The importance of seed trees in the dioecious conifer *Pilgerodendron uviferum* for passive restoration of fire disturbed southern bog forests

JAN R. BANNISTER,[1]* SVEN WAGNER,[2] PABLO J. DONOSO[3] AND JÜRGEN BAUHUS[1]

[1]*Chair of Silviculture, Faculty of Environment and Natural Resources, Albert-Ludwigs-Universität Freiburg, Tennenbacherstrasse 4, D-79106 Freiburg, Germany (Email: jan.bannister@waldbau.uni-freiburg.de)*, [2]*Institute of Silviculture and Forest Protection, TU Dresden, Tharandt, Germany; and* [3]*Institute of Silviculture, Universidad Austral de Chile, Valdivia, Chile*

Abstract Biological legacies are important for ecosystem recovery following disturbance as demonstrated by studies in the northern hemisphere. Southern bog forests dominated by the conifer *Pilgerodendron uviferum* in Northern Patagonia are a typical case of an ecosystem with low resilience to disturbance by fire, which kills most trees and seeds, on which the species depends for regeneration. In this study, we hypothesize that the natural recovery of *P. uviferum* populations in burned areas is limited by seed availability and this limitation may be exacerbated by the dioecy of the species. Using a multi-scaled approach, we quantified the seed dissemination potential from *P. uviferum* seed trees, assessed the suitability of substrates for the germination of seedlings, and finally analysed the spatial distribution of seed trees of the species at the landscape level. Our results indicate that 70 years after a fire on Chiloé Island (43°S), natural regeneration from seed trees can assist the recovery of *P. uviferum* populations following large-scale fire disturbance, but their effect is limited at a landscape level owing to a low number of reproductive female trees (0.3 trees ha^{-1}) and limited seed dispersal (<20 m). In this context, a mixed passive-active restoration approach that takes into account the spatial pattern and sex of seed trees could be the most effective and efficient option to restore not only *P. uviferum* forests in North Patagonia, but also other heavily disturbed forests with few remnant seed trees, in particular of dioecious species.

Key words: biological legacy, forest restoration, North Patagonia, seed dispersal, spatial population pattern.

INTRODUCTION

Disturbances are an integral part of ecosystems. Humans alter disturbance regimes in fundamental ways increasing scale and severity and reducing the resilience of ecosystems (Walker 2011). In forests, natural disturbances rarely eliminate all structural elements from the preceding stand. Many organisms survive, including sexually mature trees or tree regeneration. These are called 'biological legacies' (Franklin 1990; Franklin *et al.* 2002) and their importance for ecosystem recovery has been documented for a range of ecosystems, especially in the northern hemisphere (e.g. Franklin 1990; Franklin & MacMahon 2000; Hanssen 2003; Keeton & Franklin 2005; Manning *et al.* 2006; Herrera & García 2009; Kashian *et al.* 2012). In addition, previous studies of spatial patterns of plants have shown that dioecy can affect the spatial heterogeneity of plant density in tree species populations (e.g. Gibson & Menges 1994; Montesinos *et al.* 2007). Assuming an equal number of male and

female plants in a specific population, only half of the parent plants of a dioecious species will contribute to seed dispersal (Nanami *et al.* 1999). Therefore, dioecy may exacerbate any limitations in the recovery of populations by seed dissemination after large scale, intensive disturbances, especially if the species has a limited seed dispersal distance (Nanami *et al.* 1999, 2000).

This may be the case in fire-disturbed forests previously dominated by the endemic, slow-growing and long-lived conifer *Pilgerodendron uviferum* (D. Don), a wind-dispersed and dioecious tree species of Patagonia (Lara *et al.* 2006). These southernmost conifer forests of the world (Martinez 1981) cover almost 1 million ha from 40°S to 55°S (6.8% of Chilean native forests) including eastern slopes of the Andes in southern Argentina (Rovere *et al.* 2002; Lara *et al.* 2006). In Chile, they are often found in high rainfall environments (2500–8000 mm per year) and on acidic and poorly drained soils covered by *Sphagnum* bogs (Lara *et al.* 2006). In this environment, these forests develop for long periods without significant disturbances, accumulating high amounts of biomass with dense and complex understoreys (Bannister *et al.* 2012a). In the

last 200 years, humans have caused the destruction of extensive areas of these forests through broad-scale burning to facilitate access to the trees for logging (Bannister *et al*. 2008). Aboriginals and Euro-Chilean settlers have amplified fire activity to such an extent (Holz & Veblen 2011), that widespread anthropogenic fires in the last two centuries have caused dramatic changes in the structure and composition of these forests (Cruz & Lara 1981; Bannister *et al*. 2008). *Pilgerodendron uviferum* does not show any specific adaptations to fire disturbance such as thick bark, resprouting ability, protected seeds or a soil seed bank. In many areas, almost 70 years after the last fire, forest regrowth has been extremely slow and *P. uviferum* is still absent in large tracts of the landscape (Bannister *et al*. 2008). Owing to the widespread disturbance of these forests through fire, the conservation status of the species considered by the IUCN is vulnerable (Walter & Gillet 1998), and it has been included in appendix I of CITES (Lara *et al*. 2006).

Some studies have indicated the importance of seed trees, as biological legacies, for the recovery of disturbed bog forests previously dominated by the conifer *P. uviferum* (Cruz & Lara 1981; Bannister *et al*. 2008), but the effect of these seed trees for the recovery of *P. uviferum* populations at the landscape level has not been quantified. The recovery of populations may not only be limited by the availability of seeds but also by the availability of suitable sites for successful regeneration. Safe sites for natural regeneration are determined by seedbed type, moisture retention and microhabitat (Hörnberg *et al*. 1997; Cornett *et al*. 2000). For example for Scandinavian *Picea abies* bog forests, the main factor affecting seed emergence at a local scale was the microhabitat, and the most important factor for seedling mortality was overgrowth by bryophytes (Hörnberg *et al*. 1997; Hanssen 2003). This is also valid for *Picea mariana* and *Pinus sylvestris* bog forests in Canada (Roy *et al*. 1999) and Scandinavia (Gunnarsson & Rydin 1998), respectively. In this landscape context, long-term seedling survival is lower in depressions owing to vigorous *Sphagnum* growth or mortality caused by inundation (Hanssen 2003). In the case of *P. uviferum* forests, it is not known whether availability of suitable microhabitats may limit regeneration of the species in burned areas.

In this study, we aimed to assess the extent to which the recovery of *P. uviferum* populations may be facilitated through natural regeneration from seeds of remnant trees after large-scale disturbances occurred in the early 1940s (Holz & Veblen 2011). In addition, we were interested in understanding how dioecy may affect this process. Our principal hypothesis was that the natural recovery of *P. uviferum* populations in burned areas is limited by seed availability, and this limitation may be exacerbated by the dioecy of the species. Also, the availability of suitable substrates for

germination (microhabitats) or the competition with bryophytes at establishment may be limiting the recovery of *P. uviferum* populations in these areas. For this we (i) quantified the seed dissemination potential and effective seedling recruitment distance from *P. uviferum* seed trees; (ii) assessed the suitability of substrates for the germination of *P. uviferum* seedlings; and (iii) analysed the spatial distribution of sexually mature male and female trees of the species at the landscape level. This framework allowed us to address the principal constraints to seed arrival and recruitment, which are source-density, source-strength, dispersal and establishment (Clark *et al*. 1998). Based on this information, we discuss the potential for a passive restoration approach to recover disturbed *P. uviferum* bog forests in North Patagonia.

METHODS

Study area

The study area was located in Tantauco Park (~43°10'S and 74°05'W) on Chiloé Island, North Patagonia (Fig. 1). This private conservation area contains the majority of ecological types in which *P. uviferum* grows, as well as extensive disturbed areas that were burned mainly in an extensive fire in 1943 (Bannister *et al*. 2008; Holz & Veblen 2011).

Southern Chiloé has a cool-temperate climate with strong oceanic influence, a mean annual temperature of 10°C, and high annual precipitation that can reach up to 6000 mm in some places (di Castri & Hajek 1976; Pérez *et al*. 2008), belonging to the south temperate biogeographic region of Chile (Bannister *et al*. 2012b). The landscape in the study area has been shaped by the last glaciation (about 13 000 BP), which created a mix of hills from glacial till and shallow valleys, over Pre-Cambrian and Tertiary Metamorphic rocks with extremely acidic, poorly drained soils with Gley horizons (Villagrán 1988). Altitudes range between 150 and 280 m a.s.l.

The disturbed forests of the study area had been burned but subsequently not salvage-logged. This allowed us to investigate the influence of fire-disturbance separately from additional effects that subsequent logging might have had. These areas were mostly covered by *Sphagnum* bogs and cushion plants and characterized by dead trees of *P. uviferum* and *Tepualia stipularis* with some regrowth of broadleaf species like *T. stipularis*, *Nothofagus nitida*, *Drimys winteri*, and *Weinmannia trichosperma*. The study area can be divided in two topographical types: 'bog areas' located in flat areas on raised peat bogs (*Sphagnum* and cushion plants); and 'upland areas' on hills shaped by till with better drainage (see Appendix S1).

Seed dispersion and seedling recruitment around *Pilgerodendron uviferum* seed trees

To quantify the seed dissemination potential of *P. uviferum* seed trees in disturbed forests, one isolated 76-year-old seed
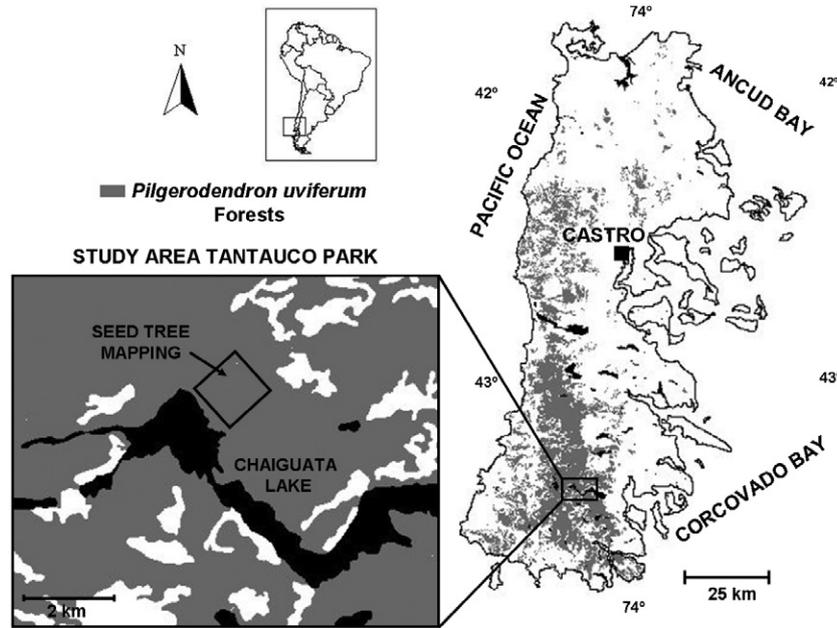
Fig. 1. Study area in the Tantauco Park on Chiloé Island, North Patagonia. Grey colour corresponds to *Pilgerodendron uviferum* dominated forests.

tree of 15.5 cm dbh and 4.8 m height, which was representative of the post-disturbance cohort, was selected to establish a dissemination assay (see Appendix S1). A total of 28 seed traps of 0.25 m² were established at 2 m distance from the seed tree and then every 5 m up to 30 m in each cardinal direction, at 30 cm height from the soil. Seeds in traps were protected from predation through nets. Once every year (May) for 3 years, seed traps were emptied and the seeds counted.

To calculate the effective seedling recruitment distance from *P. uviferum* seed trees, effective regeneration was quantified in the surroundings of 20 seed trees, which were isolated (>150 m from any other seed tree) and had already regenerated. The diameter at breast height (dbh), or root collar diameter (RCD), sex, and position in a coordinate system (x–y) were measured for each seed tree, seedling and sapling. For this, 'seedlings and saplings' were defined as plants <5 cm of dbh and younger than the central seed-tree. For the purpose of this study, no further distinction was made between seedlings and saplings, as both types of young plants, despite differences in size, originated post-disturbance from the same mother tree. To determine tree age, two increment cores were obtained at the lowest possible stem height from each seed tree and one increment core for up to three individuals of their regeneration >3 cm of dbh. Tree cores were mounted and sanded following standard procedures (Stokes & Smiley 1968).

To develop an individual tree-based model to predict the spatial distribution of seedlings and saplings, 1 m wide concentric rings were laid around each of the 20 selected trees. Regeneration frequency was counted within each ring and then transformed to density. Regeneration density around the 20 selected seed trees was then fitted with a log-normal model (Stoyan & Wagner 2001). This model was combined with an allometric component of the function used by

Ribbens *et al*. (1994) so that the final model used corresponded to Equation 1:

$$Freqln(r, dbh) = \frac{e^{\left[\frac{(\ln(r) - \mu)^2}{2\sigma^2} * (-1)\right] * N * \left[\frac{dbh}{dbhref}\right]^{\beta}}}{r\sqrt{2\pi\sigma^2}} \quad (1)$$

Where μ and σ are the logarithms of the median and the standard deviation of the distribution, N (standard total recruitment) is the number of recruits produced for a tree of a standardized dbh 'dbhref', β is a factor that modifies N and dbh is the diameter of the tree. We chose to scale N relative to a tree of 13.5 cm dbh, representing the mean of the 20 selected seed trees. Model parameters were calculated with the R software package (R Development Core Team 2012) and fitted using the least squares method for non-linear models.

Germination experiment

To evaluate the effect of different substrates found in disturbed sites on the germination of *P. uviferum* seeds, a germination experiment with locally collected seeds (weight: 523 560 seeds kg⁻¹) was performed in the nursery of Tantauco Park (see Appendix S1). This experiment comprised four different substrates: moss, mineral soil, cushion plants, and sand, which served as a control. To capture the interactions that may occur between substrate and moisture content, these substrates were kept either wet (watering each day) or were allowed to become dry (watering once a week), yielding eight treatments in total. In each of four replicates per treatment 100 seeds were sown at 3 cm apart. Following the suggestion of Donoso *et al*. (1980), the seeds were stratified for 60 days at 4°C in moist sand prior to sowing.

Seed germination rates were monitored for 6.5 months between July 2010 and February 2011, and at the end the heights of germinants were measured in each treatment (an average of 122 germinants per treatment). This experiment was limited by the assumption that the germination of seeds under optimal conditions in the greenhouse will be similar to the germination in the field.

Analyses of normality and homogeneity of variance for all variables were done with Shapiro–Wilk W, Kolmogorov Smirnov and Levene tests. Data for germination rates were normally distributed. Thus, we performed a two-way ANOVA comparing treatments (substrate and moisture) and significant differences ($P < 0.05$) were further analysed with post-hoc comparisons based on the Bonferroni method. Heights of germinants, which were, even after various transformations, not normally distributed, were compared with Kruskal–Wallis non-parametric tests and post-hoc comparisons based on Mann Whitney U-tests.

Spatial distribution of seed trees at the landscape level

Using a satellite image of the study area in the disturbed forests near Chaiguata Lake (Fig 1), we selected a representative area of 100 ha (1 km × 1 km) with both upland and bog sites (72% and 28%, respectively) to map the location of every living *P. uviferum* tree >1 m in height. In areas with clusters of living trees, we mapped only trees ≥5 cm dbh and 2 m height. For each tree, we recorded the dbh (cm), root collar diameter (cm), height (m), sex, and site condition (bog or upland). For every female tree with regeneration, we recorded abundance of seedlings and saplings in 3 categories: low (<9; 1st quartile), intermediate (between 9 and 45; 2nd and 3rd quartile), and high (>45; 4th quartile). The division between quartiles was based on the analysis of regeneration around the 20 seed trees. The age of the trees was estimated from diameters based on a regression model ($r^2 = 0.843$; $P < 0.001$) developed for the study area by Bannister *et al.* (2012a).

To characterize the spatial patterns of living *P. uviferum* trees at the landscape level, we examined the univariate and bivariate spatial point patterns of *P. uviferum* trees within the mapped area, using the Wiegand–Moloney's O-ring statistic (Wiegand *et al.* 1999). Compared to Ripley's K(t) function (Ripley 1977), the O-ring statistic has the advantage that it is not cumulative, and therefore does not confound effects at larger scales with effects at shorter distances (Wiegand & Moloney 2004). In this context, the mark-correlation function $g_{12}(r)$ is the analogue of Ripley's $K_{12}(r)$ when replacing circles by rings of radius r. The O-ring statistic $O_{12}(r) = \lambda_2 g_{12}(r)$ gives the expected number of points of pattern 2 at distance r from an arbitrary point of pattern 1, were λ is the first-order intensity of the pattern (Wiegand & Moloney 2004). In the case of bivariate spatial patterns, $O_{12}(r) = \lambda_2$ indicates independent patterns, $O_{12}(r) < \lambda_2$ indicates repulsion between seed trees, and $O_{12}(r) > \lambda_2$ points to attraction between patterns 1 and 2. For univariate patterns, $O(r)$ is calculated by setting pattern 2 equal to pattern 1. In this case $O(r) = \lambda$ indicates randomness, $O(r) < \lambda$ indicates regularity and $O(r) > \lambda$ is a sign of aggregation (Wiegand & Moloney 2004). To assess the significance of the O-ring statistic under a given null model, we generated 95% confi-

dence envelopes by calculating for each distance r the 5th lowest and highest values of the summary statistic from 99 Monte Carlo simulations of the null model.

In the mapped area, there were signs of heterogeneity in the first-order intensity λ and clusters in the patterns, which may be related to topographical conditions. Therefore, we could not use complete spatial randomness or independence as null models for univariate and bivariate second-order analyses, respectively. Alternatively, null models based on a heterogeneous Poisson process using a moving window estimate of radius $R = 100$ m were used for approximation of the heterogeneous first-order intensity λ. In the case of the bivariate analysis, we kept the locations of pattern 1 fixed and randomized pattern 2. All spatial point pattern analyses were performed with the software *Programita* (Wiegand & Moloney 2004) based on a grid of 100 × 100 cells of 10 × 10 m size. The analyses were done with a ring width of one cell and a maximum distance r of 50 cells (500 m, half of the area side).

RESULTS

Dispersion of seeds and recruitment of seedlings around *Pilgerodendron uviferum* seed trees

Over a period of 3 years, seed production of *P. uviferum* was irregular presenting mast years (2010) and years with hardly any seeds (2011). Therefore, the analysis of the pattern of seed dissemination was focused on the year 2010. We found a negative exponential seed-rain curve with distance from seed tree, where most seeds were trapped within a 20 m radius (Fig. 2a). However, throughout the whole observation period, the majority (93–100%) of seeds fell in the first 5 m from the seed tree.

The effective seedling recruitment distance from *P. uviferum* seed trees fitted well a log-normal distribution (Fig. 2b). The maximum density of seedlings and saplings occurred at 1.6 m and their mean distance to the seed tree was 4.7 m. Seedling recruitment was negligible beyond a radius of 20 m from seed trees and it was concentrated in easterly directions (70% of seedlings and saplings between 0° and 180°). No significant correlations were found between the dbh of seed trees and the maximum distance of the regeneration and seedling and sapling frequency. However, a positive correlation was found between seed tree age and maximum distance of the regeneration (r = 0.553; $P = 0.011$) and its frequency (r = 0.631; $P = 0.003$). There was also a positive correlation between seed tree height and frequency of the regeneration (r = 0.534; $P = 0.015$). From a total of 772 seedlings and saplings recorded in the vicinity of the 20 seed trees, 49% had reproductive structures and the observed male/female ratio was 1.74 (Table 1). The smallest female and male plants with cones in this regeneration cohort were about 40–50 cm tall with a root collar diameter of ca 0.5 cm.
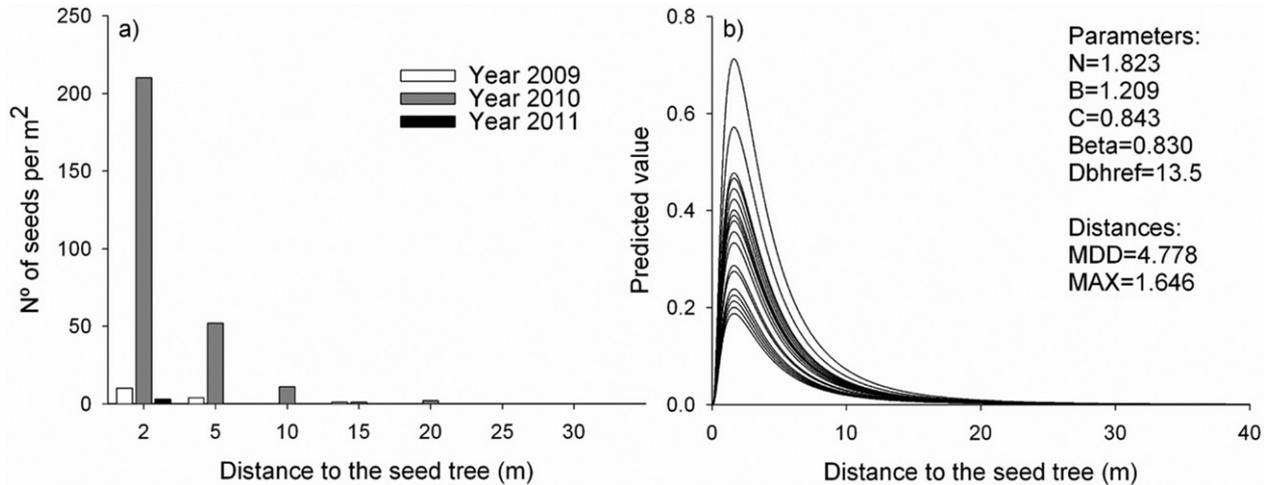
Fig. 2. Dispersion of seeds and distribution of seedlings and saplings around *Pilgerodendron uviferum* seed trees. (a) Seed dissemination over a 3-year period; (b) Log-normal density based model for the effective seedling and sapling recruitment distance from 20 trees of different dbh (diameter at breast height). B = μ; C = σ and Beta = factor of the allometric component; N = standard total recruitment; dbhref = mean dbh of the 20 selected seed trees. MDD = mean distance; MAX = distance at which the maximum density of seedlings and saplings occurs.

Table 1. Principal attributes of disturbed *Pilgerodendron uviferum* forests at the landscape level

P. uviferum trees in the mapped area (100 ha)

	n (trees per 100 ha)
Total	122 (100%)
Site	
Bogs	65 (53.3%)
Upland	57 (46.7%)
Gender	
Undefined	8 (6.6%)
Males	59 (48.4%)
Females	55 (45.1%)
M : F sex ratio	1.07
Structure	
Age[†] (years)	29–81
dbh (cm)	2–20.5
Height (m)	1–9

Associated regeneration (seedlings and saplings)

|	*n* (trees per 100 ha)
Females with regeneration	34 (27.9%)
Abundance	
Low, <9	7 (20.6%)
Intermediate, >9 to <45	17 (50.0%)
High, >45	10 (29.4%)
Gender of young trees[‡]	*n* (seedlings per 20 seed trees)
Total number	772 (100.0%)
Undefined	394 (51.0%)
Males	240 (31.1%)
Females	138 (17.9%)
M : F sex ratio	1.74

[†]Ages estimated from dbh-model from Bannister *et al.* (2012a). [‡]Regeneration data from the analysis of 20 seed trees with regeneration (see Method). dbh, diameter at breast height.

Seed germination

The first germinants emerged 3 months after sowing and their numbers increased constantly until month 5, after which germination ceased. Substrate and moisture content, as independent factors had significant effects on seed germination ($P \leq 0.001$). Germination rates were significantly higher in moist *Sphagnum* and moist mineral soil than in all the other substrates (Fig. 3a). Mortality of germinants in these substrates was only 2% and 3%, respectively, whereas it was much higher in the substrates undergoing drying-rewetting cycles. Seeds germinated also under dry conditions but with substantially lower success as indicated by extremely low germination rates in dry cushion plants and sand (Fig. 3a). The interaction between substrate and moisture content did not have a significant effect on seed germination. Final heights of germinants were not significantly different between treatments with successful germination (Fig. 3b).

Spatial distribution of seed trees at the landscape level

At a landscape level, most individuals of *P. uviferum* were found in smaller diameter classes and the estimated ages of *P. uviferum* trees were less than 81 years (Table 1). Of the mapped area, 72% was in upland sites and 28% was in bogs (Fig. 4). However, 46.7% of the *P. uviferum* trees mapped were in upland areas and 53.3% in bogs (Table 1). Male and female trees contributed 48 and 45% of the total number, respectively. In the remaining 7% of trees without
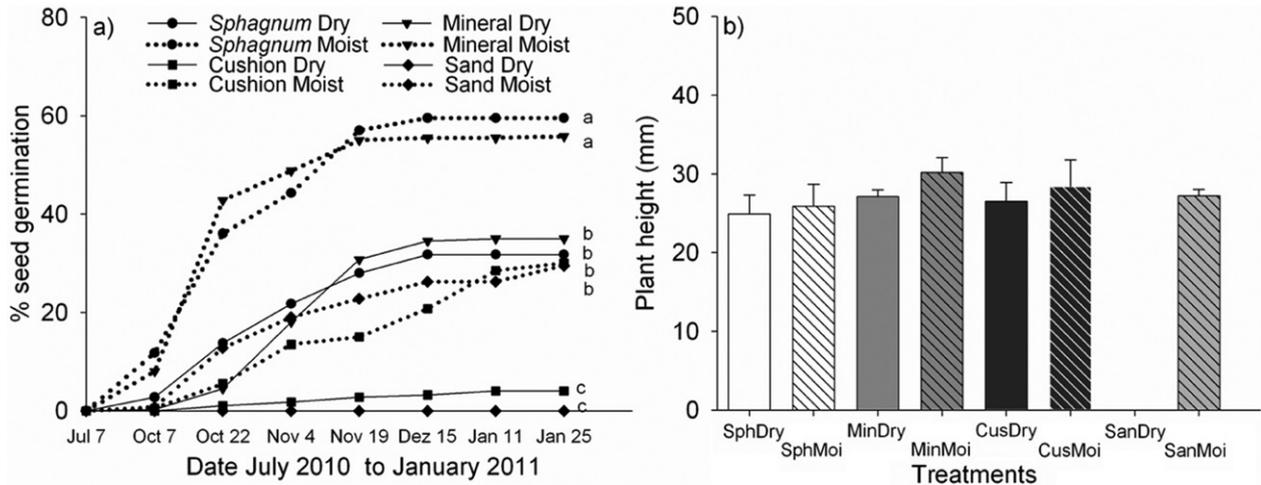
Fig. 3. (a) Mean cumulative seed germination rate for each substrate. Different letters indicate significant differences ($P \leq 0.05$) between treatments. (b) Final mean height of germinants in each treatment. No significant differences between treatments ($P > 0.05$). Treatments: SphDry = dry *Sphagnum*; SphMoist = moist *Sphagnum*; MinDry = dry mineral; MinMoi = moist mineral; CusDry = dry cushion; CusMoi = moist cushion; SanDry = dry sand; SanMoi = moist sand.
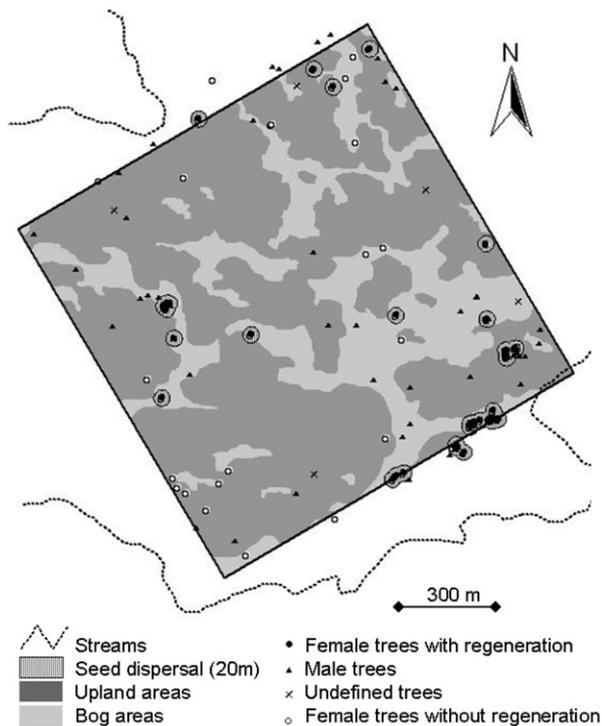
Fig. 4. Diagram showing the mapped area of 100 ha (1 km × 1 km) near Chaiguata Lake in Tantauco Park and the distribution of male and female *P. uviferum* trees.

visible reproductive structures sex could not be identified. Only 28% of the trees (0.3 trees ha^{-1}) had any regeneration in their vicinity. From the female trees with regeneration, 50% and 30% had intermediate or high seedling abundance, respectively (Table 1).

The univariate *O*-ring statistic revealed that the distribution of *P. uviferum* trees was not uniform but clustered for all trees together, as well as for males

and female trees with regeneration at scales ≤30 m (Fig. 5). Although there was some weak regularity or aggregation at some scales (70–140 and near 180 m); beyond that scale distribution patterns were almost always random up to 500 m. Female trees without regeneration had a mostly random distribution at all scales (Fig. 5d). The bivariate *O*-ring statistic revealed attraction between male and female trees with regeneration at scales ≤30 m, independency at scales between 40 and 50 m followed by repulsion at scales of 60–130 m. At larger scales, the distribution of these two groups was largely independent from each other (Fig. 5e). In contrast, the bivariate spatial pattern between males and female trees without regeneration was mostly independent at all scales, with some repulsion at scales between 40 and 90 m (Fig. 5f).

DISCUSSION

Capacity of *Pilgerodendron uviferum* to recover burned areas

The widespread fire of the early 1940s that burned the study area caused dramatic changes in the structure of the *P. uviferum* bog forests. Almost 70 years after the large fire, recovery of *P. uviferum* populations on bogs has been extremely slow, indicating a low resilience of these bog forests in relation to fire disturbance. Seed trees were extremely infrequent and their contribution to the regeneration of the disturbed area was confined to their immediate surroundings (<20 m). As only a little more than 25% of all sexually mature trees were females with regeneration, dioecy obviously decelerated the recovery of tree populations.
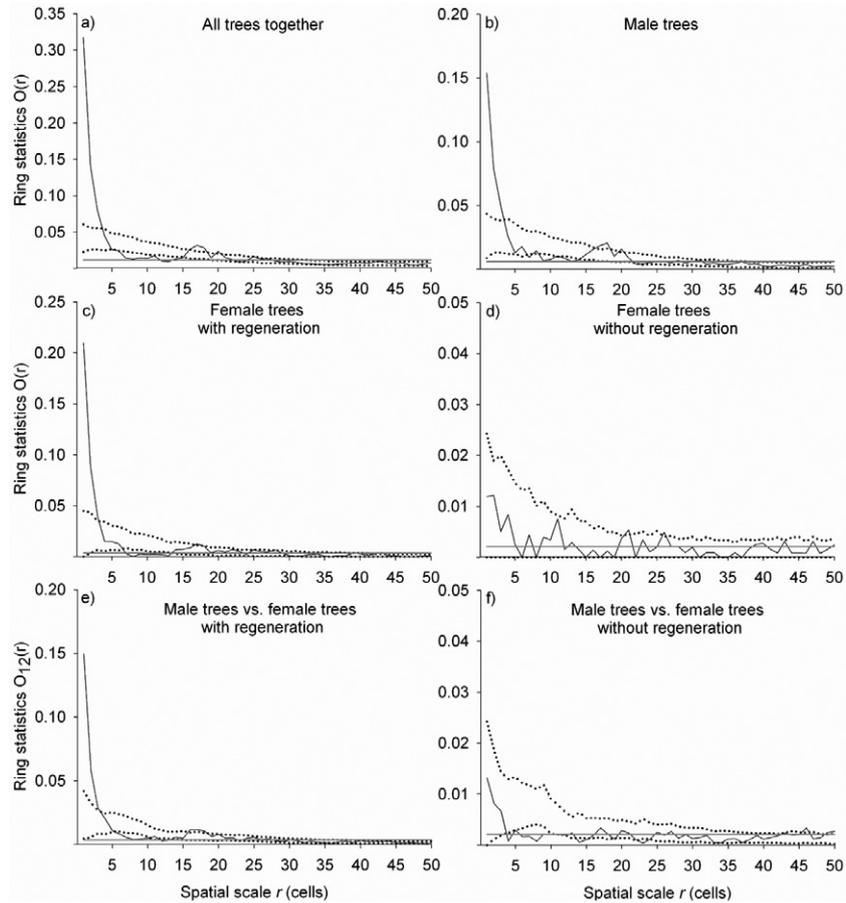
Fig. 5. Univariate (a–d) and bivariate (e–f) second-order analyses of the *Pilgerodendron uviferum* trees located in the mapped area (100 ha). The mapped area was divided in a grid of 100×100 cells, each of 10 m width. The O-ring (a–d) and O_{12}-ring (e–f) statistics are shown as solid lines and the 95% confidence envelopes of 99 randomizations of the pattern over the study area are shown as dotted lines. The solid horizontal grey line indicates the mean intensity λ of the general pattern (a–d) and the mean intensity λ_2 of pattern 2 (e–f).

Moist substrates comprising *Sphagnum* or mineral soil were the best substrates for the germination of *P. uviferum* (near 60% germination rate, 2–3% mortality), and these are precisely the most frequent substrates in the study area. Thus, it appears unlikely that availability of germination substrate may be limiting seedling establishment. However, in northern bog forests dominated by *Picea abies*, *Picea mariana* or *Pinus sylvestris*, the risk of waterlogging is lower on hummocks and elevated microsites, which are therefore safe sites for development of seedlings (Hörnberg *et al.* 1997; Gunnarsson & Rydin 1998; Roy *et al.* 1999; Hanssen 2003). Safe sites for germination are not necessarily safe sites for seedling survival, and to be overgrown by bryophytes is one of the most important mortality factors for slow-growing tree seedlings in bogs (Hörnberg *et al.* 1997). Hence only seedlings that have 'rapid' height growth are able to stay ahead of the upward growth of *Sphagnum* (Ohlson 1995). Although we did not analyse the competition between *P. uviferum* seedlings and *Sphagnum*, there was a close agreement between seed dissemination and effective seedling recruitment patterns around seed trees, indicating that although this competition exists, there must be enough safe sites for seedling survival. Sprouting, another mechanism to re-establish after disturbance and which has been reported for *P. uviferum* previously (e.g. Cruz & Lara 1981; Rovere *et al.* 2002, 2004) was extremely infrequent in the study area. Almost all post-fire regeneration originated from seed. The only vegetative reproduction was from adventitious roots in close proximity (<0.5 m) of stems. The measured seedling recruitment may potentially also be influenced by browsing. However, there are no large herbivores in the study area. Bannister *et al.* (2013) observed some browsing by the threatened and endemic Pudú deer (*Pudu puda*), but browsing by this deer was confined to partial removal of the youngest shoots and does not kill the seedlings. Hence, all available information indicates that the post-disturbance recovery of *P. uviferum* populations is limited by the low survival of seed trees or propagules during fire and subsequently the limited seed dispersal.

The short distances of seed dissemination and effective seedling recruitment patterns around *P. uviferum* seed trees (<20 m) indicate their limited capacity to provide regeneration at the landscape scale. However, in addition to the dominating short-distance dispersal, an infrequent long-distance dispersal pattern is indicated by the presence of isolated trees in the landscape (Fig. 4). All isolated *P. uviferum* trees, except for one isolated male tree, were younger than the period since the last fire (1943). Hence, these isolated trees must have originated from long-distance seed dispersal by wind. There is no available information about animal dispersal or seed predation for *P. uviferum*, but it is unlikely that these factors are responsible for the observed infrequent long-distance dispersal pattern or germination inhibition, respectively. A more likely alternative mechanism for long-distance seed dispersal is by flood flow. However, this would only occur in flat boggy areas. Additionally, more than half of the living trees were located in bogs (53%), although they only contributed to 30% of the area. Thus bogs may be either more suitable for regeneration, or the probability of seeds to survive the fire was higher in bogs than in upland forests. However, the mean estimated age of living trees was similar on bogs (49 years) and upland sites (47 years), and the number of remnant trees was equal (two trees each). Moister substrates are better for the germination of *P. uviferum* seeds (Fig. 3); therefore, it is likely that bogs offer better conditions for seedling establishment than upland sites. This is consistent with results from Filion and Morin (1996), who found that in *P. mariana* bog forests of Canada, seedlings were mostly associated with concave microsites, colonized by *Sphagnum*. However, more research is needed to asses how microtopography influences the survival of *P. uviferum* seedlings.

In boreal conifer bog forests a close connection between crown fire severity and ecosystem recovery has been observed (Arseneault 2001; Johnstone *et al.* 2009). This is consistent with the high-severity crown fire pattern described in *P. uviferum* forests in upland areas by Holz and Veblen (2009). In our case, even the oldest remnant tree (81 years) could not have participated in the crown of the previous forests and must have survived as a small seedling.

Sexual maturity in *P. uviferum* occurs already in very small trees. Almost 50% of the observed regeneration (including small plants <50 cm height) and 90% of the trees had visible reproductive structures. Despite the early fecundity and the balanced sex ratio for trees at the landscape level (Table 1), we observed an extremely low density of *P. uviferum* trees (1.2 trees ha^{-1}) and females with regeneration (0.3 trees ha^{-1}). This can be partially explained by the clustered distribution of the trees at the landscape level. There was aggregation of *P. uviferum* trees at scales up to 30 m, which is in agreement with patterns of effective regeneration around seed trees (Fig. 2). Female trees without regeneration showed no aggregation, because they were isolated from male trees (Fig. 5), contrasting with male and female trees with regeneration that showed attraction at scales up to 30 m (Fig. 5). This indicates that in the current condition of the disturbed landscape, a substantial proportion of female trees is too far away from males, also pointing to a limited effective dispersion of pollen. In this context, dioecy influenced the spatial heterogeneity of plant density in *P. uviferum* populations as was previously documented for other tree species in the northern hemisphere (Gibson & Menges 1994; Nanami *et al.* 1999, 2000; Montesinos *et al.* 2007). Given the low density, dioecy further limited the recovery of the species through natural regeneration. In addition, our results show that *P. uviferum*, like many other conifer species (Donoso *et al.* 2006; Gärtner *et al.* 2011), is a masting species with highly variable seed production between years (Fig. 2). This is consistent with Lara *et al.* (2006), who suggested that the species has periodic fluctuations in the seed production. Thus a coincidence of poor seed production and fire-disturbance in 1 year may inhibit the recovery of the species population after disturbance.

In this context, the presence or absence of *P. uviferum* seed trees in the disturbed landscape and not the availability of suitable substrate for germination is the determining biotic factor that limits the natural recovery of the species population in fire-disturbed sites. This is in agreement with our hypothesis that the natural recovery of *P. uviferum* populations in burned areas is limited by seed availability and that this limitation may be exacerbated by the dioecy of the species. This finding highlights the importance of biological legacies in the process of ecosystem recovery (e.g. Franklin 1990; Franklin & MacMahon 2000; Keeton & Franklin 2005).

Is passive restoration a suitable approach for disturbed *Pilgerodendron uviferum* forests?

It has been suggested previously that dioecy is an important factor to consider in forest restoration projects (Kuaraksa *et al.* 2012). In this context, natural regeneration from seeds of remnant female trees can effectively assist the recovery of *P. uviferum* populations. However, the extremely low density and aggregated pattern of seed trees in disturbed landscapes would result in very long times for the restoration of *P. uviferum* populations. If we consider a circular area with 20 m radius around seed trees as effectively regenerated, almost 70 years after the fire only 2.2% of the landscape has recovered passively towards *P. uviferum* forests. However, the low correlation between seed tree size and maximum distance or

frequency of the regeneration, and the small minimum size of *P. uviferum* individuals with reproductive structures, highlight the importance also of small trees to contribute to the re-establishment of the population. However, it is likely that the effectiveness of seed trees will increase with their size, leading to greater seed dispersal distances. Thus the results of this study cannot be directly extrapolated to disturbed *P. uviferum* forests with older and larger seed trees.

Restoration of degraded ecosystems depends on the removal of the influences leading to degradation but often this will not be sufficient to promote restoration (Hobbs & Norton 1996). To identify a suitable restoration approach for a specific disturbed ecosystem, information about the natural rate of recovery is required (Holl & Aide 2011). In these forests characterized by low resilience in relation to fire disturbance and low current human degradation, increasing the number of *P. uviferum* seed trees in the landscape could remove the principal biotic filter (*sensu* Hobbs & Norton 2004), which is currently retarding natural recovery. Therefore, planting male *P. uviferum* seedlings near female trees without regeneration, planting dispersed small groups comprising male and female trees, or the sowing of pretreated seeds in disturbed forests would be inexpensive measures to accelerate the restoration of *P. uviferum* forests. Also planting beneath other trees and shrubs that act as a nurse canopy appears to be a promising option for the safe establishment of seedlings (Bannister *et al.* 2013). However, the area inside a radius of 20–30 m from seed trees with regeneration can be left for natural recovery (passive restoration). All these restoration actions should take into account genetic considerations. *Pilgerodendron uviferum* has significant amounts of among-population divergence and apparent restrictions for gene flow (Premoli *et al.* 2002), and therefore seed and seedlings to be used should be collected as much as possible from local populations in order to conserve adapted genotypes.

In this context, such a mixed passive–active restoration approach that takes into account the spatial patterns and dioecy of the species appears a promising option for the restoration for disturbed *P. uviferum* dominated forests, and also for other disturbed forests dominated by dioecious tree species with substantial seed dispersal limitations. This approach will also increase genetic diversity of post-disturbance populations, which may otherwise originate from very few individuals.

ACKNOWLEDGEMENTS

REFERENCES

Arseneault D. (2001) Impact of fire behaviour on postfire forest development in a homogeneous boreal landscape. *Can. J. Forest Res.* **31**, 1367–74.

Bannister J. R., Coopman R., Donoso P. & Bauhus J. (2013) The importance of microtopography and nurse canopy for successful restoration planting of the slow-growing conifer *Pilgerodendron uviferum*. *Forests* **4**, 85–103.

Bannister J. R., Donoso P. & Bauhus J. (2012a) Persistence of the slow growing conifer *Pilgerodendron uviferum* in old growth and fire-disturbed southern bog forests. *Ecosystems* **15**, 1158–72.

Bannister J. R., Lara A. & Le Quesne C. (2008) Estructura y dinámica de bosques de *Pilgerodendron uviferum* afectados por incendios en la Cordillera de la Costa de la Isla Grande de Chiloé. *Bosque* **29**, 33–43.

Bannister J. R., Vidal O. J., Teneb E. & Sandoval V. (2012b) Latitudinal patterns and regionalization of plant diversity along a 4270-km gradient in continental Chile. *Austral Ecol.* **37**, 500–9.

Clark J. S., Macklin E. & Wood L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* **68**, 213–35.

Cornett M. W., Reich P. B., Puettmann K. J. & Lee E. F. (2000) Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. *Am. J. Bot.* **87**, 1807–14.

Cruz G. & Lara A. (1981) *Tipificación, cambio de estructura y normas de manejo para Ciprés de las Guaitecas (Pilgerodendron uviferum D. Don Florin) en la Isla Grande de Chiloé*. For. Eng. Thesis. Universidad de Chile, Santiago.

di Castri F. & Hajek E. (1976) *Bioclimatología de Chile*. Vicerrectoría Académica de la Universidad Católica de Chile, Santiago.

Donoso C., Cortes M. & Soto L. (1980) Antecedentes sobre semillas y germinación de Alerce, Ciprés de las Guaitecas, Ciprés de la Cordillera y Tineo. *Bosque* **3**, 96–100.

Donoso C., Lara A., Escobar B., Premoli A. & Souto A. (2006) *Fitzroya cupressoides* (Molina) I.M. Johnst. In: *Las especies arbóreas de los bosques templados de Chile y Argentina, Autoecología* (ed. C. Donoso) pp. 68–81. Marisa Cuneo, Valdivia.

Filion J. & Morin H. (1996) Distribution spatiale de la régénération de l'épinette noire 8 ans après un feu en forêt boréale (Québec). *Can. J. Forest Res.* **26**, 601–10.

Franklin J. F. (1990) Biological legacies: a critical management concept from Mt. St. Helens. *T. N. Am. Wildl. Nat. Res.* **55**, 215–19.

Franklin J. F. & MacMahon J. A. (2000) Messages from a Mountain. *Science* **288**, 1183–5.

Franklin J. F., Spies T. A., Van Pelt R. *et al.* (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* **155,** 399–423.

Gärtner S. M., Lieffers V. J. & Macdonald S. E. (2011) Ecology and management of natural regeneration of white spruce in the boreal forest. *Environ. Rev.* **19,** 461–78.

Gibson D. J. & Menges E. S. (1994) Population structure and spatial pattern in the dioecious shrub *Ceratiola ericoides.* *J. Veg. Sci.* **5,** 337–46.

Gunnarsson U. & Rydin H. (1998) Demography and recruitment of scots pine on raised bogs in eastern Sweden and relationships to microhabitat differentiation. *Wetlands* **18,** 133–41.

Hanssen K. H. (2003) Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. *Forest Ecol. Manage.* **180,** 199–213.

Herrera J. M. & García D. (2009) The role of remnant trees in seed dispersal through the matrix: being alone is not always so sad. *Biol. Conserv.* **142,** 149–58.

Hobbs R. & Norton D. A. (2004) Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. In: *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice* (eds V. M. Temperton, R. Hobbs, T. Nuttle & S. Halle) pp. 72–95. Island Press, Washington.

Hobbs R. J. & Norton D. A. (1996) Towards a conceptual framework for restoration Ecology. *Restor. Ecol.* **4,** 93–110.

Holl K. D. & Aide T. M. (2011) When and where to actively restore ecosystems? *Forest Ecol. Manage.* **261,** 1558–63.

Holz A. & Veblen T. T. (2009) *Pilgerodendron uviferum*: the southernmost tree-ring fire recorder species. *Ecoscience* **16,** 322–9.

Holz A. & Veblen T. T. (2011) The amplifying effects of humans on fire regimes in temperate rainforests in western Patagonia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **311,** 82–92.

Hörnberg G., Ohlson M. & Zackrisson O. (1997) Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. *Can. J. Forest Res.* **27,** 1015–23.

Johnstone J., Boby L., Tissier E., Mack M., Verbyla D. & Walker X. (2009) Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Can. J. Forest Res.* **39,** 1575–88.

Kashian D. M., Corace III R. G., Shartell L. M., Donner D. M. & Huber P. W. (2012) Variability and persistence of post-fire biological legacies in jack pine-dominated ecosystems of northern Lower Michigan. *Forest Ecol. Manage.* **263,** 148–58.

Keeton W. S. & Franklin J. F. (2005) Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecol. Monogr.* **75,** 103–18.

Kuaraksa C., Elliott S. & Hossaert-Mckey M. (2012) The phenology of dioecious *Ficus* spp. tree species and its importance for forest restoration projects. *Forest Ecol. Manage.* **265,** 82–93.

Lara A., Donoso C., Escobar B. *et al.* (2006) *Pilgerodendron uviferum* (D. Don) Florin. In: *Las especies arbóreas de los bosques templados de Chile y Argentina, Autoecología* (ed. C. Donoso) pp. 82–91. Marisa Cuneo, Valdivia.

Manning A. D., Fischer J. & Lindenmayer D. B. (2006) Scattered trees are keystone structures – implications for conservation. *Biol. Conserv.* **132,** 311–21.

Martinez O. (1981) Flora y fitosociología de un relicto de *Pilgerodendron uvifera* (D. Don) Florin en el fundo San Pablo de Tregua (Valdivia-Chile). *Bosque* **4,** 3–11.

Montesinos D., Verdú M. & García-Fayos P. (2007) Moms are better nurses than dads: gender biased self-facilitation in a dioecious *Juniperus* tree. *J. Veg. Sci.* **18,** 271–80.

Nanami S., Kawaguchi H. & Kubo T. (2000) Community dynamic models of two dioecious tree species. *Ecol. Res.* **15,** 159–64.

Nanami S., Kawaguchi H. & Yamakura T. (1999) Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. *J. Ecol.* **87,** 678–87.

Ohlson M. (1995) Growth and nutrient characteristics in bog and fen populations of Scots pine (*Pinus sylvestris*). *Plant Soil* **172,** 235–45.

Pérez C. A., Carmona M. R., Aravena J. C., Fariña J. M. & Armesto J. J. (2008) Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile. *Austral Ecol.* **28,** 591–600.

Premoli A., Souto C., Rovere A., Allnut T. & Newton A. C. (2002) Patterns of isozyme variation as indicators of biogeographic history in *Pilgerodendron uviferum* (D.Don) Florin. *Divers. Distrib.* **8,** 57–66.

R Development Core Team (2012) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna. Available from URL: http://www.R-project.org/

Ribbens E., Silander J. A. & Pacala S. W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersal. *Ecology* **75,** 1794–806.

Ripley B. D. (1977) Modelling spatial patterns. *J. Roy. Stat. Soc. B* **39,** 172–212.

Rovere A. E., Premoli A. C., Aravena J. C. & Lara A. (2004) Variación en *Pilgerodendron uviferum* (D. Don.) Florín. In: *Variación intraespecífica en las especies arbóreas de los bosques templados de Chile y Argentina* (eds C. Donoso, A. C. Premoli, L. Gallo & R. Ipinza) pp. 253–70. Editorial Universitaria, Santiago.

Rovere A. E., Premoli A. C. & Newton A. C. (2002) Estado de conservación del ciprés de las Guaitecas (*Pilgerodendron uviferum* (Don) Florín) en Argentina. *Bosque* **23,** 11–19.

Roy V., Bernier P. Y., Plamondon A. P. & Ruel J. C. (1999) Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. *Can. J. Forest Res.* **29,** 563–74.

Stokes M. A. & Smiley T. L. (1968) *An Introduction to Tree-Ring Dating.* University of Chicago Press, Chicago.

Stoyan D. & Wagner S. (2001) Estimating the fruit dispersion of anemochorous forest trees. *Ecol. Model.* **145,** 35–47.

Villagrán C. (1988) Late quaternary vegetation of southern Isla Grande de Chiloé, Chile. *Quat. Res.* **29,** 294–306.

Walker L. R. (2011) Integration of the study of natural and anthropogenic disturbances using severity gradients. *Austral Ecol.* **36,** 916–22.

Walter K. S. & Gillet H. J. (1998) *1997 IUCN Red List of Threatened Plants.* IUCN, Gland and Cambridge.

Wiegand T. & Moloney K. A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* **104,** 209–29.

Wiegand T., Moloney K. A., Naves J. & Knauer F. (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *Am. Nat.* **154,** 605–27.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Photographs of study area and sampling procedures.