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# Importance of structure for species richness and tree species regeneration niches in old-growth Patagonian swamp forests

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ABSTRACT

Swamp forests have high ecological value and significantly contribute to the productivity of the zones in which they are located because they provide important ecosystem benefits to society. *Tepualia stipularis*-dominated swamp forests, also called *tepuales*, are the most common but endangered swamp forests in Patagonia. In these forests, *T. stipularis* develops very complex structures and accumulates large amounts of biomass due to its horizontal growth habit, which leads to the formation of arboreal soils and nearly impenetrable networks of trunks. Here, we hypothesize that the complex structure of old-growth *T. stipularis*-dominated forests influences species abundance and the regeneration niches of the different tree species that grow in them. In addition, in these forests with restricted drainage, elevated microsites facilitate the development of regeneration. Using pre-harvesting inventory data from two silvicultural experiments in *T. stipularis*-dominated forests of Chiloé Island, North Patagonia, we aim to (a) characterize the structure and composition of old-growth, undisturbed stands, (b) evaluate how their structure influences the regeneration niches of the main tree species, and (c) explain the implications of these findings in the context of the traditional silvicultural management of these forests. Our results show for the first time that these forests present low anthropogenic influence (no exotic species) and contain high tree-species richness, which exceeds that of several old-growth swamp forests around the world. Also, their characteristic gap-phase dynamics and complex structures influence the regeneration niches of different coexisting tree species, which mostly germinate and establish on trunks. In this context, silvicultural methods that maintain a continuous cover should be encouraged to increase the ability of different species to reorganize and adapt to new conditions.



## 1. Introduction

Forested freshwater wetlands, including swamp forests, cover large areas extending from tropical zones to the northern and southern regions of the globe (Correa-Araneda et al., 2011; Lugo et al., 1988). These ecosystems of high ecological value, significantly contribute to the productivity of the zones in which they are located, providing important ecosystem benefits to society (Brinson and Malvárez, 2002; Correa-Araneda et al., 2011; Lugo et al., 1988). Despite their ecological and economic importance and their extensive cover, most of the available information about these ecosystems involves only floristic data (Lugo et al., 1988). Previous studies on the structure and dynamics of swamp forests have focused on forests in the Northern Hemisphere and in tropical zones (*e.g.*, Duberstein and Conner, 2009; Koponen et al., 2004; Sherman et al., 2000), whereas few studies have been performed in the Southern Hemisphere (*e.g.*, Stewart and Veblen, 1982; Veblen and Stewart, 1980), and even fewer have focused on the temperate swamp forests of the Southern Cone in Chile and Argentina (Bannister, 2015).

Most studies about swamp forests in Chile have focused on the Mediterranean zone (Correa-Araneda et al., 2011). However, many swamp forests are also located within the temperate biogeographic regions of the country (Bannister et al., 2012a) and cover 3.5 million ha (24.5% of Chilean native forests) (CONAF, 2016). Within this region, sites with restricted drainage are usually covered with forests dominated by *Tepualia stipularis*, commonly known as '*tepuales*' (Correa-Araneda et al., 2011). In these forests, *T. stipularis* develops very complex structures and accumulates a large quantity of biomass due to its horizontal growth habit, which leads to the formation of arboreal soils and nearly impenetrable networks

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of trunks. For such reasons, these forests also present low resilience to catastrophic disturbances (Bannister et al., 2012b). In addition to being difficult to access and measure, their structural complexity has inhibited studies on them, and thus, our knowledge of these forests is limited. In this context, *Tepualia stipularis* may represent one of the least-known dominant tree species in the Southern Cone of South America.

According to the few descriptive studies, *T. stipularis*-dominated forests in Chile are located in sites with restricted drainage and extremely poor nutrient conditions (Bannister et al., 2012b; Zarin et al., 1998) where they show estimated diameter growth rates of 1 mm/year (Cruz and Lara, 1981). In these sites, *T. stipularis* preferably establish on trunks and undergoes vegetative regeneration via multiple shoots (Christie and Armesto, 2003), explaining the "entangled" appearance of these forests (Donoso, 2006). Several studies performed in swamp forests in the Northern Hemisphere have found evidence that microsite heterogeneity influences the density and distribution of tree species (Duberstein and Conner, 2009; Koponen et al., 2004; Sherman et al., 2000; Vivian-Smith, 1997). For example, within a swamp forest, many tree species greatly prefer mounds (hummocks) rather than depressions (hollows), likely because mounds represent safer sites for tree species development, whereas depressions are covered with water (Duberstein and Conner, 2009). Accordingly, our first hypothesis is that the complex structure of old-growth swamp forests dominated by *T. stipularis* influences species abundance and regeneration niches of the different tree species that grow in these forests (H1). In addition, we hypothesize that elevated microsites facilitate tree species regeneration in these forests with restricted drainage (H2).

The relationship between structure and regeneration has implications for silvicultural management in these forests. Due to the large amounts of biomass accumulated in these forests and the density and calorific value of *T. stipularis* wood, which is the main fuel used for heating in North Patagonia of Chile, these forests have historically been overexploited for firewood (Neira and Bertín, 2009; Sanzana, 2012). Most of the wood extraction is informal, carried out through illegal logging or guided by forest management principles without an ecological basis. After harvesting, which generally consists of strip clear-cutting, natural regeneration has shown to be nearly null (Sanzana, 2012). As a result, the area of degraded *T. stipularis*-dominated forests increases each year in southern Chile, threatening the continuity of these forests, their structural integrity, and their provision of ecosystem services (Ramos-Jiliberto et al., 2009).

In this study, we aim to (a) characterize the structure and composition of old-growth, undisturbed *T. stipularis*-dominated forests, (b) evaluate how their structure influences the regeneration niches of the main tree species, and (c) explain the implications of these findings in the context of their traditional silvicultural management. This study is intended to be a first step in generating greater knowledge about this type of forest, whose future persistence is greatly threatened by human pressure.

## 2. Methods

### 2.1. Study area

The study area is located on Chiloé Island (41°46′S to 43°26′S) in northern Patagonia (Chile) within the transitional area between the northern and southern temperate biogeographical regions (Bannister et al., 2012a). The study area has a temperate climate with a strong oceanic influence, a relative humidity of approximately 80% and an average temperature between 10.6 °C and 11.6 °C (Di Castri and Hajek, 1976). The average annual rainfall is variable throughout the island, mostly depending on elevation. It ranges from 1598 mm at sea level (city of Castro), to 6000 mm at 900 m above sea level (masl), at the highest points of the island (Pérez et al., 2003). The total forest cover in Chiloé is 620,024 ha, of which 59.7% contains *T. stipularis* as one of the dominant tree species (CONAF, 2016). To encompass the latitudinal range of the distribution of *T. stipularis* forests in the study area, a site in the northern half of the island (Butalcura: 42°09′S, 73°50′W) and another one at the southern limit of the island (Inío: 43°21′S, 74°07′W) were selected (Fig. 1). Both sites presented old-growth and undisturbed conditions, were located on flat terrain with restricted drainage, and were saturated by water during a large part of the year. The site at Butalcura is located at ±50 masl on a soil of fluvio-glacial origin with thin (25–100 cm thick), very acidic soils (pH: 4.8), characterized by a clay-loam texture and a gley horizon with moderate P (6.9 mg/g) and N (2.4 mg/g) values. The site at Inío was located at ±10 masl on a sedimentary soil with thicker (>100 cm), very acidic soils (pH: 4.5), and a sandy-loam texture with moderate P (5.8 mg/g) and high N contents (8.3 mg/g) (Table 1).

### 2.2. Field methods

In 2014, 30 circular plots were established in each site (Butalcura and Inío), including ten 15-m-diameter plots (176.7 $m^2$), ten 10 m diameter plots (78.5 $m^2$), and ten 5 m diameter plots (19.6 $m^2$). In each plot, an inventory was performed to characterize the tree structure and composition of the forest. All trees (≥5 cm diameter at breast height (DBH) at a height of 1.3 m) in each plot were identified at the species level, and their DBH and total height (m) were measured. Height was measured using a Vertex IV ultrasound instrument (Haglöf, Sweden). Growth habit of each tree (vertical, diagonal, and horizontal) was also evaluated. To evaluate natural regeneration, four 1 m wide transects were extended from the centre of each experimental plot in four directions (N, S, E, and W, respectively) to the outer boundary. Along each transect, all of the tree species (<1.5 m high) and saplings (>1.5 m high and <5 cm DBH) were identified, and their corresponding height classes were recorded (1: 0–50 cm; 2: 50–100 cm; 3: 100–150 cm; 4: >150 cm) as was their origin (seed or vegetative), the type of microsite they grew on (mineral soil, trunk, moss-leaf litter), and the microsite elevation (1: 0–50 cm; 2: 50–100 cm; 3: 100–150 cm; 4: >150 cm). In addition, the floristic composition was described based on five 1-$m^2$ subplots, one of them located at the centre of each plot, and the other four, 2 m from the centre of the plot, along the established regeneration transects. In each subplot, all of the vascular species were identified, and their growth form was recorded (tree, shrub, subshrub, herb and fern) as well as their cover, according to the Braun-Blanquet method (Westhoff and Van der Maarel, 1978). Finally, using a soil augur, the soil depth and pH were measured at three points distributed within each plot, in the centre and 2 m to the north and south. From each point, soil samples were also extracted to a depth of 10 cm for nutrient analysis using small test pits. The nutrient levels of all of the soil samples were assessed in the Laboratory of Forest Nutrition and Soils (Laboratorio de Nutrición y Suelos Forestales) at the Universidad Austral de Chile in Valdivia, using the standardized and recommended methods of Sadzawka et al. (2006).

### 2.3. Data analysis

All plots (30 per site) were considered for the analysis of the floristic composition because they represented the same sample size of vascular species (5 subplots of 1 $m^2$). Due to the uneven sample size of the inventory plots and to prevent the potential