known (Gorresen & Willig 2004; Klingbeil & Willig 2009; Ethier & Fahrig 2011). However, nearly all of these studies do not distinguish between the effects of habitat loss from the effect of fragmentation. Understanding the relative importance of habitat loss versus habitat fragmentation *per se* as determinants of bat responses to landscape changes has important implications for bat conservation as it sets the focus for management actions. Recent work by Ethier and Fahrig (2011) provided first evidence on effects of fragmentation *per se*, independent of forest amount, on bat abundance, highlighting the importance of both process when assessing bat response to habitat modifications. However, this study was conducted in the northern temperate forests surrounded by agricultural lands. Furthermore, an important element such as potential modulating effect of landscape matrix on the response of bat assemblages has not been examined despite its managerial relevance.

Within this framework, the overall objective of this study was to examine the impacts of forest loss and fragmentation *per se* on bats and how these effects are mediated by the structural complexity of the surrounding matrix. If low contrast matrices mitigate the effects of habitat loss and fragmentation *per se* on bat abundance compared to high contrast matrices then, for the same amount of forest cover and forest fragmentation, the abundance of bats ought to be higher in patches surrounded by low contrast matrix compared to those surrounded by high contrast matrix.

Based on extensive field survey data of bats sampled on a set of human-modified landscapes obtained over the course of three years (January 2010-January 2013), I explore the following main research topics:

- **Chapter 1**: Foraging activity by bats in a fragmented landscape dominated by exotic pine plantations in central Chile.
- **Chapter 2**: Does understory vegetation reduce bat activity in forestry plantations?
- **Chapter 3**: The relative influence of habitat loss and fragmentation on insectivorous bats: does the type of matrix matter?

Diversity and relative abundance of insectivorous bats were assessed through acoustic surveys, which were supported by a bat call library created from vocalizations of individuals captured corresponding to four of the six bat species expected to occur in the study area: *Histiotus montanus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis*. A detailed description of their echolocation calls is presented in an Appendix:

- **Appendix A**: Acoustic identification of four species of bats (order chiroptera) in central Chile.

To analyze the effects of structural complexity of landscape matrix on species response to forest loss and fragmentation I will focus on insectivorous bats of central Chile, where most bat species are associated with forest habitat, (Galaz & Yáñez 2006). Of the seven species that inhabit central Chile, *Lasiurus cinereus* and *Lasiurus varius* roost exclusively in the foliage of trees, meanwhile *Histiotus macrotus*, *Histiotus montanus* and *Myotis chiloensis* may occasionally utilize this forest structure for roosting (Galaz & Yáñez 2006). Thus, I would expect a greater abundance of these species in landscapes with more forest amount that is, patches of native forest surrounded by a forested matrix, over non-forest landscapes that is, patches of native forest surrounded by a non-forested agricultural matrix. In addition to roosting sites bats also require suitable sites for foraging with some species forage within forested habitats, in forest gaps or along tracks and forest edges (Grindal 1998; Morris et al. 2010; Webala et al. 2011). Landscape configurations that maximize complementation between roosting and foraging sites should support a higher richness and abundance of *H. montanus*, *H. macrotus*, *L. cinereus*, *L. varius* and *M. chileonsis.*

This study represents a first approach to examining the effect of low versus high contrast landscape matrices on the responses of bat abundance to forest loss and fragmentation in human-modified landscapes. If low contrast matrices mitigate forest loss, it will reinforce the claim that the type of matrix can contribute significantly to biodiversity conservation in fragmented landscapes.

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Chapter 1

FORAGING ACTIVITY BY BATS IN A FRAGMENTED LANDSCAPE DOMINATED BY EXOTIC PINE PLANTATIONS IN CENTRAL CHILE[1]

Abstract. - We assessed foraging activity of insectivorous bats in a fragmented landscape of central Chile including native temperate forest, forest fragments, commercial pine plantations and local human settlements. Overall bat activity was noticeably greater along adult pine plantation edges, local human settlement and the edge of continuous forest than over interior habitats and unplanted forest plantation clear-cuts. *Tadarida brasiliensis* foraged mostly above human settlements and edges of adult pine plantations but avoided interior habitats. *Lasiurus cinereus* was more active along edges of both adult pine plantations and continuous forest than in clear-cuts and interior habitats of forest fragments. In contrast, *Lasiurus varius*, *Histiotus montanus* and *Myotis chiloensis* occurred not only along vegetation edges but also within the interior habitats of adult pine plantations. The high activity levels suggest that bats not only pass through exotic pine plantations, but that they are active in these habitats commuting and feeding, thus enhancing their capacity to persist in landscapes modified by humans in which exotic forestry plantations are an important component.

Key words: acoustic survey, insectivorous bats, forest fragmentation, pine-dominated landscape, Chile

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1.1 Introduction

Habitat conversion and fragmentation are threats to biodiversity (Sala *et al.*, 2000). A significant challenge facing conservation biologists is to know what organisms naturally occurring can survive in human-dominated landscapes and how to conserve them in these environments (Chazdon *et al.*, 2009). Due to their capability to navigate over extensive areas of fragmented landscapes, bats might exploit human-modified landscapes in ways that differ from that of terrestrial mammals (Law *et al.*, 1999; Estrada and Coates-Estrada, 2002; Avila-Flores and Fenton, 2005). The conversion of natural forests to monoculture exotic plantations is likely to reduce the diversity and abundance of insectivorous bats (Fukuda *et al.*, 2009; Phommexay *et al.*, 2011). However, more complex agroforestry systems (e.g., coffee-shaded plantations) might support high species richness of frugivorous and nectarivorous bats due to their resemblance to the original forested landscape (Estrada *et al.*, 1993; Numa, *et al.*, 2005). *Pinus radiata* plantations need to be examined to assess which of these two models they most resemble.

The landscape of central Chile is currently dominated by monocultures of Monterrey pine plantations and agricultural fields, with sparse remnants of native forests of Maulino Forest, particularly along the coastal range (Echeverria *et al.*, 2006). Despite being structurally simpler compared to the native forests, pine plantations might provide habitat for a suite of native taxa including insects, lizards, birds, small mammals, carnivores and in providing connectivity at the landscape level (Estades *et al.*, 2012). In this paper we assess the role of exotic pine plantations as foraging habitat for insectivorous bats by evaluating species richness and activity in native forest, pine plantations and human settlements. If bats also exploit plantations, it will reinforce the claim that such production-oriented landscapes might be simultaneously managed for biodiversity conservation, as required by the principles of the Convention on Biological Diversity (Estades *et al.*, 2012).

1.2 Materials and methods

1.2.1 *Study area*

The survey was conducted at Tregualemu area, in the Maulino Coastal Range of central Chile (35°59'S-72°41'W to 35°59'S-72°46'W). The study area included a 600 ha patch of coastal Maulino Forest (including the Los Queules National Reserve), Monterey pine plantations, scattered forest fragments, small villages and surrounding agricultural lands.

1.2.2 *Field work and analysis*

Bat activity was monitored in nine different habitats: (1) interior and (2) edge of continuous forest; (3) interior and (4) edge of forest fragments; (5) interior and (6) edge of mature pine plantations; (7) young pine plantations; (8) unplanted plantation clear-cuts; (9) human settlement. Sampling sites at edges were established 20 m from the border toward the interior of all habitats while interior sampling locations were placed at least 100 m from any edges or roads.

Bats were surveyed using an ultrasound bat-detector model D240X (Pettersson Elektronik AB, Uppsala, Sweden) coupled to a digital recorder (M-Audio MicroTrack II) and operated both in heterodyne and time-expanded modes. Time-expanded mode allows to record full-spectrum echolocation calls with a high-resolution sonogram of each bat vocalization. These full-spectrum echolocation calls were used to classify bat activity to species. Heterodyne recordings do not preserve duration, absolute frequencies, or the frequency–time course of the original signal, therefore, cannot be used to identify bat passes at species levels. As a consequence, heterodyne recordings were not included in the analyses at species level but were pooled with those recorded in time-expanded mode for total activity analysis, allowing full use of the recording information (Morris *et al.*, 2010).

Within each habitat we set up five to ten sampling points, all of which were at least 150 m apart. Each sampling point was visited five or six times during two years between January 2010 and January 2012. To limit seasonal variation in activity, we restricted surveys to the summer season. We sampled different habitats on different nights. Surveys began at dusk and lasted three hours to coincide with peak foraging periods of aerial insectivorous bats (Kuenzi and Morrison, 2003). Bat activity was quantified by counting the number of bat passes per 10 minutes at each point within each habitat and then we randomly move to the next sampling point. A bat pass was defined as a sequence of more than two echolocation calls (Law *et al.*, 1999). An index of activity was assessed as the number of bat passes per hour at any given habitat by each species. Further, an index of feeding activity was quantified by counting the number of feeding buzzes recorded. We digitized calls to computer and analyzed them using the Batsound 2.1 sound analysis software (Pettersson Elektronik AB, Uppsala, Sweden). Indices of feeding and bat activity levels at different habitats were compared using a Kruskall-Wallis test (data could not be transformed to fit a normal distribution) followed by a *post hoc* test. All tests were performed with STATISTICA 8.0 (StatSoft, Inc. 2007).

1.2.3 *Bat species identification*

Passes of free-flying bats were classifying to species using Quadratic Discriminant Function Analysis (DFA). Classification functions were computed using a library of validated reference calls which consisted of 264 full-spectrum recordings from hand-released (*Histiotus montanus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis*) at the location of study (Rodríguez-San Pedro and Simonetti, 2013). Variables used in this analysis were call duration, final frequency, slope frequency modulation, peak frequency, minimal and maximal frequency. DFA gave an overall correct classification rate of 90.0% for all reference calls. If there was uncertainty or inconsistency in the classification, that recording was considered unidentifiable and labeled as "unknown".

1.3 Results

A total of 100 hours were accumulated monitoring bat activity with a total of 937 echolocation sequences and 84 feeding buzzes. Of the total bat passes, we analyzed 750 time-expanded sound files that contained 490 identifiable echolocation sequences corresponding to five of the six species expected to occur in the study area: *Histiotus montanus* (66 passes), *Lasiurus varius* (127 passes), *Myotis chiloensis* (53 passes) and *Tadarida brasiliensis* (106 passes). Of the remaining 138 passes, 52 were classified as *Lasiurus cinereus* by comparing call parameters with references calls reported for this species in other regions (Barclay *et al.*, 1999; O'Farrell *et al.*, 2000) and 86 were classified as "unknown". *Histiotus macrotus* was the sixth species expected, but it was not detected.

Human settlement and habitat edges supported the highest species richness, with five species, while the interior of forest fragments, unplanted plantation clear-cuts and the interior of continuous forest exhibited the lowest, with one and two species, respectively. Overall bat activity differed significantly between habitat types (Table 1.1; $H_{(8,77)} = 65.11$,

$P < 0.01$). The highest activity rates were recorded along edges of adult pine plantation followed by local human settlement and the edge of continuous forest. The lowest bat activity levels were recorded at the interior of forest fragments and unplanted forest plantation clear-cuts. Feeding activity differ significantly between sites being slightly higher at the edges of adult pine plantations (Table 1.1; $H_{(8,77)} = 21.04$, $P < 0.01$).

Table 1.1. Median (± quartile) values of total activity (measured as total number of passes per hour) and feeding index (feeding buzzes per total number of bat passes) in nine habitats. EPL: Edge of adult forest plantation; IPL: Interior of pine plantations; EFR: Edges of forest fragments; IFR: Interior of forest fragments; ECF: Edges of continuous forest; ICF: Interior of continuous forest; YPL: Young pine plantations; HS: Human settlement; UPLC: Unplanted forest plantation clear-cuts. Different letters indicate significant differences among habitats in a posteriori test.

Habitat categories	Total activity		Index of feeding	
	Median	1st-3rd quartile	Median	1st-3rd quartile
EPL	30.00 a	19.00-35.00	0.08	0.00-0.24
IPL	5.25 bc	4.00-6.50	0.00	0.00-0.00
EFR	5.50 bc	3.00-8.00	0.00	0.00-0.00
IFR	0.00 c	0.00-0.00	0.00	0.00-0.00
ECF	18.90 ab	15.60-24.00	0.00	0.00-0.06
ICF	0.90 c	0.00-1.80	0.00	0.00-0.00
YPL	8.50 abc	3.00-11.00	0.00	0.00-0.00
HS	20.50 ab	11.00-33.00	0.00	0.00-0.23
UPLC	0.00 c	0.00-1.00	0.00	0.00-0.00

At the species level, bat activity differed between sites. Activity of *T. brasiliensis* varied significantly between habitat types (Table 1.2; $H_{(8,77)} = 54.95$, $P < 0.01$), foraging mostly in human settlement. Interior habitats were avoided as no records of *T. brasiliensis* were recorded there. Activity of *L. cinereus* was significantly higher in the edge of adult forest plantations, the edge of continuous forest and local human settlements (Table 1.2; $H_{(8,77)} = 35.77$, $P < 0.01$) but no passes were recorded in unplanted forest plantation clear-cuts and interior habitats of forest fragments. *Lasiurus varius* occurred in local human settlements and along the edge of continuous forest, as well as in the interior habitats of pine plantations (Table 1.2; $H_{(8,77)} = 49.55$, $P < 0.01$). *Histiotus montanus* was most active along adult pine plantation edges (Table 1.2; $H_{(8,77)} = 33.87$, $P < 0.01$) but also foraged in the interior of adult pine plantations and in local human settlements. It was never recorded in the interior of forest fragments or unplanted forest plantation clear-cuts. Activity of *M.*

chiloensis was significantly higher along the edge of continuous forest (Table 1.2; $H_{(8,77)} = 33.70$, $P < 0.01$) but this species also preferred the interior adult pine plantations and the edges of adult pine plantations for foraging.

Table 1.2. Median (± quartile) values of activity for each species in nine different habitats. Bat activity is expressed as the number of bat passes per hour per site. EPL: Edge of adult forest plantation; IPL: Interior of pine plantations; EFR: Edges of forest fragments; IFR: Interior of forest fragments; ECF: Edges of continuous forest; ICF: Interior of continuous forest; YPL: Young pine plantations; HS: Human settlement; UPLC: Unplanted forest plantation clear-cuts. Different letters indicate significant differences among habitats in a posteriori test

Habitat categories	*H. montanus*		*L. cinereus*		*L. varius*		*M. chiloensis*		*T. brasiliensis*	
	Median	1st-3rd quartile	Median	1st-3rd quartile	Median	1st-3rd quartile	Median	1st-3rd quartile	Median	1st-3rd quartile
EPL	2.00 a	2.00-2.00	1.50	0.00-2.00	1.00 ab	1.00-2.00	0.50 ab	0.00-1.00	2.00 ab	2.00-3.00
IPL	1.00 ab	0.50-1.00	0.00	0.00-0.50	1.00 ab	0.50-1.00	1.00 ab	0.50-1.00	0.00 c	0.00-0.00
EFR	1.00 ab	0.00-2.00	0.00	0.00-0.00	1.00 ab	0.00-2.00	0.00 ab	0.00-0.00	0.00 c	0.00-0.00
IFR	0.00 b	0.00-0.00	0.00	0.00-0.00	0.00 b	0.00-0.00	0.00 ab	0.00-0.00	0.00 c	0.00-0.00
ECF	0.00 ab	0.00-0.60	1.20	0.00-1.20	4.20 a	3.60-6.00	1.20 a	1.20-3.00	0.30 abc	0.00-0.06
ICF	0.00 ab	0.00-0.60	0.00	0.00-0.60	0.00 b	0.00-0.00	0.00 b	0.00-0.00	0.00 bc	0.00-0.00
YPL	0.00 ab	0.00-1.00	0.00	0.00-0.00	1.00 ab	0.00-3.00	0.00 ab	0.00-0.00	1.00 abc	1.00-3.00
HS	1.00 ab	1.00-1.00	1.00	0.00-1.00	3.00 a	2.00-3.00	0.00 ab	0.00-0.00	3.00 a	2.00-9.00
UPLC	0.00 b	0.00-0.00	0.00	0.00-0.00	0.00 b	0.00-0.00	0.00 b	0.00-0.00	0.00 c	0.00-0.00

1.4 Discussion

Our study reports finding five of six species of bats (*Histiotus macrotus*, *Histiotus montanus*, *Lasiurus cinereus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis*) that were expected to occur in the study area based on published distributional maps (Galaz and Yáñez, 2006). Because there are no previous studies of bats prior to fragmentation of the Maulino forest, or information on bats assemblages within forested landscapes in Chile, it is difficult to determine how different the bat assemblages of the fragmented Maulino forest is from the original assemblage. The echolocation repertoire of *Histiotus macrotus*, the single species not recorded, is unknown from anywhere in its distribution, and therefore this species may have been included in those passes we labeled as "unknown".

Fragmentation of the Maulino forest and the incorporation of commercial pine plantations are increasing the amount of edge, habitat that supports the highest bat species richness and activity levels. The combination of low physical clutter and the high insect prey availability typically found along edges (Pasek, 1988; Swystun *et al.*, 2001), might account for the importance of this habitat for foraging bats. Bats avoid structurally cluttered habitats and focus their foraging in less complex habitats presumably for the ease of navigation (Grindal and Brigham, 1999; Patriquin and Barclay, 2003). The species in our study area are aerial-hawking hunters with varying levels of tolerance for structural complexity (Sleep and Brigham, 2003, Tibbels and Kurta, 2003; Jung *et al.*, 2012) and vegetation edges may provide foraging opportunities because they are relatively open. This pattern concurs with the behavior of insectivorous bats elsewhere that also rely on edges as foraging habitats (Grindal and Brigham, 1999; Morris *et al.*, 2010).

Although monoculture plantations might reduce species richness (Ramírez and Simonetti, 2011), species richness and activity levels of bats were higher in exotic forest plantations than native forest, differing from studies of insectivorous bats in Borneo and Thailand (Fukuda *et al.*, 2009; Phommexay *et al.*, 2011). The low bat activity recorded in interior habitats of both the continuous forest and forest fragments is probably related to the high background clutter at these sites compared to pine plantations (Estades and Escobar, 2005), which probably interfere with flight maneuverability and reduces access to prey items (Brigham *et al.*, 1997; Rainho *et al.*, 2010). A factor that could explain the high bat activity recorded within adult pine plantation forests is the presence of internal service roads. Unlike continuous forest, commercial pine plantations are usually traversed by flyways (tracks, including roads and trails), which allow bats to access and use sites that are otherwise too cluttered (Adams *et al.*, 2009; Webala *et al.*, 2011). Energy requirements for foraging flights and navigation are assumed to be greater in habitats with dense vegetation, which could account for the avoidance of high-cluttered habitats (Brigham *et al.*, 1997; Sleep and Brigham, 2003). Bat activity recorded at the interior habitats of adult pine plantations was basically concentrated on the location of tracks, suggesting that these tracks provide suitable commuting and/or foraging habitats for bats within plantations forest regardless of the degree of structural clutter. This result corroborates other studies where forest tracks supported higher overall activity than off-track sites (Law and Chidel, 2002; Adams *et al.*, 2009; Webala *et al.*, 2011; Monadjem *et al.*, 2010) and emphasizes the importance of linear elements to bats.

Insectivorous bat species use differently the fragmented landscape. *Myotis chiloensis* and *H. montanus* foraged mostly along edge of continuous forest and within pine plantations possibly as they are small and maneuverable in flight (Norberg and Rayner, 1987). Their short, round wings and frequency modulated echolocation enhances their feeding in back-ground cluttered space (Schnitzler *et al.*, 2003). The high bat activity observed in local human settlements by *L. varius*, *T. brasiliensis* and *L. cinereus*, could be accounted for their ability to fly in open spaces and their reliance on insects that accumulate around streetlights (Avila-Flores and Fenton, 2005; Rydell, 1992; Jung and Kalko, 2010). The villages we surveyed were mostly illuminated, and generally scattered with small gardens and crop fields. Further, *T. brasiliensis* uses human-made buildings as roosting sites (Gaisler *et al.*, 1998; Galaz and Yáñez, 2006).

Histiotus montanus, *L. cinereus*, *L. varius*, *M. chiloensis* and *T. brasiliensis* are regarded as Least Concern (IUCN 2012). The high activity levels suggest that bats not only pass through exotic pine plantations, but that they are active in these habitats commuting and feeding, thus enhancing their capacity to persist in landscapes modified by human in which exotic forestry plantations are an important component. Exotic pine plantations provide habitats for bats which might enhance their conservation in human modified landscapes.

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Chapter 2

DOES UNDERSTORY VEGETATION REDUCE BAT ACTIVITY IN FORESTRY PLANTATIONS?[1]

Abstract. - A common feature of plantations supporting native species is the occurrence of understory vegetation. However, this environmentally friendly practice leads to increased structural clutters within forestry plantations, which could adversely affect the flight and foraging activities of bats. We used an ultrasonic bat detector, positioned on-tracks and off-tracks, to compared bat activity in plantations of Monterey pine with and without understory vegetation in central Chile. Total bat activity for all species pooled was higher on-track than off-tracks sites, with no significant difference between plantations with a developed understory and those with no or little developed vegetation. At the species level, understory vegetation significantly influenced *M. chiloensis* and *L. varius*, with more bat passes recorded in plantations with a developed understory than in simple ones. Activity of *H. montanus* and *L.cinereus* did not differ between plantations with understory and those without it. The presences of tracks provide internal linear edges in plantations with understory vegetation allowing bats to use such habitats for commuting and foraging. Promoting understory vegetation in Monterrey pine plantations could enhance the capacity of bats to persist in landscapes modified by human in which exotic forestry plantations are an important component. This could bring benefits not only to biodiversity itself, but also to plantation managers who can benefit by the presence of potential pest controllers like bats.

Key words: acoustic survey, insectivorous bats, Pinus radiata, understory vegetation

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2.1 Introduction

Forestry plantations are regarded "biological deserts" and a threat to global biodiversity (Hartley 2002). Environmental-friendly practices are demanded to mitigate their negative effects (Rousseau et al. 2005). Enhancing the occurrence of a developed understory vegetation is one such practices (Lindenmayer et al. 2004). Plantations with well-developed understory vegetation, provides many services for wildlife, such as cover, nesting sites, and food, among others, which might mitigate the impact of habitat replacement. In fact, species richness and abundance are higher in forestry plantations with a developed undergrowth than in those without it, enhancing diversity of numerous taxa including invertebrates, birds and non-flying mammals (Estades et al. 2012; Simonetti et al. 2013).

This practice however, leads to increased structural clutters within forestry plantations, which could adversely affect the presence of bats. The structural characteristics or physical clutter of the habitat influence bats' choice of foraging habitat, avoiding to navigate through structurally complex environments (Kusch et al. 2004). Increased clutter is a primary reason for reduced bat activity in forested habitats (Tibbels and Kurta 2003; Adams et al. 2009; Webala et al. 2011). Undergrowth in commercial forestry plantations might then be an acoustic clutter that could reduce flight efficiency or hamper the detection of potential prey (Norberg and Rayner 1987), (Schnitzler and Kalko 2001). Therefore, while the presence of dense understory vegetation, might enhance forestry plantations as habitat for a suite of species, it might conflict with conditions required supporting bats.

Bats can overcome physical constraints imposed by cluttered habitat flying through the networks of trails while moving through forested areas (Law and Chidel 2002). If bats similarly use service roads and tracks in forestry plantations, this fact may allow access and use sites that otherwise are inhospitable (Law and Chidel 2002; Caras and Korine 2008; Webala et al. 2011), solving the potential conflict regarding the value of understory to mitigate impacts upon biodiversity. In this framework, we assessed the effect of undergrowth on the occurrence of bats in Monterrey pine (*Pinus radiata*) plantations in central Chile. If well-developed undergrowth reduces the use of forestry plantations by bats, their activity levels ought to be lower in plantations with a developed understory than in stand with no or little understory. Similarly, bat activity would be higher along plantation tracks than away from tracks in both complex and simple plantations, due to reduced vegetation clutter.

2.2 Materials and methods

Bat surveys were conducted in plantations of Monterrey pine located at Tregualemu, coastal range of central Chile (35°59'S-72°41'W to 35°59'S-72°46'W). According to their structural complexity two types of plantations can be identified in the area: plantations with a well-development understory (classified as structurally complex plantation) and plantations in which the understory is little or absent (classified as structurally simple plantation). Plantations were classified as structurally simple when woody plant density 1 m above ground was less than 0.5 individuals/m^2, and structurally complex when density was above 0.5 individuals/m^2 (Poch and Simonetti 2013).

Bats were sampled in twenty sampling points, 10 within structurally simple and 10 structurally complex plantation sites, all of which were at least 300 m apart. Tracks are a feature of commercial forestry plantations and consist of linear flyways ranging from 1 to 5 m wide and include trails and dirt roads. At each sampling point, bat activity was recorded for 10 minutes (5 minutes on-track and 5 minutes off-track sites) per night, during nine non-consecutive nights, between January 2010 and January 2012, totaling 15 monitoring hours per type of plantations (7.5 hr on-track and 7.5 hr off-track). Off-track recordings were set > 50 m from tracks and detectors were pointed towards small gaps to minimize bat call attenuation from vegetation (Patriquin et al. 2003). Sampling began at dusk and extended for three hours to coincide with the peak foraging periods of insectivorous bats (Kuenzi and Morrison 2003). Surveys were not carried out on nights with rain or fog to avoid reduced bat activity (Pye 1971; Erickson and West 2002).

Bat activity was recorded using an ultrasound bat-detector model D240X (Pettersson Elektronic AB, Uppsala, Sweden) coupled to a digital recorder (M-Audio MicroTrack II), operated in time-expanded mode, allowing to record full-spectrum echolocation calls with a high-resolution sonogram of each bat vocalization which were used to classify activity data to species. An index of activity was assessed for each species by counting the number of bat passes per sampling point. Calls were analyzed using Batsound 2.1 software (Pettersson Elektronik AB, Uppsala, Sweden). Passes of free-flying bats were classifying to species using Quadratic Discriminant Function Analysis (DFA). Classification functions were computed using a library of validated reference calls from hand-released (*Histiotus montanus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis*) at the study area (Rodríguez-San Pedro and Simonetti 2013a). Passes of *L. cinereus* were identified by comparing call parameters with references calls reported for this specie in other regions (O'Farrell et al. 2000). Variables used in this analysis were call duration, final frequency, slope frequency modulation, peak frequency, minimal and maximal frequency. If there was uncertainty or inconsistency in the classification, that recording was considered unidentifiable and labeled as "unknown".

A two-way ANOVA (Box-Cox transformation for normality) followed by a *post hoc* Tukey tests was used to test for differences between overall bat activity according to understory development and track position. Differences between simple and complex plantations in individual species bat activity were tested using a Mann-Whitney U test (individual species data could not be transformed to fit a normal distribution).

2.3 Results

A total of 193 echolocation sequences and 13 feeding buzzes were recorded. Of the 193 passes, 84 could not be analyzed at the species level due to the low intensity of the recorded calls and were classified as "unknown". These passes were used only for overall activity analysis. The remaining 109 passes were assigned to four of the six species expected to occur in the study area: *Histiotus montanus* (32 passes), *Lasiurus varius* (32 passes), *Myotis chiloensis* (26 passes) and *Lasiurus cinereus* (19 passes). Total feeding buzzes recorded belong to *L. cinereus*.

Overall bat activity did not differ between plantations with a developed understory and those without it ($F_{(1,36)} = 0.001$, $P = 0.97$), however it was higher on-track than off-tracks sites ($F_{(1,36)} = 87.2$, $P < 0.001$) (Fig. 2.1).

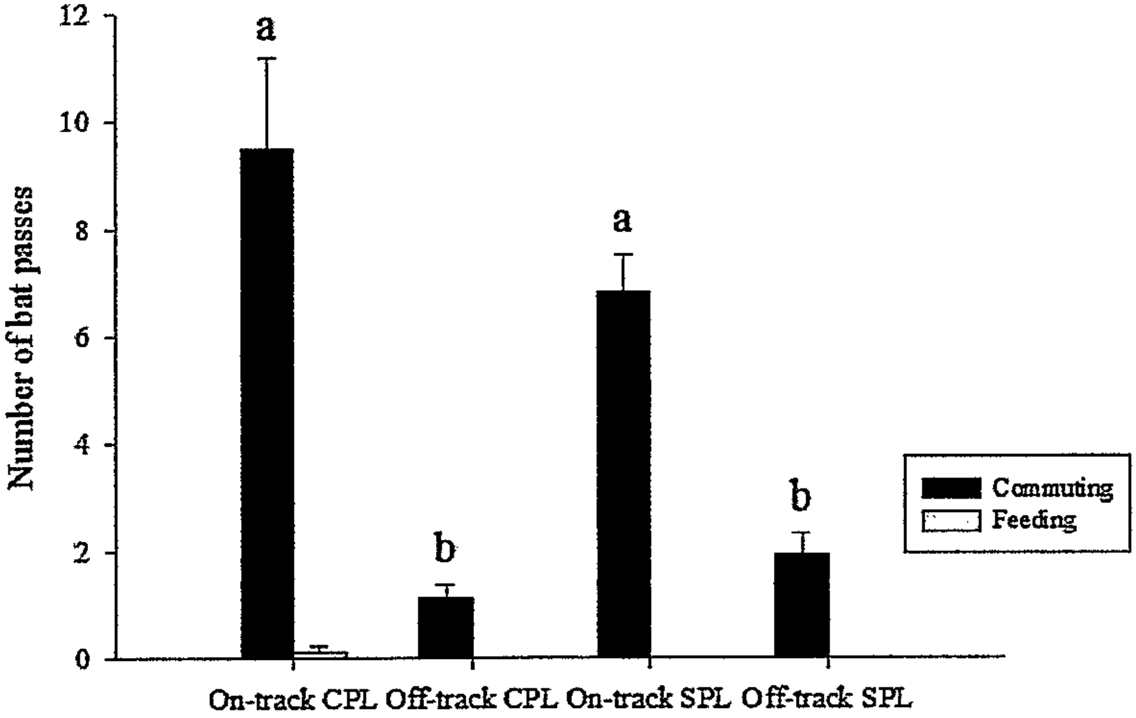

Figure 2.1. Overall bat activity and feeding activity (Mean ± SE) in complex (CPL) and simple (SPL) pine plantations, on-track and off-track. Bat passes were classified as "feeding" if they contained a feeding buzz and "commuting" if they did not. Different letters indicate significant differences at $P < 0.001$ in a posteriori test

Individual species bat activity was quantified by combining the number of passes recorded using both on-track and off-track position since almost all passes (84%) were recorded on-track sites and the results of the analysis did not change if we used only passes recorded on-track. At the species level, *M. chiloensis* and *L. varius*, were more frequently in plantations with developed understory than in simple ones for both species ($U = 20.50$, $P < 0.05$ and $U = 25.00$, $P < 0.05$ respectively) (Fig. 2.2). Activity of *H. montanus* and *L.cinereus* did not differ between plantations ($U = 27.00$, $P = 0.07$ and $U = 49.00$, $P = 0.91$). All feeding buzzes were recorded on tracks (Fig. 2.1).

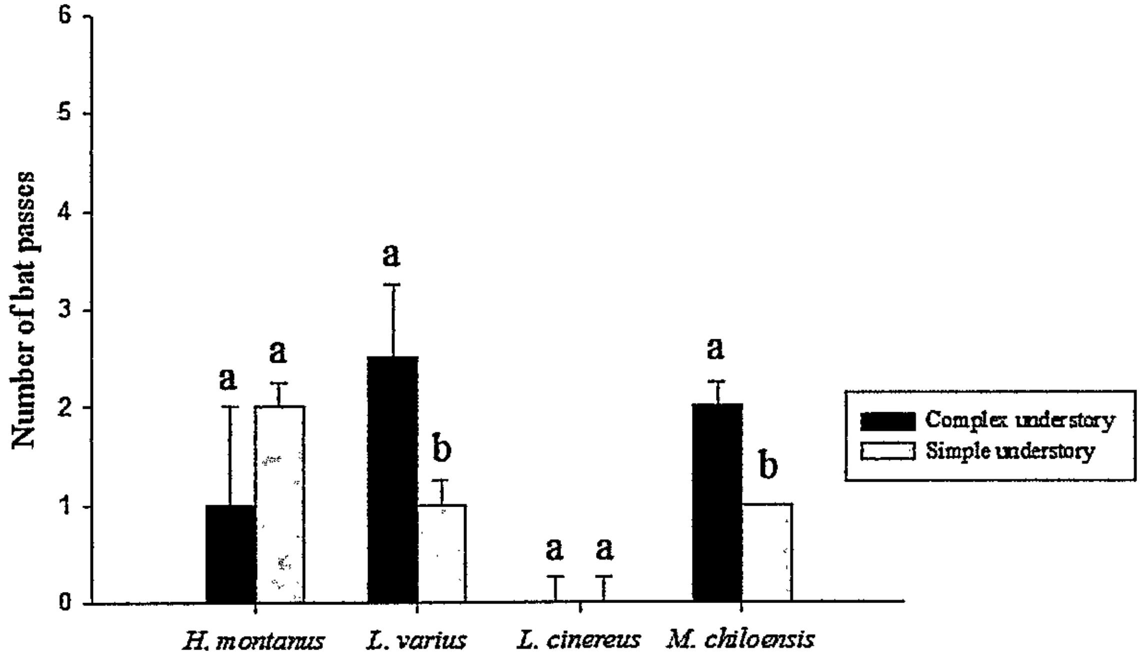

Figure 2.2. Bat activity per species (Median ± percentile) in complex and simple pine plantations. Different letters indicate significant differences at $P < 0.05$ in a posteriori test

2.4 Discussion

Bat assemblage we studied consisted of four of six species expected to occur in Tregualemu sector: *Histiotus macrotus*, *Histiotus montanus*, *Lasiurus cinereus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis* (Galaz and Yáñez 2006).The echolocation calls of *H. macrotus*, one of the unrecorded species, are unknown in their whole distribution range. Consequently, this species could be included as among the "unknown" passes and considered only in overall activity analysis. Although *T. brasiliensis* is a common species occurring in the study area (Rodríguez-San Pedro and Simonetti 2013b), it was absent in both complex and simple plantations. With long, thin wings (high aspect ratio) and relatively low frequency calls, *T. brasiliensis* could be the most clutter-sensitive bats in Chile (Schnitzler and Kalko 2001), probably avoiding clutter habitats, like interior of plantations, by only thriving in open areas (Rodríguez-San Pedro and Simonetti 2013b).

Contrary to our predictions, overall bat activity was similar between plantations with well-developed understory and plantations without it, suggesting that their activity levels are not affected by the presence of developed undergrowth. This result contrasts with studies reporting a lower bat activity in cluttered habitats (Brigham and Grindal 1997; Tibbels and Kurta 2003). A methodological consideration that could possibly explain the contradictory conclusions reported by previous studies could be ultrasonic detectors positioned away from the influence of tracks and flyways. For instance, Law and Chidel (2002) and Webala et al. (2011) found no difference in bat activity recorded on-track sites in forests with different degree of structural clutter, in contrast with detectors positioned away from tracks, which recorded a significant decrease in bat activity with increasing structural clutter. The high activity levels we recorded on-tracks sites, suggest that this landscape element provide suitable commuting and/or foraging habitats for bats in forestry plantation regardless of the degree of structural clutter (Law & Chidel 2002; Webala et al. 2011).

Individual bat species responded heterogeneously to the presence of a development understory. Species with high activity in plantations with undergrowth vegetation, *M. chiloensis* and *L. varius*, comprised both clutter-tolerant and clutter-sensitive species. *Lasiurus varius* is fast flying with low manoeuvrability (Norberg and Rayner 1987) and the use of tracks as flyways would explain how this species, that should avoid clutter, is able to inhabit successfully in otherwise structurally complex plantations. The short, round wings and frequency modulated calls of *M. chiloensis* and *H. montanus* enhances their foraging in cluttered habitats (Schnitzler and Kalko 2001).

Our results suggest that plantations with a well-developed understory are a suitable habitat for bats as for other vertebrate and invertebrate taxa (Estades et al. 2012, Simonetti et al. 2013). The presences of tracks provide internal linear edges in plantations with undergrowth vegetation allowing clutter-sensitive and clutter-tolerant bats to use such cluttered habitats for foraging. Promoting undergrowth vegetation in Monterrey pine plantations highlights the possibility of contributing to biodiversity conservation which could bring benefits not only to biodiversity itself, but also to plantation managers who can benefit by the presence of potential pest controllers like bats (Williams-Guillén et al. 2008).

Monterey pine cover over 4 million ha planted, accounting for 32% of productive plantations worldwide (FAO 2007). To the extent that forestry plantation provide wildlife habitat, such production-oriented land-use might be simultaneously managed for biodiversity conservation, as required by the Aichi targets of the Convention on Biological Diversity (CBD 2010).

2.5 Acknowledgements

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Chapter 3

THE RELATIVE INFLUENCE OF HABITAT LOSS AND FRAGMENTATION ON INSECTIVOROUS BATS: DOES THE TYPE OF MATRIX MATTER?

Summary

1. The intensity of the effects of habitat loss and fragmentation on biodiversity might also be mitigated by the nature of the surrounding matrix. Structurally similar matrix to the original habitat could provide suitable habitats for forest species and thus compensate for habitat loss more so than dissimilar structural matrix, which would be inhospitable for the original biota, reducing their species richness and abundance. To test this, we examined the effect of matrix type on the response of bats to forest loss and fragmentation of native forests in central Chile.

2. We conducted acoustic bat surveys at the centers of 18 landscapes where forest patches were immersed in a matrix of agricultural crops and 18 landscapes where patches were surrounded by a pine-dominated matrix, and relate bat activity to the amount of forest and the degree of fragmentation (estimated as the number of patches).

3. In agricultural landscapes, bat responded strongly to both forest amount and fragmentation. As the amount of forest increased, the activity of *Histiotus montanus, Lasiurus cinereus* and *Tadarida brasiliensis* increased, while the activity of *Myotis chiloensis* decreased. Similarly, as the number of forest patches increased the activity of *Lasiurus varius* and *M. chiloensis* increased, while activity of *H. montanus* decreased.

1. Submitted as Rodríguez-San Pedro A and Simonetti JA. The relative influence of habitat loss and fragmentation on insectivorous bats: does the type of matrix matter?, to *Journal of Applied Ecology*.

4. In plantation dominated landscapes, only *H. montanus* responded to forest amount, decreasing activity with increasing forest amount. Fragmentation *per se* was a stronger predictor of bat activity than forest amount with three species (*L.cinereus, M. chiloensis* and *T. brasiliensis*) responding more strongly to the number of forest patches.

5. Forest amount was a stronger predictor for agricultural than for plantation-dominated landscapes. Meanwhile, forest fragmentation was a stronger predictor in both forestry and agricultural landscapes.

6. *Synthesis and applications.* This study represent the first attempt to examine the effects of landscape matrix on the response of bats to forest loss and fragmentation, providing evidence that low contrast matrices can mitigate the effects of forest loss. Management efforts in fragmented landscapes should aim in reducing the degree of fragment-matrix contrast to mitigate the strength of forest loss, thus enhancing biodiversity in human-modified landscapes.

Key words: habitat fragmentation, habitat loss, landscape matrix, insectivorous bats, Chile

3.1 Introduction

Landscape transformations is one of the most important factors causing elevated rates of species extinction and loss of biological diversity (Wade *et al.* 2003). This process involves both habitat loss and the subdivision and isolation of the remaining habitat (fragmentation *per se*), two highly correlated processes that could triggers different effects on biodiversity (Haila 2002; Fahrig 2003). When the effects of habitat loss and fragmentation are addressed independently, habitat loss have a greater impact on biodiversity compared to the effects of fragmentation *per se* to reduce species richness of insects, amphibians, birds, and small mammals, among other taxa (Trzcinski et al. 1999; Nupp & Swihart 2000; Cushman 2006; Ritchie et al. 2009; Cerezo et al. 2010). The effects of fragmentation, meanwhile, are usually much weaker and abundance and species richness can either increase or decrease in fragmented landscapes (Fahrig 2003).

The direction and magnitude of the effects of habitat loss and fragmentation on biodiversity might also be mitigated by the structure and quality of the landscape matrix (Kupfer et al. 2006; Debinski 2006; Prevedello & Vieira 2009). The landscape matrix may compensate for habitat loss providing additional resources for many species or otherwise act as an ecological trap (With 2002; Vergara & Simonetti 2003; Ewers & Didham 2006; Harvey et al. 2006). Additionally, matrix structure could influence dispersal of fragment-dwelling biota across the landscape (Ricketts 2001; Baum et al. 2004). Landscapes with structural similarity between matrix and patches of original habitat would allow more faunal movement, while a dissimilar structural matrix would impede much movement (Gascon *et al.* 1999). As a type of forested habitat, plantations forests can contribute to improve the quality of the matrix where native forest remnants are embedded more so than other land use such as intensive agriculture, as they might provide suitable habitats for numerous forest species (Lindenmayer & Hobbs 2004; Fischer et al. 2006). Additionally, plantations may increase species richness and abundance by improving connectivity between native forest patches (Gascon et al. 1999; Lindenmayer et al. 1999; Ferreras 2001; Renjifo 2001), enhancing their survival in human-modified landscapes (Gascon et al. 1999; Kupfer et al. 2006; Rodríguez-San Pedro & Simonetti 2013a). Therefore, the effects of habitat loss and fragmentation in agricultural dominated landscapes might differ from those in forestry landscapes.

Forests are a key habitat for bats throughout the world. Many species depend on forest attributes such as foliage and cavity of mature trees for roosting, that are reduced in fragmented forest (Lacki et al. 2007). In addition to roosting sites bats also require suitable sites for foraging with some species forage within forested habitats, in forest gaps or along tracks and forest edges (Crome & Richards 1988; Morris et al. 2010; Rodríguez-San Pedro & Simonetti 2013a). In Chile, most bat species are associated with forested habitats (Galaz & Yáñez 2006). *Lasiurus cinereus* and *Lasiurus varius* roosting exclusively in the foliage of trees, while *Histiotus macrotus*, *Histiotus montanus* and *Myotis chiloensis* may utilize occasionally it for roosting (Galaz & Yáñez 2006). Thus, we would expect a greater abundance of bats in landscapes with more forested amount over non-forest landscapes. Likewise, landscape configurations that maximize complementation between roosting and foraging sites, that is, increased access to both habitats, should support a higher richness and abundance of bats.

While bat abundance is positively related to the amount of forest cover in the landscape (Gorresen & Willig 2004; Meyer & Kalko 2008; Pinto & Keitt 2008; Klingbeil & Willig 2009; Farrow & Broders 2011), the effects of fragmentation is still unclear, with some evidence of an increase in bat abundance with forest fragmentation (Estrada & Coates-Estrada 2002; Gorresen & Willig 2004; Klingbeil & Willig 2009). However, most of these studies do not distinguish between the effects of habitat loss and fragmentation, which leads to ambiguous conclusions regarding the effects of fragmentation *per se* on bats and the subsequent management actions.

To date, the only empirical test of the independent effects of forest fragmentation and habitat loss on bats was conducted by Ethier and Fahrig (2011) in Ontario, Canada. They predicted higher bat abundance in landscapes with higher forest fragmentation (but the same forest amount), based on the assumption that landscapes with more forest patches would result in higher complementation between foraging and roosting habitats. To test the generality of this prediction we examined how forest amount and fragmentation *per se* independently affect bat abundance in agricultural and plantation dominated landscapes of central Chile. If plantation forests mitigate the effects of habitat loss and fragmentation *per se* on bat abundance, providing potential roosting and foraging sites, compared to agricultural lands then, for the same amount of forest cover and forest fragmentation, the abundance and species richness of insectivorous bats ought to be higher in plantation forests dominated landscapes compared to agricultural dominated landscapes.

3.2 Materials and methods

3.2.1 *Study area and site selection*

The study was conducted in rural areas of central Chile. During the last decades, the temperate forest of central Chile has been deforested and fragmented due to agriculture and forestry plantations (Echeverria *et al.* 2006). Currently, the landscape consists of native forest patches embedded in a matrix of commercial pine (*Pinus radiata*) plantations, pastures and agricultural lands (Echeverria *et al.* 2006). The estimated cover of native forests decreased from 119,994 ha in 1975 to 39,002 ha in 2000. In other words, 67% of the native forests existing in 1975 had been replaced by other land cover types by 2000. In 2000, 69% of the total area of native forest occurred in patches of less than 100 ha and only 3% had a size greater than 1000 ha.

We selected 36 non-overlapping native forest patches (hereafter focal patches) that ranged in size from 4.0 to 25.0 ha, centered in landscapes where the dominant non-forest land cover was exclusively, pine plantations (18 focal patches) or agricultural lands (18 focal patches) (Fig. 3.1).

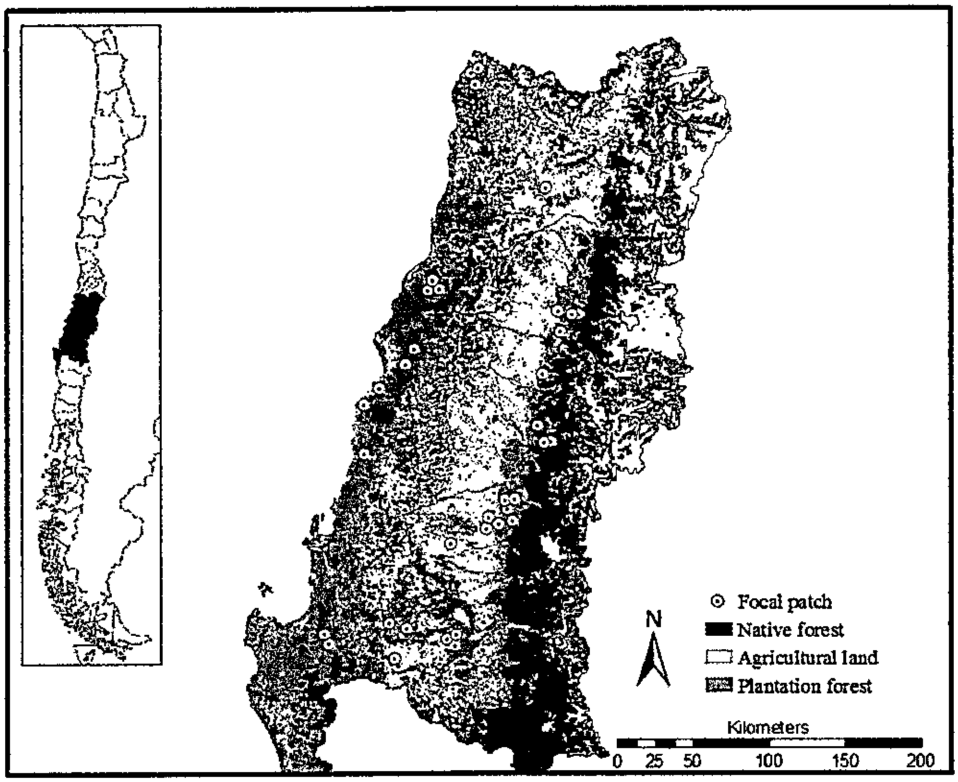

Figure 3.1. Map of south-central Chile showing the 36 surveyed focal patches.

This size range was chosen to control for potential effects of local patch size on bat activity. Forest amount ranged from 1.1 to 60.2% in agricultural landscapes and from 6.5 to 66.8% in forestry landscapes, meanwhile the number of forest patches ranged from 3 to 15 in agricultural landscapes and from 4 to 15 in forestry landscapes (see Supporting Information). We defined a "landscape" as the area within a 2.5 km radius around each of these focal patches. To account for the possibility that different bat species respond to the landscape at different scales, we also measured forest loss and fragmentation several distance intervals (buffers) from the center of each focal patch (1.0, 1.5, 2.0, 2.5, 3.0, 4.0 and 5.0 km radius. We used ArcGIS 9.3 (ESRI 2006) to calculate the proportion of native forest in the landscape within each buffer, as a measured of forest loss and the number of forest patches as a measure of fragmentation (the breaking apart of forest, independent of forest amount). To ensure independent measures of forest loss and fragmentation, buffers surrounding focal patches were chosen such that the proportion of native forest and the number of forest patches represents a gradient from landscapes containing not only the common combinations of high forest amount with low fragmentation and low forest amount with high fragmentation, but also the poorly represented combinations of low forest amount with low fragmentation and high forest amount with high fragmentation. All landscape variables were based on land cover data from the Catastro Nacional de Bosque Nativo from Corporación Nacional Forestal,Chile (http://sit.conaf.cl/).

Following Ethier and Fahrig (2011), at each focal patch, we also measured local habitat variables that might influence bat abundance (Table 3.1). These variables were temperature and wind speed. We also measure the mean density of trees across six 10 x 10 m quadrats at each focal patch, which has been found to influence insectivorous bats use of forest (Brigham & Grindal 1997; Sleep & Brigham 2003). To control for any effects of prey availability on bat activity, we used two light traps per site placed at least 50 m from the nearest bat detector (Ethier & Fahrig 2011) to capture nocturnal flying insects simultaneously with the bat surveys. We used the dry weight (biomass) of insects as a measure of prey availability at each site.

3.2.2 *Bat surveys*

After Ethier and Fahrig (2011), we conducted bat surveys at each of the 36 focal patches for one night each. To limit seasonal variation in bat activity, we restricted surveys to the austral summer season (from February to mid-March 2012 and January 2013). Surveys began at dusk and lasted for four hours to coincide with peak foraging periods of aerial insectivorous bats (Kuenzi & Morrison 2003). Bats were surveyed using two ultrasound bat-detectors model D240X (Pettersson Elektronik AB, Uppsala, Sweden) per focal patch coupled to a digital recorder (M-Audio MicroTrack II) and operated in time-expanded modes. Time-expanded mode allows to record full-spectrum echolocation calls with a high-resolution sonogram of each bat vocalization. These full-spectrum echolocation calls were used to classify bat activity to species.

We placed the first bat detector 5 m into the adjacent matrix so that it recorded bat activity along the forest edge, and the second detector 50 m into the focal patch within a partial clearing with the microphone pointing in the same direction as the first one. Echolocation calls were displayed and analyzed using BatSound 2.1 (Pettersson Elektronik AB, Uppsala, Sweden). Bat activity was quantified by counting the number of bat passes at each point within each local patch and used as a measure of relative abundance. We defined a "bat pass" as a succession of more than two echolocation pulses emitted by a bat flying on axis with the bat detector (Law et al. 1999). Since most passes were recorded along forest edges (74.7% and 66.4% in agricultural and forestry landscape, respectively), we combined the number of bat passes recorded using both bat detectors (forest edge and interior) to quantify bat activity per site. Surveys were not conducted on nights with rain or fog to avoid reduced bat activity (Pye 1971; Erickson & West 2002). Bat species were identified following Simmons (2005) and Díaz et al. (2011) for bats of southern cone of South America.

Table 3.1. Results of generalized linear models (GZLM) examining the effects of patch local variables (insect biomass, tree density, temperature and wind speed) on bat activity per species.

Species	Agricultural landscapes		
	Patch local variables	β	P
Histiotus montanus	-	-	-
Lasiurus cinereus	-	-	-
Lasiurus varius	Tree density	0.17	0.005
Myotis chiloensis	Wind speed	-0.24	0.048
Tadarida brasiliensis	Tree density	-0.14	0.015

Species	Forestry landscapes		
	Patch local variables	β	P
Histiotus montanus	Temperature	0.23	0.009
	Wind speed	-0.17	0.019
Lasiurus cinereus	Insect biomass	0.21	0.003
	Temperature	0.54	<0.001
Lasiurus varius	-	-	-
Myotis chiloensis	Wind speed	-0.07	0.028
Tadarida brasiliensis	Insect biomass	0.17	0.006

3.2.3 *Bat species identification*

Passes of free-flying bats were classifying to species using Quadratic Discriminant Function Analysis (DFA). Classification functions were computed using a library of validated reference calls from hand-released (*Histiotus montanus*, *Lasiurus varius*, *Myotis chiloensis* and *Tadarida brasiliensis*) at the study area (Rodríguez-San Pedro & Simonetti 2013b). Variables used in this analysis were call duration, final frequency, slope frequency modulation, peak frequency, minimal and maximal frequency. If there was uncertainty or inconsistency in the classification, that recording was considered unidentifiable and labeled as "unknown".

3.2.4 *Statistical analysis*

Because our landscapes (agricultural or forestry) were distributed in three different regions which differ regarding to their topography (Andes, Intermediate depression and Coastal range), we conducted a preliminary analysis (Kruskal Wallis one-way analysis of variance) to explore whether bat activity for each species varied among these landscapes. No difference on bat activity was detected (H from 0.307 to 5.282, $P > 0.05$). We check also for spatial autocorrelation on bat activity across the study areas by calculating Moran's *I* for each species.

To identify which local variables (temperature, wind speed, tree density and insect biomass) significantly affected bat activity at each landscape (agricultural and forestry), we used generalized linear models (GZLM) for each species. In each regression model we used the number of bat passes per species per site as the response variable and included as predictors each individual local variables mentioned above. For each species, we retained only those local variables with a significant effect on bat activity for inclusion in the landscape models (Table 3.1).

To estimate the relative effects of forest amount and forest fragmentation on bat activity, we used GZLM for each species at each set of landscapes (agricultural and forestry). In each model, we included the amount of native forest and the number of forest patches as predictor variables as well as any local variable that was significant in the simple GZLM for each species. Before analysis, we standardized the scales of predictors to a mean of zero and a standard deviation of one, so that the magnitude of the effects could be directly compared (Quinn & Keough 2002). The relative influence of forest loss and fragmentation was compared by examining values of standardized predictors, as well as the number of species that responded significantly to these variables. Standardized regression coefficients are one of the best methods for estimating the relative importance of forest loss and fragmentation, even when variables are highly correlated (Smith *et al.* 2009).We assessed statistical significance in all models using Wald χ^2 tests. To analyze the effects of matrix type on the response of bats to forest amount and fragmentation we performed an Analysis of Covariance (GZLM-ANCOVA) using matrix as main factor, with forest amount and number of forest patches as co-variates.

3.3 Results

Across 36 nights and 144 surveys hours, we recorded 2134 echolocation passes, 1950 of which (91%) could be identified and attributed to five of the six species expected to occur in the study area: *Histiotus montanus* (55 passes), *Lasiurus varius* (470 passes), *Myotis chiloensis* (463 passes), *Lasiurus cinereus* (145 passes) and *Tadarida brasiliensis* (817 passes). Passes of *L. cinereus* were identified by comparing call parameters with references calls reported for this specie in other regions (O'Farrell et al. 2000). The 9% of the echolocation passes could not be analyzed due to the low intensity of the recorded calls and were classified as "unknown". These passes, therefore, were not included in the analyses at species level but were considered for overall activity analysis. The most commonly encountered bat species across all landscapes were *L. varius* and *T. brasiliensis* (present at 35/36 sites) followed by *M. chiloensis* (28/36), *L. cinereus* (21/36) and *H. montanus* (16/36). Bat activity was not significantly auto-correlated in any species (Moran's I from –0.045 to 0.009, $P > 0.05$).

In agricultural landscapes, the relationship between forest amount and bat activity was significantly positive in *H. montanus* ($\beta = 0.45$, Wald $\chi^2 = 16.20$, d.f. = 1, $P < 0.001$ at 1 km), *L. cinereus* ($\beta = 0.11$, Wald $\chi^2 = 6.60$, d.f. = 1, $P = 0.010$ at 1.5 km) and *T. brasiliensis* ($\beta = 0.10$, Wald $\chi^2 = 15.81$, d.f. = 1, $P < 0.001$ at 2.0 km) and negative in *M. chiloensis* ($\beta = -0.14$, Wald $\chi^2 = 5.95$, d.f. = 1, $P = 0.015$ at 4.0 km) (Fig. 3.2). Activity of *L. varius* was not strongly associated with forest amount (Fig. 3.2). Species responses to forest fragmentation also varied in both direction and magnitude (Fig.3.2). The activity of *L. varius* and *M. chiloensis* significantly increased with increasing fragmentation ($\beta = 0.14$, Wald $\chi^2 = 6.37$, d.f. = 1, $P = 0.012$ at 3.0 km and $\beta = -0.26$, Wald $\chi^2 = 6.97$, d.f. = 1, $P = 0.008$ at 4.0 km, respectively), while activity levels decreased for *H. montanus* ($\beta = -0.44$, Wald $\chi^2 = 3.78$, d.f. = 1, $P = 0.007$ at 1.0 km) (Fig. 3.2). Activity of *L. cinereus* and *T. brasiliensis* were not strongly associated with forest fragmentation (Fig. 3.2). Based on standardized effect sizes, forest amount at the landscape level was similar in influence to forest fragmentation, with four of five species responding more strongly to forest amount than to fragmentation, compared to only three species responding more strongly to forest fragmentation (Table 3.2; Fig. 3.2).

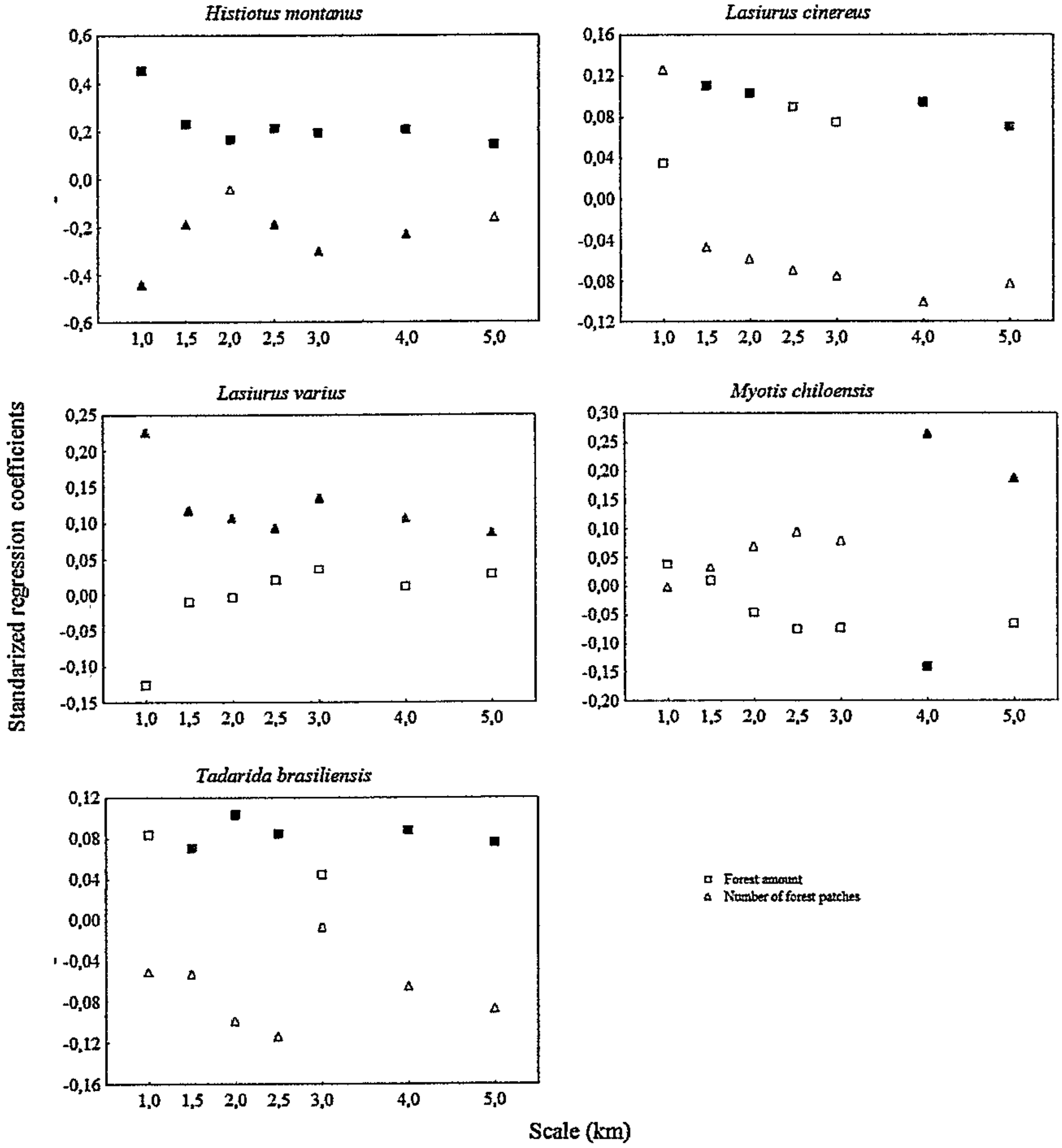

Figure 3.2. Scatter diagrams of standardized regression coefficients from GZLM examining the effects of forest amount and fragmentation *per se* on bat activity in agricultural landscapes at multiple spatial scales. The black symbols indicate statistical significant at $P < 0.05$, the gray is significant at $P < 0.10$ and unfilled symbols indicate no effect.

Table 3.2. Comparing the standardized regression coefficients obtained from the GZLM examining the effects of forest amount and fragmentation per se on bat activity between agricultural and forestry landscapes.

			Agricultural	Plantation	P
Species	Radius (km)	Variables	β	β	
Histiotus montanus	1.0	Forest amount	**0,451***	**-0,129***	**0,000**
	1.5	Number of forest patches	**0,229***	**-0,138***	**0,008**
		Number of forest patches	**-0,192***	-0,068	0,397
	2.0	Forest amount	**0,163***	**-0,150***	**0,012**
	2.5	Forest amount	**0,211***	**-0,138***	**0,013**
		Number of forest patches	**-0,191***	-0,018	0,137
	3.0	Forest amount	**0,191***	**-0,126***	**0,047**
		Number of forest patches	**-0,304***	-0,023	**0,030**
	4.0	Forest amount	**0,206***	-0,087	**0,078**
		Number of forest patches	**-0,232***	0,012	0,106
	5.0	Forest amount	**0,140***	-0,058	0,227
Lasiurus cinereus	1.5	Forest amount	**0,110***	0,142	0,630
	2.0	Forest amount	**0,103***	0,098	0,551
		Number of forest patches	-0,070	**0,107***	**0,068**
	4.0	Forest amount	**0,094***	0,064	0,340
Lasiurus varius	1.5	Number of forest patches	**0,118***	0,014	**0,065**
	2.5	Number of forest patches	**0,093***	-0,063	**0,023**
	3.0	Number of forest patches	**0,135***	-0,081	**0,006**
Myotis chiloensis	1.5	Number of forest patches	0,031	**0,146***	0,228
	4.0	Forest amount	**-0,142***	0,081	**0,023**
		Number of forest patches	**0,264***	0,115	0,968
	5.0	Number of forest patches	**0,186***	0,094	0,778
Tadarida brasiliensis		Forest amount	**0,103***	0,056	0,257
	2.5	Forest amount	**0,084***	0,081	0,765
		Number of forest patches	-0,114	**0,112***	**0,001**
	4.0	Forest amount	**0,088***	0,042	0,631
	5.0	Forest amount	**0,076***	0,033	0,397

In plantation dominated landscapes, only *H. montanus* responded significantly to forest amount, decreasing activity with increasing forest amount (β = -0.15, Wald χ^2 = 7.236, d.f. = 1, P = 0.007 at 2.0 km) (Fig. 3.3). In contrast, forest fragmentation was a better predictor of bat activity than forest amount with three (*L. cinereus*, *M. chiloensis* and *T. brasiliensis*) of the five species responding more strongly to forest fragmentation than to forest amount (Table 3.2). In all cases, bat activity increased with increasing fragmentation at the landscape level (β = 0.11, Wald χ^2 = 4.55, d.f. = 1, P = 0.033 at 2.5 km, β = 0.15, Wald χ^2 =4.30, d.f. = 1, P = 0.038 at 1.5 km, β = 0.11, Wald χ^2 = 5.20, d.f. = 1, P = 0.023 at 2.5 km, respectively) (Fig. 3.3). Activity of *L. varius* was not significantly associated with either forest amount or fragmentation (Fig. 3.3).

When compared standardized effects size of each of the two predictors between type of matrix, that forest amount was a stronger predictor for agricultural than for plantation-dominated landscapes (Table 3.2). Meanwhile, forest fragmentation was a stronger predictor in both forestry and agricultural landscapes (Table 3.2). Results of ANCOVA revealed a significant effect for matrix type only on activity of *M. chiloensis* (Table 3.3; Fig. 3.4). For the same amount of forest cover and forest fragmentation at the landscape level, activity of *M. chiloensis* species was higher in forest patches surrounded by forested matrices compared to patches embedded in agricultural matrices (Wald χ^2 = 8.012, d.f = 1, P = 0.005 at 2.5 km); meanwhile, activity of *H. montanus*, *L. cinereus*, *L. varius* and *T. brasiliensis* was similar between forest patches surrounded by either agricultural or forested matrices (Table 3.3; Fig. 3.4).

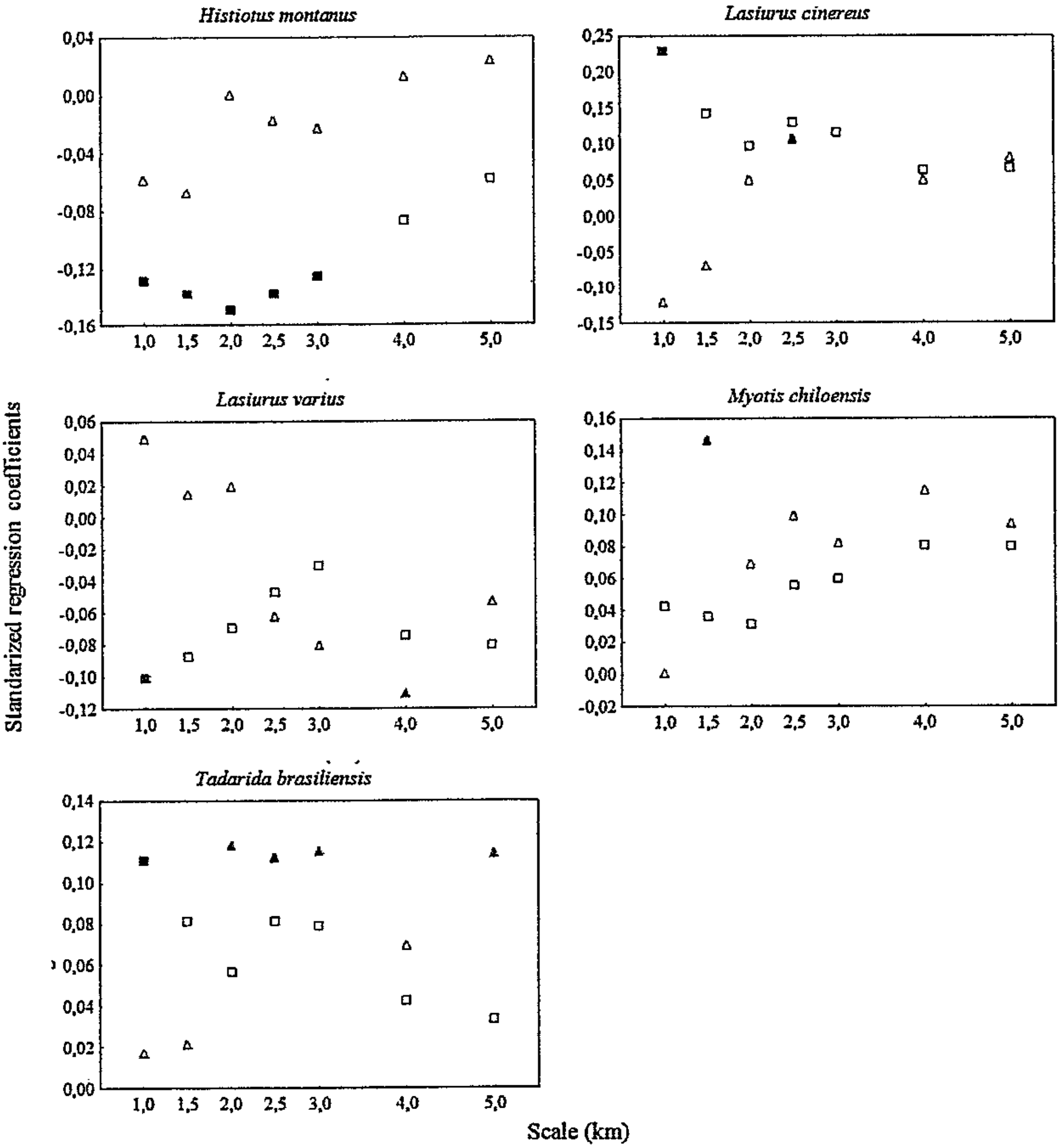

Figure 3.3. Scatter diagrams of standardized regression coefficients from GZLM examining the effects of forest amount and fragmentation *per se* on bat activity in forestry landscapes at multiple spatial scales. The black symbols indicate statistical significant at $P < 0.05$, the gray is significant at $P < 0.10$ and unfilled symbols indicate no effect.

Table 3.3. Summary statistics for the analysis of covariance (ANCOVA) to detect differences in bat activity between agricultural and forestry landscapes at spatial scale of 2.5 km

Species	Variables	Wald χ^2	P
Histiotus montanus	Matrix	5.459	**0.019**
	Forest amount	4.603	0.032
	Number of forest patches	4.199	0.040
	Matrix*Forest amount	6.190	**0.013**
	Matrix*Number of forest patches	2.215	0.137
Lasiurus cinereus	Matrix	3.117	0.077
	Forest amount	4.176	0.041
	Number of forest patches	0.392	0.531
	Matrix*Forest amount	0.735	0.391
	Matrix*Number of forest patches	3.336	0.068
Lasiurus varius	Matrix	1.553	0.213
	Forest amount	0.013	0.908
	Number of forest patches	0.540	0.462
	Matrix*Forest amount	2.021	0.155
	Matrix*Number of forest patches	5.182	0.023
Myotis chiloensis	Matrix	8.012	**0.005**
	Forest amount	0.016	0.900
	Number of forest patches	2.244	0.134
	Matrix*Forest amount	2.554	0.110
	Matrix*Number of forest patches	0.229	0.632
Tadarida brasiliensis	Matrix	0.087	0.768
	Forest amount	2.059	0.151
	Number of forest patches	0.086	0.770
	Matrix*Forest amount	0.582	0.445
	Matrix*Number of forest patches	7.887	0.005

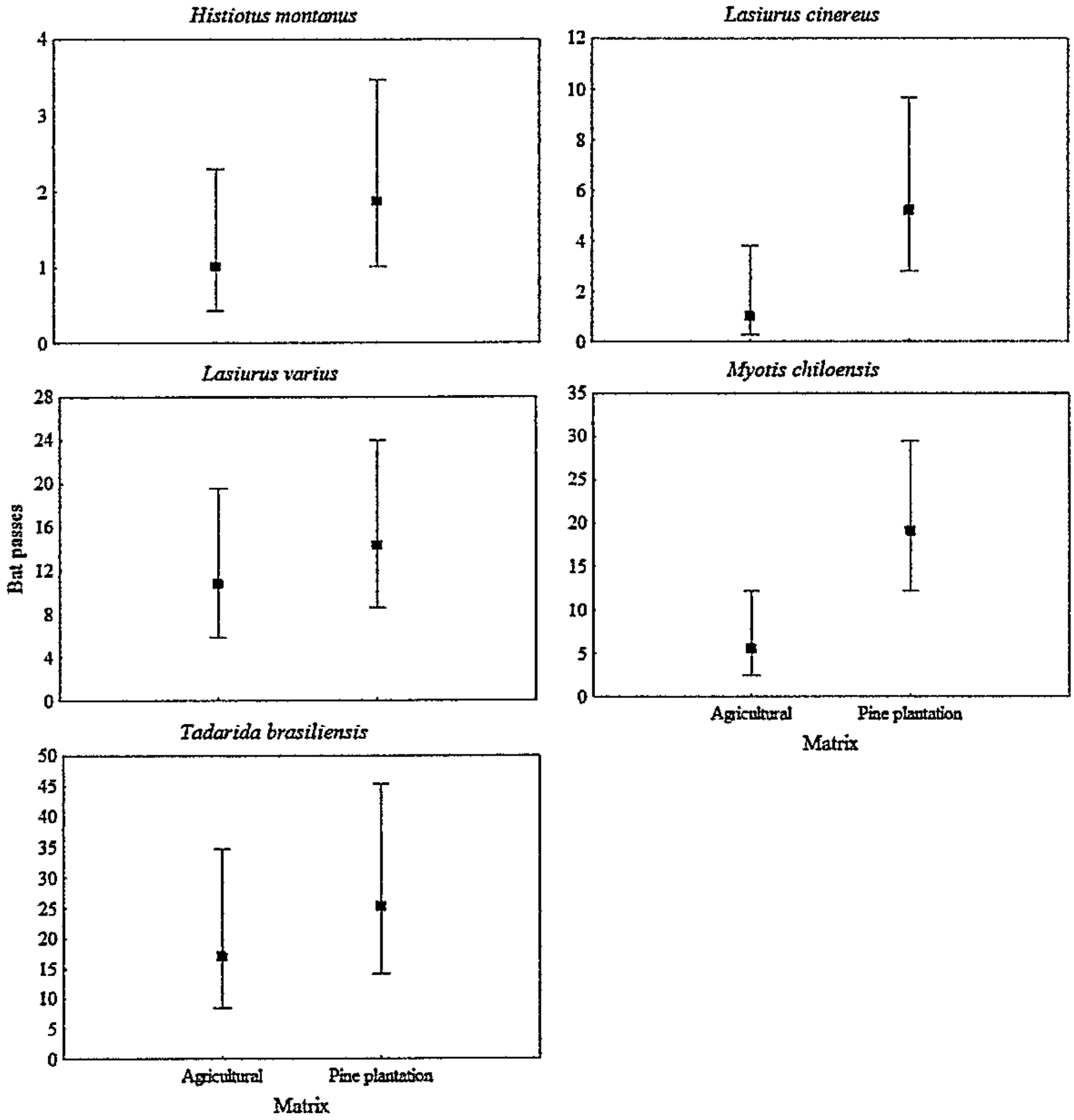

Figure 3.4. Mean ± (SE) of bat activity per species in agricultural and forestry landscapes obtained from analysis of covariance (ANCOVA) at the spatial 2.5 km radius.

3.4 Discussion

The idea that forest loss and fragmentation *per se* have independent effects on biodiversity has been shown in experimental studies that controlled for their relationship (McGarigal & McComb 1995; Trzcinski et al. 1999; Villard et al. 1999; Ethier & Fahrig 2011). These studies focused attention on the independent effects of forest loss and fragmentation *per se* on species, but did not examine how these effects are modulated by the structure of the landscape matrix (Debinski 2006).

Ethier and Fahrig (2011) examined how forest amount and fragmentation *per se* independently affect bat abundance in Ontario, Canada. They studied 22 landscapes varying in deciduous forest cover from 4.2 to 42.4%. Similar to their results, we found that the effects of forest amount were mixed across species. In addition to forest amount, they also found that when there was evidence for an effect of forest fragmentation, independent of forest amount, on bat activity, the effect was positive for most species. Ethier and Fahrig (2011) suggested that the mechanism driving this positive response of bats to fragmentation is a higher complementation between (or access to) foraging and roosting habitats in more fragmented landscapes. Another possible explanation could be a positive response to forest edge. Bats use forest edges for commuting and foraging (Grindal & Brigham 1999; Morris et al. 2010; Rodríguez-San Pedro & Simonetti 2013a) and the high number of bat passes recorded along forest edges in our study (74.7% and 66.4% in agricultural and forestry landscape, respectively) seems to support this hypothesis. However, an analysis of the relationship between bat activity and forest edge density confirmed these assumptions only for *L. varius* in agricultural landscapes, where we found a significant positive effect of forest edge, but not for the other four species. Therefore, we suggest that our results on fragmentation *per se* effects on bat activity are consistence with both the landscape complementation and the positive edge response hypotheses. In this sense, future research could help to a better understanding of the causes underlying bat response to fragmentation *per se* at the species level.

As forest amount increased, the activity of *M. chiloensis* decreased in agricultural landscapes, a surprising result for a bat species it is assumed is a forest dependent. *Myotis chiloensis* can either forage inside the forest, close to vegetation, or in edge and gaps created by natural or anthropogenic disturbance in central Chile (Galaz & Yáñez 2006;

Rodríguez-San Pedro & Simonetti 2013a). Individuals of this species is also able to use artificial structures, such as farmhouses, for roosting in rural landscapes where a considerable forest amount has been removed (Galaz & Yáñez 2006). It is therefore possible that the availability of forest edges and open areas for foraging and anthropogenic structures for roosting may be driving the observed negative relationship of *M. chiloensis* with forest amount in agricultural landscapes. Surprisingly, the activity of *L. varius* was unaffected by forest amount, even though this species have been associated with forested habitats (Galaz & Yáñez 2006; Rodríguez-San Pedro & Simonetti 2013a), suggesting that even species exhibiting a definitive association with a particular habitat type at the patch level have a great deal of variation in abundance among landscapes that could not be explained by forest amount alone. It is not surprising that activity of T. *brasiliensis*, and *L. cinereus* were not affected by fragmentation *per se*. This is probably because high wing loading and high wing aspect ratio, features characteristic of species foraging in open space (Norberg & Rayner 1987), confer high speeds that make visiting isolated patches energetically cheap. On the other hand, forest species such as *H. montanus*, that are adapted for slower and more maneuverable flight because of their lower wing loading and lower aspect ratio, probably cannot afford prolonged commuting flights over an inhospitable matrix, such as agricultural lands, to isolated patches because they are energetically very costly (Norberg & Rayner 1987).

Bat activity in our study was strongly associated with forest amount and fragmentation *per se*, however their effects varied between agricultural and forestry dominated landscapes. In accordance with other studies, forest amount was a significant predictor of abundance of most species in agricultural landscapes (McGarigal & McComb 1995; Villard et al. 1999; Klingbeil & Willig 2009; Ethier & Fahrig 2011), but not in those dominated by plantation forest where only one species responded significantly to forest amount. In contrast, fragmentation *per se* was a significant predictor of species abundance in both agricultural and forestry landscapes. The magnitude and direction of forest loss and fragmentation can be influenced by the degree of contrast between forest fragments and the matrix (Kupfer et al. 2006; Ewers & Didham 2006). Landscapes characterized by a high-contrast matrix (e.g. forest vs. agricultural) trigger the strongest negative responses to forest loss (Ewers & Didham 2006). The low contrast between forest and plantation forests, however, may provide habitat for some species of forest-dwelling bats such as *H. montanus*, *L. cinereus*, *L. varius* and *M. chiloesnis* (Rodríguez-San Pedro & Simonetti 2013a), and thus could compensate for habitat loss.

Like bats in temperate forests of Canada and tropical forests of Perú and subtropical Atlantic forest of Paraguay (Gorresen & Willig 2004; Klingbeil & Willig 2009; Ethier & Fahrig 2011), bat species in Chile displayed scale-dependent responses to forest amount and fragmentation *per se*. In agricultural landscapes, bat activity for most species was strongly determined by both forest amount and fragmentation at large spatial scales. Although limited information is available on the movements and home range size of Chilean bat species, these scales are larger than the average maximum distance traveled by similar small and medium-sized aerial insectivorous bats during foraging activity elsewhere (Elmore et al. 2005; Sparks et al. 2005; Walters et al. 2007; Henderson & Broders 2008; Kniowski & Gehrt 2014). The fact that bat activity was associated with forest amount and fragmentation *per se* at scales larger than the home range of individual bats suggests that local bat activity reflects a number of factors operating at different scales probably depending on species-specific behavioral or life-history characteristics.

In contrast to agricultural landscapes, bat activity was associated significantly with forest amount and/or fragmentation at smallest spatial scales in forestry landscapes suggesting that the type of matrix could affect not only the direction and magnitude of forest amount and fragmentation *per se* on bat abundance, but also the spatial scale at which their effects operate on species. Landscapes dominated by agricultural matrices, with smaller and more distant suitable habitat patches likely require longer commuting flights to obtain similar resources compared to landscape with greater proportions of forested cover resulting in larger home ranges and, as a consequence, they respond to larger scales in modified landscapes (Chaverri et al. 2007; Saïd et al. 2009; Kniowski & Gehrt 2014). For example, the Indiana bat (*Myotis sodalis*) home ranges within a highly agricultural landscape are larger compared to other studies in forested and rural-urban landscapes (Kniowski & Gehrt 2014).

Our results suggest that multiple-scale assessment are necessary to adequately quantifying the effects of forest amount and fragmentation *per se* on mobile species that inhabit complex landscapes where habitat patches are difficult to define and thus, may be critical to the success of management and conservation strategies in human modified landscapes.

3.4.1 *Conservation implication*

To our knowledge, this study represent the first attempt to examine the modulating effects of landscape matrix on the response of insectivorous bats to forest loss and fragmentation *per se*, providing evidence that low contrast matrices can mitigate the effects of forest loss. In our study, the relative abundance of bats was higher in moderately fragmented forest, demonstrating that landscapes with native forest distributed in a larger number of patches surrounded by a low contrast matrix may support bat diversity and abundances with no negative consequence.

Plantation forest can be viewed as "biological desert", holding depauperated assemblages of the original biota, being discarded as a suitable habitat for the local biota (Hartley 2002). The fact that landscapes with small forest patches embedded in such production-oriented land-use can mitigate the effects of forest loss, enhance the capacity of many taxa, including bats, to persist in landscapes modified by human in which forestry plantations are an important component. We suggest that management efforts in anthropogenic altered landscapes should aim in reducing the degree of fragment-matrix contrast to mitigate the strength of forest loss.

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Supporting information

Table S1. Range, mean and standard error (SE) of forest amount and number of forest patches across 18 agricultural landscapes and 18 forestry landscapes at multiple spatial scales

	Agricultural landscapes					
Scale (km)	Forest amount (ha)			Number of forest patches		
	Range	Mean	SE	Range	Mean	SE
1.0	8.41-130.29 (2.68-41.48%)	37.90	7.65	1-8	2.72	0.40
1.5	9.82-388.10 (1.39-54.91%)	85.26	21.50	1-10	4.11	0.55
2.0	13.41-739.99 (1.07-58.89%)	165.71	41.82	2-12	5.39	0.67
2.5	21.99-1181.60 (1.12-60.18)	277.95	69.34	3-15	6.94	0.88
3.0	56.98-1787.63 (2.02-63.23%)	423.49	10.48	3-22	8.00	1.17
4.0	65.50-3321.52 (1.39-66.08%)	725.79	194.28	3-27	11.50	1.75
5.0	71.84-5463.85 (0.95-72.53%)	161.05	310.49	5-33	13.78	2.05

	Forestry landscapes					
Scale (km)	Forest amount (ha)			Number of forest patches		
	Range	Mean	Range	Mean	Range	Mean
1.0	15.82-161.46 (5.04-51.40%)	60.24	10.27	2-6	3.56	0.30
1.5	32.72-304.46 (4.63-55.81%)	146.82	24.04	3-7	4.78	0.27
2.0	69.29-769.20 (5.51-61.22%)	266.01	42.92	4-11	6.83	0.46
2.5	127.67-1311.33 (6.50-66.79%)	413.13	70.08	4-15	8.67	0.74
3.0	213.01-2010.89 (7.53-71.12%)	595.67	105.28	5-21	11.06	1.04
4.0	475.92-3793.16 (9.47-75.47%)	1068.81	192.96	5-31	16.06	1.82
5.0	692.08-6294.21 (9.19-83.55%)	1694.71	331.75	6-39	20.22	2.33

Table S2. Values of standardized regression coefficients from GZLM examining the effects of the distribution range of species, forest amount and fragmentation *per se* on bat activity in agricultural and forestry landscapes at multiple spatial scales. ** indicate statistical significant at P < 0.05, * is significant at P < 0.10 and n.s indicate no significant effect.

Matrix	Scale (km)	Species	β		
			Forest amount	Number of forest patches	Andes
Agriculture	1.0	*Histiotus montanus*	0.36**	-0.32*	1.34 n.s
	1.5		0.19**	-0.15 n.s	1.87*
	2.0		0.13**	-0.02 n.s	2.11*
	2.5		0.16**	-0.11 n.s	1.73 n.s
	3.0		0.16**	-0.24 n.s	1.36 n.s
	4.0		0.16**	-0.17 n.s	1.57 n.s
	5.0		0.11**	-0.11 n.s	1.74 n.s
	1.0	*Lasiurus cinereus*	0.02 n.s	0.14 n.s	0.21 n.s
	1.5		0.11**	-0.05 n.s	0.06 n.s
	2.0		0.10**	-0.06 n.s	0.10 n.s
	2.5		0.09*	-0.07 n.s	0.03 n.s
	3.0		0.08 n.s	-0.08 n.s	-0.08 n.s
	4.0		0.10*	-0.11 n.s	-0.14 n.s
	5.0		0.07*	-0.09 n.s	-0.11 n.s
	1.0	*Lasiurus varius*	-0.15 n.s	0.31*	0.076 n.s
	1.5		-0.01 n.s	0.16**	0.07 n.s
	2.0		0.01 n.s	0.15**	-0.12 n.s
	2.5		0.06 n.s	0.13**	0.08 n.s
	3.0		0.06 n.s	0.20**	0.68 n.s
	4.0		0.05 n.s	0.16**	0.25 n.s
	5.0		0.07 n.s	0.14**	0.14 n.s

Matrix	Scale (km)	Species	β		
			Forest amount	Number of forest patches	Andes
Agriculture	1.0	*Myotis chiloensis*	0.05 n.s	0.02 n.s	0.66 n.s
	1.5		0.00 n.s	0.06 n.s	0.83 n.s
	2.0		-0.05 n.s	0.09 n.s	0.74 n.s
	2.5		-0.08*	0.12*	1.16 n.s
	3.0		-0.08 n.s	0.15 n.s	1.4 n.s
	4.0		-0.14**	0.29**	2.37**
	5.0		-0.06 n.s	0.20**	1.98**
	1.0	*Tadarida brasiliensis*	0.11**	-0.13**	-0.01 n.s
	1.5		0.09**	-0.14**	0.14 n.s
	2.0		0.09**	-0.14**	0.19 n.s
	2.5		0.09**	-0.18**	-0.24 n.s
	3.0		0.03 n.s	-0.09*	0.17 n.s
	4.0		0.08 n.s	-0.15*	0.14 n.s
	5.0		0.05**	-0.14**	0.09 n.s
Forestry	1.0	*Histiotus montanus*	-0.02 n.s	-0.14*	0.55 n.s
	1.5		-0.04 n.s	-0.12 n.s	0.73 n.s
	2.0		-0.09 n.s	-0.12 n.s	0.56 n.s
	2.5		-0.04 n.s	-0.05 n.s	0.41 n.s
	3.0		-0.03 n.s	-0.05 n.s	0.48 n.s
	4.0		-0.02 n.s	-0.06 n.s	0.49 n.s
	5.0		0.03 n.s	-0.03 n.s	0.19 n.s
	1.0	*Lasiurus cinereus*	0.28*	-0.32**	0.81 n.s
	1.5		0.05 n.s	-0.09 n.s	1.26 n.s
	2.0		-0.01 n.s	-0.04 n.s	1.34 n.s
	2.5		0.19 n.s	0.13 n.s	0.36 n.s
	3.0		0.27 n.s	0.17*	-0.41 n.s
	4.0		0.34 n.s	0.13 n.s	-0.85 n.s
	5.0		0.34 n.s	0.07 n.s	-0.79 n.s

Matrix	Scale (km)	Species	β		
			Forest amount	Number of forest patches	Andes
Forestry	1.0	*Lasiurus varius*	-0.10**	0.06 n.s	-0.25 n.s
	1.5		-0.09*	0.01 n.s	0.10 n.s
	2.0		-0.07 n.s	0.01 n.s	0.11 n.s
	2.5		-0.06 n.s	-0.08 n.s	0.50 n.s
	3.0		-0.08 n.s	-0.14**	0.83 n.s
	4.0		-0.14**	-0.17**	1.1*
	5.0		-0.15**	-0.11*	1.02 n.s
	1.0	*Myotis chiloensis*	0.05 n.s	0.01 n.s	0.24 n.s
	1.5		0.04 n.s	0.15**	-0.09 n.s
	2.0		0.04 n.s	0.06 n.s	0.16 n.s
	2.5		0.10 n.s	0.06 n.s	0.06 n.s
	3.0		0.08 n.s	0.11 n.s	-0.12 n.s
	4.0		0.14**	0.19**	-0.80 n.s
	5.0		0.13**	0.14**	-0.68 n.s
	1.0	*Tadarida brasiliensis*	0.18 n.s	-0.17**	0.71 n.s
	1.5		0.02 n.s	-0.05 n.s	0.82 n.s
	2.0		-0.03 n.s	-0.00 n.s	0.87 n.s
	2.5		0.10 n.s	0.11 n.s	0.17 n.s
	3.0		0.16 n.s	0.14*	-0.39 n.s
	4.0		0.22 n.s	0.12 n.s	-0.70 n.s
	5.0		0.22 n.s	0.09 n.s	-0.59 n.s

General conclusions

Overall, this study provides evidence that abundance of insectivorous bats in central Chile are strongly associated with both forest loss and fragmentation *per se* and that these effects are modulated by the structural complexity of the matrix in which forest patches are embedded. In my study I emphasize the need for paying attention to the structural complexity of the matrix in determining responses of species to anthropogenic modifications of the landscape.

My results stress that plantation forests might act as an alternative habitat for bats enhancing their capacity to persist in human-modified landscapes in which exotic forestry plantations are an important component. Plantations with a well-developed understory represent a suitable habitat for bats despite the higher degree of structural clutter. The presences of tracks provide internal linear edges in plantations with undergrowth vegetation allowing clutter-sensitive and clutter-tolerant bats to use such cluttered habitats for foraging. This result underscores the importance of tracks as an ameliorative measure in plantation with understory vegetation for this group of mammals.

In my thesis, I presented the first analysis of how the effects of forest loss and fragmentation *per se* are modulated by low fragment-matrix contrast versus high fragment-matrix contrast in a single study. My findings suggest that effective conservation efforts and management strategies in fragmented landscapes should aim in reducing the degree of fragment-matrix contrast to mitigate the strength of forest loss and thus the conservation of biodiversity.

Appendix 1

ACOUSTIC IDENTIFICATION OF FOUR SPECIES OF BATS (ORDER CHIROPTERA) IN CENTRAL CHILE[1]

Abstract. - Echolocation calls of four species of insectivorous bats of central Chile were recorded and characterized to determine vocal signatures that allow their identification in the field. Pulses of *Tadarida brasiliensis* were characterized by the highest duration and the lowest values for all frequencies, which do not overlap those of the remaining species. *Tadarida* emits narrowband, shallow frequency modulated search calls. All three vespertilionid species studied (*Histiotus montanus*, *Lasiurus varius* and *Myotis chiloensis*) showed similar echolocation design to one another consisting of a downward frequency modulation at the beginning of the signal followed by a narrowband quasi-constant frequency component; however, their calls differ by their spectral characteristics. Discriminant function analysis of six acoustic parameters (duration, initial frequency, slope frequency modulation, peak frequency, minimal and maximal frequency) gave an overall classification of 87.4%, suggesting species could be correctly classified based on echolocation calls. Call duration and minimal frequency were the variables most important for species identification.

Key words: echolocation calls, acoustic identification, DFA, Vespertilionidae, Molossidae

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Introduction

Aerial insectivorous bats have well-developed echolocation abilities allowing them to detect and avoid mist-nets and therefore often go underrepresented in mist-netting studies (O'Farrell and Gannon 1999). Therefore, acoustic identification of insectivorous bat species based on the shape and pattern of their echolocation calls has become a successful tool to address differential habitat use and to infer patterns of activity and behaviour (Russo and Jones 2003; Estrada et al. 2004). However, this method is only effective if each sequence of calls recorded in the field can be unequivocally assigned to a given species.

Most of the Chilean bat species are associated with forested habitats (Galaz and Yáñez 2006), yet the area covered by temperate forest in central Chile has been reduced and fragmented due to agriculture and forest plantations (Echeverría et al. 2006). Landscape-level transformations could therefore affect bat populations in Chile. Defining appropriate conservation guidelines requires identifying habitat use, particularly when land-use changes are modifying habitat availability. Further, despite the increasingly common use of bat detectors in studies of insectivorous bat activity (Law et al. 1999; Russo and Jones 2003; Estrada et al. 2004), the use of echolocation calls to conduct inventories of bats in Chile is currently hindered by a scarce knowledge of the acoustic repertoire of most species. Within this framework, we aim to examine the characteristics of echolocation calls of four species of insectivorous bats occurring in central Chile, thereby facilitating acoustic inventories of bats and assessments of interspecific variations in patterns of habitat use.

Of the four species studied, echolocation calls of *Myotis chiloensis* have been previously reported (Ossa et al. 2010), but their description was limited to only three acoustic parameters: call duration, terminal frequency and inter-pulse intervals. In order to complement its acoustic characterization, a more detailed study of their sound emissions is presented here. Call design of *Tadarida brasiliensis* is well known from populations of the northern hemisphere (Simmons et al. 1978; Ratcliffe et al., 2004). Because geographic variation in echolocation calls has been reported for other species (Thomas et al. 1987), reference calls recorded for *T. brasiliensis* in a particular region may not be applicable elsewhere, so we offer a description of echolocation calls from Chilean populations.. Finally, we present the first description of echolocation calls for *Histiotus montanus* and *Lasiurus varius*.

Material and methods

Bat captures and acoustic recordings were conducted at Tregualemu, coastal range of central Chile (35°59'S-72°41'W to 35°59'S-72°46'W), from January 2010 to October 2012. Echolocation calls of 16 *H. montanus*, 24 *L. varius* and 16 *M. chiloensis* were recorded from hand-released bats after capture using harp traps. All individual bats were recorded in the same habitat, a moderate-cluttered space over an open road (> 4m width) surrounded by low pine trees. Echolocation calls were recorded five meters from the release point when no other bats were flying over the site. Echolocation calls of *T. brasiliensis* were recorded from 20 individuals foraging up to 10 m above ground level at least 50 m away from a known roost. Captured bats were identified in the hand following Galaz and Yáñez (2006).

Echolocation calls were recorded using an ultrasound bat-detector model D240X (Pettersson Elektronic AB, Upsala, Sweden) with a flat response characteristic between 10 and 120 kHz. The output of the bat detector was coupled to a digital recorder (M-Audio MicroTrack II) and operated in time-expanded mode. Time-expanded mode allows recording full-spectrum echolocation calls so that subsequent quantitative analysis of call structure may be performed. Passes of echolocation calls were displayed simultaneously as spectrograms and oscillograms using BatSound 2.1 with a sampling rate of 44.1 kHz and a Hanning window. Spectrograms were made of consecutive Fast Fourier Transforms (FFT's) with a 99 % overlap. For spectrograms and oscillograms, time resolution was 0.1 ms. For spectrograms, the frequency resolution was 610 Hz. According to the duration of the call to be analyzed (measured in the oscillogram), power spectra were calculated using Fast Fourier Transforms obtained from 512 to 2048 data points.

From each individual, two to five pulses with good signal noise ratio (peak intensity with more than 20 dB above noise level measured in the power spectrum) were chosen. No acoustic paramaters were evaluated in pulses which did not meet this criteria. For each pulse, we manually measured the following parameters: (1) duration (time between start and end of a pulse, measured in ms in the oscillogram); (2) initial and (3) final frequency (measured in the spectrogram); (4) slope of frequency modulation (difference in kHz between the initial and final frequency of the call divided by the duration of the call); (5) peak frequency (frequency in kHz corresponding with the maximal intensity in the power spectrum); (6) maximal and (7) minimal frequency (measured 20 dB below peak intensity in the power spectrum); (8) bandwidth (difference between maximal and minimal frequency). In each call sequence, we measured interpulse interval (IPI) from the beginning of a call to the start of next call. We used Quadratic Discriminant Function Analysis (DFA) to determine if the four species could be separated in four independent groups (Russo and Jones 2002). Variables used in this analysis were call duration, final frequency, slope frequency modulation, peak frequency, maximal and minimal frequency. Wilk's λ values were obtained with a MANOVA to test for statistical significance of DFA models. The standardized discriminant function coefficients were used to determine the contribution each variable made to the ability of DFA to classify calls. For each species, descriptive statistics (Mean ± SE) were calculated. All tests were performed with STATISTICA 8.0 (StatSoft, Inc. 2007).

Results

We analyzed 62 calls from *T. brasiliensis*, 66 calls from *M. chiloensis*, 56 calls from *H. montanus* and 79 calls from *L. varius*. *Tadarida brasiliensis* showed narrowband, shallow frequency modulated (quasi-constant frequency) search calls with a single harmonic lasting 13 ms. Pulses area emitted with an average interval of 286.9 ± 18.9 ms (Figure A1; Table A1). *Tadarida brasiliensis* echolocation calls exhibited the highest call duration and showed the lowest values for all frequency variables, which do not overlap with those of the vespertilionid species. *Histiotus montanus*, *Lasiurus varius* and *Myotis chiloensis* emitted single harmonic search calls with a similar design consisting of a downward frequency modulation at the beginning of the signal followed by a narrowband quasi-constant frequency component. However, their calls differ by their spectral characteristics (Table A1). Search calls of *H. montanus* were characterized by durations shorter than 4ms and bandwidth of 13 kHz. The minimal frequency was around 31 kHz. Pulses were emitted at intervals of 136.1 ± 8.0 ms (Figure A2; Table A1). Search calls emitted by *L. varius* showed intermediate acoustic parameters (Figure A3; Table A1) with pulses longer (5 ms) than those of *H. montanus*. The minimal frequency was around 37 kHz and the inter-pulse intervals averaged 164.3 ± 9.6 ms. The calls broadcasted by *M. chiloensis* also consisted of short (< 4 ms) downward frequency-modulated signals sweeping down between 89 and 39 kHz with most energy at 47 kHz (Figure A4; Table A1).

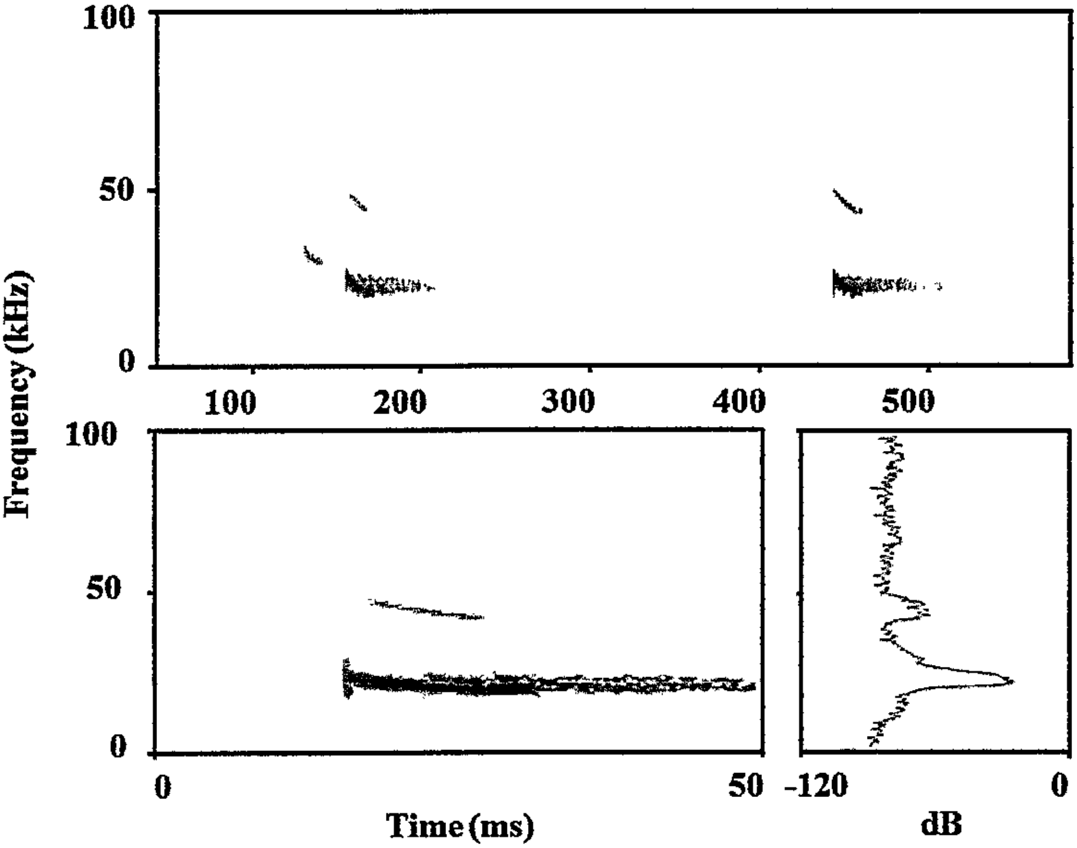

Figure A1. Sonogram of echolocation calls of *Tadarida brasiliensis* showing (a) a typical pulse sequence; (b) a single call; (c) a power spectrum of a typical echolocation call.

Multivariate discriminant function analysis of the six acoustic parameters gave an overall classification of 87.4% of the calls. Multivariate analysis of variance (MANOVA) showed that the model was significant (Wilk's λ=0.018; F=125.64; p<0.001) and that 97.2% of the variation was explained by the first two discriminant functions. Search calls of individual bats could be assigned with accuracy to their groups (Figure A5; Table A2). Search calls emitted by *T. brasiliensis* were 100% of the time correctly identified and grouped separately of the rest of the species. Identification rates of calls of *H. montanus* were also high, with 98% of recorded calls correctly identified. However, search calls of *L. varius* and *M. chiloensis* overlap in several attributes making difficult their identification.

Of the six variables used in the DFA, the most important for discriminating between species were call duration and minimal frequency (Table A3).

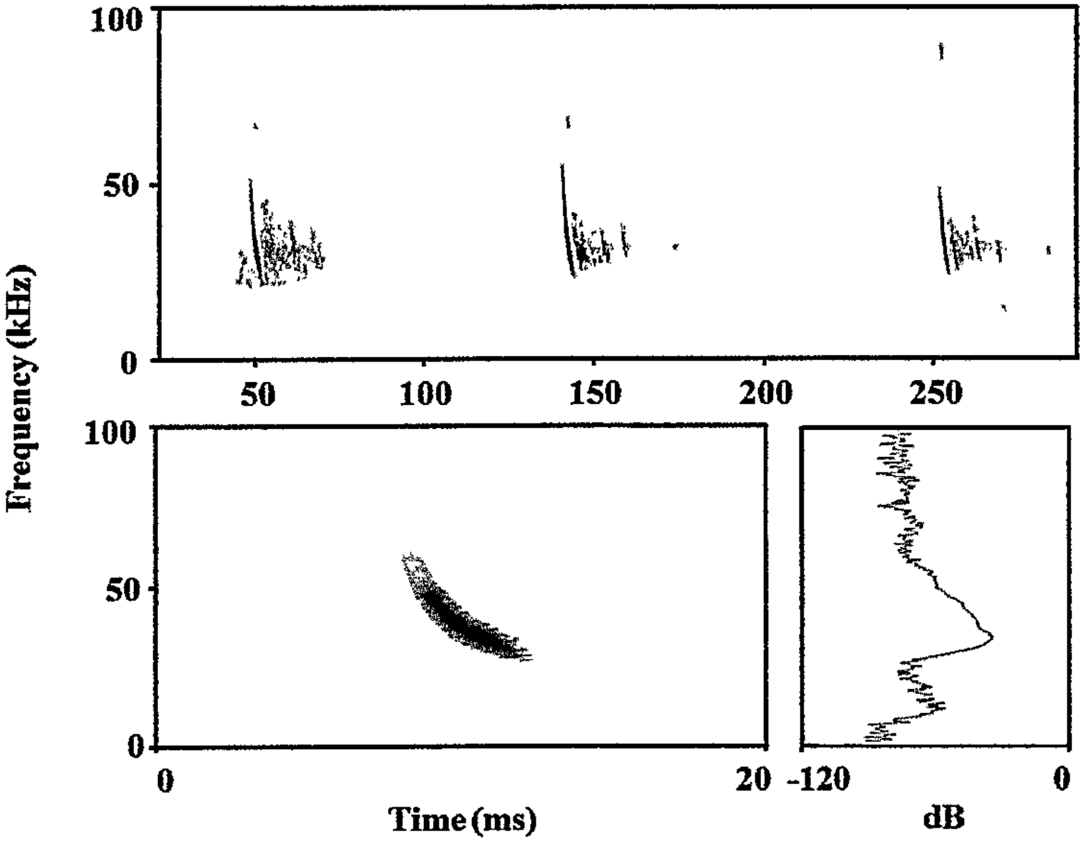

Figure A2. Sonogram of echolocation calls of *Histiotus montanus* showing (a) a typical pulse sequence; (b) a single call; (c) a power spectrum of a typical echolocation call.

Table A1. Summary statistics (Mean ± SE) for echolocation call parameters of four species of insectivorous bats in central Chile. See abbreviation of the parameters in the text.

Acoustic parameters	*Histiotus montanus* (N=16 individual bats; 56 calls)	*Lasiurus varius* (N=24 individual bats; 79 calls)	*Myotis chiloensis* (N=16 individual bats; 66 calls)	*Tadarida brasiliensis* (N=20 individual bats; 62 calls)
Duration (ms)	3.34 ± 0.08	4.91 ± 0.18	3.79 ± 0.11	13.62 ± 0.29
F-start (kHz)	53.77 ± 0.97	65.44 ± 1.56	89.29 ± 2.08	28.03 ± 0.59
F-end (kHz)	29.62 ± 0.25	35.68 ± 0.33	39.26 ± 0.26	21.05 ± 0.25
Slope (kHz/ms)	7.34 ± 0.28	6.86 ± 0.42	13.97 ± 0.73	0.53 ± 0.04
Peak frequency (kHz)	35.36 ± 0.41	41.06 ± 0.52	46.96 ± 0.49	24.31 ± 0.32
Intensity (dB)	38.29 ± 0.75	38.50 ± 0.88	38.64 ± 1.08	31.10 ± 1.50
Maximal frequency (kHz)	44.62 ± 0.91	52.73 ± 0.99	60.92 ± 1.09	27.41 ± 0.50
Minimal frequency (kHz)	31.28 ± 0.31	37.47 ± 0.34	40.38 ± 0.33	22.75 ± 0.25
Bandwidth (kHz)	13.34 ± 0.77	15.26 ± 0.77	20.54 ± 0.95	4.65 ± 0.37
IPI (ms)	136.12 ± 8.03	157.80 ± 9.74	95.06 ± 3.62	286.90 ± 18.92

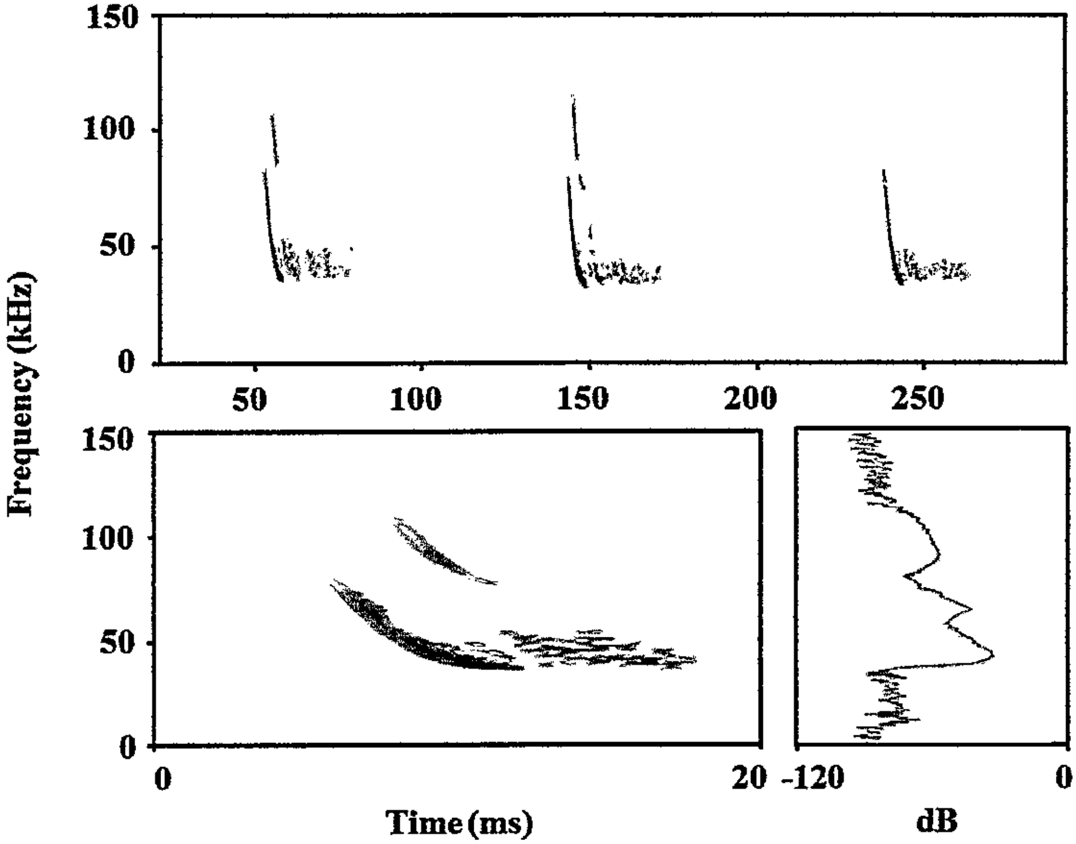

Figure A3. Sonogram of echolocation calls of *Lasiurus varius* showing (a) a typical pulse sequence; (b) a single call; (c) a power spectrum of a typical echolocation call.

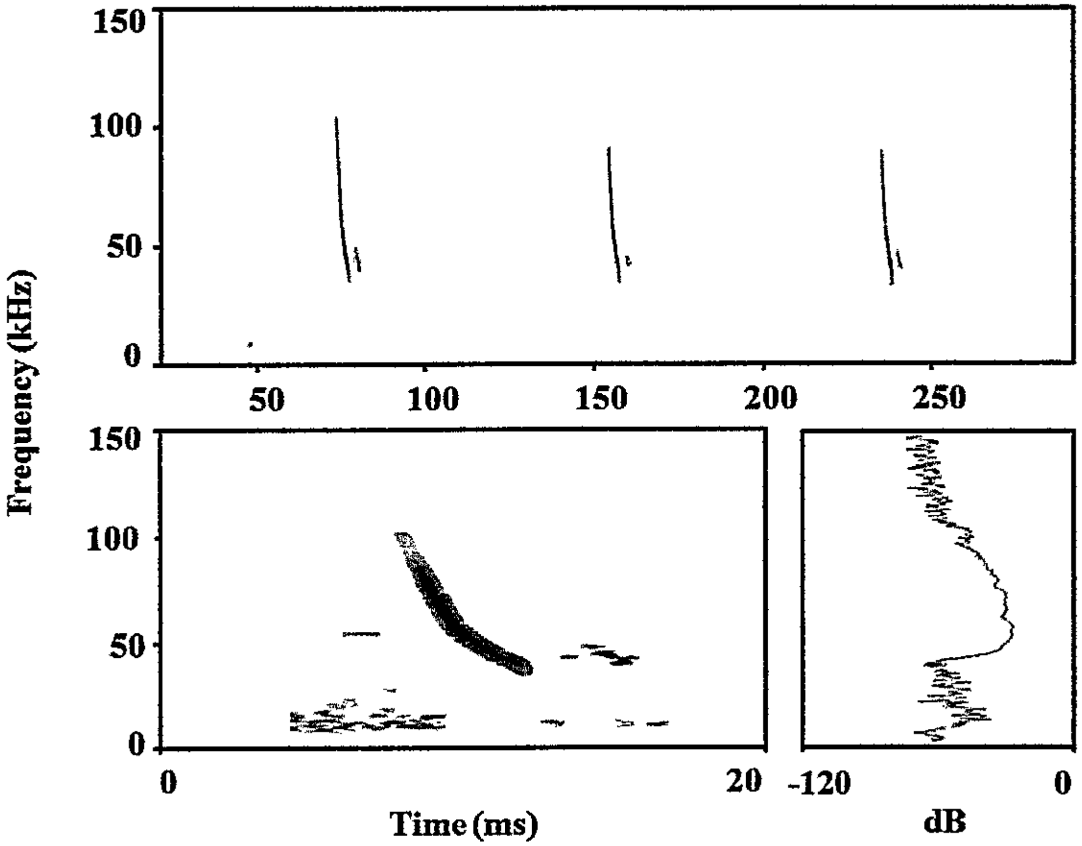

Figure A4. Sonogram of echolocation calls of *Myotis chiloensis* showing (a) a typical pulse sequence; (b) a single call; (c) a power spectrum of a typical echolocation call.

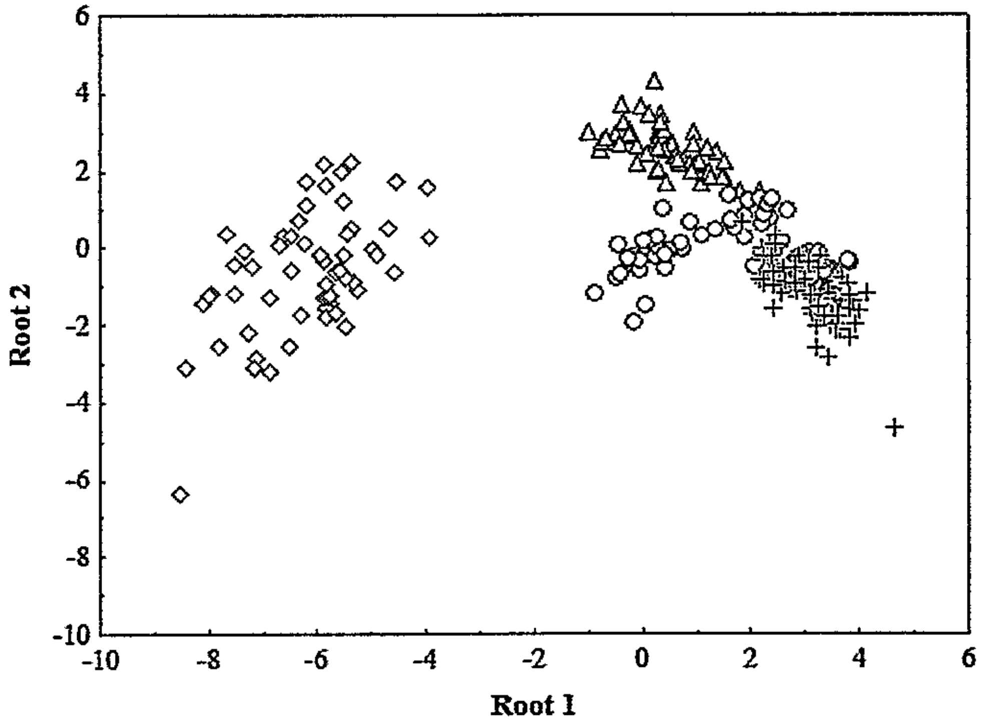

Figure A5. Results of a DFA used in the classification of the echolocation calls of *Histiotus montanus* (triangles), *Lasiurus varius* (circles), *Myotis chiloensis* (cruces) and *Tadarida brasiliensis* (rhombus) emitted during the search phase of their foraging behavior.

Table A2. Discriminant function analyses of calls from four bats species in central Chile. Figures are the number and percentage of correctly classified echolocation calls.

Classified as	True group			
	H. montanus	*L. varius*	*M. chiloensis*	*T. brasiliensis*
Histiotus montanus	55	0	0	0
Lasiurus varius	1	62	15	0
Myotis chiloensis	0	17	51	0
Tadarida brasiliensis	0	0	0	62
N total	56	79	66	62
% correct	98.2	78.5	77.3	100

Table A3. Relative importance of each call parameter in discriminating between the echolocation calls of the species by DFA. Higher standardized coefficients suggest higher discrimination power for a particular variable.

Variable	Standardized coefficients	
	Root 1	Root 2
Duration (ms)	-0.59	-0.94
F-end (kHz)	0.41	-0.76
Slope (kHz/ms)	0.01	-0.41
Peak frequency (kHz)	-0.31	0.07
Maximal frequency (kHz)	0.04	0.28
Minimal frequency (kHz)	0.57	-0.12

Discussion

We successfully described echolocation calls from four species and our discriminant analysis provided a high identification performance, potentially offering a tool for future acoustic surveys in Chile.

Among the calls from Chilean bat we considered, those of *T. brasiliensis* could be unambiguously identified because of their narrow bandwidth, long duration and low final frequency. Despite claims of geographic variation as a factor influencing echolocation calls (e.g., Gillam and McCracken 2007), pulses emitted by *T. brasiliensis* in Chile are similar to those described for populations in USA (Ratcliffe et al. 2004). Long, narrowband frequency modulated signals emitted at long interpulse intervals, are well suited for the detection of weak echoes from small insects (Simmons and Stein 1980; Schnitzler and Kalko 2001). Additionally, the longer these echolocation signals are, the better they encode target movements by carrying characteristic modulations in echo amplitude and frequency. Maximizing the range at which prey are detected will be particularly important for fast flying bats such as *T. brasiliensis*, which hunt above forest canopy. The same echolocation call structure prevails in other molossids such as *Tadarida teniotis*, *Eumops glausinus* and *Nyctinomops macrotis* (Russo and Jones 2002; Obrist et al. 2004; Mora and Torres 2008).

Echolocation call design of *M. chiloensis* described here is similar to that previously described in southern Chile, at a site 500 km away from Tregualemu (Ossa et al. 2010). *Myotis chiloensis* in southern of Chile emit signals of short duration (2.1 ± 1.0 ms) with a final frequency of 43.4 ± 1.2 kHz and inter-pulse interval of 77.5 ± 16.9 ms, which suggest no geographic variation in their echolocation calls.

The echolocation calls of *H. montanus* and *L. varius* consist mainly of single harmonic signals with a downward frequency modulated segment followed by a quasi-constant frequency component. A steep FM sweep that precedes the narrowband component is better suited to localize and characterize background targets (Schniztler and Kalko 2001). This call design is a general feature across the species of the family Vespertilionidae (Kalko and Schnitzler 1993; Siemers et al. 2001; Mora et al. 2005; Rodriguez and Mora 2006) and suggests that these bats perform two tasks while foraging. First, they search for insects near clutter, such as gaps and edges in the vegetation, and second they determine their position in space in relation to background targets (Schniztler and Kalko 2001). Even *Myotis* sp adopting a passive listening strategy to look for prey using such calls for orientation, yet call intensity may be reduced under such circumstances (e.g. Russo et al. 2007)

In our study, DFA provided a high classification rate for the four species included in the analysis (87.4%; Table 2). Correct classification rates were similar or better than previous studies (Vaughan et al. 1997; Murray et al. 1999; Parsons and Jones 2000; Russo and Jones 2002). The four bat species in our study have calls with similar spectro-temporal designs but consistently different final frequency and call duration. These particular characteristics make them much easier to distinguish acoustically than the bats of Europe or North America, for example, where sympatric *Myotis* species have calls similar in structure but overlaps in spectral and temporal parameters making them difficult to distinguish from one another (Parsons and Jones 2000; Vaughan et al. 1997). This result suggests that it should be possible to assess species-specific patterns of activity by bats in central Chile using acoustic monitoring alone. We hope this information will foster assessments of the consequences of the habitat transformation in central Chile upon its bat fauna.

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