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Accompanying vegetation in young *Pinus radiata* plantations enhances recolonization by *Ceroglossus chilensis* (Coleoptera: Carabidae) after clearcutting

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Abstract The replacement of native forests by *Pinus radiata* plantations modifies habitat availability and quality for wildlife, constituting a threat to species survival. However, the presence of understory in mature pine plantations minimizes the negative impacts of native forest replacement, rendering a secondary habitat for wildlife. Whether forest-dwelling species recolonize clear-felled areas pending on the spontaneous development of accompanying vegetation growing after harvesting is yet to be assessed. In this context, we analyze the abundance, movement and habitat selection of the endemic ground beetle *Ceroglossus chilensis* (Coleoptera: Carabidae) in an anthropic forest landscape consisting of native forest remnants, adult pine plantations (> 20 years) with a well-developed understory, and young (1–2 years) pine plantations with varying degrees of accompanying vegetation development. Particularly, we analyze the likelihood that *C. chilensis* would recolonize young pine plantations depending on the presence (> 70% cover) or the absence (< 20% cover) of this accompanying vegetation. *C. chilensis* shows a greater probability of selecting habitats with understory (pine plantations and native forest) and young plantations with accompanying vegetation (future understory) than habitats without such vegetation. Movement of *C. chilensis* also favors their permanence in habitats with understory vegetation, coinciding with higher abundances than in young pine plantations devoid of accompanying vegetation. Hence, the effect of clearcutting could be mitigated by allowing the development of accompanying vegetation into a future understory, which facilitates the recolonization of pine plantations and its use as secondary habitat for wildlife.

Keywords Carabids · Ground beetles · Habitat fragmentation · Understory · Forest landscape

Introduction

The increasing demand of wood products has resulted in a continued expansion of the forest industry worldwide (FAO 2012). Forestry plantations are also facing growing environmental requirements, as expressed in Aichi's targets. Plantations are expected to be multipurpose, as they ought to engage in the conservation of biological diversity in addition to providing goods and services (UN 2010). This goal might be challenging in plantations based on monocultures of exotic species, such as Monterey pine (*Pinus radiata*). Monoculture plantations tend to hold impoverished faunal assemblages compared to the native forest they replace, therefore posing a threat to biodiversity (see Estades et al. 2012 for a review). Monterey pine, originally from California (Mead 2013), is widely grown in several regions of the world, currently covering roughly 4 million ha in Australia, New Zealand, Spain and Chile, accounting for a third of productive plantations worldwide (Mead 2013). However, if Monterey pine plantations exhibit a developed understory, they can hold several native and even endangered species,

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therefore reducing the impact upon native fauna and contributing to satisfy Aichi's targets (Estades et al. 2012; Simonetti et al. 2013; Cerda et al. 2015).

Despite a developed understory potentially acting as a solution, pine plantations are harvested through clearcutting, a practice that removes all standing trees, further changing the habitat for the remnant biota inhabiting adult plantations and rendering logged areas unsuitable for forest-dwelling species (Brockerhoff et al. 2008; Pawson et al. 2006, 2011). In fact, faunal assemblages undergo changes in richness, composition and abundance following the clearcutting process (Pawson et al. 2009). Species richness increases in a transient fashion, due to the colonization of open-habitat as well as early successional and ruderal species that colonize exploited open areas, but the overall species response is taxon-dependent (Pawson et al. 2006; Simonetti and Estades 2015). Forest-dwellers, for instance, might suffer high mortality and emigration rates after clearcutting, leading to reduced species richness and abundance in clear-fell areas (Pawson et al. 2006; Simonetti and Estades 2015). Clearcut areas might then act as barriers for forest-dwellers, hampering their movement across the forested landscape. A key issue to fulfill Aichi's targets is the need to unravel the factors enabling forest-dwelling species to recolonize clear-fell stands and thus reduce the isolation of individuals thriving in tree bearing stands. However, recolonization of clearcut areas of monoculture plantations by native forest-dwelling species has mostly been ignored, possible due to a widely held view that considers these plantations as biological deserts (e.g., Sheil et al. 2010).

Rewilding commercial plantations of Monterey pine in Chile is a case in point. The Chestnut-throated Huet–Huet (*Pteroptochos castaneus*), an endemic bird, is reluctant to leave adult plantations or native forest remnants for harvested areas, but its movements are positively influenced by the spontaneous development of accompanying vegetation in clearcut stands (Ramirez-Collio et al. 2017). Hence, allowing the growth of accompanying vegetation in clearcuts, which ultimately develop into understory as the canopy closes, might enhance these areas as habitat for native fauna, providing food and shelter. In more complex habitats with accompanying vegetation, individuals usually have a low tendency to move and move slowly, displaying short step lengths, tortuous paths, and frequent turns, all movements that would enhance their permanence in these habitats (Goodwin and Fahrig 2002). Whether this is a general phenomenon is yet to be assessed.

Ceroglossus chilensis (Coleoptera: Carabidae) is an endemic ground-dwelling beetle, approximately 27 mm long (0.68 ± 0.005 g), which is more abundant during the fall (Henríquez et al. 2009; Cerda et al. 2015). It is a diurnal predator, feeding on insects but also carrion and fruits, while moving through leaf litter (Jiroux 1996). This species is considered a forest specialist that also inhabits adult pine plantations with well-developed understory (Donoso 2011; Cerda et al. 2015), where it exhibits slow and tortuous movements, allowing for more time to remain in them. This behavior suggests plantations with understory are a favorable habitat. In contrast, *C. chilensis* exhibits longer and straighter movements in plantations without a developed understory, which suggests these plantations represent relatively low habitat quality (Cerda et al. 2015; see also Baars 1979). In order to determine if recolonization of clear-felled areas depends on the development of vegetation other than planted trees, we test if the abundance, movement and habitat selection of *C. chilensis* can be explained by the presence of accompanying vegetation in the different habitats that compose the forested landscape of central Chile. First, we compared the abundance of *C. chilensis* in native forest, adult pine plantations and clearcut areas with and without accompanying vegetation. We expected a higher abundance of *C. chilensis* in habitats with well-developed accompanying vegetation than in clearcuts without it. Second, we studied the movement of experimentally released individuals in these four types of habitats. We expected movements to be slower and more tortuous in stands with well-developed accompanying vegetation than in stands without it. Finally, we experimentally assessed whether the selection of clearcuts by *C. chilensis* depends on the presence of accompanying vegetation, by calculating the probability of animals entering clearcuts with accompanying vegetation versus those without. We expected a higher probability of *C. chilensis* entering clearcuts with developed accompanying vegetation. If beetle abundance in clearcut areas is related to vegetation structure, manipulating the remaining vegetation after logging and in early-stage plantations might function as a management tool by enhancing recolonization of forest-dwelling species in clearcut regimes.

Materials and methods

Study site

Monterey pine accounts for 68% of forestry plantations in Chile, nears 1.9 million ha planted and contributes towards 3% of Chilean GNP (http://www.corma.cl). Pine plantations are located in the region containing the highest levels of species richness and endemism, and is regarded as a biodiversity hotspot (Mittermeier et al. 2011). We carried out our study in Tregualemu (72°43′55,59″O–35°59′37.12″S to 72°40′46,34″O–35°58′5.27″S), an area where remnants of native temperate forests, including the Los Queules National Reserve, are surrounded by commercial pine plantations of different ages, which cover 48% of the area (Acosta-Jamett and Simonetti 2004) (Online resource Fig. S1). Pine height

ranges between 0.5 m (< 1 year old) and 28 m (20 years old). We chose the following four types of habitats for use in sampling and experimental plots: adult pine plantations (Fig. 1a), native forests (Fig. 1b), young pine plantations with accompanying vegetation (Fig. 1c), and young pine plantations without accompanying vegetation (Fig. 1d). Our criteria for determining presence or absence of accompanying vegetation and plot selection consisted on vegetation cover thresholds of more than 70% (native forest, adult plantation, and young plantations with accompanying vegetation) and less than 20% (young plantations without accompanying vegetation) of accompanying vegetation aside from planted trees. For each habitat type we selected six 40×40 m plots interspersed in the landscape separated by at least 100 m.

Ceroglossus chilensis abundance

We assessed the abundance of *C. chilensis* between October 2014 and July 2015 by determining the cumulative number of individuals captured in nine Barber traps per plot. Traps operated four consecutive days per month and consisted of plastic jars (11 cm diameter and 8 cm depth) containing water and detergent as a killing-preserving solution, buried at ground level, and located 10 m apart within a 30×30 m grid of 3×3 traps. We regarded the total number of captured individuals in all nine traps as a single sample.

### *Ceroglossus chilensis* movement and habitat selection

We assessed movement and habitat selection of *C. chilensis* from April to June 2015, the period when their populations are more abundant and active (Henríquez et al. 2009; Cerda et al. 2015). We evaluated movement by direct observation of 40 individual trails per habitat type (160 total trails using always different individuals) by visual tracking in a randomly chosen subset of the plots used for determining *C. chilensis* abundance (four of each type, see Online resource S1). We avoided concurrent sampling times to avoid interference. Beetles used in these observations were captured through live-pitfall-trapping in forest remnants outside our experimental plots where they are abundant (Grez 2005;

Fig. 2 Example of an exclusion installed between native forest and young pine plantation without accompanying vegetation, 5 m into each habitat and 3 m wide. (Color figure online)

Henríquez et al. 2009). Each individual was marked with a bee tag in the pronotum, released in the center of a plot, allowed to move for 5 min prior to recording its movement, and then tracked for 30 min, marking its position with a stick every 30 s. At the end of the visual tracking, the trail was marked with a rope linking the sticks and drawn on paper, estimating the mean step-length (distance traveled in 30 s), net displacement (straight-line distance between the initial and endpoint of the path), total distance (sum of all step lengths), time spent moving, and mean turning angles (angle between the new and the last movement direction as a measurement of tortuosity) (Goodwin and Fahrig 2002; Cerda et al. 2015). Up to four different individuals were followed per day in different plots, with all observations performed during daytime (11:00 a.m. to 5:00 p.m.) on warm days.

We experimentally assessed habitat selection following a similar protocol used by Cerda et al. (2015). We set four 10×3 m enclosures delimited by plastic barriers and shared between two neighboring habitats, 5 m within each habitat type (Fig. 2, see Online resource S1 for the distribution of these enclosures). Two enclosures
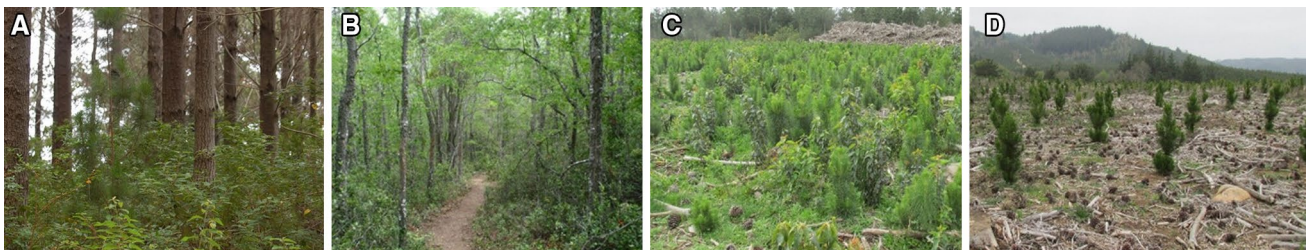
Fig. 1 Treatment plots. **a** adult pine plantations with accompanying vegetation; **b** native forest with accompanying vegetation; **c** young pine plantations with accompanying vegetation; **d** young pine plantations without accompanying vegetation. (Color figure online)

were located on the edge of native forests with young pine plantations with accompanying vegetation, and two other enclosures were shared between adult pine plantations and young pine plantations with accompanying vegetation. We installed 25 live-pitfall traps at each extreme of an enclosure. We then released 20 marked individuals per trial at the edge between habitats in each enclosure. After 48 h, we assessed the frequency of individuals captured in each habitat. We repeated this experiment 14 times in both types of edges, always using different marked individuals. Afterwards, we cut accompanying vegetation from young pine plantations and repeated the experiments 14 times, with 20 different individuals each time. This protocol allowed us to compare habitat selection probability based on the presence of accompanying vegetation in young pine plantations and type of adjacent habitat.

Data analysis

To test for differences in the abundance of *C. chilensis* between habitat types, we used a generalized linear model (GLM) with a negative binomial error structure and log link function, followed by Tukey's multiple comparisons test. We also assessed differences in net displacement, total distance, time spent moving and mean step-length between habitat types with GLMs, employing a gamma distributed error structure and log link function, again followed by Tukey's multiple comparison test. To test for differences in tortuousness, we compared mean turning angles between groups of individuals released in each habitat type with a Watson–Williams *F* test. This statitic tests for homogeneity of means between groups assuming a Von-Misis distribution, employing the same *F* statistic as Fisher's ratio commonly used in linear statistics, wherein the associated null hypothesis is that mean angles do not differ. We performed all circular statistics in Oriana 4.0 (Kovach Computing Services).

To assess habitat selection, we constructed a GLM with a binomial error structure and logit link function, and considered the frequency of *C. chilensis* captured in each habitat type (804 captured individuals from a total number of 1120 released beetles) as the dependent variable. The type of habitat adjacent to young pine plantations (adult pine plantations or native forest) and the presence or absence of accompanying vegetation in young pine plantations were considered as separate independent variables. We estimated the odds and probability of selecting young pine plantations from GLM parameter estimates. Since estimates are in logits, we calculated odds by computing the exponential function of the estimates and subsequently calculated probability as p = odds/1 − odds. We performed all GLM analyses using R ver.3.4.1 (R Core Team 2017).

Results

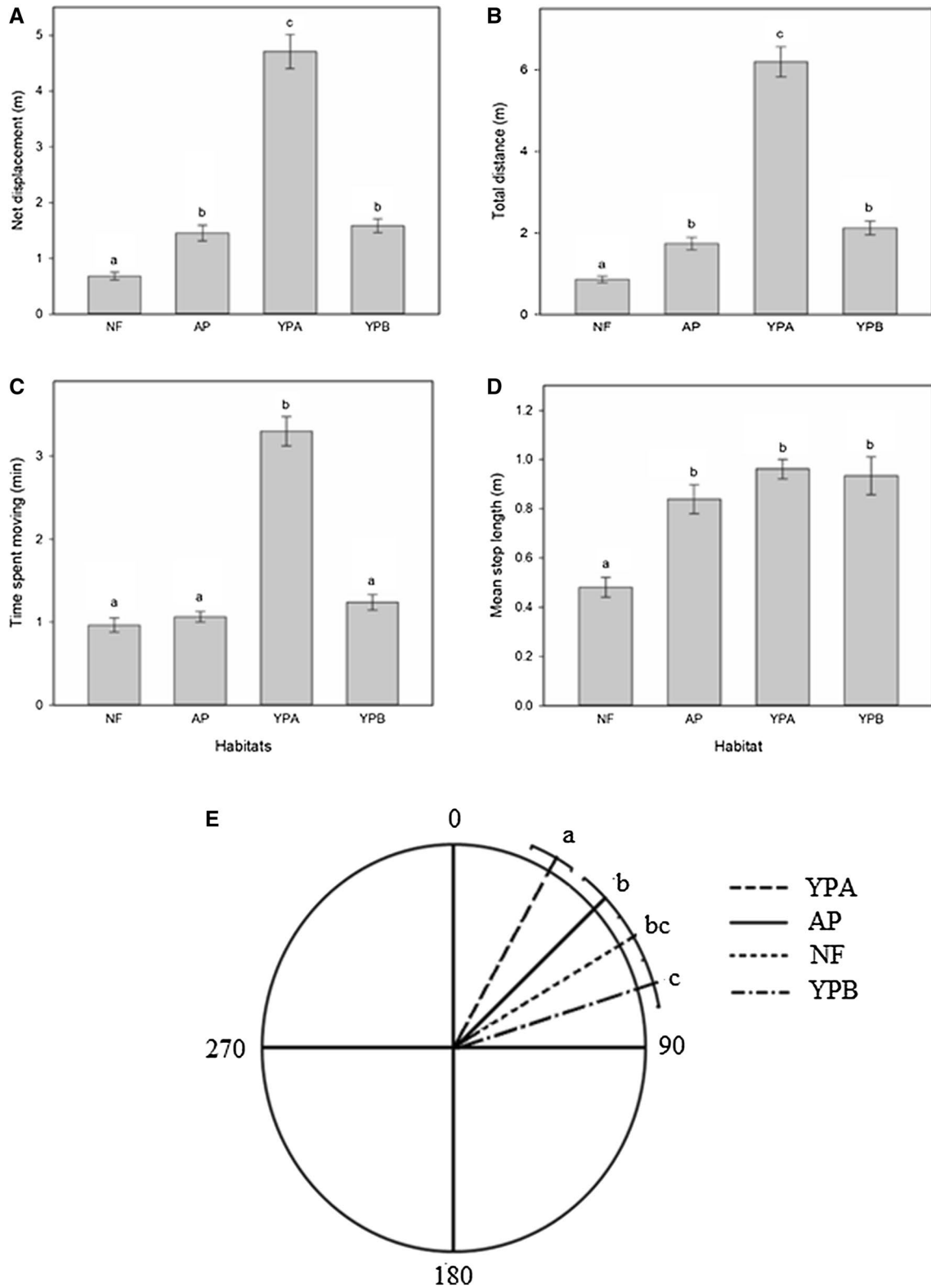### *Ceroglossus chilensis* abundance

Out of 201 individuals captured, the average abundance of *C. chilensis* was four times higher in native forests than adult plantations. Similarly, abundance in adult pine plantations and young pine plantations with accompanying vegetation was twice the amount found in young pine plantations without accompanying vegetation, although not statistically different (Fig. 3, Online resource Tables S1, S2). The fitted model (GLM: $\chi^2 = 26.407$, DF = 20, goodness of fit = 0.153) indicates that native forests and young plantations without accompanying vegetation have a significant effect on the abundance of *C. chilensis* (Online resource Table S1). However multiple comparisons reveal that only native forests boast higher abundances, while all pine plantations, regardless of accompanying vegetation, hold similar amounts of individuals (Online resource Table S2).

Ceroglossus chilensis movement

All movement variables varied with habitat type (Online resource Table S3). Net displacement was six times higher in young pine plantations without accompanying vegetation than in native forests, and three times higher than in adult pine plantations and young pine plantations with accompanying vegetation (GLM: $\chi^2 = 51.753$, DF = 156, dispersion parameter = 0.290, goodness of fit = 0.106; Fig. 4a, Online resource Table S4). Similarly, total distance was seven times higher in young pine plantations
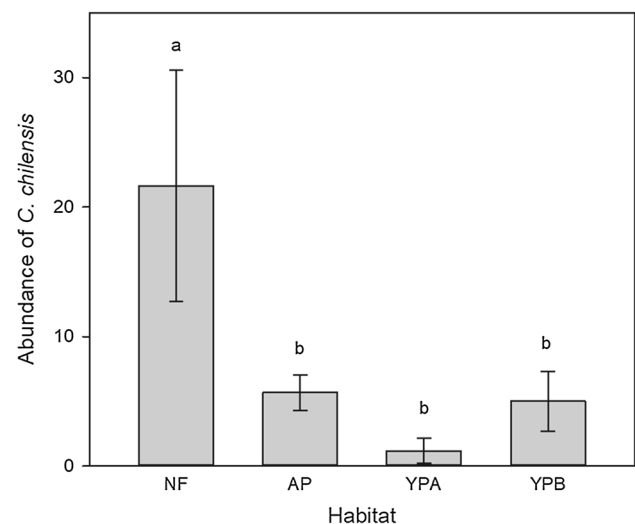
Fig. 3 *Ceroglossus chilensis* abundance in native forest (NF), adult pine plantation (AP) and young pine plantations without (YPA) and with (YPB) accompanying vegetation. Different letters above bars denote significant differences (Tukey, p < 0.05)

Fig. 4 Movement of *Ceroglossus chilensis* in native forest (NF), adult pine plantations (AP), young pine plantations with accompanying vegetation (YPB) and young pine plantations without accompanying vegetation plots (YPA), estimated by visual tracking. **a** Net displacement (mean ± SE), **b** total distance (mean ± SE), **c** time spent moving (mean ± SE), **d** mean step length (mean ± SE) and **e** mean turning angle (mean ± SE). Results of post hoc comparisons are represented by different letters indicating significant differences (Tukey, p < 0.05) in each movement measure among habitats

without accompanying vegetation than in native forests, and three times higher than in adult pine plantations and young pine plantations with accompanying vegetation (GLM: $\chi^2 = 49.917$, DF = 156, dispersion parameter = 0.271, goodness of fit = 0.063; Fig. 4b, Online resource Table S5). Time spent moving was three times higher in young pine plantations without accompanying vegetation than in all other habitats (GLM: $\chi^2 = 31.866$, DF = 156, dispersion parameter = 0.200, goodness of fit = 0.409; Fig. 4c, Online resource Table S6), and mean step length was half in native forests than in all other habitats (GLM: $\chi^2 = 34.388$, DF = 156, dispersion parameter = 0.203, goodness of fit = 0.222; Fig. 4d, Online resource Table S7). On the other hand, mean turning angles were significantly lower ($<45°$) in young pine plantations without accompanying vegetation than in all other habitats ($F_{(3, 156)} = 14.29$, p < 0.001; Fig. 4e).

Ceroglossus chilensis habitat selection

From a total of 1120 individuals released, 804 (72%) were recaptured after 48 h, of which 62% were collected in native forests and adult plantations, 25% in young pine plantations with accompanying vegetation, and 13% in young pine plantations without accompanying vegetation. We found that the presence of accompanying vegetation increases the likelihood of young plantations being selected by 2.7 times, regardless of the kind of adjacent habitat (native forest or adult pine plantations) (GLM: $\chi^2 = 24.55$, DF = 53, goodness of fit = 0.99; Tables 1, 2). In fact, when selecting young pine plantations, individuals prefer that accompanying vegetation be present rather than absent 72.8% of the time (Table 2).

Table 1 Estimated regression coefficients (β), standard errors (± SE), z values and p values for each parameter from generalized linear model explaining habitat selection by *C. chilensis* ($\chi^2 = 24.55$, DF = 53, goodness of fit = 0.999)

Parameter	β	±SE	z	p value
Intercept	−1.049	0.136	−7.698	<0.001
Plantation (native forest)	−0.002	0.150	−0.014	0.989
Accompanying vegetation presence (absence)	0.985	0.152	6.493	<0.001

Discussion

Rewilding clear-fell stands with forest-dwelling species would ease offsetting the impacts upon biodiversity carried out by replacing native forests by monospecific plantations and their harvesting through clearcutting. Plantations of *P. radiata* in New Zealand are known to act as surrogate habitats for carabids and other beetles (Brockerhoff et al. 2005; Berndt et al. 2008; Pawson et al. 2008). Similarly, in Chilean plantations, *C. chilensis* inhabits adult pine plantations, but particularly those stands that hold abundant understory (Cerda et al. 2015). Here, we show that the same situation occurs in clear-felled areas, where spontaneously growing vegetation enhances the quality of clear-cut habitats for, and hence the occurrence of *C. chilensis*. Demonstrably, tested individuals display turning angles, net displacement, total distance and time spent moving in clear-fell stands with accompanying vegetation more similar to native forest plots and adult plantations with understory than in clear-fell stands without accompanying vegetation, despite that movement was expected to be higher in good quality habitats (Jonsen and Taylor 2000; Yang 2000; Goodwin and Fahrig 2002). Additionally, the lack of discrimination when entering a given habitat when its neighboring habitat holds accompanying vegetation, and the reluctance to enter clear-felled areas without accompanying vegetation reinforce the contention that the presence of dense vegetation at low heights improves habitat quality for *C. chilensis*. Nevertheless, the occurrence of this vegetation in clear-cuts reduces, but does not eliminate the decline in abundance of *C. chilensis* when replacing native forests with plantations.

Accompanying vegetation might provide shelter from predators and suitable microclimate for *C. chilensis* (Donoso 2011; Cerda et al. 2015). Predation is a significant mortality source for carabids, including *C. chilensis* (Lövei and Sunderland 1996; Cerda et al. 2015). The most probable predators feeding on *C. chilensis* are small mammals, birds and foxes (Cerda et al. 2015 and references therein), which are common in these forested landscapes (Estades et al. 2012). However, predation of *C. chilensis* is lower in stands of adult plantations with a well-developed understory (Cerda et al. 2015), hence selecting clear-fell stands with more cover could likewise reduce predation risks. On the other hand, carabids are sensitive to abiotic conditions, like temperature and humidity (Kotze et al. 2011). Plantation stands with

Table 2 Odds ratio of habitat selection (calculated between native forest and adult plantation probabilities) and accompanying vegetation (calculated between present and absent vegetation), with respective selection probabilities by *C. chilensis*

Predictor (control)	Odds ratio	CI low (2.5%)	CI high (97.5%)	Probability
Plantation (native forest)	1.002	0.747	1.344	0.500
Vegetation presence (absence)	2.678	1.994	3.615	0.728

dense understory, like young pine plantations with accompanying vegetation, have more stable mild temperatures and higher humidity than those without this vegetation (Donoso 2011), which may improve habitat quality for *C. chilensis*. The role of other concurring factors, such as food availability, are yet to be assessed.

The mitigating effect of accompanying vegetation in pine plantations is not restricted to *C. chilensis*. Diversity and abundance of a wide array of taxa, ranging from insects to birds and mammals are higher in plantations with understory vegetation in Chile, New Zealand and Australia (Lindenmayer and Hobbs 2004; Berndt et al. 2008; Estades et al. 2012; Simonetti et al. 2013). Hence, managing plantations in order to retain accompanying vegetation could contribute to fulfilling the increasing environmental requirements toward plantations. As expected by Aichi's targets, lands dedicated to forestry should both produce goods, such as timber, and simultaneously ensure the conservation of biodiversity. Albeit simple, enhancing this vegetation has a drawback, as it competes with planted seedlings the first 2 years of growth. After clearcutting, site preparation management involves the use of herbicides to eliminate vegetation that can compete with planted seedlings, a widespread practice (Wagner et al. 2006). The elimination of such plant species during the first 2–3 years, bound to ensure seedling growth and stand productivity, precludes the initial growth of the vegetation that will comprise the understory of plantations once the canopy closes. Allowing the growth of accompanying vegetation implies controlling herbicide application, reducing its use to the minimum feasible. Concurrently, forestry practices might also consider the retention of plantation debris such as logs and dead branches. These remains could provide predator and microclimatic refuges that enhance the presence of *C. chilensis* and other ground level species, such as small mammals and saproxylic beetles, whose densities are dependent of the stage of wood decay (Saavedra and Simonetti 2005; Fierro et al. 2017). Without the structural complexity given by accompanying vegetation and woody debris, clear-cut areas might act as a barrier to these forest-dwellers, hampering their movement across the forested landscape. Populations become fragmented, facing smaller, more isolated and "hard edge" patches surrounded by a hostile matrix. In such situation, dispersal as a by-product of routine movements when searching for resources, mates or shelter, enhances recolonization of areas disturbed by clearcutting, being then a key process determining the connectivity and survival of the resulting population (Van Dyck and Baguette 2005; Ranius 2006). Therefore, modifying the traditional clearcutting system in Central Chile into a forest management that enhances the retention or development of understory vegetation and woody debris may enhance the survival of *C. chilensis* and other forest-dwelling species in forest landscapes fragmented by pine plantations. Our findings reinforce the assertion that native vegetation within plantations is not a nuisance, but instead has conservation value which should be managed to meet international biodiversity targets.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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