

The role of mutualistic interactions on post-fire recolonization: **BIRDS AS MEDIATORS OF ECOLOGICAL RESTORATION IN FORESTLANDS OF NORTHWESTERN PATAGONIA, ARGENTINA.**

Introduction

Fire has been the dominant disturbance of forestlands of northwestern Patagonia (Kitzberger & Veblen, 1999). After fire, many species have the ability of resprouting and vegetative multiplication (Rundell 1981, Mooney & Miller 1985, Fuentes et al. 1994, Raffaele & Veblen 1998, Keeley 2000). After resprouting, populations maintain the same (or even less) genetic variability they had before fire. But, recolonization of burned areas by vegetative multiplication can diminish genetic diversity of those populations. This occurs because only those individuals adapted to this disturbance can reproduce vegetatively and generates individuals with the same genotype (clones). Although better adapted genotypes proliferate, populations loose their ability to respond to future disturbances and stochastic climate variations, resulting in drastic consequences to perpetuation of native populations (Fischer et al. 2000, Dorken & Eckert 2001, Krutovskii & Neale 2001, Klekowski 2003, Carranza Almansa 2002, Leimu et al. 2006).

In recently burned areas, reproductive fitness is higher, where high availability of light and soil nutrients is found (Verboom et al. 2002, Wrobleski & Kauffman 2003, Paritsis et al. 2006). This situation has great importance because creates opportunities for sexual reproduction. This increases genetic variability, favouring genic flow in between neighbouring populations due to crossed polinization, seed dispersal, etc.

Standing dead trees are used by birds as perching structures in burned areas, increasing seedling recruitment beneath them. In Patagonian National Parks it is allowed timber harvest from dead standing trees which may limit natural recolonization of burned areas through sexual reproduction.

The results presented here have two approaches and therefore are showed in separate sections as follows:

PART I- SPATIAL HETEROGENEITY RECONSTRUCTION OF THE POST-FIRE RECOLONIZATION OF COMMUNITIES OF DIFFERENT POST-FIRE AGE OF NORTHWESTERN PATAGONIA

Materials and Methods

The study area encompassed Nahuel Huapi and Lanin National parks and to the south the area of El Bolsón (approximately 780000 ha). Within this area, 20 communities of different post-fire age (from less than 1 year to 180 years) were sampled (Figure 1). In each community 2 crossed transects of 300 meters length were carried out. In each transect the following variables were recorded:

-Spatial patterns of plant cover, at 1m intervals, with line intercept method, to estimate mean size patch of vegetation. Each transect has in total 300 points of vegetation cover and each community has 600 points in total. To determine plant cover, the vertical space was divided in three stratums: low (from 0 to 2m height), middle (from 2 to 10m height) and high (more than 10m height).



-Spatial patterns of light heterogeneity were determined with hemispherical photographs, and spatial patterns of temperature and relative humidity with a pocket weather station. Those environmental variables were recorded at 5m intervals (60 registers per transect, 120 per community).

-Number of seedlings and young shoots originated by vegetative multiplication of each woody species were recorded in $1m^2$ plots, at 5m intervals ($60m^2$ per transect, $120m^2$ per community).

Main Results

1- Plant Cover and patch sizes:

Along the sampled post-fire age gradient (0-180 years) plant cover increased gradually from 1 stratum (low) to 3 stratums of 40m of maximum height in a mature forest (Figure 2).

Mean vegetated patch size also increased with the post-fire age (Figure 3). A significant change in the mean patch size is observed from post-fires of 25 years. This may be revealing that significant changes in the vegetation structure could be occurring since the previously mentioned age. Therefore, in this report post-fire ranging between 0 and 16 years will be called *"early post-fires"*.

Deepening into patch sizes along the gradient it could be seen the following pattern: postfire recovery starts with numerous small patches, then the patch number decreases and the size increases with age, and finally a mature forest has a few big patches (Figures 4 and 5).

2- Environmental heterogeneity:

Environmental heterogeneity was assessed taking into account the Coefficient of Variation (CV%) of the temperature and relative humidity recorded along each transect. A CV was obtained for each transect and the two CVs obtained per community were averaged.

Besides, temperature and relative humidity were integrated adapting an Aridity Index (Martonne): $I_a = RH$ (%) / T (°C). The Aridity Index was calculated for each point of the transect and a CV was calculated for each transect to asses heterogeneity. The two CVs of each transect were averaged too.

In contrast with the patch size, environmental heterogeneity (CV of environmental variables recorded) decreases along the post-fire age gradient (Figure 6). This indicates that early post fires are more heterogeneous (more extreme) from an environmental perspective than intermediate and old post-fires. This could be related with the patch size and number. Communities with numerous small patches are more heterogeneous than communities with a few big patches.

3- Regeneration strategies:

To evaluate the main regeneration strategy of the dominant sprouting species, an index varying between 1 and -1 (adapted of lvlev's electivity index, Putfarken et al. 2008) was calculated for two functional groups: short (less than 2m height) and large (more than 2m height) woody species and each of the communities considered early post-fires (from 0 to 16 years). The index was calculated based on the data recorded on the seedling and sprouting censuses of $1m^2$ at 5m intervals along each transect. There are three possibilities to interpret the Regeneration Index:



* If Regeneration index = 1 \rightarrow All the individuals of a certain species found in a community are seedlings.

* If Regeneration index = -1 \rightarrow All the individuals of a certain species found in a community are sprouts.

* If Regeneration index = $0 \rightarrow$ The same proportions of seedlings and sprouts of a certain species are found in the community.

The results of the Regeneration Index are indicating that at beginning, the recolonization occurs mainly by resprouting (Figure 7). While post-fire age increases seedling strategy increases. Moreover, in large woody species the proportion of seedlings is greater than the proportion of sprouts from 5 years and henceforth (Figure 7). This could be indicating that perch effect of dead standing trees is significant from 5 years and henceforth.

To summarize, a global Regeneration Index was calculated for each species considering the data recorded in the 20 sampled communities (Figure 8). Main sprouting species registered sexual reproduction (seedlings recruitment). Specifically, the global Regeneration Index could be indicating that in the short woody species vegetative multiplication through sprouting is the main regeneration strategy. In contrast, in large woody species invest more in sexual reproduction than in vegetative multiplication.

Taking into account the total seedling density (N° of seedlings/m^{2}) and the seedling density of fleshy fruited species (Figure 9), it could be seen that species tend to reproduce sexually during the early stages of recolonization after fire (until 40 years of post-fire age), thereby indicating that perch effect of dead standing trees is significant in early post-fires through seed dispersal by birds (Figure 9, red circles).

4- Relationships between woody species dispersed by different vectors:

All woody species found in each community were classified considering its seed dispersal vector according to Aizen & Ezcurra (1998). Seed dispersal categories are: W (wind dispersed seeds), E (endozoochorus, animal dispersed seeds), M (multiple dispersing vectors) and G (gravity dispersed seeds). In the 20 communities sampled, the most dominant categories were W and E. Therefore, an index varying between 1 and -1 (adapted of lvlev's electivity index, Putfarken et al. 2008) was calculated for each community taking into account woody species plant cover at 1m intervals and seedling number at 5m intervals. There are three possibilities to interpret the E/W index:

* If E/W index = 1 \rightarrow All the adults or the seedlings in the community are species dispersed by endozoochory.

* If E/W index = -1 \longrightarrow All the adults or seedlings in the community are dispersed by wind.

* If E/W index = 0 \rightarrow The same proportions of individuals E and W are found in the community.

Not only for the adults cover, but also for the seedling number, the E/W index decreases as the post-fire age increases (Figure 10, top).

The E/W Index shows an abrupt decrease at approximately 16 years of age (Figure 10, bottom) indicating that endozoochorus dispersal is significant in early post-fires. Therefore, animal dispersed species are highly important in the early stages of post-fire recolonization. These first results are indicating that the role of birds as mediators of ecological restoration is significant during the first 16 years after fire.



PART II: BIRDS AS MEDIATORS OF ECOLOGICAL RESTORATION IN FORESTLANDS OF NORTHWESTERN PATAGONIA, ARGENTINA.

Materials and Methods

During November 2008, 450 seed traps were installed in 3 communities burned in 1999: A^o Blanco, Balcón del Gutierrez y Frey (150/community). Seed traps were constructed of plastic mesh of 0.5m x 0.5m with four wire stakes of 0.5m. Each seed trap has an area of 0.25m² and the total area of seed traps represent an area of 112.5m². In each community seed traps were arranged in a paired design: 75 were installed below perches, to evaluate the perch effect of dead standing trees in post-fire recolonization, and 75 were placed in bare soil. Seed traps were revised three times during summer at the end of January, February and March. Percentage of plant cover was measured around each seed trap to asses the degree of plant cover preferred by birds.

At the same time, bird censuses were performed when seed traps were revised, to assess bird species richness in each site.

During January 2009, 150 seedlings of *B. buxifolia* and 200 seedlings of *R. magellanicum* (two main species in post-fire recolonization) were transplanted in a field essay placed in a community burned in 1996. Seedlings were planted in two different microsites (bare soil and below shrubs) with herbivore exclosures. This essay was installed to evaluate which microsite is suitable for the seedling's recruitment and thus test if birds are efficient seed dispersers (depositing seeds in safe microsites for germination and recruitment).

Finally, collected samples were analyzed on the lab and seeds coming from bird feces were separated of the rest of seed captured by the trap.

Main Results

1- Bird censuses:

On average a total of 13 (± 2.5) bird species were observed in the sampled communities. The two main frugivores found in the three communities are *Elaenia albiceps* (fio fio) and *Turdus falcklandii* (zorzal), representing a 15% of the total species richness (Figure 11) (Amico & Aizen 2005). However, 22% of the total species richness is represented by 6 bird species that are partial frugivores (*Colaptes patio, Campephilus magellanicus, Pteroptochos tarnii, Scelorchilus rubecula, Troglodytes aedon* and *Upucerthia dumetaria*) (Amico & Aizen 2005, Christie et al. 2004). Therefore, a 37% of the total richness is represented by frugivores.

2- Seedling transplants

The response of species to different microsites was species specific. However, nurse effect of shrubs was significant for both species. For *B. buxifolia* 41.25% \pm 10.8 (mean \pm standard error) of seedlings survived bellow shrubs, while only 6.75% \pm 4.0 survived in bare soil. For *R. magellanicum* 6% \pm 2.0 survived bellow shrubs while no one survived in bare soil. These results are indicating that birds are efficient seed dispersers, depositing seeds in safe microsites where seedling recruitment are high.

3- Dead standing trees as perching structures in the post-fire recolonization



Perch effect was significant. During the whole field sampling season, 2980 seeds were captured in total, however 40% (1064 seeds) of the captured seeds were bird dispersed (Figure 12). Of the 1064 bird dispersed seeds, 84% was found in seed traps located below perches of dead standing trees.

Seed number per m² was 6.85 in seed traps located in bare soil and 11.5 in seed traps located below perches (Figure 13). In both treatments, seed numbers per m² dispersed by other vectors are similar. However, the percentage of bird dispersed seeds is significantly higher in seed traps located below perches (47%) than in seed traps located in bare soil (10%).

The proportion of seed traps with bird feces was significantly higher in traps located below perches, thereby indicating a significant perch effect of dead standing trees in post-fire recolonization (Figure 14). Perch effect was significant during the whole sampling season (Figure 14).

Finally, a Perch Selectivity Index (PSI) (based on Ivlev's electivity index, Putfarken et al. 2008) was calculated to asses the species perch preference by seed dispersing birds. The PSI takes into account three main variables:

-Perch availability of each species in the sampled community;

-N° of perches of each species that had seed traps below;

 $-N^{\circ}$ of perches of each species that were used by birds as perching sites and therefore capture bird feces with fleshy fruits seeds.

There are three possibilities to interpret the PSI:

* If PSI = 1 \rightarrow Birds are selecting the species as preferred perch, even though the availability of perches of this species is scarce.

* If PSI = -1 \rightarrow Birds does not seek this perch species, although it is abundant in the community.

The PSI shows that there are two kinds of perches being selected by birds (Figure 15). The first kind is related with feeding behaviour of frugivore birds and is reflected in perch species that have fleshy fruits. Therefore, birds use that perches because they seek fruits, thereby defecating seeds not only of the same species buy also of another species. The second kind of perches are related with another type of behaviour as reproduction, awareness, communication, etc. This kind of perching species does not have fleshy fruits and are represented by large species that are very important for commercial purposes as hard timber (*A. chilensis* and *L. hirsuta*) and firewood (*N. anctartica*) extraction. PSI of these species is higher than PSI of the fleshy fruited species, indicating that big size species develop a key role as perching structures of frugivore birds. With the second kind of perches arise the conflict between post-fire recovery and timber harvest for the subsistence of local communities.



Concluding remarks

Along this study I could understand the recover dynamics of post-fire communities.

The three most important outcomes of my project are:

- Birds develop a key role as mediators of ecological restoration post-fire communities, promoting seed flow between neighbouring communities.

- Seedling recruitment process of bird dispersed species occurs mainly during the early post-fire recolonization (specifically in this work occurs in communities between 5 and 20 post-fire age).

- Large tree species play an important role as perching structures for frugivore birds during the early recolonization after fire, thereby increasing seedling recruitment beneath them.

Considering these results I could recommend that timber harvest should be allowed between 15 and 20 years after fire had occurred. Nevertheless, there are many things that still remain unknown and are essential for management policies construction:

- Can perch availability and/or key species seedling density can be used as sustainability indicators of theses ecosystems?
- Which consequences have to harvest all timber coming from dead standing trees after 16 years that fire occurred?
- Which percentage of timber can be harvested without negatively affecting postfire recovery?
- If fallen trees generate natural exclosures that protect natural regeneration of grazing by exotic herbivores. Should its harvesting be allowed?

In a global change context, where ecosystems should adapt to constant and new disturbances, the role of birds is essential to maintain and even increase genetic diversity of these communities.

Finally, dead trees have a key function in post-fire recovery and play different roles depending on its position (vertical or horizontal) on the ecosystem. These roles vary from the generation of perching structures and therefore seedlings recruitment sites beneath them through seed dispersal by birds, passing through the generation natural exclosures that protect regeneration from grazing by exotic herbivores until the input of organic matter to the ecosystem through its decomposition.

Concluding, it is important to understand how dead individuals are fundamental to maintain ecosystems dynamics and its recover capacity to different disturbances (keep its resilience):

"Surprisingly, dead individuals can preserve life..."



Literature Cited

- AIZEN, M.A. & EZCURRA, C. 1998. "High incidente 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.

- AMICO, G.C. & AIZEN, M.A. 2005. "Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién?. Ecología Austral, 15: 89-100.

- CARRANZA ALMANSA, J. 2002. "La evolución del sexo". En: "Evolución: La base de la biología" (ed. Soler M.) pp: 177-191. Proyecto Sur de Ediciones, S.L., España.

- CHRISTIE, M.I.; RAMILO, E.J. & BETTINELLI, M.D. 2004. "Aves del Noroeste Patagonico". L.O.L.A., Buenos Aires, Argentina.

- DORKEN, M.E. & ECKERT, C.G. 2001. "Severly reduced sexual reproduction in northern populations of a clonal plant, Decodon verticillatus (Lythraceae)". Journal of Ecology, 89: 339-350.

- FISCHER, M.; VAN KLEUNEN, M. & SCHMID, B. 2000. "Genetic Allee effects on performance, plasticity and developmental stability in a clonal plant". Ecology Letters, 3: 530-539.

- FUENTES, E.R.; SEGURA, A.M. & HOLMGREN, M. 1994. "Are the responses of matorral shrubs different from those in an ecosystem with a reputed fire history?". In: "The role of fire in Mediterranean-type ecosystems" (eds. Moreno, J.M. & Oechel, W.C.), pp 16-25. Springer-Verlag, New York.

- KEELEY, J.E. 2000. "Chaparral". In "North American terrestrial vegetation" Second Edition (eds. Barbour, M.G. & Dwight Billings, W.), pp 203-225. Cambridge University Press, Cambridge, United Kingdom.

- KITZBERGER, T. & VEBLEN, T.T. 1999. "Fire induced changes in northern Patagonia landscapes". Landscape Ecology 14: 1-15.

- KLEKOWSKI, E.J. 2003. "Plant clonality, mutation, diplontic selection and mutational meltdown". Biological Journal of the Linnean Society, 79: 61-67.

- KRUTOVSKII, K.V. & NEALE, D.B. 2001. "Forest Genomics for Conserving Adaptive Genetic Diversity". Documentos de Trabajo de Recursos Genéticos Forestales, Documento de Trabajo RGF/3, Servicio de Desarrollo de Recursos Forestales, Dirección de Recursos Forestales. FAO, Roma

- LEIMU, R.; Mutikainen, P.; Koricheva, J. & Fischer, M. 2006. "How general are positive relationships between plant population size, fitness and genetic variation?". Journal of Ecology, 94: 942-952.

- MOONEY, H.A. & MILLER, P.C. 1985. "Chaparral". In: "Physiological ecology of North American plant communities" (eds. Chabot, B.F. & Mooney, H.A.), pp 213-231. Chapman and Hall, New York.

- PARITSIS, J.; RAFFAELE, E. & VEBLEN, T.T. 2006. "Vegetation disturbance by fire affects plant reproductive phenology in a shrubland community in northwestern Patagonia, Argentina". New Zealand Journal of Ecology 30: 387-395.

- PUTFARKEN, D.; DENGLER, J.; LEHMANN, S. & HA[¬]RDTLE, W. 2008. "Site use of grazing cattle and sheep in a large-scale pasture landscape: A GPS/GIS assessment". Applied Animal Behaviour Science, 111: 54–67.



- RAFFAELE, E. & VEBLEN, T.T. 1998. "Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina". Journal of Vegetation Science, 9: 693-698.

- RUNDEL, P.W. 1981. "The matorral zone of central Chile". In: "Mediterranean-type shrublands" (eds. di Castri, F.; Goodall, D.W. & Specht, R.L.), pp 175-201. Elsevier Scientific Publishing Company. Netherlands.

- VERBOOM, G.A.; STOCK, W.D. & LINDER, H.P. 2002. "Determinants of postfire flowering in the geophytic grass Ehrharta capensis". Functional Ecology, 16: 705-713.

- WROBLESKI, D.W. & KAUFFMAN, J.B. 2003. "Initial effects of prescribed fire on morphology, abundance and phenology of forbs in Big Sagebrush communities in southeastern Oregon". Restoration Ecology, 11: 82-90.