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...
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 forest 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 winteri, and Myrceugenia correifolia, the evergreen shrubs Luma chequen and Raphitamnus spinosus, one prostrate species Griselinia scandens, and several ferns in the genus Hymenophyllum (Araya et al. 1992). The scrub matrix surrounding the fragments is dominated by xeric vegetation and corresponds to the coastal steppean 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).