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**THE ROLE OF UNDERSTORY ON THE
ABUNDANCE, MOVEMENT AND SURVIVAL OF
GROUND-BEETLES IN PINE PLANTATIONS: AN
EXPERIMENTAL TEST**

Tesis

**Entregada a la
Universidad de Chile
En Cumplimiento parcial de los requisitos
Para optar al grado de**

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Por

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Director de Tesis: M.Cs. Audrey A. Grez

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INFORME DE APROBACIÓN

TESIS DE MAGÍSTER

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YENDERY FABIOLA CERDA CORTÉS

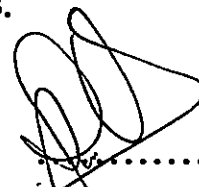
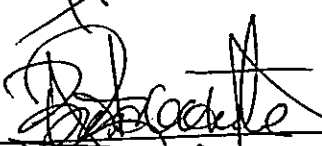
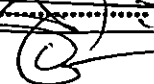
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BIOGRAFÍA



Soy bióloga con mención en medio ambiente de la Universidad de Chile. Me interesa la conservación de la biodiversidad en ambientes fragmentados. Desde 2002 he trabajado voluntariamente en una organización no gubernamental (CODEFF) cuya misión es la conservación de la fauna y flora nacional. También, he apoyado actividades de terreno de proyectos fondecyt relacionados con la conservación biológica en ambientes fragmentados. Actualmente, participo en proyectos de investigación en ciencias biológicas y soy directora nacional de CODEFF, en esta última, estoy a cargo de los temas sobre conservación en áreas silvestres protegidas privadas y centros de rehabilitación de fauna silvestre.

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RESUMEN

Las plantaciones forestales juegan un rol relevante en la conservación de la biodiversidad forestal a nivel global. A escala de paisaje, aquellas plantaciones que poseen una vegetación de sotobosque compleja les proporcionan a los organismos hábitats alternativos o vías de dispersión entre los bosques remanentes. Un experimento manipulativo fue realizado para probar si la presencia de un sotobosque denso en plantaciones de pino maduras es un factor determinante de la abundancia, movimiento y sobrevivencia de *Ceroglossus chilensis*. Entre 2009 y 2012, en diecinueve parcelas con alta, naturalmente baja cobertura y sotobosque removido experimentalmente, los carábidos fueron colectados en trampas de intercepción; el movimiento fue evaluado por observaciones directas y la sobrevivencia fue cuantificada como la proporción de días que los individuos sobrevivieron en contenedores abiertos y cerrados enterrados en el suelo hasta la mitad. Como lo esperábamos, *C. chilensis* fue más abundante en las parcelas con alta cobertura de sotobosque que en aquellas con baja cobertura o sotobosque removido. Los individuos recorrieron distancias más cortas y prefirieron quedarse en las plantaciones con alta cobertura de sotobosque. En general, la sobrevivencia de *C. chilensis* fue menor en las plantaciones con escasa cobertura de sotobosque y la mortalidad por depredadores fue significativamente mayor en estas plantaciones. Por lo tanto, la mayor abundancia de *C. chilensis* en plantaciones de pino con sotobosque denso es explicada por su comportamiento de movimiento y

sobrevivencia. Los resultados de este experimento sugieren que el desarrollo de sotobosque denso en plantaciones de pino puede contribuir a la conservación de este carábido endémico en el paisaje de bosque fragmentado.

ABSTRACT

Tree plantations play a relevant role in the conservation of global forest biodiversity. At landscape scale, those that have a complex understory vegetation provide to organisms surrogate habitats or dispersal pathways between forest remnants. A manipulative experiment was made to test if the presence of dense understory in mature pine plantations is a determining factor for the abundance, movement and survival of *Ceroglossus chilensis*. Between 2009 and 2012, in nineteen plots with high, naturally low and experimentally removed understory cover, carabids were collected in pitfall traps; movement was evaluated by direct observations, and survival was quantified as the proportion of days that individuals survived in closed and open containers half-buried into the soil. As expected, *C. chilensis* was more abundant in plots with high than low or removed understory cover. Individuals traveled shorter distances and preferred to stay in high understory cover plantations. Overall, *C. chilensis* survival was lower in plantations with scarce understory cover, and mortality by predators was significantly higher in these plantations. Therefore, the higher abundance of *C. chilensis* in dense understory pine plantations is explained by its movement behavior and survival. The results of this experiment suggest that the development of dense understory in pine plantations may contribute to the conservation of this endemic carabid beetle in the fragmented forest landscape.

INTRODUCTION

In fragmented landscapes, remnant patches have been considered a main focus in conservation of threatened populations (Banks *et al.*, 2005). However, at landscape scale, the surrounding anthropogenic matrix is increasingly recognized as an important element to biodiversity conservation (Brady *et al.*, 2009; Lindenmayer *et al.*, 2009; Prevedello & Vieira, 2010; Simonetti *et al.*, 2012). Forestry plantations have increased worldwide in recent decades (Brockhoff *et al.*, 2008; Felton *et al.*, 2010). According to the latest FAO report, forests cover around 4,000 million ha representing about 31% of planet's surface, while planted forests have grown to 264 million ha until 2010, comprising approximately 7% of the total forest area (FAO, 2010). The contribution of forest plantations to the conservation of global forest biodiversity is therefore a question of increasing relevance (Lindenmayer & Hobbs, 2004; Brockhoff *et al.*, 2008; Cummings & Reid, 2008).

Even when forest plantations have been regarded as "biological deserts" because they harbor an impoverished faunal assemblages (Carnus *et al.*, 2006), there is increasing evidence that plantations support several native species (Pawson *et al.*, 2008; see examples in Lindenmayer & Hobbs, 2004; Brockhoff *et al.*, 2008; Felton *et al.*, 2010). A common feature of these plantations is the presence of a complex understory which provides surrogate habitats or dispersal pathways between remnants of fragmented native forest (Estades *et al.*, 2012). Generally, movement of organisms in the matrix may

imply higher dispersal costs because increased predation risk and the uncertainty to reach other suitable patches of habitat compared to the dispersal cost by moving through continuous habitat (Berggren *et al.*, 2002; Haynes & Cronin, 2006), unless the matrix is structurally complex (Ricketts, 2001; Goodwin & Fahrig, 2002). Furthermore, forest plantations with a developed understory might maintain microclimatic and biotic conditions similar to forest fragments and thus promote the survival of many organisms for which original habitats have been reduced (Lindenmayer & Hobbs, 2004). In fact, understory vegetation is considered to be a good predictor of faunal diversity (Bremer & Farley, 2010; Estades *et al.*, 2012). Therefore, the conservation of understory vegetation in plantations has been suggested as a way to enhance biological diversity, particularly, species richness (Spellerberg & Sawyer, 1995).

In Chile, forest plantations began in mid-1940s. In the 70s, forest policy strongly supported them generating an advantageous scenario for forestry (Nahuelhual *et al.*, 2012). As a result, between 1995 and 2009 Chile exhibited one of the highest annual rates of afforestation (49,020 ha) and reforestation (53,610 ha) in South America (Nahuelhual *et al.*, 2012). Particularly, central-south native forests have been extensively deforested and fragmented, originally due to land clearing for farming and subsequently as a result of replacement of native forest by exotic plantations (Donoso & Lara, 1996; Echeverría *et al.*, 2006; Nahuelhual *et al.*, 2012). This landscape modification has resulted in a mosaic of small forest remnants surrounded by a matrix dominated by *Pinus radiata* D. Don (Pinaceae) plantations (Echeverría *et al.*, 2006).

Particularly, in the area of Maulino forest, a unique and threatened ecosystem harboring several distinctive and endangered animal and plant species (Bustamante *et al.*, 2006 and

references therein), pine plantations might provide habitat for populations of native plants, insects, amphibians, lizards, mammals and birds (Estades *et al.*, 2012 and references therein), and also they act as surrogate habitat for some carnivorous mammals such as kodkod (Acosta-Jamett & Simonetti, 2004). These plantations have the particularity of supporting abundant understory, consisting commonly of *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae), *Cryptocarya alba* (Mol.) Looser (Lauraceae) and *Persea lingue* Nees (Lauraceae) shrubs (Greze *et al.*, 2003; Poch, 2012).

Ceroglossus chilensis Eschscholtz (Coleoptera: Carabidae) is an endemic ground-beetle and a diurnal predator which is associated with *Nothofagus* woods including the Maulino forest (Henríquez *et al.*, 2009). In south-central Chile, it is also dominant and persistent in pine plantations, supposedly due to the presence of a developed understory cover in these plantations (Briones & Jerez, 2007). In the Maulino forest and adjacent pine plantations, *C. chilensis* is most abundant in small remnants than in pine plantations and continuous forest (Greze *et al.*, 2003; Henríquez *et al.*, 2009). Other epigeal insects, probably potential prey of *C. chilensis*, are also more abundant in small fragments than in continuous forest (Greze *et al.*, 2003; Greze, 2005); while in pine plantations their abundances are similar to the Maulino forest (Greze *et al.*, 2003). Although sex ratio and fluctuating asymmetry of *C. chilensis* are similar in fragments, continuous forest and pine plantations, fragments host smaller individuals (Henríquez *et al.*, 2009). The smaller size of *C. chilensis* in fragments suggests that forest remnants should be connected by native forest or another type of corridors (e.g., plantations with developed understory), which would facilitate dispersal of these carabids in landscape reducing possible antagonistic interactions as result of “crowding effects” (Henríquez *et al.*,

2009). Nevertheless, up to date no strong experimental evidence regarding the effect of understory in pine plantations on the abundance, dispersal and survival of this species exists.

In this work, we tested the hypothesis that the presence of dense understory in pine plantations is a determining factor for the abundance, movement and survival of *C. chilensis*. Particularly, we expected that, i) if the abundance of *C. chilensis* depends upon understory, it will significantly diminish in pine plantations where understory is experimentally removed, being similar to those observed in pine plantations with naturally low understory cover, ii) resource availability (i.e., potential prey) for *C. chilensis* will be lower in pine plantations with low understory cover compared to plantations with high understory cover, iii) *C. chilensis* will have longer and more linear displacements in pine plantations with low or experimentally removed understory cover. Additionally, they will prefer pine plantations with high understory cover than those with low understory cover and iv) survival of this carabid will be lower in plantations with low or experimentally removed understory, than in high understory cover plantations.

MATERIALS AND METHODS

Study site

The study was carried out in commercial pine plantations located at Tregualemu in Central Chile (72° 43' 55.59''W – 35° 59' 37.12''S to 72° 40' 46.34''W – 35° 58' 5.27''S). The area covers over 1,370 ha, and it is composed of remnants of Maulino forest and pine plantations with different levels of understory development, ranging from 160 to 540 m above sea level. Pine plantations consisted in mature 20 years old stands with trees 28 m high. Understory was dominated by several native species of shrubs and trees (Poch, 2012).

Experimental design

Nineteen 40 x 40 m square plots located in mature pine plantations were used in this study. These plots were established according to the understory cover level: 7 low (L, 0 - 30%) and 12 high cover (H; > 50%). L and H plots were interspersed and separated at least by 300 m. This distance is adequate for plots to be statistically independent (e.g., Vergara & Simonetti, 2004). Between November 2009 and January 2011, the abundance of *C. chilensis* was assessed in each pine plot (see methods below), establishing a baseline for comparison with the experimental plots. In February 2011, understory was removed in half of H plots, randomly selected (experimental plots, E). The understory was reduced to a cover less than 10% by manually cutting with a machete and an electric

saw, repeating this procedure in summer 2012. The remaining H and L plots kept undisturbed, acting as control.

Ceroglossus chilensis abundance

The abundance of *C. chilensis* was assessed using dry pitfall traps, consisting of plastic jars 11 cm diameter and 8 cm depth. In each sampling plot, eighteen pitfall traps were buried at ground level in a grid of 3 x 6 traps, separated by 5 or 10 m in an inner area of 30 x 30 m. Monthly, from November 2009 to July 2012, traps were opened for four consecutive days. The collected individuals were counted, marked and then released. The capture probability of pitfall traps may depend on habitat structure because structural complexity may affect the movement behavior of insects (Melbourne, 1999). More captures may be observed in less complex habitats because insects would move more in these habitats with fewer obstacles and thus be more prone to fall in a trap. This possible bias was estimated through mark-release-recapture experiments in six 4 x 4 m enclosure plots, delimited by a black plastic barrier. Three of them had less than 10% understory cover and the other three had more than 70% understory cover. Nine pitfall traps 1 m apart were placed in a 3 x 3 m grid in each of these plots. Eight *C. chilensis*, individualized with queen bee marks were released in the center of each plot, and after four days captured individuals were counted and released.

Availability of potential prey

To assess the potential invertebrate prey availability in H and L plots, between November 2009 and January 2011 (i.e., pre-understory removal period) nine of the

eighteen pitfall traps used for capturing *C. chilensis* were left opened for other additional four days. The invertebrates captured in traps without *C. chilensis* were collected, labeled and transferred to alcohol (70%). Then, they were dried at 60°C for 48 hours and weighted in an electronic analytic balance (Kern & Sohn GmbH, model ABJ 220-4M, readability 0.1 mg) to assess their biomass. Also, they were counted to estimate the cumulative abundance.

Ceroglossus chilensis movement

Movement of *C. chilensis* was evaluated by direct observations of 76 individual trails (visual tracking), 38 in H, 28 in L and 10 in E plots, during June 2010 and April to June 2011. Carabids were captured in remnant patches adjacent to pine forests through dry pitfall traps. Before beginning the observations, beetles were held in a transparent cage half-filled with soil and pine needles. Individuals were marked with a single white dot at the bottom of one elytron, using an oil paint marker. Each specimen was placed on the ground at the center of each pine plot, within an upside-down vial; after several seconds, it was carefully released trying to minimize handling effects on its movement behavior, and then tracked for 30 minutes or until it was lost, marking its position with a stick every 30 seconds (i.e., time step) (Goodwin & Fahrig, 2002). All monitoring sessions were done between 11:00 am and 5:00 pm on warm days. At the end of the visual tracking, the trail was marked with a rope linking sticks, and drawn in a paper, estimating total distance (i.e., the sum of linear distances between step points), displacement (i.e., straight-line distance between initial- and end-points of the path), displacement rate (i.e., displacement divided by total time of the monitoring session), the

proportion of time that the individual did not move (i.e., the immobile time steps divided by total time of the monitoring session), step-length (i.e., distance traced in the mobile time steps), and turning angles (i.e., the external angle between the new direction of movement and the previous direction) (Goodwin & Fahrig, 2002). Low values of the exterior angles (below 45° or above 135°) indicate a movement rather linear, whereas high values for these angles (between 45° and 135°) show rather tortuous movement.

Probability of edge crossing

Additionally, to assess the preference of *C. chilensis* for high or low understory cover, we studied the probability of edge crossing between areas with high-high, low-low and high-low understory cover. This was assessed in a 6 x 3 m enclosure delimited by a black plastic barrier in a pine stand. This enclosure was divided in two similar areas. Initially, both areas of the enclosure had high understory cover (High-High). Then, in one area of the enclosure the understory was removed, leaving it with a cover less than 10%, so the enclosure turned to be composed by one high understory cover area adjacent to a low understory cover area (High-Low). Finally, understory was removed from the remaining high understory cover area, so both areas ended with low understory cover (Low-Low). Specimens were marked with numbered queen bee marks and released at the center of one area, following its movement until it was hidden or for 5 minutes, recording whether it crossed or not the edge. Forty individuals were followed in High-High, 40 in Low-Low, 40 in High-Low, and 40 in Low-High treatments, with half of them released in each area of the enclosure.

Ceroglossus chilensis survival

Survival of *C. chilensis* was evaluated in the nineteen pine plots, using 17-L transparent plastic containers, which were cut forming windows into the top, bottom and sides. Windows were covered with a 2 mm galvanized metal mesh to allow the movement of prey in and out of the container, and strong enough to prevent the carabids from biting through and escaping (Ewers, 2008). Each container was half-buried into the soil, filling the cage with the same substrate removed from the soil. Consequently, the cages had the typical substrate of the pine stands and were connected to the above- and below-ground environments through the mesh-covered windows (Ewers, 2008). Two experimental containers were placed per plot, one was uncovered to estimate *C. chilensis* mortality by predators, and the other was covered to assess the mortality by other factors but predation (e.g., microclimate effect) on *C. chilensis*. Three specimens were added into each experimental container, and its survival was assessed once a month in two periods, from May to December 2010, and from March to December 2011. Dead individuals were removed from the container and replaced with a live carabid (Ewers, 2008). Individuals that were not found in the uncovered containers were considered as preyed upon, and replaced with a live individual. When a container was disturbed and/or broken by any animal, it was repaired and the substrate within was inspected, looking for the specimens. If the individual(s) were not found, they were replaced with a live carabid (Ewers, 2008). Parallel to these experiments, microclimatic conditions (i.e., temperature and relative humidity at ground level) were measured at noon inside the experimental containers in all pine plots with a portable thermometer-hygrometer.

Data Analysis

The effect of understory cover level on the cumulative abundance of *C. chilensis* in pine plantations before experimental understory removal (i.e., between November 2009 and January 2011) was tested using one-way ANOVA. Since the number of months sampled before and after the removal experiment differed, and considering the seasonal phenology of this species (with highly variable abundance across months, see results), to evaluate the understory manipulation effect on the cumulative abundance of *C. chilensis* in pine plantations only equivalent months in the pre- and post-understory removal periods were compared (November, December, January, April, June and July 2009-2010 and the same months in 2011-2012). These abundance data were compared using repeated measures ANOVA. If there was a significant effect of understory manipulation ($P < 0.05$), the Fisher LSD test was applied for post-hoc comparisons. For the bias estimation, the number of recaptured individuals in L and H plots was compared with a Mann-Whitney U test. The effect of understory cover level on cumulative biomass and on cumulative abundance of potential invertebrate prey during pre-understory removal period was evaluated with a one-way ANOVA.

Movement variables (i.e., total distance, displacement, displacement rate, proportion of time that the individual did not move, and step-length) were compared by one-way ANOVA and Fisher LSD. As turning angles are circular data, the mean angles, standard error of mean and the length of mean vector (r) were estimated for each understory cover type. The r is a measure of the concentration of circular data that vary from 0 (when the distribution of the turning angles is completely uniform) to 1 (when all turning angles are in the same direction) (Zar, 2010). To evaluate the effect of understory cover on this

variable a Watson-William F test was used. These circular analyses were done in Oriana 4.0 (Kovach Computing Services).

The probabilities of edge crossing (i.e., proportion of individuals that crossed) between areas with high-high and low-low, and high-low and low-high understory cover in pine stands, were compared with a χ^2 and for post hoc analysis with a multiple comparison test for proportions (Marascuilo procedure; Marascuilo, 1966).

Survival of *C. chilensis* in pine plots was quantified as the proportion of days that an individual survived related to the maximum number of days that individual could have survived (i.e., total duration of the experiment; Ewers, 2008). Data from disturbed cages were not included in the statistical analysis. The understory manipulation effect on the survival of *C. chilensis* in pine plantations was assessed with two-way ANOVA, considering understory cover (H, L and E) and lid (Covered and Uncovered cages) as factors. Fisher LSD test was applied for post-hoc comparisons. The same analysis was carried out for microclimatic data.

Data transformations ($\log_{10}(x)$ for abundance data and movement variables: total distance and displacement; $\log_{10}(x + 1)$ for step-length; (\sqrt{x}) for displacement rate; $\sin^{-1}(\sqrt{x})$ for the proportion of time that the individual did not move, and survival) were done to meet the assumptions of ANOVA when necessary. All statistical analyses were run in STATISTICA 7.0.

RESULTS

Ceroglossus chilensis abundance

Regarding bias estimation, the recaptures of *C. chilensis* in plots with distinct level of understory development did not differ significantly ($N = 3$, $U = 4.0$, $P = 0.83$). The rank sum values of individuals recaptured in the enclosures with low and high understory were 11 and 10, respectively. Therefore, it was not necessary to correct the abundance data.

During the three years of the study, most *C. chilensis* were captured between November and June, with almost nil captures in July, August and September (Fig. 1). During the pre-understory removal period, the cumulative abundance of *C. chilensis* was five times higher in H plots (mean \pm SE, 70.1 ± 29.1 individuals) than in L plots (14.9 ± 5.0 individuals; $F_{1,17} = 6.50$, $P = 0.02$).

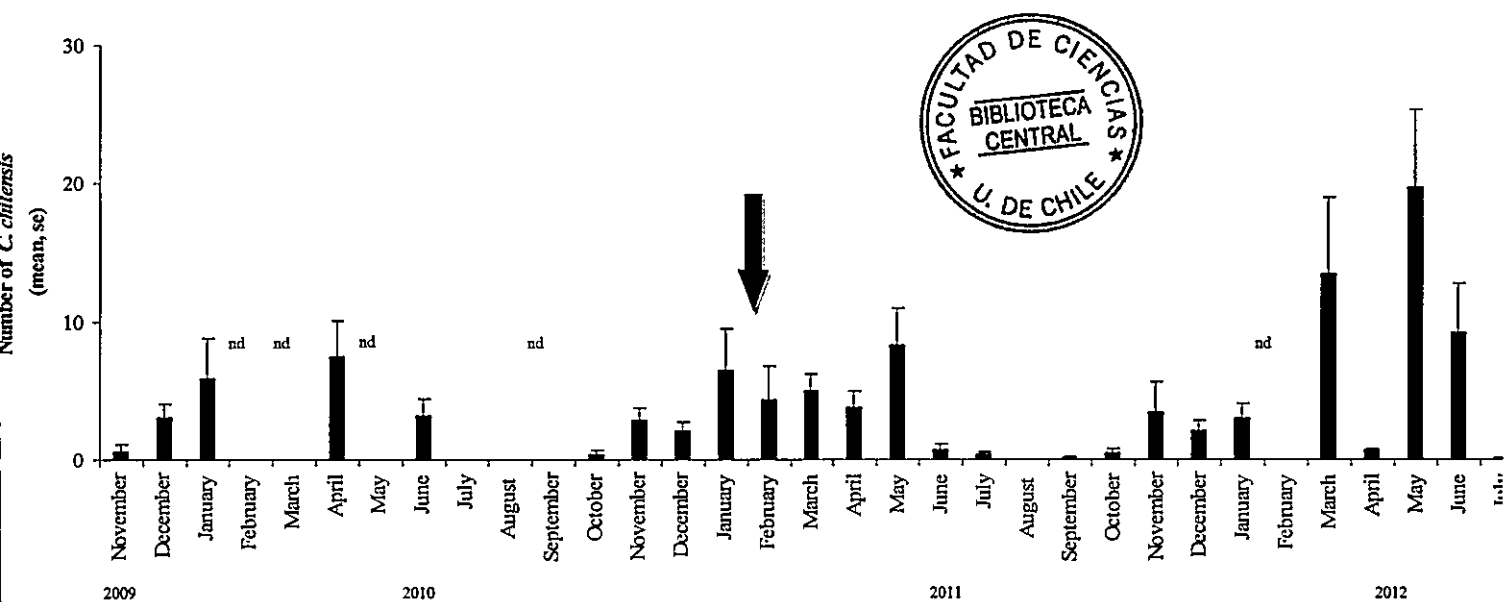


Figure 1. Abundance (mean \pm 1 se) of *C. chilensis* in pine stands from November 2009 until July 2012. Data are averages considering the seven High and seven Low understory cover plots that remained undisturbed throughout the whole study. nd: no data available for February, March, May and September 2009 and for February 2012. The arrow indicates when understory was removed from the Experimental plots.

When comparing the cumulative abundance of these carabids in H, E and L plots in equivalent months before and after understory removal, there was no significant effect of understory cover treatment ($F_{2,16} = 1.19$, $P = 0.33$) or time ($F_{1,16} = 3.61$, $P = 0.08$), with *C. chilensis* having in average similar abundances in all pine plots regardless of understory cover (H plots: 25.1 ± 5.5 individuals; L plots: 13.4 ± 3.8 individuals; E plots: 37.5 ± 22.4 individuals; in this case E plots include both pre and post understory removal periods), and similar abundances in the pre and post-removal periods (Pre-removal: 31.5 ± 11.8 individuals; Post-removal: 16.6 ± 3.6 individuals). However, there was a significant interaction time * understory cover ($F_{2,16} = 3.84$, $P = 0.04$), with the cumulative abundance of *C. chilensis* decreasing significantly in the post-removal

period, compared to the pre-removal period, only in the E plots, while maintaining similar abundances in both the H and L plots (Fig. 2).

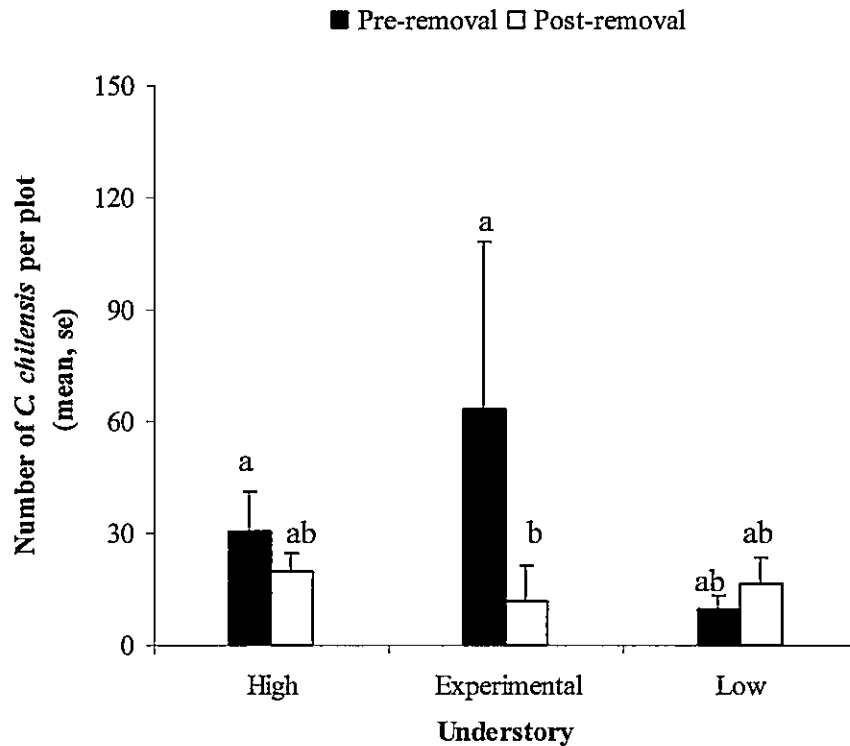


Figure 2. Cumulative abundance of *C. chilensis* in High, Experimental and Low understory cover plots comparing equivalent months between pre-removal (November–December 2009 and January–July 2010) and post-removal periods (November–December 2011 and January–July 2012). Experimental plots during pre-removal period had high understory cover. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

Availability of potential prey

The cumulative abundance of invertebrate potential prey of *C. chilensis* was similar in pine plots, independent of the level of understory cover (H plots, 149 ± 26.2 individuals; L plots, 174 ± 23.1 individuals; $F_{1,17} = 0.46$, $P = 0.51$). The cumulative biomass however

was significantly higher in L plots (3.1 ± 0.2 grams) compared with H plots (2.0 ± 0.4 grams; $F_{1,17} = 5.96$, $P = 0.03$).

Ceroglossus chilensis movement

Ceroglossus chilensis traveled significantly shorter distances and displaced less in H plots than in L and E plots (Total distance, $F_{2,73} = 6.40$, $P = 0.003$; Displacement, $F_{2,73} = 5.79$, $P = 0.005$; Fig. 3). However, displacement rate did not significantly differ between pine plots ($F_{2,73} = 2.16$, $P = 0.12$; Fig. 4). Something similar occurred with the proportion of time that the individual did not move, with no differences between plots ($F_{2,73} = 0.08$, $P = 0.92$; Fig. 4).

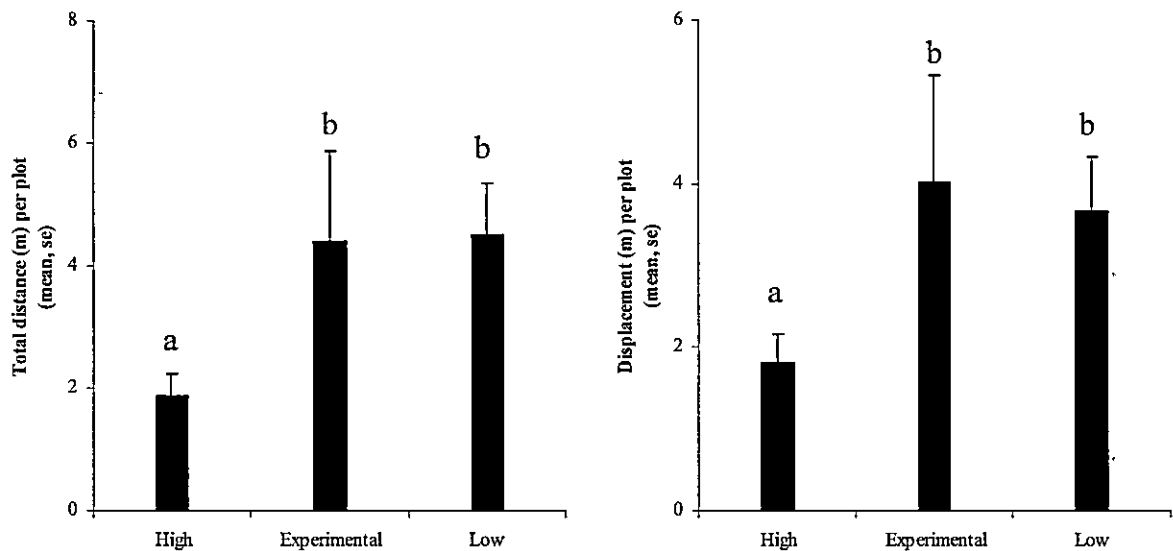


Figure 3. Movement of *C. chilensis* in High, Experimental and Low understory cover pine plots estimated by visual tracking. Left, Total distance, and right, Displacement distance. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

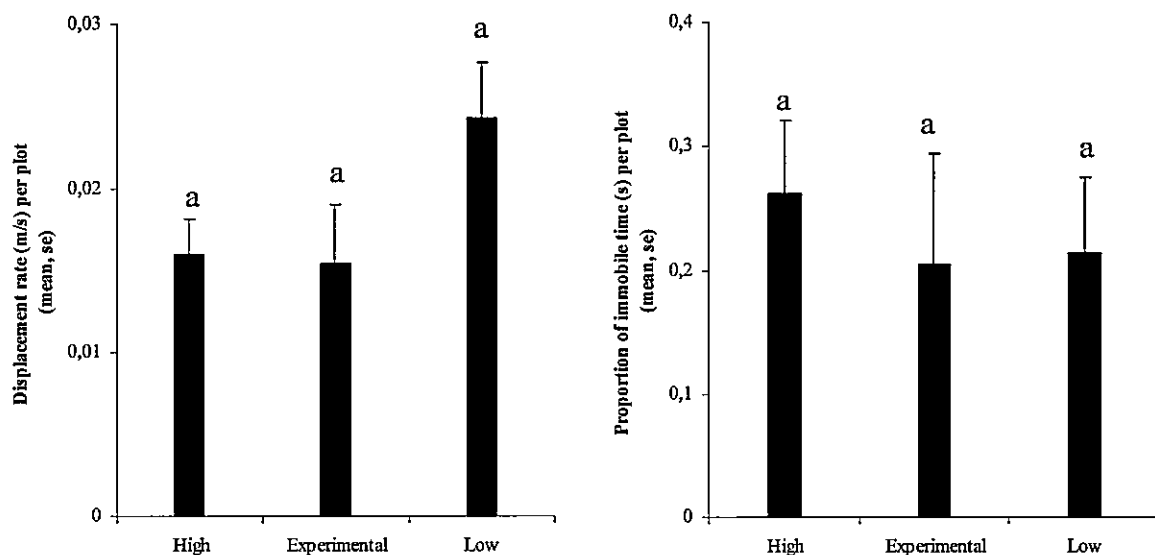


Figure 4. Movement of *C. chilensis* in High, Experimental and Low understory cover pine plots estimated by visual tracking. Left, Displacement rate, and right, Proportion of immobile time. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

On the other hand, *C. chilensis* traced significantly shorter steps in H compared with L plots, while step length in E plots was similar to H and L plots ($F_{2,73} = 8.28$, $P = 0.0006$; Fig. 5). However, turning angles were no significantly different between pine plots, with external angle values less than 45° in all treatments ($F_{2,55} = 1.66$, $P = 0.20$; Fig. 5), also they were concentrated in the same direction in each treatment (r : H plots = 0.88; L plot $s = 0.96$; E plots = 0.97).

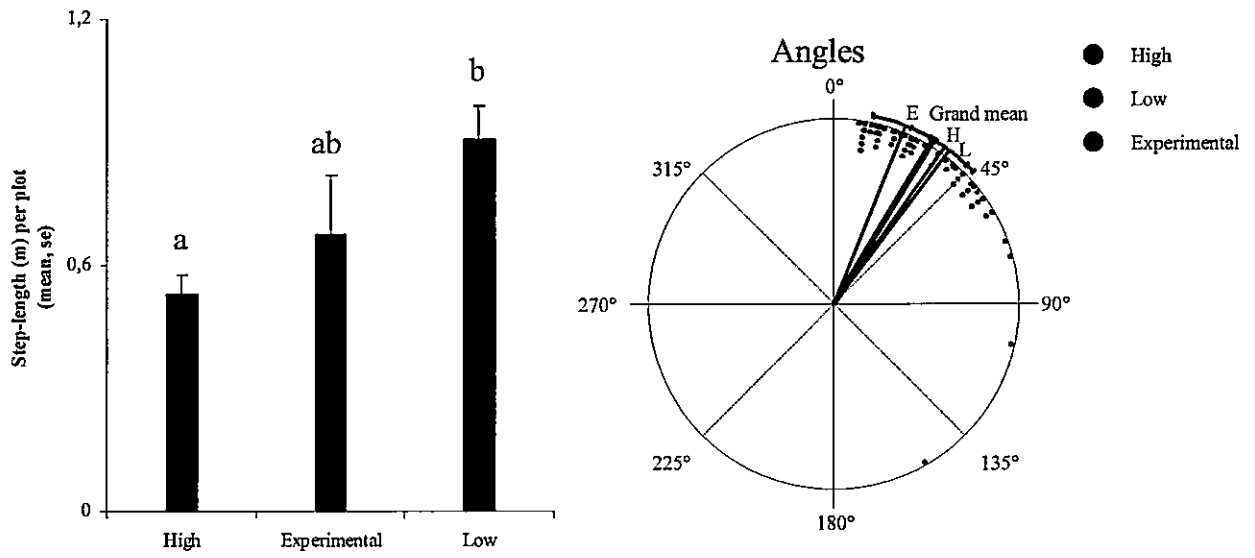


Figure 5. Movement of *C. chilensis* in High, Experimental and Low understory cover pine plots estimated by visual tracking. Left, Step length, and right, Turning angle, letters represent the type of plot and colored dots indicate the mean angle of a trail in each treatment. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

Probability of edge crossing

The proportion of individuals crossing understory edges significantly differed between treatments ($\chi^2_3 = 23.76$, $P < 0.001$; Table 1). The proportion of individuals crossing the edge in High-High, Low-Low and High-Low treatments, did not differ significantly (Table 2). But, a significantly higher proportion of individuals crossed in Low-High treatment (Table 2). Also, Low-High treatment had a significantly higher proportion of individuals crossing the edge compared to High-High and Low-Low treatments (Table 2).

Table 1. Results of the edge crossing experiments carried out in enclosure plots. N: number of released individuals.

| Edge | N | Individuals crossing |
|-----------|----|----------------------|
| High-High | 40 | 10 |
| Low-Low | 40 | 7 |
| Low-High | 40 | 22 |
| High-Low | 40 | 4 |

Table 2. Results of post hoc comparisons of the edge crossing experiments carried out in enclosure plots.

| Comparisons | $ P_i - P_j $ | Critical Value |
|------------------------|---------------|----------------|
| High-High and Low-Low | 0.075 | 0.255 |
| High-High and High-Low | 0.15 | 0.233 |
| High-High and Low-High | 0.3 | 0.291 |
| Low-Low and High-Low | 0.075 | 0.214 |
| Low-Low and Low-High | 0.375 | 0.277 |
| High-Low and Low-High | 0.45 | 0.257 |

Ceroglossus chilensis survival

There was a marginal non-significant effect of the understory cover treatment on the survival of *C. chilensis* ($F_{2,222} = 2.89$, $P = 0.06$), with ground-beetles surviving more in H than in L plots, while E plots had a survival similar to H and L plots (H: 0.55 ± 0.03 ; L: 0.48 ± 0.04 ; E: 0.52 ± 0.06). When comparing the survival between covered and uncovered cages, *C. chilensis* survived significantly more in those covered (Covered: 0.63 ± 0.03 ; Uncovered: 0.40 ± 0.03), independently of understory cover in pine plots ($F_{1,222} = 13.00$, $P = 0.0004$). Also, there was a significant understory cover * lid interaction ($F_{2,222} = 3.85$, $P = 0.02$), with the lowest proportion of days survived in the uncovered cages located in L plots compared to the H and E plots, and also compared to the covered cages in all cover treatments (Fig. 6).

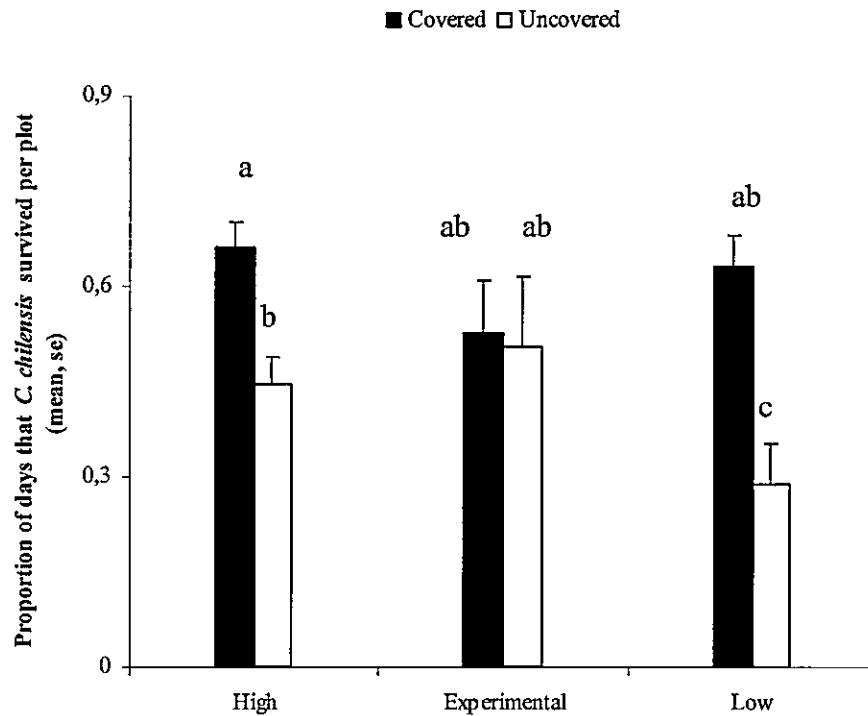


Figure 6. Proportion of days that *C. chilensis* survived in High, Experimental and Low understory cover plots, between May 2010 and December 2011 for High and Low treatments, and between March 2011 and December 2011 for Experimental treatment. Each pine plot had one covered and one uncovered container. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

Temperature and relative humidity were significantly affected by understory cover (Temperature: $F_{2,70} = 6.27$, $P = 0.003$; Relative humidity: $F_{2,70} = 11.69$, $P < 0.001$) but not by the type of cage (Temperature: $F_{1,70} = 0.001$, $P = 0.97$; Relative humidity: $F_{1,70} = 2.38$, $P = 0.13$), with temperature being higher and relative humidity lower in L and E plots than in H, respectively (Fig. 7).

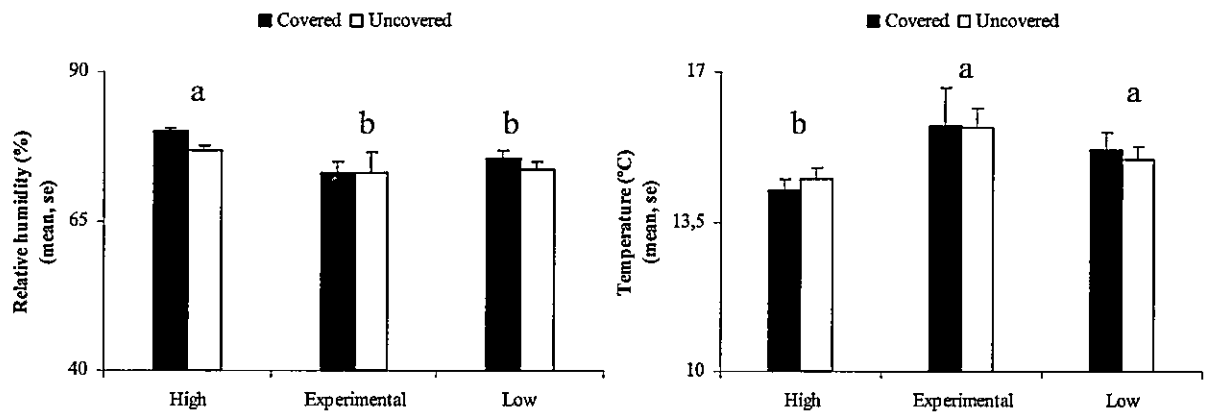


Figure 7. Microclimatic conditions in covered and uncovered containers in High, Experimental and Low understory cover pine plots, between August–December 2010 and July–December 2011. Left, Relative humidity, and right, Temperature. Letters represent Fisher LSD test for post-hoc comparisons, with different letters indicating significant differences ($p < 0.05$).

DISCUSSION



Ceroglossus chilensis was more abundant in forestry stands with dense understory cover compared to those with scarce understory development. Moreover, its abundance in pine plantations was determined by the presence of dense understory cover as our results demonstrated when the understory was experimentally removed. Several studies have documented that plantations can provide habitat for native plants and animals (see examples in Lindenmayer & Hobbs, 2004; Brockerhoff *et al.*, 2008; Felton *et al.*, 2010; Simonetti *et al.*, 2012), even for uncommon or threatened species (Brockerhoff *et al.*, 2008; Pawson *et al.*, 2010). Among invertebrates, carabids are also present in tree plantations (e.g., Magura *et al.*, 2003; Finch, 2005; Pawson *et al.*, 2009; Taboada *et al.*, 2010), including threatened or rare species (Barbaro *et al.*, 2005; Brockerhoff *et al.*, 2005). Further, they have been considered biological indicators to assess the effects of management practice of planted forests on biological diversity (see examples in Koivula & Niemelä, 2002; du Bus de Warnaffe & Lebrun, 2004; Pearce & Venier, 2006; Niemelä *et al.*, 2007; Fuller *et al.*, 2008). One practice is fostering or passively allowed the development of understory or multiple vegetation strata which enhance species richness as it might provide food and shelter, and hence better conditions for survival (e.g., Lindenmayer and Hobbs; 2004). Thus, for some ground-beetles, these human-modified landscapes can become surrogate habitats (Berndt *et al.*, 2008; Pawson *et al.*, 2008; Oxbrough *et al.*, 2010). In *C. chilensis*, even though previous research have documented its presence in pine plantations (Grez *et al.*, 2003; Briones & Jerez, 2007; Henríquez *et al.*, 2009) and evaluated aspects of its morphology (Henríquez *et al.*, 2009;

Benítez *et al.*, 2010; Benítez, 2013), this is the first study about this carabid which experimentally demonstrate that a management practice (i.e., the development of native understory cover) favored its abundance, suggesting that pine plantations with dense understory development act as surrogate habitat for *C. chilensis*. This is not an isolated case since vertebrate species are also enhanced by the occurrence of complex understory vegetation in pine plantations (Estades *et al.* 2012).

Regarding putative factors that might explain the higher abundance of *C. chilensis* in pine plantations with a developed understory cover, although invertebrate abundance was similar in forest plantations with high and low understory development, contrary to our expectations, prey biomass was higher in low understory sites, probably because of the greater abundance of larger prey in these plantations such as the red cricket *Cratomelus sp.* (Orthoptera: Grillidae). Thus, prey availability seems not to be a constraint for *C. chilensis* in low understory pine plantations.

Movement of *C. chilensis* in pine plantations had some similarities to those observed in other organisms that move in the matrix of fragmented landscapes (e.g., Haynes & Cronin, 2006; Hawkes, 2009 and references therein). Generally, matrix has been considered as an inhospitable or non-habitat (Ricketts, 2001), hence it has been expected that the movement therein should be faster and more linear than within the remnants of original habitat (Hawkes, 2009 and references therein; Kuefler *et al.*, 2010). However, movement in the matrix can be also affected by its structure or complexity (Ricketts, 2001; Goodwin & Fahrig, 2002; Bowler & Benton, 2005; Fahrig, 2007; Prevedello *et al.*, 2010), thus in a structurally complex matrix, animals may move as similar way as they do in patches of original habitat, making matrix less inhospitable for them,

contributing to landscape connectivity and population persistence. In this study, significant differences in the movement of *C. chilensis* were observed in all variables related to distances (i.e., total distance, displacement and step-length), being higher in plantations with scarce or removed understory than in those with high understory density, although they moved at the same speed and had a rather linear movement (i.e., turning angles less than 45°) in all pine plantations, independently of understory cover. A previous study in this species also demonstrated that it had higher step-lengths and displacement rates in pine plantations compared to native forest remnants (Donoso, 2011), but this study did not consider the differences in understory cover among plantations. Also, *C. chilensis* showed significant preference for dense understory plantations as demonstrated by the edge crossing probability experiments. Thus, our results suggest that its abundance in pine planted forests is modulated by its movement behavior.

Additionally, the (marginally) higher survival of this carabid in sites with high understory cover suggests that the understory protects *C. chilensis* individuals from death, particularly from predation, because of the higher mortality observed in uncovered containers in the low understory cover plantations compared to high understory cover plantations. But, contrary to our expectations, predation risk was similar in plantations with dense and experimentally removed understory. Although, carabid beetles have several antipredator defenses (Lövei & Sunderland, 1996), including chemical defenses as in *C. chilensis*, predation is an important mortality factor for adults (Lövei & Sunderland, 1996; McGuinness, 2007). The most probable predators feeding upon *C. chilensis* are small mammals, birds and foxes (Silva-Rodríguez *et al.*,

2010; Donoso, 2011). All of them have large home-ranges, greater than the 40 x 40 m plots where understory was experimentally removed, which were embedded in a stand with high understory cover. Therefore, quite probably these predators were not able to perceive these stands as low understory plantations.

The significant differences in microclimatic conditions among plantations indicate that the presence of a dense understory therein generates a distinct microclimate registering lower temperatures and higher relative humidity in these plantations. On the other hand, microclimatic condition effects of cages on survival were discarded since neither temperature nor relative humidity differed between them.

In a world where the increasing expansion of the forestry sector is threatening native forests and biodiversity, the challenge of plantations also fulfilling an active role in biodiversity conservation has raised (Hartley, 2002; Cummings & Reid, 2008; Brockerhoff *et al.*, 2008; Perrings *et al.*, 2010). It is nowadays widely recognized that they could contribute to enhance biodiversity within landscapes through complementing or supplementing species habitat or resources (Ries & Sisk, 2004), and maintaining landscape connectivity. Thus, a management allowing the presence of a dense understory composed of native species can help to achieve this role.

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