



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

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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.

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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 persis-

tence 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

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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 below 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 Cathedral Mount (41° 12' 06" S, 71° 26' 17" W; 1150 m.a.s.l.). Mean annual precipitation is approximately 1000 mm at Gutiérrez Lake and Cathedral 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* (patagonian 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

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