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## Coupled climate–forest growth shifts in the Chilean Patagonia are decoupled from trends in water–use efficiency

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### ABSTRACT

Ecological regime shifts may lead to a loss of resilience if the affected ecosystem experiences rapid and irreversible changes affecting its structure and function. Coupled regime shifts in climate variability and forest growth have been rarely described, albeit they should play a prominent role on forest dynamics. Patagonia hosts the largest forested area across the mid-latitudes of the southern Hemisphere where some unique and long-lived conifer species as *Pilgerodendron uviferum* (Cupressaceae) are found. In this region, the prominent 1970s climate shift was characterized by a very wet period leading to drier climate conditions afterwards, which caused an unprecedented drop in productivity in most forest types and tree species. However, it is unknown how such climate shift affected *P. uviferum* radial growth and intrinsic water-use efficiency (iWUE) since this species endemic to the Patagonia inhabits wet and often water-logged sites. Here we studied the response of *P. uviferum* in growth and iWUE across different sites in the Chilean Patagonia. Unexpectedly, in two out of four sites we found a positive shift in *P. uviferum* growth, which started in the 1970s. Such growth enhancement, however, was not related to trends in iWUE. Trees in sites showing growth increase presented a loss of sensitivity to the growing-season temperatures after the 1970s. Site and climate were the main predictors of growth trends, whereas the observed iWUE increase was attributed as a response to atmospheric CO<sub>2</sub> concentration increases. We conclude that the sustained growth increase observed in *P. uviferum* was not due to a CO<sub>2</sub>-fertilization effect because iWUE improvements were similar in sites with or without growth enhancement. Thus, growth and iWUE are decoupled in Patagonian *P. uviferum* forests.

### 1. Introduction

The change in the properties and processes of an ecosystem are triggered by ecological regime shifts, which involve the abrupt transition from one stable state to another leading to the reorganization of the system (Folke et al., 2004). A regime shift may also lead to a loss of ecosystem resilience, i.e. the affected ecosystem is unable to recover the same structure and function after one irreversible change (Scheffer et al., 2015). To understand and predict ecological regime shifts is therefore crucial (Carpenter et al., 2011), given that many ecosystem services are compromised, although many times it is difficult to detect the shifting between states (Scheffer, 2009). Since forests are multivariate and complex ecosystems, multiple regime shifts may occur and involve different sets of interacting variables (Bonan, 2008). However, how regime shifts are involved on forest growth dynamics and which external forcing trigger shifts is still under debate.

The abruptness and persistence of the ecological regime shifts are

scale-dependent since they are defined relative to the ecosystem dynamics under scrutiny (Hughes et al., 2013). In forests, for example, detecting shifts is a challenge because trees have long lifespans. If climate influences forest growth over a region, its role as a trigger of productivity shifts can be uncovered by detecting sudden radial-growth changes. This is the case of the Southern South America forests (latitude 38°–55°S, hereafter SSA), where radial growth experienced an unprecedented decline during the second half of the 20th century, mainly in xeric sites, caused by warming and drying trends which intensified after the 1970s (Villalba et al., 2003, 2012). This negative forest-growth shift has been largely linked to the global 1976–1977 climate shift caused by coupled changes in the Pacific sea surface temperature variability (Trenberth and Hurrell, 1994) with an intensification and poleward shift of the Southern Hemisphere westerlies (Abram et al., 2014) driven by the deepening of the Southern Annular Mode (Gong and Wang, 1999). In SSA region, the 1970s climate shift was characterized by a fast warming in austral-summer temperatures and a

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poleward shift of westerly winds, which carry precipitation to this area, leading to drier conditions after 1976 (Agosta and Compagnucci, 2008; Garreaud et al., 2009; Jacques-Coper and Garreaud, 2015). These climatic changes have been accompanied with a global increase in atmospheric CO<sub>2</sub> concentrations ( $c_a$ ) which may also improve forest growth due to a CO<sub>2</sub>-fertilization effect (Norby et al., 2005). From 1970, the  $c_a$  increase has been ~23%, so it is uncertain how much of this increase in C availability will translate into improved photosynthesis rates or enhanced radial growth in mature trees (Peñuelas et al., 2011). In SSA temperate forests subjected to wet-cool climate conditions it could be expected that rising  $c_a$  and climate warming could synergistically stimulate radial growth or lead to abrupt shifts in forest productivity (Silva and Anand, 2013). However, the role played by rising  $c_a$  on abrupt forest growth changes has not been investigated across SSA. In addition, the combined effects of sudden rises in temperature and the sustained increase in  $c_a$  could enhance growth and photosynthesis rates (but also respiration) in these wet areas, thus potentially improving the carbon uptake of SSA temperate forests (Piper et al., 2007). In contrast, it is expected that warming-triggered drought stress could reduce growth of tree species from dry areas despite rising  $c_a$  (Suarez et al., 2004).

The SSA region represents the largest continuous forested area across the mid-latitudes of the southern Hemisphere (Armesto et al., 1995). This region hosts unique temperate rainforests and it is particularly rich in endemic and long-lived conifer species (e.g. *Fitzroya cupressoides*) (Veblen et al., 2005), which may be vulnerable to declines in soil moisture availability (Camarero and Fajardo, 2017; Villalba et al., 2003, 2012), given that they prevail in humid places (sometimes > 4000 mm of annual precipitation). Warmer and drier conditions during the past century (especially since 1950) in northern, more xeric Patagonian forests in Argentina have caused forest dieback and tree mortality (Suarez et al., 2004; Villalba and Veblen, 1998), post-fire tree regeneration failure (Tercero-Bucardo et al., 2007), and insect defoliator outbreaks (Paritsis and Veblen, 2011; Piper et al., 2015). It is uncertain, however, how the 1970s ecological regime shift affected Chilean Patagonian forests, which experience oceanic and more humid conditions than their Argentine counterparts (Garreaud et al., 2013). In particular, we do not know much about how long-lived tree species common in wet, sometimes water-logged, conditions will react to a decrease in annual precipitation. In principle, these long-lived tree species may become more susceptible to sudden changes in climate like the 1976–1977 shift, because we can assume their niche breadth is rather narrow. On the other hand, the tree species here may be more resilient to shifts particularly because their longevity may act as a buffer against climate change effects (Camarero and Fajardo, 2017; Urrutia-Jalabert et al., 2015).

Here we capitalize on the 1970s-climate shift affecting SSA temperate rainforests and investigated whether it eventually translated into a forest-growth shift. To reach that aim we reconstructed growth and intrinsic water-use efficiency (hereafter iWUE), i.e. the ratio between carbon fixation and stomatal conductance, by analysing the ring widths of remote and undisturbed *Pilgerodendron uviferum* forests located in the Chilean Patagonia. We selected this conifer, endemic to the Patagonia, because it is associated to sites with poor drainage as peatlands (Lara et al., 2006). In addition, this is a very long-lived species (Holz, 2009). The occurrence of this species in sites with very high soil-water availability and the elevated maximum age make *P. uviferum* suitable as a sentinel species, good for assessing how tree species are ultimately responding to global-change effects. Based on previous climate-growth analyses (Szeicz, 1997), we expected that the abrupt post-1970s warming event (climate shift) would lead to a sudden growth enhancement in the study sites (positive forest-growth shift). Furthermore, if such coupled climate-forest shift effectively occurred, we hypothesized that iWUE would improve in response to the increase in  $c_a$  and the expected growth improvements due to a CO<sub>2</sub>-fertilization effect (Norby et al., 2005). In this context, it is worth it to recall that there are

two differences between the northern and southern hemisphere climate-change effects that should be considered regarding global-change drivers and consequences when dealing with tree species in the southern hemisphere. First,  $c_a$  continues rising and it has crossed the 400-ppm threshold in both the northern and southern hemispheres. Second, some austral regions as the SSA are among the few land areas where temperature records have not shown significant warming trends (Bidegain et al., 2016).

## 2. Material and methods

### 2.1. Study area and tree species

Western SSA (i.e. the Chilean Patagonia) is characterized by a diverse landscape chiefly dominated by broad-leaved evergreen and deciduous *Nothofagus* and mixed broadleaved-conifer forests (Armesto et al., 1995; Veblen et al., 1996). Annual precipitation here can surpass 2000 mm, where summer precipitation can even be higher than winter precipitation (Garreaud et al., 2009). Lowlands with forest islands (Supporting Information, Fig. S1) or forest-peatland ecotones developing in *Sphagnum*-dominated bogs are the habitats where *Pilgerodendron uviferum* (D. Don) Florin (Cupressaceae) is commonly found (Donoso, 1981). This corresponds to sites which were heavily glaciated in the Pleistocene and where poorly-drained, acid, and usually nutrient-deficient but rich in organic matter soils developed over metamorphic rocks (Arroyo et al., 2015).

We sampled *P. uviferum* forests just south of Cochrane city in the Aysén Region. Here the climate is temperate and oceanic, characterized by cool summers and winters and a mean annual temperature of 8.6 °C. January and June are the warmest and coldest months with means of 13.8 °C and 3.5 °C, respectively. The mean annual precipitation is ca. 800 mm and the driest and wettest months are February and August, respectively (Supporting Information, Fig. S2a). To characterize local climate conditions, we made use of meteorological data coming from the Lord Cochrane station (47.24 °S, 72.59 °W, 204 m), which holds the longest precipitation record in the study area (1971–2016 period), and it is located at 70–120 km from the study sites.

*Pilgerodendron uviferum* is the southernmost conifer on Earth with a distribution area extending from ca. 39° to 54°S in western SSA (Holz, 2009). This is a long-lived, slow-growing conifer, which usually forms small stands occurring in very wet or poorly-drained sites with acid and waterlogged soils (Lara et al., 2006). Overall, the conservation status of this species is precarious because it has been severely exploited due to its rot-resistant wood (Soto et al., 2007). *Pilgerodendron uviferum* forms distinct tree rings. Previous dendrochronological works found that its radial growth is enhanced by warm austral-summer conditions (summer is here considered from November to February) climate conditions (Holz, 2009; Roig, 1991; Roig and Boninsegna, 1992; Szeicz, 1997; Szeicz et al., 2000).

For sample collection, we selected four locations that were climatically similar but differed in slope (Table 1). All locations are temperate evergreen rainforests dominated by *P. uviferum*. Other co-occurring trees are some angiosperms (e.g. *Nothofagus betuloides*) and only another gymnosperm (*Podocarpus nubigenus*) species, which along with some shrub species (e.g. *Gaultheria mucronata*) form a dense understory (Table 1).

### 2.2. Climate data

To obtain climate data for the period 1950–2015, when tree-ring data were available for all selected tree individuals, we used monthly mean temperature and precipitation data from the Climate Research Unit (CRU) version 3.24 with gridded data at a 0.5° resolution (Harris et al., 2014). Data were extracted from grids with coordinates 48.0°–48.5°S, 73.0°–73.5°W (PO, PA and LE sites) and 47.5°–48.0°S, 73.0°–73.5°W (JA site) using the Climate Explorer webpage (<https://>

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