Seed limitation during early forest succession in a rural landscape on Chiloé Island, Chile: implications for temperate forest restoration

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Summary

1. Re-establishment of native forest species in rural landscapes may be conditioned by the proximity of seed sources, the post-disturbance composition of successional patches and the seed dispersal patterns of frugivores. Knowledge of seed dispersal rates into early seral communities, and how these are influenced by the structural and compositional characteristics of these communities is still quite poor.

2. We used an observational approach to quantify the seed rain and seed limitation (SL) (proportion of sites to which seeds were not dispersed) of woody species during two growing seasons in three early successional shrublands with contrasting species composition and attractiveness to frugivores on Chiloé Island, Chile. We compared species immigration based on dispersal types (bird- vs. wind dispersed) and life-form (shrubs vs. trees). Concomitantly, we used an experimental approach to test whether artificial perches would relieve SL and enhance seed dispersal and seedling establishment of fleshy-fruited species.

3. Most seeds collected were of pioneer shrubs already present in the early successional sites. Few (5%) were from trees appearing only in the surrounding second-growth forest. Density of seeds from fleshy-fruited trees and shrubs was seven times higher in the seral community most attractive to frugivores, whereas density of seeds from wind-dispersed trees was similar among communities. Artificial perches significantly increased the density and species richness of seeds from fleshy-fruited trees in all communities, but the magnitude of the facilitation effect depended on the ecological context of each seral community. Seed rain enhancement was higher in the community less attractive to frugivores. Seedling recruitment, however, remained low even under perches, indicating that additional constraints act during seed germination and/or seedling survival and growth.

4. *Synthesis and applications.* Forest succession in this rural landscape may be delayed or arrested by extremely low seed rain, despite the proximity (<100 m) of seed sources in older forest patches. Although artificial perches significantly enhance inputs of bird-dispersed tree seeds into shrublands, especially where fleshy-fruited pioneer species are absent from the seral community, they do not overcome other site-related barriers to establishment, as the lack of shaded places and limited soil drainage. Thus, in some ecological contexts, multiple approaches, such as direct seeding or planting, and the use of nurse plants, may be required to enhance seed rain and seedling establishment of fleshy-fruited species.

Key-words: bird perches, ecological filters, forest restoration, frugivores, land-use change, Latin America, regeneration dynamics, southern temperate rain forest

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Introduction

Understanding the causes of variation in the seed rain of tree species is an initial step toward explaining forest recovery in disturbed areas (Schupp & Fuentes 1995). The arrival of propagules is particularly important during early succession, when seed sources can be few and distant, and soil seed banks or vegetative remnants are rare or absent (Duncan & Chapman 1999; Mendoza *et al.* 2009). In some seral communities, that is, secondary successional communities of similar age but different structure, the abundance and activity patterns of avian frugivores may determine patterns of seed dispersal and seedling recruitment (García, Zamora & Amico 2010). Seed limitation (SL) probably occurs because few birds enter open, post-disturbance environments or because these sites are not attractive to foraging frugivores (Da Silva, Uhl & Murray 1996). Moreover, dispersal by avian frugivores often results in a patchy distribution of seeds, with some sites receiving high densities and other sites few or none (Da Silva, Uhl & Murray 1996; García, Zamora & Amico 2010; Herrera, Morales & García 2011). Among the factors that affect visitation rates and foraging times of avian frugivores are local food availability, that is, density and composition of pioneer fleshy-fruiting plants (Vieira, Uhl & Nepstad 1994; Da Silva, Uhl & Murray 1996) and vegetation height (McDonnell & Stiles 1983). For example, in a rural landscape of northern Chiloé Island, Chile, Jaña (2007) showed that structurally complex and taller vegetation types (riparian and upland forests) had greater abundance and species richness of frugivorous birds, and higher seed rain than simpler and shorter vegetation types (pastures and shrublands). Similarly, in northern temperate forests of New Jersey, USA, seed rain was higher in a vertically complex, 13-year-old field than in a 3-year-old field with a single vegetation layer (McDonnell & Stiles 1983). If such limitations are common, a closer examination of bird-mediated seed inputs in successional areas should offer insights into colonization patterns and their relationship with the variability of pioneer vegetation composition across the landscape (Mendoza *et al.* 2009). Knowledge of these patterns can be of great value when successional change is slow and deliberate manipulation of the colonization process seems desirable. Despite the importance of context dependency for many ecological processes (Jones & Callaway 2007), relatively few studies have considered how the community context modulates the arrival and establishment of pioneer woody plants during early secondary succession, its influence on natural forest recovery and its implications for forest restoration (e.g. Acacio *et al.* 2007; Bustamante-Sánchez, Armesto & Halpern 2011).

Over vast areas of southern Chile, the rural landscape, as in other regions of South America, is a mosaic of shrub- or tree-dominated patches of varying size and successional age resulting from differing histories of human influence (Aravena *et al.* 2002; Echeverría *et al.* 2007). In this rural landscape, recolonization of open areas by pioneer trees has often been slow and highly variable, spurring interest in the factors that limit tree establishment and growth (Aravena *et al.* 2002; Bustamante-Sánchez, Armesto & Halpern 2011). Broad-scale conversion of continuous forest cover to a patchy land-cover mosaic has presumably altered patterns of seed dispersal and tree colonization by changing the arrangement and diversity of habitat patches through which seed vectors move. These changes are especially relevant in ecosystems where avian seed dispersal has historically played a major role in tree establishment, such as the temperate rain forests of southern South America (Armesto *et al.* 1987, 2001; Armesto & Rozzi 1989).

In this study, we used observational and experimental approaches to address the question of SL in a heterogeneous rural landscape on Chiloé Island, Chile. We compared seed input rates and pioneer tree recruitment among three early seral communities of similar age, but with contrasting composition and vertical structure associated with different edaphic conditions, post-disturbance legacies and disturbance impacts (Bustamante-Sánchez, Armesto & Halpern 2011). Our objectives were threefold: (i) to quantify the seed rain of bird- and wind-dispersed seeds of woody species in each seral community; (ii) to assess whether seed rain density and potential dispersal limitation of recruitment varied among communities for two primary life-forms (shrubs vs. trees) and dispersal types (bird- vs. wind-dispersed); and (iii) to experimentally assess whether the addition of bird perches to each community would enhance seed inputs, thus relieving dispersal limitation of seedling recruitment. Because artificial perches are known to attract frugivores in low-stature early seral communities (McDonnell & Stiles 1983; McClanahan & Wolfe 1993; Holl 1998), we predicted that they should enhance seed inputs and compensate for potential SL, particularly in the community with the lowest natural seed rain. Because avian frugivores should be attracted to a site by the availability of fruits and the presence of suitable perches (e.g. McDonnell & Stiles 1983), we hypothesized that seed rain composition, richness and abundance should be greater in sites with the presence of fleshy-fruited shrubs and juvenile trees that act as natural perches. We also expected differences among sites in the inputs of fleshy-fruited species (i.e. avian-dispersed seeds) and, consequently, SL of tree recruitment. We hypothesized lower rates of seed input and greater SL for wind-dispersed seed species than for species with avian-dispersed seed.

Identification of the mechanisms that constrain tree recruitment is of vital importance for effective restoration strategy design in temperate forests. The rehabilitation of degraded and deforested lands often involves planting trees in open areas, which is a costly and not necessarily effective approach for large deforested areas (Rey Benayas, Bullock & Newton 2008). Given the financial and practical constraints of most restoration programmes, restoring

critical ecosystem processes such as seed dispersal (Méndez *et al.* 2008) to enhance successional change may be more cost-effective.

Materials and methods

STUDY AREA AND EARLY SUCCESSIONAL COMMUNITIES

The study was conducted in the rural landscape surrounding Senda Darwin Biological Station (SDBS), 15 km northeast of Ancud, northern Chiloé Island (42°S). We selected three early successional communities (30–50 years) that commonly develop after logging and burning of old-growth forests in this region (Aravena *et al.* 2002; Carmona *et al.* 2010). Named for the dominant woody species, these communities are as follows: (i) *Baccharis (B. patagonica):* dense scrub (*c.* 50% woody cover) dominated by *Baccharis patagonica* H. et A. Asteraceae, a nonfleshy-fruited, wind-dispersed pioneer shrub common on poorly drained, post-disturbance sites (Díaz & Armesto 2007); (ii) *Drimys (D. winteri):* moderately dense scrub (*c.* 30% woody cover) dominated by *B. patagonica*, but with significant presence of sparse juvenile trees, mainly 20- to 30-year-old *Drimys winteri* J.R. et G. Foster Winteraceae (Aravena *et al.* 2002); and (iii) *Berberis (B. buxifolia):* open scrub (<25% ground cover) dominated by the fleshy-fruited shrub *Berberis buxifolia* Lam. Berberidaceae on better drained soils. They differed in floristic composition, woody cover and vertical structure, but occurred on similar parent materials and were surrounded by a similar vegetation mosaic, which included older forests and pastures. For more detailed descriptions of the study area and each community see Bustamante-Sánchez, Armesto & Halpern (2011). Neighbouring forest patches (<100 m away) had a mixed canopy of mature trees of *D. winter*i, *Amomyrtus luma* Mol. and *A. meli* Phil. Legr. et Kausel Myrtaceae, *Laureliopsis philippiana* Mol. Mol Monimiaceae, and emergent *N. nitida* and *Eucryphia cordifolia* Cav. Eucryphiaceae. The proportions of wind- and bird-dispersed trees in the nearest forest edge did not differ among successional communities (ratio of wind- to bird-dispersed trees = 0·76, 0·71, and 0·72 for *Berberis*, *Baccharis* and *Drimys* shrublands, respectively; total number of trees sampled = 96, 91, 83, respectively, $\chi^2 = 0.32$, d.f. = 2, $P = 0.84$).

MEASUREMENT OF SEED RAIN IN EACH COMMUNITY

Seed rain was quantified every 2 weeks from December to May (late spring to early autumn), during the fruiting seasons of 2007 and 2008; sampling lasted 144 and 136 days in each year, respectively. All woody species in the study area bear ripe fruits predominantly between December and March (Smith-Ramírez & Armesto 1994). In each community, we used a systematic sampling design consisting of 60 sample points, distributed along parallel transects 15 m apart, covering an area of 10 125 m². The long axis of the grid was located parallel to the forest and 30–50 m from the nearest edge. At each sample point, we set a seed trap consisting of a metal ring 30 cm in diameter (surface area of 0·07 m²) supported by two PVC tubes 70 cm above the ground. A thin nylon mesh bag was attached to each ring to collect all seeds. Bags were emptied every 15 days. Seeds were stored and identified by using seed collections, literature and help from specialists.

PERCH EXPERIMENT

In January 2007, we initiated an experiment to test the effect of artificial perches. We used a randomized block design. In each of the three communities, we set up 10 blocks at least 30 m apart; in each block, two plots were subjected to one of two treatments: perch versus no perch. Treatments were randomly assigned to paired plots (1 × 1 m, separated by a 5-m buffer) (60 plots in total). Perches consisted of wooden poles 2-m tall and 15 cm in diameter. On top of each pole, two wooden bars 1-m long and 10 cm in diameter were fixed perpendicularly. Under each perch, four traps collected seeds and four traps were set in a similar arrangement (1 m spacing) in control plots without perches (240 seed traps in total). Seeds were collected every 15 days during two consecutive reproductive seasons (2007–2008) from January to May. At the end of the 2008 season, all traps were removed. Two years later (December 2010), we measured seedling recruitment beneath perches and in control plots (four 50 × 50 cm quadrats per plot) providing evidence of 2 years of seedling establishment (2009–2010).

DATA ANALYSES

Seed density

We modelled seed rain (number m^{-2} day^{-1}) using generalized least squares linear models (GLS). Separate models were fit for life-forms (trees vs. shrubs) and dispersal types (bird- *vs.* wind-dispersed trees). Models also included community type (*Berberis*, *Baccharis* and *Drimys*) and year (2007 vs. 2008; life-form model only); year was not included for the dispersal type model because of the very low density of wind-dispersed seeds collected in 2008, the seeds from both years were pooled. In contrast to GLM, GLS allows for nonconstant variance and within-group spatial dependency (spatial autocorrelation) among observations (Pinheiro & Bates 2000). We modelled two components of the variance–covariance structure of the response variable: a *variance* and a *correlation* structure. The variance structure was modelled allowing for different variances per level for each factor (i.e. seral shrubland, life-form or dispersal type group, and year). The correlation structure was modelled using the simplest serial correlation structure (compound symmetry). This correlation structure does not require the spatial coordinates of sampling points, only the groups (seral community type in our case) to which points belong; it also assumes equal correlation among within-group errors pertaining to the same group. First, different variance structures were incorporated into models, and these were then tested against each other using the Akaike Information Criterion (AIC). Then, the spatial correlation of the residuals was investigated comparing the AIC of models with and without spatial correlation. To find the minimal adequate model, we used a backward selection approach, which is recommended for mixed effect models (Diggle *et al.* 2002). GLS models were fit using the 'gls' command of the 'nlme' package in R (R Development Core Team 2005).

Seed limitation

We estimated SL for each colonizing species as the proportion of all seed traps in each community (N=60) that did not receive

seeds over the 2 years (i.e. fundamental seed limitation *sensu* Muller-Landau *et al.* 2002). Thus, SL was calculated as SL = 1 − *a*/*n*, where *a* is the number of seed traps receiving seeds of a given species during the fruiting period, and *n* is the total number of seed traps in each community. To assess the patterns of SL by dispersal type, we grouped SL values of all species sampled that were identified to species level for avian- and wind-dispersed trees and for avian-dispersed shrubs. Differences among seral communities in the SL values were assessed with Wilcoxon-paired tests.

Effects of artificial perches

We used distance-based permutational analysis of variance (McArdle & Anderson 2001) to assess the effect of presence or absence of artificial perches on seed abundance and species richness in the seed rain of each seral community, as well as for comparisons among life-forms, dispersal syndromes of woody species, and year. We used Euclidean distance as our measure of distance and 9999 permutations to calculate the significance of the pseudo-*F*-statistic. Sources of variation were the presence of artificial perch (d.f. = 1, fixed), seral community type (d.f = 2; fixed), block (nested within community, d.f = 27, random), life-form and dispersal syndrome (d.f = 1, fixed), year (d.f = 1, random) and all the respective interactions. The same analysis was used to assess the effect of presence or absence of artificial perches and seral shrubland type on woody seedling recruitment 2 years after the experiment.

Results

SPECIES RICHNESS AND COMPOSITION OF SEED RAIN

In total, 4231 seeds from 20 woody taxa were collected in seed traps over 2 years of sampling (Appendix S1). Shrubs accounted for 94% (3967 seeds) and trees for only 5% of the total seed rain. A total of 14 seed types of woody taxa were identified to species or genus (four shrubs, two vines and eight trees). Only one shrub species was non-native (*Rubus constrictus*), but because of its rarity, it was not included in subsequent analyses (Appendix S1). Among the remaining 13 native woody species, nine were fleshy-fruited and bird-dispersed and four were wind-dispersed (all trees). Of the nine bird-dispersed species, five came from nearby forests (four trees and one vine) and three (all shrubs) came either from adjacent areas or in situ. Among the shrubs, the most abundant taxon in the seed rain was *Gaultheria* spp. (two common species in the study area), whose tiny seeds represented 74% of the total seed rain of shrubs. Among trees, the most common species were *A. luma* and *D. winteri*, which accounted for 71% of tree seeds (Appendix S1). Of the total seed rain, 99% (4173 seeds) belonged to fleshy-fruited species and only 1% to dry-fruited species. Most fleshy-fruited propagules identified in the seed rain (74%) belonged to one shrub taxon, *Gaultheria* spp., which accounted for 62% and 87% of all bird-dispersed seeds in 2007 and 2008, respectively.

SEED DENSITY

For the analyses according to life-form, a different variance per life-form × seral community × year combination was included in the model; it presented the lowest AIC value (1219·2) providing a significantly better variance structure than the model that did not consider heterogeneity of variance (AIC = 3490·9, *L*-ratio test = 2625·1, d.f. = 2, *P* < 0·001). There was no spatial correlation in the seed density within sites. Hence, adding spatial correlation structure (compound symmetry, AIC = 889·7) did not improve the simplest model without correlation (AIC = 887·7). Seed rain density of shrubs and trees varied among seral communities ($F_{1,713} = 21.9$, $P \leq 0.0001$), with *Berberis* > *Baccharis* = *Drimys*, but these effects were strongly dependent on the interaction between life-form and seral community ($F_{2,713} = 9.65$, $P = 0.0001$, Fig. 1a).

For the analyses according to dispersal type, a different variance per dispersal type × seral community combination was included in the model; it presented the lowest AIC value (−1064·2) providing a significantly better variance structure than the model that did not consider heterogeneity of variance (AIC = −678·1, *L*-ratio
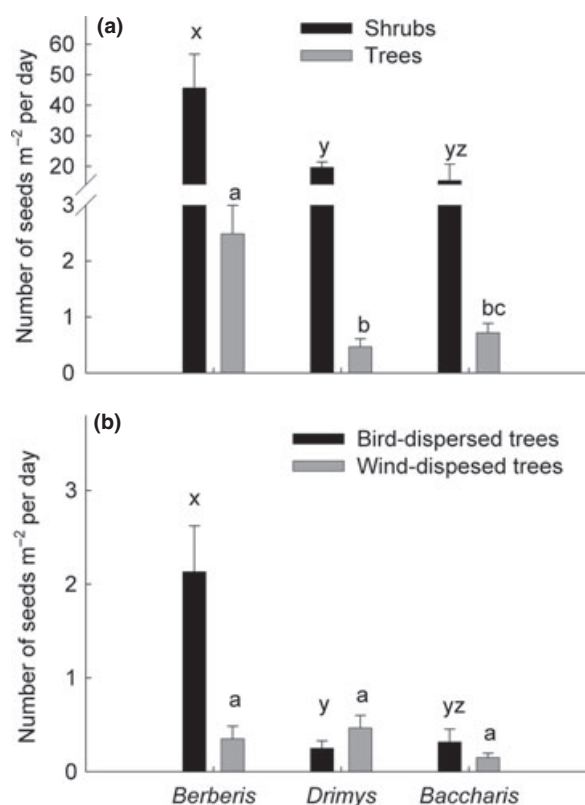

Fig. 1. Seed rain density (seeds m^{-2} day^{-1}) of woody plants in each of the three early successional shrublands, according to (a) life-form and (b) dispersal type. Values are means ± 1 SE. Results of multiple pairwise comparisons (through t-tests with correction for multiple testing) are coded by lower-case letters. Differences among communities for fleshy-fruited, bird-dispersed trees are indicated by the letters x, y, z, and differences for wind-dispersed trees by the letter a.

test = 390·09, d.f. = 2, $P < 0.001$). There was no spatial correlation in the seed density within sites. Hence, adding spatial correlation structure (AIC = −1060·2) did not improve the simplest model without correlation (AIC = −1064·2). Total seed rain density of bird (fleshy-fruited)- and wind-dispersed trees varied among the three seral communities ($F_{2,354} = 3.45$, $P = 0.03$), with *Berberis* > *Baccharis* = *Drimys*, but these effects were strongly dependent on the interaction between dispersal type and seral community ($F_{2,354} = 7.76$, $P = 0.0005$, Fig. 1b).

SEED LIMITATION

Estimated SL was strong (SL > 0·8) for the majority of colonizing woody species, regardless of dispersal type (Appendix S1). There were no differences in SL among seral communities (Wilcoxon-paired tests, all $P > 0.05$), although there was a trend towards lower SL for bird-dispersed species in the *Berberis* shrubland (Fig. 2).

PERCH EFFECTS ON SEED RAIN AND SEEDLING RECRUITMENT

A total of 47 380 seeds of 23 fleshy-fruited, bird-dispersed woody taxa were collected beneath artificial perches during the 2-year study, compared to 14,534 seeds of 15 taxa in plots without perches (Appendix S2). Among these, 15 woody taxa were identified to species or genus (six shrubs, three vines and six trees). As mentioned before, non-native *R. constrictus* was not included in the analyses. Among native woody taxa identified to species, seven originated in the surrounding forest (six trees and one vine) and nine (eight shrubs and one vine) came from early seral sites, including the sampled shrublands. Under perches, shrubs accounted for 97% (45 874), and trees for only 2% of all seeds collected. The most abundant shrub was *Gaultheria* spp. (two species pooled), representing 68% of all shrub seeds. The most common tree species in

the seed rain were *A. luma* and *D. winteri*, which accounted for 50% and 34% of all tree seeds, respectively (Appendix S2).

Perches increased the number of species of shrubs and trees in the seed rain two- to threefold (significant perch x life-form interaction: $F_{1,27} = 59.23$, $P_{(perm)} = 0.001$; Fig. 3a). In 2007, perches enhanced total species richness in the seed rain of all three shrubland communities (Fig. 3b), but in 2008, the positive effect was not significant for the *Berberis* shrubland (significant perch × seral community × year interaction: $F_{2,27} = 16.49$, $P_{(perm)} = 0.001$; Fig. 3b). Species richness of seeds from shrubs and trees also varied between years (significant life-form × year interaction: $F_{1,27} = 82.82$, $P_{(perm)} = 0.001$; Fig. 4a) and among seral communities (significant life-form × seral community interaction: $F_{2,27} = 7.66$, $P_{(perm)} = 0.003$; Fig. 4b).

Perches increased seed rain density of shrubs and trees four to nine times in the *Berberis* shrubland, but six to 11 times for shrubs and 38–159 times for trees in both the *Drimys* and *Baccharis* shrublands (perch × life-form × seral community: $F_{1,27} = 1.54$, $P_{(perm)} = 0.03$; Fig. 5). During 2007, perches increased seed rain 43 times for shrubs and 70 times for trees (all seral communities pooled), but in 2008, they did not have a significant effect (perch × life-form × year interaction: pseudo-$F_{1,27} = 11.03$, $P_{(perm)} = 0.005$; Fig. 6).

Two years after removing seed traps, five species of woody seedlings were found beneath perches in the study sites; the tree *Myrceugenia ovata* accounted for 87% (144) of these seedlings. The remainder seedlings belonged to the trees *D. winteri* (2) and *Amomyrtus* spp. (1), the shrub *Berberis darwinii* (16) and two unidentified species (3). Seedling density was higher beneath perches than in control areas (mean ± 1 SE of 4·9 ± 2 vs. 0·0; $F_{1,180} = 8.93$, $P_{(perm)} = 0.0001$), and higher below perches in the *Berberis* shrubland (13·1 ± 5·4) than in the *Baccharis* (1·5 ± 1·1) or *Drimys* shrublands (0·1 ± 0·1) (significant
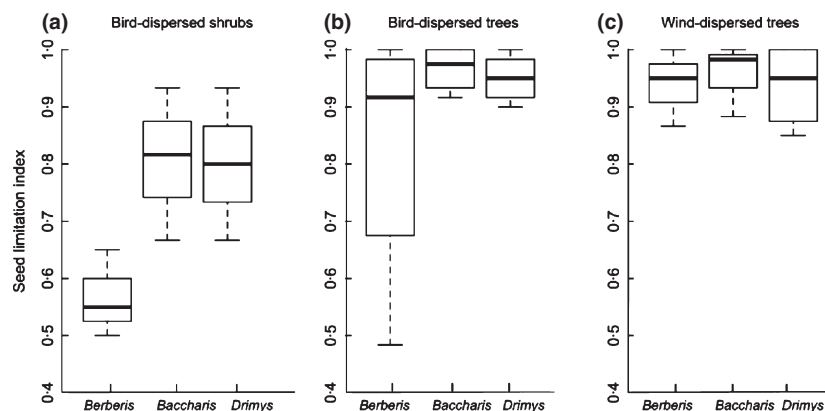

Fig. 2. Seed limitation for 11 plant species identified in the seed rain. Medians (black horizontal line) and 25–75% percentiles (boxes) are represented for: (a) bird-dispersed shrubs (*Berberis* spp., *Gaultheria* spp., *Myrteola numularia*), (b) bird-dispersed trees (*Amomyrtus luma, Amomyrtus meli, Drimys winteri, Pseudopanax laetevirens*) and (c) wind-dispersed trees (*Embothrium coccineum, Eucryphia cordifolia, Laureliopsis philippiana, Nothofagus nitida*).
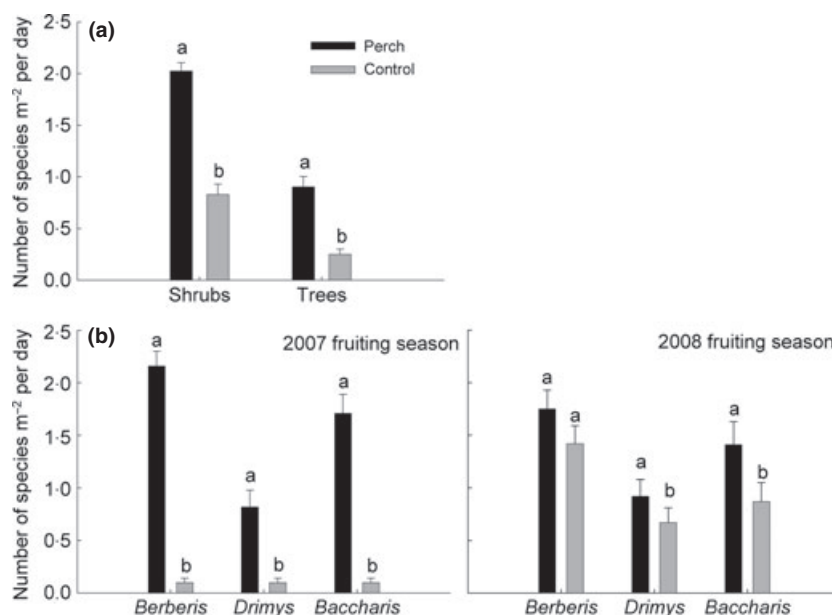
Fig. 3. Significant interaction effects of seral community type, life-form and fruiting season on species richness (species m^{-2} day^{-1}) in the seed rain below artificial perches: (a) Perch × life-form interaction and (b) Perch × seral community × season interaction. Values are means ± 1 SE. Results of multiple pairwise comparisons (through *t*-tests with correction for multiple testing) are coded by lower-case letters. Letters indicate differences between artificial perches and control treatments in each community.

perch × seral community interaction: $F_{2,27} = 4.64$, $P_{(perm)} = 0.002$).

Discussion

We studied the importance of the successional community context (current shrub and tree species composition and vertical structure of seral shrublands) to account for the heterogeneity of seed input into early successional sites of similar age, primarily for colonizing woody species with fleshy-fruited, bird-dispersed propagules. Our findings illustrate that extremely low seed rain of colonizing tree species may be delaying or impairing the progress of forest succession in the present rural landscape, despite the relatively large remaining cover of second-growth forest patches and numerous seed sources (Aravena *et al.* 2002; Echeverría *et al.* 2007). Artificial perches increased seed abundance and the number of bird-dispersed species in the seed rain in all three seral communities, but the magnitude of the facilitation effect was dependent on the ecological context of each successional community. Seed input enhancement was higher in the seral community that was less attractive to frugivorous birds.

Seed rain of local origin, from shrubs already established in these three seral sites, was the most abundant in our collections and belonged primarily to two short-statured, fleshy-fruited taxa – *Gaultheria* spp. and *M. numularia* – which have fruits with many tiny seeds (53 ± 8 and 17 ± 4 seeds per fruit, respectively). These shrubs, which often expand vegetatively, are early colonizers of many open successional sites and are abundant seeders in each of the communities studied. By contrast,

seed density of fleshy-fruited trees was very low – 0.25 ± 0.07 to 2.13 ± 0.48 seeds m^{-2} day^{-1} –, and an order of magnitude lower than that observed in nearby upland or riparian forests (Armesto *et al.* 2001; Jaña 2007). Forest interior environments in the same study area, under closed canopy and in canopy gaps, accumulate 17.5 ± 9.75 and 7.5 ± 5.05 seeds m^{-2} day^{-1}, respectively (Armesto *et al.* 2001; Jaña 2007). Such differences suggest that either bird numbers are low in these rural landscapes or there is limited movement of avian-dispersed seeds from remnant forests into adjacent shrublands. Bird surveys in the same area show that fruit-eating birds are much less common in pastures and shrublands than in upland or riparian forests (Willson *et al.* 1996; Armesto *et al.* 2005; Jaña 2007). These results highlight the role of frugivorous avifauna in enhancing the species richness and the density of tree seeds in the seed rain of early seral shrublands. They also emphasize the importance of maintaining remnant forest patches as sources of seeds of colonizing tree species (García, Zamora & Amico 2010).

Fruit production by extant pioneer plants can be an important influence on the movement of bird-dispersed seeds from surrounding forests. Studies of the transport of seeds from forests to sites under isolated remnant trees in tropical and temperate pastures show that fleshy-fruited trees receive a higher seed deposition than remnant trees without fruits or bearing dry fruits (Hernández 1995; Slocum & Horvitz 2000). These results are consistent with the observation that old fields with scattered fleshy-fruited shrubs and trees attract more frugivores and greater seed rain than sites lacking these food sources (McDonnell &
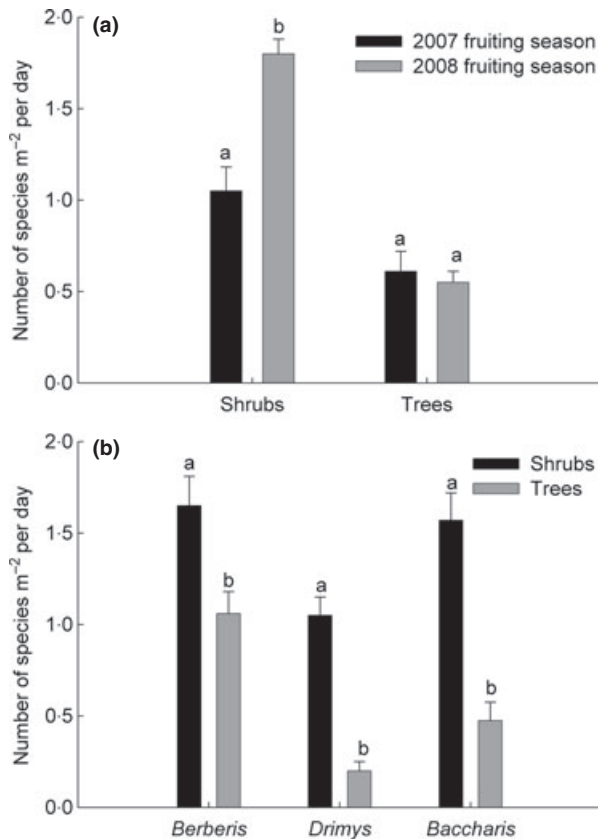
Fig. 4. Significant interaction effects of seral community, life-form and fruiting seasons on seed species richness (species m^{-2} day^{-1}): (a) Life-form x season interaction and (b) Seral community × life-form interaction. Values are means ± 1 SE. Results of multiple pairwise comparisons (through t-tests with correction for multiple testing) are coded by lower-case letters. Letters indicate differences between fruiting seasons in (a), and differences between shrubs and trees in (b).

Stiles 1983; Guevara, Purata & der Maarel 1986; da Silva, Uhl & Murray 1996). Spatial patterns of seed deposition in seral communities appear to be strongly dependent on how vertical structure and fruit production influence the behaviour of frugivorous birds (Schupp & Fuentes 1995; Jordano & Schupp 2000). Accordingly, increased frugivore activity is often associated with sites where trees have large fruit crops (García *et al.* 2001; Jaña 2007). We showed that bird-dispersed, fleshy-fruited species, particularly trees, were poorly represented in the seed rain in *Baccharis* and *Drimys* shrublands, even though fleshy-fruited tree species were frequent in the margins of surrounding forests (<100 m away). In contrast, the *Berberis* shrubland received a larger proportion of bird-dispersed seeds, consistent with its greater attractiveness to avian frugivores. On the other hand, our prediction regarding the positive effects of shrubland vertical structure on fleshy-fruited seed rain patterns was not completely supported. Although juvenile *Drimys* trees are taller than *Baccharis* shrubs, seed density of bird-dispersed woody species was similar (and uniformly low) in both seral communities. Our results provide strong evidence for the role
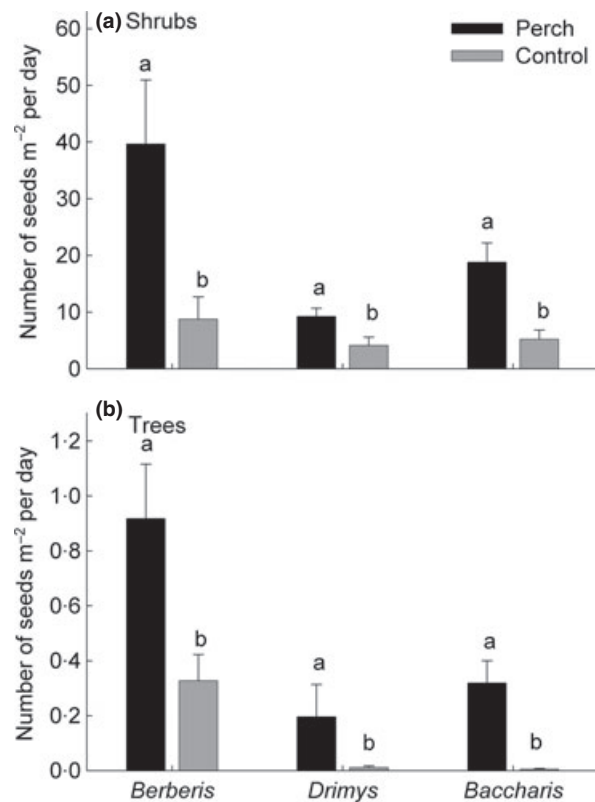

Fig. 5. Differences in seed rain densities (seeds m^{-2} day^{-1}) under artificial perches versus control areas without perches in the three seral communities for (a) shrub species and (b) tree species. Values are means ± 1 SE. Results of multiple pairwise comparisons (through *t*-tests with correction for multiple testing) are coded by lower-case letters. Letters indicate differences between perches and control treatments in each community.

of community context, that is, composition and structure of early successional communities, in setting up 'dispersal filters' that drive the process of colonization by woody species. Vegetation types such as the *Berberis* shrubland, where fleshy fruits are present, attracted more avian frugivores than neighbouring wind-dispersed shrub communities, thus increasing the probability of arrival of bird-dispersed seeds and enhancing the recruitment of fleshy-fruited trees.

SEED LIMITATION

Estimates of SL for the shrublands and species studied suggest that the seed arrival is strongly limiting recruitment of woody species, regardless of life-form and dispersal type, in all three seral communities. The abundance of many-seeded fruits of *Gaultheria* spp., coupled with low dispersal and low fruit crops of most tree species, likely contributed to the large differences among colonizing species in SL values (Appendix S1). However, the severity of SL appears to be modulated to some degree by dispersal types and community context. Wind-dispersed species were consistently and strongly seed-limited in all communities (high SL values, low variation, Fig. 2c). In
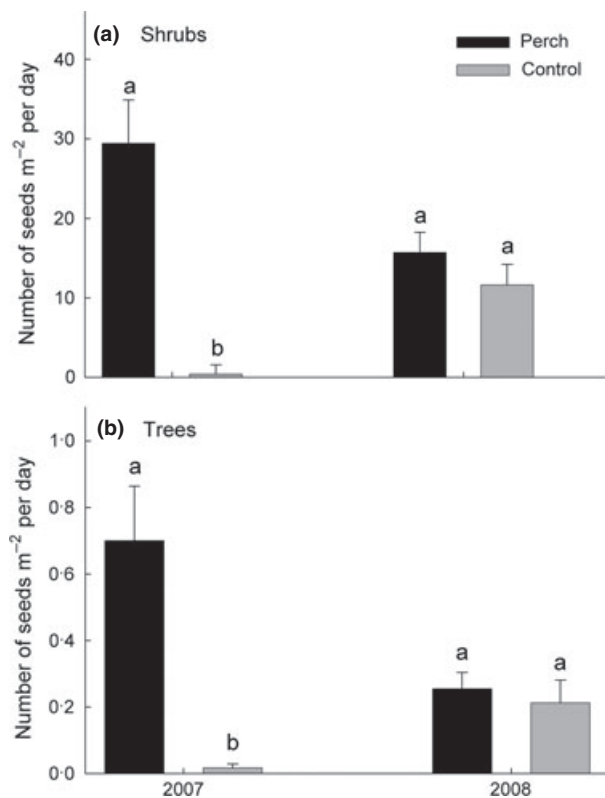
Fig. 6. Inter-annual variation in seed rain densities (seeds m^{-2} day^{-1}) under artificial perches and in controls without perches for (a) shrub species and (b) tree species. Values are means ± 1 SE. Results of multiple pairwise comparisons (through *t*-tests with correction for multiple testing) are coded by lower-case letters. Letters indicate differences between perches and control treatments in season.

contrast, for bird-dispersed species, SL was lower, and with greater variation among species in the *Berberis* shrubland. In the other two communities, bird-dispersed species consistently failed to reach a significant proportion of the seed traps (Figs. 2a & b).

SEED DISPERSAL AND SEEDLING RECRUITMENT BENEATH ARTIFICIAL PERCHES

Artificial perches serve the same function in these early successional shrublands as remnant trees do in tropical pastures (Holl 1998; Slocum & Horvitz 2000) and in Mediterranean and temperate old fields (McClanahan & Wolfe 1993; Hernández 1995).

Despite significantly higher seed inputs beneath perches, tree seedling establishment after 2 years was rather low and limited only to the *Berberis* shrubland. The absence of tree recruitment in the other seral communities may be due to lower seed input (*Drimys*) or to other physical barriers to establishment, such as the absence of protective shade and seasonal soil waterlogging (*Baccharis*) (Díaz & Armesto 2007; Bustamante-Sánchez, Armesto & Halpern 2011). Consistently with other successional studies (Miriti 1997; Holl 1998; McClanahan & Wolfe 1993), artificial

perches were unable, in the short term, to facilitate forest recovery in two of the three types of seral communities studied.

Large inter-annual differences in seed capture beneath perches illustrate the potential for temporal variation in fruit production (Armesto *et al.* 2001). The presence of artificial perches had a positive effect on seed rain density in 2007 but not in 2008, because of increased seed rain in areas without perches on the second year. Reduced fruit abundance in the nearby forest or increased fruit abundance in the successional shrubland (Fig. 4a) may have increased bird foraging in shrublands, thus explaining the pattern observed in 2008. Alternatively, in years of high fleshy fruit production in nearby forests, birds may use food resources in shrublands to a lesser extent, using perches mainly as 'stepping stones' (as observed in 2007). Consequently, the characteristics of the vegetation matrix affect frugivore behaviour and seed rain patterns in rural landscapes (Tewksbury *et al.* 2002), and reinforce the expectation that the presence of fruits in successional shrublands should have positive effects on seed rain. We suggest that years of reduced fleshy fruit production in forests surrounding the seral community, or high fruit production in shrublands, may open windows for tree regeneration through enhanced seed dispersal to successional areas.

IMPLICATIONS FOR RESTORATION

Some early successional communities will not return to tree dominance without the assistance of managers. Given that restoration programmes have financial and practical constraints, it may be more efficient and less expensive to work toward restoring critical ecosystem processes (Méndez *et al.* 2008), such as biotic seed dispersal, which is fundamental for the colonization of disturbed southern temperate forests (Armesto & Rozzi 1989) and may be disrupted by disturbance. Studies have shown that seed dispersal is severely altered by extensive land conversion or fragmentation of forests (Dosch, Peterson & Haines 2007; Jaña 2007; García, Zamora & Amico 2010). Artificial perches increase the arrival of propagules of forest trees in successional shrublands. However, we have shown that bird perching structures address only one of the obstacles to forest recovery. Although perches enhance seed dispersal in some contexts – especially where fleshy-fruited pioneer species are absent from the seral community – they do not overcome barriers to seedling establishment (Holl 1998). We showed previously that limited soil drainage might impose severe constraints on post-fire woody seedling establishment in *Baccharis* shrublands in Chiloé Island (Díaz & Armesto 2007; Díaz, Bigelow & Armesto 2007; Bustamante-Sánchez, Armesto & Halpern 2011). Hence, multiple approaches may be required to enhance tree recruitment in this community context, such as adding elevated substrates (soil mounds or woody debris; Armesto *et al.* 2009), combined with perches

to attract avian frugivores, and nurse plants to offer shelter from direct sun exposure or cold temperatures. Additionally, as seeds and seedlings of wind-dispersed trees are scarce in seral communities because of distance-restricted seed dispersal, direct seeding or planting of seedlings and juveniles may be required to accelerate the establishment of this group of species. Planting juveniles of fleshy-fruited species, on the other hand, could have a self-reinforcing effect on the arrival and establishment of additional avian-dispersed, fleshy-fruited species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Number of seed traps, total number of seeds and seed limitation index in each community.

Appendix S2. Total number of seeds of fleshy-fruited woody species collected below artificial perches and control plots in each successional community.

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