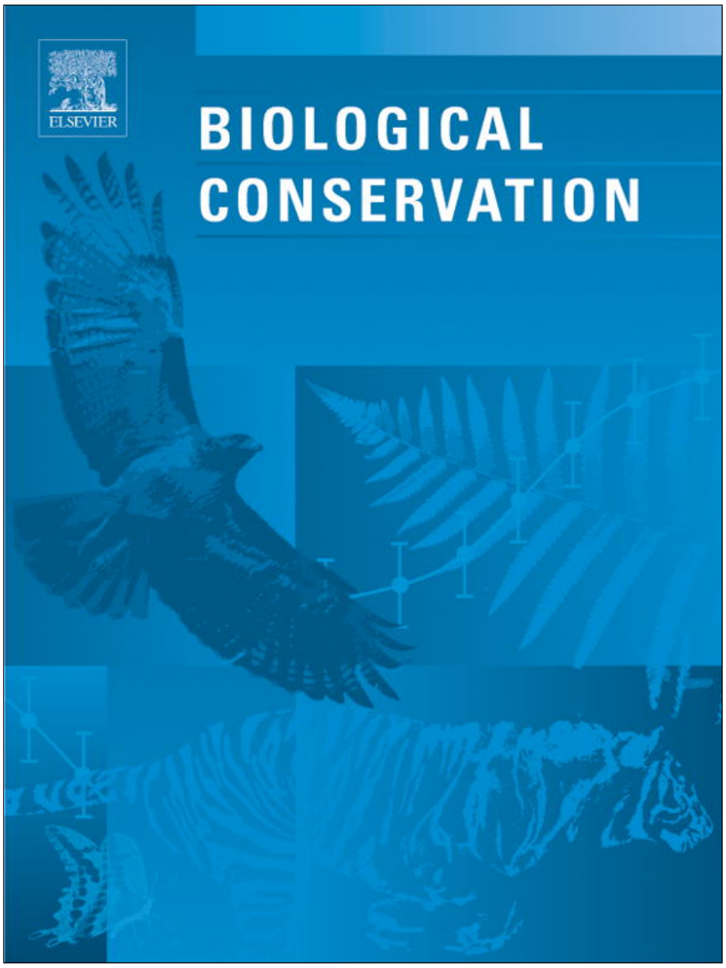
ELSEVIER
BIOLOGICAL
CONSERVATION

Biological Conservation 158 (2013) 342–350

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Birds as mediators of passive restoration during early post-fire recovery

Laura Cavallero *, Estela Raffaele, Marcelo A. Aizen

Laboratorio Ecotono, Universidad Nacional del Comahue-CONICET (INIBIOMA), Quintral 1250, S.C. de Bariloche (8400), Pcia. de Río Negro, Argentina

ARTICLE INFO

Article history:
Received 30 June 2012
Received in revised form 2 October 2012
Accepted 8 October 2012

Keywords:
Standing burned trees
Seed dispersal
Frugivory
Mobile-links
Seedlings
Seed rain

ABSTRACT

Remnant trees or artificial perches in burned areas can favor passive restoration through the perch effect. Birds consuming fruits in remnant vegetation patches or unburned adjacent communities are expected to defecate or regurgitate seeds as they perch on standing burned trees and shrubs in post-fire areas. The purpose of this study was to determine whether standing burned trees and shrubs are used by frugivorous birds as perching structures and if their maintenance promotes passive restoration of burned ecosystems. We: (a) recorded the seed rain of woody species in microsites underneath perches and in the open, (b) recorded seedling survival underneath the canopy of resprouting individuals and in the open, and (c) quantified seed rain and seedling recruitment of endozoochorous species at hectare level. Standing burned trees and shrubs were used as natural perches by frugivorous birds and increased seed arrival into recently burned communities. In addition, seedling survival was greater below the canopy of resprouting woody vegetation than in the open. Thus, standing burned trees and shrubs provide an important structural component attracting frugivorous birds, and therefore seeds during early post-fire regeneration. Resprouting trees and shrubs were also critical during post-fire recovery, because they act as seed traps, facilitate seedling survival and produce fruits that attract frugivorous birds, promoting seed flow among different communities at a landscape level. Therefore, the maintenance of standing burned woody vegetation could favor passive restoration of burned areas.

1. Introduction

Seed dispersal controls vegetation recovery in disturbed habitats (Howe and Miriti, 2004). In many temperate and tropical terrestrial ecosystems, seed dispersal is carried out mostly by mutualistic vertebrates, mainly birds (Reid 1989; Herrera et al., 1994; Wenny and Levey, 1998; Carlo and Yang 2011), and to a lesser degree, canids (Bustamante et al., 1992; Santos et al., 2003; Silva et al., 2005) and bats (Medellín and Gaona, 1999; Reiter et al., 2006). These mutualistic dispersers can enhance plant recruitment by depositing seeds in microsites with a high probability of germination and seedling emergence and survival (Reid 1989; Schupp et al., 2010). Seed dispersers are called 'mobile links' because they have the ability to connect different habitats within the landscape through seed transfer (Lundberg and Moberg, 2003). This landscape scale connection increases ecosystem resilience because it promotes gene flow between populations, especially when seed transport occurs from undisturbed to disturbed habitats. Therefore, large scale connection through mobile links leads to the persistence of plant meta-populations in fragmented landscapes (Lundberg and Moberg 2003; García et al., 2010). The importance of seed dispersal by vertebrates for the regeneration of woody species has been studied mostly in undisturbed habitats (e.g., Herrera 1989; Armesto et al., 2001), while relatively few studies have evaluated the relevance of this mutualism in the restoration of disturbed environments (García et al., 2010; Carlo and Yang 2011).

Standing burned trees and shrubs could favor passive restoration of post-fire areas through the so called "perch effect". Natural or artificial perches attract birds into degraded areas, acting as recolonization 'hot spots' and thus promoting plant recruitment. This perch effect has been recorded in abandoned agricultural lands in both tropical (Wunderle, 1997; Holl, 1998; Shiels and Walker, 2003; Zanini and Ganade, 2005; Carlo and Yang 2011) and temperate ecosystems (McDonnell and Stiles 1983; McClanahan and Wolfe 1993). Moreover, in some studies it has been documented that birds usually prefer natural over artificial perches (Holl 1998; Zanini and Ganade 2005). Thus, standing burned trees and shrubs could represent a key resource for frugivorous birds in mostly denuded sites, as it is the case in recently burned areas. These 'mobile links' are expected to consume fruits in remnant vegetation patches or unburned adjacent communities, and defecate or regurgitate seeds as they perch on standing woody vegetation in burned areas, thus favoring their recolonization. In Patagonian forests, fire is a frequent disturbance (Kitzberger and

---

* Corresponding author. Tel.: +54 294 4423374; fax: +54 294 4422111.
E-mail addresses: laucavallero@yahoo.com.ar, cavallerol@comahue-conicet.gob.ar (L. Cavallero), estelaraffaele@yahoo.com.ar (E. Raffaele), marcelo.aizen@gmail.com (M.A. Aizen).

0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2012.10.004

Veblen 1999; Veblen et al., 2003) and over 50% of the woody species produce fleshy fruits (Aizen and Ezcurra, 1998), suggesting that many species depend on 'mobile links' for seed dispersal and recolonization of recently burned areas. Consequently, to fully understand forest dynamics it is critical to assess if standing burned trees and shrubs are used as perches by frugivorous birds, increasing seed arrival into post-fire areas and thus, favoring their passive restoration.

In contrast to the potential benefits of leaving standing burned woody vegetation, post-fire logging may decrease propagule arrival to burned areas by eliminating the vertical structures used by birds as perches. This management practice is very common worldwide (Morissette et al., 2002; Beschta et al., 2004; Donato et al., 2006; Lindenmayer and Noss, 2006; Castro et al., 2010) and involves the logging of burned trees, together with the elimination of remaining woody debris (branches, logs, and stumps) (Marañón-Jimenez et al., 2011). Due to the use of heavy machinery, road openings, and low soil protection against erosive agents, the removal of burned trees and woody debris cause soil erosion and compaction, and reduce nutrient availability and soil respiration (Beschta et al., 2004; Lindenmayer and Noss 2006; Marañón-Jimenez et al., 2011). In addition, post-fire logged sites have recorded low richness and diversity of plants, insects, birds, and mammals, mainly due to the loss of resources that provide habitat for such species (Hutto 1995; Morissette et al., 2002; Beschta et al., 2004; Donato et al., 2006; Lindenmayer and Noss 2006; Castro et al., 2010). Consequently, many authors suggest that post-fire logging constrains natural recovery of terrestrial ecosystems, thereby affecting the dynamics of aquatic ecosystems located nearby or downstream, due to changes in matter, energy, and water flows (Beschta et al., 2004; Lindenmayer and Noss 2006).

The lack of seeds is also one of the main factors limiting the recovery of disturbed ecosystems (McDonnell and Stiles 1983; Holl 1998; Shiels and Walker 2003; Zanini and Ganade 2005). Therefore, propagule arrival from other sites through 'mobile links' and its deposition in microsites with a high likelihood of germination and survival are a key process affecting the speed and even the direction of recovery in disturbed ecosystems (Lundberg and Moberg 2003; Gómez-Aparicio et al., 2009). The effect of post-fire logging on ecosystem recovery dynamics has been studied from many different perspectives (Morissette et al., 2002; Beschta et al., 2004; Lindenmayer and Noss 2006; Donato et al., 2006; Castro et al., 2010; Marañón-Jimenez et al., 2011). However, to our knowledge none of the studies conducted so far have evaluated the role of standing burned trees and shrubs as recolonization 'hot spots' by their perch effect in post-fire areas. The purpose of this study is to determine the importance of standing burned trees and shrubs during early post-fire recovery in Patagonian forests. We hypothesized that standing burned trees and shrubs are used by frugivorous birds as perching structures and their maintenance promotes passive restoration of burned ecosystems. Specifically, we addressed the following questions: (a) Are endozoochorous species seeds deposited in greater proportion bellow perches than in the open, in comparison with the seeds of species with other dispersal modes (e.g. anemochorous and barochorous)? (b) Is there any perch-species more used than others? If so, it is more used because of its abundance or because it is actively selected by birds? (c) Is there any fleshy fruit species more dispersed than others? If so, it is more dispersed because of its abundance or because it is actively sought by birds? (d) Are dispersed seeds more associated with homospecific perches or with heterospecific perches? (e) Do frugivorous birds deposit seeds in microsites that facilitate seedling survival? (f) How many seeds per hectare would be dispersed by frugivorous birds underneath perches of standing burned trees and shrubs? Here we show that standing burned trees and shrubs, particularly of some species, represent key elements that can foster forest regeneration of recently burned areas via the perch effect.

2. Materials and methods

2.1. Study area

The study was conducted in Nahuel Huapi National Park during the summer of 2008–2009. We selected three sites burned in 1999 unlogged after fire. These sites are located nearby Los Moscos Lake (41° 21′ 65″ S, 71° 38′ 54″ W; 950 m.a.s.l.), Gutiérrez Lake (41° 11′ 42″ S, 71° 25′ 15″ W; 939 m.a.s.l.), and on the slopes of Catedral Mount (41° 12′ 06″ S, 71° 26′ 17″ W; 1150 m.a.s.l.). Mean annual precipitation is approximately 1000 mm at Gutierrez Lake and Catedral Mt and 1400 mm at Los Moscos Lake (Barros et al., 1983), with nearly 60% of the annual precipitation falling in the winter season (from May to August). Soils are mostly derived from volcanic ash (andisols). Before burning, plant communities were dominated by two tree species, *Austrocedrus chilensis* (hereafter *Au. chilensis*) and *Nothofagus antarctica*. Other common species were the trees *Lomatia hirsuta* and *Maytenus boaria*, the small trees *Schinus patagonicus* and *Aristotelia chilensis* (hereafter *Ar. chilensis*), and the shrubs *Diostea juncea*, *Berberis* spp., and *Ribes* spp. Except for *Au. chilensis*, the other species have the ability to resprout after fire. The two main frugivorous birds present at all the three sites and throughout the fruiting period of fleshy-fruited species were the migrant *Elaenia albiceps* (white-crested Elaenias) and the resident *Turdus falcklandii* (patagonic thrush). Also six partly frugivorous species occurred at least in one of the sites: *Colaptes pitio*, *Campephilus magellanicus*, *Pteroptochos tarnii*, *Scelorchilus rubecula*, *Troglodytes aedon*, and *Upucerthia dumetaria* (see Appendix A for methodological sampling details). When we performed the study, woody species cover varied between 30% and 50%, while bare ground cover ranged between 25% and 55%. Among 28–44% of the woody species cover belonged to fleshy-fruited species, of which 32 – 49% were large enough to bear fruit.

2.2. Sampling procedure

2.2.1. Effects of perching structures on the seed rain

We characterized the seed rain at each study site to assess whether birds used standing burned trees and shrubs as perches in post-fire areas. Seed rain was recorded by funnel-shaped 50 × 50 cm seed traps constructed of plastic mesh and supported by four 50 cm wire legs that raise the funnel above ground to prevent seed predation by rodents (García et al., 2010). In December 2008, we placed the seed traps in 75 blocks (1 × 3 m) randomly distributed within a relatively homogeneous 300 × 300 m plot at each site, considering a minimum distance of 10 m between nearest blocks. In each block, we assigned two paired treatments (i.e., one trap per treatment): (1) below perches of standing burned trees or shrubs and (2) areas without woody species cover (i.e., in the open). We selected as perches to standing burned shrubs whose height varied between 1.5 and 5 m with trunk diameter greater than 5 cm, and standing burned trees whose height ranged from 5 to 20 m with dbh greater than 15 cm. At each site, each of the 150 seed traps (i.e., 75 blocks × 2 traps per block) was checked in January, February, and March, when most woody species bear fruits (Armesto et al., 2001; Cavallero and Raffaele 2010; García et al., 2010). Seeds found in each trap were collected and placed in individual paper bags. Species determination was made based on seed morphology using a reference collection. In some cases seeds from a few genera with more than one species occurring locally could be identified to the genus level only (e.g. *Berberis* spp.). In the case of species with fleshy fruits, we considered only seeds found without pulp (i.e., indicating they come from bird feces or regurgitations), while discarding whole fruits that may have fallen into traps directly from the maternal plant. In order to assess whether the use of perches was related to the woody vegetation underneath, we estimated woody species cover on 1-m^2 plots centered on each trap using the Braun Blanquet method (Mueller-Dombois and Ellenberg, 1974). To compare the seed rain among plant species, we estimated seed rain in terms of number of fruits rather than seeds because fleshy-fruited species differ in the number of seeds per fruit. To calculate seed dispersal in fruit units (hereafter "dispersed fruits") we divided the number of seeds of each fleshy-fruited species per m^2 by the mean number of seeds per fruit of each species (Gimenez Gowland, 2000).

We estimated the following variables related to the specific questions:

(a) Cumulative seed number per m^2 by species in each dispersal mode (endozoochory, anemochory, and barochory). The number of seeds of each woody species per trap (0.25 m^2) was expressed as the total seed number per m^2 (sensu Armesto et al., 2001), considering the 3 months when traps were checked (i.e., January, February, and March).

(b) Differential use of perch-species by birds considering two variables: the estimated cumulative number of fleshy fruits deposited below each perch-species and the Perch Selectivity Index (PSI). For each site, we calculated the estimated cumulative number of fleshy fruits per m^2 under individuals of each perch-species that allowed us to determine which perch-species received more fleshy fruits. In addition, we calculated PSI by adapting the Ivlev's selectivity index (Jacobs 1974; Putfarken et al., 2008) as follows:

$$\mathrm{PSI}_i = (U_i - \mathrm{Ab}_i)/(U_i + \mathrm{Ab}_i)$$

where U_i represents the proportion of used perches of species i based on the total number of used perches at a given site (i.e., including perches from all species). The perches in which we found endozoochorous seeds in the traps placed below them, were considered as used perches. Ab_i represents the relative abundance of species i perches at a given site. PSI ranges from +1 (perch-species highly selected) to −1 (perch-species completely avoided). PSI is zero when the proportion of used perches of species i was equal to species i number of individuals at a given site (i.e., species i was used as a perch in the same proportion of its availability). By considering the total perch availability, PSI allowed us to evaluate whether birds use different perch-species based only on their abundance or actively selected certain perch-species.

(c) Differential fruit consumption and seed dispersal by birds of fleshy-fruited species by considering the proportion of dispersed seeds of each fleshy-fruited species (expressed in fruit units, see above) and an index of selectivity, the Fleshy-fruited species Selectivity Index (FSI) (Jacobs 1974; Putfarken et al., 2008) for each species and site:

$$\mathrm{FSI}_i = (\mathrm{Prop}_i - \mathrm{Cov}_i)/(\mathrm{Prop}_i + \mathrm{Cov}_i)$$

where Prop_i represents the proportion of species i dispersed fruits based on the total number of dispersed fruits at a given site. Cov_i represents the proportion of species i cover at a given site. Fleshy-fruited species cover was estimated in each site by the point-intercept method (Mueller-Dombois and Ellenberg 1974), at 1 m intervals, using two 300 m transects. The index varies between +1 (actively sought fruits) and −1 (completely avoided fruits). For dioecious *Ar. chilensis* and *M. boaria* we divided plant cover by two assuming a 1:1 sex ratio (Charnov, 1982). When we found seeds of a particular species but this species was not present at the site, we assigned it a cover value of zero. By taking into account the proportion of dispersed fruits and the cover of each species producing fleshy fruits, the FSI allowed us to assess whether birds consume fruits from fleshy-fruited species based on their abundance or actively seek certain fleshy-fruited species.

(d) Real dispersal events by calculating for each fleshy-fruited species the estimated cumulative number of fleshy fruits per m^2 recorded below perches from the same species and below perches from other species (i.e., events resulting with certainty in real movement away from the maternal plant). This variable allowed us to evaluate the proportion of dispersed fruits deposited below homospecific perches (i.e., when a bird consumed fruits from a plant defecating the seeds in situ) vs. heterospecific perches (i.e., when a bird consumed fruits from a plant of a certain species and then settled on a plant from another species, defecating the seeds from the former plant). This variable represents a conservative estimation of real dispersal events because it did not include the seeds of individuals from a given species that were transported and deposited by birds below perches of other individuals from the same species.

2.2.2. Seedling survival in different microsites

To examine the relationship between seed rain and establishment, we transplanted seedlings from four fleshy-fruited species (*B. buxifolia*, *M. boaria*, *R. magellanicum*, and *S. patagonicus*) into two types of microsites: underneath the canopy of individuals of resprouting species and in the open (i.e., exposed areas 2–3 m apart from the nearest resprouting shrub or tree). All seedlings were grown in a greenhouse from seeds collected in nearby local forests, and transplanted into the field when they displayed cotyledons or 2–4 fully developed leaves. We carried out seedling transplants at one site burned in 1996 (located in Catedral Mt 41° 07′17″S, 71° 26′ 10″ W, 854 m.a.s.l.) that previous to the fire was dominated by *Au. chilensis* and *N. antarctica*. In May 2009, we transplanted a total of 144 seedlings of *B. buxifolia* and 200 of *R. magellanicum*. In May 2010, at the same site, we transplanted a total of 64 seedlings of *M. boaria* and 80 of *S. patagonicus* distributed between the two types of microsites. Transplants were carried out in May when evapotranspiration was low enough to minimize post-transplant mortality (Gallopín, 1978). Due to the presence of hares in the site, seedlings were protected from herbivory by 50 cm diameter exclosures constructed with wire mesh rolled into a cylinder and nailed to the ground with iron stakes. For each species, we placed the exclosures in randomized blocks, each block containing the two levels of microsite factor (underneath the canopy of individuals of resprouting species and in the open) with a total of four blocks (i.e., four pairs of an exclosure placed underneath the canopy of a resprouting individual and one placed in the open). In summary 18, 25, 8, and 10 seedlings of *B. buxifolia*, *R. magellanicum*, *M. boaria* and *S. patagonicus*, respectively, were transplanted in each exclosure. The exclosures placed underneath the canopy of resprouting individuals were installed below one of three possible species: the trees *L. hirsuta* and *N. antarctica*, and the small tree *S. patagonicus*. Ten days after transplantation, we recorded seedling survival to determine post-transplant mortality. Finally, we recorded seedling survival 1 year after transplanting (i.e., April 2010 or 2011 depending on the species) to assess the effect of microsite on mortality.

2.2.3. Seed rain and seedling survival per hectare

In order to assess the potential benefit of leaving standing burned woody vegetation as a passive restoration practice in post-fire areas, we quantified seed rain and seedling recruitment of endozoochorous species at hectare level. The data obtained from seed traps was used to estimate the perch effect of standing burned trees and shrubs in the seed rain of endozoochorous species per hectare (see Appendix A for methodological details). We used the information obtained from seedling transplants to calculate seedling recruitment underneath standing burned trees and shrubs at hectare level (see Appendix A for methodological details).

2.3. Data analysis

To evaluate the effect of standing burned trees and shrubs on seed rain, we compared the cumulative seed number per m^2 underneath perches and in the open for three seed dispersal modes (i.e., endozoochory, anemochory, and barochory) using Generalized Linear Mixed Models (GLMMs). To perform the GLMMs we considered completely randomized blocks (CRBs) nested within a main plot (i.e., site). When fitting the GLMMs we included Perch as a fixed factor with two levels (i.e., underneath perches and in the open), whereas Block (i.e., including the two paired levels of the perch factor) and Site (i.e., Gutierrez Lake, Catedral Mount, and Los Moscos Lake) were included as random factors. To test whether endozoochorous seeds were deposited in higher proportion bellow perches than in the open in comparison with anemochorous and barochorous seeds, we performed another GLMM including Mode (i.e., Anemochory, Endozoochory, and Barochory), Perch (i.e., underneath perches and in the open) and its interaction, as fixed factors. Block and Site were included as random factors. Because our data were counts (i.e., number of seeds), we fitted the GLMMs considering a Poisson distribution and a log link function.

To assess if some perch-species were more used than others, and if they were more used because they were more abundant or because they were actively selected by birds, we compared the cumulative estimated fleshy fruit number per m^2 and PSI between perch-species by using Linear Mixed Models (LMMs). We considered Perch-species as a fixed factor with eight levels (*Au. chilensis*, *B. buxifolia*, *D. juncea*, *L. hirsuta*, *M. boaria*, *N. antarctica*, *R. magellanicum*, and *S. patagonicus*) and Site as a random factor. To test whether some fleshy-fruited species were more dispersed than others and if this was related to their abundance, we compared the proportion of dispersed fruits and the FSI between fleshy-fruited species using a LMM. Fleshy-fruited species was included as a fixed factor with five levels (*Ar. chilensis*, *Berberis spp*., *M. boaria*, *R. magellanicum*, and *S. patagonicus*) and Site as a random factor. When we detected significant differences, we performed post hoc multiple comparisons through Tukey's test.

In order to assess whether the seeds were deposited differentially below homospecific than heterospecific perches, we compared the estimated number of fleshy fruits deposited below homospecific vs. heterospecific perches by means of a LMM. We considered two fixed factors: (a) Seed dispersal with two levels (estimated fleshy fruit number per m^2 recorded below homospecific and heterospecific perches); (b) Fleshy-fruited species with five levels (*Ar. chilensis*, *Berberis* spp., *M. boaria*, *R. magellanicum*, and *S. patagonicus*) and its interaction. Site was included as a random factor.

To assess whether frugivorous birds deposit seeds differentially in microsites that facilitate seedling survival we compared seedling survival of transplanted individuals between microsites, by means of a LMM in CRB. For each species (*B. buxifolia*, *M. boaria*, *R. magellanicum*, and *S. patagonicus*), we compared seedling survival considering Microsite as a fixed factor with two levels (underneath the canopy of a resprouting individual and in the open) and Block as a random factor. All analyses were performed using R software (R Development Core Team 2006). Significance level in all tests was $\alpha = 0.05$. Normality and homoscedasticity were corroborated prior to each analysis as required by LMMs (Quinn and Keough, 2002).

3. Results

3.1. Effects of perching structures on the seed rain

Throughout the sampling season, we collected a total of 2980 seeds of 16 woody species (Appendix B) from which five species were dispersed by birds. Of this total, 1064 were dispersed by birds and 89% of those seeds were collected from traps placed underneath standing burned trees and shrubs. On average, we recorded twice the number of seeds in traps underneath perches (12.5 seeds/m^2) than in the open (6.7 seeds/m^2), summing across all dispersal mode categories. In the three study sites, the average cumulative seed number per m^2 was significantly higher under perches than in the open for all three dispersal modes (Table 1). When we included dispersal mode in the model, the factors perch ($\chi^2 = 729.09$; $p < 0.0001$) and mode ($\chi^2 = 671.29$; $p < 0.0001$) and its interaction ($\chi^2 = 389.16$; $p < 0.0001$) were all significant. The interaction shows that differences in seed numbers between microsites were greatest for endozoochorous species (Fig. 1). Specifically, the number of seeds dispersed by birds was nine times higher in traps underneath perches than in the open (17.25 vs. 1.92 seeds/m^2).

We recorded eight native woody species used as perches (five trees and three shrubs) and five native woody species used as fleshy fruit sources (three small trees and two shrubs). We detected significant differences among perch-species for the estimated cumulative number of fleshy fruits per m^2 and PSI (Fig. 2, Table 2). The highest estimated cumulative number of fleshy fruits per m^2 was found underneath perches of *R. magellanicum* and *Au. chilensis*, while *B. buxifolia*, *D. juncea*, *L. hirsuta*, *M. boaria*, and *N. antarctica* received the lowest estimated number of fruits per m^2 (Fig. 2a). Considering perch availability, birds mainly selected two anemochorous tree species *Au. chilensis* and *L. hirsuta* (Fig. 2b, Table 2). On the other hand, the proportion of dispersed fruits was similar between fleshy-fruited species (Fig. 3, Table 2). However, when considering fleshy-fruited species cover, the most abundant species (i.e., *S. patagonicus*) was the least selected, whereas two rare species (i.e., *Ar. chilensis* and *R. magellanicum*) were actively selected by birds (FSI, Fig. 3, Table 2). It must be remarked that we recorded seeds of *Ar. chilensis* and *M. boaria*, although these species were not present at two of the study sites.

Table 1

Results of Generalized Linear Mixed Models (GLMMs) for cumulative seed number per m^2 of endozoochorous (E), anemochorous (A) and barochorous (B) woody species. Fixed effects: degrees of freedom (*df*), *t*-statistic (*t*) for fixed effects and associated *p*-values (*p*). Random effects: variance (var.) and standard deviation (SD) of site, block nested within site, and residual variability. *n* = 450 observations.

Variables	Fixed effects			Random effects					
	Perch			Site		Block (Site)		Residual	
	df	*t*	*p*	Var.	SD	Var.	SD	Var.	SD
Seed number, m^2 (E)	221	−35.99	**<0.0001**	0.1928	0.4391	0.6051	0.7779	0.3559	0.5965
Seed number, m^2 (A)	221	−3.49	**0.0020**	0.0000	0.0001	0.0006	0.0008	0.0009	0.0003
Seed number, m^2 (B)	221	−11.80	**<0.0001**	0.0000	0.0000	0.1586	0.3983	0.0249	0.1579

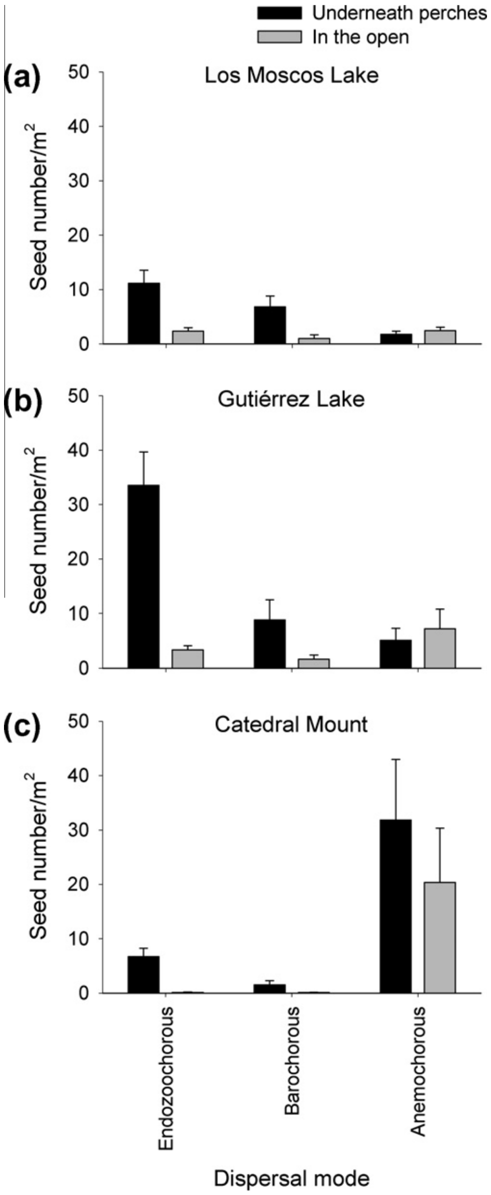

Fig. 1. Average cumulative seed number per m^2 of endozoochorous, barochorous and anemochorous species recorded underneath perches and in the open, in Los Moscos Lake (a), Gutiérrez Lake (b) and Catedral Mount (c).

From the total number of dispersed fruits, 85% of them were found underneath perches from heterospecific species (Fig. 4). Thus, the estimated number of fruits per m^2 was significantly greater below heterospecific than homospecific perches ($F_{1,15} = 15.26$; $p = 0.0013$) for all fleshy fruit species ($F_{4,16} = 1.02$; $p = 0.4233$), recording no significant interaction between factors ($F_{4,15} = 0.36$; $p = 0.8319$) (Fig. 4). Notably, the most abundant species (i.e., *S. patagonicus*) for which we recorded the lowest FSI value, recorded the highest number of fruits below homospecific perches (Fig. 4).

3.2. Seedling survival in different microsites

Post-transplant stress mortality differed greatly among species. We found that 19.4% of the seedlings of *B. buxifolia*, 41.7% of *M. boaria*, 55.5% of *R. magellanicum*, and 14.6% of *S. patagonicus* died after transplant. Seedling survival 1 year after transplant was significantly higher underneath the canopy of resprouting woody plants than in the open for *B. buxifolia*, *R. magellanicum*, and *S. patagonicus* (Fig. 5, Table 2). For *M. boaria* no significant differences were found between microsites (Fig. 5, Table 2).

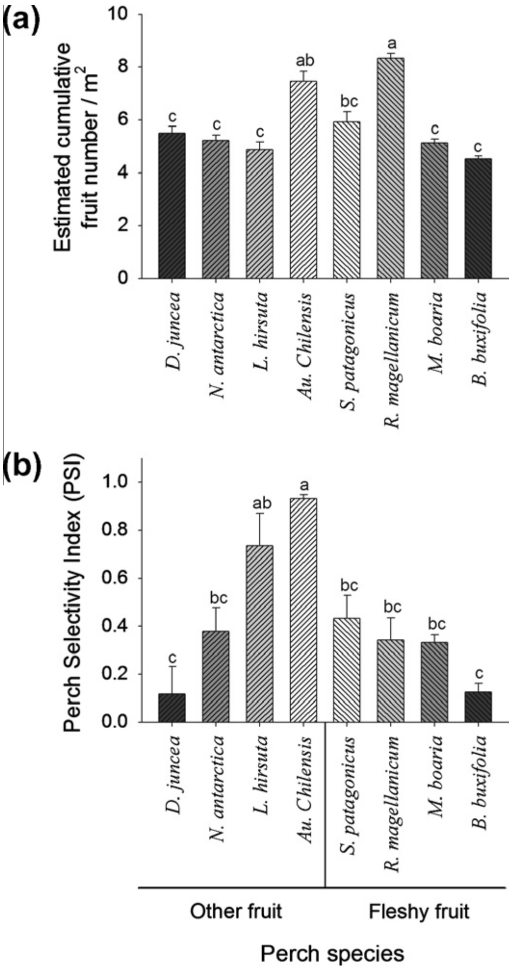

Fig. 2. Estimated cumulative fruit number per m^2 (a) and Perch Selectivity Index (b) of each perch-species. Distinct letters indicate significant differences between species ($p \leqslant 0.05$).

3.3. Seed arrival and seedling survival per hectare

We estimated that standing burned trees and shrubs facilitated the arrival of between 29,452 and 59,919 seeds/ha, depending on perch-availability and m^2 of available microsites (Appendix C). In addition, seedling number per hectare associated with these seeds ranged from 270 to 11,818 seedlings/ha depending on seed viability, germination capacity, and survival underneath perches (Appendix C). These number are conservative because a lack of data on survival of *Ar. chilensis*. Natural seedling occurrence of endozoochorous species varied between 3056 and 5486 seedlings/ha. Three perch-species (*Au. chilensis*, *L. hirsuta*, and *S. patagonicus*) had a considerably positive effect on seed rain and establishment, accounting for 75% of the seed rain and 80% of the seedling recruitment (Appendix C).

4. Discussion

4.1. Effects of perching structures on the seed rain

Standing burned trees and shrubs, which were used as natural perches by frugivorous birds, represented a key structural compo-

Table 2
Results of Linear Mixed Models (LMM) for comparisons of the estimated cumulative number of fleshy fruits per m^2 deposited below each perch-species, Perch Selectivity Index (PSI), proportion of dispersed fruits, Fleshy-fruited species Selectivity Index (FSI), and seedling survival on different microsites. Fixed effects: degrees of freedom (*df*), *F*-statistics for fixed effects (*F*) and associated *p*-values (*p*). Random effects: variance (var.) and standard deviation (SD) for site or block, depending on the variable, and residual variability. $n = 21$ observations for perch-species variables, $n = 15$ observations for fleshy-fruited species variables and $n = 8$ observations for seedling survival.

Variables	Fixed effects			Random effects			
	Species			Site		Residual	
	df	*F*	*p*	Var.	SD	Var.	SD
Estimated cumulative number of fleshy fruits (m^2)	6/12	2.68	**0.0500**	0.0005	0.0080	0.0624	0.0235
Perch Selectivity Index (PSI)	6/12	8.93	**0.0003**	−0.0018	0.0016	0.0245	0.0092
Proportion of dispersed fruits	4/8	0.47	**0.7572**	0.0069	0.0036	0.0360	0.0180
Fleshy-fruited species Selectivity Index (FSI)	4/8	3.71	**0.0539**	0.0046	0.0160	0.0900	0.0450
	Microsite			Block		Residual	
Survival of *B. buxifolia* seedlings	1/3	14.31	**0.0324**	35.97	167.26	251.48	205.34
Survival of *M. boaria* seedlings	1/3	6.86	0.0790	0.00	160.56	278.11	227.07
Survival of *R. magellanicum* seedlings	1/3	55.67	**0.0050**	0.00	4.99	8.64	7.06
Survival of *S. patagonicus* seedlings	1/3	13.57	**0.0347**	64.83	259.77	380.41	310.61

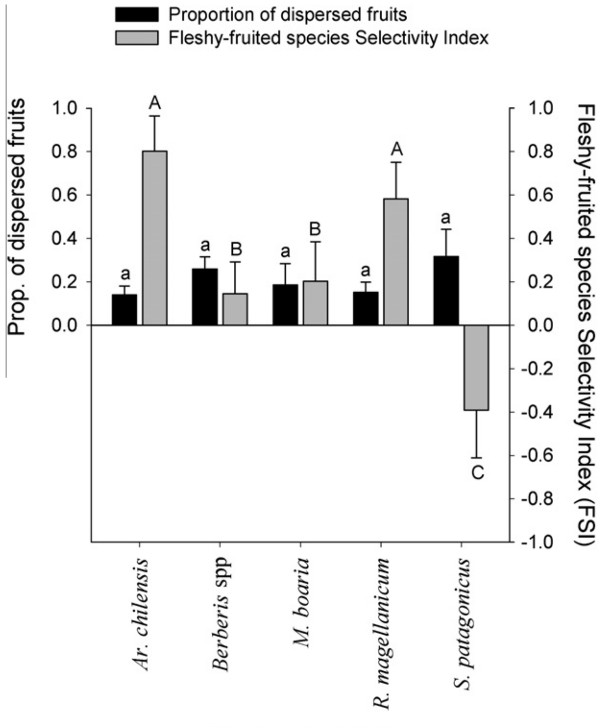

Fig. 3. Proportion of dispersed fruits and Fleshy-fruited species Selectivity Index (FSI) for each bird dispersed species. Distinct lowercase letters indicate significant differences among species for the proportion of dispersed fruits ($p \leqslant 0.05$). Distinct uppercase letters indicate significant differences among species for the Fleshy-fruited species Selectivity Index (FSI) ($p \leqslant 0.05$).

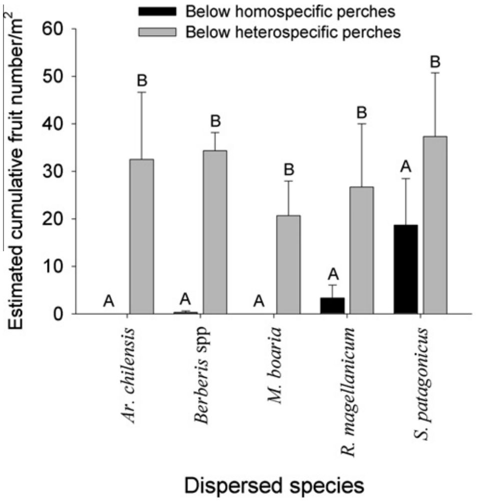

Fig. 4. Estimated cumulative fruit number per m^2 recorded in seed traps placed below homospecific and heterospecific perches. Distinct uppercase letters indicate significant differences for dispersion factor ($p \leqslant 0.05$).

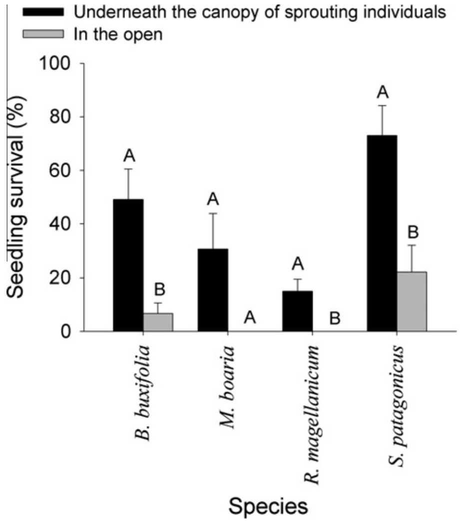

Fig. 5. Seedling survival percentage in different microsites (underneath the canopy of resprouting individuals vs. in the open) by species. Distinct letters indicate significant differences between microsites ($p \leqslant 0.05$).

nent during early regeneration of recently burned *Au. chilensis* and *N. antarctica* forests. The number of seeds per m^2 was higher underneath perches than in the open independent of dispersal mode, but this difference was most striking in the case of endozoochorous species (Fig. 1). Therefore, birds disproportionately dispersed seeds from fleshy fruited species below perches. The results from this and other studies in both temperate and tropical forests show that perches serve as attractors for bird dispersers (McDonnell and Stiles 1983; McClanahan and Wolfe 1993; Wunderle 1997; Holl 1998; Shiels and Walker 2003; Zanini and Ganade 2005; Carlo and Yang 2011). In our study, the number of seeds found in traps located under perches was nine times greater than in traps placed in the open. This is consistent with results from other studies in tropical forests where the number of seeds under perches was 15 (Holl 1998), 13 (Andrade Melo et al., 2000), and 10 (Shiels and Walker 2003; Zanini and Ganade 2005) times greater than the number of seeds recorded in areas without perches. In contrast, the number of seeds of anemochorous species as a group was only twice as high in traps underneath perches as in the open. Nevertheless, this higher number of seeds underneath perches for wind-borne seeds could be due to the fact that shrubs and trees act as seed traps by interrupting wind flow, especially in ecosystems where spatial configuration of the community is characterized by relatively isolated vegetated patches immersed within a bare soil matrix (Aguiar and Sala 1999; Walker and del Moral 2009). In any event, anemochory was the dispersal mode that recorded the highest number of seeds per m^2 in open areas (i.e., 45% of the trapped seeds fell into traps without perches) (Fig. 1). This could be due to the dependence of anemochorous species on an 'unspecific' vector regarding seed transport to particular microsites (Cavallero et al., 2012). Finally, the presence of barochorous seeds in seed traps below perches could be due to fruits/seeds produced by some of the resprouting shrubs with this dispersal mode were large enough to bear fruit that fell by gravity into the traps (Fig. 1). Consequently, the results of this study suggest that resprouting trees or shrubs play an important role in the recolonization of burned areas acting not only as bird perches, but also as seed traps and seed sources. However, our results emphasize the importance and differential role of standing burned woody vegetation for the recruitment of endozoochorous species after fire.

An anemochorous tree (*Au. chilensis*) and an endozoochorous shrub (*R. magellanicum*) were the perch-species that received the highest number of endozoochorous seeds per area unit (Fig. 2a). In the case of *Au. chilensis*, birds probably deposited a large number of seeds under perches of this tall anemochorous conifer because they use this species for mating, nesting, and/or territory monitoring (Hutto 1995; Morissette et al., 2002; Carlo and Aukema 2005). In the case of *R. magellanicum*, birds dispersed large numbers of seeds under perches of this endozoochorous shrub because they use this species as a food resource (McDonnell and Stiles 1983). Considering Perch Selectivity Index, the two anemochorous tallest and largest trees (i.e., *Au. chilensis* and *L. hirsuta*, reaching a maximum height of 15–30 m) were the most selected perches (Fig. 2b), suggesting that birds did not only use the species that offer a food reward but also actively selected species which provide key habitat resources (e.g. roosting, and/or breeding sites) (McDonnell and Stiles 1983; Hutto 1995; Morissette et al., 2002; Carlo and Aukema 2005). These large-sized species provide spatial and vertical complexity in highly simplified burned forests. Structural complexity is essential to attract birds to disturbed areas and therefore, to maintain landscape-scale connectivity among undisturbed areas (McDonnell and Stiles 1983; Wunderle 1997).

The proportion of dispersed seeds underneath perches was similar between fleshy-fruited species (Fig. 3, Table 2). However, fleshy-fruited species were differentially selected by birds (FSI, Fig. 3, Table 2). Specifically, the most abundant species (i.e., *S. patagonicus*) was the least selected, whereas two rare species (i.e., *Ar. chilensis* and *R. magellanicum*) were disproportionately represented in the seed rain regarding their cover. These two species could be particularly rewarding, compared to the other fleshy-fruited species, because they produce a high number of fruits per cover unit and/or of high quality. For instance, *Ar. chilensis* and *R. magellanicum* produce fruits with 20–30% more pulp and with higher mineral content than the fruits of *Berberis* spp. (Damascos et al., 2008). It should be noted that *R. magellanicum* was also highly used as a perch, suggesting that their widespread use could be due to the food reward provided by this species. Therefore, resprouting species bearing fleshy fruits can play an important role in post-fire recovery because they attract fruit-eating birds, promoting seed flow among nearby plant communities, at the same time that they provide perches for processing fruits and defecating or regurgitating seeds.

Our results also provide strong evidence that birds, through seed transfer, act as mobile-links fostering the recovery of disturbed ecosystems. The number of seeds from fleshy-fruited species deposited below a heterospecific perch-species was significantly higher (about 85%) than the number of seeds deposited below perches of the same species, for all fleshy-fruited species. Even though 15% of the seeds were dispersed underneath homospecific perches, most of them (80%) belong to the most abundant species *S. patagonicus*, which increase the chance of seed transfer from and to individuals of the same species (Figs. 3 and 4). Therefore, most of the seeds found below perches were literally 'dispersed' by birds away from the mother plant. Moreover, we found seeds of two species (i.e., *Ar. chilensis* and *M. boaria*) even when these species were not recorded in two of the study sites. This suggests that seed flow occurred at scales of at least several hundreds of meters over the landscape, supporting the view that birds act as mobile-links transporting seeds among different communities (Lundberg and Moberg 2003). Propagule arrival from other communities through mobile-links is critical during post-disturbance recolonization when local seed sources are scarce (Gómez-Aparicio et al., 2009; Lundberg and Moberg 2003).

4.2. Seedling survival in different microsites

Summer water deficit is the main cause of high seedling mortality in Mediterranean climate ecosystems, such as the shrublands and forests of NW Patagonia, and reducing its severity favors seedling survival (Kitzberger et al., 2000; Rey and Alcántara 2000; Gómez-Aparicio et al., 2005). In this study, seedling survival was higher underneath the canopy of resprouting individuals than in the open for three of the four species tested. In the case of *M. boaria*, although there were no significant differences between microsites, no seedling survived in the open. This was probably due to the low number of seedlings of this species available for transplanting. Thus, our results indicate that resprouting individuals buffer extreme environmental conditions in recently burned sites, favoring seedling survival (Castro et al., 2010). In this context, perches used by birds had between 40% and 60% of woody cover below them. This suggests that birds deposit seeds in microsites where vegetation cover 'facilitates' seedling survival (Wenny 2001; Cavallero et al., 2012). Several authors reported that the benefit produced by natural perches (as recolonization hot spots in disturbed sites) is lost when these structures are not combined with vegetation or other structures such as woody debris which facilitate seedling survival (Holl 1998; Shiels and Walker 2003; Zanini and Ganade 2005). Therefore, birds favored recolonization of burned areas using resprouting species as perches and depositing the seeds in microsites with greater survival probability. Consequently, the combined effect of different plant–animal (i.e., mutualistic seed dispersal) and plant–plant interactions (i.e., facilitation) is what ultimately promotes recolonization of disturbed areas.

4.3. Seed arrival and seedling survival per hectare

The maintenance of standing burned trees and shrubs could produce on average an input of 44,685 (±15,233) endozoochorous seeds/ha into burned areas through their use as perching structures by mobile-links (Appendix C). Moreover, considering that birds used perches that had between 40% and 60% of woody species cover underneath, on average 6044 (±5774) seedlings of endozoochorous species/ha could be recruited below perches (Appendix C). However, natural seedling occurrence was lower

(4236 ± 993 endozoochorous seedlings/ha), indicating that other effects not considered in this study (e.g., density and diversity of frugivores, annual fruit and seed production, seed predation, pathogen attack, seedling emergence, herbivory, and competition) would decrease the number of seedlings effectively recruited via the perch effect. However, the 30% difference between estimated and recorded seedling recruitment indicate that the perch effect by itself can explain most seedling establishment of endozoochorous species.

Finally, three perch-species had a considerably high effect on seed rain and seedling recruitment (i.e., *Au. chilensis*, *L. hirsuta*, and *S. patagonicus*; Appendix C). The high preference of birds for the anemochorous trees (i.e., *Au. chilensis* and *L. hirsuta*) could be due to their large size, providing structural complexity in mostly denuded areas after fire (McDonnell and Stiles 1983; Hutto 1995; Carlo and Aukema 2005). In contrast, the great effect of the endozoochorous small tree (i.e., *S. patagonicus*) on seedling recruitment could be related to its great abundance and wide distribution (see Figs. 3 and 4). The high effect of anemochorous and endozoochorous trees on seed rain and seedling recruitment, suggests that standing burned woody vegetation is a key resource during the early post-fire recovery process.

4.4. Conclusions

Frugivorous birds could be considered as landscape architects because their activity determines in part, vegetation recovery in disturbed habitats (Howe and Miriti 2004). Our results show that birds acted as mobile-links transferring seeds of fleshy-fruited species across the landscape. Standing burned trees and shrubs were used as natural perches by frugivorous birds, acted as seed traps for wind dispersed seeds, and facilitated the survival of seedlings spatially associated with them, thereby promoting woody species recolonization. Therefore, standing burned trees and shrubs are a key structural component during the early post-fire regeneration of the studied *Au. chilensis* and *N. antarctica* forests. Therefore, the maintenance of standing woody vegetation favored passive restoration of those burned areas. Consequently, post-fire logging could limit early recovery (<10 years after fire) of forests of northwestern Patagonia.

Acknowledgments

We thank National Parks Administration (APN) by allowing us to work in the Nahuel Huapi National Park. We also thank Dardo López, Alejandra Lostaunau, Manuel de Paz, Santiago Quiroga and Silvia Castañeda for helping in the field and in the laboratory. Eugene Schupp, Tomás Carlo, Enrique Chaneton, Leonardo Galetto, Florencia Urretavizcaya, and two anonimous reviewers provided valuable comments and suggestions on an earlier draft. This study was funded by The Rufford Maurice Laing Foundation (RSG 28.11.07). Laura Cavallero acknowledges a PhD. fellowship from CONICET.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.10.004.

References

Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol. Evol. 14, 273–277.

Aizen, M.A., Ezcurra, C., 1998. High incidence of plant–animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance. Ecología Austral 8, 217–236.

Andrade Melo, V., Jackson Griffith, G., De Marco Junior, P., Silva, E., Lopes de Souza, A., Carneiro Guedes, M., Faria Ozório, T., 2000. Efeito de poleiros artificiais na dispersão de sementes por aves. Revista Arvore 24, 235–240.

Armesto, J.J., Díaz, I., Papic, C., Willson, M.F., 2001. Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloé island, Chile. Austral Ecol. 26, 311–320.

Barros, V., Cordón, V., Moyano, C., Méndez, R., Forquera, J., Pizzio, O., 1983. Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén. Universidad Nacional del Comahue, Cinco Saltos, Neuquén, Argentina.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire management on forested public lands of the western United States. Conserv. Biol. 18, 957–967.

Bustamante, R.O., Simonetti, J.A., Mella, J.E., 1992. Are foxes legitimate and efficient seed dispersers? A field test. Acta Oecol. 13, 203–208.

Carlo, T.A., Aukema, J.E., 2005. Female-directed dispersal and facilitation between a tropical mistletoe and a dioecious host. Ecology 86, 3245–3251.

Carlo, T.A., Yang, S., 2011. Network models of frugivory and seed dispersal: challenges and opportunities. Acta Oecol. 37, 619–624.

Castro, J., Allen, C.D., Molina-Morales, M., Maranón-Jiménez, S., Sánchez-Miranda, A., Zamora, R., 2010. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. Restor. Ecol. 19. http://dx.doi.org/10.1111/j.1526-100X.2009.00619.x.

Cavallero, L., Aizen, M.A., Raffaele, E., 2012. Endozoochory decreases environmental filtering imposed to seedlings. J. Veg. Sci. 23, 677–689.

Cavallero, L., Raffaele, E., 2010. Fire enhances the 'competition-free' space of an invader shrub: *Rosa rubiginosa* in northwestern Patagonia. Biol. Invasions 12, 3395–3404.

Charnov, E.L., 1982. The Theory of Sex Allocation. Princeton University Press, New Jersey.

Damascos, M.A., Arribere, M., Svriz, M., Bran, D., 2008. Fruit mineral contents of six wild species of the north Andean Patagonia, Argentina. Biol. Trace Elem. Res. 125, 72–80.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311, 352.

Gallopín, G., 1978. Estudio ecológico integrado de la cuenca superior del Río Manso (Río Negro, Argentina). Descripción general de la Cuenca. In: Anales de Parques Nacionales. Administración de Parques Nacionales, pp. 251–255.

García, D., Zamora, R., Amico, G.C., 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conserv. Biol. 24, 1070–1079.

Gimenez Gowland, M.B., 2000. Flora nativa norpatagonica ilustrada. Instituto Nacional de Tecnología Agropecuaria – Fundación Vida Silvestre Argentina – Administración de Parques Nacionales, Bariloche.

Gómez-Aparicio, L., Valladares, F., Zamora, R., Quero, J.L., 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28, 757–768.

Gómez-Aparicio, L., Zavala, M.A., Bonet, F.J., Zamora, R., 2009. Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. Ecol. Appl. 19, 2124–2141.

Herrera, C.M., 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55, 250–262.

Herrera, C.M., Jordano, P., López-Soria, L., Amat, J.A., 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecol. Monogr. 64, 315–344.

Holl, K.D., 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restor. Ecol. 6, 253–261.

Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. Bioscience 54, 651–660.

Hutto, R.L., 1995. Composition of bird communities following stand replacement fires in northern Rocky mountain (USA) conifer forests. Conserv. Biol. 9, 1041–1058.

Jacobs, J., 1974. Quantitative measurement of food selection. Oecologia 14, 413–417.

Kitzberger, T., Veblen, T.T., 1999. Fire-induced changes in northern Patagonian landscapes. Landscape Ecol. 14, 1–15.

Kitzberger, T., Steinaker, D.F., Veblen, T.T., 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81, 1914–1924.

Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20, 949–958.

Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. Ecosystems 6, 87–98.

Marañón-Jimenez, S., Castro, J., Kowalski, A.S., Serrano-Ortiz, P., Reverter, B.R., Sánchez-Cañete, E.P., Zamora, R., 2011. Post-fire soil respiration in relation to burnt wood management in a Mediterranean mountain ecosystem. For. Ecol. Manage. 261, 1436–1447.

McClanahan, T.R., Wolfe, R.W., 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conserv. Biol. 7, 279–288.

McDonnell, M.J., Stiles, E.W., 1983. The structural complexity of old field vegetation and the recruitment of bird–dispersed plant species. Oecologia 56, 109–116.

Medellín, R.A., Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica 31, 478–485.

Morissette, J.L., Cobb, T.P., Brigham, R.M., James, P.C., 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Can. J. For. Res. 32, 2169–2183.

Mueller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, Inc., New York–London–Sydney–Toronto.

Putfarken, D., Dengler, J., Lehmann, S., Hardtle, W., 2008. Site use of grazing cattle and sheep in a large-scale pasture landscape: a GPS/GIS assessment. Appl. Anim. Behav. Sci. 111, 54–67.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, United Kingdom.

R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, N., 1989. Dispersal of misteltoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology 70, 137–145.

Reiter, J., Curio, E., Tacud, B., Urbina, H., Geronimo, F., 2006. Tracking bat-dispersed seeds using fluorescent pigment. Biotropica 38, 64–68.

Rey, P.J., Alcántara, J.M., 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J. Ecol. 88, 622–633.

Santos, E.F., Setz, E.Z.F., Gobbi, N., 2003. Diet of the maned wolf (*Chrysocyon brachyurus*) and its role in seed dispersal on a cattle ranch in Brazil. J. Zool. 260, 203–208.

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Tansley review: seed dispersal effectiveness revisited: a conceptual review. New Phytol. 188, 333–353.

Shiels, A.B., Walker, L.R., 2003. Bird perches increase forest seeds on Puerto Rican landslides. Restor. Ecol. 11, 457–465.

Silva, S.I., Bozinovic, F., Jaksic, F.M., 2005. Frugivory and seed dispersal by foxes in relation to mammalian prey abundance in a semiarid thornscrub. Austral Ecol. 30, 739–746.

Veblen, T.T., Kitzberger, T., Raffaele, E., Lorenz, D., 2003. Fire history and vegetation changes in northern Patagonia, Argentina. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York, pp. 265–295.

Walker, L.R., del Moral, R., 2009. Transition dynamics in succession: implications for rates, trajectories and restoration. In: Hobbs, R.J., Suding, K.N. (Eds.), New Models for Ecosystem Dynamics and Restoration. Island Press, Washington, pp. 33–49.

Wenny, D.G., Levey, D.J., 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proc. Nat. Acad. Sci. 95, 6204–6207.

Wenny, D.G., 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evol. Ecol. Res. 3, 51–74.

Wunderle, J.M., 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 223–235.

Zanini, L., Ganade, G., 2005. Restoration of Araucaria forest: the role of perches, pioneer vegetation, and soil fertility. Restor. Ecol. 13, 207–514.