ÉCOSCIENCE

13 (3): 360-371 (2006)

Effect of fire on ground beetles and ant assemblages along an environmental gradient in NW Patagonia: Does habitat type matter?[1]

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Abstract: The response of beetle and ant assemblages to fire (2–5 y old) and the dependence of that response on habitat type were analyzed. Using pitfall traps, beetles (Coleoptera) and ants (Formicidae) were sampled in replicated forest, scrub, and steppe areas including paired unburnt and burnt plots. A total of 176 species of beetles (8245 individuals) and 22 species of ants (115,056 individuals) were captured. Most beetle families (65%) were captured in the forest, while most ant species were most frequently captured in the steppe (45%). Beetle abundance was the same in unburnt and burnt plots in the three habitats, but ant abundance was higher in burnt than in unburnt plots. Fire usually decreased species richness of both taxa, but the strength of this effect depended on the habitat type. Coleoptera richness was lower in burnt than in unburnt plots in the forest and steppe but was the same in unburnt and burnt scrub plots. Ant richness was lower in burnt forest and scrub plots and was similar between burnt and unburnt steppe plots. For both taxa, species composition of the forest assemblages was different between unburnt and burnt forest plots (difference almost significant for ants) but not between unburnt and burnt steppe plots. Beetle species composition in the scrub was different between unburnt and burnt plots, but ant species composition was the same. Our results support the idea that the consequences of fire on native beetle and ant assemblages depend on the habitat type but also on the taxonomic group under analysis. Beetles and ants showed differences in their habitat preference and in the way that they use the habitats (*e.g.,* preference for vegetated or bare soil patches) along the environmental gradient. These differences explain why beetles were in general more severely affected than ants, and why fire differentially affected both taxa in the scrub (habitat of intermediate complexity). A good knowledge of the habitat utilization by different groups at the local scale and a regional perspective (*e.g.,* habitat preference along an environmental gradient) are necessary to fully understand the effect of disturbances on native arthropod assemblages.

Keywords: assemblage composition, burning, Coleoptera, environmental gradient, Formicidae, Patagonia.

Résumé : La réponse au feu (pour des feux de 2 à 5 ans) d’assemblages de coléoptères et de fourmis et la dépendance de cette réponse au type d’habitat ont été analysés. Des coléoptères (Coleoptera) et des fourmis (Formicidae) ont été échantillonnés à l’aide de pièges à fosse dans des réplicats d’aires de forêt, de broussailles et de steppe incluant des paires de parcelles brûlées et intactes. Au total, 176 espèces de coléoptères (8245 individus) et 22 espèces de fourmis (115 056 individus) ont été capturés. La majorité des familles de coléoptères ont été capturées dans la forêt (65%) alors que la majorité des espèces de fourmis ont été capturées plus fréquemment dans la steppe (45%). L’abondance de coléoptères était la même pour les parcelles intactes et brûlées des trois types d’habitat mais les fourmis étaient plus abondantes dans les parcelles brûlées que dans celles intactes. En général, le feu causait une diminution de la richesse en espèces des deux taxons mais la force de cet effet dépendait du type d’habitat. La richesse en espèces de coléoptères était plus faible dans les parcelles de forêt et de steppe brûlées que dans celles intactes mais était la même entre les parcelles de broussailles brûlées et intactes. La richesse en espèces de fourmis était plus faible dans les parcelles brûlées de forêt et de broussailles mais était similaire entre les parcelles brûlées et intactes de steppe. Pour les deux taxons, la composition en espèces des assemblages forestiers était différente entre les parcelles intactes et brûlées (une différence presque significative pour les fourmis) mais ce n’était pas le cas entre les parcelles intactes et brûlées de steppe. La composition en espèces des assemblages de coléoptères était différente entre les parcelles de broussailles intactes et brûlées mais était la même pour les assemblages de fourmis. Nos résultats supportent l’idée que les conséquences du feu sur les assemblages indigènes de coléoptères et de fourmis dépendent non seulement du type d’habitat mais aussi du groupe taxonomique analysé. Les coléoptères et les fourmis ont démontré des différences au niveau des préférences d’habitat et dans la façon de l’utiliser (*e.g.*, préférence pour des sols nus ou pourvus de végétation) le long du gradient environnemental. Ces différences expliquent pourquoi les coléoptères étaient en général affectés plus sévèrement par le feu que les fourmis et pourquoi dans les parcelles de broussailles (un habitat de complexité intermédiaire), le feu avait un effet différent sur les deux taxons. Une bonne connaissance de l’utilisation de l’habitat par différents groupes à l’échelle locale et une perspective régionale (*e.g.*, les préférences d’habitat le long d’un gradient environnemental) sont nécessaires pour avoir une compréhension complète de l’effet des perturbations sur les assemblages indigènes d’arthropodes.

Mots-clés : Coleoptera, composition des assemblages, feu, Formicidae, gradient environnemental, Patagonie.

Nomenclature: Dimitri, 1962; Flores, 1997; Roig-Juñent, 2002; Fernández, 2003.

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[1] Rec. 2005-09-06; acc. 2006-01-16.
Associate Editor: André Desrochers.

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Introduction

Fire is a common environmental disturbance that can increase, decrease, or have no effect on arthropod diversity. These varying effects depend on the characteristics of the fire, assemblage composition, and habitat type (Andersen, 1991; York, 1994; 1999; 2000; Orgeas & Andersen, 2001; Farji-Brener, Corley & Bettinelli, 2002; Moretti *et al.,* 2002; Moretti, Obrist & Duelli, 2004; Parr *et al.,* 2004). Habitat type (distinguished by complexity level) is one of the most important factors as it usually modulates the effect of other agents on natural communities (Picket & White, 1985; Pimm, 1991). For example, different studies have shown that the effect of fire frequency or time since fire on ant assemblages depends on the habitats complexity (*e.g.,* number of vegetation strata; Andersen, 1991; Hoffmann, 2003; Parr *et al.,* 2004). In some ecosystems, habitats can become less complex after fire because of the reduction of vegetation cover and/or number of layers. In consequence, differences between post- and pre-fire habitat conditions can be more pronounced in complex habitats than in simpler ones. This means that fire, like other disturbances, can have different effects depending on habitat type, and the response of communities will vary depending on the capacity of their species to deal with the post-disturbance conditions (Picket & White, 1985; Pimm, 1991). Species adapted to more complex habitats, for example habitats with more vegetation layers, which can mean more environmental niches and more foraging opportunities for the species, will be more severely affected than species that prefer less complex habitats (*e.g.,* habitat with fewer vegetation layers; Andersen, 1991; York, 2000; Farji-Brener, Corley & Bettinelli, 2002).

In northwestern Patagonia, Farji-Brener, Corley, and Bettinelli (2002) studied the response of ant communities to fire and found that habitat type (scrub or steppe) and the regional species composition of the ant fauna determine the extent to which burning affects ant assemblages. They showed that the effect of fire on ant diversity was greater in the scrub habitat (structurally complex habitat) than in the steppe (structurally simple habitat). However, that study did not include a wide range of habitats; it only studied the effect of fire on scrub and steppe assemblages, excluding the forest habitat, which markedly differs in structural complexity from the others (*e.g.,* high percentage of tree cover). In addition, the study analyzed the effect of fire on ant assemblages only, leaving aside other important and diverse taxa such as beetles. If habitat type is indeed important, it can be expected that the response to fire of beetles and ants (*e.g.,* difference in abundance, richness, and species composition) will vary between habitats. However, the pattern of response after fire could be group specific.

Northwestern Patagonia provides an ideal location to study the relationship between the effect of fire and habitat type on arthropod assemblages. Fire is a common feature in the dynamics of these natural systems (Veblen *et al.,* 1999; Kitzberger, 2003), and this region is exposed to a remarkable environmental gradient featuring a large and rapid variation in habitat complexity (*e.g.,* vegetation cover and number of plant strata). Over a distance of only 100 km, annual rainfall drops from 3500 mm·y^{-1} to 350 mm·y^{-1} (Barros *et al.,* 1983; Veblen *et al.,* 1996), resulting in a strong change in the floristic composition and physiognomy of vegetation. From west to east, at least three major habitats that decline in complexity (see Methods) can be distinguished: (1) evergreen forest, which is characterized by a well-developed tree cover and understory; (2) scrub dominated by abundant shrub and bamboo vegetation, which almost lacks trees and has a low proportion of bare ground; and (3) xeric steppe, which is dominated mainly by grasses and eventually by short shrubs and has a high proportion of bare soil (Dimitri, 1962; see pictures in Figure 1 and Table I).

Beetles and ants are tightly linked to ecosystem functioning; they can attain large biomass and represent a great proportion of the total species diversity of an ecosystem (Wilson, 1987). These taxa have proven to be sensitive to habitat burning (Orgeas & Andersen, 2001; Izhaki, Levey & Silva, 2003), but in only a few cases has the effect of fire been studied or discussed simultaneously for these two groups (Siemann, Haarstad & Tilman, 1996; York, 1999). It has been proposed that more taxa should be simultaneously included in analyses of the effect of fire on arthropod assemblages to better understand the complex ecological interactions and minimize the risk of making general statements based on studies of only a limited number of taxa (Prodon, Fons & Athias-Binche, 1987). The strategy of identifying taxa that show similar responses to environmental disturbances has been useful in other regions of the world (Australia: Oliver & Beattie, 1996) as a way to establish groups that can be used as surrogates of each other in ecological studies (Hammond, 1994).

In the present study we analyze the effect of fire on beetle (Coleoptera) and ant (Formicidae) assemblages along three habitat types. Our hypothesis is that fire affects ground-dwelling beetle and ant assemblages, but that this effect will depend strongly on the habitat type. We expect that the abundance, richness, and species composition of ground-dwelling beetles and ants will be different between unburnt and burnt plots, and that the differences in those response variables between unburnt and burnt plots will be greater in forest assemblages (habitat with high structural complexity) than on scrub assemblages (intermediate complexity) and, in turn, that the differences on scrub assemblages will be greater than on steppe assemblages (lower complexity). We expect to find the same pattern for vegetation cover (canopy and ground cover).

Methods

STUDY AREA

The study was conducted in 2001 along a 63-km-long west-to-east transect within the Nahuel Huapi National Park, Bariloche, Argentina (40º 20'–41º 35' S, 71º–72º W, altitude from 800 to 1400 m asl; Figure 1). Approximately 60% of annual precipitation falls from May through August, and more than 90% of fires occur during the warm and dry season from October through March (Kitzberger, Veblen & Villalba, 1997). Fire is a common feature in the dynamics of all the habitats along the environmental gradient. It has been estimated that for the last 100 y, successive fire intervals have ranged from 3 to 17 y (Veblen *et al.,* 1999). In the

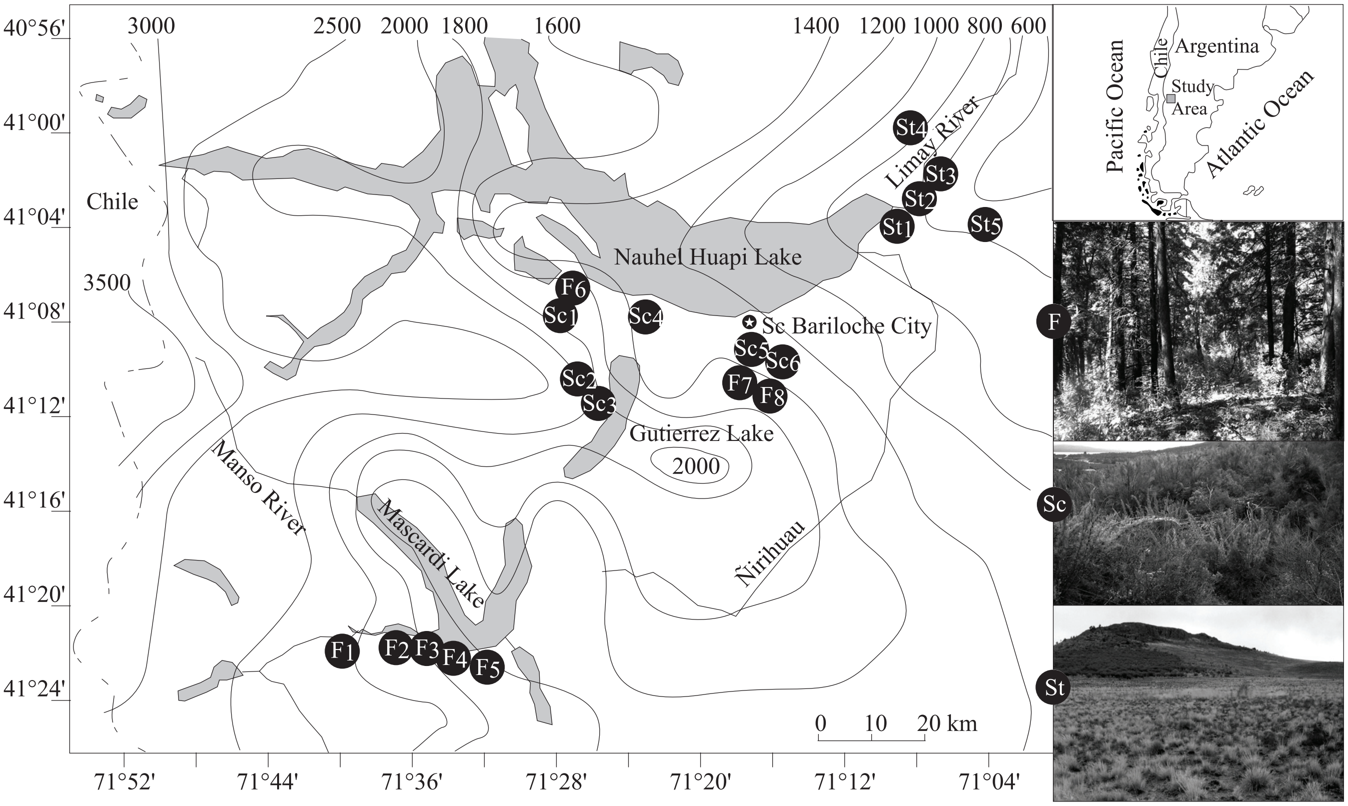

FIGURE 1. Study area. The location of the 19 study sites along the west-to-east transect is indicated. Abbreviations correspond to sites in F = forest, Sc = scrub, and St = steppe. Isolines of mean annual precipitation (mm) are also shown.

summers of 1996 and 1999 more than 22,000 ha of forest (both mesic and xeric), scrubland, and steppe ecosystems burned. The spring and summer of both years were very dry and hot, and in particular the 1999 fire coincided with La Niña event, which typically promotes dry springs in northwestern Patagonia (Veblen *et al.,* 2003). The mean annual temperature is 8 ºC, though temperature can fluctuate from a mean minimum of –2 ºC in the coldest month (July) to a mean maximum of 23 ºC in the warmest (January). Although the air temperature regime is the same along the transect covered in our study, because of differences in vegetation structure the highest temperature measured at soil surface in summer ranged from 65 ºC in the steppe to 25 ºC in forest and scrub sites (A. Farji-Brener, J. Paritsis & N. Tercero, unpubl. data). Introduced livestock and cervids are present in all habitat types along the region and can have consequences on fire regime and the composition of vegetation (Veblen *et al.,* 2003).

The Andean mountains act as a barrier to westerly airflow at temperate latitudes, resulting in a pronounced eastward rain shadow. Humid winds from the Pacific rise up and cross the Andean crests, causing the most intense rainfalls on the western (Chilean) side of the Cordillera and a marked west-to-east gradient on the eastern (Argentinean) side. The mean annual precipitation along this gradient drastically declines from > 3000 mm in the west of the Nahuel Huapi National Park to < 500 mm just 100 km to the east (Barros *et al.,* 1983). Major climatic, soil, and biotic differences along the west-to-east gradient allow the distinction of three major habitat types (see Figure 1): (1) evergreen forest, in sites with 2000–1600 mm of mean annual precipitation; (2) scrub, in sites with 2000–1200 mm of mean annual precipitation; and (3) xeric steppe, in sites with 800–400 mm of mean annual precipitation (Dimitri, 1962). In the western zone of the Nahuel Huapi National Park, there are temperate rainforests that are dominated by *Nothofagus dombeyii* up to 900 m above sea level. Above this altitude, the dominant species is *Nothofagus pumilio*. The forest habitat is characterized by at least three vegetation layers, determined by the presence of trees, shrubs, and grasses and/or herbs. Semi-arid scrub vegetation grows along the foothill zone; here, *Nothofagus antarctica* in its shrub-like form is dominant and is usually mixed with other shrubs such as *Diostea juncea* and *Chusquea culeou*. Trees are rarely present in this habitat, but forbs and grasses grow under the shrubs. In the eastern zone, the steppe lacks tall vegetation except for isolated shrubs and small groups of shrubs. Steppe vegetation is mainly composed of short xerophytic shrubs and herbs. Dominant species include *Senecio bracteolatus*, *Mulinum spinosum,* and *Stipa speciosa*. These habitats were characterized elsewhere (Ruggiero, Farji-Brener & Ezcurra, unpubl. data) using six variables (% bare soil, % litter cover, % tree cover, % herbs and grasses cover, % shrub cover, and mean relative humidity [HR%]) sampling nine forest, three scrub, and nine steppe areas of 100 m^2 in the same study area as the present research (see Table I). According to the Coops and Catling (1997) visual method for scoring habitat complexity, the forest can be classified as the most complex habitat and the steppe as the least complex, while the scrub has an intermediate complexity.

TABLE I. Habitat characterization based on six environmental variables (Ruggiero, Farji-Brener & Ezcurra, unpubl. data). According to the Coops and Catling (1997) visual method for scoring habitat complexity, the forest is the most complex habitat (highest vegetation cover and number of plant layers) and the steppe is the least complex habitat (lowest vegetation cover). Nine forest, three scrub, and nine steppe areas of 100 m^2 were sampled in the same study area as the present research. Means ± SE are shown.

Habitat	Logs, rocks, etc. (%)	Leaf litter cover (%)	Tree canopy (%)	Shrub canopy (%)	Ground cover (%)	Soil moisture**	Coops and Catling score
Forest	2 ± 5	82 ± 6	70 ± 3	37 ± 7	24 ± 9	Moist	11
Scrub	25 ± 9	47 ± 11	40 ± 6*	33 ± 15	47 ± 12	Dry	8
Steppe	47 ± 5	11 ± 6	0 ± 0	12 ± 7	48 ± 9	Dry	6

*The scrub areas sampled included areas with isolated trees. In the present research we sampled only in scrub areas dominated by *Nothofagus antarctica* (shrub-like form) and bamboo (*Chusquea culeou*) that lacked trees.

**Assessed during the summer.

INSECT SAMPLING AND IDENTIFICATION

Nineteen sites were selected along the west-to-east transect (Figure 1), capturing the three major habitat types (eight forest, six scrub, and five steppe sites). While the forest and steppe sites were much like those characterized by Ruggiero, Farji-Brener & Ezcurra (unpubl. data), the scrub sites we sampled were dominated by *N. antarctica* (shrub-like form) and bamboo (*C. culeou*) and lacked trees. Each site covered approximately 0.25 ha and was bisected by a fire border, providing two paired plots, one burnt and one unburnt, which enabled us to exclude gradient effects. Because sites were selected to include both burnt and unburnt plots within each habitat type, we were limited by the availability of this condition within the area. Fires occurred in the summers of 1996 (one steppe, one scrub, and three forest sites) and 1999 (four steppe, five scrub, and five forest sites), so at the time of sampling, fires had occurred between 2 and 5 y before. In all of the sites it was still obvious which side had burnt. A total of 38 plots (19 sites × 2 plots at each site) were thus established. The minimum distance separating the two closest sites (SC2 and SC3 in Figure 1) was 300 m, whereas plots within each site were at least 80 m apart (each plot was 40 m from the fire border). These separation distances are within the range of those reported in previous studies (Porter & Savignano, 1990; Rykken, Capen & Mahabir, 1997; Koivula *et al.,* 1999; Eubanks, 2001; Cook, 2003) and can be assumed to provide independent information for ecological analysis of ground-dwelling arthropods (Moretti, Obrist & Duelli, 2004).

Beetles and ants were collected using pitfall traps, which provide a standard and replicable sampling method and which have been satisfactorily used in comparative studies concerned with both qualitative and quantitative data (Luff, 1975; Spence & Niemelä, 1994; Ausden, 1996; Ribera *et al.,* 2001). A total of 342 pitfall traps were used, at an intensity of nine traps·100 m^{-2} in each plot. Traps (plastic cups of 9 cm diameter and 12 cm depth, partly filled with water, ethylene glycol, and detergent) were placed in a 5 × 5 m grid for 3 weeks between mid-January and mid-February 2000. The contents of the nine traps at each collection station were pooled into one sample. All samples ($n = 38$) were preserved in ethylic alcohol 70% and taken to the laboratory for identification of taxa.

Beetle and ant specimens were first identified to family level and, within each family, sorted to species (beetles: 40%; ants: 96%) or morphospecies (beetles: 60%; ants: 4%). We observed morphological characters and used identification keys published by Kusnezov (1953), Peña Guzmán (1987), and Borror, Triplehorn, and Johnson (1992). All the material was sent to specialists for definitive identification and then was stored in a reference collection at Laboratorio Ecotono, Centro Regional Universitario Bariloche, Argentina. For simplicity, both species and morphospecies will be referred to as species throughout the paper.

VEGETATION COVER ESTIMATION

Grass and shrub cover (ground) in all habitats and tree cover (canopy) in forest sites were estimated in order to have a measure of the effect of past fires on vegetation in each site. We considered that the greater the effect of fire was, the greater the difference in vegetation cover between unburnt and burnt plots would be. Ground and canopy cover were also used as descriptors of habitat complexity (*e.g.,* higher canopy cover meant higher complexity; see Coops & Catling, 1997). Following Belanger and Anderson (1989), at each collection station (burnt and unburnt) we randomly selected 10 points to estimate ground and canopy cover. At each point, we compared the vegetation pattern within a 50- × 50-cm square with a reference card of covers to visually estimate the proportion of ground and canopy cover. An average ground and canopy cover was then calculated for each site.

DATA ANALYSIS

We measured the effect of past fires on abundance of Coleoptera and Formicidae and ground vegetation cover using General Linear Model (GLM) ANOVA, with habitat (forest, scrub, and steppe), disturbance (burnt and unburnt), and site (19 blocks) as factors. Habitat and disturbances were fixed factors, while site was a random factor and was nested into habitat (Grafen & Hails, 2002). The Fisher LSD test was used for doing *a posteriori* comparisons. In addition, we investigated the effect of fire on the Coleoptera families and ant species to better understand the response to fire of general assemblages. Because Coleoptera families and ant species were not abundant enough in all plot types (three habitats, two fire treatments), the effect of fire (unburnt *versus* burnt plots) was analyzed using paired t-tests only for those habitats where the groups were abundant. The same analysis was also performed on canopy cover data. Data were transformed to meet ANOVA assumptions: vegetation cover data were transformed as $x' = \arcsin \sqrt{x}$, and abundance data were transformed as $x' = \log (x + 1)$.

Because estimates of species richness can be influenced by differences in sample size, expected richness was calculated and compared using sample-based rarefaction curves (Gotelli & Colwell, 2001). Rarefaction eliminates variation in species richness due to differences in sample size (*e.g.,* number of beetles captured at each collecting station) by re-sampling a pool of *n* individuals repeatedly at random (Gotelli & Colwell, 2001). Rarefaction was used to estimate beetle and ant species richness in each unburnt and burnt plot of the three habitats. We re-scaled rarefaction curves to the number of individuals captured and compared different curves (*e.g.,* expected beetle richness in unburnt and burnt forest) at the highest value shared among curves (*e.g.,* $n = 2500$ to compare expected beetle richness in unburnt and burnt forest). Calculations were made using the software EstimateS 6.1 (Colwell, 2000).

We used Analysis of Similarity (ANOSIM) with the Bray–Curtis similarity index to determine if there were significant differences in assemblage composition between plot types (different habitat type, burnt and unburnt) (Clarke & Green, 1988). To reduce the weight of very abundant species, data were fourth-root transformed. ANOSIM is a nonparametric permutation procedure applied to rank similarity matrices underlying sample ordinations. The test is based on comparing distances between groups with distances within groups. ANOSIM produces an R-statistic that is an absolute measure of distance between groups. A large positive R (up to 1) means high dissimilarity between groups. Significance is computed by permutation of group membership. To display the relationships between different plots we used non-metric multidimensional scaling (NMDS) with the Bray–Curtis similarity coefficient (Kruskal & Wish, 1978). The NMDS algorithm attempts to place data points in a coordinate system such that ranked distances are preserved. This method is well suited for non-normal data and does not assume linear relationships among variables. Both ANOSIM and NMDS were performed with PAST 1.34 (Hammer, Harper & Ryan, 2001)

We also determined the preferred habitat for each beetle family and ant species as the habitat where a higher proportion of total sampled sites were occupied by a family or species. Secondly, we took into account the abundance of the groups in the unburned plots to decide. In same cases when data was insufficient we used the literature (Kusnezov, 1953; Peña Guzmán, 1987 and Borror *et al.*, 1992) to assigned the preferred habitat.

Results

A total of 176 species of beetles (8245 individuals) and 22 species of ants (115,056 individuals) were captured. While the number of beetle species represents 73% of the expected richness for the study area, the number of ants represents 85% (expected richness was calculated using the Chao1 and Jack1 indexes respectively; Sackmann *et al.,* 2006). Of the beetle families, 64.5% were most frequently captured in the forest, 15.4% were most frequently captured in the scrub, and 19.2% were most frequently captured in the steppe (Table II). A similar pattern was observed at the species level (forest: 50%, scrub: 25%, and steppe: 25%). On the other hand, 40.9% of the ant species were most frequently captured in the forest, 13.6% were most frequently captured in the scrub, and 45.5% were most frequently captured in the steppe.

According to ANOVA results (Table III) the abundance of beetles varied but not significantly between habitats (more individuals in the forest than in the steppe, with intermediate abundance in the scrub; Figure 2). Abundance was not significantly different in unburnt and burnt plots in the three habitats (Figure 2); however, abundance tended to be higher in unburnt plots in the forest and scrub but the same in the steppe. Because abundance varied greatly between sites, the effects of fire, habitat, and the interaction term were not significant (*e.g., P* between 0.12 and 0.25; see Table III and Figure 2). The abundance of the Coleoptera families showed different responses to fire (Table II). Seventeen families were not abundant enough to statistically assess differences between unburnt and burnt plots; but of the other nine families three had higher abundance in unburnt than in burnt plots (the difference for Leiodidae was marginally significant [*P* between 0.09-0.10]) and six had similar abundance in unburnt and burnt plots (Table II). The abundance of ants was higher in the steppe than in the scrub, while abundance in the scrub was higher than abundance in the forest (Table III and Figure 2; Fisher LSD $P < 0.02$). It was also typically higher in the burnt plots (Table III, Figure 2). Fifteen species were not abundant enough to statistically analyze the effect of fire on their abundance, but of the analyzed ant species three out of seven became more abundant after fire; only one (*Monomorium denticulatum*) was less abundant in the burnt plots, and the rest had similar abundances between the two kinds of plots (Table IV). It is interesting to note that the abundance of *Camponotus chilensis* and *Dorymyrmex tener* increased in burnt plots in the forest but not in the other habitats (Table IV).

Coleoptera expected richness was 18% lower in burnt than unburnt forest plots (2500 individuals captured) and 30% lower in burnt than unburnt steppe plots (290 individuals captured), but expected species richness was the same in unburnt and burnt scrub plots (470 individuals captured, Figure 3). Fire reduced ant expected species richness in the forest and scrub areas (37 and 29% for 420 and 2000 individuals captured, respectively), but the expected richness in the steppe was almost the same in unburnt and burnt plots at 38,000 captured individuals (Figure 3).

ANOSIM and NMDS ordination revealed that fire affected the composition of beetle and ant assemblages differentially (Table V, Figure 4). Coleoptera assemblages in the forest and scrub differed between unburnt and burnt plots but were similar between unburnt and burnt plots in the steppe. Ant assemblages in the forest were marginally different between unburnt and burnt plots but were similar in the scrub and steppe. However, for both groups, similarity between assemblages in unburnt and burnt plots increased from the forest to the steppe (minimum similarity between unburnt and burnt forest, intermediate in the scrub, and maximum in the steppe; Table V). In addition, the type of habitat (when undisturbed) also affected the assemblages' species composition. For both taxa the forest and scrub assemblages were similar to each other and different from the steppe assemblages. But the similarity between forest and scrub assemblages was stronger for Coleoptera than for ants (Table V, Figure 4). On the other hand, in the burnt plots all the assemblages appeared to be different. In

TABLE II. Abundance of Coleoptera families in unburnt and burnt plots (mean ± SD). Paired *t*-tests were performed only for families occurring in at least five sites and with abundance ≥ 20 individuals. *n* is the number of sites where individuals of the family were captured. Total abundance means the total number of individuals captured in the habitat (unburnt and burnt plots). "Preferred habitat" (the habitat where the highest proportion of total sampled sites was occupied by a family; but see Methods for details) is shown in bold. The proportion of sites where the family was captured is shown in parentheses after habitat type. F = Forest, Sc = Scrub, and St = Steppe.

Taxa	Habitat	Unburnt	Burnt	Total abundance	*n*	*t*	df	*P*
Carabidae	**F (1)**	270 ± 435	305 ± 301	4605	8	-0.23	7	0.82
	Sc (1)	60 ± 60.9	29.6 ± 24.9	538	6	-1.8	5	0.13
	St (0.8)	16.5 ± 9.9	32.7 ± 28.2	197	4			
Staphylinidae	F (1)	29.7 ± 56.7	7.3 ± 9.8	297	8	1.3	7	0.23
	Sc (1)	56.5 ± 101.8	6.6 ± 7	379	6	1.2	5	0.28
Cryptophagidae	**F (0.8)**	77.3 ± 117.5	6.3 ± 6.8	251	5			
	Sc (0.4)	21.4 ± 21.8	27.6 ± 60.0	245	3	-0.3	4	0.76
Leiodidae	**F (0.9)**	45.8 ± 61.0	1.14 ± 1.4	329	7	1.9	6	0.10
	Sc (0.8)	22.0 ± 25.6	2.8 ± 5.2	125	5	2.05	4	0.11
Tenebrionidae	F (0.4)	1.3 ± 1.5	28.6 ± 19.2	90	3			
	Sc (0.5)	2.3 ± 3.2	7.3 ± 1.1	29	3			
	St (1)	32.6 ± 10.6	29.2 ± 9.2	309	5	0.46	4	0.67
Curculionidae	**F (0.9)**	11.7 ± 21.8	3.1 ± 3.6	104	7	1.02	6	0.34
	Sc (1)	7.3 ± 13.7	1.8 ± 1.3	55	6	0.97	5	0.37
	St (1)	5.2 ± 4.2	4.4 ± 6.7	48	5	0.57	4	0.57
Histeridae	F (0.1)	0	61	61	1			
	Sc (0.3)	0 ± 0	22.5 ± 27.5	45	2			
	St (0.6)	2.7 ± 2.3	10.3 ± 10.4	39	3			
Cantharidae	**F (1)**	7.1 ± 6.2	2 ± 2.1	73	8	2.98	7	0.02
	Sc (1)	9.5 ± 8.5	1.8 ± 2.2	68	6	2.9	5	0.03
Scaraboideae	F (0.9)	6.3 ± 5.5	0.7 ± 0.7	49	7	2.77	6	0.03
	Sc (1)	9.8 ± 8.6	1.7 ± 1.9	69	6	2.3	5	0.06
	St (0.8)	3.5 ± 2.6	1 ± 0.8	18	4			
Coccinellidae	F (0.1)	0	1	1	1			
	Sc (0.3)	0 ± 0	4 ± 2.8	8	2			
	St (0.8)	1.75 ± 2.8	17.2 ± 20.0	76	4			
Lampyridae	F (0.2)	1.5 ± 0.6	0 ± 0	6	4			
	Sc (0.5)	3 ± 4.3	2 ± 2.6	15	3			
Lucanidae	**F (0.6)**	1.0 ± 0.7	1.8 ± 1.3	14	5	-1.35	4	0.24
Melyridae	F (0.1)	5	0	5	1			
	Sc (0.5)	1 ± 0	0.3 ± 0.6	4	3			
	St (0.4)	1.5 ± 0.7	0 ± 0	3	2			
Pselaphidae	**F (0.7)**	2 ± 2	1 ± 1	18	6			
Mordellidae	**St (1)**	1.8 ± 2.2	0.6 ± .9	12	5			
Lyctidae	**F (0.5)**	0 ± 0	2.7 ± 2.0	11	4			
Salpingidae	**F (0.7)**	1 ± 0.6	0.5 ± 0.5	9	6			
Nitidulidae	**F (0.1)**	0	1	1	1			
	Sc (0.5)	2.3 ± 2.3	0 ± 0	7	3			
Pedilidae	**F (0.2)**	2.5 ± 0.7	0 ± 0	5	2			
	Sc (0.2)	1	0	1	1			
Ptinidae	**F (0.6)**	0.8 ± 0.4	0.2 ± 0.4	5	5			
Chrysomelidae	**F (0.1)**	1	1	2	4			
	Sc (0.3)	0 ± 0	1 ± 1	2				
Elateridae	**F (0.4)**	1 ± 0	0.3 ± 0.5	4	3			
Meloideae	**St (0.2)**	1	3	4	1			
Scirtidae	**F (0.2)**	1.5 ± 0.7	0 ± 0	3	2			
Cerambycidae	**F (0.1)**	1	1	2	1			
Anobiidae	**F (0.1)**	1	0	1	1			

TABLE III. Results of ANOVA tests on the effect of fire on the abundance of Coleoptera and Formicidae in three habitat types. Factors: Fire (unburnt, burnt), Habitat (forest, scrub, and steppe), Block (19 sites). Fire and Habitat were fixed factors and Block was random and nested into Habitat. *P*-values lower than 0.05 are in bold. MS is mean square.

	Coleoptera				Formicidae			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Fire	1	0.60	1.83	0.19	1	1.14	5.34	**0.03**
Habitat	2	0.24	2.62	0.12	2	8.16	8.81	**0.002**
Fire × Habitat	2	0.14	1.50	0.25	2	0.32	1.52	0.24
Block	16	0.32	3.50	**0.008**	16	0.92	4.35	**0.002**
Error	16	0.09			16	0.21		

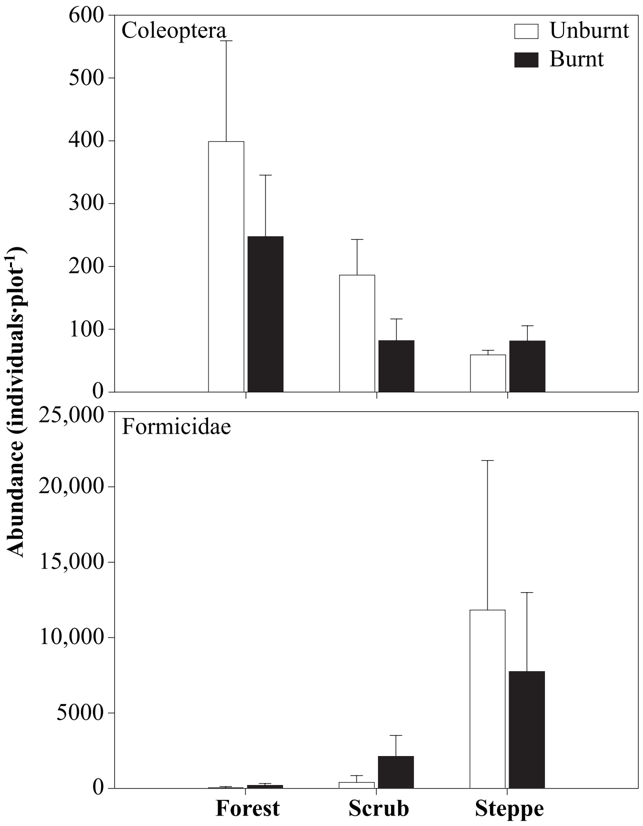

Figure 2. Abundance (mean ± SE) of beetles (Coleoptera) and ants (Formicidae) in unburnt and burnt plot in three habitat types.

contrast, fire had almost no effect on the ant assemblages' similarity relationships (Table V, Figure 4).

The effect of fire on ground vegetation cover wasn't the same in the three habitats ($F_{2,\ 16} = 4.1$, $P = 0.04$, Figure 5). While burning reduced ground vegetation cover in the scrub and steppe (for both comparisons, Fisher LSD test $P < 0.05$), ground vegetation cover was similar between unburnt and burnt forests (Fisher LSD test $P > 0.05$, Figure 5). However, tree canopy cover was significantly higher in unburnt than in burnt forests (76.1 ± 8.0 *versus* 5.0 ± 4.4, $t = 26.1$, $P < 0.001$). These results mean, according to Coops and Catling (1997) (see Methods), that the complexity of the three habitats was reduced after fire because of the loss of vegetation layers (*e.g.,* the burnt forest plots lost almost all the tree cover) and/or vegetation cover.

Discussion

Both beetle and ant assemblages were affected by fire: in general, we found differences in abundance, richness, and species composition between unburnt and burnt plots. However, the strength of these changes usually depended on the habitat type. General beetle abundance was the same in unburnt than in burnt plots; however, abundance tended to be slightly higher in the unburnt plots. In contrast, ant abundance was significantly lower in the unburnt than in the burnt plots. Although for many families the differences in abundance could not be statistically assessed, in general fire tended to reduce the abundance of many beetle families (*e.g.,* Staphylinidae, Leiodidade, Cantharidae, Scaraboideae). Most of those families were associated with dense vegetation (80% of beetle families were found more frequently in the forest and scrub) and were probably affected by the habitat simplification produced after burning (*e.g.,* reduction of tree and shrub cover). Previous studies have shown a decline of groups associated with woody vegetation in sites that become more open and structurally simplified after fire (Niwa & Peck, 2002; Moretti, Obrist & Duelli, 2004). However, other families in the present study that were associated with open habitats seemed to have benefited from the habitat modification induced by fire (differences were not statistically tested: Histeridae, Tenebrionidae, Coccinellidae). Bess *et al.* (2002) showed that certain Coleoptera species that preferred open, bare-ground habitat also increased after fire. Similarly, Niwa and Peck (2002) found that active hunting spiders were collected more often in burnt than in unburnt sites. In the present study the reduction in abundance of some families was compensated for by an increase in others, so overall Coleoptera abundance was similar between unburnt and burnt plots.

The abundance of many ant species increased in burnt plots (*e.g., Dorymyrmex tener* [Dolichoderinae] and *Camponotus chilensis* [Formicinae] in the forest and *Ephebomyrmex odoratus* [Myrmicinae] in the forest and scrub). *Dorymyrmex* spp. in particular attained very high numbers in the disturbed plots (9300–17,700 *D. tener* individuals/plot), and *D. richteri* was only captured there (this species was the second most abundant species in burnt plots). *Dorymyrmex richteri* usually prefers more open habitats, and thus it benefited from the general increase in the proportion of bare ground after fire. However, the abundance of a minor proportion of species that were usually associated with dense vegetation decreased with fire (*e.g., Lasiophanes atriventris*, *Myrmelachista vicina* [Formicinae], *Monomorium denticulatum* [Myrmicinae]). In Australia, when fire causes habitat simplification and increased insolation at ground level the abundance of aggressive species favouring hot, open areas and of species adapted to arid conditions usually increases (*e.g.,* some Dolichoderinae and Myrmicinae). By contrast, species that forage within litter (*e.g.,* some Myrmicinae) usually decrease their abundance after habitat simplification (Hoffmann & Andersen, 2003).

Both beetle and ant richness was, in general, negatively affected by fire, but apparently by different mechanisms. While the impoverishment of structural complexity (*e.g.,* loss of vegetation cover) may have caused the decline of beetle species that were mainly forest dwellers, ant richness may have been mainly lowered by competitive exclusion (Sackmann, 2005). The increase in *Dorymyrmex* spp. abundance in burnt plots may have prevented other species from becoming much more abundant (Farji-Brener, Corley & Bettinelli, 2002; Sackmann, 2005). In Argentina, most *Dorymyrmex* species are subordinate to other species in the xerophilous subtropical forest of the Chaco region (*circa* 25° s) (Bestlemeyer & Wiens, 1996; Bestlemeyer, 1997; 2000), but are numerically and behaviourally dominant in the harsher areas of Patagonia (Farji-Brener, Corley & Bettinelli, 2002). Moreover, in northwestern Patagonia, *Dorymyrmex* spp. can enhance their dominance when the

Table IV. Ant abundance in burnt and unburnt plots (mean ± SD). Paired *t*-tests were performed only for species occurring in at least five sites and with abundance ≥ 20 individuals. *n* is the number of sites where species were captured. Total abundance means the total number of individuals captured in the habitat (unburnt and burnt plots). "Preferred habitat" (the habitat where the highest proportion of total sampled sites was occupied by a species; but see Methods for details) is shown in bold. The proportion of sites where the species was captured is shown in parentheses after habitat type. F = Forest, Sc = Scrub, and St = Steppe.

Species	Habitat	Unburnt	Burnt	Total abundance	*n*	*t*	df	*P*
Formicinae								
Camponotus chilensis	F (0.6)	16.4 ± 23.2	41.2 ± 25.4	288	5	-2.9	4	0.04
	Sc (0.8)	28.4 ± 31.4	24.8 ± 20	266	5	0.25	4	0.8
Brachymyrmex patagonica	Sc (0.2)	1	0	1	1			
	St (0.8)	25.7 ± 49.5	38.5 ± 75.7	256	3			
Lasiophanes sp.	**St (0.6)**	4.0 ± 6.9	2.7 ± 1.5	220	3			
Camponotus distinguendus	F (0.4)	1 ± 1	42.27	129	3			
	Sc (0.3)	17.5 ± 13.4	11.3 ± 5	51	2			
	St (0.2)	0	6	6	1			
Lasiophanes picinus	**F (0.7)**	6.5 ± 10.6	4.3 ± 7.2	65	6	0.38	5	0.7
	Sc (0.3)	4 ± 3.6	0.3 ± 0.6	13	2			
	St (0.2)	43	1	44	1			
Lasiophanes atriventris	**F (0.4)**	9.3 ± 14.5	1.3 ± 2.3	32	3			
Lasiophanes valdiviensis	F (0.5)	7.5 ± 6.5	41.8 ± 42	19	4			
	Sc (0.2)	0	1	1	1			
Myrmelachista vicina	**F (0.1)**	9	0	9	1			
Camponotus punctulatus	F (0.2)	0.5 ± 0.5	0.5 ± 0.5	2	2			
	Sc (0.3)	2.0 ± 1.4	1.0 ± 0	5	2			
Dolichoderinae								
Dorymyrmex tener	F (0.6)	36.4 ± 68.2	205 ±166.1	1207	5	-2.57	4	0.06
	Sc (0.7)	539 ± 1079	773 ± 1433	5252	4			
	St (1)	11,318 ± 22,265	7238 ± 11640	92,781	5	0.83	4	0.45
Dorymyrmex richteri	Sc (0.2)	0 ± 0	6722	6722	1			
	St (0.6)	0 ± 0	79.3 ± 121.8	238	3			
Dorymyrmex antarcticus	F (0.4)	0 ± 0	16.6 ± 26.2	50	3			
	Sc (0.7)	2 ± 1..8	656 ± 1250	2633	4			
	St (1)	458 ± 785	365 ± 601	4120	5	0.91	4	0.41
Dorymyrmex minutus	**St (0.4)**	10.5 ± 14.8	28.0 ± 28.3	77	2			
Dorymyrmex exsanguis	**St (0.2)**	1	0	1	1			
Forelius chalybea	**F (0.1)**	1	0	1	1			
Myrmicinae								
Ephebomyrmex odoratus	**F (1)**	0.87 ± 1.3	15.6 ± 19	132	8	-2.2	7	0.06
	Sc (0.8)	1 ± 1.7	25.8 ± 25	134	5	-2.2	4	0.08
Pogonomyrmex carbonarius	**St (1)**	11.4 ± 11.2	14.8 ± 20.6	131	5	0.01	4	0.98
Acromyrmex lobicornis	Sc (0.2)	43	0	43	1			
	St (0.2)	0	26	26	1			
Solenopsis patagonica	F (0.2)	3 ± 4.2	14.5 ± 19.1	35	2			
	Sc (0.2)	0	1	1	1			
	St (0.2)	11	0	11	1			
Monomorium denticulatum	**F (0.6)**	6.0 ± 1.7	0.6 ± 0.8	34	5	6.32	4	**0.003**
Ephebomyrmex angustus	F (0.2)	3 ± 4.2	4 ± 4.2	14	2			
	Sc (0.2)	1	0	1	1			
Monomorium bidentatum	**F (0.1)**	1	0	5	1			

area they inhabit becomes harsher for other ants (Farji-Brener, Corley & Bettinelli, 2002). A similar situation was reported by Izhaki, Levey, and Silva (2003): ant species richness in Florida pine savanna was initially depressed by fire, probably because of the sudden dominance of a *Forelius pruinosus* (Dolichoderinae). Also, large increases in the abundance of generalist ant species proportionally reduced the dominance of detritivore insects in a riparian forest in New Mexico (Bess *et al.,* 2002).

Fire differentially affected beetle and ant richness in the scrub: while the number of beetle species was similar between unburnt and burnt plots, ant richness differed between the two plot types. The intrinsic heterogeneity of the habitat (occurrence of vegetated and bare soil patches) and spatial segregation of taxa within the habitat (use of different micro-habitats) may explain this result. The scrub is a heterogeneous habitat that varies in the proportion of vegetated and bare ground patches it has (between 40% and 20% in this study and Sackmann, 2005). While bare ground patches can be used by species that prefer open habitats (*e.g.,* steppe dwellers) species that are usually associated with vegetation (*e.g.*, forest dwellers) may be able to use the more vegetated areas of the habitat. Indeed, Kusnezov (1959) pointed out that in northwestern Patagonia the transition between the forest and steppe acts as an ecological barrier, impeding the movement of forest dweller ant species from that habitat. But some species (*e.g., Camponotus distinguendus* and *Lasiophanes picinus*) are able to penetrate the more open habitats by following the vegetation that grows in the more humid areas of these habitats (*e.g.,* where subterranean water makes soil more humid). It has also been shown for the same area that some beetle spe-

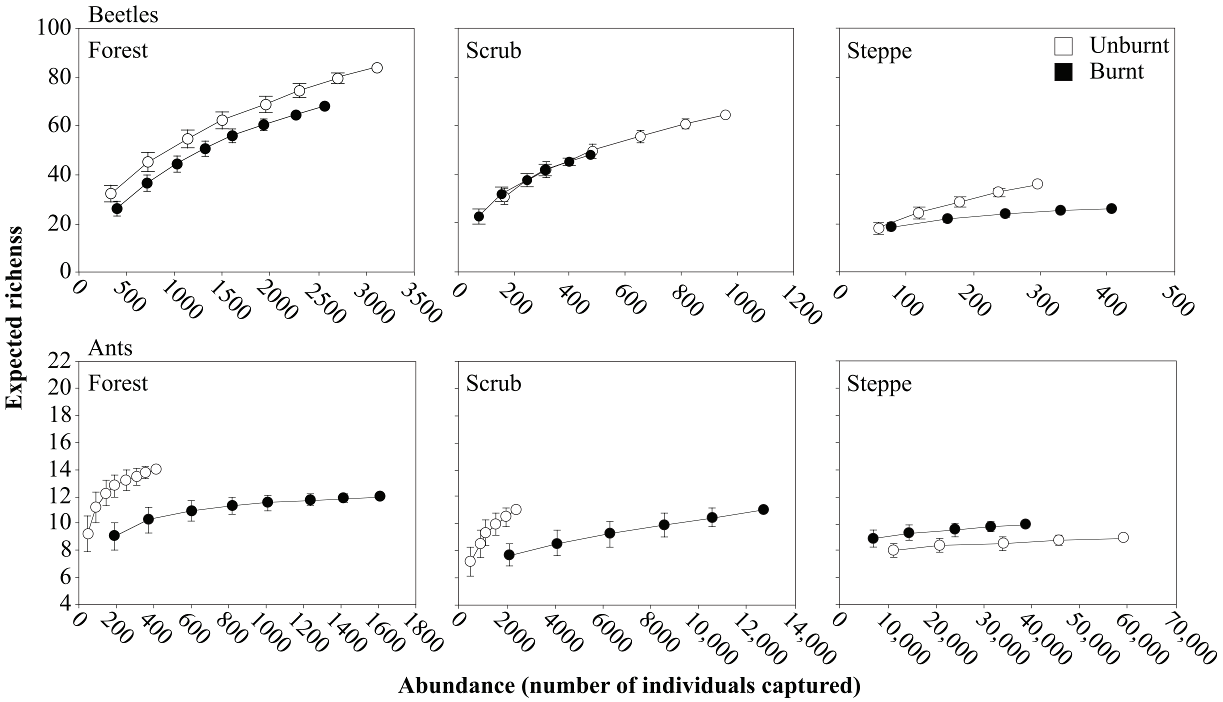

FIGURE 3. Sample-based rarefaction curves rescaled to individuals used to compare expected species richness of beetles (Coleoptera) and ants (Formicidae) in unburnt and burnt plots of three habitat types. Data are means ± SD after randomization.

TABLE V. Analysis of similarity for Coleoptera and Formicidae assemblages between plot types (unburnt and burnt forest, scrub, and steppe). R reflects the degree of separation of the assemblages based in their species composition: if R is close to one, the compared assemblages are dissimilar. Significant *P* are in bold (critical *P* values were adjusted by the Benjamini–Hochberg method [Verhoeven *et al.*, 2005]).

	Coleoptera		Formicidae	
Comparison	R	*P*	R	*P*
UBF *versus* BF	0.34	**0.006**	0.20	0.05
UBSc *versus* BSc	0.31	**0.026**	0.10	0.18
UBSt *versus* BSt	-0.02	0.50	-0.18	0.95
UBF *versus* UBSc	-0.09	0.84	0.11	0.16
UBF versus UBSt	0.98	**< 0.001**	0.55	**0.001**
UBSc *versus* UBSt	0.89	**0.005**	0.38	**0.01**
BF *versus* BSc	0.28	**0.023**	-0.06	0.68
BF *versus* BSt	0.76	**0.002**	0.72	**0.004**
BSc *versus* BSt	0.53	**0.01**	0.52	**0.005**

cies (*e.g., Emmalodera obesa*, *Nyctelia ritundipennis,* and *Cnemalobus deplanatus*) use vegetated patches more frequently than bare ground patches (Mazía *et al.,* 2006). It follows that fire in the scrub habitat, by reducing vegetation cover, will negatively affect species associated with vegetated patches and favour or not affect at all species that make use of bare ground patches. Indeed, after burning, the scrub lost 39 beetle species (17 of which were also captured in the unburnt forest), but gained 24 (eight of which were also captured in the steppe). Because the scrub and the steppe habitats are neighbouring habitats, a flux of individuals between them is plausible. A small proportion of ant species uses vegetated patches in the scrub (*e.g., Lasiophanes picinus*) and so was affected by fire in the scrub. However, as stated above, the main cause of ant richness reduction was probably competitive exclusion triggered by the disproportionate increase in *Dorymyrmex* species. Indeed, the greatest increase in *Dorymyrmex* spp. abundance happened in the scrub.

Beetle and ant richness also showed different responses to fire in the steppe: while beetle richness was reduced, ant richness was not. Fire also reduced the size of vegetated patches in this habitat (average reduction = 34%). In spite of being species that inhabit an open habitat, most beetles in arid environments usually spend much of their time inside vegetation patches (Mazía *et al.*, 2006). In contrast to what happened in the scrub, where similar numbers of species were lost and gained, in the steppe 10 species were lost after fire and only three were gained. Finally, ant richness was the same between unburnt and burnt plots because most ant species make use of bare ground patches when they are outside their nests (Kusnezov, 1959; Sackmann, pers. observ.).

As we had expected, fire changed beetle and ant assemblages' composition in the forest (complex habitat) but had no effect on the steppe (simple habitat) assemblages. However, the response of the scrub assemblages differed between the two taxa: while beetle species composition in the scrub changed after fire, ant species composition remained unchanged. In addition, the degree of variation in the forest assemblages with fire was higher for beetles than for ants (for which, the change was only marginally significant). We consider that the overall effect of fire was greater for beetle assemblages than for ant assemblages.

It has been proposed that the course that ant diversity changes take after disturbances may depend on both the changes in habitat structure and on the ant assemblage structure (Bestlemeyer & Wiens, 1996; Farji-Brener, Corley &

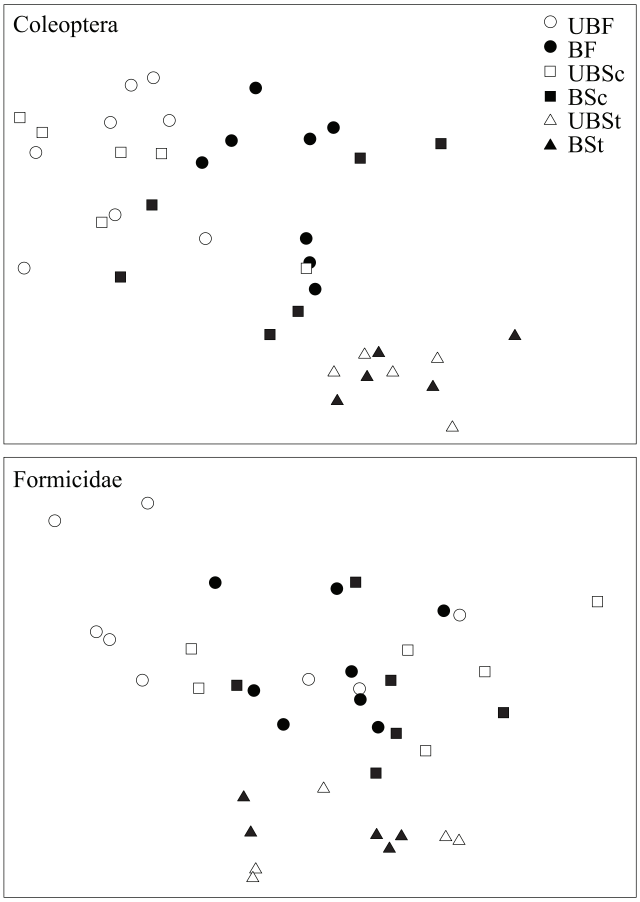

FIGURE 4. Non-metric multidimensional scaling of beetle and ant assemblages composition based on Bray–Curtis similarity index (Stress: beetles = 0.20; ants = 0.23). Each point is a two-dimensional representation of the assemblages composition in each plot type (unburnt and burnt forest, scrub, and steppe). Points that are close together have ant assemblages that are more similar in species composition than points that are far apart.

Bettinelli, 2002). For example, ant diversity in tropical forest declines with habitat simplification because the regional ant fauna consists largely of forest-habitat–adapted taxa (Roth, Perfecto & Rathcke, 1994; Perfecto & Snelling, 1995; Vasconcelos, 1999; Vasconcelos, Vilhena & Caliri, 2000). Moreover, disturbance is likely to have an adverse effect when a species occurs in its most preferred habitat, whereas disturbance might actually improve habitat suitability when a species occurs in a non-preferred habitat (Hoffman & Andersen, 2003). Because the proportion of beetle and ant species inhabiting the three unburnt habitats was different (a greater proportion of ant species inhabited the more open habitat, while more beetle families were forest dwellers), the overall effect of fire on these groups differed too.

Beetle species composition in the scrub differed between unburnt and burnt plots, but ant assemblages did not. In the case of beetles, although species richness and abundance was the same between unburnt and burnt plots in the scrub, species composition changed with fire in that habitat. As stated above, fire negatively affected many beetle species in the scrub through habitat simplification, but it facilitated the immigration of steppe-dweller species. As a consequence, species composition changed with fire although richness did not. In the case of ants, it seems that the effect of fire on species richness and abundance (see above) was not strong enough to change the assemblages' species composition. This may also have been the case for beetle assemblages in the steppe.

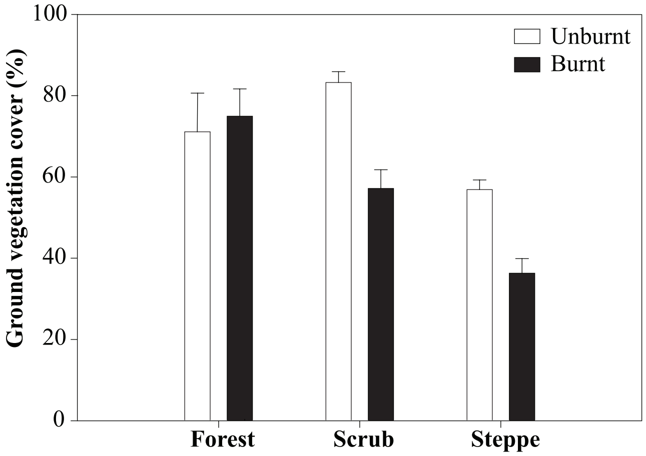

FIGURE 5. Ground vegetation cover (shrubs and grasses) in three unburnt and burnt habitat types. Means + SE for each type of plot are shown.

In contrast to the results reported by Farji-Brener, Corley, and Bettinelli (2002) (see also Parr *et al.,* 2004), the response of ground plant cover did not parallel the insect pattern of response. Although the forest lost almost all its canopy cover after fire (90% reduction), vegetation cover at ground level was similar between unburnt and burnt plots, making it difficult to assess whether ground-dwelling beetles and ants could distinguish any difference. Furthermore, vegetation cover reduction in the scrub and in the steppe was similar (30% and 40%, respectively). The lack of concordance between the vegetation and the insect assemblage responses and the differing responses of the beetle and ant assemblages suggest that a factor or factors (*e.g.,* most preferred habitat and/or habitat use) other than differences in a simple estimator of habitat structure complexity such as plant cover may explain why the effect of fire varied between different habitats.

Although fire is a common feature in the dynamics of the ecosystems in northwest Patagonia, 2–5 y after the fires we still found differences in plant cover (canopy cover in the forest and ground cover in the scrub and steppe) and in beetle and ant species composition between burnt and unburnt sites in all the studied habitats. When ecosystems are exposed to chronic fire regimes it is usual to see rapid post-fire recovery of their different elements. For example, Izhaki, Levey, and Silva (2003) showed that only 0.5 y after a fire, the ant assemblage of longleaf pine savanna in Florida, USA returned to the pre-fire state. In northwest Patagonia, harsh climatic conditions may impede rapid recovery of the affected communities after fire. It is possible, however, that beetle and ant assemblages recover as vegetation does (Bess *et al.,* 2002; Izhaki, Levey & Silva, 2003), because fire occurs in a patchy fashion and the recovery process could be aided by immigration of individuals from unburnt patches.

Our results support the idea that the consequences of fire on native beetle and ant assemblages depend on habitat type (*e.g.,* differences in structural complexity) but also, as previously stated by Farji-Brener, Corley, and Bettinelli (2002), on regional species composition. In particular, the distribution of species among the different habitats in the region (*e.g.,* forest or steppe species) and the way that those species use the habitats (*e.g.,* preference for vegetated or bare soil patches) will determine their ability to deal with post-disturbance conditions. This implies that a good knowledge of both the habitat utilization of different groups at the local scale and how this habitat utilization may change along a regional gradient is necessary to fully understand the effect of disturbances on native arthropod assemblages.

Acknowledgements

We deeply thank those professional taxonomists who generously devoted their time to species determination, namely, S. Roig-Juñent (Carabidae, Chrysomelidae, Bruchidae), G. Flores (Tenebrionidae), F. Ocampo (Scarabaeidae, Trogidae, Geotrupidae, Lucanidae), V. Gusarov (Staphylinidae), P. Posadas (Curculionidae), M. Elgueta (many Coleoptera families), and F. Cuezzo (Formicidae). We thank M. Kun for helping sort Coleoptera species, M. Mermoz (Delegación Técnica Patagonia, APN) for assisting us with fire maps and historical records, and J. C. Corley and T. Erwin for helpful comments on the manuscript. P. Sackmann has a Postgraduate Fellowship (CONICET). We acknowledge funding from the Agencia Nacional de Promoción Científica y Tecnológica.

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