Converting clear cutting into a less hostile habitat: The importance of understory for the abundance and movement of the Chestnut-throated Huet-Huet (*Pteroptochos castaneus*: Rhinocryptidae)

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ABSTRACT

Sustainable forest management of commercial monoculture plantations may be difficult to achieve in plantations of Monterrey pine because these commercial monocultures are managed under a clear cutting system, where the understory vegetation is initially damaged by harvesting, and subsequently, by herbicide application. Despite its marked structural changes following harvesting, the ecological role of understory in mitigating the negative impact of clear cutting on biodiversity is scarcely known. We test for the positive effect of the understory vegetation present in clearcut pine stands on the abundance and movement ability of the Chestnut-throated Huet-Huet (*Pteroptochos castaneus*), an insectivorous bird sensitive to adult pine plantations with scarce understory cover. Abundance was assessed through passive and broadcasting surveys during reproductive and pos-reproductive season at native forests, mature pine stands and cleacut areas. Movement was experimentally assessed as the willingness of individual Huet-Huets to enter into clearcuts from adjacent mature pint stands of native forest. The understory vegetation was the main predictor of *P. castaneus* abundance in native forest and mature pine plantations, but not into clearcut stands. Although Huet-Huets tended to be reluctant to enter into clearcuttings, their displacement into clearcuttings was positively influenced by the understory present in both the clearcut stands and the habitats where they had been experimentally attracted by playbacks (i.e., native forest or mature pine). We conclude that the conservation of *P. castaneus* in forest plantations involves modifying the traditional clearcutting system into a forest management that minimizes the use of herbicides while promoting the retention of understory vegetation and woody debris.

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1. Introduction

Forestry plantations represent 7% of the global area covered by forests, ca. 228 million ha (Payn et al., 2015). Since 2010, forestry plantations have increased at an average annual rate of 1.2% (i.e., 3.2 million ha per year), while during this same period, native forests have decreased 6.6 million ha per year (FAO, 2015). The increasing global demand for forest products, such as pulpwood, timber, firewood, and biomass energy is the main factor responsible for the rapid expansion of forestry plantations (WWF, 2015; FAO, 2015). Management of these plantations increasingly faces societal demands, as expressed in the Strategic Plan for Biodiversity 2011–2020 of the Convention on Biological Diversity, which states that by 2020: "areas under agriculture, aquaculture and for-estry are managed sustainably, ensuring conservation of biodiversity" (UN, 2010). Therefore, plantations ought to fulfill the demand for forest products while reducing pressure on biodiversity derived of the replacement of native forest (Paquette and Messier, 2009). Within this context, one of the main challenges for sustainable forest management is to contribute to the conservation of biodiversity in areas devoted to forestry plantations (Hartley, 2002; Hayes et al., 2005; Lindenmayer and Hobbs, 2004).

Sustainability may be difficult to achieve in the widespread plantations of Monterrey pine (*Pinus radiata*) and Eucalyptus (*Eucalyptus* spp.) because these commercial monocultures are managed under a clearcutting system, a disruptive forestry practices involving the simultaneous removal of all standing trees (Pawson et al., 2006; Keenan and Kimmins, 1993). Clearcutting is questioned by its ecological and visual impacts, including changes of vegetation structure and composition, soil propriaties as well as environmental services (Niklitschek, 2015). In terms of biodiver-

sity, available evidence of its effects upon biodiversity in commercial plantations is scarce. Hence, the information required to unravel the effects of clearcutting on biodiversity and the potential of clear-felled areas to be re-colonized is insufficient (Simonetti and Estades, 2015). Clearcutting may reduce the richness and abundance of forest-dwelling species at the expense of an increase in open-habitat generalist species (Pawson et al., 2006; Acuña and Estades, 2011), although such an effect is less marked after second post-logging year (Simonetti and Estades, 2015). At the landscape-level, clear-cut stands might act as a barrier for the movement of wildlife, thus reducing their functional connectivity (Popescu and Hunter, 2011; Acuña and Estades, 2011).

Mature pine plantations in central Chile often support a dense understory vegetation whose diversity and structural complexity improve habitat quality for forest dwellers (Vergara and Simonetti, 2003; Estades and Escobar, 2005). There is increasing evidence that the habitat quality for native wildlife in forestry plantations is enhanced through a well-developed and structurally complex understory (Lindenmayer and Hobbs, 2004; Simonetti et al., 2013). Depending on the presence of a dense understory vegetation, several native animal species of central Chile forests use pine plantations as an alternative habitat, providing them with shelter and feeding resources. For instance, the abundance of endangered mammals, like the kodkod (*Leopardus guigna*), and ground-dwelling insects, such as *Ceroglossus chilensis* (Coleoptera; Carabidae) is positively associated with the percentage of understory cover present in mature and juvenile pine stands (Simonetti, 2006; Simonetti et al., 2012; Saavedra and Simonetti, 2005; Acosta-Jamett and Simonetti, 2004; Cerda et al., 2015; Grez et al., 2003). In fact, some fitness component of forest dwelling rodents and ground beetles, such as sex ratio, age structure and body conditions do not differ between individuals thriving in plantations and native forests, suggesting these habitats are of comparable quality (Estades et al., 2012). Similarly, the per capita food abundance, nest success and clutch size of forest insectivore bird species tend to be higher in plantations than native forests, thus adding support to the assertion that habitat quality offered by plantations is relatively similar than that offered by native forest (see Estades et al., 2012 for a review).

As for other wildlife, pine plantations might also function a secondary habitat for Tapaculo (Rhinocryptidae) birds as their abundance and movement are positively related with understory cover in pine plantations (Estades and Temple, 1999; Estades and Escobar, 2005; Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). Tapaculos are territorial and particularly sensitive to habitat fragmentation because they have poor dispersal capability due to their terrestrial habits and lower flight capacity (Willson et al., 1994; Sieving et al., 1996; Vergara and Simonetti, 2006). Among Tapaculos, the Chestnut-throated Huet-Huet (*Pteroptochos castaneus*), endemic to the deciduous forest of Central Chile is the most sensitive species to the absence of understory cover (Vergara and Simonetti, 2003, 2004, 2006). *P. castaneus* has been willing to move to pine plantations if pine stand supports a well-developed understory when experimentally attracted by broadcasted songs (Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). Although the understory vegetation can improve habitat conditions for Tapaculos in pine plantations, its role as a key factor in enhancing habitat quality and recovery of biodiversity after clearcutting has not yet been well established. The lack of knowledge about how understory vegetation facilitates the re-establishment of biodiversity contrasts with the progress in silvicultural practices that ensure the establishment of new plantations (Kogan et al., 2002). Here, we explore if understory vegetation might contribute to convert clearcuttings into a less hostile habitat for forest dwelling species such as Tapaculos.

Within this study we tested two hypotheses. First, understory vegetation has a positive effect upon abundance of *P. castaneus*, but this effect is less pronounced in clearcut stands compared with native forest and mature pine plantations because habitat suitability improves as the canopy closes. Second, understory vegetation improves the movement ability of *P. castaneus* by enhancing both their willingness to move to clearcut stands and the distance they enter into the clearcutting.

2. Materials and methods

2.1. Study area

Our study was conducted in central Chile (72°40′W, 35°60′S), in a geographical area which comprises Los Queules National Reserve (35°59′ S, 72°41′ W) and nearby (<100 ha) fragments of temperate deciduous forest, surrounded by plantations of pine Monterrey harvested by clearcutting with rotations of 15–20 yr (Vergara and Simonetti, 2004). Temperate deciduous forest includes *Lophozonia glauca* and *L. obliqua* as dominant species, and the evergreen *Cryptocarya alba* and *Peumus boldus* (Bustamante et al., 2005). Understory vegetation is composed by native shrubs, such as *Chusquea cumingii* and *Aristotelia chilensis*.

We used mature pine plantations of 15 or more years of age, whose height is equal or higher than 8–10 m (Tomasevic and Estades, 2008). Understory vegetation in mature pine plantation is a combination of *A. chilensis*, *P. boldus* with exotic species, such as *Teline monspessulana* and *Rubus ulmifolius* (Poch and Simonetti, 2013). We used clearcutting stands consisting of a 5–10 ha that were harvested the year before the survey (i.e., year 2013). Ground vegetation (henceforth "understory" in clearcut) that originate the understory is composed mainly by shrubs (e.g. *Aristotelia chilensis*, *Genista monspessulana*, *Rubus ulmifolius*), woody and herbaceous species (e.g. *Silybum marianum*, *Hypochaeris* sp.) including small trees of pine.

2.2. Bird abundance and understory survey

Abundance of *P. castaneus* was recorded of a total of 30 sample points using 50 m fixed radius point counts (see Vergara and Simonetti, 2006). Point count surveys involved a combination of two different survey methods: passive survey and broadcast survey. We designed a repeated measures design to simultaneously model occupancy and detect probabilities resulting from both survey methods. At each visit to point-count, we used a method involving an 8-min broadcast survey (Saracco et al., 2011). Broadcast surveys consisted of playing vocalizations and territorial songs using a portable speaker for two 1-min periods, each one separated by 3 min to detect birds (1 + 3 + 1 + 3 = 8 min). We set 18, 6, and 6 points in clearcutting, mature pine and native forest fragments, respectively. Points were located at the center of forest stands, i.e. >100 m from the nearest edge and >200 m from the other sampled stands. Sampling points at clearfelled areas were located 138 ± 17 m from native forest remnants and 189 ± 37 m from mature pine stands. The abundance of *P. castaneus* in mature pine and clearcut stands was not influenced by distance to the nearest stand of native forest (r = 0.44, p = 0.20).

At each sampling point, we conducted four bird surveys during the breeding season of *P. castaneus* (Sep-Dec 2014, the austral spring) and 4 bird surveys during their post-breeding season (Jan-March 2015, the austral summer), resulting in a total of 240 visits to sampling points (i.e., 3.2 h). Surveys began at dawn (05:30 h) and continued until 12:00 h.

Understory cover was measured in each habitat using 50 m line-intercept transects centered at the sampling point of birds,

quantifying the proportion of the line covered by woody vegetation, including native (e.g., *Aristotelia chilensis*, *Chusquea* sp., *Cryptocarya alba* and *Peumus boldus*) and exotic species (*Genista monspessulana* and *Rubus ulmofolius*) (Higgins et al., 1996).

2.3. Bird movement

We used playback experiments to assess the willingness of *P. castaneus* to move from native forest and mature pine stands into adjacent clearcut stands. We selected 20 clearcut stands adjacent to a native forest fragment and 20 clearcut stands adjacent to a mature pine plantation stand. Trials were repeated 2 or 3 times (Table 1). Playback trials involved playing vocalizations and territorial songs using a portable speaker. We followed the protocol described by Tomasevic and Estades (2008), consisting of playing vocalizations and territorial songs during three 1-min periods separated by 3 min (1 + 3 + 1 + 3 + 1 + 3 = 12 min). First, the bird was attracted to the edge between the clearcutting and either, a native forest or a mature pine stand. Then, the playback experiment started only if the attracted bird approached to less than 2 m from the edge. Failed attempts of attracting birds to the edge were discarded for later analysis (Table 1). Second, one successful trial involved the observer moving 25 m into the clearcut stand, perpendicularly to the edge. Third, if the bird was observed crossing to the clearcut stand, the observer moved an additional 25 m into the stand, with a new playback session carried out at 50 from the edge. We recorded two edge crossing responses, firstly, the binary response of Huet-Huet to move, or not to move, into de clearcut stand, and secondly, the distance traveled by the bird, measured with 1 m resolution (i.e., 0–1, 1–2, 2–3, ..., 49–50 m). Experimental playback trials started at dawn (05:30 h) and continued until 12:00 h.

In order to assess the effect of understory development upon the movement of *P. castaneus*, we measured the understory cover in each edge type (native forest-clearcut and mature pine-clearcut) along a 102 m linear transect, perpendicular to the forest edge, 51 m toward the clearcut and 51 m into the native forest or pine plantation.

2.4. Data analysis

We used a Poisson-binomial mixture Bayesian model, as proposed by Royle (2004a, 2004b) (see also Kéry et al., 2005), to assess the abundance of *P. castaneus* from samples of repeated point counts ($j = 1, 2, ..., k$; with k being the number of survey visits at the point i) while accounting for imperfect detections of bird individuals resulting from sampling related factors. This modeling approach assumes that the *P. castaneus* observed on repeated counts at the same point (C_{ij}) are k independent realizations of a Binomial random variable, $C_{ij} \sim Binomial\ (N_i, p_{ij})$. Parameter N_i is an unknown latent Poisson distributed variable, $N_i \sim Poisson\ (z_i \lambda_i)$, such that λ_i is the mean abundance in the point i and z_i a coefficient (ranging between 0 and 1) accounting for over-dispersion resulting from zero inflation (Kéry and Schaub, 2012). The detection probability, p_{ij}, varies over repeated counts and depends on

temporal covariates. The function establishing the relationship between the local mean abundance (λ) and habitat covariates is:

$$\log(\lambda_i) = \beta_0 + \beta_1 UC_i + \beta_2 H_i + \beta_3 (UC_i \times H_i) \tag{1}$$

where β_l ($l = 0, 1, ..., 4$) are the fixed-effect model coefficients (including an intercept), UC_i is the understory (%) covering the point i, H_i is a factor giving the habitat type in the point i (i.e., clearcut, native forest or mature pine). $UC_i \times H_i$ is an interaction term between the latter two covariates accounting for an understory cover effect depending on the type overstory habitat. Detection probability, p_{ij}, at site i during the time period j was estimated with the following logit function:

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 SM_{ij} + \alpha_2 S_j \tag{2}$$

where SM_{ij} is the survey method (passive or broadcast survey) used during the survey repetition j at the point i whereas S_j is the season (breeding or post-breeding) during which the point was surveyed.

For each successful experiment trial i carried out in the experimental clearcut stand j the distance moved by *P. castaneus* into the stand was evaluated using a zero-inflated Poisson (ZIP) model. ZIP models were appropriate for analyzing our movement data because they included excess zeros that resulted from birds deciding not to enter into the clearcut. The discrete response variable (the distance interval; see above) is modeled with a likelihood function that combines the Bernoulli-distributed binary response of *P. castaenus* to move into the clearcut stand (with probability P) and the distance (m) traveled by the *P. castaneus* into the clearcut stand, which is drawn from a Poisson distribution, with parameter Λ being the mean distance moved. Λ was modeled as a function of habitat covariates:

$$\log(\Lambda_{ji}) = \beta_0 + \beta_1 UC_j + \beta_2 UF_j + \beta_3 (UC_j \times ET_j) + \beta_4 (UF_i \times ET_j) \tag{3}$$

where UC_j is the understory cover (%) in the clearcut stand j, UF_j is the understory cover (%) in either, the native forest or pine plantation, adjacent to the experimental clearcut stand j, ET_j is the habitat or "edge" type adjacent to the clearcut stand (i.e., native forest or mature pine). The interaction terms $UC_j \times ET_j$ and $UF_j \times ET_j$ assess if the effect of understory cover changes with the edge type. The probability a *P. castaneus* enters into the clearcut (P) was modeled as:

$$\text{logit}(P_{ij}) = \alpha_0 + \gamma_j \tag{4}$$

This is basically a function of a random effect coefficient (γj) for the experimental stand j ($j = 1, 2, ..., 40$) representing the effect of individuals responding differently to vocalizations and territorial songs in each spatial location.

We developed models containing all possible combinations of covariates, including Poisson-binomial mixture models for bird abundance (Eqs. (1) and (2)) and ZIP models for movement distance (Eqs. (3) and (4)). The Deviance Information Criteria (DIC) and differences in DIC (ΔDIC) were used to interpret the strength of evidence for each competing model (Spiegelhalter et al., 2003). Models with ΔDIC < 2 were considered to be supported by the data. The importance of each fixed effect coefficient was evaluated

Table 1
Summary of playback experiments designed to evaluate the movement of *P. castaneus*, including the number of experimental locations, number of attempts for attracting birds to edges, number of trials and success rate for each edge type (native forest or mature pine) and season (breeding or post-breeding season).

Edge type	Stand (n)	Season	Attempts (n)	Trials (n)	Success (%)
Mature pine	20	Breeding	42	33	78.6
Mature pine		Post-breeding	39	25	64.1
Native forest	20	Breeding	41	33	80.5
Native forest		Post-breeding	47	34	72.3
Total	40		169	125	73.9

by examining their Bayesian Credible Intervals (BIC) estimated from posterior distribution of parameters. The 95% BCIs that did not overlap zero were considered as being significant. We used vague non-informative prior distributions for all model parameters. Parameters γ_r were assumed to be Gaussian distributed associated to each experimental stand. Parameter distributions were based on three Markov Chain Monte Carlo (MCMC) samples, each with 20,000 iterations, discarding the first 10,000 iterations and thinning by 3. MCMC Convergence was visually examined and by using the Potential Scale Reduction factor. Models were run using OpenBUGS via the R2 OpenBUGS package of R.

3. Results

3.1. Understory cover

Understory coverage differed between habitats (ANOVA; F-value = 35.95, p-value = 2.45×10^{-8}). Clearcut stands (14.1 ± 1.4%) exhibit less understory cover than the native forest fragments (30.2 ± 1.6%) (Tukey test; p-value = 1.6×10^{-6}) and mature pine plantations (31.1 ± 1.1%) (Tukey test; p-value = 6.3×10^{-7}) (Fig. 1).

3.2. Abundance of P. castaneus

The observed abundance of *P. castaneus* varied between habitat and season (Fig. 2). *P. castaneus* does not dwell clearcut stands. Even more, in 144 visits to the clearcut stands, only one individual (0.69%) was observed in the post-breeding season by broadcast survey (Fig. 2). Nevertheless, the observed abundance of *P. castaneus* in both breeding and post-breeding season, in native forest was higher than in mature pine (F = 6.37; P = 0.01, n = 96). Bayesian estimates of detection probabilities using playbacks increased two times when compared with passive surveys (Appendix A).

The two models with better fit to the data (Table 2) included as covariates understory cover (UC) and its interaction with habitat type (UC × H). Abundance of Chestnut-throated Huet-Huet is positively associated whit the understory cover in both native forest and mature pine plantations (understory cover vegetation was approximately 30%) but not in clearcut stands (Table 3). The significant interaction between understory cover and habitat type (UC × H; Table 3) indicates that Chestnut-throated Huet-Huet responds to the understory cover only in those habitats that provide them with a canopy developed such as pine plantations and native forest.
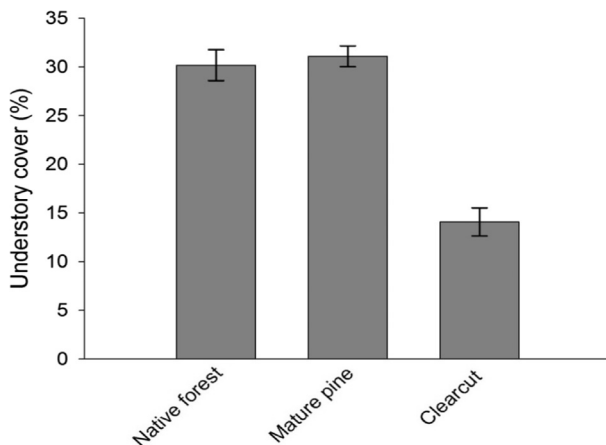

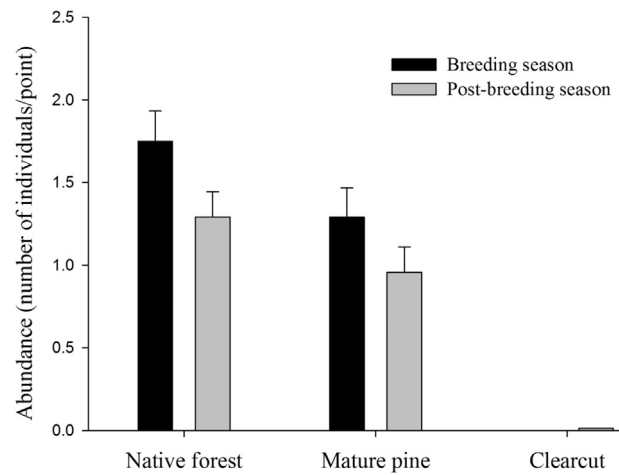**Fig. 1.** Understory cover (%) in native forest, mature pine and clearcut.

Fig. 2. Observed abundance (number of individuals/point) of *P. castaneus* in native forest, mature pine and clearcut in breeding season (black bars) and post-breeding season (grey bars).

3.3. Bird movement

3.3.1. Understory cover
The understory cover within the native forest and mature pine stands was 4.4 and 3.2 times higher than the understory cover at the adjacent clearcut stand respectively (*t*-test; p-value = 5.84×10^{-12}).

3.3.2. Bird movement
Movements of *P. castaneus* to clearcutting stand were scarce. From a total of 125 trials, birds crossed to clearcutting only 18 times (14.4%) (Table 4). The proportion of Chestnut-throated Huet-Huet that moved from native forest to clearcut stand was not different from the proportion that moved from mature pine to clearcut stand (Table 5).

Although *P. castaneus* individuals were reluctant to enter into clearcutting at high frequencies (distance intrusion = 0) in both breeding and post-breeding season, some birds did do so. Distance of intrusion traveled by a *P. castaneus* to clearcutting is greater when coming from native forest (Figs. 3 and 4).

The covariates of the three best-supported candidate ZIP models (Table 6) and the values of the coefficients associated with each of these fixed effects (Table 7) indicate that the mean distance *P. castaneus* moved into the clearcutting is positively associated with the understory cover present in clearcut stands as well as the understory cover present in the habitat from where they move to (i.e., native forest or mature pine).The effect of the understory cover on the mean movement distance, however, was significantly larger when individuals entered from mature pine plantations than when doing from native forest (Table 7).

4. Discussion

The presence of a structurally complex and diverse understory vegetation could mitigate the negative effects of clearcutting by improving habitat quality and increasing biological connectivity between remaining habitat patches (Popescu and Hunter, 2011; Acuña, 2010). This positive understory effect could be especially beneficial for understory specialist bird species with a low dispersal capability, such as the Chestnut-throated Huet-Huet (*Pteroptochos castaneus*). In fact, improving the quality of the intervening matrix, such a plantation, favors animal movement through the landscape contributing to connect remnants of forest patches

Table 2
Poisson-binomial mixture Bayesian models to predict the abundance of *Pteroptochos castaneus*. Covariates of abundance and detectability models are shown separately. The mean, standard deviations (SD), 95% lower and upper Bayesian credible intervals, Deviance's Information Criterion (DIC) and difference DIC with the lowest model (ΔDIC) are shown. Codes of covariates of the detectability model are: SM = survey method and S = season. Codes for covariates of the abundance model are: UC = understory cover and H = habitat.

Detectability model	Abundance model	Deviance				DIC	ΔDIC
		Mean	SD	2.50%	97.50%		
SM + S	UC	434.83	5.36	427.1	447.6	449.17	0.00
SM + S	UC × H	435.42	5.59	420.6	450.2	450.22	1.05
SM	UC	438.56	5.14	431.3	450.9	451.76	2.59
SM + S	H	434.69	6.42	425.4	450.1	455.21	6.04
SM + S	UC + H	437.09	6.06	428.0	451.3	455.29	6.11
SM	UC × H	440.58	5.54	432.3	453.6	455.90	6.73
SM + S	UC + UC × H	437.58	6.19	428.3	452.0	456.71	7.54
SM	UC + H	441.41	5.85	432.4	454.6	458.53	9.36
SM + S	UC + H + UC × H	438.81	6.91	428.8	455.7	462.27	13.10
SM	UC + H + UC × H	442.45	6.38	432.9	457.3	462.70	13.52
SM	UC + UC × H	442.11	6.69	432.4	458.6	464.42	15.25
SM	H	439.92	7.32	429.5	457.2	466.13	16.96
SM + S	H + UC × H	438.69	11.05	425.9	468.3	497.23	48.05
SM	H + UC × H	454.05	16.22	430.9	479.3	524.17	75.00

Table 3
Coefficient values of the best-supported zero-inflated Poisson (ZIP) model of Table 2. The means, standard deviations (SD) and 95% lower and upper Bayesian credible intervals are shown. Codes of covariates for the abundance model are: UC = understory cover and H = habitat. Codes of covariates of the detectability model are: SM = survey method and S = season.

Effect	Mean	SD	2.50%	97.50%
Abundance model				
UC	0.13	0.03	0.08	0.18
UC × H (native forest)	0.34	0.12	0.15	0.65
UC × H (mature pine)	0.33	0.12	0.14	0.64
Detectability model				
SM	0.86	0.19	0.49	1.25
S	−0.35	0.18	−0.71	−0.01

Table 4
Results playback experiments to assess movement Chestnut-throated Huet-Huet (*Pteroptochos castaneus*) to clearcut stands.

Edge type/season	To clearcut stand	
	Crossing	Not cross
Native forest/breeding season	6 (18.2%)	27 (81.8%)
Native forest/post-breeding season	4 (11.8%)	30 (88.2%)
Mature pine/breeding season	3 (9.1%)	30 (90.9%)
Mature pine/post-breeding season	5 (20%)	20 (80%)
Total	18 (14.4%)	107 (85.6%)

while promoting the function of forest plantation as source habitats for wildlife (e.g., Valdovinos et al., 2009; Vergara, 2011; Estades et al., 2012). However, our results clearly indicate that understory vegetation at clearcut stands less than 3–4 years old is insufficient to improve the habitat quality for *P. castaneus*. In contrast, as assessed by previous studies, its abundance in mature pine stands and native forests is directly associated with understory cover (Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). Growing evidence further suggests that Tapaculos are also nesting within plantations, along banks (unpublished observations).

The understory vegetation can also promote the movement of animals by improving their willingness to cross open habitats (Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). Although our results showed that *P. castaneus* tends to be reluctant to move to harvested areas, some individuals entered into clearcuttings. These findings are consistent with previous studies of Tapaculos, where both the willingness to enter into mature pine plantations and the distance of intrusion were positively associated with the presence of understory (Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). Clearcut stands are extensive open areas whose sparse understory vegetation does not supply *P. castaneus* with shelter and foraging resources, thus acting as a hostile matrix of high resistance for the movement (Willson et al., 1994). The negative effect of clearcutting on forest bird population is consistent with the negative perception of forest birds to open habitats, such as cattle grasslands (Sieving et al., 1996, 2000). In fact, Tapaculos inhabiting native forest fragments surrounded by grasslands in agricultural landscapes of southern Chile perceive the open matrix as a barrier, compelling them to move between fragments through riparian corridors (Sieving et al., 1996, 2000).

Several studies in fragmented landscapes support that the structural contrast between vegetation of native forest fragments and the matrix influences the ability of wildlife to cross these boundaries and move to other fragments (Collinge and Palmer,

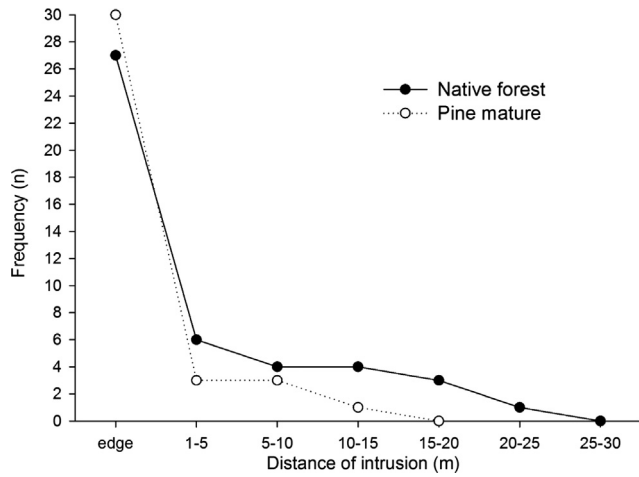**Table 5**
Total number of *Pteroptochos castaneus* that crossed from native forest or mature pine plantation to clearcut (n), mean distance of intrusion and total numbers of playback experiments (trials) are shown. Differences in proportions between individuals moving from a given habitat to clearcut stand are tested by Fisher exact test (one-tailed).

Edge type	Crossing (n)	Mean distance of intrusion (m)	SE	Trials (#)	Fisher (p)
Native forest	10	11.3	2.4	67	0.66
Mature pine	8	8.4	1.3	58	

Fig. 3. Frequency of *P. castaneus* crossing edge from native forest or mature pine plantation, entering to clearcut stand in breeding season.
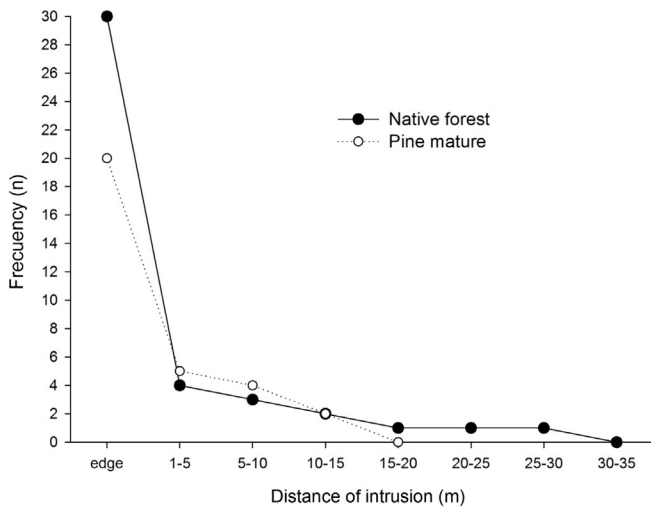

Fig. 4. Frequency of *P. castaneus* that crossing edge from native forest or mature pine plantation, entering to clearcut stand in post-breeding season.

2002; Kupfer et al., 2006). In our study, the vegetation contrast across boundaries of mature pine plantation-clearcut stand is less abrupt when compared to the boundary between native forests

and clearcut stands. The less marked structural differences between mature pine and clearcutting would explain the stronger understory vegetation effect on individuals moving from pine plantations (see Table 7). Therefore, gradual gradients in the understory vegetation, as observed between pine stands and clearcutting, could lead boundaries to act as soft barriers (Schieck et al., 1995). Foresters could reduce the contrast between the native forest and clearcuts through promoting understory vegetation in clearcuts. Enhancing it will facilitate the use of such areas by Tapaculos, as a first step to fulfill the Aichi's target that areas under forestry are managed in order to ensure conservation of biodiversity (Simonetti et al., 2013)

Intensively managed plantations usually have a detrimental effect on the biodiversity (Hayes et al., 2005). Hence, we propose that forestry management should provide to forest-dwelling birds with understory vegetation through adopting stand- and landscape-level silvicultural practices that promote the retention and growth of understory plants (Paquette and Messier, 2009; Tomasevic and Estades, 2008; Acuña, 2010; Simonetti et al., 2012; Simonetti and Estades, 2015) for example, through the reducing in the use of herbicides. Understory vegetation in clearcutting is suppressed by up to 80% percent by using herbicides before seeding and may be repeated one or two seasons after the establishment of the plantation (Kogan et al., 2002). Herbicides are used to ensure the productivity of forest stands through reducing competition for water resources and nutrients of understory plants with planted pine trees (Kogan et al., 2002). Thus, weed control involves a trade-off between the economic gains from forestry and biodiversity conservation. Forestry practices improving the abundance and movement of Tapaculos may also include the retention of woody debris such as logs, stumps and dead branches in the understory (Vergara and Simonetti, 2006; Tomasevic and Estades, 2008). At the landscape scale, the negative effect of clearcutting may be reduced though wildlife corridors connecting isolated native forest fragments and/or mature pine plantations (Franklin and Forman, 1987; Popescu and Hunter, 2011). In addition, leaving hedges of standing pines after the harvest time could promote the movement of wildlife. These movement corridors should increase the diversity of habitat and ensure the persistence of forest specialist species while maintaining the habitat of early successional species (Constantine et al., 2004). Such corridors might be standing plots of mature plantations holding understory vegetation (Simonetti et al., 2013; Cerda et al., 2015). Hence, the conservation of forest-dwelling species in forest plantation landscapes might require adjusting the spatial pattern of harvesting

Table 6
ZIP models explaining the distance moved by *P. castaneus* into clearcut. Codes of covariates are: UF = understory cover in the forest (mature pine or native forest), UC = understory in clearcutting, ET = edge type, S = season.

Model	Deviance				DIC	ΔDIC
	Mean	SD	2.50%	97.50%		
ET × UC + ET × UF + UC + UF	150.3	4.3	143.0	159.9	157.8	0.0
ET × UC + ET × UF + UC + UF + ET	152.5	4.2	145.6	162.0	159.7	1.9
UC + UF + UC × UF + ET	151.3	4.9	143.0	162.2	159.7	1.9
ET × UC + ET × UF + UC + UC × UF	154.2	3.9	147.7	163.2	160.9	3.1
ET × UC + ET × UF + UC + UF + S	153.9	4.1	147.0	163.1	161.5	3.7
ET × UC + ET × UF + UF + UC + UC × UF	154.6	4.3	147.4	164.2	162.0	4.2
ET × UC + ET × UF + UC	157.1	3.8	150.6	165.5	163.0	5.2
UC + UF + UC × UF	159.0	5.1	150.2	170.2	165.5	7.8
UC	160.3	4.7	152.1	170.2	166.6	8.8
UC + S	161.5	5.0	152.7	172.3	168.5	10.7
UC + UF	161.6	4.8	153.1	172.0	168.8	11.1
UC + UF + ET	162.0	4.9	153.3	172.6	169.8	12.0
UC + UF + S	162.7	5.1	154.0	173.5	170.7	12.9
UC + UC × UF + ET	163.6	5.1	154.8	174.4	171.3	13.5
UC + UF + ET + S	162.9	4.9	154.2	173.6	171.4	13.6
ET × UC + ET × UF	168.4	5.0	159.8	179.4	174.6	16.8
UF	177.7	5.1	168.5	188.7	183.4	25.6

Table 7
Coefficient values of the best-supported ZIP models shown in Table 6. The means, standard deviations (SD) and 95% lower and upper Bayesian credible intervals are shown. Codes for independent variables are: UF = understory cover in the forest (mature pine or native forest), UC = understory in the clearcut and ET = edge type.

Effect	Mean	SD	2.50(%)	97.50(%)
UC	0.91	0.15	0.58	1.17
UF	0.73	0.39	−0.13	1.43
ET × UC	2.09	0.61	0.95	3.33
ET × UF	1.26	1.22	−1.07	3.77
ET	−1.32	0.84	−3.05	0.18
UF	2.97	0.86	1.19	4.53
UC × UF	−3.12	0.93	−4.79	−1.21

(e.g. Harris, 1984), improving the odds to conserve native species into a monoculture of exotic species, advancing the sustainability of forestry practices.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.11.005.

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