Effects of the structure of pine plantations on their ''softness'' as barriers for ground-dwelling forest birds in south-central Chile

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Abstract

Fragmentation combined with habitat loss can affect population persistence mainly by isolating habitat fragments. However, this isolation depends, in part, on the species' perception of the surrounding matrix compared to remnant characteristics. Coastal forests of the Maule region have been severely fragmented. Surprisingly, forest remnants embedded in a pine plantation matrix hold most of the avian species expected for this kind of forest. This pattern has been explained by the fact that the structure of pine plantations may not be too different from that of native forests, allowing plantations to act as a ''soft barrier'' to dispersal among fragments. With playback experiments, we evaluated the effect of the structure of Monterey pine plantations, expressed as stand age, and understory cover, on the willingness of three ground-dwelling forest species (Rhinocryptidae: *Pteropotochos castaneus*, *Scytalopus fuscus*, and *Eugralla paradoxa*) to move from native remnants into pine plantation matrix during the breeding season 2004–2005 in the coastal range of south-central Chile. The distance of intrusion into the matrix of all species was positively related to understory cover. Only the movement of *P. castaneus* was significantly related to stand age. These attributes and their spatial array may affect functional connectivity and therefore species dispersal and population persistence in this fragmented landscape.

Keywords: Rhinocryptidae; Matrix permeability; Habitat barrier; Pine plantations; Maulino forest; Understory birds

1. Introduction

Forest fragmentation combined with habitat loss (Fahrig, 2003) has become one of the most important causes behind the loss of biodiversity during the last decades (Myers, 1994; Noss and Csuti, 1994). Although there are several mechanisms by which these processes can threaten the persistence of forest bird populations (Saunders et al., 1991; Noss and Csuti, 1994), isolation between forest remnants may play a major role especially for species with poor dispersal capacity (Lens et al., 2002), such as understory insectivorous species (Willson et al., 1994; Sievieng et al., 1996; Sekercioglu et al., 2002). Usually, it has been argued that in fragmented forest landscapes the matrix is a ''hostile'' habitat (e.g. agricultural crops) for most forest species, constituting a ''hard barrier'' (sensu Stamps et al., 1987) to individuals' movement through the landscape. However, little attention has been given to cases when the matrix can act as ''soft barrier'' (sensu Stamps et al., 1987)

allowing some degree of movement through it (Estades and Temple, 1999; Castellon and Sieving, 2006), thus diminishing the negative effects of isolation (Noss and Csuti, 1994; Witt and Huntly, 2001).

The coastal range of south-central Chile was originally covered by *Nothofagus*-dominated forests (Maulino forest), composed mainly by deciduous *Nothofagus glauca*, *N. obliqua*, and evergreen species such as *N. dombeyi*, *Cryptocaria alba*, *Persea lingue*, and *Aristotelia chilensis*, among others (San Martín and Donoso, 1996). But, after more than a century of modern human exploitation and landscape modification, the natural vegetation is extremely fragmented (Bustamante and Castor, 1998; Grez et al., 1998). In addition, the native forest cover has been reduced to less than 10% of its original extension (Estades and Temple, 1999; Echeverría et al., 2006), and the remnant patches of native forest show a significant degree of degradation (Olave, 1984; San Martín and Donoso, 1996). These detrimental human activities include the clearing of forests for agriculture, the production of timber, firewood, and charcoal (San Martín and Donoso, 1996), and the massive introduction of exotic pine plantations in the last two decades.

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Studies on the avifauna of this region have shown that even very small patches of forest maintain a relatively high number of species compared to larger fragments present in the same area (Estades and Temple, 1999; Vergara and Simonetti, 2004). This pattern is the opposite of what is found in fragmented forest surrounded by a semi-arid (Cornelius et al., 2000) or agricultural matrix (Willson et al., 1994), or even in actual islands of the Chiloé Archipelago in southern Chile (Rozzi et al., 1996a). Estades and Temple (1999) argued that such a pattern was due to the fact that most forest patches were surrounded by pine plantations, which, due to their forest structure, are not as inhospitable for forest birds as open areas, but act as a ''soft barrier'' (after Schieck et al., 1995) for birds inhabiting forest remnants, as pine plantations have shown to allow foraging (Lindenmayer et al., 2002) and some degree of movement between native forest fragments (Dale et al., 1994) in other forest systems.

Indeed, the importance of the characteristics of the matrix on the effects of fragmentation on biodiversity has been recognized in the last decade (Estades and Temple, 1999; Renjifo, 2001; Lindenmayer et al., 2002; Kupfer et al., 2006). The matrix can affect positively on the presence of several bird species by providing foraging resources and/or nesting sites (Sisk et al., 1997; Estades, 2001) configuring a mosaic of resources in the landscape. Thus, a ''Landscape Mosaic'' approach (Wiens, 1994) would be better approach than an ''Island Biogeography'' approach (MacArthur and Wilson, 1967) to understand patterns of species distribution in this type of landscape.

However, pine plantations are very dynamic forest systems, and the continuity of canopy cover is frequently broken up by clearcutting. Additionally, intensive management of pine plantations tends to limit the development of native understory that competes for water and nutrients with pines (Zutter and Miller, 1998) which has been found to have positive effects on the avifauna occupying these plantations (Pérez, 2004). Therefore, the role of pine plantations in the conservation of forest birds living in fragmented forests may depend on plantation development and management schemes, which in turn, might affect the capability of birds of moving through the matrix.

Birds from the Neotropical family Rhinocryptidae are characterized by their almost exclusively terrestrial habits, showing a very low flight capacity (Krabbe and Schulenberg, 2003). Most rhinocryptids present in Chile are forest species (Johnson, 1967; Araya et al., 1996; Jaramillo, 2003), endemic to the southern South America's temperate forests (Vuilleumier, 1985; Rozzi et al., 1996b) which are an important part of the Central Chile Biodiversity Hotspot (Myers et al., 2000). Their poor dispersal capacity makes these birds especially sensitive to habitat connectivity loss (Willson, 2004) which is particularly true in agricultural-dominated landscapes where their abundance showed a marked decrease in small native forest fragments related to larger fragments (Willson et al., 1994). However, this pattern is not found in pine plantations-dominated landscapes where the degree of functional isolation of native remnants seems to be lower, possibly because of the lack of structural contrast (Kupfer et al., 2006) between natural forests and pine plantations (Estades and Temple, 1999; Vergara and Simonetti, 2006).

In addition, the abundance of these species is positively related to the density of the understory (Estades, 1997; Reid et al., 2004; Díaz et al., 2005) even in pine plantations (Estades and Temple, 1999; Vergara, 2001; Estades and Escobar, 2005; Vergara and Simonetti, 2006). Along with this positive effect on rhinocryptid abundance, the density of the understory may be positively related to the movement of these birds in a landscape (Estades and Temple, 1999; Castellon and Sieving, 2006; Vergara and Simonetti, 2006). For example, Sievieng et al. (1996) found that the presence of shrubs can positively affect the willingness of some of these species to enter into the matrix in an agricultural landscape in Southern Chile. Using a playback experiment we tested the prediction that territorial rhinocryptids living in native forests patches will be more willing to move into the neighboring pine plantations when stands are older and/or understory cover is higher.

2. Methods

Our study was conducted at the Pantanillos Forest Research Station of the University of Chile (35°26′S, 72°17′W) and its surrounding areas in the Maule region of central Chile. The area is dominated by exotic Monterey pine (*Pinus radiata*) plantations and scattered native forests fragments cover no more than 10% of the landscape (Estades and Temple, 1999; Echeverría et al., 2006). Most pine plantations in the area are thinned two to three times during rotation allowing enough light to reach the ground to stimulate the development of an important native understory (Estades and Escobar, 2005). This understory is composed mainly by shrubs (e.g. *Azara integrifolia*, *Escallonia pulverulenta*) and small trees (e.g. *N. glauca*, *C. alba*, *Lithraea caustica*, and *Luma apiculata*) that are also present in native forest remnants in the area (Pérez, 2004).

All field work was carried out during the austral breeding season of 2004–2005. Of a total of 120 trials (see experiment description), 37 were conducted on October 2004, 30 on November 2004, and 53 on February 2005. We defined two experimental factors with two levels each. In order to assess the effect of plantation development we distinguished between young (3 years or younger) and mature (15 years or more) stands. Since we had no information on the exact age of each stand, we used the actual height as a surrogate of age, where stands with less than 3 years old may not exceed 4 m in height; and mature stands do not have less than 8–10 m in height (authors, personal observation). Within these plantations we visually assessed the understory cover and divided sites in areas with sparse (less than 30%) and dense (more than 50%) understory cover. We avoided misclassification using these non-overlapping and easily definable categories. In these sites we evaluated the willingness to enter pine plantations of the three rhinocryptid species present in the study area: the Dusky Tapaculo (*Scytalopus fuscus*, a former subspecies of *S. magellanicus*, but now considered as a separate species, Riveros and Villegas, 1994; Jaramillo, 2003), the Ochre-flanked Tapaculo (*Eugralla paradoxa*) and the Chestnut-throated Huethuet (*Pteroptochos castaneus*).

The experiment consisted in locating a native forest patch where there was a territorial individual of one of the target

species conducting territory-defense vocalizations in a well defined location assessed by the observer (JAT). Because this behavior is observed only in adult individuals, we are confident that we did not include juveniles in the trials, even in February (end of the austral breeding season), when a larger proportion of juveniles in the area can be expected. Since these species have been found previously in pine plantations (Estades and Temple, 1999; Vergara, 2001), the experiment was only conducted if there was not another individual present in the plantations around sampling points (e.g. answering the territorial call of the bird in the native forest). The adjacent pine plantations were then classified into one of the four types that resulted from combining the two studied factors (i.e. mature stand/dense understory, mature stand/sparse understory, young stand/dense understory, and young stand/sparse understory). If the latter was not possible (e.g. the understory had an "intermediate" cover or the plantation was between 4 and 14 years old) the point was discarded. In order to avoid pseudoreplication problems (MacGregor, 2000) two sample points for the same target species were never located closer than 200 m from each other, and a single bird was not sampled for more than one treatment (as many territories were in narrow strips of native forest around creeks, some of them where adjacent to two different types of plantations). Indeed, the mean distance between neighboring plots was 835 m (S.D. = 642) for *P. castaneus*, 726 m (S.D. = 703) for *E. paradoxa*, and 759 m (S.D. = 791), for *S. fuscus*. We consider that these distances are enough to ensure an acceptable level of independence among trials. For each species and factor we conducted a number of 10 replicates ($n = 3 \times 2 \times 2 \times 10 = 120$). All experiments were conducted in the morning (06:45–11:30) during non-rainy days.

The playback protocol was developed *in situ* after several days of trials at the beginning of the breeding season. The observer stayed in the plantation at 50 m from the edge of the native vegetation, approximately in front of the presumed location of the singing bird (Sievieng et al., 1996). The position of the observer (the same as the speaker) was chosen in order to allow him to hide from the approaching bird but, at the same time, to allow him to study the bird's behavior. In order to minimize the observer's effect on the behavior of the target bird, the observer wore camouflaged clothing and lay on the ground. Using a 20-W monophonic tape player the observer played the territorial call of the species (recorded early in October season by us in the same area) during three 1-min periods, each one separated by a 2-min wait. After that, the observer waited for other 5 min after which the experiment was considered finished (total experiment duration = $1 + 2 + 1 + 2 + 1 + 5 = 12$ min). The same output volume was used for *S. fuscus* and *E. paradoxa*, whereas for the larger *P. castaneus* a higher volume was chosen in order to match the higher power of this bird's calls. During the experiment the observer visually estimated the maximum distance (in 5-m intervals) at which the bird moved into the plantation when approaching the speaker. In cases when the bird arrived to the speaker's position before the end of the 12-min period, the experiment was terminated. Cases when the birds completely stopped singing after the playback experiment had begun, or when they stayed in the same original location showing no change in their behavior (i.e. no change in vocalization pattern and/or no change in its original location) were dropped from the analysis. Cases where birds only moved out to native forest edge were considered zero penetration into the plantations.

Data were expressed as the percentage of the maximum travel distance (50 m) that the birds moved during the experiment and they were normalized using the arcsin-transformation (Sokal and Rohlf, 2003). We analyzed data using ANOVA and multiple linear regressions.

3. Results

The overall number of individuals that entered the plantations during the experiments differed between species. From a total of 40 observations of individuals that actively responded to the experiment for each species, *S. fuscus* entered more frequently the plantations ($n = 27$), followed by *P. castaneus* ($n = 17$), and finally by *E. paradoxa* ($n = 12$). The remaining birds were reluctant to enter into the pine plantation matrix (i.e. they showed an intrusion distance = 0).
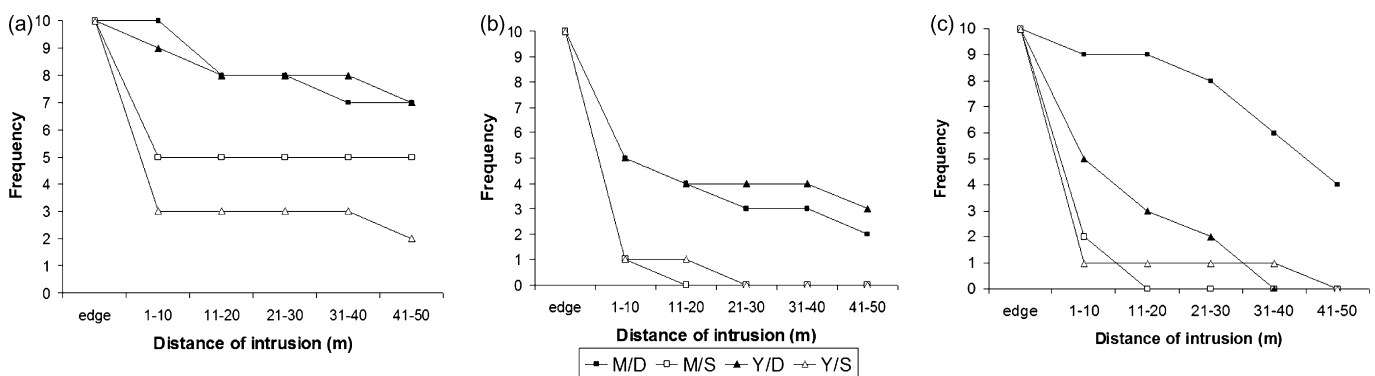

Fig. 1. Frequency of birds that entered the plantation to, at least, the distance expressed in the *X*-axis while defending territory, from native forest into pine plantations matrix by three Rhinocryptidae species: (a) *Scytalopus fuscus*, (b) *Eugralla paradoxa*, and (c) *Pteroptochos castaneus*. Bifactorial experiment (stand age/understory cover) results are shown as follows: M/D (mature stand/dense understory), M/S (mature stand/sparse understory), Y/D (young stand/dense understory), and Y/S (young stand/sparse understory).

Table 1
ANOVA table showing the effect of structural variables of pine plantations on Arcsin-transfomed % of distance of intrusion from native forest by three Rhinocryptidae species

Source	Sum of squares	d.f.	Mean square	F ratio	P
Species	28152.3	2	14076.1	16.8	0.000
Stand age	3123.2	1	3123.2	3.7	0.056
Understory cover	36203.2	1	36203.2	43.3	0.000
Species × age	2742.9	2	1371.4	1.6	0.199
Species × understory	673.5	2	336.7	0.4	0.669
Age × understory	278.4	1	278.4	0.3	0.565
Species × age × understory	5403.1	2	2701.5	3.2	0.043
Error	90263.5	108	835.8		

Of all treatments, the mature stands with dense understory achieved the largest number of intrusions, all species pooled. Fig. 1 shows the frequency of birds that entered the plantation to, at least, the distance expressed in the X-axis for each species sorted by species and treatment.

Despite the fact that an important proportion of birds did not enter the matrix, we found that for those who did, the distance at which they moved into the pine plantation when approaching the speaker was significantly affected by understory cover and bird species (Table 1). There was also a significant interaction between species, stand age, and understory cover (Table 1).

In fact, although all three species tended to move farther into the plantation in sites with dense understory (multiple regression analysis: *S. fuscus*, $t = 3.64$, $P = 0.001$; *E. paradoxa*, $t = 3.32$, $P = 0.002$, and *P. castaneus*, $t = 4.55$, $P < 0.001$), distance traveled by *P. castaneus* showed also a significant positive relationship with stand age (multiple regression analysis: $t = 2.78$, $P = 0.008$). Movement distance of the other species were not affected by stand age (*S. fuscus*, $t = 1.07$, $P = 0.293$, *E. paradoxa* ($t = -0.26$, $P = 0.797$).

Most of the times *S. fuscus* and *E. paradoxa* approached the speaker silently, but started singing loudly at the point where they stopped their approach. *P. castaneus*, on the other hand, used to approach to the speaker emitting loud alarm calls continuously and trying to determine the location of the intruder.

4. Discussion

Although evidence shows that rhinocriptids are reluctant to move into sparsely vegetated areas, in our experiment some birds did do so. Moreover, studies such as ours deal only with adult territorial birds that may be less adventurous than dispersing juveniles (Sievieng et al., 2000), that are less experienced assessing predation risk and habitat suitability (Yoder et al., 2004). Therefore, playback experiments may overestimate the effect of fragmentation on total movements of ground-dwelling birds. Other techniques, such as radiotracking may provide a less biased picture of the effect of plantation structure on bird movements, but certainly require a significant amount of additional resources.

Despite some methodological differences (e.g. more than one observer vs. one, or 20 min trials vs. 12 min, in our study), our results agree with the observations by Sievieng et al. (1996) in finding that *S. magellanicus* (*S. fuscus* in our case) was the most likely species to leave the native forest to move into the matrix, followed by *Pteroptochos tarnii* (Black-throated Huethuet, a sister species to *P. castaneus*), and *E. paradoxa* in the last place. Sievieng et al. (1996) also observed that the shrub cover affected the willingness of these species to move into the matrix. Therefore, our results show that these three species exhibit consistent behaviors even in different ecological situations: a high remnant/matrix contrast (native forest vs. pastures, Willson et al., 1994; Sievieng et al., 1996), and where the matrix is less structurally different to forest remnants (native forest vs. pine plantations, the present study). In both cases bird willingness to abandon their territories and move into the matrix was significantly affected by the understory (shrub) cover.

Vergara and Simonetti (2006) also used playbacks to study habitat use and movements by rhinocriptids from native forest into pine plantations in a similar landscape, but did not address the effect of stand age as a factor. Although they did not treat understory cover as a factor independent from forest type (i.e. they used pine plantations with poor understory as the only treatment) their results suggest that individuals of *P. castaneus* may be reluctant to move from native vegetation into plantations with sparse understory.

Although we cannot completely rule out an effect of differential territorial responses between the studied species, the different responses of the three species to the playback experiment may have to do with their relative perception of danger. The fact that the only species sensitive to stand age (*P. castaneus*, 150 g, 24 cm) is substantially larger than the other two (*S. fuscus*, 15 g, 10 cm, and *E. paradoxa*, 30 g, 14 cm) suggests that birds may differ in what they consider to be an acceptably safe cover to move through. Because of its size, usually *P. castaneus* cannot move easily through dense shrubs and has to travel using paths in between shrub patches (authors, personal observation), making it more visible to raptors, such as *Accipiter chilensis*, a known predator of this species (Sievieng et al., 2000; JAT, personal observation). The latter may force these birds to seek habitats with a relatively closed canopy. This pattern was also documented by Belisle and Desrochers (2002) who found that larger species tended to be more conservative when crossing forest gaps, also because of predation risk. Creegan and Oborne (2005), on the other hand, found that larger species were more likely to cross gaps, but they argued that larger birds were more able to avoid predators. In any event, predation risk seems to be a constant factor in gap-crossing decision (Harris and Reed, 2002).

In our study, five (50%) individuals of *S. fuscus* did reach the speaker on the mature stand with sparse understory treatment (Fig. 1), but in most cases these movements where favored by the presence of pruning debris on the ground, that may be enough to conceal the presence of these small birds. This finding agrees with the observation of Vergara and Simonetti (2006) of a positive effect of pruning debris on the abundance of *S. fuscus* and *E. paradoxa*.

An important number of birds do use Monterey pine plantations in central Chile as breeding, foraging and roosting

habitat (Estades, 1999a,b; Estades and Temple, 1999, 2001; Vergara, 2001), and the abundance of many of them is positively associated to the degree of development of the understory (Estades and Temple, 1999; Pérez, 2004; Estades and Escobar, 2005). Understory can influence local density of breeding forest birds in pine plantations by providing more foraging resources (arthropods in this case), nesting sites (especially for open-nesting and understory birds, Morrison, 1992; Willson and Comet, 1996; López and Moro, 1997; Díaz et al., 1998), and safe places to avoid predator attacks (Lima, 1993; Reid et al., 2004).

Therefore, management of plantations to benefit ground-dwelling birds should strive to maintain a developed understory (Thomas et al., 1999). However, there is a clear trade-off between commercial (primary use) and conservation role of plantations. There is enough evidence showing that shrubs compete for nutrients, light and water with commercial trees, significantly reducing their growth (Zutter and Miller, 1998; Chang and Preston, 2000; Matsushima and Chang, 2006), particularly during the first years of the plantation. For that reason the use of herbicides plays an important role in the establishment of modern pine plantations throughout the world (Wagner et al., 2006), including Chile (Kogan et al., 2002). However, management schemes based on single herbicide applications and that do not include mechanical site treatments tend to have only temporary effects, as many plant communities show important levels of resilience (Miller and Miller, 2004). Additionally, during the early stages of plantations, it is possible that young unpruned trees may act structurally as shrubs counteracting the effects of herbicides on the native understory. In Chile, most plantations are established without much mechanical site preparation and herbicides are seldom used beyond the first year of the plantation (M. Toral, personal communication), indicating that current pine plantation management practices allow the development of an understory in most sites. However, this pattern might change in the future if management schemes become more herbicide-intensive.

It is believed that corridors are less necessary when there is movement of organisms through the matrix (Hudgens and Haddad, 2003). In the present study, the only species that might need corridors is *P. castaneus*, due to its clear requirement of both mature plantations and high understory cover. Creating such corridors in pine plantations may be done by leaving uncut strips (Estades, unpublished data), or by organizing clearcutting in such a way that areas grow up together to form large continuous mature patches of forest (Ohman, 2000; Rebain and McDill, 2003). Additionally, riparian areas with native vegetation may serve as corridors for birds in landscapes dominated by pine plantations (Desrochers and Hannon, 1997; Estades and Temple, 1999; Estades, unpublished data).

Pine plantations in central Chile do allow the movement of birds living in native forest fragments. This pattern has been observed in other plantations systems worldwide (Marsden et al., 2001; Lindenmayer et al., 2002; Creegan and Oborne, 2005; Barbaro et al., 2007). The latter, along with the fact that plantations with well developed understory supply an important amount of foraging resources for most bird species (Estades and

Escobar, 2005), creates a ''soft barrier'' that can reduce the negative effects of fragmentation on population density (Estades, 2001), and ease the movement and exchange of individuals among populations.

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