

Nucleation-driven regeneration promotes post-fire recovery in a Chilean temperate forest

Felipe E. Albornoz · Aurora Gaxiola ·
Bárbara J. Seaman · Francisco I. Pugnaire ·
Juan J. Armesto

Received: 12 November 2012 / Accepted: 26 April 2013 / Published online: 10 May 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Nucleation is a successional process in which extant vegetation facilitates seed dispersal and recruitment of other individuals and species around focal points in the landscape, leading to ecosystem recovery. This is an important process in disturbed sites where regeneration is limited by abiotic conditions or restrictive seed dispersal. We investigated forest recovery in a large burned area of evergreen temperate rainforest in southern Chile subjected to seasonal soil waterlogging, and assessed the relevance of nucleation processes in overcoming biotic and

physical barriers for tree species regeneration. We measured richness and abundance of woody species in relation to patch size, as well as abiotic factors such as light and soil moisture within and outside patches. We found higher tree regeneration in existing patches than in open areas. We recorded an increase of patch size over time, associated with the increase in number of individuals and tree species. Soils in open areas were waterlogged, especially in winter, while patches were not. Trees in patches also acted as perches, enhancing bird-mediated seed rain. Seeds of fleshy-fruited tree species arrived first at patches and seedlings were

F. E. Albornoz (✉) · B. J. Seaman
Departamento de Ecología, Pontificia Universidad
Católica de Chile, Casilla 114-D, Santiago, Chile
e-mail: felipealbornoz.ramirez@gmail.com;
alborf01@student.uwa.edu.au

B. J. Seaman
e-mail: b.seaman.e@gmail.com

F. E. Albornoz · B. J. Seaman
Instituto de Ecología & Biodiversidad (IEB), Santiago,
Chile

Present Address:

F. E. Albornoz
School of Plant Biology, University of Western Australia,
35 Stirling Highway, Crawley, WA 6009, Australia

A. Gaxiola · J. J. Armesto
Departamento de Ecología y Laboratorio Internacional de
Cambio Global, Pontificia Universidad Católica de Chile,
Casilla 114-D, Santiago, Chile
e-mail: Aurora.Gaxiola@cantab.net

J. J. Armesto
e-mail: jarmesto@bio.puc.cl

A. Gaxiola · J. J. Armesto
Instituto de Ecología y Biodiversidad, Casilla 653,
Santiago, Chile

F. I. Pugnaire
Laboratorio Internacional de Cambio Global (LINC-
Global), Estación Experimental de Zonas Áridas, CSIC,
Almería, Spain
e-mail: fip@eeza.csic.es

more frequent in smaller, younger patches, while the number of seedlings of trees with wind-dispersed seeds increased in larger, older patches. Our study shows that woody species seem incapable of recruiting in open and waterlogged soils and depend strongly on extant vegetation patches to establish. In this fire-disturbed evergreen temperate forest regeneration occurs via nucleation, where new individuals contribute to a centrifugal kind of patch growth.

Keywords Dispersal syndrome · Facilitation · Forest fire · Nurse plant · Perch effect · Restoration · Soil waterlogging · Temperate rainforest

Introduction

Nucleated regeneration is a specific process of succession whereby plants in circumscribed areas facilitate colonization by late-successional species due to locally enhanced soil, water, or light conditions, as well as by accumulation of seeds and seedlings (Yarranton and Morrison 1974; Rubio-Casal et al. 2001; Franks 2003). Nucleation, and facilitation in general, may enhance species colonization and establishment in areas where succession is arrested or severely impaired by physical or biotic constraints (Bertness and Callaway 1994). For example, in low resource environments such as salt marshes, where environmental conditions in the open (i.e., high salinity and low soil pH) hamper survival and establishment of late-successional species such as *Salicornia ramosissima*, which can only survive under *Arthrocnemum macrostachyum* (Rubio-Casal et al. 2001), nucleation occurs when *Salicornia* individuals grow around *Arthrocnemum* forming large patches where further *Salicornia* individuals can establish (Rubio-Casal et al. 2001). Similarly, nucleation has been observed following anthropogenic disturbance, where remnant vegetation promotes species establishment (Verdú and García-Fayos 1996; Pausas et al. 2006; Schlawin and Zahawi 2008). Pausas et al. (2006) showed that in old, abandoned fields remnant trees act as “nuclei,” providing perches that promote recruitment of bird-dispersed species (see also McDonnell and Stiles 1983; Guevara et al. 1986). Moreover, canopy species had positive effects on seed germination and seedling establishment, thus remnant vegetation can have a significant role on ecosystem recovery with long-lasting effects, which may spread over the entire landscape (Corbin and Holl 2012).

Perch effects, and positive effects of canopy species on germination and establishment of seedlings, have been identified as key processes promoting ecosystem regeneration via nucleation, especially after human-induced disturbances (Pausas et al. 2006; Milton et al. 2007; Schlawin and Zahawi 2008; Kinhal and Parthasarathy 2010). Holl et al. (2000), for instance, found significant differences between both dispersal syndromes under the canopy of scattered remnant individuals of tropical woody species in an abandoned pasture in Costa Rica. This study also showed that seedling growth was higher under remnant trees than in open areas, which fostered vegetation recovering through nucleation. In a Mediterranean forest in Spain, Verdú and García-Fayos (1996) found that isolated remnant trees not only promoted seedling establishment under their canopies, but also acted as regeneration foci by enhancing seed accretion and seedling establishment particularly of bird-dispersed species. Therefore, during nucleated regeneration at least two mechanisms are operating simultaneously, facilitation and perch effect, although the relative importance of each in different landscapes has not been assessed (but see Pausas et al. 2006).

The importance of nucleation processes has been explored mainly in systems where plant growth is limited by low resource availability and the relevance of facilitative interactions has been for long acknowledged (Tewksbury and Lloyd 2001; Gómez-Aparicio 2009). Bertness and Callaway (1994) hypothesized that competitive interactions would be more relevant under high resource availability, whereas under more extreme environmental conditions with low resource supply facilitative interactions would be more common. This hypothesis, known as the “stress gradient hypothesis,” has been supported by several studies (Kawai and Tokeshi 2007; Armas et al. 2011; Baribault and Kobe 2011; He et al. 2013). For example, Holzapfel et al. (2006) found along an aridity gradient that positive plant interactions decreased with increasing rainfall. In less stressful environments, the role of positive interactions is considered less important in structuring ecosystems, although recent studies have highlighted the importance of facilitative interactions for seedling survival and establishment in temperate rainforests (Gaxiola et al. 2008; Bustamante-Sánchez et al. 2011).

In areas of Chiloé Island, where the canopy of temperate forests has been removed by fire or logging,

soils often become waterlogged due to reduced canopy interception and evapotranspiration, which diminishes the chances of tree seedling establishment (Díaz and Armesto, 2007; Díaz et al. 2007). This is due to the fact that fires are not a natural disturbance and the native flora lacks adaptations to regenerate after fire disturbance, and hence forest recovery can be greatly impaired and must rely largely on seed inputs (Carmona et al. 2002). Hence, in human-disturbed sites over poorly drained soils tree regeneration is often constrained to elevated surfaces, such as remnant logs or *Sphagnum* mounds (Lusk 1995; Díaz and Armesto 2007). Also, in Chilean temperate rain forests fruit-eating birds play a key role in forest regeneration by transporting seeds to forest margins, tree-fall gaps, and open areas (Armesto et al. 2001). Furthermore, a high proportion (i.e., >70 %) of tree species have fleshy fruits with seeds disseminated by birds. Wind-dispersed species are present in much lower proportion in the canopy of these temperate forests compared to forests in the northern hemisphere (Armesto and Rozzi 1989; Willson et al. 1989).

Here we test the existence of a nucleated tree regeneration process following anthropogenic forest fire in a temperate southern Chilean forest. After loss of the tree canopy the disturbed area becomes seasonally waterlogged, and, therefore, we explore the hypothesis that nucleation around mounds and remnant vegetation is the primary mechanism behind the forest recovery process. We hypothesize that “legacies” (e.g., surviving trees, logs, and stumps) from the original forest enhance seed accumulation and facilitate seedling survival by providing safe sites in an otherwise unsuitable environment for recruitment in order to promote a nucleated forest recovery. Our specific goals were to (1) identify the co-occurrence of perch and facilitation processes as potential mechanisms of nucleation, and (2) assess abiotic conditions that may be promoting a patchy ecosystem regeneration.

Materials and methods

Study area

The study was conducted in a 50-year-old post man-made fire (Holz and Veblen 2011) successional area of ca. 5 ha at Senda Darwin Biological Station (SDBS;

Fig. 2) in northern Chiloé Island, Chile (41°50' S; Fig. 1), about 20 km north of Ancud. The current landscape in this part of the island has been shaped by widespread use of fire to clear land for pastures and farming during the past century, followed by the removal of firewood (Willson and Armesto 1996; Carmona et al. 2002), generating large areas of waterlogged soils and seemingly arrested succession similar to our study site. Current vegetation is a mosaic of deforested areas and remnant fragments of Valdivian and North-Patagonian evergreen broad-leaved rainforests, which includes a mixture of conifer and angiosperm trees with different seed dispersal modes. The canopy is dominated by *Podocarpus nubigena* (Podocarpaceae), *Drimys winteri* (Winteraceae), and *Nothofagus nitida* (Nothofagaceae), with an understorey of *Tepualia stipularis* and other Myrtaceous tree species (Gutiérrez et al. 2004). The climate is wet-temperate with strong oceanic influence (Di Castri and Hajek 1976) and mean annual precipitation of 2,000–2,500 mm; mean minimum and maximum monthly temperatures are 3 °C in July and 17 °C in January, respectively (SDBS, meteorological records 1999–2007). Soils are primarily *n̄adis*, characterized by an impermeable hardpan at ca. 50–60 cm depth (Veith and Garleff 1996), which results in a shallow water table and water-saturated soils in winter (June–August), especially in logged or burned areas subjected to lower evapotranspiration rates (Díaz and Armesto 2007).

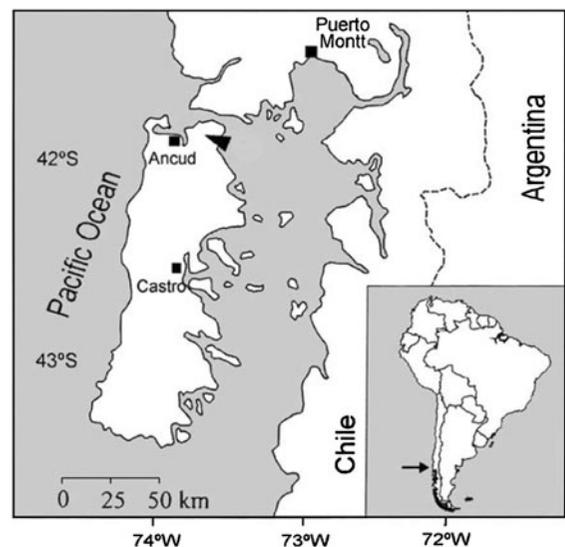


Fig. 1 Study area at Senda Darwin Biological Station (SDBS; black arrow), northern Chiloé Island, Chile

Characterization of post-fire forest recovery

To assess whether post-fire forest recovery occurred via nucleated regeneration, we measured tree species composition under remnant tree patches and in the surrounding open areas. We sampled forest patches present within a five-hectare area (about 10 % of the burned area) and recorded each patch's area, species composition, age of individual trees, as well as abiotic conditions inside and outside patches. We defined a patch as a conspicuous aggregation of trees of any age with at least one tree taller than 2 m and a diameter at breast height greater than 5 cm. We distinguished a patch in a successional shrubland matrix as a group of trees without other trees present within a surrounding ring of one meter. The surrounding ring was established from the projected canopy crown of all the trees composing the patch. We categorized patches by size in three groups of equal patch numbers; small (0.4–8.0 m²), medium (8.1–19.9 m²), and large (20.0–146.0 m²). This categorization was used in order to keep approximately the same sample size of patches in each size category for statistical purposes.

Vegetation under patches and in the surrounding matrix was dominated by low ferns—*Blechnum pennamarina* and *Gleichenia* spp., prostrated bushes such as *Gaultheria mucronata* and *Myrteola numularia*, and occasional taller shrubs of *Baccharis magellanica*. To estimate the area occupied by tree patches we measured the maximum diameter beneath the tree crowns and its perpendicular and calculated the area using the formula of an ellipse. The tree having the largest DBH was considered the oldest in the patch, henceforth referred to as the focal tree. We used the basal area of the focal tree as *proxy* for patch age, based on reported correlations between DBH and age for tree species in the same forest (Gutiérrez et al. 2004).

We classified trees in age classes as follows. A tree was classified as “*adult*” when taller than 2 m and with DBH >5 cm; “*juveniles*” were 1–2 m tall, with a DBH <5 cm; “*saplings*” were all woody plants between 30 cm and 1 m in height; and “*seedlings*” were regenerating individuals smaller than 30 cm. Tree species found in patches are summarized in Table 1. For non-tree species only the presence was recorded (see Appendix Table 2). Additionally, we quantified tree recruitment in the disturbed area by counting all tree seedlings and saplings present every

50 cm along eight 50-m-long transects. Six transects were established from east to west and two from south to north in the entire disturbed area (Fig. 2). We recorded whether each recruiting trees were present in open areas between patches or within patches, and whether seedlings or saplings found in transects were growing on an elevated substrate (e.g., logs or stumps) or on bare soil.

Perch effect and environmental conditions

We defined “perch” effect as the facilitative role of the tallest tree present in a patch on the recruitment of bird-dispersed species. To evaluate its role as perch, we correlated height of the tallest tree with the total number of seedlings and saplings recorded in that patch. To avoid confusions between perch effect and passive seed rain we removed from the database all seedlings that had an adult of the same species within the same patch. To evaluate temporal differences in colonization between different seed dispersal syndromes, we calculated the ratio between bird- and wind-dispersed species (DIS index hereafter) for each patch. By only using number of species we ensured that the arrival of every new species came from outside the respective patch.

To test whether patches exerted a positive influence on tree species regeneration and establishment, we calculated the Relative interaction index (RII, sensu Armas et al. 2004) as a function of tree seedlings inside and outside patches. For each 50-m transect we assigned sample points to open areas or to small, medium, and large patches and then calculated the RII for each patch category (i.e., small, medium, and large). We used the equation $RII = (\text{seedlings inside patches} - \text{seedlings in open area}) / (\text{seedlings inside patches} + \text{seedlings in open area})$.

Finally, we measured environmental conditions inside and outside patches, including the fraction of photosynthetically active radiation (PAR) reaching patch understories (compared to the open during cloudy days). Soil moisture (first 10 cm) was measured in 27 randomly chosen patches and in 27 surrounding open areas using a portable TDR probe (TDR 100, Sensor Meter, Plainfield, IL, USA). Finally, we measured soil pH in 15 patches and 15 neighboring open areas. Soil pH was determined in a 1:2 suspension in water.

Table 1 Tree species found in the post-fire, disturbed area and their dispersal syndromes (from Armesto and Rozzi 1989)

Species	Family	Seed dispersal syndrome	Number of individuals	Times recorded as focal	Percentage of young		Percentage on elevated surfaces	
					Inside	Outside	Inside	Outside
<i>Drimys winteri</i>	Winteraceae	Ornithochory	293	57	94.84	5.16	1.0	87.5
<i>Eucryphia cordifolia</i>	Eucryphiaceae	Anemochory	191	16	96.61	3.39	25.0	100
<i>Tepualia stipularis</i>	Myrtaceae	Anemochory	144	9	100	0	0	–
<i>Amomyrtus</i> sp	Myrtaceae	Ornithochory	122	7	98.81	1.19	50.0	100
<i>Podocarpus nubigenus</i>	Podocarpaceae	Ornithochory	126	7	93.48	6.52	53.8	100
<i>Raukaua laetevirens</i>	Araliaceae	Ornithochory	96	2	100	0	12.5	–
<i>Gevuina avellana</i>	Proteaceae	Mammalochory	30	2	89.47	10.53	0	100
<i>Embothrium coccineum</i>	Proteaceae	Anemochory	18	10	100	0	0	–
<i>Nothofagus nitida</i>	Nothofagaceae	Anemochory	18	7	100	0	66.6	0
<i>Weinmannia trichosperma</i>	Cunoniaceae	Anemochory	10	0	100	0	0	–
<i>Caldcluvia paniculata</i>	Cunoniaceae	Ornithochory	4	0	100	0	0	–

Trees of all ages were counted inside 117 forest patches and outside patches along eight, 50-m-long transects. Species are ordered according to their abundances (number of individuals counted). “Young” comprises both seedlings and saplings

Statistical analysis

To test whether patches acted as regeneration nuclei, we correlated the basal area of the focal tree with the number of established trees, tree species richness, and total patch area. We used standard major axis regression, which is more appropriate than standard linear regression, when both the dependent and the independent variables are measured with error (Warton et al. 2006). To assess whether open areas and patches differed in number of seedlings and preferred substrates, we used a χ^2 test.

The relationship between total number of seedlings and perch height was determined using quantile regression (*quantreg* package in R), which allows regression lines to be fit to the upper boundary of a bivariate dataset as well as through the center of the relationship (Cade and Noon 2003). This approach was used because the bivariate plot, between perch height (i.e., height of the tallest tree and number of seedlings) appeared wedge-shaped, with much greater variance in number of seedlings for large trees. This could suggest that perch height only limits seedling numbers when other (unquantified) factors are no longer limiting, and so defining the upper boundary of the relationship is important (Cade and Noon 2003). We also evaluated whether

the relationship between perch height and regenerating individuals differed between bird- and wind-dispersed species using a logistic regression where the presence of seedlings was the dependent variable and perch height was the independent variable. We used a *glm* function with a logit link in R; models were run independently for individuals of wind- and bird-dispersed origin.

Data on soil pH, soil water content, and % PAR were compared among patch categories and between patches and open areas. A one-way ANOVA and a posteriori Tukey’s test were used to assess the significance of differences between patch-size categories and open areas.

Finally, to evaluate facilitation we ran a one-way ANOVA and a posteriori Tukey’s tests to evaluate differences in RII among patch-size categories. Statistical analyses were conducted using R 2.5.1 software (R Development Core Team 2005).

Results

Evidence for nucleation

A total of 117 regenerating patches were identified in our 5-ha field site (Fig. 2); mean patch size was

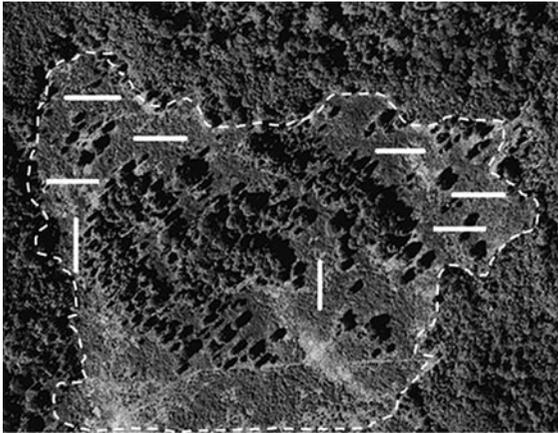


Fig. 2 Aerial photograph of the five-hectare area affected by an anthropogenic fire 50 years ago in SDBD, Chiloé Island, Chile. Discrete tree patches and the matrix of ferns and prostrate shrubs can be distinguished. Surrounding areas are remnant evergreen forests, not burned. White lines represent the eight 50-m-long transects, six of them with W–E orientation and two with N–S orientation. Dashed line shows the limits of the study area

$15.4 \pm 2.6 \text{ m}^2$ (mean ± 1 SE) ranging from 0.03 to 160 m^2 , and mean height and DBH of focal trees were $4.9 \pm 0.3 \text{ m}$ and $14.5 \pm 1.3 \text{ cm}$, respectively. We found a total of 1,052 trees of all ages in the 117 regenerating patches. *Drimys winteri* was the most common tree species in regenerating patches, with 293 individuals present in 86 % of the patches. Four species followed in frequency: *Eucryphia cordifolia* (49 %), *Tepualia stipularis* (42 %), *Amomyrtus* spp. (combining *A. meli* and *A. luma*, 39 %), and *P. nubigena* (31 %). A fleshy-fruited species with bird-dispersed seeds, *D. winteri*, was the focal tree in about half (49 %) the patches, while *Eucryphia cordifolia* and *Embothrium coccineum*, both wind-dispersed, were the focal trees in 14 and 8 % of patches, respectively. The remaining 29 % of patches had other seven tree species as focal trees (Table 1).

Larger and older focal trees in patches were associated with richer assemblages of tree species of all ages, which in turn were associated with increasing patch area. The positive correlation between basal area of the focal tree in a given patch and the number of all trees in the patch ($R^2 = 0.36$, $F_{1,59} = 34$, $P < 0.0001$; Fig. 3a) indicated that recruitment increased as patches aged. The same relationship was found for number of woody species per patch ($R^2 = 0.41$, $F_{1,59} = 41$, $P < 0.0001$; Fig. 3b). Overall, there was a positive relationship between basal area of the focal

tree and total patch area ($R^2 = 0.65$, $F_{1,59} = 113$, $P < 0.0001$; Fig. 3c).

As expected, there were clear differences in tree recruitment between patches and the open matrix without trees, with higher regeneration in patches and almost null outside them. We recorded 11 species in all patches and only 5 species of trees in open areas with more than 60 % juveniles (Table 1). Along the eight transects in the disturbed area, we found a total of 310 tree seedlings, from which 94 % occurred in patches and only 6 % in open areas ($\chi^2 = 556$; $P < 0.0001$). We found twice as many seedlings of fleshy-fruited than non-fleshy-fruited species in the entire field site (67 vs. 29 %, respectively, $\chi^2 = 85$; $P < 0.0001$). This difference held for seedlings and saplings found within patches (67 % bird, vs. 30 % wind, $\chi^2 = 78$; $P < 0.0001$) and outside patches (67 % bird, vs. 22 % wind, $\chi^2 = 5.5$; $P < 0.02$). Finally, RII increased with patch-size category; however, significant differences were only found between small and large patches ($F_{2,21} = 4.28$, $P = 0.02$; Tukey's test, $P = 0.02$; Fig. 4). Differences between small and medium, and medium and large patches were not statistically different (Tukey's test, $P = 0.3$ and $P = 0.36$, respectively; Fig. 4). Furthermore, small patches had higher variance and larger patches had the lowest ($\sigma^2 = 0.43$ and 0.009 , respectively; Fig. 4).

Perch effect

Patches with taller trees accumulated more seedlings and saplings than patches with shorter trees, or shorter perches, irrespective of the dispersal syndrome of the recruited individuals. In general, there was a positive relationship between height of focal trees and the number of seedlings and saplings recruited in any given patch (Fig. 5a); however, the 65th quantile line was the first to be significantly different from zero (Fig. 5a) which suggests that this correlation does not hold for short trees. The slopes of the 75th and 95th lines differed from one another ($t = 8.23$, $df = 189$, $P < 0.001$), thus taller trees indeed promoted species recruitment across regenerating patches (Fig. 5a). This was further confirmed by the results of the logistic regression, particularly for individuals with bird-dispersed seeds. Seedlings and saplings of bird-dispersed seeds increased with perch height ($a = 0.16 \pm 0.05$, $Z = 3.24$, $P < 0.001$, $n = 105$),

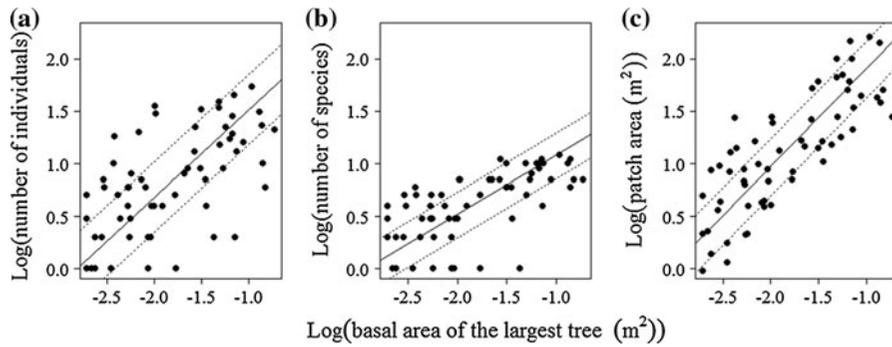


Fig. 3 Positive relationships between basal area of focal trees with DBH greater than 5 cm ($n = 60$), and number of trees of all ages present in a patch (a), number of tree species of all woody species (b) and total patch area (c). The solid lines drawn in each panel are type II regressions; dashed lines represent 95 %

confidence intervals. For a slope = 0.83, 95 % CI = 0.68, 1.02, and elevation = 2.34, 95 % CI = 2.01, 2.68; b slope = 0.57, 95 % CI = 0.47, 0.69, and elevation = 1.64, 95 % CI = 1.42, 1.86; and c slope = 0.94, 95 % CI = 0.81, 1.10, and elevation = 2.83, 95 % CI = 2.56, 3.10

whereas tree height was irrelevant for the abundance of wind-dispersed species ($a = 0.05 \pm 0.03$, $Z = 1.49$, $P = 0.13$, $n = 105$). When we analyzed the proportion of bird versus wind-dispersed species, we found that wind-dispersed tree species were less frequently present in patches than bird-dispersed species; in only 7 out of 117 patches the DIS index remained below 1, which is the value when species with bird or wind dispersal syndromes are equally present in a patch. Thus, those 7 patches had more recruitment of wind-dispersed than bird-dispersed species. In the other 110 patches bird-dispersed species dominated the assemblage and remained dominant through successional time. Species with wind-dispersed seeds showed a tendency to arrive in

greater numbers to bigger, potentially older patches, and thus the DIS index tended to decline from about 5 to 1.5 with patch area (Fig. 5b).

Environmental conditions

Abiotic conditions differed significantly between established patches and surrounding open areas (Fig. 6). PAR inside patches was 41 % lower than that measured in open areas ($F_{1,52} = 34.09$, $P < 0.0001$). No differences in PAR were recorded among patches ($F_{2,24} = 1.26$, $P = 0.3$; Fig. 6a). Soil water content was 25 % higher in open areas compared to regeneration patches ($F_{2,213} = 20.43$, $P < 0.0001$) all year round ($F_{9,200} = 20.88$, $P < 0.0001$), with the highest difference recorded in winter (June–August), when soils in open areas become saturated ($F_{3,212} = 9.8$, $P < 0.0001$; Fig. 6b). Among patches, soil moisture was higher in small patches (area $< 8 \text{ m}^2$), compared to medium and large patches, but this only happened during winter months ($F_{6,96} = 4.8$, $P < 0.001$, Tukey’s test, $P < 0.0001$; Fig. 6b). No differences were detected in soil pH between patches and open areas (4.58 ± 0.07 and 4.7 ± 0.08 , respectively; $F_{1,28} = 2.15$, $P = 0.15$), or among patches ($F_{3,26} = 1.08$, $P = 0.37$). Finally, analyses of substrate showed that 82 % of tree seedlings found outside the patches were growing on elevated substrates, while inside the patches only 28 % of the seedlings were found to be growing on elevated substrates ($\chi^2 = 21.57$; $P < 0.0001$; Table 1).

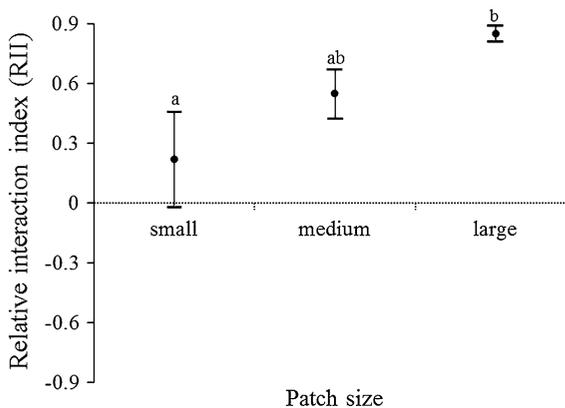


Fig. 4 Positive effect of patch size on relative interaction index (RII). Points represent mean values of RII for the three different patch-size categories (mean \pm SE, $n = 8$). Different letters indicate statistically significant differences among patch sizes (Tukey’s HSD test; $P < 0.001$)

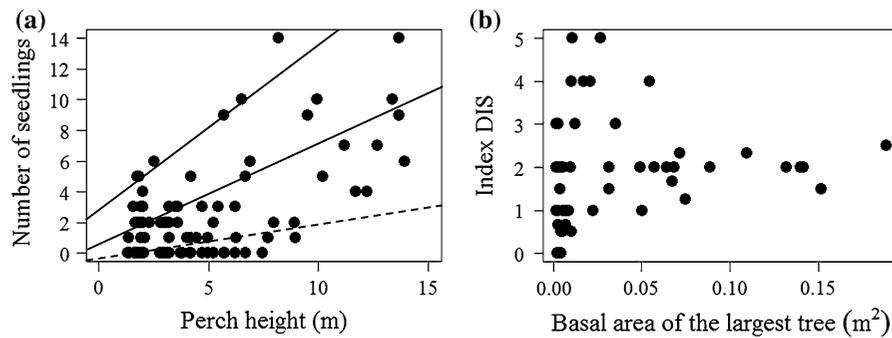


Fig. 5 **a** Number of seedlings growing on patches as a function of height of the tallest tree or perch. *Dotted* and *dashed* lines represent 20th and 50th quantile lines with slopes no different from zero (slopes = 0.16, 95 % CI = 0, 0.29). *Solid* lines represent 70th and 95th quantile lines (slopes = 0.64, 95 %

CI = 0.53, 1.02 and 1.03, 95 % CI = 0.75, 1.66, respectively). **b** Changes in the ratio between the number of bird-dispersed/wind-dispersed woody species (DIS Index) as a function of the basal area of the focal tree (a proxy of patch age)

Discussion

Our results show that 50 years after a human-set fire, forest succession occurs through nucleation where remnant patches acted as recruitment “nuclei,” disseminating seeds for the establishment of new patches, but also acting as “sinks” for propagules produced by trees in other patches or nearby forests. In addition, seed rain in the shrubland matrix was much lower than in patches with tall trees; hence patches facilitated recruitment by providing more suitable sites and shelter, while at the same time attracted dispersers of fleshy fruits.

Existing patches in the burned area, irrespective of whether focal trees were fire remnants or new colonisers, grew and expanded over time, leading by coalescence to a closed canopy (Fig. 2). The positive correlation between basal area of the focal tree in each patch (a proxy of patch age) and whole patch area supports the argument that patches are expanding into the surrounding open areas (Fig. 3). Furthermore, we only found 18 woody seedlings and saplings growing in areas outside patches. By contrast, in a similar area under tree patches we recorded around 300 tree seedlings and saplings. Studies of secondary forest succession have reported that tree seedling abundance

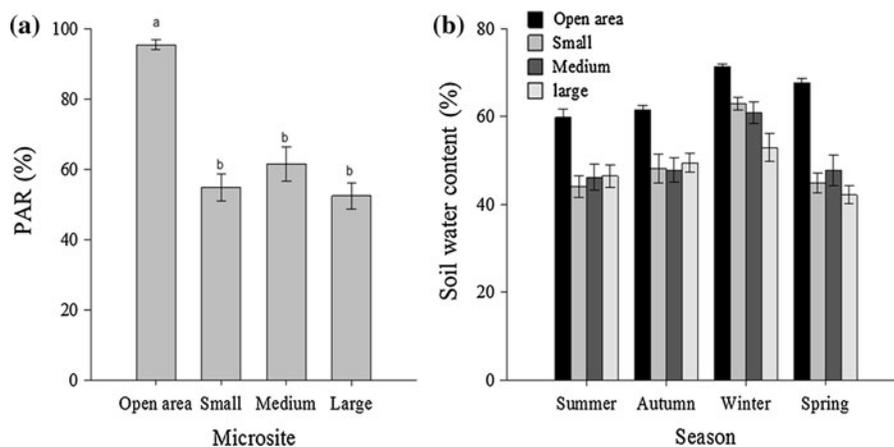


Fig. 6 **a** Percentage of photosynthetically active radiation, PAR (mean \pm SE, $n = 9$), measured in small, medium, and large patches and in the matrix of ferns and prostate shrubs. *Different letters* indicate statistically significant differences

among microsites (Tukey’s HSD test; $P < 0.001$). **b** Differences in soil water content (%) between microsites in different size tree patches and in open areas (mean \pm SE, $n = 9$)

under post-disturbance “legacies” tends to be higher than in open areas without woody cover because of different constraints on recruitment (Verdú and García-Fayos 1996; Bustamante-Sánchez et al. 2011). We conclude from our results that conditions outside patches are unsuitable for tree recruitment, while trees established in regenerating patches modify their immediate surroundings to facilitate the recruitment of additional tree species (Fig. 4).

One effective mechanism that promotes patch expansion is the perch effect that tall trees have within *regeneration nuclei*. We found that tall trees have strong positive effects on the number of seedlings and saplings in patches (Fig. 5a), emphasizing the importance of bird dispersal in the process of forest recovery (Armesto et al. 1996, 2001; Bustamante-Sánchez et al. 2011). Our quantile regression results suggest that smaller trees are less effective as perches, since patches with small trees tend to accumulate fewer individuals; thus the strongest correlation between perch height and number of seedlings was found for tall trees. This is in accordance with previous studies; in a degraded sub-tropical forest in eastern Australia, bird-dispersed seeds were more abundant under artificial perches that were 6 m tall than under 3-m-tall perches (Toh et al. 1999). However, as perch effect alone cannot explain nucleation it is important to evaluate facilitation processes as well. We found that facilitation is also crucial for forest recovery given that soil waterlogging seems to be a strong abiotic filter for tree seedling establishment in these post-disturbed soils (Díaz and Armesto 2007). Thus although we found that soil humidity was lower in larger patches, and these patches offered more favorable conditions for seedling establishment (Fig. 4), further studies are required to disentangle the relative effects of these co-varying factors.

Soil waterlogging has been identified as a major impediment for tree species survival and growth (Sun et al. 1995; Díaz et al. 2007; Gaxiola et al. 2010). Hence, human disturbances can create new conditions where only few species from temperate forests thrive (Díaz et al. 2007). This may explain why more than 90 % of established trees were found in regenerating patches. Furthermore, those tree seedlings and saplings that were found outside patches were actually restricted to elevated surfaces of forest legacies left after the fire (Table 1). In our study site, soil moisture in open areas remained above 60 % throughout the

year and exceeded 70 % during winter months (Fig. 6b). In a previous study, Pérez et al. (2009) also reported that in temperate forests of Chiloé island, southern Chile, soil moisture was significantly higher in logged than in intact forests. Furthermore, hydrologic models confirmed that soil waterlogging is a common consequence of deforestation in southern Chile and other high-latitude forests due to the combination of poor soil drainage and reduced evapotranspiration (Read and Hill 1983; Díaz et al. 2007). Hence alterations of forest structure modify soil drainage and thus conditions for species survival, favoring the development of a dense ground cover of ferns and prostrate shrubs that further restricts seedling establishment.

Soil waterlogging hampers regeneration of woody species by impeding seed germination and plant growth (Kozłowski 1997; Gibbs and Greenway 2003; Díaz et al. 2007; Gaxiola et al. 2010). Thus, elevated surfaces can provide safe sites for tree recruitment because seedlings can establish above the water table level and the herbaceous and fern cover (Read and Hill 1983; Díaz and Armesto 2007; Gaxiola et al. 2008). Studies in a temperate rain forest in southern New Zealand support this argument by showing that tree seedling recruitment occurred with higher probability on the surface of elevated trunks of tree-ferns where species escaped flooded soil conditions (Gaxiola et al. 2008). Accordingly, the overall results from the RII analysis show a clear facilitative effect of patches on the seedling presence, and this effect increases with patch size (Fig. 4). Furthermore, small patches presented a high variance of RII values and half the transects had either negative or non-interaction at all, suggesting that smaller patches still lack the necessary properties to fully improve seedling survival. Interestingly, the only abiotic condition that presented an inverse relationship with the RII values was soil moisture. These results, together with the low number and high proportion of tree seedlings growing on elevated surfaces in the open area, evidence that waterlogged soils hamper seedling survival and that this limitation can be overcome by recruiting in medium and large patches, especially large patches that had the lowest soil moisture.

Succession theory suggests that wind-dispersed tree species may be the first colonisers of early successional sites in temperate forest, where few trees can act as perches and few bird-dispersed seeds arrive

(McDonnell and Stiles 1983). However, only 5.9 % of all patches in our study site had more wind-dispersed individuals than bird-dispersed species (Fig. 5b), and only 38 % of patches ($n = 117$) had a focal wind-dispersed tree species. Because of their large DBH and basal area in all cases, we suspect that established wind-dispersed trees are remnants from the forest before the fire, likely to have been dominated by *Nothofagus* (Aravena et al. 2002). Except for these legacies, most focal trees in patches were bird-dispersed species. We found that seedlings of wind-dispersed species were nearly absent from open areas, and bird-dispersed tree species were more frequent than those of wind-dispersed species in both open areas and patches. Most tree seedlings found outside patches were accounted for by *P. nubigena* and *D. winteri*, which have bird-dispersed syndromes (Table 1). *D. winteri* was the focal tree in 49 % of the regenerating patches, and is often considered a pioneer species in these temperate forests (Donoso et al. 2006). Feild et al. (1998) associated the presence of stomatal plugs in leaves of *D. winteri* with high survival in extremely wet soils. Similarly, Feild and Holbrook (2000) correlated poor stomata closure of *Drimys granadensis* with a higher water requirements and persistence in wet soils. Accordingly, *D. winteri*, may be the best suited species to colonize these highly wet soils left after fire or logging. By contrast, other common tree species from Chilean forests, *P. nubigena* and *Nothofagus dombeyi*, can be negatively affected by excess soil moisture; Gaxiola et al. (2010) reported extremely poor tolerance to soil waterlogging in sister species of *Podocarpus* and *Nothofagus* in New Zealand. Finally, the lack of differences in soil pH between patches and surrounding areas agree with previous reports which did not find differences in pH among successional sites (Aravena et al. 2002), suggesting that acidity is not a factor arresting succession.

Our study provides key information on natural responses of temperate rainforest to anthropogenic disturbance. We propose two complementary mechanisms, via nucleation, for the recovery of forest cover in post-fire sites that should be taken into account by restoration programs: (i) the ability to overcome waterlogging in winter, as recruiting trees must be established under remnant trees in pre-existent tree patches, or elevated surfaces where soil moisture is reduced, and (ii) the ability of newly established or

remnant trees to act as perches and attract fruit-eating birds and thus enhance recruitment of fleshy-fruited species. These two mechanisms lead to patch growth and coalescence. Further studies should focus on the relative contributions of the perch effect and facilitation processes.

Acknowledgments We acknowledge support from Fondecyt-FONDAP 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Iniciativa Científica Milenio P05-002, and Grant PFB 23 from CONICYT to the Instituto de Ecología y Biodiversidad (IEB). This is a contribution to the Research Program of the LTSER Network at Estación Biológica Senda Darwin, Chiloé, Chile, and to the Biogeochemistry Laboratory, Pontificia Universidad Católica de Chile. We appreciate the field assistance and advice of Cristina Armas, Juan de Dios Miranda, Francisco Padilla, Juan Luis Celis, and Lorena Suárez.

Appendix

See Table 2.

Table 2 Non-tree woody species found in the post-fire, disturbed area and their dispersal syndromes (Armesto and Rozzi 1989)

Species	Family	Seed dispersal syndrome
<i>Chusquea quila</i>	Poaceae	Mammalochory
<i>Griselinia</i> sp	Griselinaceae	Ornithochory
<i>Luzuriaga</i> sp	Luzuriagaceae	Ornithochory
<i>Myrceugenia parviflora</i>	Myrtaceae	Ornithochory
<i>Philesia magellanica</i>	Philesiaceae	Ornithochory

For non-tree woody species only the presence or absence was recorded

References

- Aravena JC, Carmona MR, Pérez CA, Armesto JJ (2002) Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Rev Chil Hist Nat* 75:339–360
- Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686
- Armas C, Rodríguez-Echeverría S, Pugnaire FI (2011) A field test of the stress-gradient hypothesis along an aridity gradient. *J Veg Sci* 22:818–827
- Armesto JJ, Rozzi R (1989) Seed dispersal syndromes in the rain forest of Chiloé: evidence for the importance of biotic dispersal in a temperate rain forest. *J Biogeogr* 16:219–226

- Armesto JJ, Aravena JC, Pérez C, Arroyo MTK (1996) Bosques templados de la Cordillera de la Costa. In: Armesto JJ, Villagrán C, Arroyo MTK (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp 199–214
- Armesto JJ, Díaz I, Papic C, Willson MF (2001) Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloé Island, Chile. *Austral Ecol* 26:311–320
- Baribault TW, Kobe RK (2011) Neighbour interactions strengthen with increased soil resources in a northern hardwood forest. *J Ecol* 99:1358–1372
- Bertness MD, Callaway RM (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bustamante-Sánchez M, Armesto JJ, Halpern CB (2011) Biotic and abiotic controls on tree colonization in three early successional communities of Chiloé Island, Chile. *J Ecol* 99:288–299
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420
- Carmona MR, Armesto JJ, Aravena JC, Perez CA (2002) Coarse woody debris biomass in successional and primary temperate forests in Chiloé Island, Chile. *For Ecol Manag* 164:265–275
- Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. *For Ecol Manag* 265:37–46
- Di Castri F, Hajek ER. 1976. *Bioclimatología de Chile*. Vice-rectoría Académica, Universidad de Chile, Santiago, Chile
- Díaz MF, Armesto JJ (2007) Limitantes físicos y bióticos de la regeneración arbórea en matorrales sucesionales de la Isla Grande de Chiloé, Chile. *Rev Chil Hist Nat* 80:13–26
- Díaz MF, Bigelow S, Armesto JJ (2007) Alteration of the hydrologic cycle due to forest clearing and its consequences for rainforest succession. *For Ecol Manag* 244:32–40
- Donoso C, Escobar B, Donoso P, Utreras F (2006) *Drimys winteri*. In: Donoso C (ed) *Las especies arbóreas de los bosques templados de Chile y Argentina*, 1a edn. Autoecología, Chile, pp 220–232
- Feild TS, Holbrook NM (2000) Xylem sap flow and stem hydraulics of the vesselless angiosperm *Drimys granadensis* (Winteraceae) in a Costa Rican elfin forest. *Plant, Cell Environ* 23:1067–1077
- Feild TS, Zwieniecki MA, Donoghue MJ, Holbrook NM (1998) Stomatal plugs of *Drimys winteri* (Winteraceae) protect leaves from mist but not drought. *Proc Natl Acad Sci USA* 95:14256–14259
- Franks SJ (2003) Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecol* 168:1–11
- Gaxiola A, Burrows LE, Coomes DA (2008) Tree fern trunks facilitate seedling regeneration in a productive lowland temperate rain forest. *Oecologia* 155:325–335
- Gaxiola A, McNeill SM, Coomes DA (2010) What drives retrogressive succession? Plant strategies to tolerate infertile and poorly drained soils. *Funct Ecol* 24:714–722
- Gibbs J, Greenway H (2003) Mechanism of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. *Funct Plant Biol* 30:1–47
- Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *J Ecol* 97:1202–1214
- Guevara S, Purata SE, Maarel E (1986) The role of remnant forest trees in tropical secondary succession. *Plant Ecol* 66:77–84
- Gutiérrez AG, Armesto JJ, Aravena JC (2004) Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *J Ecol* 92:598–608
- He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett.* (in press)
- Holl KD, Loik ME, Lin EH V, Ia Samuels (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor Ecol* 8:339–349
- Holz A, Veblen TT (2011) The amplifying effects of humans on fire regimes in temperate rainforests in western Patagonia. *Palaeogeogr Palaeoclimatol Palaeoecol* 311:82–92
- Holzappel C, Tielbörger K, Parag HA, Kigel J, Sternberg M (2006) Annual plant–shrub interactions along an aridity gradient. *Basic Appl Ecol* 7:268–279
- Kawai T, Tokeshi M (2007) Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proc Biol Sci* 274:2503–2508
- Kinhal V, Parthasarathy N (2010) Nucleated succession by an endemic palm *Phoenix pusilla* enhances diversity of woody species in the arid Coromandel Coast of India. *AoB Plants* 2010:plq007
- Kozłowski TT (1997) Responses of woody plants to flooding and salinity. *Tree Physiol* 17:490–490
- Lusk CH (1995) Seed size, establishment sites and species coexistence in a Chilean rainforest. *J Veg Sci* 6:249–256
- McDonnell MJ, Stiles EW (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–116
- Milton SJ, Wilson JRU, Richardson DM, Seymour CL, Dean WRJ, Iponga DM, Procheş Ş (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *J Ecol* 95:648–661
- Pausas JG, Bonet A, Maestre FT, Climent A (2006) The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecol* 29:346–352
- Pérez CA, Carmona MR, Fariña JM, Armesto JJ (2009) Selective logging of lowland evergreen rainforests in Chiloé Island, Chile: effects of changing tree species composition on soil nitrogen transformations. *For Ecol Manag* 258:1660–1668
- R Development Core Team (2005) ROYAL: a language and environment for statistical computing. R Foundation for Statistical Computing. *J R Stat Soc Ser B* 67:289–300
- Read J, Hill R (1983) Rainforest invasion onto Tasmanian old-fields. *Aust J Ecol* 8:149–161
- Rubio-Casal AE, Castillo JM, Luque CJ, Figueroa ME (2001) Nucleation and facilitation in salt pans in Mediterranean salt marshes. *J Veg Sci* 12:761–770
- Schlawin JR, Zahawi RA (2008) “Nucleating” succession in recovering neotropical wet forests: the legacy of remnant trees. *J Veg Sci* 19:485–492
- Sun OJ, Sweet GB, Whitehead D, Buchan GD (1995) Physiological responses to water stress and waterlogging in *Nothofagus* species. *Tree Physiol* 15:629–638
- Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425–434

- Toh I, Gillespie M, Lamb D (1999) The role of isolated trees in facilitating tree seedling recruitment at a degraded subtropical rainforest site. *Restor Ecol* 7:288–297
- Veith H, Garleff K (1996) Evolución del paisaje cuaternario y los suelos en Chile central-sur. In: Armesto JJ, Villagrán C, Arroyo MTK (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp 29–50
- Verdú M, García-Fayos P (1996) Nucleation processes in a Mediterranean bird-dispersed plant. *Funct Ecol* 10: 275–280
- Warton DI, Wrights DF, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Willson MF, Armesto JJ (1996) The natural history of Chiloé: on Darwin's trail. *Rev Chil Hist Nat* 69:149–161
- Willson MF, Irvine AK, Walsh NG (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities with geographic comparisons. *Biotropica* 21:133–147
- Yarranton AGA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation. *J Ecol* 62:417–428