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Bats of the Chilean temperate rainforest: patterns of landscape use in a mosaic of native forests, eucalyptus plantations and grasslands within a South American biodiversity hotspot

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Abstract   Forestry plantations represent about 4 % of the global land cover and demand for wood is steadily increasing worldwide. Impacts of forest plantations on biodiversity are controversial; forest plantations could positively influence biodiversity by producing a buffer zone between native forests and agriculture, while replacement of native forests with plantations could reduce biodiversity. Chile is one of the main producers of wood worldwide, and production is largely based on intensively managed monocultures of exotic tree species. Only a few studies have looked at the effects of forestry plantations on biodiversity in Chile, mainly focusing on pine plantations. The aim of this study was to characterize habitat use and richness of bats between native forests, eucalyptus plantations and grasslands in a biodiversity hotspot in southern Chile to determine how land use affects an important mammalian taxa. We found no difference in use or richness of bats in eucalyptus plantations versus native forests. Regional context within the larger Valdivian watershed (Andes, central valley, coastal range) had a stronger influence on bat activity

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and richness than land use type (native forest, plantation, grassland), with the Andean region being the most diverse and where most bat activity is concentrated. Our results suggest that the composition and structure of the surrounding landscape mosaic may be fundamental to determine the impacts of forestry and human land use on biodiversity.

Introduction

Whether or not forestry plantations may have a positive or a negative impact on conservation efforts is highly context-dependent (Brockerhoff et al. 2008; Paquette and Messier 2010). Some have argued that having intensive monocultures in limited areas of the world could actually help conservation efforts in several ways (Brockerhoff et al. 2008; Paquette and Messier 2010; Pawson et al. 2013). First, by efficiently producing large amounts of wood in a small area, there would be release of pressure to exploit other pristine native forests. Second, forestry plantations may have lower impacts on biodiversity than other agricultural practices. For instance, if agricultural lands are replaced by forestry plantations, as opposed to replacing native forests, this would likely improve chances of persistence of species that can either survive and reproduce in plantations or use them for dispersal. And third, by managing landscapes as mosaics of different land uses, plantations could be used as buffers around remnant native forest patches to reduce the effects of fragmentation (e.g. decrease edge effects) and as corridors between patches to reduce patch isolation. All this makes it likely that the effects of forestry plantations will be highly context-dependent and assumes that the landscape can be managed to maximize several outputs at the same time (e.g. maximize wood production, biodiversity conservation and ecosystem services such as water regulation) (Brockerhoff et al. 2008; Paquette and Messier 2010). To better understand the conservation impacts of plantation forestry, we urgently need a deeper understanding of how wildlife species use plantation habitats and whether this depends on landscape context and configuration (Paquette and Messier 2010).

Many studies have addressed the potential effects of agroforestry on biodiversity at large. For example, a study carried out in the Brazilian amazon and comparing diversity of multiple taxa between plantation forests (dominated by *Eucalyptus urograndis*), secondary and primary native forests showed that multiple taxa responded idiosyncratically to this gradient of landscape modification (Barlow et al. 2007). From 15 different taxa surveyed, only five showed the expected pattern of richness decreasing from primary to plantation forests, while the others showed either no predictable pattern along this gradient or similar species richness across all habitat types (Barlow et al. 2007, 2012). Among the unexpected results, bats showed similar species richness in plantation forests as compared to secondary forests, and moths presented their lowest species richness in primary forests. A similar study in Indonesia encompassing a wider habitat spectrum (including annual agriculture, agroforestry plantations, as well as primary and secondary forests) showed a more consistent decrease in species numbers from the least to the most disturbed habitat type between six different taxa including trees, understory plants, insects and birds (Schulze et al. 2004). Some have argued that taxa with higher dispersal abilities, such as birds and bats, would be less affected by plantations than the less vagile taxa (Barlow et al. 2012;

Bhagwat et al. 2008). Forestry plantations would therefore be a more promising conservation tool for these taxa than for others. However, these results must be interpreted with caution for at least two reasons. First, several studies have shown that species richness may be similar, but species composition or community structure may significantly change between habitat types (Barlow et al. 2007, 2012; Harvey and Villalobos 2007). And second, the outcome of habitat configuration may be highly context-dependent and may vary, for example, with respect to the distance to the nearest intact native forests (Harvey and Villalobos 2007) or to the type of plantation in question (e.g. Phommexay et al. (2011) found lower understory insectivorous bat diversity within rubber plantations as compared to native forests). Overall these results point to the fact that it is difficult to predict a priori how a particular group will respond to land use changes in a given context.

Chile is one of the main producers of wood worldwide, and this production is largely based on intensively managed monocultures of exotic species of *Pine* and *Eucalyptus* (Paquette and Messier 2010). Only a few studies have looked at the effects of pine plantations on biodiversity. Consistent with some of the general ideas regarding forestry and conservation presented above, the few studies concerning biodiversity in Chile have revealed that bird diversity is high within pine plantations that are managed to maintain a native understory (Estades and Temple 1999). Pine plantations seem to host a mix of species coming from open habitats as well as native forests, sometimes presenting higher species richness than native forests (Estades and Temple 1999; Tomasevic and Estades 2008; Vergara and Simonetti 2004). A recent study carried out in a site in central Chile showed that bats are sensitive to edge effects, preferring edges of adult pine plantations or native forests over interior habitats for feeding (Rodriguez-San Pedro and Simonetti 2013b). Overall, taxa that are negatively affected by pine plantations are highly dependent on specific elements of the mature native forests, such as old tree trunk cavities for cavity-nesting birds, or debris found on the floor for ground-dwelling animals (Estades and Temple 1999; Tomasevic and Estades 2008; Vergara and Simonetti 2004). However, there are at least two caveats to these results. First, most of these studies have been carried out in forestry plantations owned by universities and managed using pruning two to three times during each rotation to maximize the growth of understory. This is not a common practice in commercially-owned plantations, and may have a large influence on diversity, especially for the species that depend on a high understory cover (Vergara and Simonetti 2006). In fact, studies comparing native forest diversity with highly managed plantations and their surrounding grasslands in southern Chile present contrasting results, with plantations presenting lower diversity and representing an important dispersal filter in the landscape (Sieving et al. 2000; Willson 2004; Willson et al. 1994; Saavedra and Simonetti 2005). Second, eucalyptus plantations have not been studied in the area, and they usually have a poorer understory, representing a different scenario for biodiversity compared to native forests or pine plantations.

Bats are major components of wildlife diversity and account for a quarter of mammalian diversity globally (Wilson and Reeder 1993). Bat species are susceptible to landscape perturbations from human activities, such as forest fragmentation and degradation, as well as water pollution (Racey and Entwistle 2003). Landscape studies in other regions of the world have revealed that bat activity may differ greatly according to habitat type and food availability (Jaberg and Guisan 2001; Law et al. 1999; Gehrt and Chelsvig 2003; Mehr et al. 2011). However, some studies have shown negative impacts of plantations and agroforestry on bat diversity (e.g. Phommexay et al. 2011; Williams-Guillen and Perfecto 2010) whereas others have found the opposite pattern (e.g. Barlow et al. 2007; Bhagwat et al. 2008). Very little is known about bat ecology and distributions in Chile (Jaksic 1997),

despite the fact that the country contains important global conservation priority areas and a high percentage of endemism for other taxa (Brooks et al. 2006). Some isolated publications have dealt with particular aspects of bat ecology in the region. For example, Canals et al. (2005) summarized ecological characteristics of eight bat species by gathering information from general mammal textbooks for the Neotropics, and related them to morphological characteristics of each species. Medical studies have been targeted at identifying the species that can carry and transmit rabies (Favi et al. 1999). And, more recently, a field study was targeted at characterizing echolocation calls of different populations of *Myotis chiloensis* in southern Chile (Ossa et al. 2010) and echolocation characteristics for four species in central Chile (Rodriguez-San Pedro and Simonetti 2013a). However more specific studies related to bat ecology and landscape features in Chile have been lacking (but see Rodriguez-San Pedro and Simonetti (2013b) for edge effects). All bat species described for the region are insectivorous, and could provide important ecosystem functions such as suppression of insect outbreaks in a forestry and agricultural dominated landscape (Boyles et al. 2011; Cleveland et al. 2006).

The aim of this study was to characterize habitat use and species richness of bats between native forests, eucalyptus plantations and grasslands in a biodiversity hotspot in southern Chile. We focused on the Valdivian watershed, which is at the core of the Chilean rainforest biodiversity hotspot (Brooks et al. 2006). This mosaic landscape presents a mixture of the three land uses, and encompasses sharp altitudinal gradients in a relatively small extent. Since bat responses have been shown to be sometimes opposite to the usually expected decreasing gradient from pristine forests to plantations, it was difficult to predict which response would be expected in this particular context. We therefore hypothesized that species richness and bat activity would differ in native forest habitats compared to eucalyptus plantations and grasslands, given the structural differences between habitats. Also, given that previous studies have shown the importance of landscape context in the type of response biodiversity shows to different land uses, we also hypothesized that these differences may depend on regional context. We therefore compared habitat use and activity among the three habitat types (native forest, plantation, and grassland) in three distinct regions of the Valdivian watershed that represent different landscape contexts (Andean mountains, coastal range, and central valley).

Materials and methods

Study area and site selection criteria

In southern Chile, the Valdivian rainforest is home to the highest biodiversity in the country and is one of 25 global biodiversity hotspots. The Valdivian watershed, from its origin in the Andean mountains to its end in the Pacific Ocean, encompasses a wide altitudinal and vegetation range and includes one of the largest wetlands in the region. Major land uses include pine and eucalyptus plantations, pasture for livestock grazing, and native forest (Fig. 1) (Echeverria et al. 2012).

The study area can be divided from east to west in three different regions (Fig. 1) that are distinct with respect to their topography and anthropogenic activities. The first is the Andean range to the east and its adjacent sub-alpine forests, which are characterized by sharp altitudinal gradients as well as a high snow fall during winter. This region is dominated by native forests, which constitutes the vast majority of the landscape, and forestry plantations, and open grasslands are rather scarce, occupying less than 10 % of the
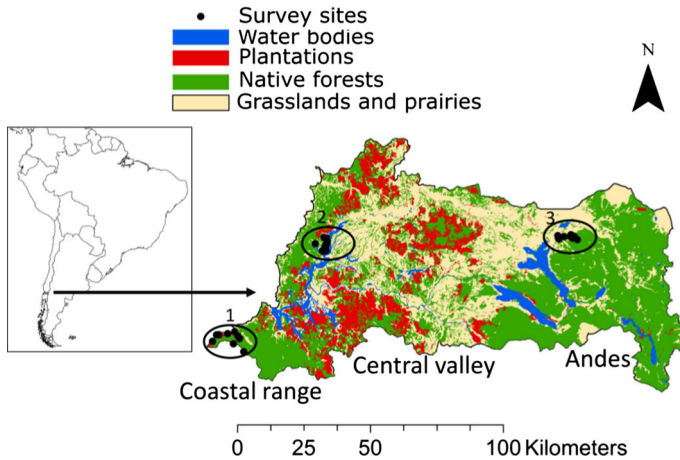
Fig. 1 Study area. The study area is located in southern Chile. The Andes to the east and the coastal range to the west are separated by the central valley, where most human activities are concentrated. The coastal range is fairly narrow at some places and falls directly into the Pacific Sea. Pasturelands for livestock grazing dominate the central valley, plantations being the second main land use type. The three study landscapes sampled here were: *1* Chaihuín in the coastal range, *2* San Martin in the central valley, and *3* San Pablo de Tregua in the Andes

landscapes. In this context, grasslands and plantations are immersed in a native forest matrix. Economic activities here are often limited to ecotourism, although some agriculture and forestry can be found in the lower elevations. The second region is the central valley, which is flatter and dominated by pasturelands for livestock grazing and, to a lesser degree, pine and eucalyptus plantations. This is where human influences are the most prevalent and where deforestation has a longer history, probably starting at the beginning of the XIXth century (Echeverria et al. 2012). Contrary to the Andes, here native forest fragments are isolated remnants often surrounded by pasturelands, and occasionally by pine and eucalyptus plantations. The third region is the coastal range, which is dominated by coastal mountains that fall directly into the sea. Compared to the Andean range, the coastal range is narrower and mountain peaks are lower. The coast remains dominated by native forests, and pasturelands and plantations are less common than in the central valley. Compared to the other two regions, the coastal range also has very little grasslands and open spaces similar to the Andes, but plantations and secondary forests are more common than in the Andes creating a more equitable mix between plantations, young native forests, and old-growth native forests. There are also many large meandering rivers crossing the coastal range. Both the coastal and Andean ranges have large water bodies (Fig. 1), as the study area is within the Chilean Lake District.

We chose to survey one landscape in each of these three regions. The first criterion used to select landscapes within each region was that they had to have a mixture of the three land uses (native forests, forestry plantations and grasslands) at distances that would make the logistics associated with the bat monitoring feasible. The main logistic constraint was that we were sampling simultaneously all land use types within each region, which meant that the nine sampling locations per region (3 sampling sites per habitat type × 3 habitat types) had to be accessible within the same day to be able to change the batteries and check for equipment failure. This resulted in an overall combination of nine survey sites per

region, and nine survey sites per land use type, and a total of 27 survey sites (3 regions × 3 land use types × 3 survey sites in each). However, we had to drop results from one plantation survey in the coastal range, and one grassland site in the Andes due to equipment failure, resulting in a total of 25 survey sites. Survey sites in the same region and land use type were located in different fragments so as to make surveys as independent as possible. For this reason, we chose the following sites: (1) Chaihuín representing the coastal range; (2) San Martin, representing the central valley; and (3) San Pablo de Tregua, representing the Andes (Fig. 1). All sites surveyed in Chaihuín and San Martin were between 0 and 30 m.a.m.s.l., while those in San Pablo de Tregua were between 600 and 750 m.a.m.s.l. Chaihuín is a 59,000 ha reserve with 36 km of coastlines, and is managed by The Nature Conservancy (TNC) since 2006. Prior to 2006, the land was owned by a private forestry company that replaced part of the native forests with eucalyptus plantations. Native forests in the coastal area of Chaihuín are dominated by olivillo (*Aextoxicon punctatum*) and interior forests include *Fitzroya cupressoides* and *Nothofagus betuloides*. There are local human communities living out of small businesses that do not interfere with the forest, such as small artisanal fisheries and subsistence agriculture. San Martin is a small forest field station owned by the Universidad Austral since 1973. The station itself is situated in the central valley on a 80 ha fragment of Valdivian temperate rainforest dominated by species of the family *Myrtacea* and *Nothofagus spp* and is surrounded by private properties consisting of other small native forest fragments interspersed with grasslands and eucalyptus plantations. Grassland habitats in San Martin were associated with cattle or horse grazing properties, usually bordered by native forest fragments. San Pablo de Tregua is a field experimental station in the Andean range owned by Universidad Austral since 1973 and covers an area of 2,900 ha, including a mixture of land uses of forest plantations, native forest and grassland habitats.

Within each study area we aimed to provide a minimum distance between sampling points within the same land use type >1.5 km to achieve distinct sampling replicates and reduce the chance of spatial correlation in bat activity. However, this was a challenge in some of the areas, especially in the central valley, because of the high degree of fragmentation and average size of fragments. Therefore, in San Martin two of the plantation points are located at about 1 km from each other. The Anabat echolocation monitoring equipment was placed at a minimal distance of 100 m from the habitat border at the interior of the habitat of interest, and habitat fragments were at least 1 km long, with the exception of two of the native forest fragments in San Martin which were still more than 600 m long and 250 m wide.

Sampling bat echolocation activity

At the time of the surveys, there was no available reference library for Chilean bats. Therefore, at the beginning of our study, mist-net surveys were conducted for nine nights in January 2009 at the San Martin field site and were used to verify identification of species detected with acoustic sampling and build an echolocation call reference library from hand-release recordings. Hand-release recordings were conducted using Anapocket (Corben 2004) and a bright spotlight. Bats were released and recorded as long as they remained in constant view in the spotlight. We developed a graphical and descriptive key of spectrographs of echolocation calls based on a reference call library developed from active acoustic monitoring and hand-release recordings from captured bats in the study region. Anabat uses a zero-crossings analysis (Parsons et al. 2000) which produces output files displaying echolocation calls on time versus frequency graphs. All files were analyzed by a

Table 1 Number of survey nights for each region and each land use type

	Number of survey nights							
	3	4	5	6	7	8	9	Total
Region								
Andes	0	1	1	1	0	0	5	60
Coastal range	0	0	0	0	2	6	0	62
Central valley	2	1	4	2	0	0	0	42
Land use								
Grassland	0	0	3	0	1	2	2	56
Native forest	1	2	1	1	0	3	1	55
Plantation	1	0	1	2	1	1	2	53

The numbers in each cell represents the number of survey sites with the given number of survey nights. The column with the total number of survey nights therefore represents the sum of the number of survey nights for each category

single observer in AnalookW v.3.2. The five species detected and identified in this study generally had distinct echolocation signatures that were easily visually classifiable to species. A recent study of the echolocation calls of four of these bats species from central Chile showed that discriminant function analysis had a correct classification rate of 87 % among these taxa (Rodriguez-San Pedro and Simonetti 2013a). Misclassification of echolocation calls from bats is possible given interspecific similarity and intraspecific variation in call characteristics (Parsons and Szewczak 2009). In our study, some calls from *Tadarida brasiliensis* and *Lasiurus cinereus* shared similar characteristics, such as terminal frequencies, but these species also produce distinct calls that were classifiable to species.

Call parameters such as characteristic frequency (flattest part of the call), minimum and maximum frequency, characteristic slope (slope of the flattest part of the call), call duration, interpulse interval, and overall call shape were measured from known reference calls and used in the key to characterize species-specific call sequences (Gehrt and Chelsvig 2004). Sequences were identified at the species level if they had greater than two diagnostic pulses that met defined criteria based on reference calls.

Echolocation call sequences can be unidentifiable at the species-level for several reasons, including poor recording quality that results in excess noise or echo that obscures diagnostic properties of the echolocation pulses or sufficient overlap in call properties to be confused with another species. These types of sequences were placed in either fragment or phonic groups, respectively, and were not used for species identification. We defined a bat 'pass' as echolocation call sequences separated by greater than 5 s and interpret this as an index of relative bat activity at sampling points.

We then recorded bat echolocation activity with broadband ultrasonic bat detectors (Anabat II; Titley Electronics) to determine species presence and relative foraging activity (Gehrt and Chelsvig 2004; Hayes 1997; O'Farrell et al. 1999) within the 27 survey sites. Passive monitoring stations contained an Anabat II (Titley Electronics) bat detector with high-frequency microphone housed in a waterproof shroud with a 45° reflector (Messina 2004) extended on a 1 m pole and connected to an Anabat Compact Flash Zero-Crossings

Fig. 2 Box plots of bat activity (log of number of passes per night and per site) by land use type and region. ▶
The *line* within the *box* indicates the median; the *box* indicates the distribution of values of the middle 50 %
of the data; bars indicate the minimum and maximum values excluding potential outliers; *single dots* are
potential outliers. On the *left column* the land use types (*G* grasslands, *N* native forests, *P* plantations) are
compared, and on the right side the regions (*A* Andes, *C* coastal range, *V* valley). *Different letters* above or
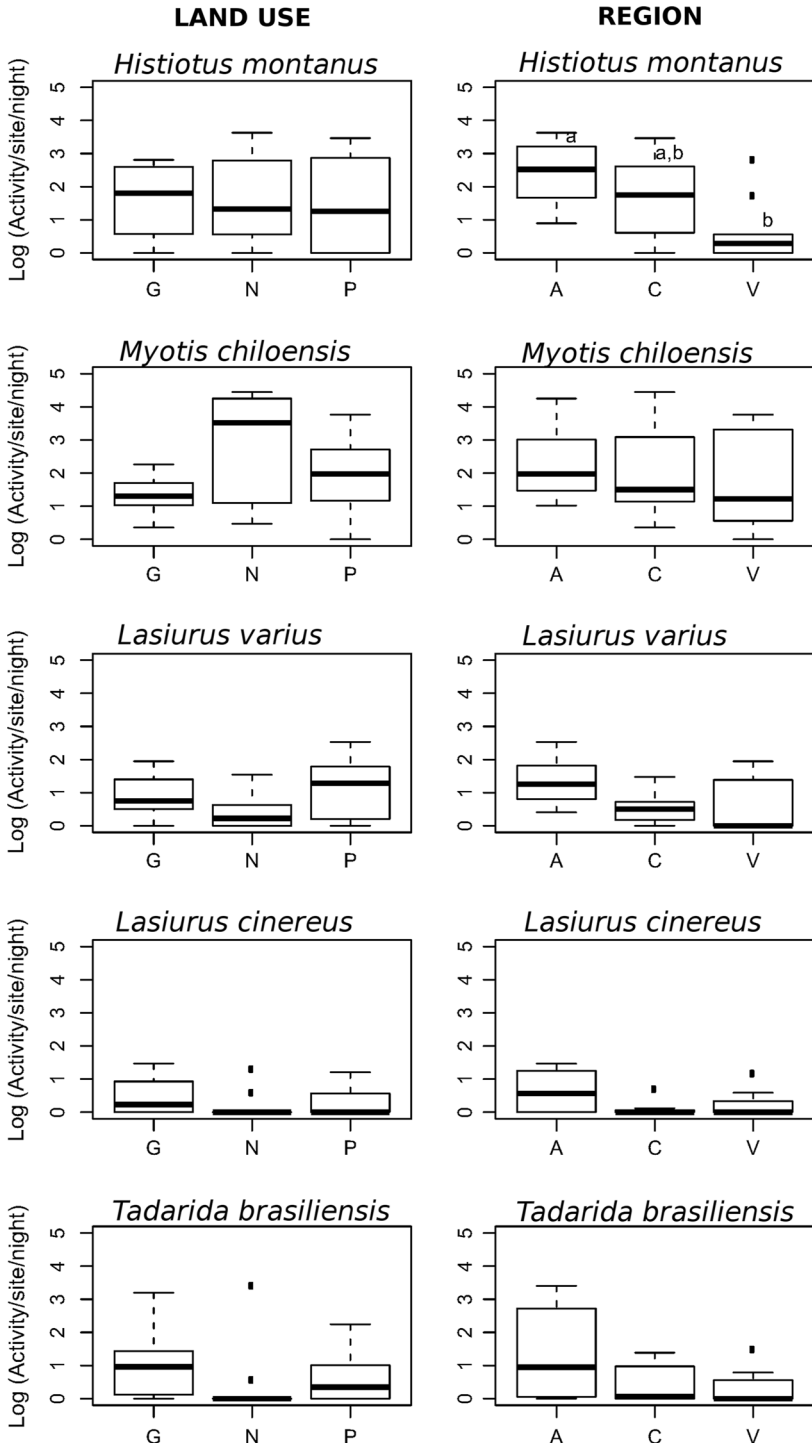below the bars indicate significant differences between groups (Tukey HSD, *p* value <0.05)

Interface Module (Titley Electonics) recording device to store real-time recordings of bat
echolocation data for five consecutive nights. We chose the Anabat recording system
because it was the most cost-effective approach at the time to record bat echolocation calls
from sunset to sunrise for multiple consecutive nights allowing for temporal and spatial
replication necessary for the objectives of our study (Frick 2013). Echolocation monitoring
systems vary in their ultra-sonic microphone sensitivities and therefore caution is advised
if comparing results of other studies that use different monitoring systems (Adams et al.
2012). All Anabat equipment was set to record during 12 h at night, between 6 PM and 6
AM, so that duration of surveys is the same in all survey sites. This resulted in a total of
164 nights of survey (Table 1), equivalent to 1,968 h of recordings. All surveys were
carried out during the austral summer in January and February 2009. All sites (and
therefore all habitat types) within a region were surveyed simultaneously in the following
order: January 6th–January 14th 2009—central valley; January 30th–February 6th—
coastal range; and February 9th–February 17th—Andes. This allowed us to control for
potential effects of weather variability across land use types, but not across regions.

Statistical analysis

We conducted a preliminary analysis (Supplementary Material S1) to investigate whether
probability of detection for each species varied among land use types. This analysis found
no effect of habitat type on probability of detection, so we present below analyses
assuming probability of detection was equal among habitat types (Supplementary Material
S1). All the following statistical analysis was carried out using Rv2.11.1 (R Development
Core Team 2011).

Occurrence and activity by bat species

Data consisted of number of passes per night at each site. This type of acoustic monitoring
provides information on the level of use of a site by bats. Although greater levels of
activity presumably reflect greater use by bats, causal relationships are not clear and
activity levels remain an indicator of population status rather than of abundance (Frick
2013). In our study, some of the sites had more survey-nights than others because of
logistical reasons (e.g. cows ate some of the cables in one site; a microphone was stolen
from another site; bad weather) (Table 1). We transformed this data into presence/absence
per site (occurrence data), and number of passes/night/site (activity data). We used a GLM
on occurrence and log-transformed activity data to determine whether there were any
significant factors (region or land use) explaining occurrence or activity patterns using
binomial or Gaussian distributions respectively. All GLM were checked for normality of
residuals and random distribution of fitted versus observed values, as well as for over-
dispersion. If any relationships came out significant, we applied a posteriori Tukey HSD
test, which corrects for multiple comparisons, to check which regions (Andes, coastal

LAND USE

REGION

Histiotus montanus

Histiotus montanus

Myotis chiloensis

Myotis chiloensis

Lasiurus varius

Lasiurus varius

Lasiurus cinereus

Lasiurus cinereus

Tadarida brasiliensis

Tadarida brasiliensis

range, central valley) or land use types (native forest, plantation, grassland) were significantly different.

Species richness

The total number of species detected at each site was summed across all surveys. We applied a GLM with Poisson distribution and a posteriori Tukey HSD test as in the previous analysis to check on significant differences in species richness between land use types and regions.

Results

Bat occurrence and activity by species

Patterns of species occupancy do not vary significantly across habitat types and region. Most species are present in almost every site. Overall, we found no significant relationship between species occurrence and land use. Although *Histiotus montanus* and *L. varius* are more prevalent in the coastal and Andean ranges as compared to the central valley, these relationships are not statistically significant (0.05 < HSD *p* values <0.07). *M. chiloensis* is present in every site, except in one plantation site in the central valley. *H. montanus*, is present in all sites in the Andes, absent from only one coastal site (in a eucalyptus plantation), and absent from several sites in the central valley (two plantations, one native forest, and one grassland). *L. varius* is absent from 6 out of 25 sites, and *L. cinereus* is absent in 15 out of 25 sites, in both cases with different habitat types and regions represented among the absence sites.

None of the species in the study area showed differences in activity patterns between land use types (Fig. 2, left column). For *L. varius*, activity is higher in plantations, but the difference with the other land use types is not significant (Fig. 2). For *L. cinereus* and *T. brasiliensis* activity seems lower within native forests, but no significant relationships were detected in these cases either (Fig. 2). The region seems to have a stronger effect on species activity than land use, with most species showing higher activity in the Andes than in the other regions (Fig. 2, right column). However, the only significant difference is found in *H. montanus*, which is significantly more active in the Andes as compared to the central valley (Tukey HSD, *p* value = 0.01, Fig. 2).

Species richness

There was a significant effect of the region on species richness (GLM *p* value = 0.045), with the contrast between the Andean sites and those in the central valley being significant (Tukey HSD, *p* value = 0.029) (Fig. 3).

Discussion

Here we have studied the relative occupancy and activity patterns of insectivorous bat species in a mosaic of native forests, eucalyptus plantations and grasslands in a Chilean rainforest biodiversity hotspot. Our results do not reveal any evidence of a negative impact
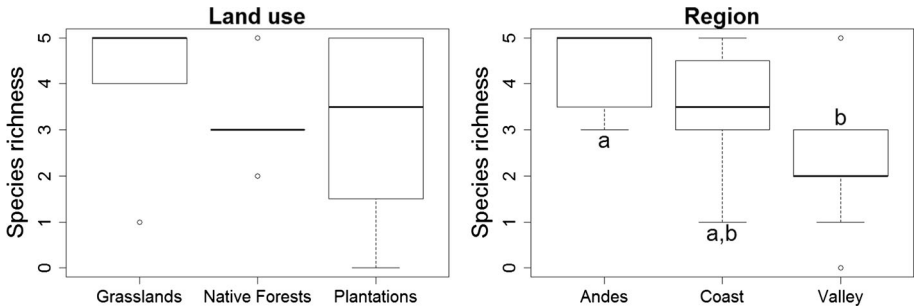
Fig. 3 Species richness by land use type (*left*) and region (*right*). The *line* within the *box* indicates the median; the *box* indicates the distribution of values of the middle 50 % of the data; *error bars* indicate the minimum and maximum values excluding potential outliers; *single dots* are potential outliers. *Different letters* above or below the *s* indicate significant differences between groups (*p* value <0.05)

of eucalyptus plantations on bats. There are only 11 bat species described in Chile, five of which have a known range overlapping the study area. We found all five species in our study area. According to their activity patterns, only *H. montanus* and *M. chiloensis* appear to have high activity levels in native forests, but these activity levels are not significantly different to the other land use types (Fig. 2). At the opposite, *L. varius* is more active in plantations as compared to native forests, but again these differences are not significant (Fig. 2). Indeed, the effects of the region seem to be stronger than the effects of land use type, with higher activity levels for most species in the Andes than in the central valley (Fig. 2), and species richness reflecting this same pattern (Fig. 3).

The fact that plantations do not show lower diversity or activity of bats is not surprising. Previous studies including bats have shown both positive and negative types of responses. For example Faria et al. (2006) found that cacao plantations harbored more species than the surrounding Atlantic forests of Brazil. Barlow et al. (2007) found that bats and orchid bees were more diverse in secondary forests than in primary forests, whereas Clarke et al. (2005) found that bats were more diverse in logged forests than they were in primary forests. These previous studies point to idiosyncratic responses of bats to land use types, responses that can depend on the species life-history traits. In our study area, all species are insectivorous. A recently published study in central Chile, including four of the five species detected here, found that these species prefer habitat edges, and forage at the edge of native forests or pine plantations (Rodriguez-San Pedro and Simonetti 2013b). Contrary to our results, Rodriguez-San Pedro and Simonetti (2013b) found significant differences between habitat types, the highest species richness being in open habitats such as urban areas and forest edges, and lower diversity and bat activity being in forest interior. In our study, we avoided edges (all equipment was placed in habitat interiors) and therefore the patterns that we see are not due to edge effects, and we did not survey near human settlements. However effects of land use type were controlled for by the effects of the region, which seems to be more important but is confounded by several potential causal effects. The central valley, which is dominated by open habitats and where native forest fragments and plantations are less prevalent, has the lowest species richness, as compared to the Andes, which is the most pristine region with a dominant native forest matrix surrounding the other land uses. These regional differences may explain the difference in results, but there are a number of other factors that could also explain part of the differences. For example, Fischer et al. (2010), studying birds and bats, suggested that a few scattered trees may significantly increase

species diversity in an overall open landscape. In the coastal sites surveyed here, the grasslands were mostly surrounded by forests (native or plantations), so that the proximity of a few trees may have influenced those surveys. At the opposite end of the spectrum, remnant forests and plantation fragments in the central valley may have acted as attractors for bats foraging in the area, which is mostly dominated by grasslands. The fact that we did not find differences between land use types but we did find differences between regions support the idea that the landscape context is fundamental to determine bat diversity. In other words, in a conservation context it will be very difficult to isolate the effects of habitat type per se from those of landscape structure such as distance to the nearest forest fragments, distance to forest edges, and nature of the surrounding matrix.

As a preliminary study, we could not control for all these factors at once. In our study, we did not have detailed information regarding these landscape characteristics, and we did not have enough replication within each habitat type and region to incorporate them in a statistical analysis. Indeed the relationship between area and diversity would predict that species richness should be lowest in the smallest fragments. In our study, the smallest forest fragments are located in the central valley, which also harbor the lowest species richness, and the largest fragments are located in the Andes, where species richness is highest (Fig. 3). Also, our surveys were carried out simultaneously between land uses, but they were first carried out in the central valley, then in the coastal range, and finally in the Andes. Although all surveys were done at the peak of the summer season in a fairly short time window, we cannot rule out that this strategy may have influenced the results regarding the regional effects. A final confounding effect relates to altitude. Altitude often has either a negative impact on diversity, or a bell-shaped relationship with higher diversity found at intermediate altitude (Rahbek 1997; Willig et al. 2011). Here again, coastal and central valley sites did not differ in altitude, but the Andean sites are significantly higher than the others. The fact that diversity is higher in the Andes rules out a negative relationship between diversity and altitude. However, 600–750 m.a.m.s.l. could be considered an intermediate altitude at which diversity could peak if the relationship is bell-shaped. Further research should try to tease apart the potential effects of area, landscape mosaic, and time within a season, on bat activity and richness to have a better understanding of the causal effects driving these regional effects on bat diversity.

A recent meta-analysis (García-Morales et al. 2013) showed that the impact of land use on Neotropical bats depends on feeding habits, with gleaning and aerial insectivore species showing no effect size to forest disturbance. Most species found in our study are adapted to forage and fly in open areas. For example, Canals et al. (2005) studied their morphological features and classed the molossids (which include *T. brasiliensis*) in a group of highly aerodynamic fast-flying species, the vespertilionids *M. chiloensis* and *H. montanus* in a group of slower-flying but with increased maneuverability, and *L. cinereus* as in an intermediate fast-flying but with increased agility group. *M. chiloensis* and *H. montanus* would therefore be better adapted morphologically to forage and use wooded areas than the other species. In our results *M. chiloensis* has a higher median activity (although statistically not significant) in native forests, than in plantations, and higher in plantations than in grasslands (Fig. 2). *H. montanus* is more active in grasslands, and median activity levels between all land use types is very similar (Fig. 2). Therefore while *M. chiloensis* might be adapted to more structurally complex habitats, *H. montanus* might be a generalist in terms of habitat types. However, these conclusions based on morphological differences do not result in differences in activity for these two species between native forests and grassland habitats in our study. This highlights the importance of characterizing habitat use and other

ecological features on the ground, especially for species with large distribution ranges that can show significant regional or local variability in different aspects of their ecology.

Overall, we did not find any reason to believe that eucalyptus plantations are negatively impacting bat diversity in the region. This goes somewhat against patterns shown for birds in areas with little understory cover in the region (Sieving et al. 2000; Willson et al. 1994), indicating that bats may not be good indicators for biodiversity response at large in Chilean temperate forests. However, it highlights the benefits of understanding the relationships between different economic activities and patterns of biodiversity and shows the potential of managing the landscape to optimize different economic activities (Brockerhoff et al. 2008). Further research should be carried out, using a larger number of survey localities, a larger geographic extent, and studying population dynamics and dispersal in more detail. In particular, it would be very useful to understand exactly what factors are driving the effects of the region on the patterns of activity shown here. The possibility that these patterns may be the result of a longer exploitation history in the central valley, with all the counfounding effects that this carries (e.g. fragment area, landscape mosaic composition) prevents us from discarding the possibility of plantations and grasslands having negative impacts on this fauna. However, our results also open the door to promote a more positive human perception of bats. If bat species that live in exotic plantations and pasturelands are eating a large quantity of potentially damaging insects, or if there are potential benefits of having a land use mosaic of grasslands, plantations and native forests, all this may play in favor of bat conservation in the region. But these possibilities require extensive field testing at a regional scale and should be looked at in more detail in future work (Paquette and Messier 2010; Gehrt and Chelsvig 2004; O'Farrell et al. 1999).

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