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Ecological Research

ISSN 0912-3814

Ecol Res
DOI 10.1007/s11284-015-1302-2

Springer

Ecol Res
DOI 10.1007/s11284-015-1302-2

ORIGINAL ARTICLE

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Received: 23 October 2014 / Accepted: 25 August 2015

Abstract Understanding the responses of natural communities to disturbances remains a challenging task in ecology. In northwestern Patagonia, the most important disturbances are fire and introduced ungulates. Although these disturbances have been present in this region since late eighteen century, their effects on arthropods diversity have been poorly studied. Here, we examined the short-term response of ground beetles (Coleoptera) to fire (burnt and unburnt) in browsed forests and to cattle browsing (cattle and no cattle) in post-fire forests. We collected ground beetles with pitfall traps and estimated beetle abundance, species richness, assemblage composition, abundance of trophic guilds and beetle characteristic species, and measured some habitat parameters. We found that burnt browsed forest had lower diversity and different assemblage composition than unburnt forest. Beetle abundance, assemblage composition and abundance of trophic guilds were similar in post-fire forests with and without cattle browsing. Conversely, beetle species richness was higher in cattle than in no cattle forests. Fire had a strong negative effect on beetle diversity probably by its effect changing habitat structure. Whereas fire had a homogenizing influence on beetle diversity with and without cattle, at small-spatial scales, browsing of cattle probably generate habitat heterogeneity enhancing beetle richness. The implementation of policies aimed to reduce the risk of fire and to maintain low-moderate cattle pressure appears to be vital to conserve the beetle assemblage in the Patagonian region.

Electronic supplementary material The online version of this article (doi:10.1007/s11284-015-1302-2) contains supplementary material, which is available to authorized users.

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Keywords Andean forest · Coleoptera · Diversity · Introduced ungulates · Post-fire

Introduction

One of the greatest issues in contemporary ecology is to understand how disturbances will influence the assembly of communities and the functioning of ecosystems (Turner 2010). Disturbances are often defined as discrete events that disrupt ecosystem, community, or population structure and change resource availability, or the physical environment (White and Pickett 1985). Moreover, disturbances may differentially affect the abundance of species in distinctive trophic levels and can therefore alter the spatial patterns of species diversity and composition (Knight and Holt 2005). Thus, knowing the effects of disturbances on some composite values, like species diversity and ecosystem functioning, is a relevant issue to adequately suggest conservation management practices (Turner 2010).

In northwestern Patagonia, the two most important disturbances in forests and shrublands ecosystems are fire (Kitzberger and Veblen 1999; Veblen et al. 2003, 2011) and introduced ungulates (Veblen et al. 1992; Relva and Veblen 1998; Vázquez 2002; Relva et al. 2010). Fire, both natural and anthropogenic, has been the dominant disturbance determining plant community structure and landscape pattern (Veblen et al. 2003; 2011). For example, fire affected vegetation dynamics with consequences depending on spatial heterogeneity, vegetation type, abiotic conditions and human activities (Veblen et al. 2003; Mermoz et al. 2005; Paritsis et al. 2006). On the other hand, cattle (*Bos taurus*) were introduced by Europeans by the late eighteenth century (Veblen et al. 1992), and game animals such as red deer (*Cervus elaphus*) were introduced around 1904 (Jaksic et al. 2002). Currently they are the most widespread introduced ungulates in these forests (Navas 1987; Jaksic 1998). Introduced ungulates change the physiognomy of seedlings and recruits of dominant canopy trees (Veblen et al. 1992; Vázquez 2002; Vázquez & Simberloff 2003; Blackhall et al. 2008) and understory plants (Dimitri 1962; Veblen et al. 1992; Vázquez and Simberloff 2002; Barrios-Garcia et al. 2012), and disrupt plant-animal mutualisms (Vázquez and Simberloff 2004; Rodriguez-Cabal et al. 2013). Additionally, it is well recognized that introduced ungulates greatly affect post-fire regeneration in natural communities, modifying vegetation structure and composition, retarding the plant succession and growth (Raffaele and Veblen 2001; Blackhall et al. 2008; Raffaele et al. 2011; de Paz and Raffaele 2013) and facilitating the introduction of exotic species (Nuñez et al. 2008). Although in this region fire and introduced ungulates have been present since late eighteen century, their effects on arthropods diversity have been poorly studied.

Arthropods, the most diverse component of terrestrial ecosystems, are highly sensitive to changes in environmental conditions, which characterize them as good indicators of disturbance level (Orgeas and Andersen 2001; Gaspar et al. 2010). Beetles (Coleoptera) are by far one of the most diverse groups with more than 350,000 species in the world (Borror et al. 1992; New 2010). In Patagonian ecosystems ground beetles are diverse, abundant, with high levels of endemism (Morrone and Roig-Juñent 1995; Morrone and Coscarón 1998; Claps et al. 2008), taxonomically quite well known (Morrone and Roig-Juñent 1995), sensitive to environmental conditions (Sackmann and Farji-Brener 2006; Paritsis and Aizen 2008; Ruggiero et al. 2009), and have short generation times that provide a fine-grained view of ecological change (Rainio and Niemelä 2003; Work et al. 2008). Consequently, ground beetles are ideal organisms for the study of how fire and introduced ungulates disturbances affect diversity.

We examined the response of ground beetles (Coleoptera) to fire and introduced ungulates. In particular, we studied the effect of fire by comparison of burnt and unburnt areas in forest exposed to cattle browsing and the effect of cattle browsing in burnt forest by an exclusion experiment. We ask the following questions: (1) How fire in cattle browsed forest (burnt vs. unburnt), and (2) How ungulates in burnt forest (cattle vs. no cattle) affect ground beetle diversity and trophic guilds? (3) Are particular beetle species associated to each disturbance? and (4) Does exist a relationship between ground beetle assemblages and habitat parameters that may differ between disturbances?

Methods

Study site

We conducted the study in the Nahuel Huapi National Park, Patagonia, Argentina (40° 38′ S–71° 42′ W; 850 m above sea level) during the austral summers of 2006 and 2007. In this region, the mean annual temperature is 8º C and it ranges from a minimum of 2 °C (July) to a maximum of 23 ° C (January). Precipitation is concentrated mainly in autumn and winter as snow with an annual rainfall of 2000 mm (Barros et al. 1983). Native forest vegetation in the area belongs to the Subantartic biogeographical region (Cabrera 1994). Dominant trees are the evergreen southern-beech *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. The understory is dominated by Valdivian temperate rain forest species like bamboos, ferns, and evergreen angiosperm and conifer trees.

In January 1999 approximately 9 ha of the forest were affected by an intense wildfire that was quickly suppressed (Administración de Parques Nacionales 1999). The fire severity was high and it consumed the forest floor litter and killed the above-ground vegetation, leaving only dead standing trees. Post-fire stands of tall *Nothofagus* and/or *Austrocedrus* forests are characterized by very low regeneration due to the obligate seed reproduction, and are often replaced by shrublands with vigorous post-fire resprouting plant species (Kitzberger and Veblen 1999; Veblen et al. 2003). This burnt area is characterized by dead tree trunks standing or fallen with an understory dominated by shrubs such as *Ribes magellanicum*, *Aristotelia chilensis*, *Berberis darwinii*, *Vicia nigricans*, *Buddleja globosa*, the bamboo *Chusquea culeou* and herbaceous species like *Acaena pinnatifida*, *Oxalis valdiviensis* and *Ozmorhiza chilensis*.

In the near unburnt forest the tree species *N. dombeyi* and *A. chilensis* reach heights of 40 and 35 m, respectively. Dominant individuals of both species are 1–1.2 m diameter at breast height (dbh). Probably this forest was originated after severe fires in the early part of the 19th century (Veblen 1989), however is considered as unburnt site because was unaffected by fire for > 50 years (Suarez and Kitzberger 2010). The understory is dominated by shrubs like *Azara lanceolata*, *Desfontainea spinosa*, *Berberis darwinii*, *Aristotelia chilensis*, *Ribes magellanicum*, the bamboo *Chusquea culeou*, the climber *Vicia nigricans* and herbs like *Osmorhiza chilensis*, *Adenocaulon chilense*, and *Viola sp.*

The burnt and unburnt areas are both affected by browsing and trampling of cattle which are allowed to freely range over extensive areas. Currently, cattle (*Bos taurus*) is the most widespread exotic ungulate in these forests (Navas 1987; Lauria-Sorge and Romero 1999; Jaksic et al. 2002). The distance between burnt and unburnt study areas was 500 m, and they slightly differed in altitude; burnt area was at 890 m a. s. l. and unburnt at 840 m a. s. l.

Experimental design

In March 2002, we placed eight 25 × 25 m plots in a burnt forest positioned at least 50 m apart: four plots were fenced against cattle, 1.20 m height, and the other four were left unfenced. In unburnt forest we place four 25 × 25 m plots unfenced. In consequence, the three treatments were: cattle in burnt forest (Fire-Cattle = F-C) and cattle removal in burnt forest (Fire-No Cattle = F-NC) as parts of the cattle exclusion experiment, and unburnt forest with cattle browsing (No Fire-Cattle = NF-C). To study the fire effect in cattle browsed forest, we compare the treatments: burnt (F-C) vs. unburnt (NF-C) with cattle browsing. On the other hand, to study cattle effects in burnt forest, we compared the treatments: cattle (F-C) and no cattle (F-NC) in burnt forest.

Ground beetle sampling

Ground beetles were sampled by pitfall trapping during the austral summers (January to March) of 2006 and 2007. The summer season correspond to the most active period for arthropods in this temperate region. Traps were 500 ml plastic cups partially filled with water and propylene glycol (95:5) and buried flush with the ground. On each plot, we placed five pitfall traps arranged four in a square and one in the middle, and no closer than 5 m from each other (n = 60 traps). These traps were active in the field in three periods of five days each during each sampling period (January, February, and March) in the summers of 2006 and 2007. The contents of the 15 traps (i.e., five traps repeated in three consecutive months per plot) were pooled into one sample per plot per year, and sorted in the laboratory where we counted each individual and identified them to species or morphospecies. Voucher specimens are held at the Laboratorio Ecotono, Universidad Nacional del Comahue, Río Negro, Argentina.

Environmental variables

To better understand the possible mechanisms affecting beetle assemblages we recorded environmental variables. We measured: light availability in the first sampling season, air temperature and air humidity in the second sampling season. During both sampling seasons we measured understory vegetation cover, height, and species richness; and cattle browsing. All these variables may affect the diversity of beetles (Buddle et al. 2006; New 2010). Light availability was estimated by taking 6 hemispherical photographs in each plot. Photographs were taken at a height of 1 m above the ground using a leveled digital camera (CoolPix 995 digital camera, Nikon, Japan) aimed at the zenith, using a fish-eye lens with a 180° field of view (FCE8, Nikon). All photographs were taken in overcast weather to ensure homogeneous illumination and adequate canopy-sky contrast. Photographs were analyzed using software WinSCANOPY TM for hemispherical image analysis, estimating the parameter direct site factor (DSF) which is defined as the proportion of direct radiation received below the canopy as a fraction of that received above the canopy (Gómez et al. 2004). Air temperature (T°) and air relative humidity were recorded with 6 thermal and relative humidity sensors (HOBO ® TMC6-HA) installed from November 2006 to May 2007. Air temperature and relative humidity measurements were taken at 2-h intervals. We placed two sensors per treatment, which were located 1 m above the ground in shaded areas. Daily temperature and relative humidity were averaged per hour. We measured understory vegetation and degree of browsing at each 25 × 25 m plot using 20 permanent 2 m^2 subplots located systematically in two lines of 10 subplots. We recorded percentage cover of all vascular plant species and maximum heights of all woody and climbers species in each subplot. The total mean cover was estimated as the sum of each species cover; hence it could greater than 100 %. The degree of browsing by cattle was also estimated in each of those 20 subplots by observing the number of browsed branches on each woody and climber species. For each species was assigned a browsing rating ranging from 0 to 3, following Veblen et al. (1992) methodology (3 = heavy, most of the branches browsed, 2 = moderate, more than two branches browsed, 1 = light, one or two branches browsed and 0 = none, no evidence of browsing). Browsing rates per subplot were used to compute the mean browsing index (MBI) per plot, which is the summary statistic indicating the intensity of browsing on all species in the area sampled. MBI = Σ (BI for all species)/N, where BI is the estimation of the total amount of browsing on each species growing in the area sampled, and N is the number of subplots.

Data analysis

Beetle abundance, species richness, and assemblage composition were estimated for each plot. Beetle abundance was expressed as the total number of individuals per plot, disturbance type, and year. Species richness can be strongly influenced by differences in sample size, thus we estimated richness by a randomization process using EcoSim® (Gotelli and Entsminger 2001). Differences in abundance among samples were standardized by using rarefaction (Gotelli and Colwell 2001). Assemblage composition describes the collection of beetle species co-occurring per plot, disturbance type and year. Additionally, beetles were grouped into four trophic guilds: predators, herbivores, scavengers and fungivorous. Grouping species according to feeding is a useful way to show the ecological role of arthropods (Petchey and Gaston 2006). Beetle abundance of each trophic guild was expressed as the total number of individuals per plot, disturbance type, and year. To determine fire effects in browsed forest on ground beetle diversity and trophic guilds over time we performed repeated-measures ANOVA. "Fire" was considered a fixed factor with two levels (burnt and unburnt) and "years" as fixed factor with two levels (2006–2007). The years factor were considered as fixed factor since they were only 2 consecutive years and they are not random samples within all possible (Sokal and Rohlf 1999). On the other hand, to determine cattle effects on ground beetle diversity in burnt forest over time we performed repeated-measures ANOVA, "cattle" (cattle and no cattle) and "years" (2006–2007) were considered fixed factors with two levels. These repeated measures ANOVA were performed for beetles abundance, rarefied species richness and abundance of trophic guilds. These variables were transformed when necessary to meet assumptions of normality and homoscedasticity (Sokal and Rohlf 1999). The analysis was done with the function aov in the stats package of R statistical software (R Development Core Team 2014).

Changes in beetle community composition were performed using analysis of similarity (ANOSIM) with Bray-Curtis index to determine if there were significant differences in beetle assemblages between burnt and unburnt browsed forests, and between cattle and no cattle in burnt forests, during both years. ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke and Warwick 2001), that produces a global R-statistic, which is an absolute measure of distance between groups. A value of 0 indicates there is complete overlap in the community composition between groups, while a value of 1 indicates that there is no overlap (Clarke and Gorley 2006). We visualized these results using non-parametric multidimensional scaling analysis (NMDS) on Bray-Curtis dissimilarity values in PRIMER v.6 (Clarke and Gorley 2006).

Indicator beetle species for each disturbance type were identified using the Indicator Value method (Dufrêne and Legendre 1997). This method assesses the degree to which a species fulfills the criteria of specificity (uniqueness to a particular habitat) and fidelity (frequency of occurrence). A higher indicator value implied that a species can be considered characteristic of a particular habitat or site (McGeoch and Chown 1998). Indicator values for each species were estimated based on a species abundance matrix and Dufrêne and Legendre's (1997) random reallocation procedure of plots among plot groups was used to test for the significance of IndVal measures. Dufrêne and Legendre (1997) assume a characteristic species for a given treatment if the species IndVal is >25 % and significant at $P < 0.05$. This analysis was done with the function indval in the indicspecies package of R statistical software (R Development Core Team 2014).

Given that the environmental variables: light availability, air temperature and air humidity were measured during one season, we performed one-way ANOVA. However, for the variables measured during two seasons: mean vegetation cover, mean maximum vegetation height, mean species richness, and mean cattle browsing index we performed repeated-measures ANOVA. "Fire" was considered a fixed factor with two levels (burnt and unburnt), "years" a fixed factor with two levels (2006–2007). And "cattle" (cattle and cattle removal) and "years" (2006–2007) were considered fixed factors with two levels. This analysis was done with the function aov in the stats package of R statistical software (R Development Core Team 2014).

Results

Fire effects in cattle browsed forests

We collected a total of 685 ground beetles belonging to 18 families and 70 species during both years across burnt and unburnt forests browsed by cattle (Table S1). The dominant families were Carabidae with 11 species and 48 % of the total catch, Trachypachidae with 2 species (25 %), Staphylinidae with 14 species (9 %), Scarabeidae with 7 species (5 %), and Leiodidae with 8 species (2 %) (Table S1).

Beetle abundance was 66 % higher in unburnt than in burnt forests (ANOVA, $F_{1,6} = 9.26$, $P = 0.02$, Fig. 1a) and was 44 % higher on second sampling season (ANOVA, $F_{1,6} = 20.62$, $P = 0.004$). Similarly, beetle species richness, estimated by rarefaction, was different between burnt and unburnt forest (ANOVA, $F_{1,6} = 6.43$, $P = 0.04$; Fig. 1c), with unburnt forest having one more species than burnt forest. However, beetle species richness was similar between sampling seasons (ANOVA, $F_{1,6} = 0.29$, $P = 0.61$).

Beetle assemblages differed significantly between unburnt and burnt forests with cattle browsing (ANOSIM,

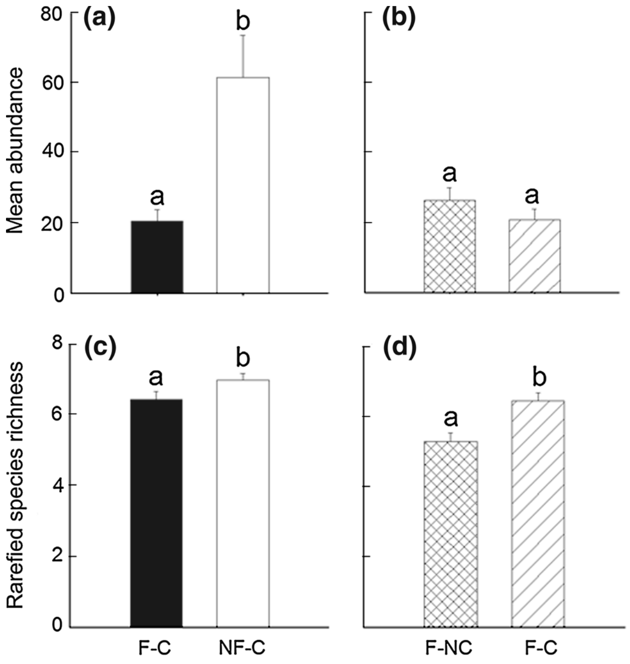

Fig. 1 Mean (± SE) beetle abundance and rarefied specific richness per plot for: **a** and **c** fire effects in browsed forests (F-C: burnt with cattle and NF-C: unburnt with cattle), and **b** and **d** cattle browsing effects in burnt forest (F-NC: burnt without cattle and F-C: burnt with cattle). Different letters above error bars denote significant differences between treatments as denoted by ANOVA results

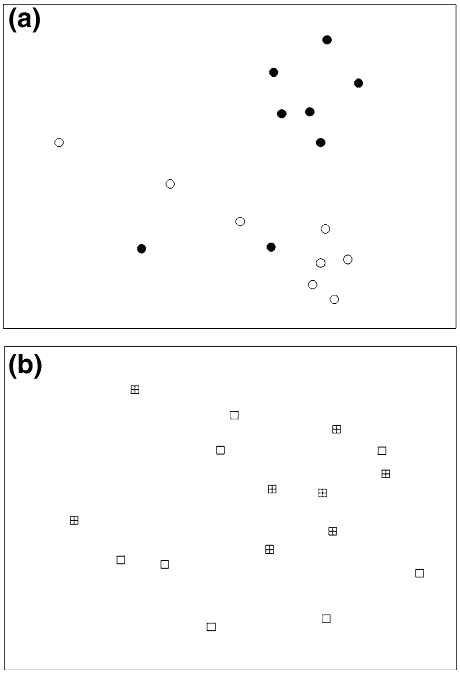

Fig. 2 Non-metric multidimensional scaling (NMS) ordination of beetle species assemblages in: **a** burnt (*filled circle*) and unburnt (*unfilled circle*) forests with cattle (ANOSIM, $R = 0.6$, $P = 0.005$, stress = 0.14); and **b** burnt forest with cattle (*unfilled square*) and without cattle (*squared plus*) (ANOSIM, $R = 0.10$, $P = 0.76$, stress = 0.18)

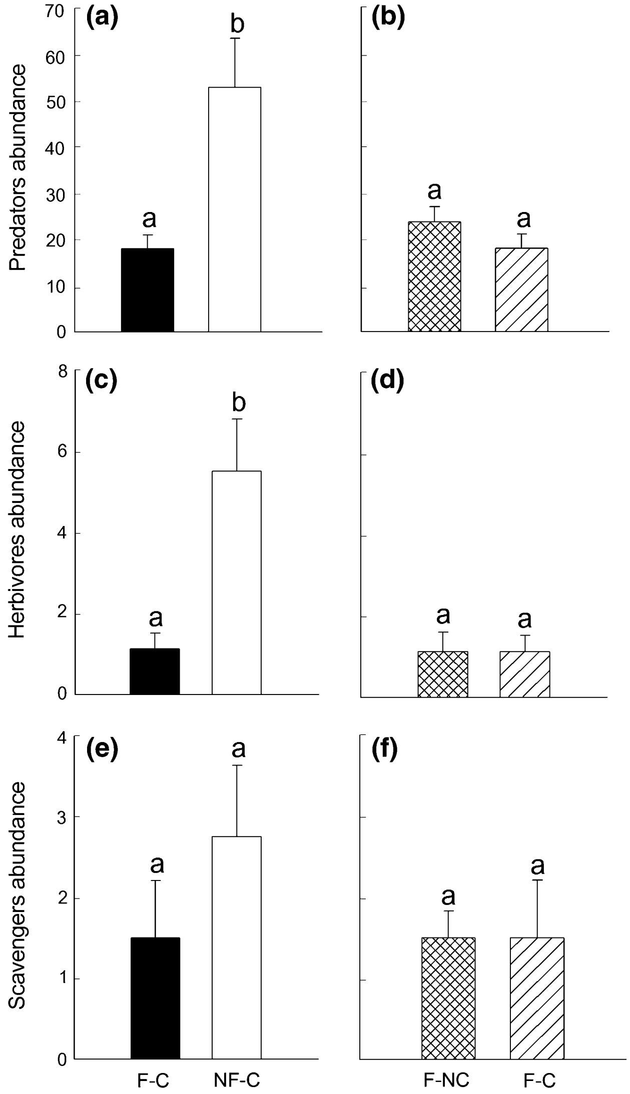

Fig. 3 Mean (± SE) beetle abundance per trophic guild (predators, herbivores and scavengers) for: **a**, **c**, **e** fire effects in browsed forests (F-C: burnt with cattle and NF-C: unburnt with cattle), and **b**, **d**, **e** cattle browsing effects in burnt forest (F-NC: burnt without cattle and F-C: burnt with cattle). Different letters above error bars denote significant differences between treatments as denoted by ANOVA results

$R = 0.6$, $P = 0.005$; Fig. 2a), and was similar among sampling seasons (ANOSIM, $R = 0.17$, $P = 0.13$). The IndVal analysis revealed that there were two species characteristic of unburnt browsed forest. The species were *Systolosoma lateritum* (Trachypachidae) ($IV = 1$, $P = 0.03$) and *Trechini sp.1* (Carabidae) ($IV = 1$, $P = 0.02$).

Beetles from burnt and unburnt browsed forests were assigned into four trophic guilds: 86 % predators, 8 % herbivores, 5 % scavengers, and 1 % fungivorous (Table S1). The abundance of predators and herbivores beetles were higher in unburnt than in burnt forests (ANOVA, $F_{1,6} = 7.99$, $P = 0.03$, Fig. 3a; $F_{1,6} = 5.86$, $P = 0.05$, Fig. 3c). The abundance of predators beetles was 43 % higher on the second sampling season (ANOVA, $F_{1,6} = 10.38$, $P = 0.02$) and the abundance of herbivores beetles was similar over sampling seasons (ANOVA, $F_{1,6} = 0.67$, $P = 0.44$). However, scavengers beetle abundance was similar in burnt and unburnt forests (ANOVA, $F_{1,6} = 1.92$, $P = 0.21$, Fig. 3e) and the difference between sampling seasons was not significant (ANOVA, $F_{1,6} = 5.40$, $P = 0.06$). In the case of the fungivorous guild, we found only 4 individuals in unburnt forest; therefore we did not perform ANOVA analysis (Table S1).

Some environmental variables showed significant differences between burnt and unburnt browsed forests. Light availability measured as direct site factor was 46 % lower in unburnt forest than in burnt forest (Table 1) due to the lack of canopy in the burnt forest. Air temperature and air relative humidity were similar in unburnt and burnt forests (Table 1). The mean understory vegetation cover (%) of all vascular plants was 23 % higher in burnt than in unburnt forests (Table 1) and similar between sampling seasons (ANOVA, $F_{1,6} = 0.23$, $P = 0.65$). Understory vegetation richness was also 23 % higher in burnt than in unburnt forest (Table 1), however was similar between sampling seasons (ANOVA, $F_{1,6} = 5.65$, $P = 0.06$). Mean vegetation height (m) was similar between burnt and unburnt forests (Table 1), however was 15 % higher in second than first sampling season (ANOVA, $F_{1,6} = 6.29$, $P = 0.04$). Cattle impact on all species in the area

Table 1 Mean ± SE and ANOVA results of habitat parameters for fire effects with cattle browsing (F-C: burnt with cattle and NF-C: unburnt with cattle) and cattle browsing effects in post fire forests (F-NC: burnt without cattle and F-C: burnt with cattle)

Parameter	Fire effects				Cattle effects			
	F-C	NF-C	*F*	*P*	F-NC	F-C	*F*	*P*
Light availability	0.60 ± 0.03	0.32 ± 0.02	58.80	0.0003	0.65 ± 0.03	0.60 ± 0.03	1.07	0.34
Air temperature (°C)	11.47 ± 1.42	10.30 ± 0.89	0.48	0.50	13.08 ± 1.66	11.47 ± 1.42	0.55	0.47
Air relative humidity (HR %)	75.29 ± 5.85	82.12 ± 3.38	1.02	0.32	48.76 ± 3.97	75.29 ± 5.85	14.07	0.001
Understory mean vegetation cover (%)	115.89 ± 7.05	88.80 ± 4.52	6.63	0.04	124.06 ± 6.03	115.89 ± 7.05	0.47	0.58
Understory vegetation height (m)	98.92 ± 6.44	69.44 ± 7.92	4.90	0.07	150.82 ± 12.30	98.92 ± 6.44	7.06	0.04
Understory vegetation richness	30.00 ± 1.69	23.00 ± 1.12	7.44	0.03	27.25 ± 2.00	30.00 ± 1.69	0.60	0.47
Cattle browsing	1.74 ± 0.43	3.44 ± 0.66	4.72	0.04				

sampled, assessed as mean browsing index, was 49 % higher in unburnt than in burnt forests (Table 1).

Cattle effects in burnt forest

We collected a total of 375 ground beetles belonging to 15 families and 52 species during both years across cattle and no cattle burnt forests (Table S1). The dominant families were Carabidae with 11 species corresponding to 60 % of the total catch, followed by Staphylinidae with 11 species (22 %), Leiodidae with 9 species (5 %) and Trachypachidae with 2 species (4 %) (Table S1).

The mean abundance of ground beetles was similar between no cattle and cattle forests (ANOVA, $F_{1,6} = 0.99$, $P = 0.36$, Fig. 1b) and similar between sampling seasons (ANOVA, $F_{1,6} = 2.54$, $P = 0.16$). Beetle species richness, estimated by rarefaction, was 18 % higher in cattle than in no cattle forests (ANOVA, $F_{1,6} = 20.64$, $P = 0.0004$; Fig. 1d) and similar between sampling seasons (ANOVA, $F_{1,6} = 0.22$, $P = 0.65$). Ground beetle species composition was similar between forests with and without cattle (ANOSIM, $R = 0.10$, $P = 0.76$, Fig. 2b), and was similar among years (ANOSIM, $R = 0.20$, $P = 0.11$). Indicator species analysis to identify characteristics species of disturbance revealed there were no significant species for burnt forests with and without cattle.

Beetles were grouped in three trophic guilds: 89 % were predators, 5 % herbivores and 6 % scavengers, with no fungivorous beetles in burnt forest (Table S1). Predator, herbivore and scavenger beetle abundances were similar in burnt forest between cattle and no cattle (ANOVA, $F_{1,6} = 1.19$, $P = 0.32$, Fig. 3b; $F_{1,6} = 0.02$, $P = 0.89$, Fig. 3d; $F_{1,6} = 0.46$, $P = 0.52$, Fig. 3f) and was similar between sampling seasons (ANOVA, $F_{1,6} = 2.10$, $P = 0.20$; $F_{1,6} = 0.64$, $P = 0.45$; $F_{1,6} = 1.63$, $P = 0.25$).

Habitat parameters were quite similar between cattle and no cattle forests. Light availability measured as direct site factor and air temperature were similar in cattle and no cattle forests (Table 1). However, air relative humidity was 35 % higher in no cattle than in cattle forests (Table 1). The understory mean cover (%) of all vascular plants and species richness were similar in cattle and no cattle forests (Table 1) and similar between sampling seasons (ANOVA, $F_{1,6} = 2.43$, $P = 0.17$; $F_{1,6} = 5.17$, $P = 0.06$). The vegetation height was 66 % lower in cattle than in no cattle forests (Table 1) and was 11 % higher in second than in first sampling season (ANOVA, $F_{1,6} = 9.01$, $P = 0.02$). In no cattle forests there was no browsing because of the fence against cattle, while in the cattle forests the mean browsing index of all the species sampled was 2.4 ± 0.45 in 2006 and 1.08 ± 0.81 in 2007 (mean ± SE).

Discussion

Fire effects in cattle browsed forests

Burnt forest showed lower beetle diversity than unburnt forest. Burnt forest had lower beetle abundance, lower species richness and different assemblage composition compared with unburnt forest (Figs. 1a, c and 2a). These patterns of impoverished beetle diversity could be explained by different mechanisms related to the temporal scale from the time since fire. In general, the immediate effect of fire on arthropods is often direct mortality and forced migration of mobile species (Andersen and Müller 2000). In the short-period after fire (the case of our study) modifications of environmental characteristics may play a bigger role than direct mortality, negatively affecting food supplies, refuges, oviposition and foraging sites, and modifying interspecific competition and predation rates (Blanche et al. 2001). Beetle diversity could be affected directly or indirectly by environmental changes caused by fire, such as canopy loss and light increase (Table 1). Also, fire increased understory cover vegetation and plant species richness because many plants resprouted vigorously after fire (Veblen et al. 2003) (Table 1). These changes in structural complexity of habitat (canopy loss and plant understory changes) could explain the impoverishment of beetle diversity in burnt forest because of loss beetle niches (i.e., woody vegetation). There are few studies describing beetle colonization patterns of post-fired areas (Swengel 2001; Sasal et al. 2010; Pryke and Samways 2012) which showed that colonization could take many years since fire and it depends on several factors such as fire characteristic (i.e., severity, intensity, and extension), study group, habitat type, and climatic conditions. Our results are consistent with studies conducted in the region that also found lower beetle diversity in burnt forest compared with unburnt forest (Sackmann and Farji-Brener 2006). All these post-fire succession mechanisms may have contributed to explain the impoverishment of beetle diversity in burnt forest observed in this study.

Disturbances produced changes in resource availability that may differentially impact in arthropods communities, for instance some trophic guilds might be more affected than others (Hawkins and MacMahon 1989).The more abundant trophic guilds were predators and herbivores which represent secondary and primary consumers respectively. The abundance of both trophic guilds was lower in burnt than in unburnt forest (Fig. 3a, c). Fire could cause habitat simplification and a decline in niche availability that decreases the abundance of predator and herbivores beetles. Less abundant guilds such as scavengers showed no significant differences between burnt and unburnt forests (Fig. 3e) and only four fungivorous individuals were found in unburnt forest. In sum, trophic guilds are a useful way to relate diversity and ecosystem function (Bengtsson 1998). Therefore, diversity and trophic guilds decreased in burnt forest.

Because beetles had high sensitivity to environmental conditions, they have been used as bioindicators in many environmental monitoring and assessments providing a fine scale view of ecological changes (Orgeas and Andersen 2001). Regarding beetle characteristic species, unburnt forest had two characteristic species out of 70 species found in burnt and unburnt forests, belonging to two families Carabidae and Trachypachidae, both predators. These species can be used to identify early indicators of restoration success (González et al. 2013), and could also reflect the responses of other species or the overall biodiversity (Rainio and Niemelä 2003). In sum, characteristic beetles species could be good indicators of fire effects.

Cattle effects in burnt forest

We observed that forests with and without cattle had similar beetle abundance, assemblage composition, abundance of trophic guilds (predators, herbivores and scavengers) and non-particular species (Figs. 1b, 2b, 3b, d, f). On the other hand beetle species richness in cattle forest was 18 % higher than in no cattle forest (Fig. 1d). The observed patterns on beetle diversity could be explained by the effects of two types of disturbances.

Post-fire sites are characterized by the removal of large parts or all the aboveground biomass with an homogenizing effect (Bond and van Wilgen 1996). This homogenization may produce the similar beetle abundance (Fig. 1b), community composition (Fig. 2b) and abundance of trophic guilds (Fig. 3b, d, f) independently of the presence of cattle browsing. Unlike other measures of beetle diversity, beetle richness was higher in forests with cattle than in forest without (Fig. 1d). Introduced ungulates is a biotic disturbance that affect at smaller scales and have heterogeneous effects compared with fire (Hobbs 1996; Vázquez 2002; Allred et al. 2011). Ungulate herbivory may increase the available niche for beetles, through changes in quality and quantity of litter, dead wood, flowers, seeds, cover, egg laying sites, nesting sites, and vegetation structure (van Wieren and Bakker 2008). In the habitat parameters measured, we found that cattle forest have 35 % higher air relative humidity and 66 % lower vegetation height than no cattle forest (Table 1). Cattle disturbance could favor beetle species richness directly through their presence, browsing, trampling and feces, or indirectly through effects on soil and vegetation structure (van Wieren and Bakker 2008). For instance, cattle feces could favor the presence of dung beetles like some scarab beetles (Scarabaeidae) and some rove beetles species (Staphylinidae) over other taxa (Bustamante-Sánchez et al. 2004), although these specialized beetles have no contributed to the difference in diversity found in our study. Soil organic compounds could be modified by feces, and cattle trampling could affect soil properties. Moreover, through selective feeding and trampling, cattle could affect vertical complexity, reducing plant heights and sometimes changing species assemblage (Raffaele and Veblen 2001; Blackhall et al. 2008). For example, in grasslands and forest ecosystems ungulates in post-fire areas increased arthropod diversity because of their effects on habitat heterogeneity (Fay 2003; York and Tarnawski 2004). Although not tested in this study, the positive effect of cattle on environmental heterogeneity could be considered as the main mechanism explaining the high beetle richness between post-fire cattle browsed forests.

Conclusion

Our study is a snapshot of a long post-fire succession process combined with a particular intensity of cattle browsing that contributes to better understand the ecological consequences of cattle removal in burnt areas. However, increase in disturbance frequency and intensity as a result of climate change enhances the need for better conceptual and mechanistic understanding of ecosystem response to both disturbances. Our results suggest that the inclusion of a poorer studied—but ecological relevant- focal group, like arthropods, is needed to better understand the effect of disturbances on diversity. Particularly, we found that fire disturbance provoked strong changes in beetle community over time. This may be of particular relevance since in the Patagonian-Andean region wildfire events will increase substantially during the first half of the 21st century (Veblen et al. 2011). Therefore, the implementation of policies reducing the risk of fire appears to be vital to conserve the beetle assemblage in the Patagonian region. On the other hand, we found that in a recent post-fire forest, low-moderate cattle browsing could enhance beetle richness. For management decisions it is important to regulate the ungulate grazing pressure in post-fire areas; apparently low-moderate cattle grazing could help to restore beetle diversity. However further research is needed to understand the effect of ungulates in other arthropods and vertebrate groups, and the appropriate moment after fire to allow cattle in post-fire areas.

Acknowledgments We thank Juan Karlanian, Melisa Blackhall, Emiliano and Daniela Sasal for field assistance, and Juan Paritsis, Carolina Quintero, Mariano Rodriguez-Cabal and Martín A. Nuñez for manuscript suggestions. We also thank SergioRoig-Juñet (Carabidae), Mariana Chani (Saphilinidae), Eider Ruíz-Manzanos (Scarabeidae), Gustavo Flores (Tenebrionidae) and Alfred Newton (Leiodidae) for their assistance with beetle identifications. The "Administración de ParquesNacionales" allowed access to the study site. Y. S., E. R. and A. F.-B. are researchers for CONICET.

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