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The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context

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Abstract. We investigated the effects of recent fires on the native ant communities in two habitats of north-west Patagonia that differ in vegetation structural complexity. Using bait traps, we sampled ants in replicated scrub and steppe areas including paired burned and unburned sites. Fires significantly reduced plant cover and ant diversity only in scrub sites. The drop in diversity was due to (a) a reduction in the abundance of rare species associated with woody vegetation, and (b) an increase in the abundance of the dominant species, which thrive in more xeric microclimatic conditions. Consequently, ant assemblage structure of burned scrub approaches that of steppe sites. Our findings suggest that the effects of disturbances on ant assemblages depends both on habitat characteristics, which in turn determine the extent of the changes induced by the disturbance, and on the regional context of the ant fauna, which in turn determines the ability of the ants to deal with the post-disturbance conditions.

Key words. Ants, diversity, disturbance, fire, Patagonia, regional species pool, vegetation structure.

INTRODUCTION

Natural disturbances are important events affecting community structure. Disturbances, by reducing biomass and creating variations in the availability of resources, can alter species numbers and/or dominance relationships. If the disturbance reduces the abundance of the dominant species, by preventing the monopolization of limiting resources, diversity can increase (Connell, 1978). In contrast, a reduction in diversity may be expected when the changes caused by the disturbances result in the elimination of species and/or favour the dominant species (Pickett & White, 1985). Whether diversity will increase or decrease after a disturbance depends on intrinsic characteristics of the disturbances (e.g. frequency), the characteristics of the disturbed habitat (e.g. habitat heterogeneity) and also the community structure (e.g. the existence of competitive hierarchies).

Fire is one of the most common disturbances that can cause large scale and dramatic changes in species diversity and therefore has attracted considerable research effort (see Whelan, 1995). Fire frequency can increase due to climatic and land-use changes (Chandler *et al.*, 1983; Clark, 1990; Johnson & Larsen, 1991; Kitzberger & Veblen, 1997, 1999; Veblen *et al.*, 1999). Most studies of the effects of fire on natural communities have focused on the intrinsic characteristics of the disturbances and their impact on vegetation. For example, several studies have looked at how different fire regimes and their severity has affected plant community structure (Veblen & Lorenz, 1987, 1988; Medina & Silva, 1990; Swetnam, 1993; Kitzberger & Veblen, 1997, 1999). However, the effects of fire on insect communities in relation to habitat structure are less well known.

Ants are abundant and widely distributed insects that are considered important in ecosystem function as they can play a central role in processes such as nutrient cycling, seed dispersal and the population regulation of other insects (Hölldobler & Wilson, 1990; Folgarait, 1988). In addition, ant assemblages are frequently structured through competitive hierarchies (Hölldobler & Wilson, 1990). These reasons make ant assemblages appropriate to study the effects of disturbance on insect community structure in different habitats. Recent studies have shown that land use through habitat simplification reduces ant species numbers and alters dominance relationships (Roth *et al.*, 1994; Perfecto & Snelling, 1995; Bestelmeyer & Wiens, 1996; Kidd & Longair, 1997; Vasconcelos, 1999; Vasconcelos *et al.*, 2000). Fire can simplify natural environments affecting, in turn, ant community attributes (Andersen, 1991; MacKay *et al.*, 1991; York, 2000). Fires can reduce nest sites and food for ants, and modify some microclimatic variables, such as ground temperature (Andersen, 1991; MacKay *et al.*, 1991).

In Northern Patagonia, a region that includes habitats including scrub and steppe, fires are a common feature in the dynamics of these natural systems. It has been estimated that for the last 100 years, successive fire intervals have ranged from 3 and 17 years (Veblen *et al.*, 1999). In this region, despite their abundance, ants have been poorly studied. As far as we know, there is no detailed description of ant community composition after Kusnezov (1953), much less, an examination of the role of fire on such communities. We investigate the effects of recent fires on the ant assemblages in two habitats of north-western Patagonia, scrub and steppe, which differ in vegetation structural complexity.

METHODS

Study area

The study area was located at the eastern boundary of the Nahuel Huapi National Park, within ecotonal areas of a marked west-east rainfall gradient (3500–350 mm year^{-1} in approximately 100 km) characteristic of north-western Patagonia (41°S–71°W). Following this gradient, the vegetation physiognomy determines at least 3 distinctive habitats: (a) evergreen forest dominated by *Nothofagus dombeyi*, (b) scrub dominated by mixed tree and shrub vegetation including *Austrocedrus chilensis*, *Lomatia hirsuta*, *Maytenus boaria* and *Schinus patagonicus*, and (c) xeric steppe dominated by patches of tussock grasses such as *Stipa speciosa* and small shrubs such as and *Mulinum spinosum* (Dimitri, 1962). Mean annual temperature is 8 °C. Mean minimum in July, the coldest month, is −2 °C, and the mean maximum in January, the warmest month, is 23 °C.

During the summer of 1996, a great part of the study area experienced extensive fires, which, in a patch-like fashion, affected mainly scrub and steppe zones. Therefore, a mosaic including both burned and unburned sites defined by sharp borders were delimited. Natural features that could directly influence ant communities did not determine the limits of the burned subsites. Contrasts across borders allowed the comparison of changes in a given local ant assemblage due to fires. Furthermore, the presence of several borders enabled consideration of these changes across different assemblages within the same habitat, thus providing replication. Sampling units (henceforth referred to as sites) were defined as an area of approximately 2 ha bisected by the fire border. Thus, each site includes 2 plots of approximately 1 ha, each corresponding to the burned and unburned areas delimited by the fire border. A total of 12 sites (4 in steppe and 8 in scrub) were located within an area of approximately 150 km^2. Within each habitat, sampling sites were separated by 3–6 km. Sampling was carried out during the first summer following the fires (December–March 1997).

Ant and vegetation sampling

A total of 80 bait traps were randomly placed in each site, 40 in the burned plot and 40 in the unburned plot. Traps consisted of open plastic containers (10 cm in diameter and 10 cm deep) baited either with tuna or honey (20 traps with each bait) in order to attract ground ants with different foraging habits. Containers were neatly buried in the soil to facilitate ant access to the baits. We avoided locating trap within 20 m from the border to prevent ants foraging in either burned or unburned areas from falling in traps located in the opposite plot. Although bait traps can underestimate species richness and may give a biased representation of ant species composition (Folgarait, 1988; Fisher, 1999), such method has been successfully used in comparative studies (Andersen, 1992; Medel & Vásquez, 1994; Roth *et al.*, 1994; Perfecto & Snelling, 1995; Bestelmeyer, 1997). Additionally, because bait traps permit ant recruitment, abundance at baits can also be used as a guide to behavioural dominance (Andersen, 1997b). Baits were diurnally placed because in the study area nocturnal ant activity is practically absent (A.G. Farji-Brener, unpublished data).

At each site, traps were placed at peak daily ant foraging activity. Daily peak activity patterns were checked through preliminary sampling and adjusted as the season progressed. After 3 h, traps were collected, covered and carried to the laboratory for species identification and tallying. Ants were identified using a specific key for the ants of north-west Patagonia (Kusnezov, 1953).

Because no single diversity index encompasses all the characteristics of an ideal index (Magurran, 1988; Krebs, 1989), a combination of them that reflects richness, dominance, evenness, relative abundance, and similarity were used. In accordance with recent ant community studies, we chose to use S (species richness), H (Shanon-Wiener's diversity index), E (evenness) and IS (Index of similarity) to examine the effect of fire on ant assemblages (Andersen, 1992; Roth *et al.*, 1994; Perfecto & Snelling, 1995; Cerdá *et al.*, 1997; Cros *et al.*, 1997). Shannon's diversity index (H), was calculated in each burned and unburned sites as, $H = -\Sigma(P_i \times \ln P_i)$, where P_i was the proportion of individuals of species *i*. Evenness index was calculated as: $E = H/\ln S$. Similitude index was calculated as $IS = S_{ij}/(S_i + S_j - S_{ij})$ where S_{ij} is the number of species found in both sites that are being compared, S_i is the number of species founded in the site *i* and S_j number of species founded in the site *j*. The index of similitude goes from 0 (no species in common) to 1 (100% of species in common).

Results were examined across two spatial scales. For scrub and steppe areas separately, ant abundance for each species were pooled across burned and unburned sites. This allows us to view a broader scenario of the effects of fire on the ant assemblages in each habitat. At this large scale, we compared H-values using a specific test for the comparison of diversity (Zar, 1984). In turn, by looking at each site as a replicate, the local variation of the effects of burning within scrub and steppe areas may be observed. At this scale we compared ant diversity between burned and unburned sites (separately for steppe and scrub areas) by means of a one-way blocked nonparametric ANOVA (Friedman's test), where each site was considered as a block (see Roth *et al.*, 1994). Species abundance between burned and unburned sites was compared using paired *t*-tests. In addition, a Principal Component Analysis (PCA) was used to ordinate sites according to ant species composition and abundance. Species abundance (ln transformed) of all the species sampled was included in the analysis.

Vegetation cover (basal) in each site (both grasses and shrubs) was sampled to describe the effect of the recent fire on vegetation in each site. At each subsite, ten 10-m long transects were randomly located and the presence of living plant cover was sampled at 10-cm intervals. A cover index (CI) was made as follows CI = no. of points with cover/100[total number of points]. This index takes values between 0 (no plant cover) to 1 (maximum plant cover).

RESULTS

We caught a total of 9774 ants assigned to 11 species (*c.* 75% of the total ant species described for the sampling region, Kusnezov, 1953). Seven of these species were recorded in the steppe and 8 in the scrubland. However, in spite of the fact that both habitats had a similar number of species, the simililarity index was low (IS = 0.36). Shared species, such as *Dorymyrmex richtieri* and *D. tener*, were common in open habitats (Table 1).

Vegetation cover was affected differentially by fire in the different areas. In the scrubland, plant cover in unburned sites was approximately 72.6 ± 7% vs. nearly 14.8 ± 3% in the burned subsites (mean ± 1 SE, $P < 0.001$, paired-*t*-test). In contrast, for steppe areas, plant cover was only slightly affected by fire (42.7 ± 9% for burned sites vs. 58.7 ± 13% for unburned sites $P > 0.10$, paired-*t*-test).

The effect of fire on the ant assemblage resembles the pattern described for the vegetation cover. In steppe areas, average ant diversity was similar between burned and unburned sites (mean ± 1 SE, 0.30 ± 0.12 vs. 0.32 ± 0.09, respectively, Friedman's test $\chi^2 = 0.05$, $P > 0.9$). In contrast, fire significantly reduced average diversity in scrubland (0.40 ± 0.1 for burned scrub vs. 0.55 ± 0.1 for

Table 1 Total number of individuals per ant species in scrub and steppe habitats, north-west Patagonia. Numbers in parenthesis are the percentage of sites in which each species was found. $^*P < 0.05$

Species	Scrub (8 sites)		Steppe (4 sites)	
	Unburned	Burned	Unburned	Burned
Camponotus chilensis	24 (25%)	20 (25%)	–	—
Camponotus distenguendus	225 (37.5%)	138 (50%)	2 (25%)	—
Dorymyrmex antarcticus	—	—	104 (25%)	204 (25%)
Dorymyrmex exsanguis	—	—	10 (50%)	47 (25%)
Dorymyrmex richteri	374 (62.5%)	412 (87.5%)	1234 (100%)	517 (100%)
Dorymyrmex tener	322 (75%)	1282 (100%)	1933 (100%)	2575 (100%)
Ephebomyrmex angustus	13 (37.5%)	—	—	—
Ephebomyrmex odouratus	13 (25%)	96 (37.5%)	—	—
Lasiophanes sp. 1	91 (37.5%)	3 (12.5%)	—	—
Lasiophanes valdiviensis	9 (25%)	—	—	1 (25%)
Pogonomyrmex carbonarius	—	—	36 (50%)	59 (50%)
Total richness	8	6	6	6
Total no. of individuals	1071	1951	3319	3403
Diversity (H)	0.65	0.43*	0.37	0.35
Evenness (E)	0.73	0.55*	0.47	0.45
Similitude (IS)	0.75	(0.36)	0.86	

unburned scrub, Friedman's test $\chi^2 = 4.5$, $P < 0.03$). The same pattern was obtained when data from burned and unburned sites were pooled for either steppe and scrub areas (Table 1). The lower ant diversity recorded in burned sites within scrubland, was a consequence of both species loss and changes in ant abundance, as fire affected ant species differentially. For instance, *Camponotus distingendus* and *Lasiophanes* sp. 1 suffered reductions of two- and thirty-fold, respectively, in burned scrub. Other, more rare species such as *Lasiophanes valdiviensis* and *Ephebomyrmex angustus* were absent from burned sites. On the other hand, some species increased their numbers after the fire. For example, *Dorymyrmex tener* and *Ephebomyrmex odouratus* underwent a four-fold and a seven-fold increase in abundance, respectively (Table 1 and Fig. 1).

In the PCA analysis, only the unburned scrub subsites could be identified as a group along the first axis, which accounted for 25% of variance (Fig. 2). Burned and unburned steppe as well as the burned scrub subsites cannot be separated through species composition along this axis. Axis 1 correlates positively with ant abundance of *Ephebomyrmex angustus* and *Lasiophanes* sp. 1, and negatively with that of *Dorymyrmex tener* ($r = 0.84$, 0.78 and -0.69, respectively, $P < 0.05$). The second axis (17% variance) does not separate subsites according to fire occurrence. We found significant correlation between this axis and the abundance of *D. antarcticus* and *Pogonomyrmex carbonarius* ($r = 0.95$ and 0.94, $P < 0.05$), both species were found exclusively in steppe areas.

DISCUSSION

In north-west Patagonia, the consequences of recent fires on the native ant assemblages varied with habitat. Whereas ant diversity was similar in both burned and unburned sites in the steppe, it was significantly reduced by fire in scrub areas. Fire largely affects ant assemblages indirectly, through fire-induced modifications to habitat, food supplies, and interspecific competition (Andersen, 1991; York, 2000). In the steppe, an area with natural bare ground patches, low vegetation fuel biomass and rapid regeneration; plant cover was similar in burned and unburned sites after only 1 year. Thus, fire-related changes for ants in this habitat are probably small and short-term. In contrast, fire represented a major disturbance in scrub sites, reducing vegetation cover by approximately 80%. Following such changes, ant

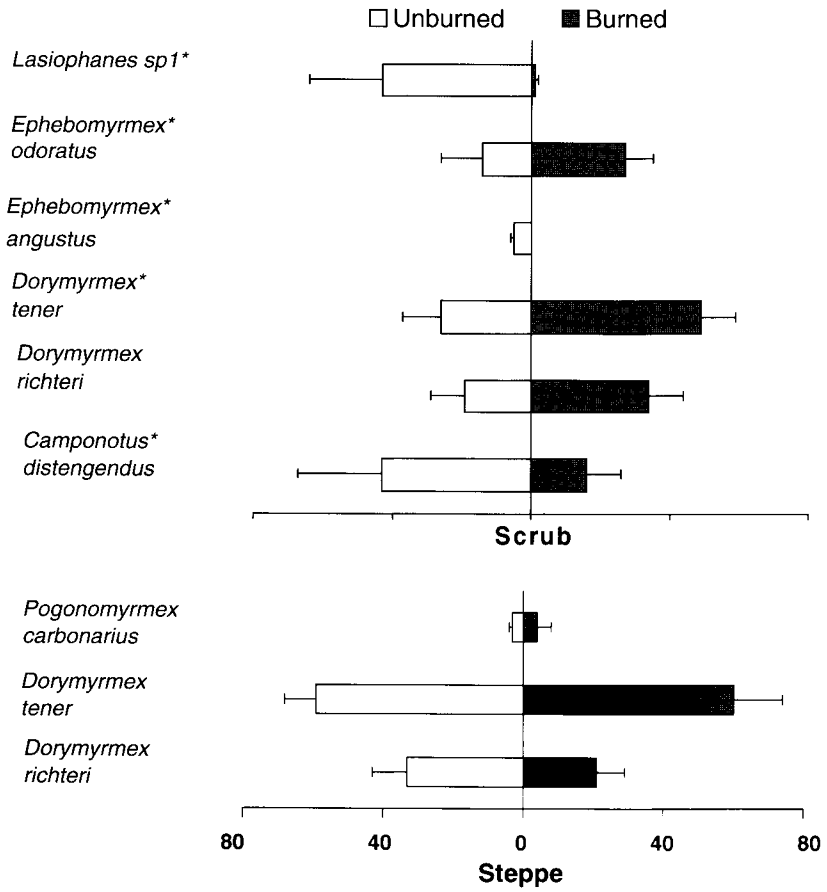

Fig. 1 Relative abundance (mean ± 1 SE, in percent) of the most common ant species captured in burned and unburned steppe and scrub. Only species present in more than the 25% of the sites are shown. $*P < 0.05$, paired *t*-tests.

diversity was significantly reduced in the burned scrubland.

Both species loss and changes in the dominance relationships explained this reduction in diversity. In general, the ants absent in burned scrub were rare species associated with the woody vegetation of mesic areas (see also Andersen, 1991; MacKay *et al.*, 1991; York, 2000). For instance, *Ephebomyrmex angustus* and *Lasiophanes* spp. are endemic species with distributions restricted to the humid areas of Patagonia (Kuznesov, 1953) and thus were probably affected by changes in soil microclimate as well as by the reduction in food and nest sites due to fires. On the other hand, other more frequent species become significantly less abundant. This is the case for *Camponotus distinguendus*, an ant that can live and feed on trees and shrubs, which is presumably affected by the reduction in plant cover. Ants are considered to be good bio-indicators of the degree of habitat disturbance, because many species are responsive to environmental change (Roth *et al.*, 1994; Andersen, 1997a; York, 2000). Additionally, the changes in ant communities can reflect those of other fauna (Majer, 1983; York, 2000). Therefore, the relative abundance of *Camponotus distingendus*, *Ephebomyrmex angustus* and *Lasiophanes* spp. in north-west Patagonia could be used to monitor scrub ecosystem recovery from disturbances (see Andersen, 1991, 1993; Cabrera *et al.*, 1998).

In contrast, other species become more frequent in burned scrub sites. *Ephebomyrmex*

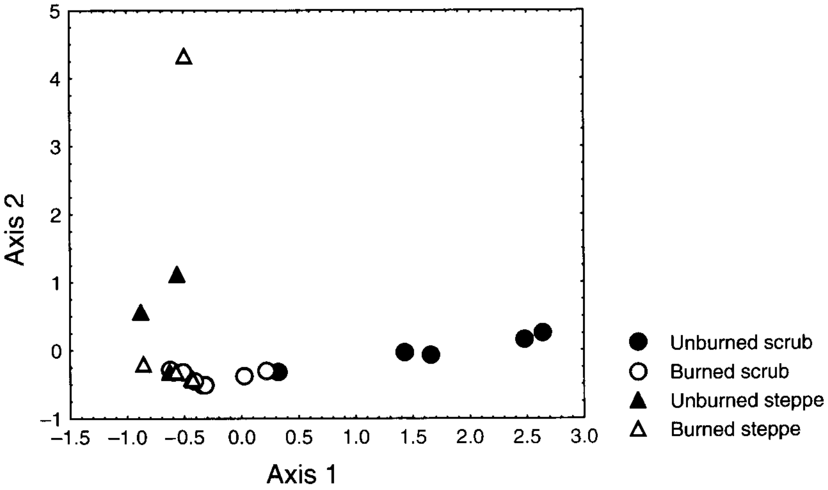

Fig. 2 PCA bidimensional ordination plot for 24 plots (8 burned and unburned scrub, and 4 burned and unburned steppe sites) according ant species abundance.

odouratus, a rare species whose geographical distribution includes more xeric areas (Kusnezov, 1953), undergoes an increase in abundance (Table 1, Fig. 1). Further work is needed to establish if this increase is due to a release of competitive pressure held by its congeneric species *Ephebomyrmex angustus*, and/or to this species' ability to live in more xeric conditions. However, the drop in diversity in burned scrub sites is coincident with the remarkable increase in abundance of *Dorymyrmex tener.* Considering all sites together, this species undergoes an increase from nearly 300 to 1300 individuals, representing a change from 30% to 67% of all ants being caught (Table 1). This pattern is similar to that observed when each site was analysed as an independent sample (Fig. 1). *Dorymyrmex tener* is a generalist predatory ant which lives and forages in open soil and rocks (Kusnezov, 1953). This ant species, which is behaviourally dominant in disturbed and open areas (Farji-Brener, unpublished data), is also common in the unburned scrub. *Dorymyrmex tener* is also the most abundant species in the steppe (*c.* 70% of all captured ants) and does not suffer a reduction in abundance by the effects of fire in this habitat. Given that this ant species lives in xeric microclimatic conditions, it may be better pre-adapted to the postfire scrub structure (Kusnezov, 1953).

In other regions, *Dorymyrmex* spp. are generally subordinate in aggressive interactions with other species of ants (Andersen, 1997b; Bestelmeyer, 1997, 2000). Subordinate ant species are known to have broader physiological tolerances than many of their competitors, allowing them to forage under extreme daily temperature conditions to avoid dominant ants (Fellers, 1987; Andersen, 1992; Cerdá *et al.*, 1997, 1998; Bestelmeyer, 2000). It has been suggested that such tolerance to large daily microclimatic fluctuations may permit their expansion into climatically extreme regions where they may become the dominant species (Bestelmeyer, 1997). Our findings support this view. In Argentina, most of the *Dorymyrmex* species are subordinate in the xerophilous subtropical forests of the Chaco region (c.25°S) (Bestelmeyer & Wiens, 1996; Bestelmeyer, 1997, 2000), but are numerical and behavioural dominant in the harsher areas of Patagonia (c.41°S, Table 1 and Fig. 1, Farji-Brener, unpublished data). Moreover, in north-west Patagonia, *Dorymyrmex tener* can enhance their dominance when the area they inhabit becomes harsher for other ants. The existence of a woody vegetation cover naturally buffers local soil temperature fluctuations, creating microclimatic heterogeneity, allowing *D. tener* to share its numerical dominance with other less heat-tolerant ant species in scrub habitats (Table 1).

Fires, by reducing plant cover, increase the availability of open habitats that are ideal for such heat-tolerant ant species (Andersen, 1991, 1992; Kidd & Longair, 1997).

Past work has also noted that the reduction of vegetative structure may lead to lower diversity and to the increase in dominance of stress-tolerant species in ant communities (Greenslade & Greenslade, 1977: Risch & Carroll. 1982: MacKay *et al.*, 1991). However. others have shown that reductions in vegetative structure may also enhance ant diversity by reducing the activity of dominant species (Andersen & Yen, 1985; Andersen. 1991). The course ant diversity changes take after disturbances may depend on both the changes in habitat structure and on the ant assemblage structure (Bestelmeyer & Wiens, 1996). For example, ant diversity in tropical forest declines strongly with structural simplification of the vegetation because the regional ant fauna consists largely of forest-habitat adapted taxa (Roth *et al.*, 1994; Perfecto & Snelling, 1995; Vasconcelos, 1999; Vasconcelos *et al.*, 2000). In contrast, ant diversity is lower in the wooded sites of the Australian semiarid zones where open-habitat adapted species are more common (Andersen, 1992, 1997b). In addition, because ant assemblages are commonly structured through competitive hierarchies (reviewed in Hölldobler & Wilson, 1990), the characteristics of the dominant group can also determine the effects of disturbance on ant diversity. If the dominant species are intolerant to the habitat changes generated through the disturbance, their reduction may be accompanied by an increase in the subdominant groups implying an increment in diversity (Cros *et al.*, 1997). In contrast. if the assemblage is dominated by ant species pre-adapted to the post-disturbance conditions, we can expect an increase in the dominance of this species causing a decrease in diversity. It would be interesting to explore in what cases the post-disturbance conditions increase habitat favourability for dominant ants, decreasing diversity. We may expect that this effect will be more important at higher latitudes, given that abiotic stress increases with latitude (Kaufman, 1995) and probably so does the dominance of stress-tolerant ants.

Because our study was limited to 1 year following fire, we cannot ascertain whether the changes induced by fire on the Patagonian ant communities will be sustained in time (see Brian *et al.*, 1976; York, 2000). However, given that fires occur repeatedly in different scrub sites throughout the region, the changes in ant assemblages may be sustained in a patchwork fashion at a regional scale. It is well known that in northern Patagonia the composition of some plant assemblies can be dynamically sustained by disturbances (Veblen *et al.*, 1992; Kitzberger & Veblen, 1997, 1999). Our results indicate that this may be also true for ants.

Several studies have shown that the intrinsic characteristics of the disturbances, such as intensity and frequency, are important factors determining the changes in the structure and/or composition of natural communities (see Pickett & White, 1985). The implication stemming from our work is that the intrinsic characteristics of the disturbed habitat, such as structural complexity and regional context, can also be very important in order to understand the effects of disturbance on species assemblages (Pimm, 1991).

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