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**SEED RAIN OF BIRD-DISPERSED SPECIES IN  
RIPARIAN AND UPLAND FORESTS IN A RURAL  
LANDSCAPE OF NORTHERN CHILOÉ ISLAND,  
CHILE**

**Tesis**

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## ABSTRACT

In rural landscapes of Chiloé Island, southern Chile, linear-shaped remnants of riparian forest are immersed in a mosaic of grazing pastures, secondary shrublands and upland forest fragments. Riparian forests in Chiloé Island are dominated by fleshy-fruited tree species with endozoochoral dispersal syndromes and are recognized as important habitats for native plants and animals; hence, they are expected to enhance dispersal and landscape connectivity in human-modified environments. Few studies, however, have examined this prediction. To assess the role of riparian forest vegetation in seed dispersal in this rural area of Chiloé Island, we investigated the deposition of avian-dispersed propagules to these riparian forests, in contrast to upland forests patches, pastures and shrublands in the same landscape (<1 km apart), and examined some of the possible determinants of species richness and composition of seed inputs in each habitat. We used seed traps to collect the seed rain during two consecutive fruiting seasons (2002-2003, 6 seed traps per habitat type, surface area per trap = 1 m<sup>2</sup>; 2003-2004, 21 seed traps per habitat type, surface area per trap = 0.07 m<sup>2</sup>). Because riparian forest strips are linear-shaped and predominantly edge habitat (<100 m wide), we compared the riparian seed rain to seed rain in the interior and edges of upland forest patches. Total seed rain of fleshy-fruited species was at least eight times higher in forests (both riparian and upland) than in pastures and shrublands in the same landscape. Seed rain of avian-dispersed propagules was at least two-fold higher (depending on sampling season) in riparian than in upland forests, including seeds from species only present in other habitat inside the same landscape unit (> 1 km away). Total bird abundance did not differ between forest habitats (upland vs. riparian); however, relative abundance of frugivorous and non-frugivorous birds was higher in

forests than in shrubland-pasture habitats. A canonical correspondence analysis showed that percent canopy cover and fleshy-fruited-species richness are highly correlated with the magnitude and species composition of the seed rain of bird dispersed species in one riparian forest studied, differing greatly from upland forest edges. This riparian forest presents unique species associated, not present in upland forests. The other riparian forest studied is more related with species present in upland forests. We conclude that riparian forests constitute critical habitats for avian seed disperser-plant interactions in this rural landscape, receiving a qualitatively and quantitatively different seed rain than do other forest and non-forest habitats in the same area, thus representing hot-spots for mutualistic dispersal interactions and premium sites for immigrants from habitats located outside the patches in the immediate neighborhood. These results have important consequences management and conservation of biodiversity in rural areas.

## RESUMEN

El paisaje rural de la Isla Grande de Chiloé, en el sur de Chile, se caracteriza por poseer remanentes de bosques ribereños inmersos en un mosaico de pastizales para ganado, matorrales y fragmentos de bosques no ribereños o de tierras más altas. Los bosques ribereños de Chiloé están dominados por especies de árboles de fruto carnosos, con síndrome de dispersión endozoócora y son reconocidos como hábitats importantes para las especies de plantas y animales nativos, por lo que se espera que incrementen el movimiento de las especies y la conectividad dentro del paisaje antropogénico. Sin embargo, pocos estudios han examinado esta predicción. Para evaluar el rol de los bosques ribereños en la dispersión de semillas en áreas rurales del norte de la Isla Grande de Chiloé investigamos la deposición de propágulos dispersados por aves hacia estos hábitats, contrastándolos con bosques no ribereños, pastizales y matorral en el mismo paisaje (<1 km de distancia entre hábitats). Además examinamos algunos de los posibles determinantes de la riqueza y composición de especies en la lluvia de semillas en cada hábitat. Para coleccionar la lluvia de semillas utilizamos trampas de semillas durante dos temporadas de fructificación (2002-2003, 6 trampas de semillas por tipo de hábitat, área de colecta por trampa = 1 m<sup>2</sup>; 2003-2004, 21 trampas de semillas por tipo de hábitat, área de colecta por trampa = 0.07 m<sup>2</sup>). Los remanentes de bosque ribereño son generalmente de forma lineal, con alta influencia del borde (<100 m de ancho), por lo que comparamos la lluvia de semillas del bosque ribereño con la lluvia de semillas en el interior y bordes de fragmentos de bosque no-ribereño. La lluvia de propágulos dispersados por aves fue al menos el doble (dependiendo de la temporada de muestreo) en los bosques ribereños que en los no-ribereños, incluyendo semillas de especies presentes en otros tipos de hábitat de la

unidad de paisaje (< 1 km de distancia). La abundancia de aves no difirió entre los distintos tipos de hábitat de bosque (ribereño vs. no-ribereño); sin embargo, la abundancia relativa de aves frugívoras y no-frugívoras fue mayor en los bosques que en los hábitats de pastizal y matorral. Un análisis de correspondencia canónica mostró que el porcentaje de cobertura del dosel, junto a la riqueza de especies leñosas de fruto carnoso, se encuentran fuertemente correlacionadas con la magnitud y composición de especies de la lluvia de semillas dispersadas por aves, principalmente en uno de los bosques ribereños estudiados, difiriendo del bosque no-ribereño (borde e interior). Este bosque de ribera presenta una asociación de especies única, no presente en los bosques no-ribereños. El segundo bosque ribereño posee una asociación más similar a los bosques no-ribereños. Concluimos que en este paisaje rural los bosques de ribera de río constituyen hábitats críticos para las interacciones entre aves dispersoras y plantas, recibiendo una lluvia de semillas diferente tanto en magnitud como en composición, en comparación a la recibida por otros tipos de hábitats de bosque, matorral y pastizal. Los bosques ribereños estarían constituyendo puntos calientes para interacciones mutualistas de dispersión, y sitios privilegiados para las semillas inmigrantes desde otros hábitats ubicados fuera de los parches, en el vecindario inmediato. Estos resultados tienen importantes consecuencias para el manejo y la conservación de la biodiversidad en los sectores rurales del sur de Chile.

## INTRODUCTION

Riparian ecosystems are key elements for biodiversity and ecosystem functions in agricultural landscapes. The importance of riparian zones far exceeds their low percent cover in the landscape because of their prominent role as ecological linkages among habitats, strong biotic and abiotic interactions, and function as interface between terrestrial and aquatic ecosystems (Gregory et al. 1991, Naiman and Decamps 1997). From a hydrological point of view, riparian ecosystems strongly influence the neighboring landscape as a consequence of their variable flood regimes, geographic channel processes, altitudinal climate shifts and upland influences on the fluvial corridor (Naiman and Decamps 1997). From a biogeographical point of view, rivers form a network throughout the drainage basin and provide important pathways for the dispersal and migration of organisms associated with them (Pedroli et al. 2002). In addition, riparian zones are considered as three-dimensional zones, as their influences go further away than the limits of flooding and channeling, influencing even upward into the canopy of streamside vegetation. Dissolved nutrients movement from terrestrial to stream ecosystems and vice versa, differences in soil processes close versus far from the stream, dissolved and particulate matter flows, channeling of organisms moving across the landscape, and differences in microclimate between riparian and upland vegetation, all constitute examples of riparian influences on the surrounding landscape (Gregory et al. 1991, Naiman and Decamps 1997, Tabacchi et al. 1998).

The linear nature of riparian ecosystems enhance their importance as key elements for landscape connectivity, maintaining biological fluxes across extended and dynamic environmental gradients (Gregory et al. 1991, Naiman and Decamps 1997, Ward et al.

2002). Stream ecosystems have been described as corridors for nutrients, energy, and matter; as well for plant propagules, rodents, mammals and even disturbance agents, such as fire and pathogens (Puth and Wilson 2001). Riparian vegetation strips constitute ideal pathways for active and passive dispersion of plant and animal species across human-modified landscapes (Gregory et al. 1991, Johansson et al. 1996, Tabacchi et al. 1998, Godoy et al. 1999, Pedrolí et al. 2002). Previous studies in temperate forests have shown that birds use linear shaped riparian forests as corridors for movement in deforested landscapes, where corridor width is an important habitat attribute (Hodges and Kremenitz 1996, Sieving et al. 2000, Shirley and Smith 2005). In boreal forests, moths and songbird abundance is as high in riparian and upland old-growth continuous forest, respectively, as in riparian forest corridors, and during bird reproductive season riparian corridor use is even stronger than upland forest use (Monkkonen and Mutanen 2003, Mosley et al. 2006). However, the same characteristics that make riparian ecosystems valuable and unique make them also very vulnerable to ecological influences from the surrounding landscape (Martin et al. 2006). For example, small rivers and creeks receive constant inputs of organic matter from riparian vegetation and neighboring terrestrial ecosystem, but their ecological buffer capacity is low compared to higher order streams, making them vulnerable to the effects of changes in land cover (Tabacchi et al. 1998). Consequently, riparian ecosystems may constitute not only corridors, but also ecological boundaries or ecotones, with unique characteristics defined by space and time scale, and by the strength of interactions with adjacent ecosystems (Naiman and Decamps 1997, Puth and Wilson 2001).

Biodiversity and productivity of riparian ecosystems are tightly related (Ward and Tockner 2001). The intermediate disturbance hypothesis (dynamic equilibrium model, Huston 1979) has been applied to explain the differences in productivity between riparian and upland ecosystems. The model predicts that the disturbance level required to attain maximum species diversity varies as a function of the ecosystem productivity, as productivity increases greater disturbance is needed to prevent competitive exclusion (Ward et al. 2002). Periodic flooding constitutes a frequent disturbance in most riparian ecosystems, creating heterogeneity within the riparian zone (Naiman and Decamps 1997, Pollock et al. 1998). Productivity of riparian forests is related to their location along rivers, often receiving large amounts of dissolved, particulate and coarse organic matter and nutrients from upstream. In agricultural headwaters, riparian zones are subject to large subsurface nitrate inputs from the uplands (Tabacchi et al. 1998). Microbiological processes are intensified through flooding and particle sizes, increasing nutrient cycling and, therefore, their availability for plants. These characteristics lead riparian ecosystems to maintain a high productivity, and consequently, riparian plant communities exhibit high degree of structural and compositional diversity, often having a higher species richness than other habitats in the landscape (Gregory et al. 1991, Naiman and Decamps 1997, Tabacchi et al. 1998, Ward and Tockner 2001). Many studies have evaluated species richness and composition in different types of riparian ecosystems, frequently assuming their function as corridors in landscapes. Results have demonstrated that riparian forests corridors generally support high numbers of bird species and vertebrate predators, depending on corridor width (Keller et al. 1993, Hodges and Kremetz 1996, Sieving et al. 2000, Hilty and Merenlender 2004), when compared with upland habitats (but see Sabo et al. 2005).



Plant-animal interactions are significant ecological processes of riparian communities (Naiman and Decamps 1997). However, to our knowledge, studies about the importance and consequences of ecological interactions in these ecosystems are lacking (Tabacchi et al. 1998). Plant-animal interactions (such as zoochoral seed dispersal) in riparian forests are an important subject of study still largely unexplored (Tabacchi et al. 1998). To understand the role of riparian habitat networks in landscape connectivity, and their consequences for population and community dynamics, a better understanding of the movements of seed-dispersing animals, commonly birds, mammals and ants, across the landscape is required (Chambers and MacMahon 1994).

In temperate rain forests of Chiloé Island, southern Chile, seed dispersal by birds is a major plant-animal interaction (Armesto et al. 1987, 1996). Between the 67% and 72% of the woody species (between 48 and 51 species), including epiphytes and vines, are fleshy-fruited (Armesto and Rozzi 1989, Willson 1991). When compared to different types of temperate forest in North America, New Zealand and Australia, this percentage is one of the highest frequencies of fleshy-fruited species (Willson 1991). However, the frugivorous guild of Chilean forests is impoverished relative to the high diversity of fleshy-fruited plant species (Armesto et al. 1987, Armesto and Rozzi 1989, Willson 1991). The major frugivores and potential seed dispersers in Chiloé forests are generalist birds (17 species), which, regularly or occasionally, consume fruits of several fleshy-fruited species (Armesto et al. 1987, Armesto and Rozzi 1989, Sabag 1993). The main dispersers are *Turdus falcklandii* and *Elaenia albiceps*, generalist in habitat use as well as in foraging preferences (Sabag 1993, Aizen et al. 2002, Díaz et al. 2005). As in northern hemisphere temperate forests, avian frugivores in Chiloé are more frequently

recorded in forest gaps and edges (Willson et al. 1994, Rozzi et al. 1996a). Thus, for avian-dispersed tree species, the spatial pattern of disseminating seeds or 'seed shadow' is expected to show some peaks associated with particular habitats (for example, riparian edge-corridors) where bird activity is greater (Levey et al. 2005).

Riparian vegetation strips are a distinct element in the rural landscape of northern Chiloé. These forests usually constitute remnants of continuous forests, which landowners maintain for firewood and timber extraction and cattle shelter, to prevent erosion or simply as a consequence of inaccessibility. Riparian vegetation is also protected by Chilean law (for example: DL 701, management rules for different *Nothofagus* forests types) however, law enforcing is almost inexistent. These linear fragments constitute natural corridors for native species, such as understory specialist birds belonging to the families *Rhinocryptidae* and *Furnaridae*, and for the small wild-cat predator, *Oncifelis guigna* (guigna) which moves across the agricultural landscape through forested and inaccessible ravines (Sieving et al. 2000, Sanderson et al. 2002).

Considering the important function of riparian habitats and the use of riparian forests by native bird species, this study evaluates seed rain of bird-dispersed species in riparian forests in a rural landscape of northern Chiloé Island. We expect that the quantity and quality of seed dispersal by birds will be higher in these riparian habitats than in adjacent upland forests, shrublands and pastures, but more similar to the seed rain in forest edges than in forest interior. We asked the following main questions: a. Does the magnitude and composition of seed rain differ between riparian and upland forests, in northern Chiloé island? b. Are there differences in abundance and diversity of frugivorous birds among habitat types? c. What are the determinants of differences in

seed rain between riparian forests and other habitats in the rural landscape mosaic? d. What is the evidence that riparian forests function as critical landscape elements for seed dispersal by birds and for the conservation of tree diversity in rural landscapes of northern Chiloé?

## METHODS

### *Study site*

The study site was located in Northern Chiloé Island, in the agricultural landscape surrounding Senda Darwin Biological Station (SDBS, 41°50'S, 73°40'W, Fig. 1). The predominant forest type is North-Patagonian dominated by evergreen broad-leaved tree species, such as *Drimys winteri*, *Podocarpus nubigena* and *Nothofagus nitida* (Veblen et al. 1983). Climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek 1976). Mean annual temperature is 10°C, annual precipitation has been estimated between 2000 and 2500 mm, with a dryer period during the austral summer, particularly between January and February, austral summer (representing approximately 11% of the total annual precipitation) (Di Castri and Hajek 1976). The present landscape in northern Chiloé (Ancud district) is dominated by human activities, mainly pastures for cattle grazing, rural houses, roads, secondary forest fragments and shrublands. Native forest cover persists as an important land use, covering the 55.66% (90,180 ha) of the land. However, almost 21% of this category consists of secondary growth and open, logged or burned forests. Pastures for cattle grazing cover the 25.6% of the land, and shrublands represent 9.3%. The remnant fragments of native forest in Chiloé island range from 0.02 to 4,872 ha. Fragment sizes between 10 and 50 ha are the most frequent (59% of total fragments) in the landscape; however, they comprise only the 5.3% of the total native forest area. Fragments between 100 and 500 ha size ads up 41% of remnant native forest (CONAF-CONAMA-BIRF 1999).

This study was designed to test for the differences in seed rain of bird-dispersed species, quantity and composition, between riparian forests and non-riparian upland

forests and other common habitat in the rural landscape. Because of the patterns of human occupation and use of the landscape, riparian fragments were frequently linear or dendritic remnants less than 100 m wide, but non-riparian linear fragments were not found. Therefore, we sampled forest interior and edges in each patch of upland forest, to control for the effects of linear shaped, narrow riparian forest remnants with significant edge effect.

We defined three main forest habitat types for comparisons: non-riparian or upland forest interior (UFI), non-riparian or upland forest edge (UFE) and riparian forest (RF). We were able to work in two comparable landscape units containing representative areas of each habitat type. The Landscape (L1), in SDBS, had the three habitat types we were looking for: forest interior, forest edge and riparian forest, within <500 m of separation. The second landscape (L2) was about 1.5 miles away, crossing the main road, representing upland non-riparian forest (edge and interior) and riparian forest within a radius of <1 km. All fragments were on lowland areas (50-100 m elevation.).

#### *Riparian forests*

Riparian vegetation at both sites was secondary growth forest, with dominance of fleshy-fruited species and individuals of *Amomyrtus luma*, *Amomyrtus meli* (both Myrtaceae), *Raphitamnus spinosus* (Verbenaceae), *Drimys winteri* (Winteraceae), and *Luma apiculata* (Myrtaceae) among others (Fig. 2). Canopy height was about 15-25 m and vegetation strips varied mostly between 3 and 20 m in width (in the areas selected for sampling transects, see below). Riparian forest at SDBS (L1RF) was adjacent to "Huicha" river, a second order, gentle sloping river, with continuous water flow all-year round. Some parts of the riparian habitat may be flooded in winter. Vegetation

bordering Huicha river (L1RF) is continuous along about 4 km. However, at the second site, L2RF, the river runs along the forest for about 300 m and then it connects with a small forest fragment (of about 80 ha approximately). Riparian fragments are generally surrounded by cattle pastures, which in SDBS are currently not in use. Occasional timber takes place in L2RF, reducing the presence of larger individuals in comparison with the riparian strip of Huicha river.

#### *Non riparian forest*

Non-riparian sampling sites consisted of forest patches of about 160 and 135 ha (L1 and L2, respectively). Fragment at L1, at SDBS, is an old-growth forest (about 300 yr old) dominated by *Drimys winteri*, *Podocarpus nubigena*, *Tepualia stipularis* and *Weinmannia trichosperma*. Dominant species at L2 forest fragment (about 70 yr old), were *Amomyrtus luma*, *Drimys winteri*, *Eucryphia cordifolia* and *Nothofagus nitida* (Aravena et al. 2002). Fleshy-fruited species dominated both forests, but varied between L1 and 2, and between forest interior and edge (Fig. 2). Canopy height in both fragments varied between 25 and 30 m (Armesto et al. 2001). These forests have not been subjected to large-scale logging, but timber extraction has been more intense in L2. Forest edges are dominated by shade-intolerant low shrubs as *Berberis darwini* and *Baccharis sp*, typical of early succession after fire (Willson and Armesto 1996), fast growing trees of *Drimys winteri* and some Myrtaceae, such as *Tepualia stipularis* and *Amomyrtus luma*.

#### *Sampling design: first and second fruiting seasons*

We used an adaptative design in our study, responding to the results from the first fruiting season sampled (2002-03). In first season we included four habitat types

(riparian forest, non-riparian forest, shrubland and pasture) and 6 big seed traps per habitat type. For second sampling season (2003-04) we intensified sampling effort reducing seed trap size, incrementing seed traps number and eliminating shrubland and pasture of sampling habitats, because it received very little seed rain. Thus, we will describe both sampling seasons (2002-03, 2003-04) separately below.

#### *First fruiting season*

In the 2002-2003 fruiting season our study was designed to evaluate the magnitude of seed dispersal and bird use of three different land cover types available in the rural landscape. The study site was SDBS. We sampled bird species composition and abundance as well as seed rain in riparian and non-riparian (upland) forest, abandoned pasture, and secondary shrubland (dominated by *Baccharis sp.*). For seed rain assessment six large seed traps (1 m<sup>2</sup> collection surface), placed 40 cm above the ground level, were set up in each habitat, except for riparian forests, where a total of 18 seed traps were set up along three transects following the riparian vegetation strip, within 20-25 m of the river edge. A trap consisted of a plastic surface held to a wooden frame (1x1 m) covered with a thin nylon bag to collect the seeds. Traps were separated by 15 m along 75 m linear transects at each site. Bi-weekly collections of all seeds received were conducted between December 2002 and June 2003. However, after April, seed rain of bird dispersed species decreased to almost zero. Therefore, statistical analysis focused on the peak fruiting period, from December 2002 to April 2003 (143 sampling days).

In parallel, bird surveys were conducted on December and January in each habitat. Bird assemblages were sampled between 7 and 9.30 am in rainless days during the peak

fruiting period for most woody species. All passerine birds, parrots and doves heard or seen within a rectangular plot of 50 by 5 meters along the river side to include the riparian vegetation were recorded during 5 min period.

#### *Second fruiting season*

During the second fruiting season, sampling of birds and seed rain was based on the same a 300-m linear transect, in each of the three forest habitats types compared (non riparian forest interior, non riparian forest edge and riparian forest) in both landscape units. In the second year, we did not include pastures and shrublands in comparisons because bird abundance and seed rain was significantly lower in these habitats than in forests. Sampling effort was identical in each habitat, regardless of differences in patch size or riparian forest width.

#### *Seed rain*

We set up 21 seed traps, every 15 m along each 300 m transect in each forest habitat sampled per landscape unit. Forest interior was sampled at least 50 m away from the nearest forest edge. Forest edge was defined as a 20-m wide strip beginning from the position of edge trees toward the forest interior. Seed traps for fruiting season two consisted of metal rings, 30 cm in diameter (surface area = 0.07 m<sup>2</sup>), placed at approximately 70 cm above the ground. A thin nylon bag (1 mm mesh size) was attached to each ring, to collect the seeds. Almost all seeds of woody species in the forest can be captured by this mesh size, but some small seeded species (e.g., *Asteranthera ovata*) may be underestimated. Seed collectors were emptied every fifteen days, to prevent material decomposition inside the bags. Seed collectors were activated between December 2003 and April 2004 (129 sampling days). During this



period most (>90%) of the fleshy-fruited species in the site bear ripe fruits (Smith-Ramírez and Armesto 1994). Seed and fruit samples were stored in paper bags for one week to 3 months before identification and seeds were identified under a 0.8x-3.5x dissecting scope, using a reference seed collection of all the woody plants fruiting within each landscape unit.

The contents of seed traps from both fruiting seasons were analyzed as follows:

- 1- All seeds present in each seed trap for a given sampling period were counted, except for seeds smaller than 2 mm, as these were difficult to identify from the detritus and some may be lost through the mesh.
- 2- Seeds and fruits were identified to the lowest taxonomic level, most frequently species level.
- 3- Seeds from fleshy and dry fruits were separated, and classified as biotic and non-biotic dispersal syndromes. Naked seeds from fleshy-fruited species with biotic dispersal syndrome (without skins and presumably passed through a bird's gut) were considered as actively dispersed seeds (see e.g., Jordano et al. 2007) , and complete fruits present in traps were considered as non-dispersed seeds, fallen by gravity, wind storms or animal movement in the canopy. In arillated species (e.g., *Podocarpus nubigena*) the presence of the aril attached to the seed was considered as an indicator of the absence of dispersal.
- 4- Species that accounted for more than 10% of all collected seeds in each fruiting season were analyzed separately to assess their temporal pattern of dispersal.

Plant species were classified as trees, shrubs or other (including mainly vine, epiphyte and one hemiparasite species) following Armesto and Rozzi (1989), and Smith-Ramírez and Armesto (1994).

To control for the influence of surrounding vegetation and trees located above the seed traps in the quantity and composition of the seed rain, we identified and counted all the individuals trees or shrubs located within a circular plot of 4 m radius centered on each seed trap. The variables measured for woody species present within the circular plots were: presence of fleshy and non-fleshy fruited woody species (trees and epiphytes), number and identity of individuals with DBH (diameter at breast high) >10 cm and percentage canopy cover directly above the seed trap.

#### *Bird surveys*

Bird surveys during the second fruiting season followed the point-centered counting method as described by Willson et al. (1994) in a previous study of avian communities in Chiloé rainforests. We defined three 30-m radius census points in each forest habitat (UFI, UFE, RF) within the two landscape units. Census points were separated by about 100 m from each other along the 300-m long transect. All birds seen or heard within the 30-m radius plots were recorded for an 8-min period at each point. Each plot was surveyed six times during the fruiting season (December to April), between 1 and 4 hours after sunrise in non-rainy days. Sampling of each habitat was repeated in two different days each month, changing the order of recording sites in order to control for the effect of sampling on different days and different times in the day. In riparian forest fragments, because of the linear shape of riparian vegetation strip, the area surveyed

per point was often larger than the width of the forest strip, therefore including some adjacent habitat (generally pastures). This effect was not considered a problem because we were interested in determining whether birds were attracted to riparian habitats regardless of the area of the riparian forest strip.

### *Data analyses*

#### *Seed rain*

Seed rain data were analyzed according to i) dispersal syndrome (biotic versus abiotic), ii) seed condition (dispersed versus non-dispersed) iii) and growth habit of species (tree versus shrub versus others). In addition, we estimated intra-season (bi-weekly) variation in seed rain quantity and composition, and similarity in seed rain composition across the different habitats surveyed. To contrast between dispersal syndromes, seed rain was analyzed using factorial ANOVA (first and second season separately), data were log-transformed ( $\log x+1$ ) to meet ANOVA assumptions. For the 2002-2003 fruiting season, factors and levels considered in the ANOVA for seed rain were: i) habitat type (riparian forest, upland forest, shrubland and pasture) and ii) seed dispersal syndrome. In the second sampling season (2003-2004), we considered i) landscape unit as a factor (L1 vs L2) and ii) forest habitat type (riparian forest, upland forest edge, upland forest interior) iii) and seed dispersal syndrome.

Other analyses of seed rain quantity were carried out on frequency data. This type of analysis requires a balanced design, which was not possible for the first fruiting season; therefore, six of the 18 riparian forest seed traps were randomly selected for comparison with the other habitats (in the second season we had the same number of

traps per habitat). To estimate the proportion of the seed rain derived from the trees above or surrounding (<2 m away) the location of the collector and seeds derived from sources outside this area, we counted all dispersed seeds (naked seeds) that fell in the trap from species not present above or within 2 m of the collector. These seeds were called 'allochthonous seed rain'.

Seed condition (dispersed versus non-dispersed) and growth habits (tree, shrub or other) of fleshy-fruited species were compared among habitats by pooling the seed rain data for the entire fruiting season in each habitat. Habitat fruit production was quantified indirectly through fallen seeds contained inside fruits (Zhang and Wang 1995). Differences between observed and expected frequencies of seeds in each category of dispersal condition and growth habit were evaluated with  $\chi^2$  and goodness of fit (G test) tests for each fruiting season. Frequency of collected seeds was contrasted with the proportion of seeds belonging to each category collected at landscape level ( $H_0$ : no differences in seed rain proportion between habitats). Similarly, the number of species of seeds collected in different habitat types was compared with total number of collected species at landscape level belonging to each category of dispersal condition or growth habit (pooling all habitat types). Goodness of fit (G test) tests does not accept expected values <1, therefore in the first season we did not compare seed rain data for shrubland and pasture habitats separated by habit growth, where seed inputs become too low. Species that accounted for >10% of all bird dispersed seeds collected in one fruiting season were analyzed for temporal patterns of seed fall, using repeated measures ANOVA when assumptions were met, and Tukey HSD post-hoc test when necessary. For the first fruiting season temporal patterns analysis were performed on (log x+1) transformed data. Repeated measures analyses for the second season data

were not possible, because data did not meet ANOVA assumptions, even under log transformation. Similarity in species composition of bird dispersed seed rain across the different habitats surveyed was assessed using a cluster analysis, which is based on Morisita-Horn similarity index (Magurran 1998) This index constitutes one of the most robust similarity indexes, as it is relatively independent of species richness and performs satisfactorily when sample sizes are large, however, it is highly sensitive to the most abundant species (Magurran 1998, Chao et al. 2006). A dendrogram based on Morisita-Horn index was constructed, following the UPGMA clustering algorithm (Krebs 1989). Statistical significance of observed clusters was determined through a randomization test (Manly 2001).

### *Birds*

Total number of species as well as frugivorous and non-frugivorous bird abundance and species richness (number of individuals per point or per transect per day, depending of the year) was compared between forest habitats using repeated measures ANOVA, and with Tukey HSD post-hoc test when necessary. Frugivorous bird species were defined by the presence of fruits in the diet, regardless of the importance of this item relative to other food items. Classification of species in feeding guilds was based on the published literature (according to Armesto et al. 1987, Willson et al. 1994, Rozzi et al. 1996b, Willson et al. 1996, Estades and Temple 1999). Factors for repeated measures analysis were habitat (forest type vs. shrubland and pasture) and diet for first season, and habitat type, landscape unit and diet for the second season. Bird abundance cannot be compared between the two years of study because different sampling methods were used (transect versus point), but we focused on comparisons among habitats.

### *Seed rain, bird diversity and habitat variables*

To evaluate the dependence of the seed rain on different possible causal variables, a canonical correspondence analysis (CCA) was performed for the second year data. Data were organized in a species matrix containing the total number of dispersed seeds per habitat type and landscape unit (L1UFI, L1UFE, L1RF, L2UFI, L2UFE, and L2RF) for each species (habitat types were rows and different plant species were columns). This matrix was compared with an explanatory data matrix comprising five variables (columns): 1) mean seed rain (considering dispersed and non-dispersed seeds as an indirect measure of seed production of each habitat type) of fleshy fruited species, 2) mean seed rain of non-fleshy fruited species, 3) mean percent canopy cover, 4) mean total bird abundance, and 5) mean number of frugivorous bird species in each sampled site and habitat type. This analysis is based on a Monte Carlo test of independence between species and habitat explanatory matrices ( $H_0$ : no relation or correspondence between matrices).

Univariate and frequency analysis were conducted using the software Statistica 6.0 (StatSoft Inc. 1984-2001) and Poptools v. 2.7 (2006). Cluster and multivariate analysis was conducted with Multi-Variate Statistical Package (MVSP) version 3.12 and PC-ord for windows (McCune and Mefford 1999), respectively.

## RESULTS

### *Seed rain*

A total of 46,663 seeds from 34 woody species were collected in the two seasons of study in all habitats. Of these, the 42% (19,725 seeds) belonged to wind dispersed species, and the 58% (26,938 seeds) to fleshy-fruited species (Appendix 1). However, 24% (6,445 seeds) of all seeds of fleshy-fruited species belonged to one species, *Gaultheria* sp. (primarily *Gaultheria mucronata* and some *G. phylliraefolia*), and were collected during second season, mainly in riparian forest. This species alone accounted for 77% of all seeds having biotic dispersal syndromes collected during the second season, and hence this species was omitted from most subsequent analyses of seed rain, and considered an outlier. From the total seed rain of seeds belonging to fleshy fruited species, 54% (14,426 seeds) were already dispersed, that is, were found without skin (pericarp). Riparian forests received 91% (42,385 seeds) of all collected seeds, upland forest (edge and interior) 9%; in shrubland and pastures seed rain was <1% of the total for all habitats (only one fruiting season).

### *i. Abiotic versus biotic dispersal syndromes*

The abundance of fallen seeds, classified according to abiotic or biotic dispersal syndromes, varied between habitats. During both seasons seed rain was consistently larger in riparian forests than in upland forests and species with biotic dispersal syndromes dominated in number over species with abiotic dispersal syndromes (Fig. 3, Table 1). Seed rain responses to habitat type depended on dispersal syndrome. The seed rain of species dispersed abiotically did not change between habitats, with the exception of *N. nitida* which produced an outstanding seed rain in the first season, due

to a single tree located above one seed trap (see Appendix 1). In contrast, the seed rain of vertebrate-dispersed species was higher in riparian forests than in all other habitats (Fig 3, Table 1). Seed rain in shrubland and pastures was extremely low (first season results), and both habitats received only dispersed seeds (i.e. not contained within fruits) belonging mainly to vertebrate-dispersed species. During the entire fruiting season, shrubland habitat received one seed, and pastures 14 seeds, two of which belonged to a wind-dispersed species, *Embothrium coccinum*) (Appendix 1).

#### *ii. Seed condition*

The frequencies of dispersed and non-dispersed seeds (naked seeds versus gravity fallen fruits) belonging to species with biotic dispersal syndrome differed across the different habitats. In both seasons riparian forests accumulated the highest seed rain of all habitats, considering both dispersed and non-dispersed seeds (Fig. 4). Seed rain was different from the expectation based on the null hypothesis of equal distribution of seeds across habitats, both for dispersed and non-dispersed, fallen seeds (Chi<sup>2</sup> tests, first season: dispersed seeds  $\chi^2 = 4\ 340$ ,  $df = 3$ ,  $P < 0.0001$ , non-dispersed seeds  $\chi^2 = 13\ 378$ ,  $df = 3$ ,  $P < 0.0001$ ; second season: dispersed seeds  $\chi^2 = 1\ 025$ ,  $df = 2$ ,  $P < 0.0001$ , non-dispersed seeds  $\chi^2 = 1\ 576$ ,  $df = 2$ ,  $P < 0.0001$ ). Riparian forests concentrated the majority of dispersed seeds, capturing >60% of the total seeds dispersed in each fruiting season. Based on the total number of entire fruits fallen in each habitat, riparian forest showed the highest relative fruit production of fleshy-fruited, vertebrate-dispersed species, concentrating 81% to 95% of all the fallen seeds contained inside fruits in each season (Fig. 4).



The influence of surrounding vegetation on seed traps is the same independent of whether *Gaultheria* is included or excluded from the analysis. The interior of upland forests, together with one of the two upland forest edges showed the highest proportion of seeds belonging to allochthonous species (>0.5, Table 2), but the highest numbers of allochthonous seeds, by about one order of magnitude, fall in the riparian environments. Riparian forests also had the highest total seed rain (Table 2).

### *iii. Growth habits*

The frequency of collected seeds belonging to species with different growth habits in each habitat type was significantly different from the proportion of seeds from each growth habit collected at landscape level (pooling all habitat types) (Chi<sup>2</sup> tests, first season:  $\chi^2 = 111.8$ , df = 6, P < 0.0001; second season:  $\chi^2 = 277.8$ , df = 4, P < 0.0001; Fig. 5). Riparian forests received 65% and 91% (first and second fruiting season, respectively) of all dispersed seeds from trees. Tree seeds were the most common dispersed seeds in riparian forests during the first fruiting season (95% of all collected seeds in this habitat). However, in the second season shrub seeds (excluding *Gaultheria*) constituted 60% of all dispersed seeds in riparian habitats in contrast to 39% of seeds from trees (Fig. 5). Like riparian forests, the seed rain of upland forest interior was dominated by trees (99% of the total) over shrubs in the first season, in contrast to 25% and 29% of the seed rain corresponding to trees and shrubs respectively in the second season.

The proportion of species of seeds collected in each habitat belonging to each growth habit did not differ from the proportion of the total number of collected species at landscape level (pooling all habitat types), neither in the first season nor in the second

(goodness of fit test, first season analyses consider only forest habitats:  $G = 0.74$ ,  $df = 2$ ,  $P = 0.98$ ; second season:  $G = 2.25$ ,  $df = 4$ ,  $P = 0.97$ ).

*iv. Variation in seed rain within and between years*

Species that accounted for more than 10% of total seed rain, within each season were separately analyzed. For each species, the seed rain varied considerably during the season (Fig. 6), and the mean seed number per square meter of seed trap differed among habitats sampling dates and landscape units (in the second fruiting season). For the first fruiting season there was a significant difference in the total number of dispersed seeds of *Amomyrtus luma* seeds between riparian forest and upland forest interior (habitat:  $F_{1,10} = 11.14$ ,  $P < 0.01$ ), but this difference was not uniform through the fruiting season (interaction month\*habitat type:  $F_{7,70} = 6.39$ ,  $P < 0.0001$ ). Between January 19 and March 3 (year 2003), the seed rain of *A. luma* was higher in riparian forest than in upland forest (time\*habitat: Tukey HSD  $P < 0.05$ , Fig. 6). In contrast, *Drimys winteri* seed rain did not differ between riparian and non-riparian forests (habitat:  $F_{1,10} = 0.29$ ,  $P = 0.60$ ), although seed rain varied over the fruiting season (tiempo\*habitat:  $F_{8,80} = 2.81$ ,  $P < 0.01$ ). During the second fruiting season, seed rain was dominated by *A. luma*, *Fuchsia magellanica*, *Myrteola nummularia* and *Ribes magellanicum*. The temporal pattern of seed rain of *A. luma* was similar to the previous fruiting season, and it was higher in riparian than in upland forest, mainly between January and February 15. Seeds of the shrubs *F. magellanica* and *R. magellanicum* were collected predominantly in riparian forest. Seeds of *M. nummularia* were collected later in the fruiting season compared to all other species, and were more common in upland forest edge than in riparian forest (Fig. 6).

#### *v. Similarity in seed rain composition and abundance between habitats*

The cluster analysis for the first fruiting season considered riparian forest, upland forest and pastures, because of the small number of seeds collected in shrubland. Seed rain in riparian forest and upland forest were floristically similar (Morisita-Horn similarity index=0.95), but pastures diverged from this group, showing a low similarity (Morisita-Horn similarity index=0.66, Fig. 7). In the second fruiting season, maximum similarity was found between upland forest edges of both landscapes units (Morisita-Horn similarity index=0.86). Upland forest interior and riparian forests presented lower similarities with forest edges than with each other (Fig. 7). None of the observed clusters were significantly different from those expected randomly (randomization tests performed).

#### *Bird diversity and abundance*

Bird abundance was relatively similar in forested habitats between sampling seasons. In both season total bird abundance did not differ between riparian and non-riparian forests, but it was higher in riparian forest than in pasture (first season), (Table 3, Fig. 8). Frugivorous birds were about twice or three times more abundant in forested habitats than in pasture and shrubland, but the opposite was true for non-frugivorous (insectivores plus granivores) birds (Fig. 8). This difference was marginally significant in the second season, as frugivorous birds tended to be more abundant than non-frugivorous birds in riparian and upland forest interior, but showed similar abundances in upland forest edge. Species richness of all birds followed the same patterns as abundance in both fruiting seasons (Table 4, Fig. 8).

#### *Relation between seed rain, bird diversity and habitat variables*

Canonical correspondence analysis showed that for some woody species seed rain was strongly correlated with some habitat types (Fig. 9, Table 5). Riparian forest on Landscape unit 1 was characterized by the presence of seeds of *Amomyrtus meli*, *Fuchsia magellanica*, *Ribes magellanicum*, *Berberis darwini*, *B. buxifolia* and *T. corymbosus*. Forest edges (landscapes 1 and 2) were distinguished by the presence of seeds of two anemochorous species, the vine *Campsidium valdivianum* and the tree *Embothrium coccineum*, in addition to vertebrate-dispersed *Myrteola nummularia* and *Griselinia racemosa* (Fig. 9).

Dispersed seeds were not independent of habitat variables measured and included in the explanatory matrix (Monte Carlo test for axis 1 and axis 2,  $P = 0.01$ ). Axis 1 was positively correlated with the mean seed rain of fleshy fruited (BSR, vertebrate-dispersed) species, with number of fleshy fruited species present in the habitat type (OS) and with the percentage of canopy cover (cover). Axis 1 and 2 were negatively correlated with mean seed rain of non-fleshy fruited (wind or gravity-dispersed) species (ASR, table 5). The number of fleshy-fruited species (OS) was highly correlated with mean seed rain of fleshy fruited species (BSR, weighted correlation: 0.969, weighted by habitat totals in main matrix). The number of fleshy fruited species and of seeds belonging to these species (OS and BSR explanatory variables), in addition to canopy cover (cover), were positively correlated with the number of dispersed seeds in the riparian forest of Landscape Unit 1 (Fig. 9). Seed rain of species with abiotic dispersal syndrome was more related to mean seed rain in the interior of the upland forest in Landscape Unit 2 (Fig. 9).

## DISCUSSION

This study documents that riparian forests are important elements in the process of seed dispersal by birds in rural landscapes of Chiloé Island, southern Chile. Floristic composition of riparian forest strips differs, in some case notably, from adjacent non-riparian forest habitats. Riparian forests harbor more fleshy-fruited species and individuals than upland forests. Seed dispersal by birds to riparian forest habitats was higher than to upland forests, and much higher than to shrubland and pastures, thus rejecting the null hypothesis of no difference in biotic seed dispersal between riparian forests and the other habitats, particularly other forest patches in the rural environment. The proportion of dispersed seeds belonging to species not present above or around each trap is higher in interior of upland forests than in other habitat types, indicating that dispersers often move seeds among different tree species. However, the total amount of alochtonous seeds is still higher in riparian environments, in accordance with the higher total seed rain. The plant species that accounted for the majority of dispersed seeds differ between upland and riparian forest habitats: riparian forests have a seed rain that is significantly richer in species composition than upland forest patches, and the latter is a nested subset of the former. However, bird species composition and abundance did not change significantly when comparing upland with riparian forest, although frugivorous bird abundance in both forested habitats (riparian and non-riparian) was clearly higher than in non-forested habitats (shrublands and pastures).

### *Seed rain in different habitat types*

Previous studies of seed dispersal in northern Chiloé have suggested that the composition and magnitude of seed rain in each habitat may be strongly influenced by

the identity, age and size of fruiting trees (Armesto et al. 2001). Riparian forests in the study area are dominated largely by early successional, shade intolerant tree species and small tree sizes in comparison to some upland forest patches which may have older canopy trees (Aravena et al. 2002). Therefore, differences in crop size of fleshy fruits and dispersal activity of frugivores could be the causes of the higher seed rain in riparian forests compared to forest interior and forest edges in older patches in the same landscape. Riparian habitats have been broadly described in the literature as highly productive environments because of high nutrient fluxes, organic material levels and faster nutrient cycling (Gregory et al. 1991, Pollock et al. 1998, Tabacchi et al. 1998). Moreover, generally narrow riparian forest strips (<100 m) in northern Chiloé and other agricultural landscapes are more exposed to sunlight, and, hence could have increased plant productivity, contributing to bigger fruit crops than upland forests (Bentley and Catterall 1997, Armesto et al. 2001).

Edge species as the shrubs *Gaultheria phillyearifolia*, *G. mucronata*, *Berberis spp.* and *Myrteola nummularia* are more frequent found along riparian vegetation strips than in upland forests, including edges. This difference is reflected in the composition of the seed rain. However, forest trees such as *Amomyrtus luma*, *Gevuina avellana* and *Eucryphia cordifolia* are common to both riparian forests and upland forests which is reflected in their relatively similar seed rain in both habitats. Understorey species such as *Fuchsia magellanica* and *Raphitamnus spinosus* were present exclusively in riparian forests, but their seeds were collected in the interior of upland forest. These data suggest that riparian forests of northern Chiloé Island could be acting as concentrators of plant diversity through enhanced seed rain compared to upland forest patches in this

rural landscape and, probably, may function as propagule sources for the other landscape elements.

Most woody species in each season showed their maximum seed dispersal in the middle of the austral summer, somewhere between December and March (e. g., *Amomyrtus luma*, *Fuchsia magellanica*, *Drimys winteri*, *Ribes magellanicum*), while *Myrteola nummularia*, a shrub species characteristic of edges, disperses in April. These data are coincident with the phenological patterns proposed by Smith-Ramírez and Armesto (1994), where the majority of fleshy-fruited species in Chiloé forests had their peak of ripe fruit production between December and March. Their study also showed that the length and peaks of the flowering and fruiting periods for tree species are strongly correlated with their pollination and dispersal modes rather than with habitat features (Smith-Ramírez and Armesto 1994) and hence we did not expect to find differences in the peak fruiting month between riparian and upland forests. Seed rain of *Drimys winteri*, a common pioneer tree species in all forests (Aravena et al. 2002), was higher during December in the first fruiting season in both riparian and non-riparian forests. In the second season, however, this species was nearly absent from the seed rain, showing large inter-annual differences in fruit crops which are broadly synchronous. Similar differences in seed rain for this species between consecutive years were documented by Armesto et al. (2001). This alternating pattern of high and low fruit crops between years observed in *Drimys* was also postulated for species of Myrtaceae in rainforests of Chiloé (Smith-Ramírez and Armesto 1994). However, in the present study, *Amomyrtus luma* bore abundant ripe fruits in both fruiting seasons. Long-term phenological records are needed to establish the inter-annual variability of fruiting patterns in tree species of Chiloé rainforests.

### *Landscape, habitat structure and seed dispersal by birds*

Other studies have shown that the abundance of avian frugivores remains unaffected by local variation in fruit production, although their patterns of activity may change spatially (e.g., Restrepo et al. 1999). In the present study, neither the total number of species nor the abundance of frugivores changed between riparian and upland forests in rural areas of Chiloé. However, when comparing both types of forests to non-forested habitats which cover large fractions of the rural environment such as pasture and shrubland, frugivores become significantly less common relative to non-frugivores. Forested habitats presumably represent a greater abundance and more reliable resource base of fruits for foraging frugivores compared to pastures and shrublands in this rural landscape. Even though pastures and shrublands contain some low-stature, fleshy-fruited shrub species, such as *Berberis buxifolia*, *B. darwini*, and *Myrteola nummularia*, which are early colonizers of open sites, they appear to be less attractive to frugivores and more appealing to insectivores and granivores. Some studies have suggested that the height of woody colonizers necessary for frugivorous bird activity may be limiting their use of shrublands and pastures (Mc Donnell and Stiles 1983).

The dominant bird species in pastures was *Tachycineta meyeni* (Chilean Swallow), and shrublands were dominated by *Anairetes parulus* (Tufted Tit-tyrant) along with other insectivorous and granivorous bird species (Fig. 10). These species have been described as shrub (and edge) users and *T. meyeni* as a large-tree user because it nests in big trees, but it feeds in open habitats (Díaz et al. 2005). Understory species and big-tree users, both habitat-use guilds characteristic of old-growth forest stands (Díaz et al. 2005), were present in riparian forests, however, structural components of riparian forest are predominantly mid-successional with few large trees (Jaña et al., non



published data). It seems likely that ecological legacies (as dead or alive large trees), the high productivity of riparian habitats and the dense understory are incentives to the occupation of this habitat by species from old-growth stands. Riparian forests therefore provide resources and habitat structures to different habitat-use guilds which may otherwise be restricted in their patch occupation in rural landscapes. Our results suggest that habitat structure of riparian forest can be important for bird species which are sensitive to habitat fragmentation such as understory birds (Sieving et al. 2002).

The two main avian frugivores in Chiloé forests, *Turdus* and *Elaenia* are open habitat users and vertical profile generalists (Armesto et al. 2001, Díaz et al. 2005). These species may consequently use edges and vegetation strips for foraging and moving between patches of forest habitat. In this case, corridor width and understory cover, attributes used as a measure of corridor quality may be of different relevance for the focal species (Levey et al. 2005). In addition, fleshy fruited trees in the riparian forest edge are more exposed to sunlight and less water-limited, and hence they may produce larger crops which attract large numbers of *Turdus* and *Elaenia* (Restrepo et al. 1999, Armesto et al. 2001). The abundance of *Turdus* and *Elaenia* did not differ between riparian and upland forest, in contrast to large differences in the quantity of bird dispersed seeds. This suggests that bird foraging activity and perching times should be different between upland forest interior, edges and riparian forests. Frugivorous birds would be consume more fruits per capita and disperse more seed in riparian forests than in upland forests.

Habitat variables such as fruit production (indirectly measured as total seed and fruit rain), canopy cover and frequency of fleshy-fruited plant species can be identified as

possible drivers of differential seed dispersal in riparian forests, with respect to other patches of bird habitat in the rural landscape. However, differences between the two riparian forests sampled are also important. Sampling design in future studies should be improved, defining more consolidated experimental units (here called landscapes). Riparian fragment at González (Landscape Unit 2) was not connected with upland forest (unlike Landscape Unit 1) this could make comparisons and block analysis less robust. In addition, this forest was putted under selecting logging by the owners, in spite of their intention of conservation for future generations and as consequence of traditional forest use rooted on native people. Extraction of remnant big trees from riparian woodlands may influence on fruit availability, constraining the potential seed dispersal and plant recruitment in the community (Armesto et al. 2001), and consequently changing the initial conditions for succession and tree regeneration.

#### *Rural landscape configuration and riparian forests*

Riparian forests could be expected to perform as forest edge habitats in the landscape, because of their linear shape and narrow widths. However, in the study site, seed rain in riparian forests differed greatly from forest edges, and it is relatively more similar to that of forest patch interior. Following Puth and Wilson (2001) nomenclature: "an edge or *boundary* is defined as an area of sharp gradients in ecological flows that slows or redirects flows of organisms, matter, or energy between patches (Wiens et al. 1985) and a *corridor* as a structure that channels and directs the flow of organisms, materials, or energy between patches". Streams and their immediate context (in this case, riparian forest strip) constitute a mix of both, a natural edge and corridor that can modulate the movement of species and propagules in the landscape (Naiman and Decamps 1997, Puth and Wilson 2001). For example, in this study, we have found evidence that

supports this mixed role of riparian vegetation strips: First, they seem to play an important role within the rural landscape as corridors for plant dispersal (Gregory et al. 1991) through composition differences and enhanced quantity of seed rain, modulated by mutualistic plant-animal interactions (Levey et al. 2005). Secondly, for birds, riparian forests may be similar to edge habitats in upland forests, which may produce greater fruit crops and increase bird activity, especially of frugivores (Thompson & Willson 1981). The added complexity and productivity of riparian vegetation would compensate possible negative effects of habitat size and tree structure (Fink et al. 2006). Riparian forests therefore may act both as corridors and as rich sources of resources for birds, especially frugivores, thus facilitating relatively long-distance plant movement through seed dispersal across the rural landscape. Preliminary studies shows that seed predation on riparian forests of northern Chiloé is lower than in upland forest edge and interior (M. Bustamante-Sánchez et al., unpublished data). Other studies have documented higher seed predation in corridor connected patches (Orrock and Damschen 2005), but higher intensity of pollination and seed dispersal has been described for this habitat type too (Tewksbury et al. 2002, Levey et al. 2005, Sabo et al. 2005). More comprehensive studies of plant-animal interactions in riparian forests are necessary in order to understand their role regarding population and genetic patterns across the rural landscape (Puth and Wilson 2001, Tewksbury et al. 2002, Haddad et al. 2003, Orrock and Damschen 2005, Sabo et al. 2005). When seen from a broad point of view, the ecological function of riparian forests in the rural environments become more complex than just corridor or edge habitats.

Previous studies have documented that riparian corridors are important landscape elements for the maintenance of regional biodiversity (Johansson et al. 1996, Sabo et

al. 2005). Species richness of plants may be higher than in neighboring upland habitats, as suggested by the enhanced seed rain of avian-dispersed propagules in our study. Therefore, an important characteristic of riparian habitats is their heterogeneity (Sabo et al. 2005). Riparian forest habitats within a predominantly non-forest land cover as characteristic of many rural landscapes (Mayfield and Daily 2005) are important landscape features that sustain species diversity by serving as refugia (e.g., as both living and passing habitat) for several plant and animal species (Heartsill-Scalley and Aide 2003). Most ecological processes and interactions depend on spatial scales much larger than that of a single forest fragment (Murphy and Lovett-Doust 2004). Therefore, planning cohesive conservation networks in human-dominated landscapes, including and considering species interactions (such as plant-animal mutualisms) and ecological processes (such as seed dispersal, predation and recruitment) will be much more effective than conserving a limited number of species and isolated habitats (Pedroli et al. 2002).

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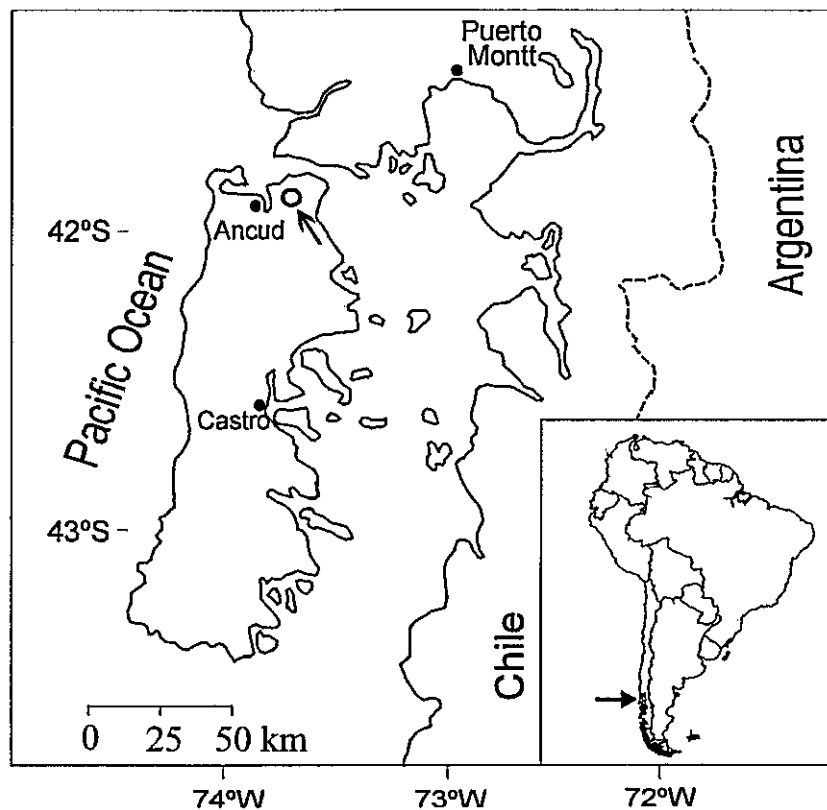


Figure 1: Study area location in a rural landscape in northern Chiloé Island, southern Chile (empty circle indicated by the arrow).

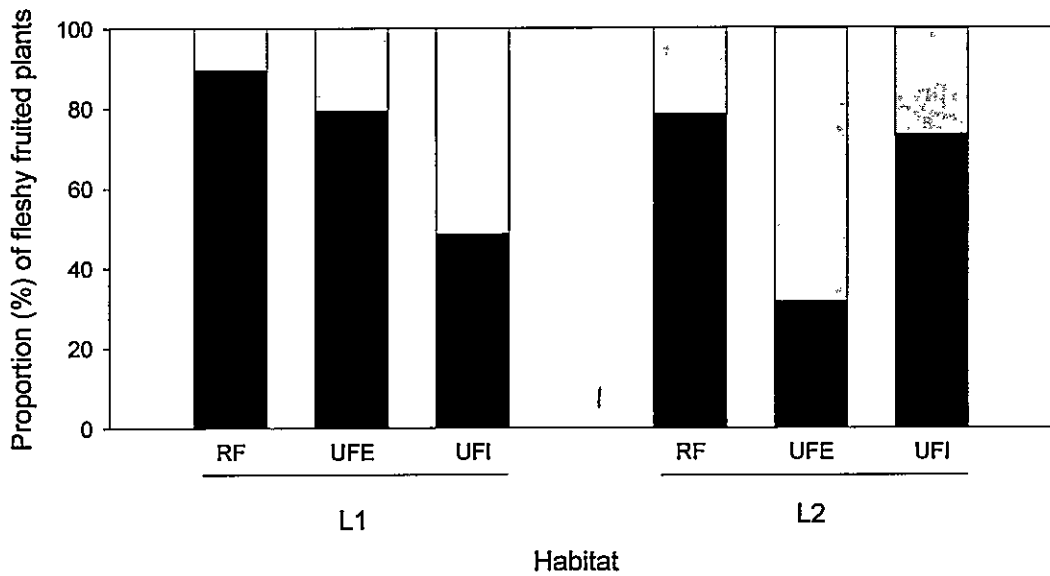


Figure 2: Relative abundance of individual trees (with DBH >10 cm) belonging to fleshy fruited species in the different forest habitats sampled in fruiting season two (2003-2004). Black bars: fleshy-fruited species. Gray bar: Other fruit types. See text for habitat names. Sample size of individual trees in each habitat: landscape 1 (L1) RF n = 68, UFE n = 34, UFI n = 76; landscape 2 (L2) RF n = 70 UFE = 101, UFI n = 73.

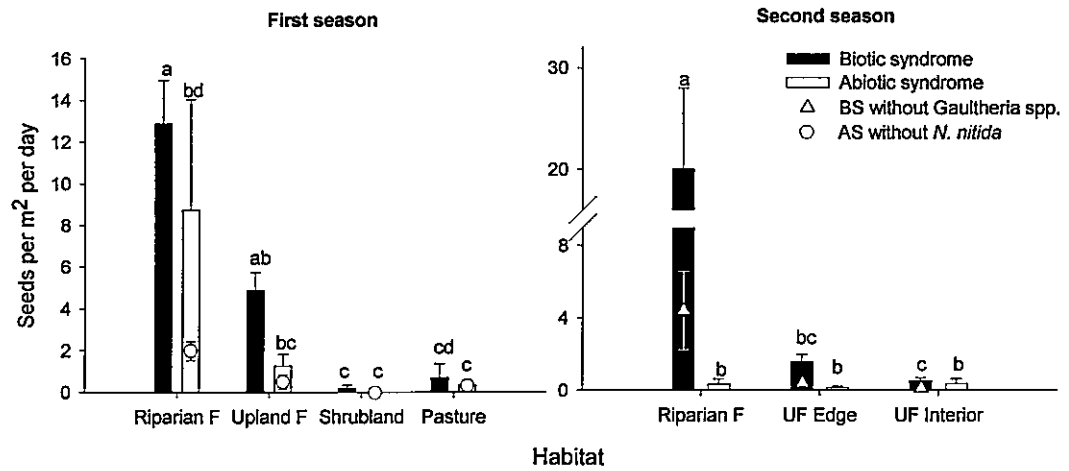


Figure 3: Mean number of collected seeds in each season ( $\pm 1$  SE), pooling dispersed and non-dispersed seeds of biotically and abiotically-dispersed species. Please note the different habitat types compared in the first and second fruiting season. Different letters above bars indicate significant differences among habitats and dispersal syndromes.

Table 1: Factorial ANOVA results for the total number of collected seeds in each season, considering differences among habitats and between dispersal syndromes (biotic vs. abiotic dispersal). Analysis was performed on log-transformed data.

First season				
	df	MS	F	P
Habitat type	3	2.78	28.47	0.000
Dispersal syndrome	1	0.95	9.71	0.003
H*DS	3	0.28	2.89	0.042
Error	64	0.10		
Second season				
	df	MS	F	P
Habitat type	2	2.16	26.16	0.000
Landscape Unit	1	0.98	11.90	0.001
Dispersal syndrome	1	7.09	86.00	0.000
H*LU	2	0.51	6.18	0.002
H*DS	2	2.22	26.97	0.000
LU*DS	1	0.79	9.57	0.002
H*LU*DS	2	1.07	12.96	0.000
Error	240	0.08		

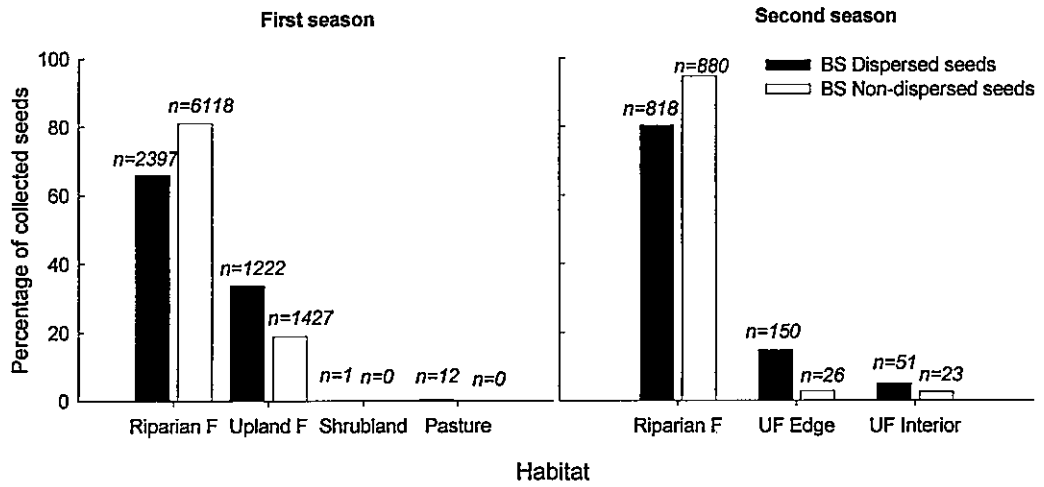


Figure 4: Percentage of seeds from fleshy-fruited species that were found in the dispersed condition (naked seeds) vs. non-dispersed condition (whole fruit fallen by gravity). Numbers above bars are the total number of collected seeds per habitat per season.



Table 2: Seed rain of collected seeds from allochthonous species in each one of sampled habitats. Seeds are considered from allochthonous species when the species was absent from the sampled vegetation around the trap. a) shows the seeds and species number including *Gaultheria* species, b) seeds and species without *Gaultheria* species. See text for habitat names. Mean number of seeds/species per trap is shown  $\pm$  standard deviation.

a. *With Gaultheria* spp.

		Total number of species collected	Number of allochthonous species collected	Total seed rain	Number of naked seeds collected	Number of allochthonous seeds collected	Proportion of allochthonous seeds
UF interior 1	Total	18		68	48	28	0.58
	Mean per trap	$0.9 \pm 0.9$	$0.5 \pm 0.7$	$3 \pm 6$	$2 \pm 4$	$1 \pm 3$	
UF interior 2	Total	20		129	121	112	0.93
	Mean per trap	$1.4 \pm 1.3$	$1.0 \pm 1.2$	$6 \pm 20$	$6 \pm 11$	$5 \pm 11$	
UF edge 1	Total	17		372	305	137	0.45
	Mean per trap	$1.8 \pm 1.4$	$1.1 \pm 1.2$	$18 \pm 25$	$15 \pm 22$	$7 \pm 12$	
UF edge 2	Total	18		212	205	189	0.92
	Mean per trap	$1.4 \pm 1.1$	$0.9 \pm 0.8$	$10 \pm 20$	$10 \pm 19$	$9 \pm 19$	
Riparian F 1	Total	23		6851	3849	950	0.25
	Mean per trap	$7.1 \pm 2.0$	$4.2 \pm 2.2$	$326 \pm 628$	$183 \pm 329$	$45 \pm 81$	
Riparian F 2	Total	17		761	744	216	0.29
	Mean per trap	$1.6 \pm 1.0$	$0.7 \pm 0.9$	$36 \pm 70$	$35 \pm 70$	$10 \pm 29$	

b. *Without Gaultheria* spp.

		Total number of species collected	Number of allochthonous species collected	Total seed rain	Number of naked seeds collected	Number of allochthonous seeds collected	Proportion of allochthonous seeds
UF interior 1	Total	17		41	26	21	0.81
	Mean per trap	$0.6 \pm 0.7$	$0.3 \pm 0.6$	$2.0 \pm 4.7$	$1.2 \pm 3.4$	$1.0 \pm 3.5$	
UF interior 2	Total	19		33	25	16	0.64
	Mean per trap	$0.9 \pm 1.1$	$0.5 \pm 0.9$	$1.6 \pm 2.4$	$1.2 \pm 1.6$	$0.8 \pm 1.6$	
UF edge 1	Total	16		132	113	39	0.35
	Mean per trap	$1.3 \pm 1.1$	$0.8 \pm 1.0$	$6.3 \pm 12.7$	$5.4 \pm 12.2$	$1.9 \pm 2.7$	
UF edge 2	Total	17		44	37	21	0.57
	Mean per trap	$0.9 \pm 0.9$	$0.3 \pm 0.6$	$2.1 \pm 2.7$	$1.8 \pm 2.5$	$1.0 \pm 2.4$	
Riparian F 1	Total	22		1675	801	215	0.27
	Mean per trap	$6.2 \pm 2.0$	$3.7 \pm 1.9$	$79.8 \pm 172.9$	$38.1 \pm 54.4$	$10.2 \pm 10.3$	
Riparian F 2	Total	16		23	17	6	0.35
	Mean per trap	$0.8 \pm 0.9$	$0.3 \pm 0.6$	$1.1 \pm 1.7$	$0.8 \pm 1.1$	$0.3 \pm 0.6$	

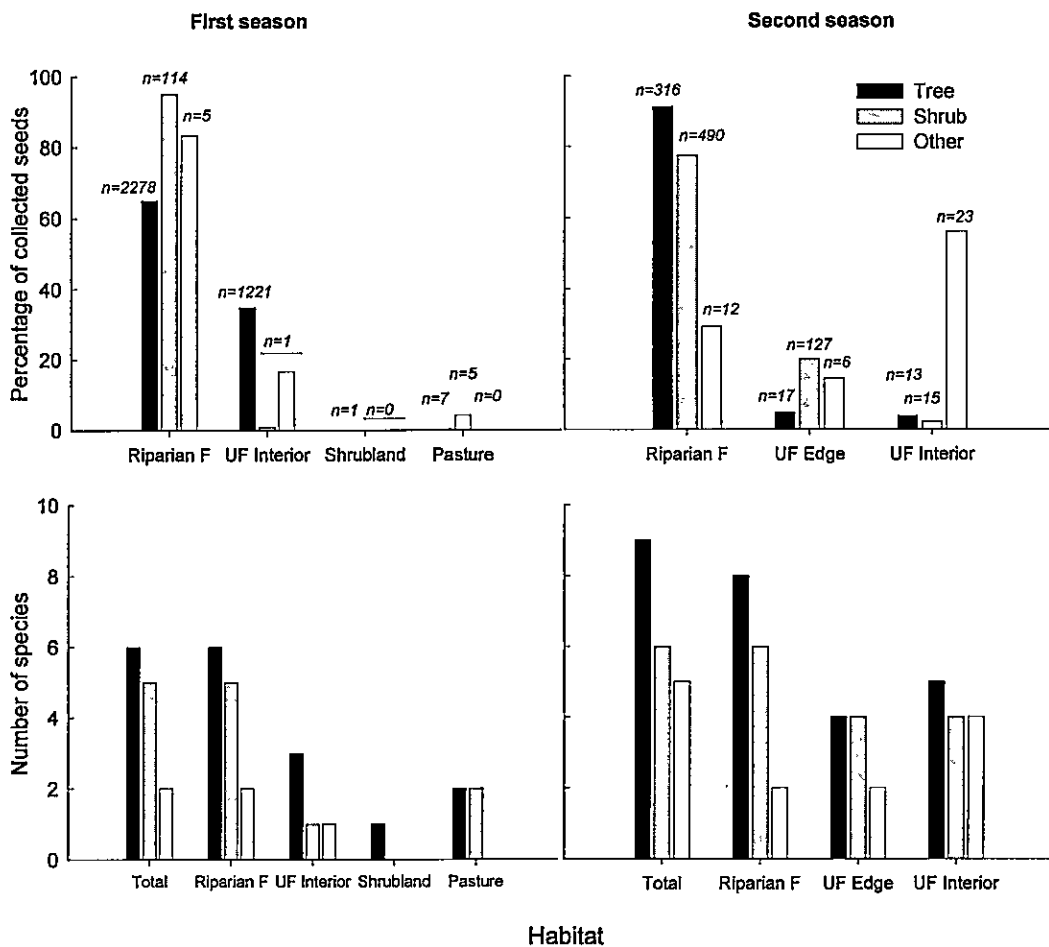


Figure 5: Percentage of all dispersed seeds (upper two panels) and total number of fleshy-fruited species (lower two panels) of each growth habit (trees, shrubs and other including vines) collected in the seed traps each season. Numbers above bars are the total number of collected seeds per habitat per season. For species numbers, total represents the accumulated number of species collected across all habitats for each growth habit.

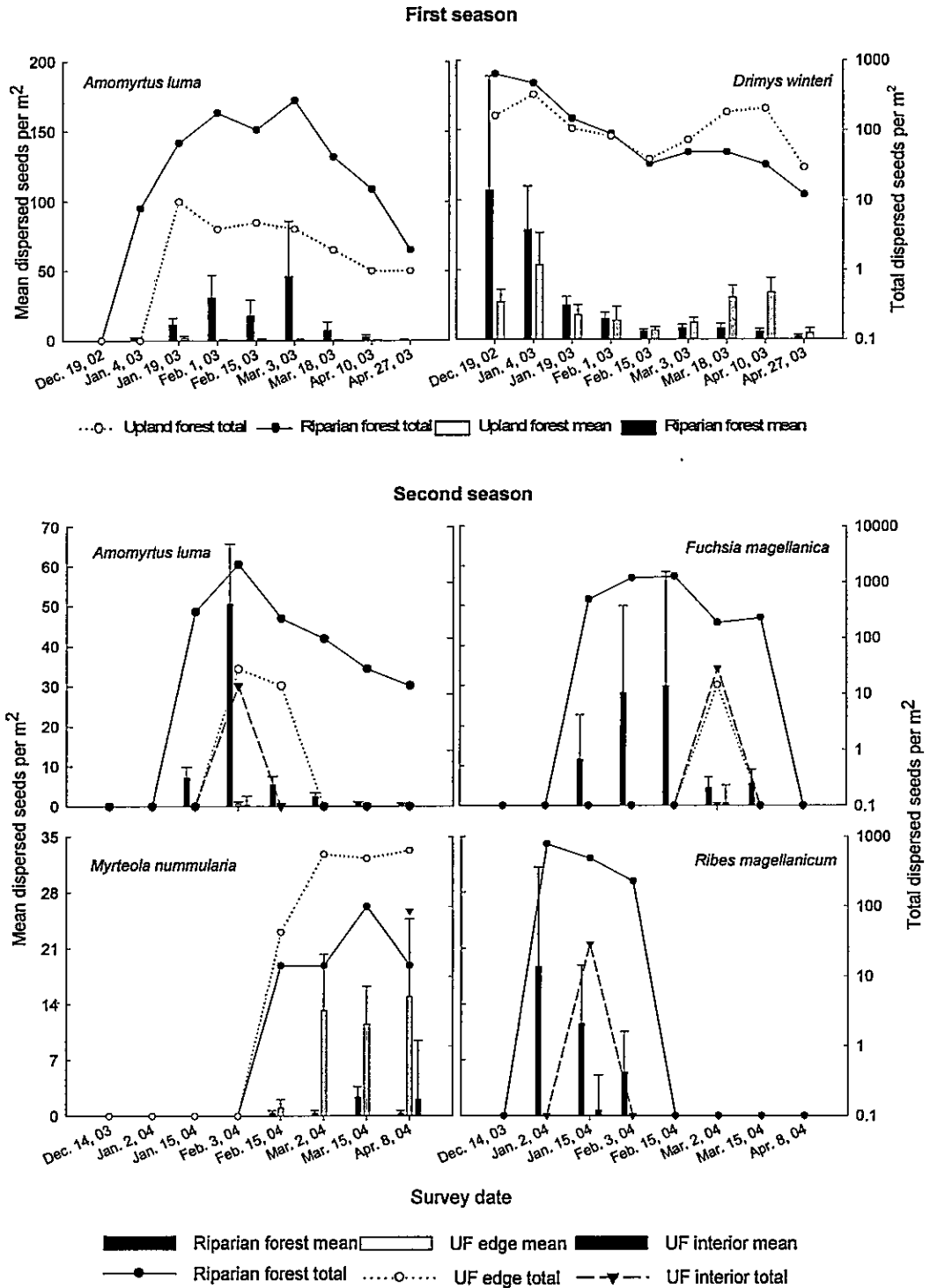


Figure 6: Temporal variation of seed rain over the fruiting season. Only species that accounted for the 10% or more of all dispersed seeds in the seed rain are shown.

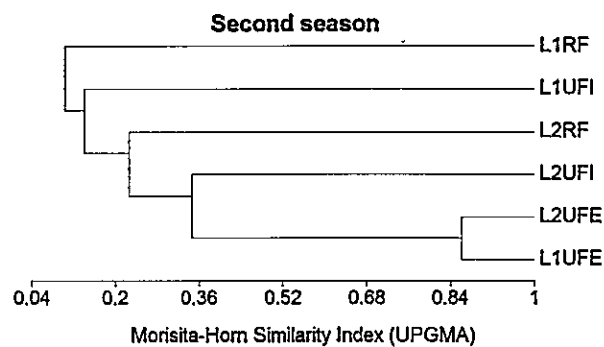
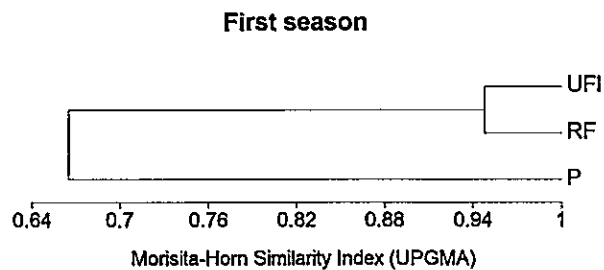


Figure 7: Dendrogram of similarities (Morisita-Horn index) of biotically-dispersed seeds collected on each season. UFI: upland forest interior, UFE: upland forest edge, RF: riparian forest, P: pasture, L1: landscape 1, L2: landscape 2. Non statistical significance of groups was found, neither in first nor second season.

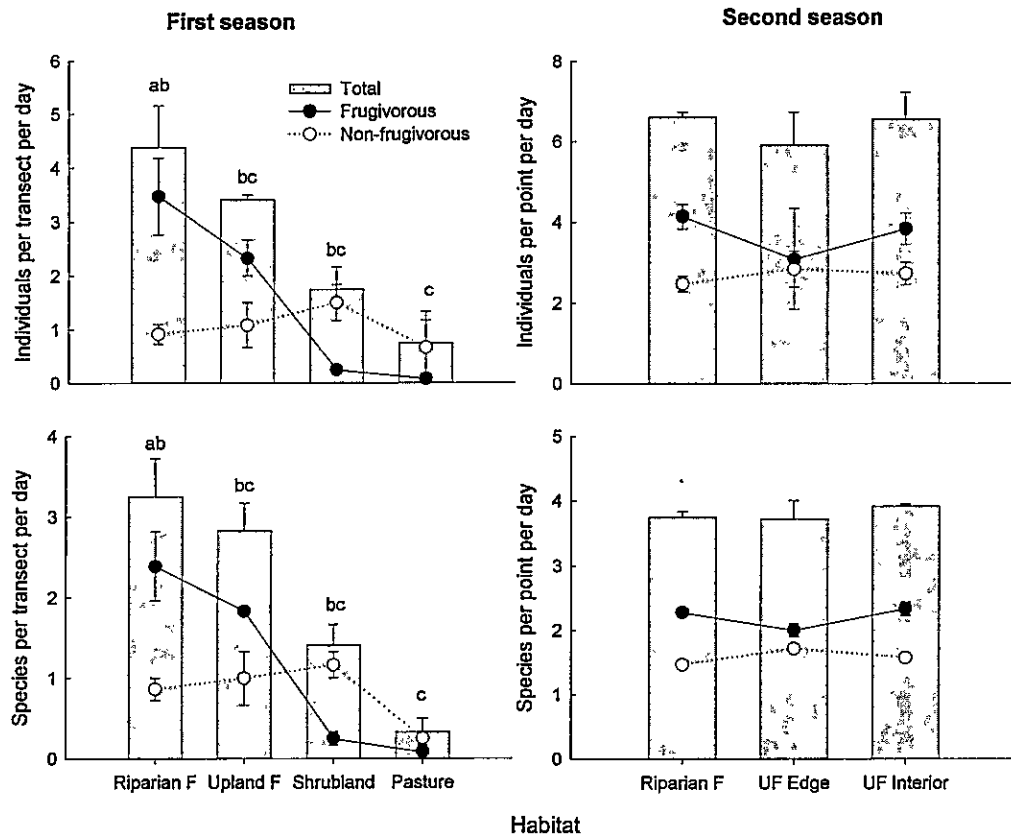


Figure 8: Mean bird abundance and species richness, for all species, frugivorous and non-frugivorous birds, in both fruiting seasons studied. Please note the different habitat categories each season. In first season, different letters above bars denote significant differences between habitats. No significant differences were found for bird abundances in the second season.

Table 3: Factorial ANOVA for bird abundances for each fruiting season. Between-subject represents the variation between groups (between the different levels inside a factor). Within-subject represents variation inside of the groups, through time.

First season					Second season				
	df	MS	F	P		df	MS	F	P
<i>Between-subject</i>					<i>Between-subject</i>				
Habitat	3	24.78	3.78	0.032*	Landscape	1	11.12	3.24	0.085
Diet	1	7.00	1.07	0.317	Habitat	2	2.68	0.78	0.470
H*D	3	29.39	4.48	0.018*	Diet	1	55.00	16.01	0.001*
Error	16	6.56			L*H	2	4.39	1.28	0.297
<i>Within-subject</i>					<i>Within-subject</i>				
Time	5	0.64	0.72	0.607	L*D	1	10.23	2.98	0.097
T*H	15	1.67	1.88	0.037*	H*D	2	9.17	2.67	0.090
T*D	5	1.78	2.00	0.088*	L*H*D	2	23.09	6.72	0.005*
T*H*D	15	1.92	2.16	0.015*	Error	24	3.44		
Error	80	0.89			<i>Within-subject</i>				
					Time	5	30.28	6.47	0.000*
					T*L	5	14.28	3.05	0.013*
					T*H	10	6.98	1.49	0.151
					T*D	5	2.55	0.54	0.742
					T*L*H	10	10.49	2.24	0.020*
					T*L*D	5	2.68	0.57	0.720
					T*H*D	10	6.58	1.41	0.185
					T*L*H*D	10	7.54	1.61	0.111
					Error	120	4.68		

Table 4: Factorial ANOVA for bird species richness in each fruiting season. Between-subject represents the variation between groups (between the different levels inside a factor). Within-subject represents variation inside of the groups, through time.

First season					Second season				
	df	MS	F	P		df	MS	F	P
<i>Between-subject</i>					<i>Between-subject</i>				
Habitat	3	15.19	6.35	0.005*	Landscape	1	0.17	0.22	0.646
Diet	1	2.94	1.23	0.284	Habitat	2	0.20	0.26	0.774
H*D	3	10.87	4.54	0.017*	Diet	1	20.17	26.24	0.000*
Error	16	2.39			L*H	2	0.68	0.89	0.426
<i>Within-subject</i>					<i>Within-subject</i>				
Time	5	0.23	0.53	0.753	L*D	1	2.24	2.92	0.101
T*H	15	0.71	1.63	0.084	H*D	2	1.51	1.97	0.161
T*D	5	0.61	1.41	0.229	L*H*D	2	3.64	4.74	0.018*
T*H*D	15	1.06	2.44	0.006*	Error	24	0.77		
Error	80	0.43			<i>Within-subject</i>				
					Time	5	6.09	5.85	0.000*
					T*L	5	2.48	2.38	0.042*
					T*H	10	1.54	1.48	0.154
					T*D	5	1.43	1.38	0.238
					T*L*H	10	1.69	1.63	0.107
					T*L*D	5	0.82	0.79	0.561
					T*H*D	10	0.71	0.69	0.736
					T*L*H*D	10	1.22	1.17	0.315
					Error	120	1.04		

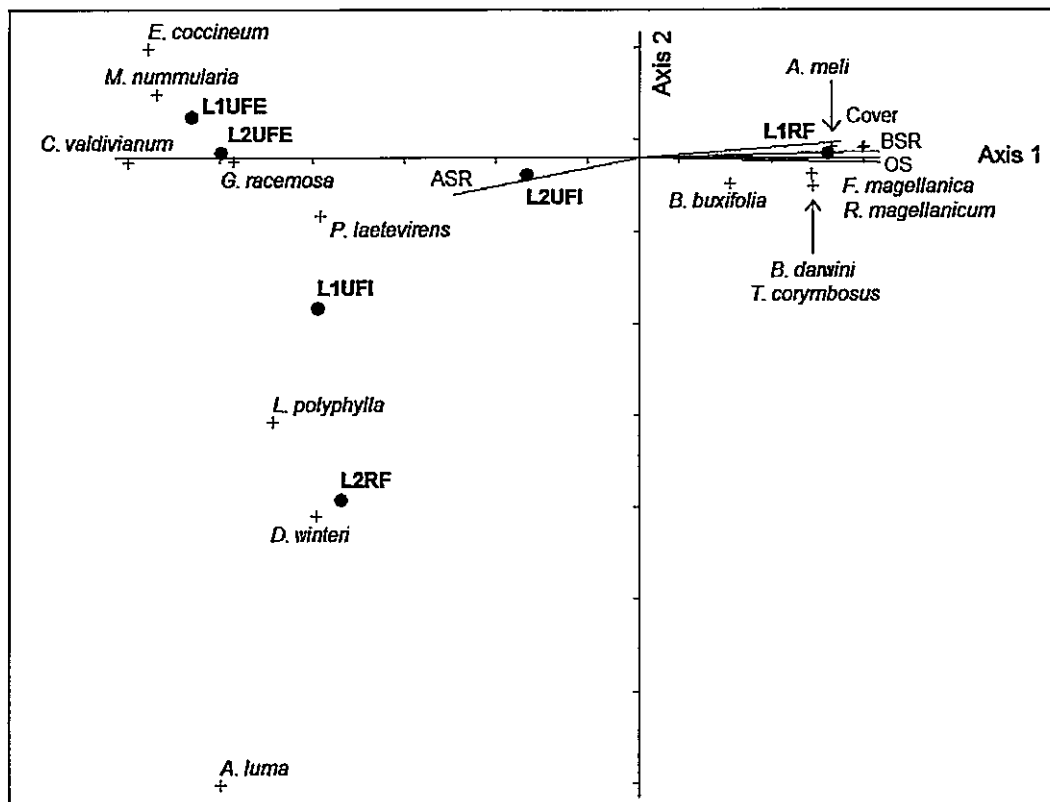


Figure 9: Position of habitat types and seed rain by species, in the space defined by a canonical correspondence analysis (CCA). Explanatory variables are depicted as vectors (OS: number of fleshy-fruited species, cover: percentage canopy cover, BSR: mean seed rain of fleshy fruited species, ASR: mean seed rain of non-fleshy fruited species). The position of a site or habitat with respect to each explanatory variable is approximated by projecting the point in the diagram perpendicularly on the explanatory vector (OS, BSR, ASR, cover). The length of the line representing the explanatory vector indicates the relative importance of a given explanatory variable in the model, and the direction of the line how well the environmental variable is correlated with each axis. Complete species names are given in appendix 1.



Table 5: Summary of statistics for the first two CCA axes. Correlations between explanatory variables (OS: number of fleshy-fruited species, cover: percentage canopy cover, BSR: mean seed rain of fleshy fruited species, ASR: mean seed rain of non-fleshy fruited species) and canonical axes are shown (inter-set correlations).

<b>Statistic</b>	<b>CCA axis 1</b>	<b>CCA axis 2</b>
<i>Eigenvalues</i>	0.815	0.351
Variance in species data		
percentage of explained variance	50%	21.5%
<i>Inter-set correlations</i>		
BSR	0.974	0.119
ASR	-0.670	-0.639
OS	0.973	-0.094
Cover	0.727	0.268
BA	-0.016	-0.069

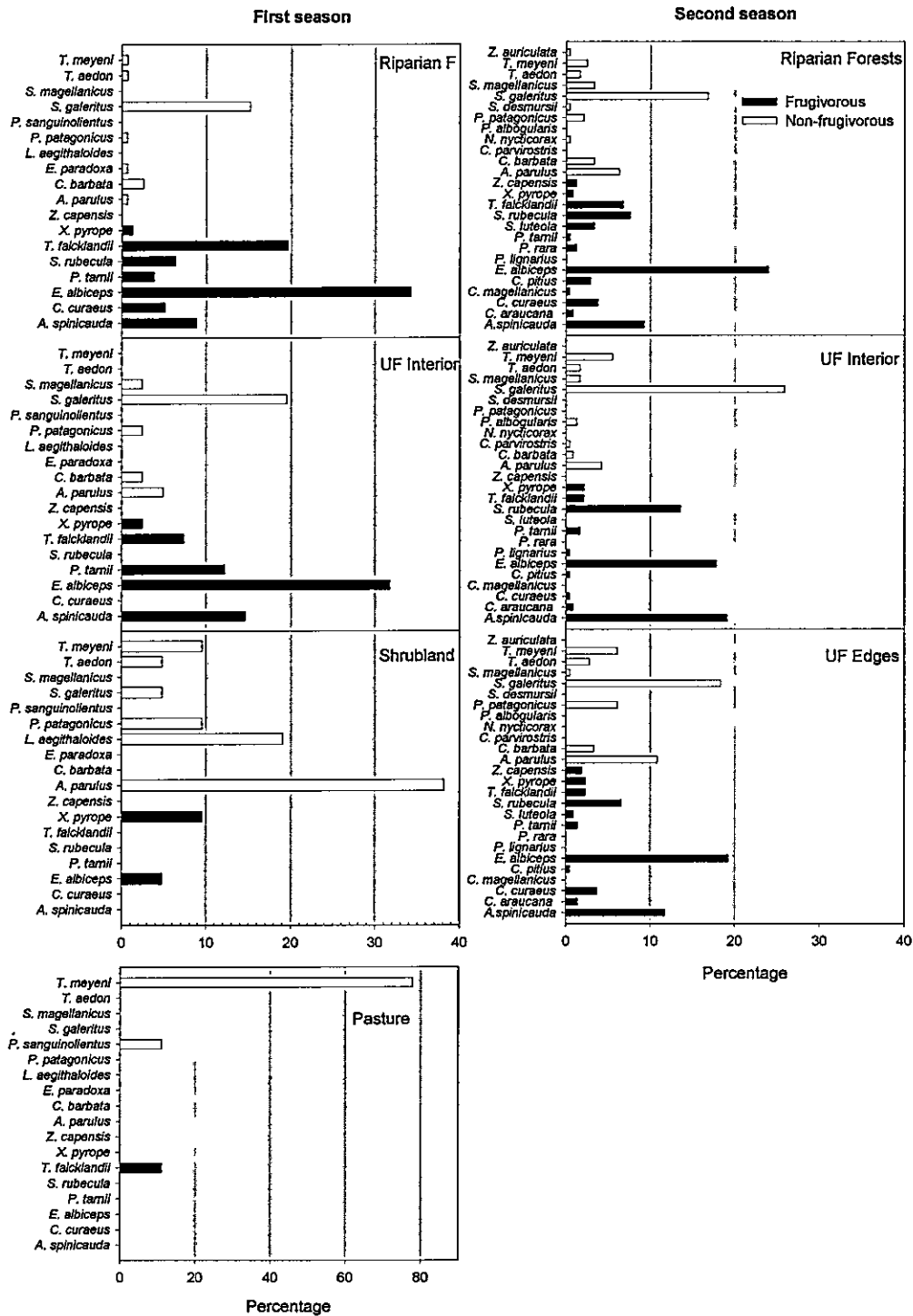


Figure 10: Relative abundance of birds in different rural habitats during two consecutive fruiting seasons. For the second fruiting season (left panels), data for equivalent habitats in landscapes 1 and 2 were pooled.

Appendix 1: Plant species present as growing individuals or as seeds in different habitats of Chiloé Island, during two consecutive fruiting seasons. UFI: upland forest interior, UFE: riparian forest edge, RF: riparian forest, S: shrubland, P: pasture. Dispersal syndrome codes E: endozoochory (fleshy-fruited), A: anemochory, H: hydrochory, (both included as abiotic dispersal syndromes) M: mammalochory, (included as others dispersal syndromes): ?= indicates uncertain dispersal vector or unknown, \* dry fruits that may open and release the seeds when still on the plant (RJP personal observation). Letters in parentheses indicate the main vertebrate disperser identified for each species B: birds M: mammals. †Aizen et al. 2002 ‡Celis-Diez unpublished data. Data in parentheses for each fruiting season indicates: total collecting trap area and number of sampling days. Dispersal syndromes and growth habits according to Armeisto and Rozzi (1989), Smith-Ramirez and Armeisto (1994).

Plant species	Family	Dispersal syndrome	Growth Habit	HABITATS	Total number of seeds collected per habitat								
					UFI		UFE		RF		S		P
					First season (6 m <sup>2</sup> , 143 days)	Second season (1.47m <sup>2</sup> , 129 days)	Second season (1.47m <sup>2</sup> , 129 days)	Second season (1.47m <sup>2</sup> , 129 days)	First season (18 m <sup>2</sup> , 143 days)	Second season (1.47m <sup>2</sup> , 129 days)	First season (6 m <sup>2</sup> , 143 days)	Second season (6 m <sup>2</sup> , 143 days)	First season (6 m <sup>2</sup> , 143 days)
<i>Aextoxicicon punctatum</i>	Aextoxicaceae	E (B)	Tree	UFI-RF	0	0	0	0	11	9	0	0	0
<i>Amomyrtus luma</i>	Myrtaceae	E (B)	Tree	UFI-UFE-RF	53	1	3	5610	259	0	0	0	0
<i>Amomyrtus meli</i>	Myrtaceae	E (B)	Tree	UFI-UFE-RF	0	2	1	114	69	0	0	2	2
<i>Aristolelia chilensis</i>	Elaeocarpaceae	E (B)	Tree	-	0	0	0	53	2	0	0	0	0
<i>Berberis buxifolia</i>	Berberidaceae	E (B)	Shrub	UFE-RF	0	5	3	38	42	0	0	4	4
<i>Berberis darwinii</i>	Berberidaceae	E (B)	Shrub	UFE-RF	1	0	3	116	144	0	0	1	1
<i>Caldcluvia paniculata</i>	Cunoniaceae	A	Tree	UFI-UFE-RF	0	0	0	0	0	0	0	0	0
<i>Campsidium valdivianum</i>	Bignoniaceae	A	Vine	UFI-UFE-RF	0	1	6	0	0	0	0	0	0
<i>Chusquea</i> spp.	Poaceae	M?	Shrub	UFI (gap)-UFE-RF	0	0	0	0	0	0	0	0	0
<i>Cissus striata</i>	Vitaceae	E (B)	Vine	RF	0	0	0	0	0	0	0	0	0
<i>Crinodendron hookerianum</i>	Elaeocarpaceae	H-E†	Shrub	UFI-UFE-RF	0	0	0	0	1	0	0	0	0
<i>Desfontainea spinosa</i>	Desfontaineaceae	E (B)	Shrub	UFI-UFE-RF	0	0	0	0	0	0	0	0	0

Total number of seeds collected per habitat

Plant species	Family	Dispersal syndrome	Growth Habit	HABITATS	UFI		UFE		RF		S	P
					First season (6 m <sup>2</sup> , 143 days)	Second season (1.47 m <sup>2</sup> , 129 days)	First season (18 m <sup>2</sup> , 143 days)	Second season (1.47 m <sup>2</sup> , 129 days)	First season (6 m <sup>2</sup> , 143 days)	Second season (1.47 m <sup>2</sup> , 129 days)	First season (6 m <sup>2</sup> , 143 days)	First season (6 m <sup>2</sup> , 143 days)
<i>Drimys winteri</i>	Winteraceae	E (B)	Tree	UFI-UFE-RF	2437	1	21	7290	7	1	1	5
<i>Embothrium coccineum</i>	Proteaceae	A	Tree	UFE-RF	0	0	25	185	2	0	0	2
<i>Eucryphia cordifolia</i>	Eucryphiaceae	A	Tree	UFI-UFE-RF	6	0	1	1049	3	0	0	0
<i>Fuchsia magellanica</i>	Onagraceae	E (B)	Shrub	RF	0	17	1	2101	775	0	0	0
<i>Gaultheria phillyearifolia</i>	Ericaceae	E (B)	Shrub	UFI (gaps) - UFE-RF	150	123	408	0	5914	0	0	0
<i>Gevuina avellana</i>	Proteaceae	E (M)	Tree	UFI-UFE-RF	1	0	0	36	1	0	0	0
<i>Griselinia racemosa</i>	Cornaceae	E (B)	Vine	UFI-UFE-RF	0	2	5	0	0	0	0	0
<i>Laurelopsis philippiana</i>	Monimiaceae	A	Tree	UFI-RF	2	0	0	201	0	0	0	0
<i>Luma apiculata</i>	Myrtaceae	E (B)	Tree	UFI-UFE-RF	0	0	0	0	12	0	0	0
<i>Luzuriaga polyphylla</i>	Philesiaceae	E (B-M <sup>+</sup> )	Vine	UFI-UFE-RF	0	4	1	0	0	0	0	0
<i>Luzuriaga radicans</i>	Philesiaceae	E (B)	Vine	UFI-RF	0	0	0	0	2	0	0	0
<i>Mitrasia coccinea</i>	Gesneriaceae	E (B)	Epiphyte	UFE-UFI-RF	0	16	0	0	0	0	0	0
<i>Myrceugenia ovata</i>	Myrtaceae	E (B)	Tree	UFE	0	0	0	0	0	0	0	0
<i>Myrceugenia parvifolia</i>	Myrtaceae	E (B)	Tree	UFI-UFE-RF	0	0	0	0	0	0	0	0
<i>Myrceugenia planipes</i>	Myrtaceae	E (B)	Tree	RF	0	0	0	44	0	0	0	0
<i>Myrteola nummularia</i>	Myrtaceae	E (B)	Shrub	UFE	0	6	120	47	10	0	0	0

Total number of seeds collected per habitat

Plant species	Family	Dispersal syndrome	Growth Habit	HABITATS	UFI		UFE		RF		P
					First season (6 m <sup>2</sup> , 143 days)	Second season (1.47m <sup>2</sup> , 129 days)	Second season (1.47m <sup>2</sup> , 129 days)	First season (18 m <sup>2</sup> , 143 days)	First season (6 m <sup>2</sup> , 143 days)	Second season (6 m <sup>2</sup> , 143 days)	
<i>Nothofagus nitida</i>	Nothofagaceae	A	Tree	UFI-UFE-RF	639	3	0	17329	0	0	0
<i>Pernettya insana</i>	Ericaceae	E (B)	Shrub	UFI-UFE-RF	0	0	0	0	0	0	0
<i>Philesia magellanica</i>	Philesiaceae	E (B)	Vine	UFI-UFE-RF	0	0	1	0	0	0	0
<i>Pilgerodendron uviferum</i>	Cupressaceae	A?	Tree	UFE	0	0	0	0	0	0	0
<i>Podocarpus nubigena</i>	Podocarpaceae	Z (B)	Tree	UFI-UFE-RF	0	13	4	0	0	0	0
<i>Pseudopanax laetevirens</i>	Araliaceae	E (B)*	Tree Vine	UFI-UFE-RF	0	4	13	0	3	0	0
<i>Rhaphithamnus spinosus</i>	Verbenaceae	E (B)	Tree	RF	2	0	0	290	108	0	0
<i>Ribes magellanicum</i>	Saxifragaceae	E (B)*	Shrub	RF	0	2	0	48	190	0	0
<i>Rubus constrictus</i>	Rosaceae	E (B)	Shrub	RF	0	0	0	58	55	0	0
<i>Saxe-gothea conspicua</i>	Podocarpaceae	?	Tree	UFI-UFE-RF	0	0	0	0	0	0	0
<i>Tepualia stipularis</i>	Myrtaceae	A	Shrub	UFI-UFE-RF	n	8	n	n	0	0	0
<i>Tristerix corymbosus</i>	Loranthaceae	E (M <sup>+</sup> )	Hemi-parasite	UFI-UFE-RF	5	1	0	13	10	0	0
<i>Weinmannia trichosperma</i>	Cunoniaceae	A	Tree	UFI-UFE-RF	0	120	22	0	120	0	0
Total					3296	329	638	34633	7738	1	14