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Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile

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Abstract Habitat fragmentation is recognized as one of the main factors associated with species extinction and is particularly acute in South American forest habitats. In this study, we examined the effects of forest fragmentation on the beetle assemblage at the relict temperate forest of Fray Jorge (Chile). We evaluated the following hypotheses: (1) there is a strong edge effect, so that the number of beetle species and individuals increases away from the edge, towards the inner part of each fragment, (2) this pattern should be apparent in the larger fragments but not in the smaller ones, where edge effects are expected to be stronger, and (3) there should be a significant interaction between number of species/individuals found inside and outside fragments (i.e., in the matrix) and season, because of an increase in aridity and water stress during austral summer months. We found that the relationship between the number of individuals and number of species vs distance from the matrix towards the forest interior was affected by fragment size and season. In general, both number of species and individuals tended to increase from the matrix towards the forest edge and then either decrease, increase or maintain a constant level, depending on fragment size and season. The result of an ANOVA analysis, which used season, size, and position (inside vs outside fragments) as factors and number of individuals as the response variable, showed a significant effect of fragment size, position, and season and a significant interaction between fragment size and season, season and position, and size and position. ANOVA analysis using number of species as the response variable showed that area, season, and position all had significant effects. The results also showed a significant interaction

between size and season and between season and position. Our results emphasize the existence of strong fragment-size and seasonal effects modulating both the response of beetles to fragmentation and their abundance and distribution in temperate areas. Thus, seasonal dynamic effects can be of paramount importance to demonstrate and understand the effect of habitat fragmentation upon arthropod assemblages in temperate areas.

Keywords Temperate forest · Insects · Fragmentation · South America

Introduction

The fragmentation of habitats features among the top disrupters of ecosystem functioning and underlies most of the current biodiversity losses at a global scale (Saunders et al. 1991; Vitousek 1994). Forest landscapes in South America are currently threatened due to habitat degradation, loss, and fragmentation (WRI 1990). Among the few well studied systems in South America (for overviews, see Schelhas and Greensberg 1996; Laurance and Bierregaard 1997), are the tropical rainforest in Brazil (Lovejoy et al. 1984, 1986; Bierregaard and Lovejoy 1989; Bierregaard et al. 1992), the Chaco dry forest in Argentina (Aizen and Feinsinger 1994a, b), the western Andean cloud forest in Colombia (Kattan et al. 1994), and the coastal forest of western Ecuador (Parker and Carr 1992). Although these studies differ in terms of the taxonomic groups studied, sample size, duration, and methodologies, they underscore the adverse effect forest fragmentation has, e.g., fostering local extinction of species, severe population declines, and disruption of important ecological processes, such as pollination and fruit dispersal. Temperate forests in southern South America are not an exception to this unfortunate trend (Estades 1994; Willson et al. 1994; Sieving et al. 1996; Cornelius et al. 2000). In this area, human encroachment, fire use, agriculture, and commercial logging have caused intense fragmentation and reduction of

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forest area (Armesto et al. 1994; Bustamante and Grez 1995; Lara et al. 1996).

The fragmentation of habitats results in edge effects, as a consequence of modifications in the physical conditions, such as wind, water, and solar radiation fluxes (Saunders et al. 1991), thus exposing the organisms that remain in the fragments to the conditions of a different surrounding ecosystem (Murcia 1995). Edge effects are not only related to physical changes, but also to biotic changes related to the exposure of plant and animal populations to new ecological interactions (Wilcove et al. 1986).

In general, three types of edge effects can be recognized: abiotic effects, direct biological effects, and indirect biological effects (Murcia 1995). These effects usually penetrate deep into forest fragments, leading to changes in the distribution, abundance, interaction, and diversity of species (Laurance and Yensen 1991; Schelhas and Greensberg 1996; Laurance and Bierregaard 1997; Gascon and Lovejoy 1998). It is becoming increasingly clear that edge effects are highly dynamic in both time and space (Gascon et al. 2000; Newmark 2001) as a result of the interaction between the forest fragment and the matrix attributes. In particular, Gascon et al. (2000) show that, when the harshness of the matrix is high, in terms of degrading the forest habitat within fragments, the edges usually recede, resulting in a greater penetration of edge effects and in the reduction of fragment area.

The effects of habitat fragmentation have been studied in many vertebrate species but less often in arthropods living in natural forest landscapes. This should be of concern, because arthropods represent a large proportion (over 90%) of the known biodiversity (Erwin 1982) and because available evidence suggests that fragmentation may cause the disruption of key biological processes that maintain biodiversity and ecosystem functioning, such as pollination, seed dispersal, and nutrient recycling, all of which are insect-mediated processes (e.g., Jennersten 1988; Aizen and Feinsinger 1994a, b; Didham et al. 1996).

Fragmentation has been shown to affect insect species richness and abundance (Didham 1997; Carvalho and Vasconcelos 1999; Golden and Crist 1999; Martikainen et al. 2000). In particular, insects have been shown to be sensitive to changes in fragment area and/or edge proximity (Webb et al. 1984; Klein 1989; Webb 1989; Margules et al. 1994; Didham 1997; Didham et al. 1998a; Harris and Burns 2000). Thus, insect species can be useful bioindicators of the type of habitat change and degradation usually associated with fragmentation (Fournier and Loreau 1999).

In this study, we examined the effects of forest fragmentation on the beetle assemblage at the relict temperate forest of Fray Jorge. The relict character of this forest, restricted to the coastal range of semi-arid Chile since the Pleistocene and currently located 1,000 km from the continuous temperate forest of southern Chile, provides an extreme scenario to study the effects of for-

est fragmentation upon insects, in terms of isolation and contrasting climatic regime. We evaluated the following hypotheses:

1. There is a strong edge effect which causes the number of beetle species and individuals to increase towards the inner part of each fragment (Didham et al. 1998a, b). We hypothesize this because forest habitat increases from the edge towards the inner part of fragments and because these are relict temperate forest fragments surrounded by a matrix of semi-arid vegetation.
2. This pattern should be more apparent in the larger fragments than in the smaller ones, where edge effects are expected to be stronger due to their low area:perimeter ratio.
3. We expect a significant interaction between the number of species and individuals found inside and outside fragments (i.e., in the matrix) and the season. We hypothesize this because the study area is embedded in a region characterized by strong seasonal changes in average temperature and precipitation, such that the contrast between the matrix and the forest fragment habitat (and its biological consequences) changes through time. Further, we expect it to be stronger during the austral summer months, characterized by an increase in aridity and water stress.

Materials and methods

Study area

The study was carried out at a relict temperate forest in the Fray Jorge National Park (30° 40' S, 71° 30' W), located 110 km south of the city of La Serena, Chile. The climate is mediterranean-arid, with dry and hot summers and cool winters (Di Castri and Hajek 1976). Mean annual precipitation is 85 mm, distributed mainly between May and September (austral winter, Fig. 1). The forest fragments are restricted to sea-facing slopes on top of the coastal range (600 m elevation), where the humidity brought by moisture-laden "camanchaca" fog enables their existence. Forest fragments range over 0.3–21 ha in size. The fragmentation of this system is the result of natural processes linked to spatial heterogeneity in fog intensity and to human perturbations that occurred before Fray Jorge was declared a National Park in 1941.

Dominant plant species are the trees *Aextoxicon punctatum*, *Drimys winterii*, and *Myrceugenia correifolia*, the evergreen shrubs *Luma chequen* and *Raphitamnus spinosus*, one prostrate species *Griselinia scandens*, and several ferns in the genus *Hymnophyllum* (Araya et al. 1992). The scrub matrix surrounding the fragments is dominated by xeric vegetation and corresponds to the coastal stepparian Matorral of Coquimbo (Araya et al. 1992; Gajardo 1993), which also extends to the lowland area (200 m elevation).

The species composition of both plants and birds and the soil chemistry of the Fray Jorge forest closely resembles that of the Valdivian temperate forest currently distributed 1,000 km south of Fray Jorge (Villagrán and Armesto 1980; Pérez and Villagrán 1985, 1994; Cornelius et al. 2000). Recent floristic and paleontological studies indicate that this relict forest was derived from a widely distributed flora (the mixed and subtropical flora of coastal Chile), which became increasingly isolated due to climatic changes towards the end of the Tertiary (Troncoso et al. 1980; Villagrán and Armesto 1980; Hinojosa and Villagrán 1997; Villagrán and Hinojosa 1997). It became restricted to its present location, associated to the coastal mountain range, during the Quaternary (Troncoso et al. 1980; Villagrán and Hinojosa 1997).

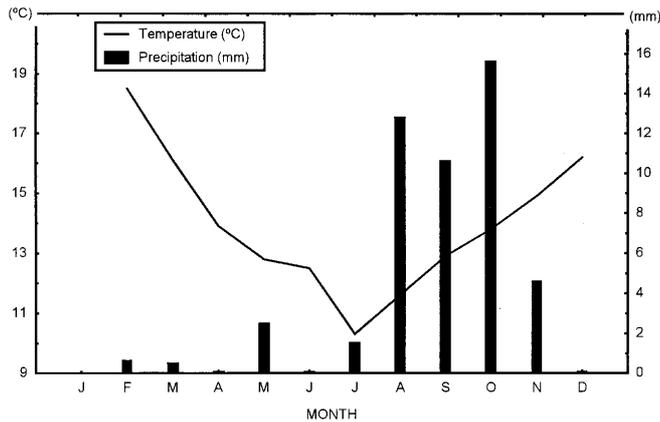


Fig. 1 Mean monthly temperatures and total precipitation at La Serena in 1999

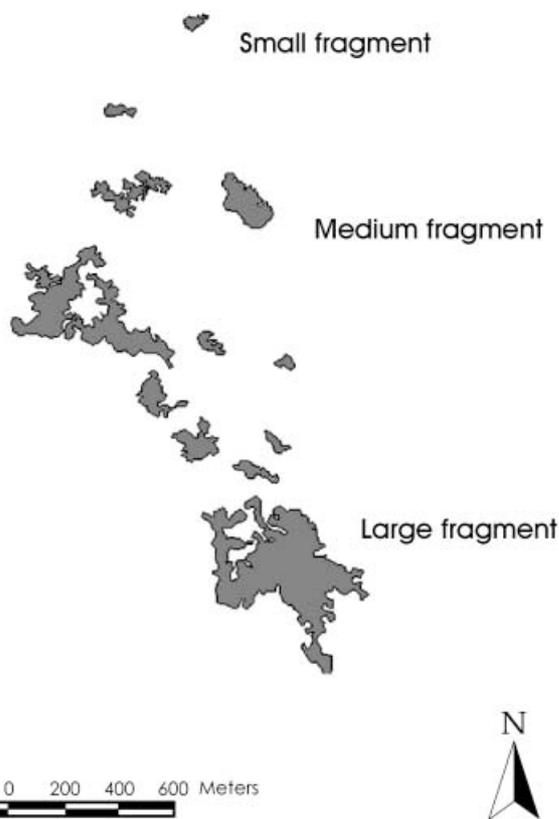


Fig. 2 The northern part of the Fray Jorge study area, showing the location of the small, medium, and large fragments used in this study

Methodology

At Fray Jorge, we used aerial photographs (1:20,000 scale) taken in 1993 to select three forest fragments. We selected fragments so as to obtain a wide range of fragment areas (0.3–14.2 ha) and to maximize the distance between them (to assure independence), which ranged over 360–3,130 m (Fig. 2). The final selection of sites was subject to accessibility and permission from the National Park Administration. Because these forest fragments are in a protected area, minimal changes in their size have occurred during 1993–1998. Fragment sizes were 0.3 ha, 2 ha, and 14.2 ha.

We sampled ground beetles by placing 30 pitfall traps in each fragment (Greenslade 1964; Fournier and Loreau 1999). Traps were made of small plastic cups (200 cm³) and were arrayed in linear transects in each fragment, running perpendicular from the fragment's edge to the center. The distance between traps was 5 m in all transects. In the small- and medium-sized fragments, we placed three 45-m transects with 10 pitfall traps in each. In the largest fragment, we placed two 70-m transects, with 15 pitfall traps in each to ensure that they ran from the matrix to the center of the fragment. Thus, for each fragment we had 30 pitfall traps, 15 traps inside and 15 outside the fragment.

Fragments were sampled during each season [austral summer (January 1998), autumn (May 1998), winter (August 1998), spring (October 1998)]. Traps were operated for 48 h, encompassing 2 nights and 2 days. Because ours was a comparative analysis and the same trapping effort was used on all occasions, species richness was calculated as number of species captured per trap.

Our first hypothesis was assessed using curvilinear regression analysis (Sokal and Rohlf 1995) and fitting models of the form: $y = a + bx^q + cx^b + dx^p$, where distance from the matrix to the center of the fragment was used as the independent or predictor variable and number of species or individuals (previously transformed to logarithms, pooling data for traps located at the same distance) was the response or dependent variable. This analysis was repeated for each fragment and for each season. Model fitting was carried out in S-PLUS, using the GLM procedure (Venables and Ripley 1997). To discriminate among models we used Mallows's C_p statistic (Venables and Ripley 1997).

Our second hypothesis was analyzed using three-way ANOVAs; and the response variables were: number of individuals and number of species. The explanatory variables of the model were: season (with four levels: winter, spring, summer, autumn), size of fragment (with three levels: large, medium, small), and position within fragment (with two levels: outside, inside the fragment). To test our third hypothesis, we looked for the significance of the interaction between season, position, and size.

Results

We collected 2,644 individuals during the four seasons, corresponding to 32 beetle species in 16 families (Table 1). The most species-rich families were: Tenebrionidae (5 spp), Curculionidae (5 spp), and Melyridae (3 spp).

Distribution and abundance along transects

The relationship between number of individuals and distance from the matrix varies as a result of fragment size and season (Fig. 3, Table 2). In general, no relationship was apparent for the small fragment, while relationships tended to be monotonic and positive for the medium-sized fragment and were positive but non-monotonic for the large fragment. One exception to the trends is represented by the small fragment in autumn, with a nonlinear relationship between number of individuals and distance that peaked at the edge of the fragment. Similarly, the medium fragment in winter showed a negative relationship, such that the number of individuals decreased from the matrix to the fragment, while the opposite was observed during the other seasons. Finally, the large fragment in winter showed a peaked relationship, with the number of individuals increasing at the edge and de-

Fig. 3a–l Plots of the relationship between number of individuals and distance from the matrix. **a–d** Small fragment in summer, autumn, winter, and spring, **e–h** medium fragment in summer, autumn, winter, and spring, and **i–l** large fragment in summer, autumn, winter, and spring. The *dashed line* indicates the location of the edge

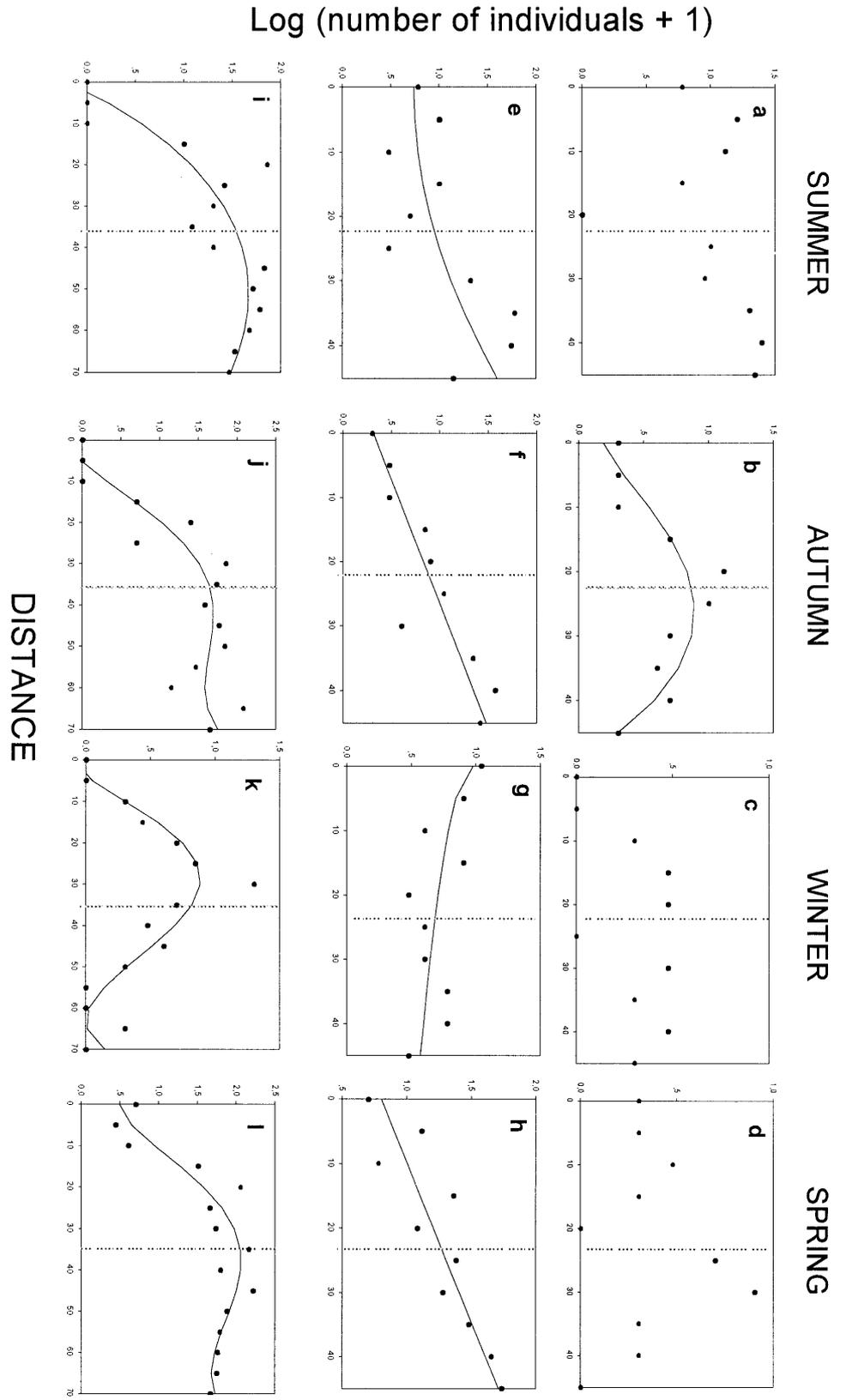


Table 1 Beetle species captured in Fray Jorge, with season and position of capture. A autumn, I inside fragment, O outside fragment, S summer, SP spring, W winter

Family	Species	Season captured	Trap position
Tenebrionidae	<i>Enneboens chilensis</i>	S, A, SP	I-O
	<i>Tribolium</i> sp.	W	O
	<i>Myrmecodema michelbacheri</i>	SP	I-O
	<i>Praocis</i> sp.	SP	O
	<i>Nictopetus</i> sp.	S	O
Scolytidae	<i>Gnatotrichus cortiloides</i>	S, SP	I-O
Biphylidae	<i>Diplocoelus</i> sp.	S, A, W, SP	I-O
Staphylinidae	sp. 1	S, A, W, SP	I-O
	<i>Longivilius</i> sp.	S, W, SP	I-O
Lagriidae	sp. 1	S, A, W, SP	I-O
	sp. 2	SP	I
Chrysomelidae	<i>Chaetochema</i> sp. nov.	S, A, W, SP	I-O
	<i>Protosilapha</i> sp.	W, SP	I-O
Melyridae	<i>Amecocerus girandi</i>	S, SP	O
	<i>Amecocerus</i> sp.	S	I-O
	<i>Arthrobrachus nigromaculatus</i>	SP	O
Languriidae	<i>Loberus</i> sp.	S, W, SP	I-O
Leiodidae	sp. 1	S, SP	I-O
	<i>Eunemadus</i> sp.	A, SP	I-O
Curculionidae	<i>Acalles rotundatum</i>	S, A, W, SP	I-O
	<i>Puranius inecualis</i>	A, W	O
	<i>Chemecoelus valparadisi</i>	W	O
	<i>Sibinia albovitata</i>	SP	I
	<i>Euophryum</i> sp.	SP	I-O
Elateridae	sp. 1	A	I-O
Scarabaeidae	<i>Trox (Polynoneus) ballatus</i>	S, A, W, SP	O
	<i>Sericoides</i> sp.	W	O
Ptiniidae	sp. 1	A, SP	I-O
	<i>Ptinus</i> sp.	W, SP	I-O
Anthixidae	<i>Licanurus</i> sp.	A	I
Colydiidae	<i>Synchita</i> sp.	SP	O
Bruchidae	<i>Lithraeus egenus</i>	SP	O

Table 2 Relationship between number of individuals (response variable) and distance from the matrix to the center of the fragment (independent or predictor variable), for fragments of different size and at different seasons. n.s. Not significant, P probability, r^2 coefficient of determination

Season	Small	Medium	Large
Summer	n.s.	$y = a + bx^2$ ($r^2 = 0.42$, $P = 0.042$)	$y = a + bx + cx^{1.5}$ ($r^2 = 0.7724$, $P = 0.0001$)
Autumn	$y = a + bx^{1.5} + cx^2$ ($r^2 = 0.7101$, $P = 0.013$)	$y = a + bx$ ($r^2 = 0.7996$, $P = 0.0005$)	$y = a + bx^2 + cx^{2.5} + dx^3$ ($r^2 = 0.8325$, $P = 0.0001$)
Winter	n.s.	$y = a + bx^{0.5}$ ($r^2 = 0.4207$, $P = 0.0425$)	$y = a + bx^2 + cx^{2.5} + dx^3$ ($r^2 = 0.7604$, $P = 0.0029$)
Spring	n.s.	$y = a + bx^{0.5}$ ($r^2 = 0.7973$, $P = 0.0005$)	$y = a + bx^2 + cx^{2.5} + dx^3$ ($r^2 = 0.8361$, $P = 0.0001$)

creasing towards the matrix and towards the forest interior area while, during the other seasons, the number of individuals inside the forest fragment remained relatively constant and were not affected by the distance to the edge.

In agreement with the patterns detected for the number of individuals, no relationship between number of species and position along the transect was detected for the small fragment, except in autumn (Fig 4, Table 3). For the medium fragment, the relationship tended to be monotonic and increasing except in winter, when richness decreased with distance, and in summer, when no relationship was apparent. Finally, the large fragment

showed a nonlinear and peaked relationship between richness and distance, with richness increasing toward the edge and then decreasing toward the forest interior. The only exception to this trend was observed during summer (Fig. 4).

The effect of fragment size, season, and position

The results of the ANOVA using season, size, and position as factors and number of individuals as the response variable (Table 4) show a significant effect of fragment size, position, and season, and a significant interaction

Fig. 4a–l Plots of the relationship between number of species and distance from the matrix. **a–d** Small fragment in summer, autumn, winter, and spring, **e–h** medium fragment in summer, autumn, winter, and spring, and **i–l** large fragment in summer, autumn, winter, and spring. The *dashed line* indicates the location of the edge

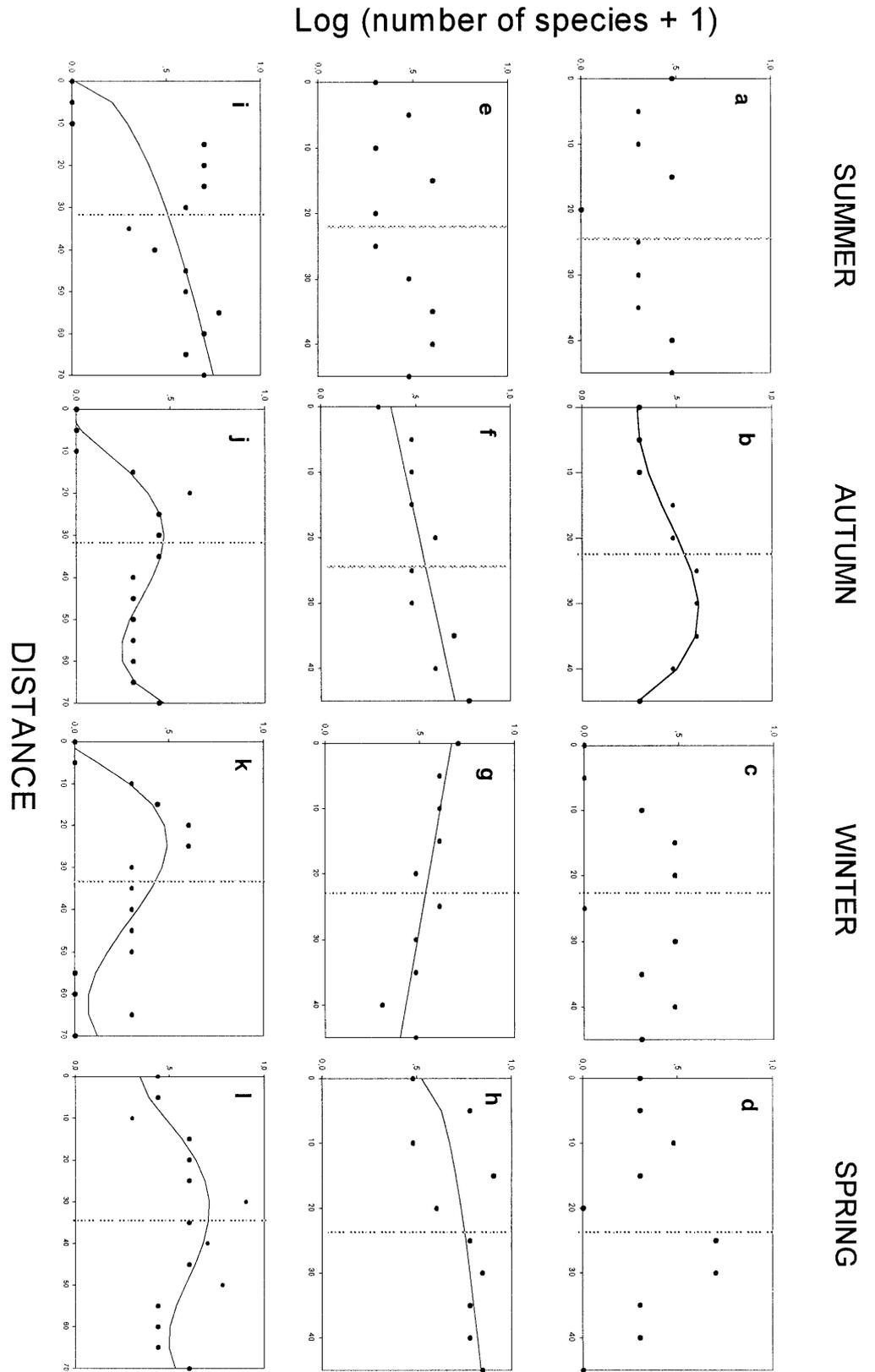


Fig. 5 Mean number of individuals by season, size of fragment, and position in the fragment (continuous lines inside fragments, dashed lines outside fragments). Large fragment (L) is 14.2 ha, medium fragment (M) is 2 ha, small fragment (S) is 0.3 ha

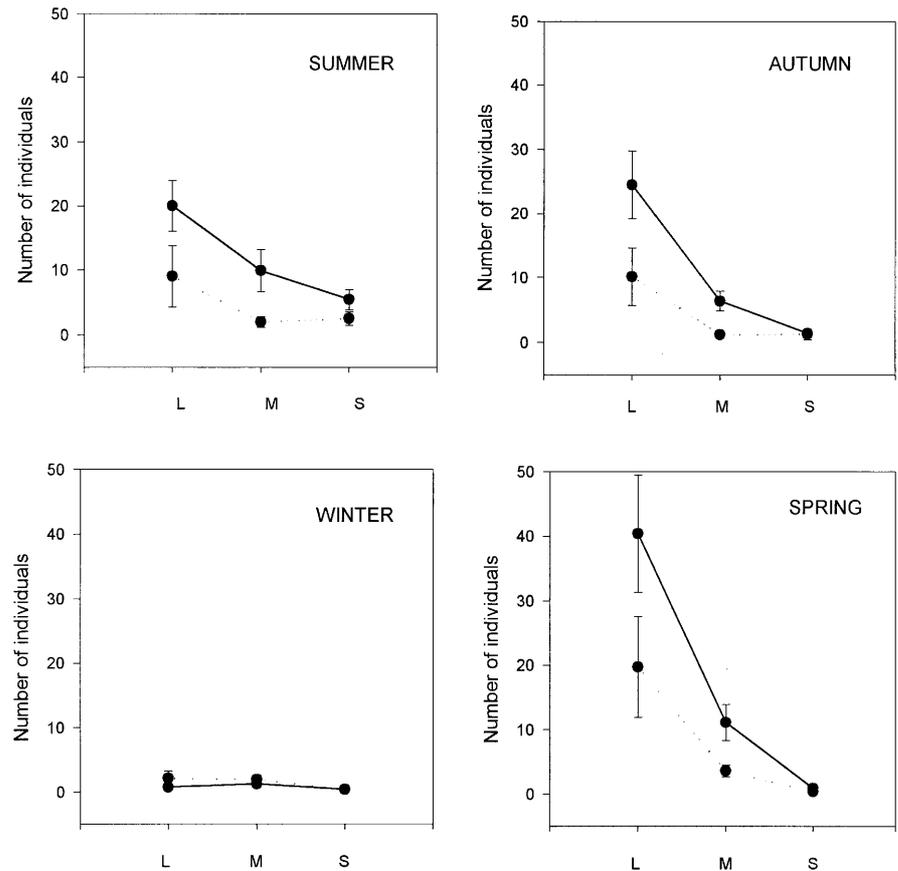


Table 3 Relationship between number of species (response variable) and distance from the matrix to the center of the fragment (independent or predictor variable), for fragments of different size and at different seasons

Season	Small	Medium	Large
Summer	n.s.	n.s.	$y=a+bx^{0.5}$ ($r^2=0.5423$, $P=0.0017$)
Autumn	$y=a+bx^{2.5}+cx^3$ ($r^2=0.9519$, $P=0.0001$)	$y=a+bx$ ($r^2=0.6892$, $P=0.0029$)	$y=a+bx^2+cx^{2.5}+dx^3$ ($r^2=0.7810$, $P=0.0006$)
Winter	n.s.	$y=a+bx$ ($r^2=0.6654$, $P=0.0040$)	$y=a+bx^{1.5}+cx^2+dx^{2.5}$ ($r^2=0.6936$, $P=0.0036$)
Spring	n.s.	$y=a+bx^{0.5}$ ($r^2=0.4005$, $P=0.0495$)	$y=a+bx^2+cx^{2.5}+dx^3$ ($r^2=0.5209$, $P=0.0379$)

Table 4 Results of the three-way ANOVA for the response variable number of individuals

Source	Sum of squares	Degrees of freedom	Mean squares	F-ratio	P
Season	6098.689	3	2032.896	12.584	0.001
Size	13519.072	2	6759.536	41.843	0.001
Position	2901.344	1	2901.344	17.960	0.001
Season × size	7135.394	6	1189.232	7.362	0.001
Season × position	1329.122	3	443.041	2.742	0.043
Size × position	1593.574	2	796.786	4.932	0.008
Season × size × position	1008.494	6	168.082	1.040	0.399
Error	54279.600	336	161.546	—	—

between fragment size and season, season and position, and size and position. The large fragment contains the highest number of individuals; and the number decreases with fragment size (Fig. 5), a phenomenon observed during all seasons but winter. The total number of individu-

als was higher inside than outside fragments (i.e., in the matrix, Fig. 5), but this difference disappeared during winter and was dependent on fragment area, such that it decreased as fragments become smaller. In addition, it is interesting to note that the number of individuals inside

Fig. 6 Mean number of species by season, size of fragment, and position in the fragment (continuous lines inside fragments, dashed lines outside fragments). Large fragment (*L*) is 14.2 ha, medium fragment (*M*) is 2 ha, small fragment (*S*) is 0.3 ha

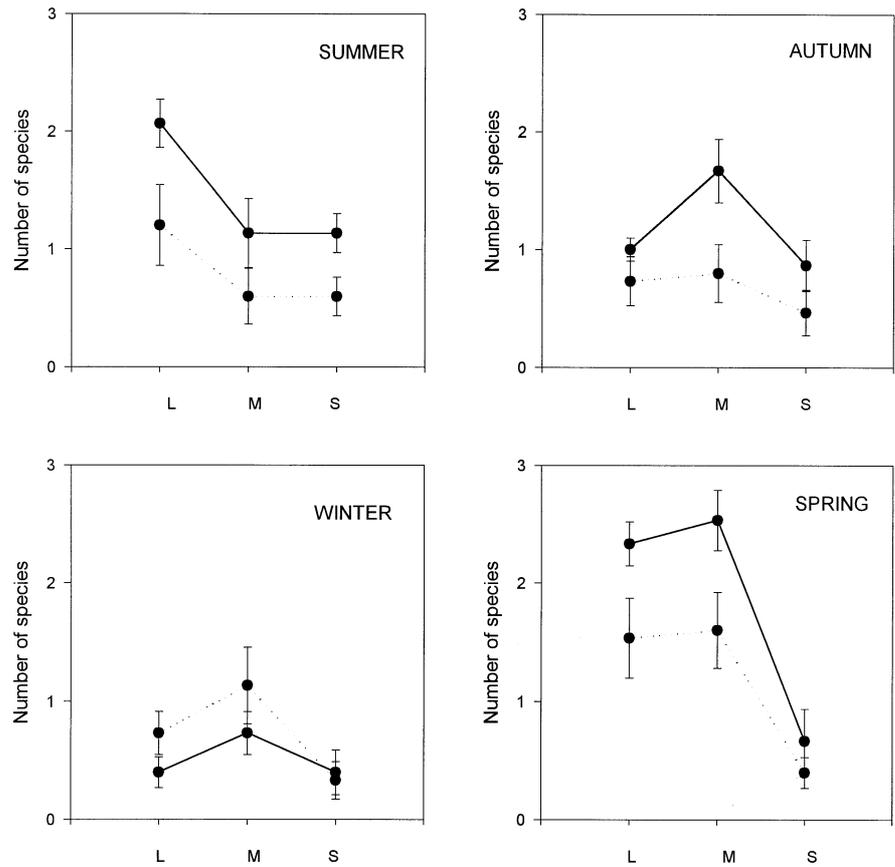


Table 5 Results of the three-way ANOVA for the response variable number of species

Source	Sum of squares	Degrees of freedom	Mean squares	<i>F</i> -ratio	<i>P</i>
Season	37.533	3	12.511	15.709	0.001
Size	34.272	2	17.136	21.516	0.001
Position	14.400	1	14.400	18.081	0.001
Season × size	30.683	6	5.114	6.421	0.001
Season × position	11.933	3	3.978	4.995	0.002
Size × position	0.417	2	0.208	0.262	0.770
Season × size × position	4.450	6	0.742	0.931	0.473
Error	267.600	336	0.796	—	—

and outside fragments decreased in a similar way with fragment area. The seasonal effect upon number of individuals is apparent in this, being lower during winter.

The ANOVA using number of species as the response variable showed that area, season, and position all had significant effects (Table 5). The result also shows significant interactions between size and season and between season and position. The number of species was higher in the medium fragment and lower in the small and large fragments (Fig. 6). Nonetheless, this pattern changed seasonally, such that, during summer, the large fragment had more species than either the medium or the small fragments. The number of species was generally higher inside fragments than outside, in the matrix (Fig. 6), but this trend reversed during winter, when more species were observed outside than inside. As with the number of individuals, the number of species inside and outside frag-

ments changed with fragment area, in a similar way. Finally, the number of species was high during spring and summer and decreased during autumn and winter (Fig. 6).

Discussion

We have shown that fragmentation affects the structure of beetle assemblages found in a southern temperate forest. In particular, we have shown that beetle species abundance and richness tends to increase from the matrix to the forest edge in large and medium-sized fragments in most seasons. However, no significant trends in either abundance or richness were found for the small fragment. Similarly, we found that the number of individuals and species varied significantly with position (inside vs outside fragments), size of fragment, and season.

Several studies have shown that beetle abundance and/or species richness increases significantly from the forest interior towards the forest edge (Didham et al. 1998a, b; Fournier and Loreau 1999). In contrast, our results show that, in general, the forest interior has the highest abundance and there is no general increase towards the edge. Further, the observed patterns are dependent on fragment size and season. For the medium-sized fragment, abundance decreases from the forest interior towards the edge and matrix habitat. However, for the large fragment, abundance does not change from the forest interior towards the edge, but it decreases sharply from the edge towards the matrix. Thus, in the medium-sized fragment (2 ha), beetle abundance changes in the same way as it does between the matrix and the edge in large-sized fragments. This is likely a result of the steep gradient in abiotic conditions between the matrix and the forest interior, which can only be ameliorated in large fragments (14.2 ha). These relict forest fragments are surrounded by a semi-arid matrix composed of small shrubs and grasses, where environmental temperature differences between matrix and the forest interior can reach 5 °C (Muñoz and Pisano 1947). This difference can be especially strong for insect species restricted to temperate forests (e.g., *Myrmecodema michelbacheri*).

A similar pattern is observed for richness, although richness does increase from the forest interior towards the forest edge in the large fragment. That this pattern is not apparent in summer (Fig. 4i), when the gradient in abiotic conditions is higher, supports the existence of dynamic edge-effects mediated either by the movement of species (see Niemelä 1988) across the forest and the matrix habitat continuum or by the seasonal turnover of species during the year. Data in the seasonal occurrence of species (Table 1), suggest that seasonal turnover may be important, with species associated with different habitats showing up in different seasons. However, the fact that the most abundant species were found in most seasons suggests that individual movement between microhabitats is also involved. Further studies should include: (1) a larger number of different-sized fragments to better characterize critical patch areas correlated with changes in the way abundance and richness change from forest to matrix habitats and (2) longer periods of time, in order to characterize the natural variability of this pattern. It is likely that edge- and size-effects not only change in intensity through the annual cycle, but also over larger scales, linked to climatic events, such as El Niño, which strongly affect the dynamics of ecosystems in central Chile (Jaksic 2001).

In agreement with theory, the small fragment has a low abundance and richness because of its small area and likely also because of strong edge-effects, due to its proportionally higher perimeter (e.g., Murcia 1995; but see Bolger et al. 2000). This is consistent with the ANOVA results, where position (inside vs outside fragments) affected the number of individuals and species and its effect varied with the size of the fragment, such that differences in abundance and species richness be-

tween inside and outside fragments decreased as fragments become smaller (Figs. 5, 6). However, the fact that changes in number of individuals and species inside and outside fragments followed similar trends as area increased suggests that fragments also affect matrix conditions in their surroundings (see Power 1996) and that these influences become stronger as area increases. This sort of mass effect implies that large-sized fragments are not only less affected by the edge-effect created by matrix conditions but also have a stronger effect on the matrix habitat surrounding them.

Our results showed that, within fragments, abundance was higher in all seasons, except winter, and was affected by fragment area, such that it decreased as fragments become smaller. Area-effects on arthropod abundance and richness have been well established in both experimental and field studies (e.g., Kareiva 1990; Collinge 2000; but see Golden and Crist 2000). Nonetheless, seasonal effects (Bolger et al. 2000) have not been fully analyzed with regard to their interaction with area- or edge-effects in fragmented landscapes. In our study, season significantly interacted with the effects of area and position. This is expected for insects in a temperate region with a strong seasonal climatic pattern (Di Castri and Hajek 1976). We expected that a seasonal effect would be strong in our system (hypothesis 3), considering its relict character and current distribution within a semiarid area. Our results support this contention. In fact, area-effects on abundance disappeared in winter and the effect of position was reversed (Figs. 5, 6). Both results are likely the outcome of seasonal changes in hydric stress and arthropod activity patterns associated with temperature and the amount of precipitation. Interestingly, although it is stronger in the spring (Cereceda et al. 1997), fog intensity appears not to be involved. However, further work is needed to understand the impact and interactions among the environmental factors responsible for the observed seasonal changes. The most important point is that, at least for temperate systems, seasonal dynamic effects can be of paramount importance to demonstrate and understand the effect of habitat fragmentation upon arthropod assemblages.

With regard to the effect of area upon species richness, field observations and experiments have reported a positive relationship, with larger fragments harboring more species (Didham et al. 1998a; Debinski and Holt 2000; Rukke 2000). We found that species richness was slightly higher in the medium fragment in all seasons but summer (Fig. 6). This is probably an anomaly associated with its position inside a small creek with a pronounced slope, which may affect the environmental characteristic of the fragment, particularly in terms of reduced temperature and increased fog retention. In another study (Cornelius et al. 2000), we found that the number of bird species was higher in this same medium-sized fragment.

A final word of caution is in order. As with most non-experimental field studies, our area treatment was not adequately replicated so as to capture the range of variability associated with area effects. In this regard, we in-

curred simple pseudoreplication (sensu Hurlbert 1984). This could affect our type I error rate. However, considering the significance of our ANOVA results and their consistency, we consider them as representative of the system's natural variability and as adequately reflecting the response of arthropod assemblages to fragmentation in our system. Further studies in the area should find ways to deal with the difficulties associated with finding exact replicates for fragments (fragments differ in many variables other than area) and the existence of logistic constraints linked to accessibility.

It is well known that insects are important players in biological processes that maintain biodiversity and ecosystem functions (Jennersten 1988; Didham et al. 1996; Mooney et al. 1996). Beetles participate in many processes, such as nutrient-recycling in the tropics, are strongly affected by habitat fragmentation (Klein 1989; Didham et al. 1998b), and are edge-avoiders (Didham et al. 1998a), so that they usually disappear from small fragments or near the edges. We have little information about the exact guild or trophic level to which beetles belong. However, available evidence suggests that species in the families Tenebrionidae, Staphilinidae, and Ptiinidae are decomposers (Peña 1996). Interestingly, we found that species in these families are the ones that disappear from the small fragment and from near the edge. As pointed out by Mares (1992) and Ojeda and Mares (1989), the lack of basic scientific knowledge on species natural history is one of the major threats to biodiversity conservation in South America. This is particularly relevant for inconspicuous species such as insects, which, despite their importance for ecosystem function, remain largely unknown.

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