

THE ROLE OF BIRDS AND MICROSITES IN THE REGENERATION OF SOUTH-  
TEMPERATE RAINFOREST

By

MICHAEL P. MILLESON

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Michael P. Milleson

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By

Michael P. Milleson

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Chair: Kathryn E. Sieving

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Determining the mechanisms of arrested succession at restoration sites can influence understanding and management of landscape scale patterns and processes. On Isla Grande de Chiloé, a large continental island in southern Chile, conversion of south-temperate rainforest to pasture is occurring at a high rate. In some cleared sites agricultural activity cannot be implemented due to invasion of persistent shrub fields comprised of *Baccharis spp.*, a scrubby bush in the Asteraceae. *Baccharis*-dominated fields serve no economic purpose and are of limited use to wildlife. If they could be restored to native forest then landowners and endangered endemic wildlife species would accrue greater benefit. The goal of this study was to identify the relative importance of two likely limitations on natural regeneration of native forest in *Baccharis*-invaded sites on Isla Grande de Chiloé, Chile.

I tested two alternative hypotheses for arrested succession in my system: that shrub fields persist because of lack of seed dispersal, and lack of appropriate substrates for seed

germination and seedling establishment. In chapter 1 I present findings of field studies (experiments and comparative observations) showing that both ample seed dispersal and provision of suitable germination sites must occur to increase the rate of forest regeneration in *Baccharis*-dominated shrub fields. Sites with few or scattered trees received significantly less avian seed-disperser visitation than did sites with more than approximately 30 trees/ha or with trees in clumps of several individuals. Additionally, substrate types with the greatest seedling density were the rarest of the substrates available.

In the second chapter, I develop a dynamic systems model that incorporates processes actuating both hypothesized mechanisms of arrested succession to address realistic scenarios for restoration given constraints and goals relevant to local landowners. I use field data and findings reported in the literature to parameterize the model. Based on the model, the following suggestions are made. First, areas selected for forest regeneration should be adjacent to mid-successional or old growth forest stands in order to ensure sufficient avian seed dispersal. Second, the focus should be on providing sufficient germination substrates and making the field attractive to avian dispersers. The model also showed that given both avian seed dispersers and suitable germination sites, the most important deterrents to forest succession are the competitive effects of *Sphagnum* and *Baccharis* cover in the fields. Finally, the model demonstrates how these deterrents to regeneration can be overcome simply by planting a few trees each year in old fields that have minimal germination sites – a realistic recommendation given landowner constraints.

CHAPTER 1  
AVIAN SEED DISPERSER ACTIVITY AND AVAILABILITY OF GERMINATION  
SUBSTRATE IN *BACCHARIS*-DOMINATED OLD-FIELDS IN SOUTHERN CHILE

**Introduction**

A common goal of ecological restoration is to quicken the natural pace of secondary succession (Hobbs & Norton 1996). However, in cases of arrested succession, when a damaged or degraded ecosystem does not return to the original state (Brown & Lugo 1994), the causes of the arrest must first be identified and removed, if possible, before secondary succession can proceed (Parker 1997). Three general types of factors can cause arrested succession. Sites can be colonized by species that inhibit the growth or spread of species more characteristic of the desired ecological state (Connell & Slatyer 1977); abiotic factors pushed outside the local species' ranges of tolerance by the disturbance can prevent establishment by representative colonizers (Milchunas & Lauenroth 1995); or, finally, disturbance can bring about conditions (biotic or abiotic) that favor the influx of an entirely different set of species to the site (Suding & Goldberg 2001).

Determining the mechanisms of arrested succession at small scales can influence understanding and management of larger landscape scale patterns and processes (Bell et al. 1997). Once succession becomes arrested, site characteristics may change considerably, pushing the site over a threshold toward the "basin of attraction" of an alternate state (Laycock 1991; Lewontin 1969). When undesirable alternate stable states arise in landscapes, restoration ecological approaches can be used to identify and release

the mechanisms that generate and maintain them. The goal of this research was to identify mechanisms that may be inhibiting forest succession in previously cleared fields in the Valdivian temperate rainforest region of southern Chile. The persistent shrub fields that may develop following clearing of Chilean temperate rainforest can occupy significant areas (30% or more in regions where forest clearing is advanced) and provide little to no ecological or economic productivity (Gude, 2000; personal observation). Therefore, these persistent shrub fields are manifest as an undesirable alternate ecosystem state at the landscape scale. In this study I examine alternative causes of arrested forest succession at a community-scale, in shrub fields at forest edges, with the goal of identifying factors maintaining persistent shrub lands that, via restoration work, could be released or altered to allow forest succession to proceed.

### **Chilean South-temperate Rainforest**

The South temperate rainforest of the Valdivian region of Chile (35°- 48° S) receives between 1,000 and 6,000 mm of rain per year, and is characterized by emergent evergreen broad-leaved trees (e.g., *Nothofagus oblique*, *N. alpina*, and *N. dombeyi*) and conifers (e.g., *Podocarpus nubigena*). Typical canopy and understory species include *Drimys winterii*, *Weinmannia trichosperma*, and several trees in the family *Myrtaceae* (Willson et al. 1994). Endemism is very high (Stattersfield et al. 1998), ranging from 45% in vertebrates to 90% in seed plants (Armesto et al. 1996; Villagran & Hinojosa 1997). The typical disturbance regime is characterized by periodic catastrophic disturbances such as earthquakes, volcanic activity, and fire. Windthrow and treefall gap creation are common occurrences (Veblen 1979). This disturbance regime prevents shade tolerant tree species such as *Laurelia philippiana* and *Saxegothea conspicua* from out-competing the shade intolerant *Nothofagus* (Bustamante & Armesto 1995). Due to

human settlement and agricultural land uses, much of the remaining Valdivian rainforest exists as fragmented patches in a matrix of pastoral, agricultural, and industrial forestry land uses, where increased gap creation, fire, and windthrow frequencies along forest edge have intensified disturbances in remaining forests (Willson & Armesto 1996). Forest clearing and associated human activities in remaining forest have resulted in global endangerment of endemic flora (Armesto et al. 1998) and fauna of the region (Stattersfield et al. 1998).

### **Disturbance, Arrested Succession, and Consequences**

On Isla Grande de Chiloé, a large continental island serviced by a system of ferries, forest conversion has been slower than on adjacent mainland (Rozzi et al. 2000) due to its greater economic isolation. Here, the rural life style is characterized by pasture creation (via tree cutting followed by fire) for milk and meat cows and sheep, by non-mechanized row crop production (oxen teams are often used to till the soil), and by fuel wood acquisition in the most accessible forest patches (Armesto et al. 1998). Large scale forestry (via clear-cutting) also occurs in the island's southern sectors, and plantations of pine and eucalyptus are increasing throughout Chiloé's rural landscapes (Armesto et al. 2001b). In rural communities, economic productivity for the people is partly determined by availability of pasture for livestock and wood fiber for cooking and building materials. This can be limited by the development of persistent shrub fields (dominated by *Baccharis magellanica*) following forest clearing that cannot be used for livestock or row crop production. Moreover, native forest succession does not occur readily in *Baccharis*-dominated sites.

While native forest frequently reinvades logged sites that are not further disturbed by fire, and in some agricultural old fields left fallow, *Baccharis* fields frequently

develop after forest clearing. It appears that *Baccharis* takes over especially where the water table may be higher than elsewhere, and significant soil inundation prevents establishment of both native trees (Bewley & Black 1982) and cultivars. The shrubs can be burned back but, without prohibitively expensive ditching and draining, fire alone does not often improve site utility for either agriculture or forest regeneration. *Baccharis* overstory may prevent establishment by forest tree species (Céspedes et al. 2002; Putz & Canham 1992), and is underused by the local avifauna (Gude, 2000). Therefore this shrub land formation is of low economic and ecological value, and it appears to be highly persistent. In the landscape of NE Chiloé, *Baccharis* fields comprise around 30% of the land cover and are virtually unused by native wildlife species (T. M. Darnell, K. E. Sieving, unpublished data). Since farmers that clear forest for pasture or wood products and get *Baccharis* development in the cleared area usually move to clear a different site, if available, I view these fields as a restoration priority. Regeneration of forest on arrested successional sites would provide wildlife habitat and at least minimal economic benefit (forest products) for people, and this might protect forest in other sites from additional clearing (Fig. 1). In this study I focused on understanding factors limiting natural forest regeneration in sites dominated by *Baccharis* shrubs.

#### **Alternative Hypotheses for Arrested Succession: Seed Dispersal vs. Germination Limitation**

Forest regeneration can be limited by several factors, including competition, lack of nutrients, irregular disturbance regime, or allelopathy (Brewer 2002; Connell & Slatyer 1977; Kirkman et al. 2004; Mallik 2003; Wilson & Shure 1993; Céspedes et al. 2002). While all of these factors likely play a role in creating and maintaining a state of arrested

succession, this study focuses on dispersal and germination due to their importance in this system (Armesto & Rozzi 1989; Papic & Armesto 2000).

### **Seed dispersal limitation**

Insufficient seed dispersal can limit opportunities for establishment and growth of diverse plant species and, thereby, reduce vegetative structural heterogeneity. Given that more than 70% of all trees, shrubs, and vines in the Valdivian rainforests are bird dispersed (Armesto & Rozzi 1989), access to *Baccharis* fields by frugivorous birds and their activities in them are likely to define many parameters of regeneration. In a study by Armesto et al. (2001a), only 10% of the fleshy fruits collected in seed traps placed in rainforest fragments reached the margins of the forest patch, suggesting that even fewer would reach beyond forest edges and into shrub fields. Moreover, since the principal seed dispersing birds are forest species (Willson et al. 1994), the absence of suitable habitat for them in cleared fields could contribute to arrested succession. Seed dispersal is important in this site if seeds are able to establish in open areas or if they are deposited on suitable microsites for germination (Howe & Mirti 2004).

Three possible factors have been identified that might make a site, such as an anthropogenic shrub field, unsuitable for use by frugivorous birds: a lack of perches, a lack of structural diversity, and a lack of food. Several studies have found that seed rain is positively correlated with vegetation that offers natural perching sites (Debussche & Isenmann 1994; Ferguson & Drake 1999; Harvey 2000; Kollman & Pirl 1995) and with the availability of manmade perches (but see Holl 1999; McClanahan & Wolfe 1993; McDonnell & Stiles 1983). In this study, I assessed the importance of natural (tree) perch availability in *Baccharis* fields on avian frugivore activity.

A lack of vegetative structural complexity may also result in decreased visitation to a site by seed dispersers. Holl (1998) and McDonnell and Stiles (1983) found that perches that are more complex received more seed rain. Cardoso da Silva, et al. (1996) also found a positive correlation between structural complexity and bird use of a site. Structural complexity, and its positive effect on bird use, is also increased when trees are found in close proximity to one another (Toh et al. 1999). Complex vegetative structure may appeal to birds for reasons such as increased cover and more diverse microhabitats. In sum, enhancing complexity in target degraded sites may be an important factor in restoration where bird dispersal is a central constraint on inputs of seeds. To address this aspect of seed dispersal limitation into shrub fields, I assessed the effect of simple natural perches (lone trees) versus more complex perching and cover for frugivorous birds, represented by clumps of trees.

A third factor limiting seed dispersal may be lack of food; fruiting vegetation in a restoration site can attract birds to make more visits during which they are more likely to defecate seeds. Although Holl (1998) found that using fruit as bait did not increase bird visitation, Cardoso da Silva, et al. (1996) found an increase in the use of an abandoned field when naturally occurring fruit resources were higher. Moreover, Slocum and Horvitz (2000) found greater seed dispersal beneath fleshy fruit producing trees in Costa Rica. Wunderle (1997) also suggests that, in general, the presence of fruit plays an important role in attracting seed dispersers. Thus, a potential consideration in restoration efforts is the availability of fruit to frugivores in the target sites. In this study, I addressed this possibility by assessing the relative influence of fruiting and non-fruiting trees in shrub fields on frugivore visitation and activity.

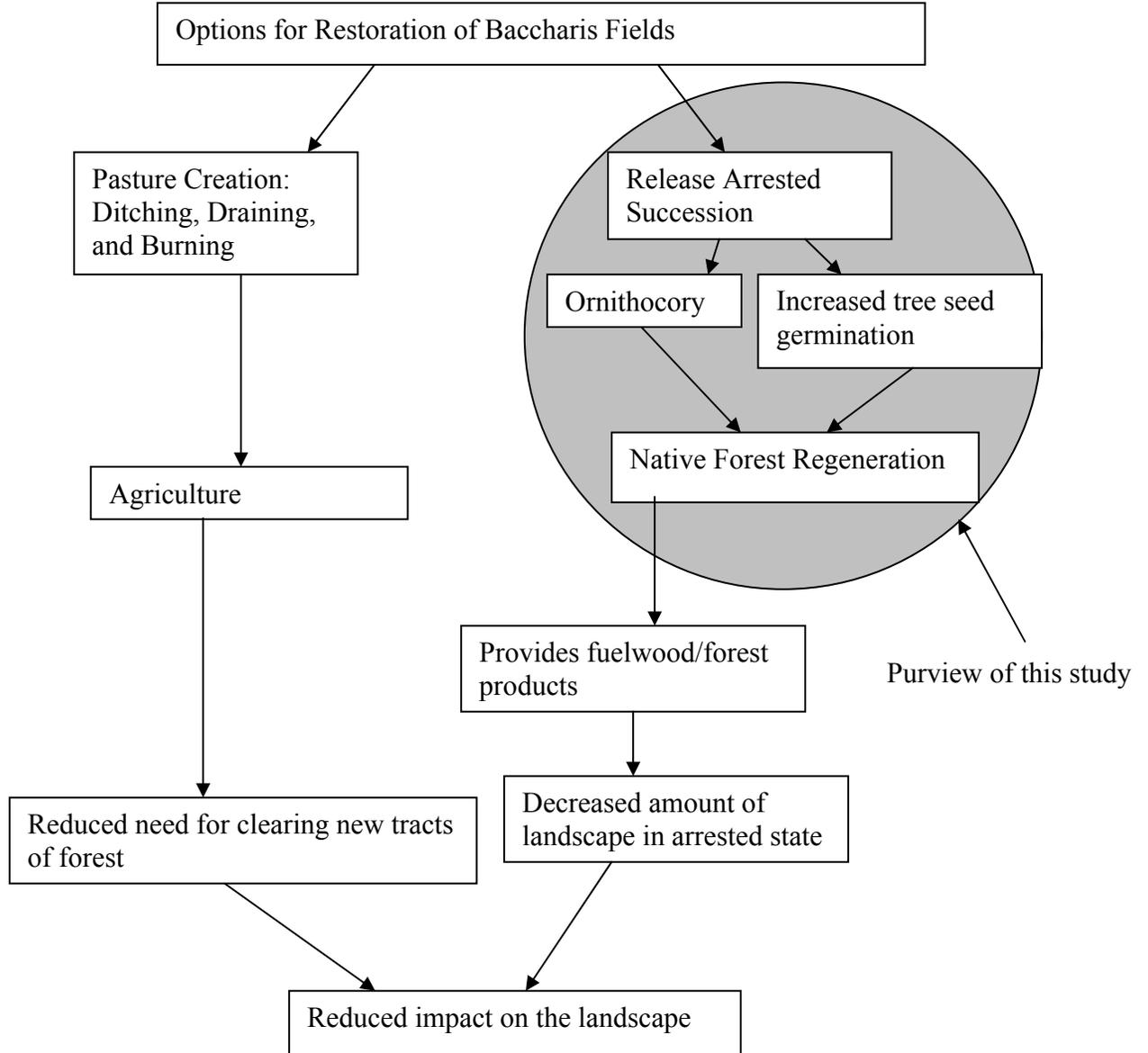


Figure 1. Conceptual model of options for use of an arrested successional site. The left path helps alleviate continued fragmentation pressure on temperate rainforests in S. Chile, but is expensive. The right path enhances regeneration of forest and wildlife habitat in areas that would otherwise have no wildlife or economic values. Both have the same end result from a landscape level perspective; however, fully identifying how to enhance regeneration is the purview of this study.

### **Seed germination and seedling establishment limitation**

Once successfully dispersed to a site, tree establishment and growth can be limited at various life stages. Germination of dispersed seeds can be prevented by physical characteristics of the microsite (insolation, moisture, litter depth, pH, etc.; Houle 1992; Peterson & Pickett 1990; Streng et al. 1989), and by seed predation (Hulme 2002). Other critical life-stages include the seedling and sapling stages, at which point plants are especially vulnerable to herbivory (Hanley 1998) and fungal attack (Rey & Alcantara 2000). In *Baccharis* fields, inundation, desiccation, and nutrient limitation may all affect seed germination. Year round surface water inhibits germination of most tree species (Bewley & Black 1982), and is likely to do so under the hydric conditions that characterize *Baccharis* fields (Papic & Armesto 2000). Moreover, as *Baccharis* becomes established in cleared sites development of a surface layer of *Sphagnum* is commonly observed (Ruthsatz & Villagran 1991) and could reduce germination of seeds in at least two ways. When *Sphagnum* accumulates in a disturbed site, it creates acidic and nutrient poor conditions that are known to exclude colonization by forest species (Van Breeman 1995, J. Armesto, K. Clark, pers. comm.). Seeds may also desiccate readily when deposited on top of *Sphagnum* mats, because while this lichen requires standing water to grow, the top layers can be well above available moisture (Van Breeman 1995).

It has been suggested that all of these extreme conditions limiting seed germination in hydric forests and old-fields can be alleviated by the availability of dead wood on the ground (Papic & Armesto 2000; Takahashi et al. 2000). Woody debris in *Baccharis* fields fluctuates less in water content relative to soils (Papic & Armesto 2000), and therefore, could ameliorate both low and high water stresses on seeds falling in bare ground or *Sphagnum*-laden sites. Moreover, large pieces of woody debris from tree

trunks (commonly called nurse logs) can collect organic debris, preventing nutrient limitations (Harmon et al. 1986). After germinating on dead wood, seedlings subsequently become established by growing down into the soil. With sufficient maturity attained while supported by nurse logs, tree seedlings/saplings of wet forest can then tolerate, and even alter conditions of the soil. In other wet temperate forest systems, conifer germination is largely dependent on the availability of nurse logs (Hofgaard 1993; Simard et al. 1998), and in northern hardwood forests, yellow birch and red spruce densities are 24 and 5 times greater, respectively, on nurse logs than on the forest floor (McGee & Birmingham 1997). In premontane Costa Rican pastures, four of the most common woody species were found significantly more often on logs than on surrounding microsites (Peterson & Haines 2000). In a temperate Chilean forest system, seedlings of eight tree species common to the forests of Chiloé, were found growing primarily on dead wood on the forest floor (Christie & Armesto 2003; Lusk 1995). Additionally, Papić and Armesto (2000) showed that survivorship of one-year-old seedlings of the five most dominant tree species found in the region is higher on woody debris in logged fields. Thus, it is likely that post-clearing fire applied by land owners in my study system reduces the availability of deadwood and that this is a limitation on germination success of seeds arriving into these fields.

### **Research Design**

I considered two potentially interacting hypotheses to better understand the processes inhibiting succession in south temperate old-fields and the potential for manipulating them during restoration to forest. The first hypothesis, that a lack of avian frugivore activity is limiting forest regeneration, is based on the possibility that a lack of perches, structural diversity providing cover, and/or a lack of food is making the

*Baccharis* fields unsuitable for use by frugivorous birds. Rather than use artificial perches, I conducted three comparative observational studies to examine the influence of naturally occurring variation in tree density and fruiting activity on bird activity at the scale of 0.5 ha old-fields. To test the second hypothesis, that the limited availability of suitable germination microsites is limiting forest regeneration, I conducted one comparative-observational study examining the relationship between the presence of seedlings on various substrates and the availability of these sites, and one experimental study examining germination rates on different substrates.

This study was conducted along forest/old-field boundaries at sites occurring over a 400-km<sup>2</sup> area. At the scale of my study plots, the phenomena of interest are localized bird movements, microhabitat choices (e.g., perches and feeding sites), and small-scale changes in substrate availability, which influence individual tree growth and distribution. At larger scales, other forces such as economics, large-scale disturbances, and patch context are operating to determine overall extent of forest versus other land uses in the regional landscape. But the purpose of this study was to examine small-scale processes potentially under the control of individual landowners seeking recommendations for managing their small parcels comprising the total area (*sensu* Hostetler 1999). Within the context of a given field, the study was conducted close to the forest edge because successional processes fostering forest intrusion into hydric fields (e.g., frugivore activity, seed fall, and deadwood accumulation) occur from the forest edge outward (Armesto et al. 2001a; Armesto & Rozzi 1989). Data generated here were used to identify limitations on seedling establishment and to parameterize a systems model for comparison of different forest restoration scenarios (Chapter 2).

### **Frugivore activity hypothesis**

Assuming that increasing frugivore activity correlates strongly with seed movement (Westcott & Graham 2000), I studied frugivore visitation rates to old-fields with varying numbers of trees (Debussche & Isenmann 1994; Ferguson & Drake 1999; Harvey 2000; Kollman & Pirl 1995), clusters versus single trees (Cardoso da Silva et al. 1996; Holl 1998; McDonnell & Stiles 1983; Toh et al. 1999), and fruiting versus non-fruiting trees (Cardoso da Silva et al. 1996).

I predicted that bird activity would be influenced by type (fruiting vs. non-fruiting), occurrence, and distribution (solitary vs. clumped) of trees in fields and proximity to forest. Specifically, I predicted that avian frugivore abundance would be greatest in old-fields with greatest numbers of remnant trees, that avian frugivores would be most often associated with clusters of trees rather than single trees, that avian frugivores would be more often associated with fruiting trees rather than non-fruiting trees, and that avian seed deposition would be greatest beneath trees.

### **Germination site hypothesis**

To test whether germination sites for forest trees are limiting in old fields, I surveyed fields for tree seedlings and identified 6 relevant micro-site types; beneath trees, coarse woody debris (CWD), CWD beneath a tree, beneath *Baccharis*, *Sphagnum*, and bare ground. I then surveyed fields for the availability of micro-sites that were relevant to seedling establishment, and tested to see if sites promoting seedling establishment were limited. I predicted that I would most often find seedlings growing on dead wood beneath trees, and least often on *Sphagnum* moss. I also tested actual establishment rates by planting seeds on three different substrates (decaying wood, bare dirt, and *Sphagnum*) and comparing their germination and survival success. I expected to see greater rates of

establishment on dead wood when compared to *Sphagnum* moss and bare ground (Papic & Armesto 2000). The major assumption is that sites that are suitable for germination are also suitable for further survival, which is not always true (Gunnarsson & Rydin 1998). This assumption was not tested, however Papic and Armesto (2000) found that seedling survival is higher on coarse woody debris than on bare ground.

## Methods

### Study Site

The study was conducted during the months of January and February 2001-2002, at and near Estación Biológica Senda Darwin, a field station located on Isla Grande de Chiloé (9,600 km<sup>2</sup>) roughly 10 km from the coast of Chile (41°55'S, 73°35'W). The main woody tree species colonizing disturbed habitat are the avian dispersed *D. winterii*, and *E. cordifolia*, and the wind dispersed *N. nitida* (Veblen 1985). The study fields are located in the northeastern part of the island, near the towns of Manao and Linao. Mean annual rainfall is 1906 mm (peaks in Austral winter; June-September) and the mean annual temperature is 11° C (Armesto & Figueroa 1987).

### Study Species

The primary seed dispersers in this system are *Elaenia albiceps* (white crested elaenia or fio fio) and *Turdus falklandi* (austral thrush or zorzal; Willson et al. 1994). The white crested elaenia occupies forest interior, edges, and clearings in *Nothofagus* forest. Its breeding season is from November to February (Fjeldså & Krabbe 1990). The austral thrush makes use of a variety of habitats ranging from *Nothofagus* understory to gardens, parks, or brushy country. Its breeding season begins in October and ends in February (Fjeldså & Krabbe 1990). *Nothofagus nitida* was the numerically dominant tree

species in the post-disturbance shrub fields, followed by *Drimys winterii*, *Amomyrtus meli*, *Eucryphia cordifolia*, and *Podocarpus nubigena*.

## **Frugivore Activity Hypothesis**

### **Bird censuses**

I conducted bird censuses during the breeding season (January and February 2001-2002) between the hours of 06:30 and 09:30 to examine the effect of trees in fields on the number of avian visits to fields. A total of 12 0.5 ha rectangular old field sites were selected, including 4 sites in each of the following categories based on the density of emergent forest trees (> 10cm dbh); low (with zero to 18 trees/ha), medium (30- 48 trees/ha), and high (more than 58 trees/ha). Site selection was constrained by proximity to the field station and thus was non-random. However, sites were at least 200m apart, and in most cases greater than 1000m apart, limiting the chances of non-independence. For each sample, I delimited a 100m by 50m section of old-field adjacent to a forest edge that contained *Baccharis magellanica*. Nine sites were sampled 3 times each in 2001, and an additional three sites were added in 2002. In order to avoid confusing temporal effects on frugivore abundance with site effects, all sites were censused once before any site was censused a second time (with two exceptions, due to travel restrictions). Censuses were only conducted on non-rainy mornings. For each sample, I recorded each frugivore seen moving from forest into the 0.5 ha section during a 10 minute period. Ten-minute point counts probably allowed double counting to occur. However, I was not concerned with movement from forest to field per individual bird, but rather total number of field visits per unit time. Whether by one or by several birds, each visit has an equal probability of resulting in a defecated seed. Since all of my sites were located near forest patches large enough to support many individuals of my study species, I assumed that

linear densities of these bird's territories along forest edges were comparable among sites. Thus, my census plots sampled visits by an equal number of individuals. The effect of field type (high, medium, or low number of trees) on number of avian frugivore visits was subjected to a Kruskal-Wallis one way analysis of variance.

### **Focal samples**

I used a sub-set of the sites described above to conduct 30-censuses of two specific trees or tree clusters between the hours of 07:00 and 10:00. Sites were selected based on the availability of trees that fit the following design. To compare clusters of trees to single trees, I selected a cluster of trees, usually mixed species, and a single tree, equidistant from the forest edge and within 20m of one another. I defined a cluster as a group of two or more trees where each tree was within 0.5m of the foliage edge of its nearest neighbor. Mean cluster size was 10.18m ( $\pm$  1 S.E. = 0.8430m) circumference at the outer edge of the crown. The mean crown circumference of a single tree was 4.00m ( $\pm$  0.4624m). After selecting the trees, I placed myself in an inconspicuous location that provided an unobstructed view of both trees and clusters and counted the number of avian frugivore visits to either the cluster of trees or the single tree during a 30-minute period. 24 single-cluster pairs were censused. I also conducted focal samples comparing fruiting tree species (*Drimys winterii*) to non-fruiting tree species, using the same methods described above. *Drimys winterii* were not presently bearing fruit in four of the 14 pairs sampled. The effect of cluster type (cluster or single) and tree type (fruiting or non-fruiting) on the number of avian frugivore visits was analyzed using Mann-Whitney U tests.

### **Seed traps**

To test for a difference in seed rain with distance from the forest edge, I placed 120 seed traps in clusters of three throughout four fields located at and near Senda Darwin. Seed traps were placed in clusters of three to increase the area sampled at each location. Seed traps were modeled after those used by Amesto et al. (2001a). The traps were constructed from a metal ring 30cm in diameter, supported by three metal stakes approximately 50cm above the ground. Seed catching area for each trap was approximately 0.07 m<sup>2</sup>. Plastic netting (mesh size = 2mm) was attached to each ring to collect the seeds. I placed 20 of the trap clusters within 25 meters of the forest edge, and 20 from 25 - 50 m from the edge. The design was slightly unbalanced, because there were insufficient trees within 25 meters of the edge. To determine whether avian seed dispersal was higher beneath trees, I placed 19 of the traps directly beneath a tree, and the other 21 at randomly chosen, non-tree locations. Traps were placed at the end of January 2001, and were checked at the end of February 2001, the beginning of January 2002, and the end of February 2002. Only seeds that were of a different species than the tree above the trap were counted, unless there was good evidence that the seed had been dropped by a bird (i.e., fecal material evident). I tested for the effect of distance from edge on seed rain and the effect of location (tree or non-tree) on seed rain using Mann-Whitney U tests.

### **Germination Site Hypothesis**

#### **Seedling transects**

In 2001 I set up five transects in each of nine fields to determine where seedlings were actually growing. Fields were chosen at random from the 12 fields that I sampled for frugivore activity. I placed 100-m transects parallel to the edge at 10, 20, 30, 40, and 50 meters from the edge, in order to control for distance from edge. Along each transect,

I searched at three randomly selected points for each of the following substrates: bare ground, dead wood, bare ground beneath a tree, dead wood beneath a tree, beneath *Baccharis magellanica*, and on *Sphagnum* moss for a total of 18 randomly chosen points on each transect. At each point, I searched a 5m radius for the presence of the substrate, and counted the presence and number of seedlings growing on the nearest one-meter square area of the substrate. All trees less than one centimeter in diameter were considered seedlings. Seedlings were not identified to species, but were differentiated from non-woody species.

### **Substrate availability transects**

In 2002, I randomly chose six of the 12 fields to analyze substrate/cover type availability. In each field, I established five 50-m transects perpendicular to the forest edge, in order to incorporate any variability along this gradient. Using a measuring tape I paced the transects, visually estimating the percentage cover of each substrate type for each meter of distance, arriving at a percent cover for each substrate type over the total 50 meters. A Chi-squared test was then used to compare the number of seedlings found at each substrate or cover type to the percent occurrence of each type.

### **Germination and survival experiment**

In February 2001, I planted 1080 seeds of two species; *Drimys winterii* and *Amomyrtus meli*, on three substrates; dead wood, bare ground, and *Sphagnum* moss to compare rates of germination and survival on different substrates. *Drimys* and *Amomyrtus* were chosen based on availability and their prevalence in successional fields. At each of 18 locations, in two large *Baccharis* fields at Senda Darwin, I placed 10 seeds of each species on 0.1m<sup>2</sup> area of each substrate. Only locations where all three substrates occurred within 2m of each other were chosen, to control for localized site effects. Due

to this constraint sites were chosen based on availability, and thus were non-random. At each location, I placed seeds in three microhabitats, each of which constituted a treatment: (1) dead wood, (2) bare ground, (3) and *Sphagnum* moss. Prior to planting, any existing seedlings were removed, and the substrate surface was lightly scraped to remove any existing seeds. Seeds were lightly pressed into exposed soil or *Sphagnum* moss and dropped onto crevasses or pressed into soft portions of CWD. In an actual defecation event, seeds would be accompanied by fecal material, and would have been subjected to intestinal acids, which may enhance germination (Traveset et al. 2001). Each location was marked with small metal stakes and flagging tape. In January of 2002,, I recorded the percentage of seeds that had germinated and survived. The effect of substrate type on germination and survival was evaluated using a Kruskal\_Wallace test.

## Results

### Frugivore Activity Hypothesis

#### Bird Censuses

The mean number of frugivores counted during 10-minute point counts for fields with low, medium, and high numbers of trees was highest for the sites with the most trees (> 29) and lowest for the sites with less than nine trees (Fig. 2). In total, 75 frugivore visits were recorded. *Elaenia albiceps* accounted for 64% of the observations, and *Turdus falklandi* made up the 36%. Mean number of frugivore visits at high sites was ~4 times higher than and medium sites, where mean frugivore visits was ~5 times higher than low sites. Sites with low and medium numbers of trees were both found to be significantly different from high tree sites, but not from each other ( $X^2(2)= 7.78$ ,  $P =0.02$   $N=12$ ; Fig. 3).

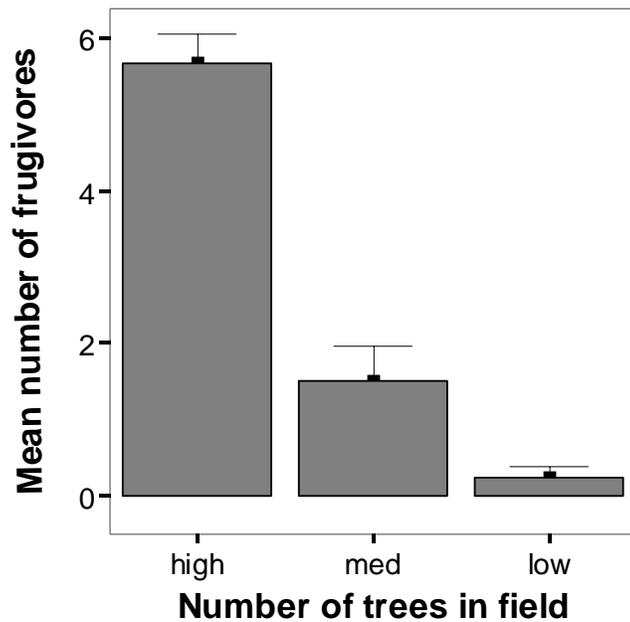


Figure 2. Average number of frugivores counted during 10 minute point counts at 12 sites in Chiloé, Chile. Sites are grouped as high (>29 trees), medium (15-24 trees), and low (0-9 trees) numbers of trees (N = 12). Error bars represent +/- 1 SE.

### Focal samples

During focal tree sampling, clusters of trees received significantly more bird visits on average than single trees ( $Z(46) = -3.38$ ,  $P = 0.001$ ,  $N=24$ ; Fig. 3). When circumference was controlled for, clusters still received significantly more visits ( $Z(44) = -2.396$ ,  $P=0.02$ ,  $N=46$ ). Clusters received 6.6 times more visits on average than single trees. However, there was no significant difference in the number of visits to fruiting and non-fruiting trees, though the sample size was lower ( $Z(26) = -0.48$ ,  $P = 0.73$ ,  $N=14$ ; Fig. 4) Fruiting tree species received approximately twice as many visits on average as non-fruiting tree species.

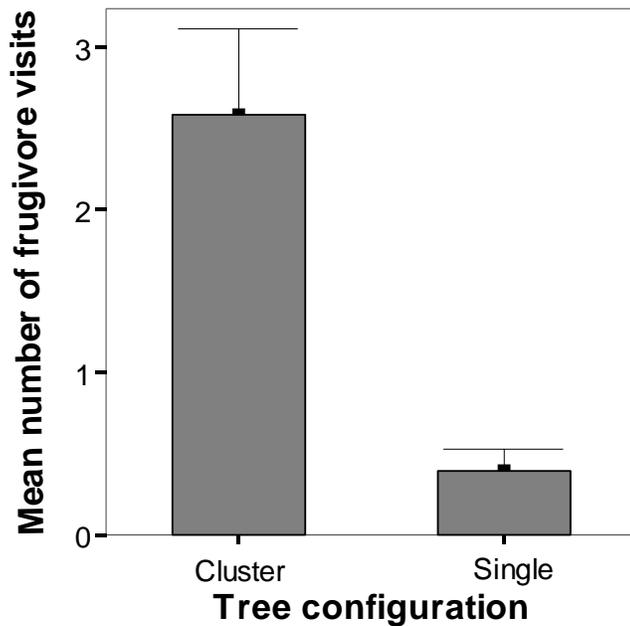


Figure 3. Mean number of frugivore visits during 30-minute focal samples to clusters of trees and adjacent single trees in degraded old-fields in Chiloé, Chile (N = 24). Error bars represent +/- 1 S.E.

### Seed traps

Four hundred and ninety four seeds from fruiting tree species were collected in the seed traps over the course of one year. Of these, 482 were found beneath trees (out of 16 trap clusters) and 12 were found in random non-tree locations (out of 2 non-tree trap clusters). After discounting seeds that I was unable to verify as being bird dispersed (i.e. seeds of the same species as the tree above the trap and not embedded in fecal material), there were 110 seeds dispersed to locations beneath trees and 12 dispersed to random non-tree locations. Seed rain of verifiably dispersed seeds within 25 meters of the edge did not vary significantly from seed rain between 25 and 50 meters from the edge ( $Z(38)=-0.03$ ,  $P=0.98$ ,  $N=20$ ). Dispersed seeds were significantly more common beneath trees than in random non-tree locations ( $Z(38)=-3.33$ ,  $P = 0.004$ ,  $N=20$ ).

## Germination Site Hypothesis

### Seedling transects

I found the highest density of seedlings beneath trees, followed by dead wood beneath trees, *Baccharis*, bare ground, dead wood, and *Sphagnum* (Fig.5).

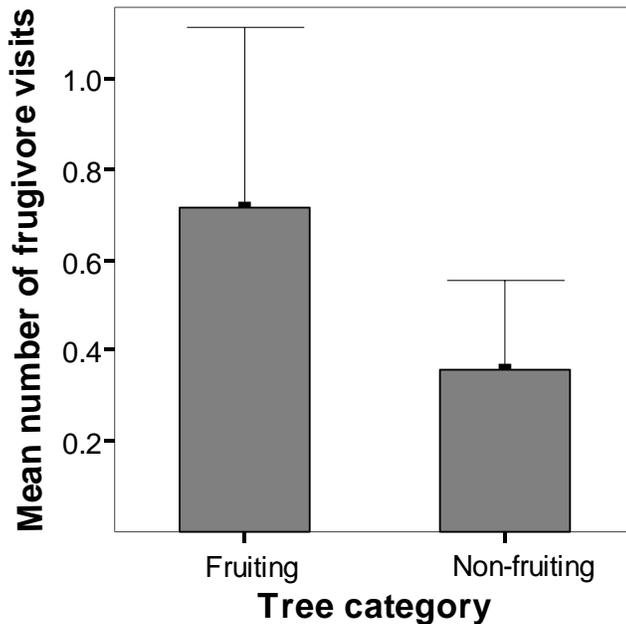


Figure 4. Mean number of frugivore visits during 30-minute focal samples to fruiting and non-fruiting trees in degraded old-fields in Chiloé, Chile (N = 14). Error bars represent +/- 1 S.E.

### Substrate availability transects

*Baccharis* was the most common substrate type, covering 34.57% of the sampled area followed by ferns, *Sphagnum* and bare soil. Trees, trees with dead wood, and dead wood were the least common substrate types (Fig. 6). Seedlings were found in significantly higher numbers than would be expected beneath trees, and on dead wood beneath trees, and in significantly lower numbers than expected on *Sphagnum* moss ( $X^2(5)=192$ ,  $P < 0.001$ ,  $N=157$ ).

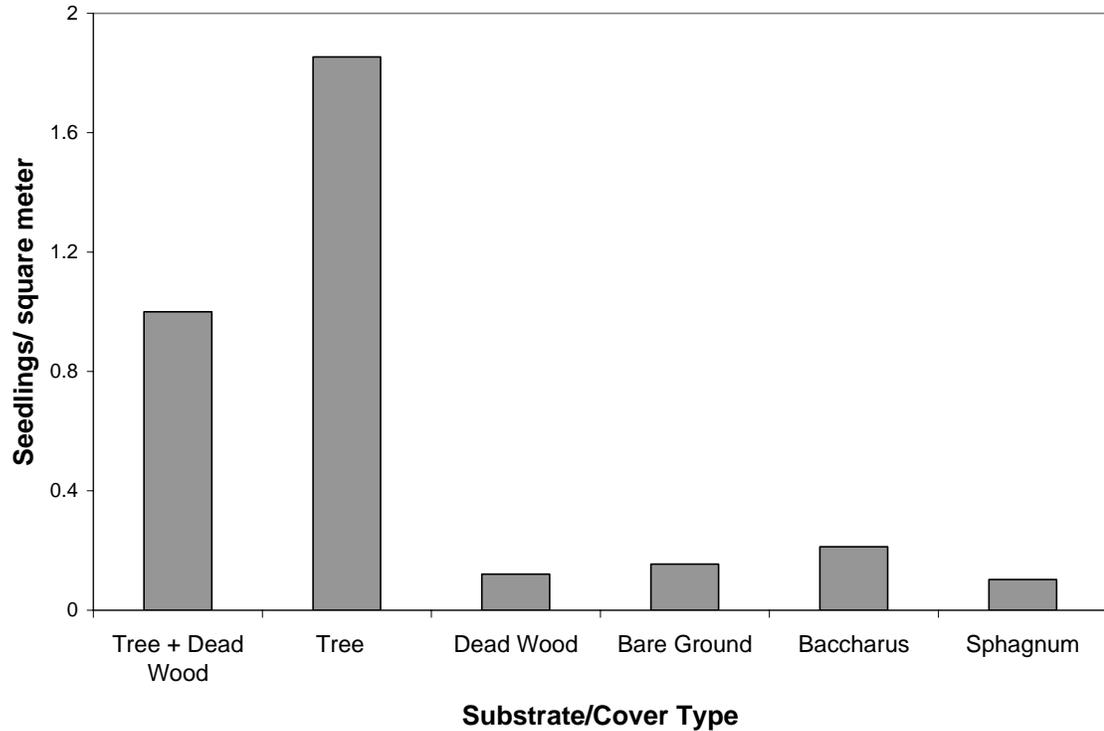


Figure 5. Density of seedlings found growing on each substrate type in 9 degraded old-fields in Chiloé, Chile.

### Germination

Of 1080 planted seeds (N=360 on each substrate type), only 7 *Drimys* seeds germinated and survived for one year. Five of these were on dead wood, two were on bare ground, and no seeds placed on *Sphagnum* moss germinated and survived (Fig. 7).

### Discussion

I conclude that seed dispersal limitation is the most important factor limiting regeneration of *Baccharis* fields for the following reasons. Fields with no or very few trees received almost no frugivore visits. Since very few seeds were found in traps placed in open areas, some sort of perching structure appears to be necessary to “jumpstart” regeneration. Availability of suitable germination substrate, while also important, seems to be secondary to seed dispersal, since some seedlings were found in

all substrate types. The latter finding suggests that although some substrates might be better for germination, increased overall dispersal into any sites could increase germination rates. While the history of the study fields is not fully known, most were logged at least 30-50 years ago (I. Díaz, Pers. Comm.). Presence of seedlings and trees in some of my study plots suggests that succession to forest is not actually arrested close to forest edges, but slowed enough to be experiencing limitations on regeneration representative of truly arrested sites.

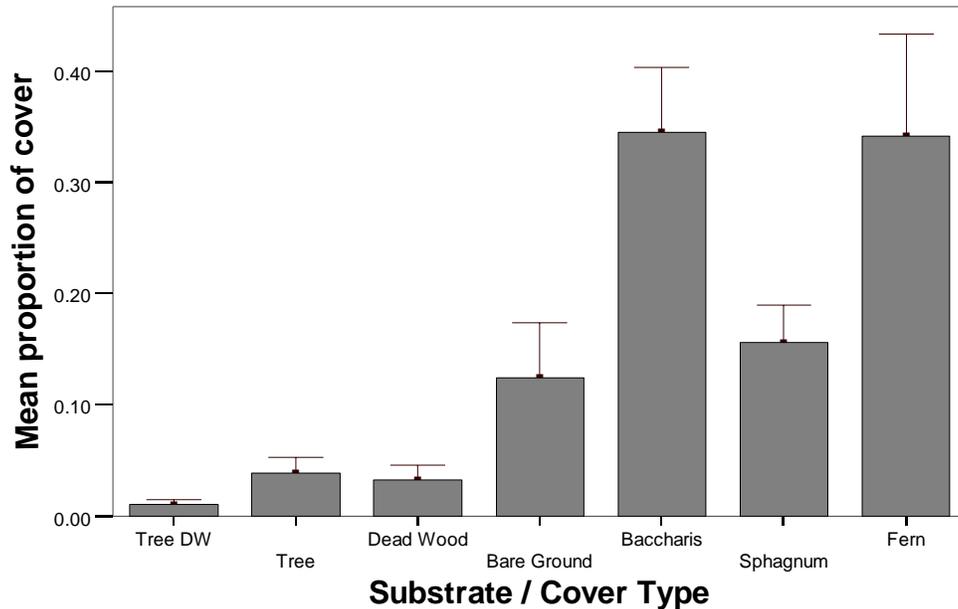


Figure 6. Percent cover of various substrate types across six degraded old-fields in Chiloé, Chile. Error bars represent  $\pm 1$  SE.

### Frugivore Activity

Following my predictions, fields with more trees received more visitations from frugivorous birds than fields with fewer trees. However, lack of a significant difference between low and medium tree density suggests the existence of a threshold value for the number of trees required to significantly increase the number of visitations, alternatively,

my sample size may have been too low to detect a difference. Based on my study design, the threshold could be around 15 trees per hectare. Therefore, at minimum, my results imply that if forest is logged and the land owner wants forest to regrow, then leaving at least 15 trees/ha will positively influence the number of frugivorous birds frequenting the area (and enhance the rate of regrowth; see Chapter 2). Due to the limited area of my study plots, however, point counts on a larger set of fields varying more systematically in the number of remnant trees should be conducted to obtain a more accurate determination of numbers of trees needed to attract seed dispersers.

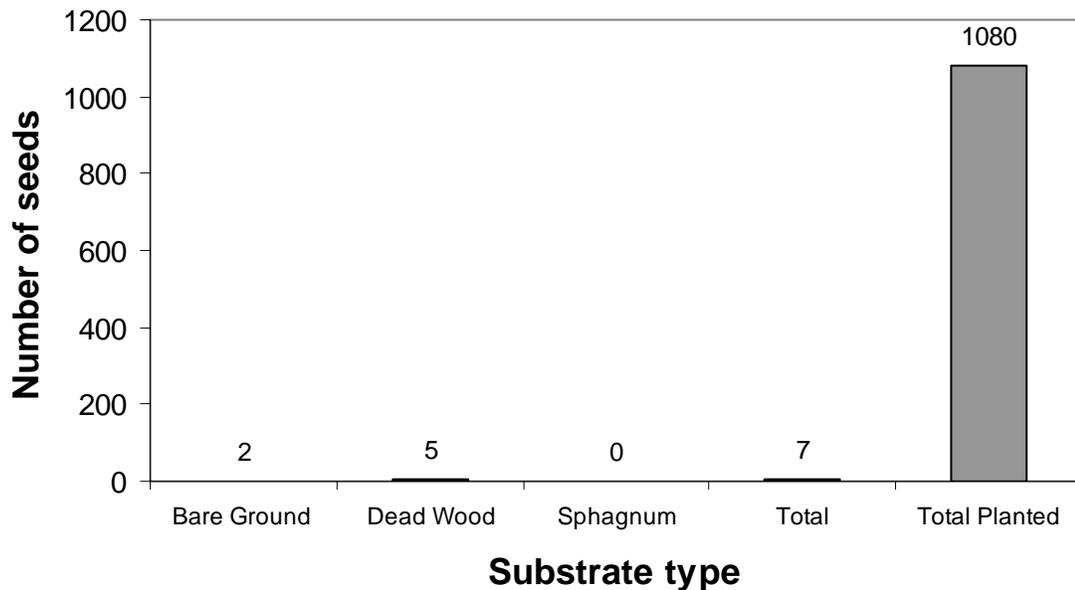


Figure 7. Number of seeds germinating on each substrate type in 18 trials, in degraded old-fields in Chiloé, Chile.

Focal sampling revealed that trees growing in large clusters attract more frugivores than trees growing singly. This may be due to the fact that a cluster of trees provides greater cover from predators and is more likely to contain multiple food resources than a single tree (Debussche & Isenmann 1994; Ferguson & Drake 1999; Holl 1999;

McClanahan & Wolfe 1993; Slocum & Horvitz 2000). It is also possible that clusters of trees simply receive more visitors due to their greater volume and likelihood of being in the path of birds moving across open areas. But in any case, it may be more effective, when leaving remnant trees during forest clearing, to leave them in small clumps.

Although, this may seem counterintuitive for pasture creation, trees can be useful in providing shade and windbreaks for cattle. Additionally, if pasture creation is successful, remaining trees can be used for fuel wood when it has become apparent that *Baccharis* and *Sphagnum* are not becoming established.

Data from the seed trap study suggest that frugivores overwhelmingly deposit seeds beneath trees. Although density dependent mortality can be greater beneath trees (Howe & Smallwood 1982; Janzen 1970; but see Hubbell 1979; 1980), in this system it may be compensated by conditions under trees that are significantly better for germination and survival (i.e., elevated and drier soils, reduced daily variations in temperature and humidity, and a lack of competition from shrubs and grasses; Nepstad et al. 1996). This combination of seed attraction and favorable conditions for germination and growth characterizes what has been called “recruitment foci”, or points in old fields from which regenerating forest grows outward (McDonnell & Stiles 1983; Slocum & Horvitz 2000; Toh et al. 1999).

### **Seedling Establishment**

The location of seedlings in fields further suggests that some of the seeds deposited beneath trees survive to the seedling stage. Seedlings were significantly less prevalent on other substrate types. After trees and trees with dead wood, the next most common location for seedlings was beneath *Baccharis*. Because *Baccharis* is so common relative to colonizing or remnant trees, on a per plant basis, *Baccharis* shrubs receive much less

seed input than trees in old-fields. However, *Baccharis* is occasionally used as a perching site by the smaller bird species, and some seedling establishment might occur in the absence of trees, albeit at an extremely slow rate. When seedling density is divided by substrate availability, it becomes apparent that the rarest sites represent the highest seedling establishment (Fig. 8).

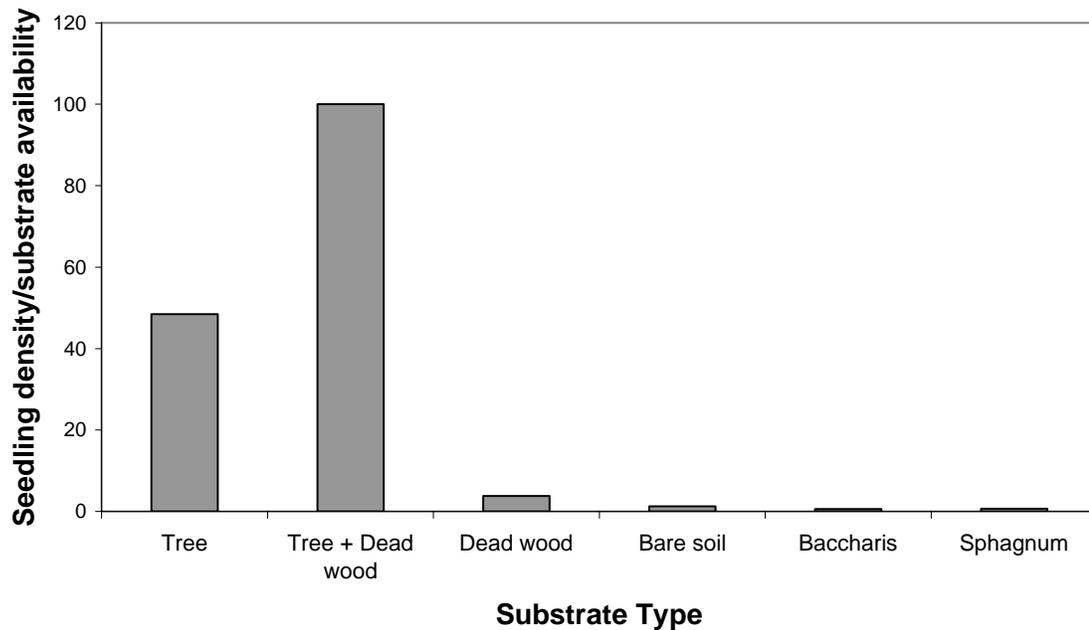


Figure 8. Seedling density divided by substrate availability for various substrates in *Baccharis*-dominated oldfields throughout Chiloé, Chile.

Testing germination success on different substrates yielded little data. Low germination and survival rates in my study (0.97 %) may accurately reflect an extremely low germination rate under natural conditions. In a study of germination of the same species under green house conditions, however, a much greater percentage of seeds germinated (~75 %; Figueroa et al. 1996). Actual germination rates may have been higher, however, because I was unable to check for germination between field seasons. It is quite possible that germination rates were much higher, and that subsequent survival

was low. Moreover, it is not yet known for this system how gut passage affects the seed germination process (Traveset & Willson 1997). Further testing of seed germination on a variety of substrate types after frugivore gut processing would be beneficial.

### **Recruitment Foci**

I found more seedlings growing beneath trees than any other location. This is somewhat expected a priori (Nepstad et al. 1996; Slocum & Horvitz 2000), and my work also suggests that this is due to some combination of increased seed input and better conditions for survival of seeds and seedlings beneath trees (Figs 2, 5). From the seed trap portion of the study, we know that seeds are being dispersed, and that the area beneath trees is the main recipient of these dispersed seeds. What we don't know is whether this area is also better for seed germination. However, the presence of a tree suggests that the area was historically a favorable microsite, particularly because most trees used for this study probably came in after the fields were created; the oldest tree that I cored was 54 years old. Typically, dispersal away from a parent tree is thought to increase seed survival by decreasing intraspecific competition (Hubbell 1979), as well as by providing escape from predators and pathogens (Connell 1971; Janzen 1970). However, in the case of *Baccharis* dominated old-fields, survival away from the parent tree is likely much lower, unless the seed is dispersed beneath the canopy of another tree. For future work it will be important to examine how distance from a tree influences germination success in sites where succession is arrested, as the rate of survival should reach a maximum closer to the tree, then drop off drastically, reflecting the unfavorable conditions of the site (Houle 1995). Ascertaining how close to a tree a seed needs to fall to maximize its germination success would facilitate restoration planning, by allowing estimation of optimal tree planting density.

## Conclusions

In order to speed-up or initiate forest regeneration in *Baccharis* dominated shrub fields, lack of seed dispersal and a lack of suitable germination sites must both be overcome. My study suggests most strongly that seed dispersal is the main limiting factor. Moreover, I can conclude that the simplest means of overcoming arrested succession will be to plant tree saplings in fields where forest regeneration is desired. And while my work did not find overwhelming evidence that the presence of dead wood (nurse logs) is necessary to overcome germination limitation, evidence that this would be important is mounting from this and other rainforest systems (Harmon et al. 1986; Papp & Armesto 2000; Takahashi et al. 2000). Therefore, based on the field studies and literature review presented here, I put forward the following conservative recommendations for reducing *Baccharis* coverage where it exists, or fostering forest development rather than shrub development where forest is freshly cleared. (1) Plant, or preferably leave behind, a small number of forest trees after clearing; at least some in clumps. (2) Leave a significant amount of coarse woody debris throughout the area of interest to provide safe germination sites. In the next chapter I explore recommendations in greater detail using an empirical systems model of forest regeneration under different starting conditions in order to allow landowners greater certainty in applying these simple recommendations to their own fields which may vary in starting conditions that could affect the outcome.

CHAPTER 2  
RAINFOREST RESTORATION SCENARIOS FOR *BACCHARIS*- DOMINATED  
OLD-FIELDS IN SOUTHERN CHILE: A SIMPLE ECOSYSTEM MODEL AS A  
DECISION MAKING TOOL

**Introduction**

Determining the underlying mechanisms of arrested succession at local restoration sites can influence understanding and management of larger landscape scale patterns and processes (Bell et al. 1997). For example, arrested succession is one way that stable and widespread community types (or alternate stable states; (Laycock 1991; Lewontin 1969) can arise that, in turn, define the mosaic of ecological and socioeconomic characteristics of human landscapes (Naveh 1994). Therefore, when undesirable alternate stable states arise in landscapes, restoration ecological approaches can be used to identify and release mechanisms that generate and maintain them. In this study, I identified potential mechanisms of arrested succession in mesic old-fields resulting from anthropogenic clearing of south-temperate rainforest in Chile. The community type produced that is undesirable, from both socioeconomic and ecological perspectives, is a persistent shrub community dominated by *Baccharis* spp.

**Chilean South-temperate Rainforest: Natural Disturbance Regime and Arrested Succession**

The South temperate rainforest in the Valdivian region of Chile (35°- 48° S) receives between 1,000 and 6,000 mm of rain per year, and is characterized by emergent evergreen broad-leaved trees (e.g., *Nothofagus oblique*, *N. alpina*, and *N. dombeyi*) and evergreen conifers (e.g., *Podocarpus nubigina*). Canopy species include *Drimys winterii*,

*Weinmannia trichosperma*, and several trees in the family *Myrtaceae* (Willson et al. 1994). Vertebrate dispersed species make up approximately 70% of the flora (Armesto & Rozzi 1989) and include *Drimys winterii*, *Amomyrtus luma*, *A. meli*, *Eucryphia cordifolia*, *Weinmannia trichosperma*, *Podocarpus nubigena*, *Laurelia philippiana*, and *N. nitida*. Two bird species, *Eleania albiceps*, and *Turdus falklandii* disperse the majority of seeds. Endemism is very high in this biome (Stattersfield et al. 1998), ranging from 45 % in vertebrates to 90% in some groups of seed plants (Armesto et al. 1996; Villagran & Hinojosa 1997).

The natural forest disturbance regime is characterized by large-scale periodic catastrophes including earthquakes, volcanic activity, and fire that occur relatively rarely in a given site. Wind throw and tree fall gap creation occur much more frequently at any given location and at smaller scales (Veblen 1979). The natural disturbance regime prevents shade tolerant tree species such as *Laurelia philippiana* and *Saxegothea conspicua* from out competing the shade intolerant *Nothofagus* (Bustamante & Armesto 1995) and helps maintain a typically diverse tree canopy composition across scales and throughout the Valdivian region. Human disturbances include widespread clearing of forest followed by burning and then conversion to agriculture (especially in the lowlands) and to industrial forestry plantations of exotic pine and eucalyptus. Typical farm and plantation plots are much larger, and more highly altered, than natural clearings.

Productivity of cleared lands can be limited by the development of persistent shrubs (dominated by *Baccharis magellanica*) following forest clearing that prevent livestock or row crop production and natural forest succession. Apparently the *Baccharis* shrub canopy develops where the water table is, or becomes, elevated following forest

clearing. While soil inundation alone can prevent establishment of native trees (Bewley & Black 1982), *Baccharis* overstory may also prevent establishment by desirable species (Céspedes et al. 2002); Putz and Canham 1992). Landowners can burn back the shrubs but without prohibitively expensive ditching and draining, fire alone does not reliably improve site utility for either agriculture or forest regeneration (Pers. Obs.). *Baccharis* species are common disturbance-related site invaders in many regions where they are native, as in this study (Stylinski and Allen 1999; Sarmiento et al. 2003). A natural ecotonal vegetation type called Magellanic moorland, occurring at higher elevations in Chile, has similar plant community properties to the *Baccharis* shrublands that represent arrested succession in the lowlands (Ruthsatz and Villagren 1991). But monospecific *Baccharis* shrublands are not naturally widely distributed in the study area and are a direct result of clearing at a larger scale than the natural disturbance regime.

On Isla Grande de Chiloé, up to 30% or more of local landscapes currently persist in this arrested state, and extensive areas have been dominated by uniform *Baccharis* stands for more than 50 years (T. M. Darnell, unpublished data). *Baccharis* shrublands are resource poor and not productive of native wildlife (Sieving unpubl. data) or agricultural produce. Farmers that clear forest and then see the development of *Baccharis* shrub in the cleared area will move on to clear another site, if available, to try again. Therefore, from the perspective of maximizing biotic productivity in this landscape, restoration of *Baccharis* fields to either pasture or native forest would be beneficial. Regeneration of forest would provide wildlife habitat and forest products for people, and viable pasture creation would stave off further clearing of native forest (Fig. 1). Given that forest clearing and human activity in southern Chile have resulted in

global endangerment of endemic flora (Armesto et al. 1998) and fauna of the region (Stattersfield et al. 1998), native forest restoration is a high priority. In this chapter I explore two likely causes of arrested forest succession in through systems modeling of restoration scenarios I developed based on field data (from Chapter 1).

In Chapter 1 I tested two alternative hypotheses for arrested succession in my system: that shrub fields persist because of lack of seed dispersal into them, and that they persist because associated conditions prevent seed germination and seedling establishment. I found evidence that both mechanisms are operating to suppress succession in *Baccharis* fields on Chiloé Island, in addition to supporting justification based on the work of others. Therefore, in this chapter I develop a dynamic systems model that incorporates processes actuating both mechanisms of arrested succession in order to address realistic scenarios for restoration given constraints and goals relevant to local landowners.

### **Modeling Restoration Scenarios**

Several restoration scenarios are possible for the patchwork of cleared old-fields that exist in the temperate rainforests of southern Chile. One possibility involves the creation of drainage ditches followed by controlled burning, to dry out the shrub fields and create pasture. While this does not replace forest, it does reduce the amount of additional forest that needs to be cleared. A second potential approach is to plant rows of trees with high rates of evapotranspiration (Ferro et al. 2003); trees can function as “pumps” in this scenario, reducing the hydric conditions and allowing easier conversion to pasture or forest. However, both of these approaches are costly, and depend on monetary resources of individual landowners; many farmers in the region do not have the resources to employ these techniques (Personal Observation). A third general approach,

and the focus of this modeling exercise, is the restoration of native forest via restoration of secondary forest succession in shrub-dominated fields. Forest regeneration on arrested sites could lead to some economic gain for landowners (from forest products or provision of livestock shelter and understory browse during winter) and may, thereby, lessen pressures to clear more forest.

In Chapter 1 I presented evidence that seed dispersal can be limited if birds are not attracted to shrub fields. Attractiveness is determined by the number of trees, whether they are fruiting, and their spatial distribution. Planting trees can help attract seed-dispersing birds into shrub fields, and potentially provide better microsites for germination and seedling establishment. It is also clear that because ground-level substrates where seeds might fall can be either too wet (bare ground) or too dry or acidic (*Sphagnum*), coarse woody debris (CWD) coarse woody debris is the best germination substrate because it will catch and germinate seeds that would otherwise be inundated in water or desiccated in the *Sphagnum* layer (Lusk 1995; Papic & Armesto 2000). Therefore, suitability of germination and seedling establishment sites are determined by relative availability of CWD versus adverse substrate conditions. Both planting trees and adding CWD cost money and labor. Therefore, the goal of the model is to assess the gain (in rate of forest regeneration) against the estimated relative costs of inputs.

This chapter presents a dynamic systems model of seed disperser response to field characteristics, seed germination processes, and tree establishment and growth in the old-fields adjacent to south-temperate rainforest on Isla Grande de Chiloé, Chile (41°55'S, 73°35'W). The purpose of this model is threefold. The first is to expand our understanding of the relative importance of seed dispersal by birds and the limitations of

seed germination as key components of forest succession. The second is to explore methods for restoring rainforest by simulating removal of limitations to the process of succession (i.e. lack of trees, insufficient germination sites). The third objective is to assess the model as a predictive tool that can be used by managers and landowners who want to restore native forest, given certain constraints (i.e., time, money, labor). I use field data (Chapter 1) and information from other studies, to parameterize the model, which necessarily simplifies certain aspects of the regenerative process. For example, interactions between tree species, soil properties, and nutrient levels are ignored. Sensitivity analyses were applied in cases where model parameters are estimated or derived from the literature to analyze their importance, to provide a range of outcomes when a parameter is not well known, and to generate useful hypotheses for further testing.

## **Model Description**

### **Overview**

The model is comprised of five subsystems: old-field characteristics (size, cover and substrate types, length of edge), seed rain, seed germination and seedling survival, creation of new recruitment foci, and tree growth and survival (Fig. 9). The underlying premise of the model is that succession acts as a positive feedback loop during early stages such that trees present in the old-field act as an attractant for avian seed dispersers. As seeds are dispersed to suitable germination sites, the number of trees increases as does area covered by tree canopy and, in turn, this attracts more seed dispersers and alters the habitat to create more germination sites (Alcantara et al. 2000; Slocum 2001). At later stages, as tree density increases, homeostatic properties slow forest growth (e.g., Tappeiner et al. 1997; Wills et al. 1997). Rather than attempt to explicitly model

every aspect of the ecosystem, select attributes are modeled incorporating available data from field studies. For example, instead of modeling all processes that could influence tree growth rates; I incorporated rates of tree growth recorded in nearby systems (see below). Stella 7.0 (Wallis et al. 2001), an icon based modeling environment, was used to create this model. Following is a brief description of key model equations. The model is presented in its entirety in Appendix 1 (iconographic form) and Appendix 2 (equation form).

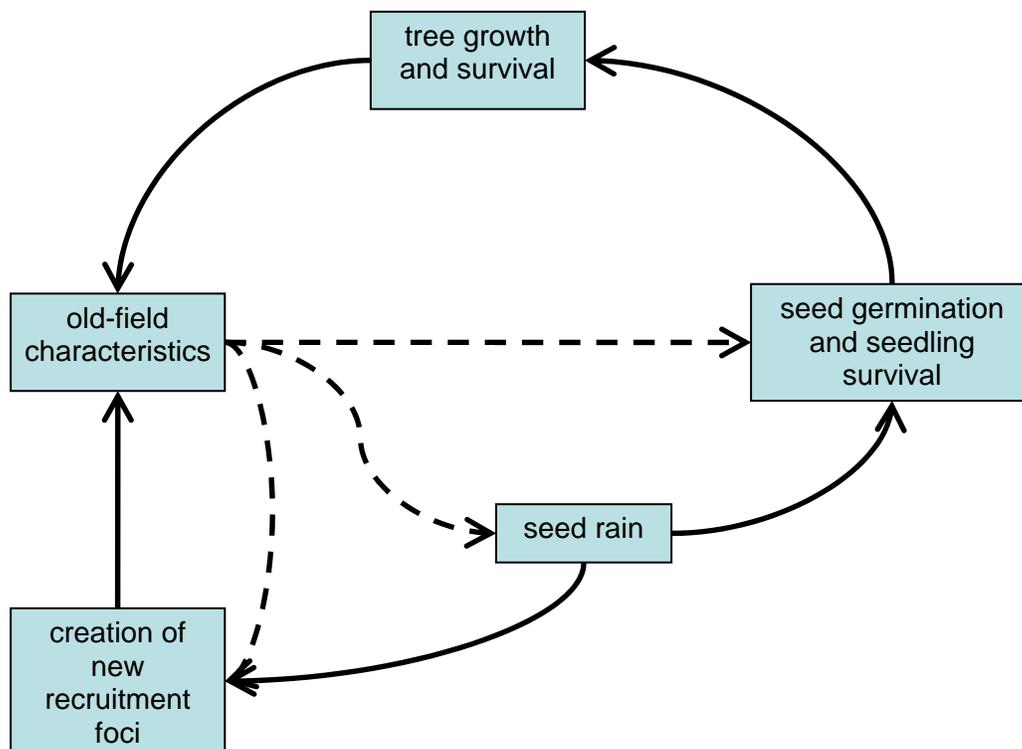


Figure 9. A simple representation of old-field regeneration as conceptualized by the model. Dark arrows represent the flow of material (through space or time – i.e. seeds or tree growth), dashed arrows represent the influence of one component on another.

### Old-field Characteristics

The parameters I defined to reflect old-field characteristics include: area of ground cover of 5 different types; area of tree canopy cover; and the rate of spread of tree cover in the face of competition with other ground cover types. Cover types defined here (and observed in the field; Chapter 1) are trees, *Sphagnum* moss, coarse woody debris (CWD), *Baccharis*, grasses and ferns, and bare ground. The category “grasses and ferns” refers to vegetation that is greater than 0.25 m in height and that is sufficiently dense to limit the amount of light striking the soil. The category “bare ground” refers to either exposed soil or patches of sparse grasses and soil. Each of these cover-types either promotes or inhibits tree growth. Tree growth in this instance refers to the increase in total tree canopy area throughout the old-field. Other trees, CWD, and bare ground act as promoters of tree growth (i.e., area of canopy cover can increase in and around areas with these cover types). On the other hand, tree seedlings have difficulty getting established in areas with *Sphagnum*, *Baccharis*, and grasses and ferns. Therefore, growth of forest area is inhibited where these substrate types occur (Chapter 1).

To represent proportion of canopy coverage, the canopy cover of trees in the old-field is calculated relative to the size of the old-field. This is shown in Eq. 1

$$C_a = \sum F_a / O_a \quad (1)$$

where  $F_a$  is the area of ground covered by tree or tree canopy (also referred to as a focus), and  $O_a$  is the area of the old-field. When determining the actual area available for tree growth, the various substrate types are subtracted from the total size of the old-field, as in Eq. 2

$$G_a = O_a - (SPcov + Bcov + GFcov) \quad (2)$$

where  $G_a$  is the area available for trees to grow,  $SP_{cov}$  is the area of old-field covered by *Sphagnum* moss,  $B_{cov}$  is the area of old-field covered by *Baccharis*, and  $GF_{cov}$  is the area of old-field covered by grasses and ferns. This means that trees are in competition for resources with grasses, shrubs, and mosses. In other words, when shrubs and mosses dominate an old-field, the area available for new tree growth is much lower than in an old-field without competing cover types because there is less available space and resources for the trees to grow.

Little data are available concerning the rate of spread of *Sphagnum* moss. However, it has been shown that *Sphagnum* out-competes small plants by creating acidic, anoxic, and nutrient poor conditions (Van Breeman 1995). This model incorporates *Sphagnum* as a static feature that is slowly out-competed by trees, which, once rooted with a canopy over the top of the shrub layer, can grow uninhibited. Although the actual mechanisms underlying tree-shrub and tree-*Sphagnum* competition are poorly understood at present, it is assumed that as forest trees grow, microclimatic changes occur, making the habitat more suitable for trees and less suitable for *Baccharis* and *Sphagnum*. Figueroa and Lusk (2001), for example, found that *Baccharis* shrub canopy is highly shade intolerant. Additionally, Ohlson et al. (2001) describe the impedance of *Sphagnum* growth by *Pinus sylvestris* in a boreal bog ecosystem. Eq. 3 calculates the rate at which growing trees can out-compete *Sphagnum* moss.

$$SP_{cov}(t) = SP_{cov}(t - dt) - (IF P > 0.99 THEN \sum F_c *(1/180) ELSE 0) * dt \quad (3)$$

where  $SP_{cov}$  is the area covered by *Sphagnum* at time  $t$ ,  $P$  is the proportion of the old-field covered by any substrate type other than bare ground (including forest),  $F_c$  is the circumference of the recruitment foci, and  $dt$  is equal to one month. The value in

parentheses, 1/180, is an estimate, subjected to sensitivity analyses, as little data regarding *Sphagnum*-tree competition is available. Therefore, as the edge of the recruitment focus meets a patch of *Sphagnum* moss, it takes 15 years to shade out each square meter of *Sphagnum* moss that is adjacent to the regenerating patch of trees. The time required for forest to out-compete opposing cover types is unknown, and requires further research. Therefore, very conservative values were chosen.

Eq. 4 and 5 show how *Baccharis* and grasses and ferns are similarly handled.

$$Bcov(t) = Bcov(t - dt) - (IF P > 0.99 THEN \sum Fc *(1/288) ELSE 0) * dt \quad (4)$$

$$GFcov(t) = GFcov(t - dt) - (IF P > 0.99 THEN \sum Fc *(1/48) ELSE 0) * dt \quad (5)$$

It takes 24 years to shade out 1m<sup>2</sup> of *Baccharis*, and four years to shade out 1m<sup>2</sup> of grass or ferns.

Other old-field parameters include the length of forested edge bordering the field, and the number and size of existing trees in the old-field, and are chosen to represent the field of interest.

### **Seed rain**

Based on data collected (Chapter 1), it is assumed that avian-dispersed seed rain occurs with equal frequency within 50m of the forest edge, given appropriate conditions (this was the scale of the field studies in Chapter 1). Hence, the dynamics of this model are relevant to forest growth within 50m of the forest edge – at larger distances into shrub fields, certain rates may differ.

Two measurements were used to calculate the potential for seed dispersal into a field; the number of avian frugivores inhabiting forest adjacent to the old-field, and the seed rain beneath trees in old-fields. Bird censuses were conducted in forest edge habitat adjacent to *Baccharis* dominated old fields to estimate the number of frugivores in

adjacent forests. Between 07:00 and 10:00 during January and February 2002, I walked two 200m line transects into each of three different forest patches and counted frugivores seen or heard within 40m of the transect. Due to the dense nature of the forest, distance was estimated, not measured. Forest patches were chosen based on proximity to pre-existing study sites and transect direction was chosen randomly. The average number of frugivores counted was 12.5 per 80m wide transect. *Elaenia albiceps* will travel hundreds of meters from the forest and into the adjacent old-field, if there is sufficient structure in the field (Willson et al. 1994). This means that for each meter of edge there are 0.16 birds with access to the old-field. This method is prone to under-counting (Bibby et al. 2000), but to avoid over predicting rates of forest regeneration, the outcome was not modified. This is high relative to linear densities of most breeding birds, but the primary seed disperser, *Elaenia albiceps*, occurs at very high densities in this system (Rozzi et al. 1996; Willson et al. 1994). To simplify the model, *Turdus falklandi* was not included.

To estimate seed rain, 60 seed traps of roughly 0.07 m<sup>2</sup> in surface area were placed beneath trees in 2 old fields (see Chapter 1 for details). Over a one-year period, 92 verifiably dispersed seeds were found in 60 traps. Hence, 4.2m<sup>2</sup> of old-field received 92 seeds in one year, generating a rate of 21.9 seeds/ m<sup>2</sup>\*year, or 1.83 seeds/ m<sup>2</sup>\*month beneath trees.

Eq. (6) shows how the potential seed rain (PSR) was calculated.

$$PSR = (Sr * Oa) * (L/100) * (Db/.015625) \quad (6)$$

where Sr is the number of seeds dispersed per unit of attractive habitat in the old field, L is the length of the edge, and Db is the density of birds in the forest edge with access to

the old-field. As the number of trees in the old-field increases, the ability of the birds to disperse seeds equally to all areas decreases. However, this levels off to some degree because as the old-field becomes converted to forest it begins to provide suitable habitat, increasing the seed disperser population (Figure 10 shows how the value of  $S$  changes with the number of trees present in the old-field). The second part of this equation,  $(L/100)*(N/16)$ , adjusts the amount of seed rain for the length of edge, based on the bird survey data suggesting that there are 16 frugivorous birds per 100 meters of edge. Because the value of  $S$  is derived from real-world sampling efforts where the edge and density were 100m and  $\sim 0.16$  birds/m of edge, respectively, these values allow the model to adjust  $S$  to varying conditions (i.e. when there is 100m of edge  $N = 16$ , if there are more or less than 100m of edge the model adjusts  $N$ ).

Actual seed rain is based on the proportion of old-field covered by trees. The portion of the potential seed rain that is dispersed is equal to the ratio of area beneath trees to total field size (0.5 ha). However, most of this seed rain does not contribute to the expansion of recruitment foci. In many systems, seeds that fall under existing canopy tend to die off or form a seedling bank where they replace adults that die (Antos et al. 2000; Stewart et al. 1991; Szwagrzyk et al. 2001). From the tree's perspective, avian frugivores both bring seeds from other species and individuals as well as disperse seeds for the tree. In any case, this results in a seed shadow that typically results in a leptokurtic distribution conforming to a negative exponential curve (Willson & Traveset 2000). Long distance dispersal events are dealt with below via the creation of new foci. For the purposes of the model, it is the short distance dispersal that we are mainly interested in, as seeds dispersed too far from the tree are likely to be dispersed in poor

quality habitat unsuitable for germination, and would not influence regeneration in focal sites at this scale. Based on this traditional model of seed shadows, I expect seed rain to be highest beneath the tree canopy (where it contributes to replacement of existing trees) and, due to the lack of alternative perching sites, to drop off quickly as distance from the canopy increases. Additionally, I expect conditions in most of the old-field to be unsuitable for germination such that with the exception of rare conditions (discussed below) survival is only possible in the immediate vicinity of existing tree canopy, resulting in a process of “nucleation” (Debussche & Isenmann 1994), where the only seed rain that contributes to tree growth occurs in the outer edge of the tree canopy. Therefore, only the seeds that fall in the outer 0.5 meters of a tree canopy actually contribute to the growth of recruitment foci in the model. This is represented by Eq. (7).

$$F_g = A_f - (\sqrt{(A_f/\pi) - 0.5^2 * \pi}) / A_f \quad (7)$$

where  $F_g$  is the part of the focus where seed rain contributes to growth in area and  $A_f$  is the area of the focus ( $m^2$ ). For simplicity, recruitment foci are assumed to be circular in shape. Eq. (8) describes the actual seed rain (ASR).

$$ASR = PSR * (\sum A_f / O_a) * \sum F_g \quad (8)$$

### **Seed Germination and Seedling Survival**

Germination rates were determined by planting seeds of two species in various substrates throughout an old field (see Chapter 1). Because the rate of germination and survival was 0.97% and may not have adequately mimicked natural conditions, I compared it to the germination rates obtained by Figueroa and Lusk (2001) for *Drimys winterii*; these were observed to be ~75% annually in gap conditions, and as low as 16% in low light conditions. However, in this study, seeds were protected from predation. In a study on seed predation in the same area, as many as 65% of seeds were removed by

predators (Díaz et al. 1999). Taking a conservative approach, I chose 6% (65% of 16%) as the germination rate for the model. To account for the large difference, I ran a sensitivity analysis to determine the impact of changes in the germination rate (see results section). At rates below 1%, changes in the germination rate have a large impact on rates of forest growth; above 1% the difference is much less. Eq. (9) shows how germination is calculated.

$$G = Sf * Gr \quad (9)$$

where G is germination, Sf is the number of seeds in the recruitment focus, and Gr is the germination rate.

The proportion of seedlings that become established as saplings is based on a mortality of 1% per week (for *Drimys winterii*) under controlled conditions in high light and 4% per week in low light (Lusk & Del Pozo 2002). I took the conservative approach and chose 4% per week to arrive at a number for the model. This value may be low because it was determined under controlled conditions, but I explored this also with sensitivity analyses. Due to the prevalence of standing water in arrested old-fields, the presence of dead wood, acting as “nurse-logs”, increases the chance of seedling survival. Pápic and Armesto (2000) found that survival was 12 times greater on dead wood than on surrounding terrain. This is reflected in the model by setting the death rate for seedlings on dead wood 12 times lower than that of other seedlings.

### **Creation of New Foci**

In addition to the growth of any existing recruitment foci in the old-field, there is some chance that new foci will be created as time passes. Since birds perch on *Baccharis* or other small shrubs in the field (Personal Observation) or occasionally defecate while flying, there is a small possibility that a seedling will become established at a new

location in the old-field each month. Determining the value of this likelihood requires further research, and estimating it is quite difficult. However, I made the assumption that there is a 100% chance of a seedling becoming established below a tree in any given year (Slocum 2000), and that the proportion of the various cover types influences this probability of occurrence. Adjusting for area, I then compared the number of seedlings that I found beneath non-tree cover types (Chapter 1) to the number found beneath trees to calculate the odds that a seedling would be established there annually (Table 1). However, the presence of a seedling does not necessarily guarantee a surviving sapling. To further represent the likelihood of sapling establishment, I included the transition probabilities (e.g., Rey & Alcantara 2000) determined by Papic and Armesto (2000) for survival of seedlings. However, because the process of survival from seed to established sapling in the harsh conditions of a cleared old-field is poorly understood, I erred on the side of caution and assumed that only 10% of the sites were suitable for new foci establishment to occur. Eq. (11) shows how the random chance of new foci appearing is handled.

$$\begin{aligned}
 & \text{IF } Af = 0 \\
 & \text{(on dead wood) THEN MONTECARLO}^1 \left( (0.10/12) * DW \right) * 0.23 * r \\
 & \text{or} \\
 & \text{(on bare ground) THEN MONTECARLO} \left( (0.06/12) * BG \right) * 0.02 * r \\
 & \text{ELSE } 0
 \end{aligned} \tag{11}$$

where DW is the percent cover of dead wood in the old-field but not part of an existing focus, BG is the percent cover of bare ground in the old-field, and r is the additional

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<sup>1</sup> Monte Carlo is a function that returns either a 1 or a 0 each time step. The number in parentheses determines the frequency that a 1 is generated.

rarity of new focus formation ( $r=0.1$  in this case). Values are divided by 12 to convert the annual value to the monthly time step used in the model. (To adequately represent multiple foci with the Stella software, it is necessary to “array” many of the variables in the model. The if-then-else structure of the equation ensures that new foci do not appear where one already exists.) This equation generates a random chance of a seed falling, germinating and surviving, which increases with the presence of dead wood and bare ground.

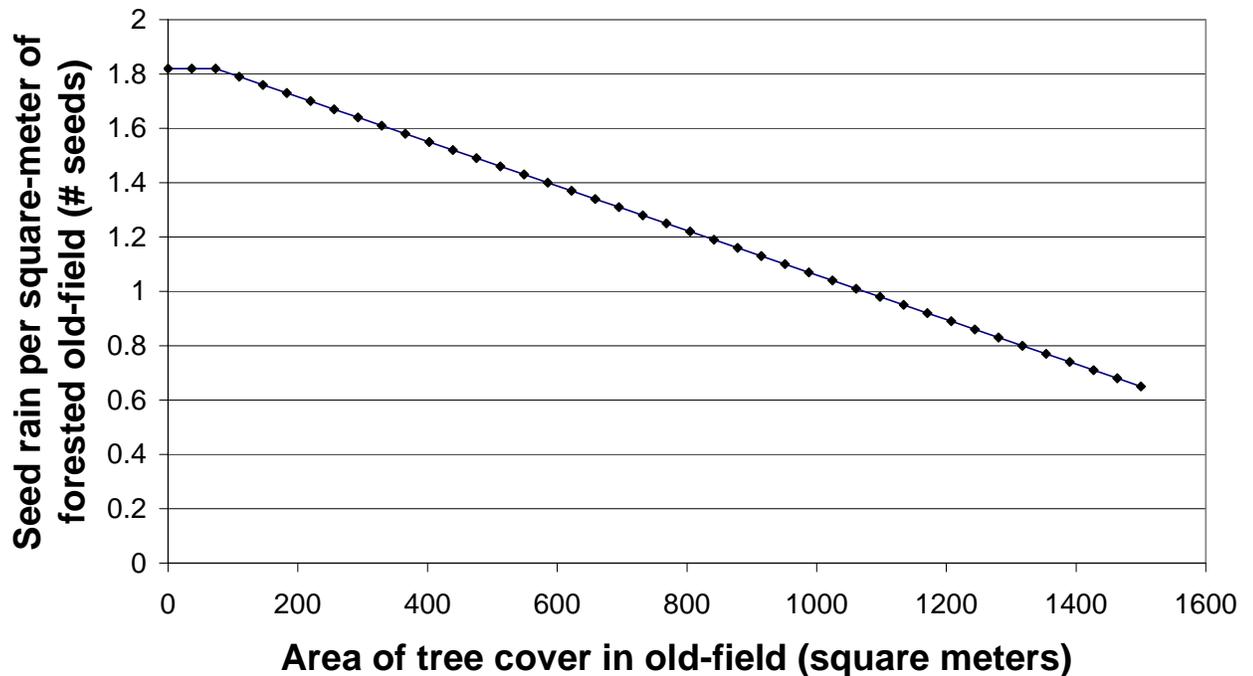


Figure 10. The value of  $S$ , or seed rain per meter of forest in the old-field, changes with increasing tree cover in the old-field. This is because the existing seed disperser population becomes less able to distribute seeds as more attractive habitat opens up. Eventually, seed disperser population should increase, allowing the curve to level out.

### Tree Growth and Survival

Ages of 16 trees in old fields were determined by coring in order to estimate the tree growth rate. Tree cores were extracted as close to the ground as possible, then

sanded with progressively finer sand paper. After repeated sanding, growth rings were visible and were counted under a binocular microscope (Stokes et al. 1968). Cores were not cross-dated, so missing and false rings may be a potential source of error (Lusk 1999).

Table 1. Comparison of the number of seedlings found beneath non-tree cover types to the number found beneath trees to estimate the odds that a seedling would be established there.

Cover type	# of seedlings found (x)	Proportion of cover type to total area surveyed (p)	Number of seedlings in field if entire 5000m <sup>2</sup> field were same as cover type ( $[(1/p)*x]=n$ )	Seedlings per meter <sup>2</sup> (n/5000)	Compared to tree
Tree	89.00	0.04	2225	0.44	1.00
Dead Wood	7.00	0.03	233	0.05	0.10
Bare Ground	17.00	0.12	141	0.03	0.06
<i>Baccharis</i>	27.00	0.35	77	0.01	0.03
<i>Sphagnum</i>	8.00	0.15	53	0.02	0.04

Tree growth rate is based on the positive correlation found between age and DBH (Fig. 11) and age and height (Fig. 12). The standard “tree” for this model is a 10cm DBH tree with a canopy covering 1.68 m<sup>2</sup> of old-field. This was determined by measuring the canopy cover of 15 adult trees and averaging the area covered. Trees in this model are broken down into 5 size classes; saplings with a DBH < 5cm, and trees with a DBH of 5cm, 10cm, 20cm, and 30cm or more. Between the size classes, canopy cover area is assumed proportional to DBH. The growth rate for *D. winteri* to each size class is based on commercial forestry data (Navarro et al. 1997).

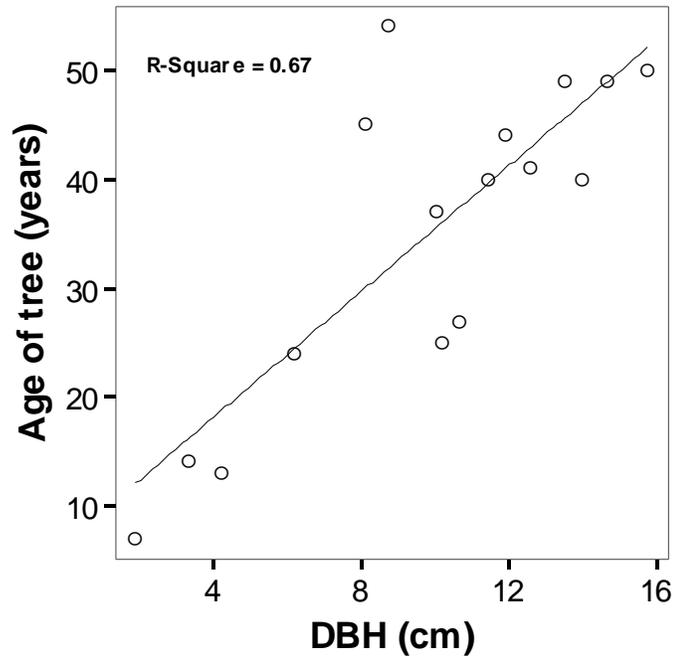


Figure 11. Correlation between age of *Drymis winterii* (as determined by coring) and diameter at breast height (DBH).

Navarro et al. (1997) reported an annual mortality rate for *D. winterii* of 2.17%, which equals 0.181% mortality per month. The number of trees in each size class is governed by Eq. 12

$$SC_x(t) = SC_x(t - dt) + (G_{in} - G_{out} - D_x) * dt \quad (12)$$

where  $SC_x$  is the size class at time  $t$ ,  $G_{in}$  is the input of trees growing to that size class,  $G_{out}$  is the trees growing out of the size class, and  $D_x$  is the death of trees.

### Sensitivity Analyses

I conducted sensitivity analyses in order to examine the impacts of changes in key components of the model on model predictions (e.g., Halpern et al. 2005). A base set of conditions representing an “average” field were used for all sensitivity runs (Table 2).

These values were determined by line transect sampling. The proportion of

cover/substrate type was visually estimated at each meter along five 50 meter transects in each of six fields. The proportions of cover and substrate types were then averaged.

Table 2. Parameters used for sensitivity analyses. Values represent mean of 6 fields.

Parameter	Initial value (m <sup>2</sup> ) used in sensitivity analyses
Cover of <i>Baccharis</i>	1728.5 m <sup>2</sup>
Cover of <i>Sphagnum</i>	762.5 m <sup>2</sup>
Cover of Bare soil	603.5 m <sup>2</sup>
Cover of Tree	(30 trees of size class 2)
Cover of Deadwood	312 m <sup>2</sup>
Cover of Ferns and grasses	1513 m <sup>2</sup>
Field size	5000 m <sup>2</sup>
Edge length	100 m
Bird density	0.16 birds with access/m of edge
Germination rate	0.60% of seeds per month

Each parameter in question was then run repeatedly through an incremental series of values centered on the mean value reported in Table 1 (e.g., Hallgren & Pitman 2000). Sensitivity analyses that were run are listed in Table 2, and include characteristics of the field and model parameters such as germination rate and rates of competition between forest trees and other cover types

Given that field data were collected in old-fields with less than 50% tree cover, it is doubtful the model, parameterized with such data, will sufficiently reflect the population and community dynamics of largely forested sites. Controls on, and relationships among,

bird density, inter-specific competition, and microclimatic conditions are likely to change over time, especially as forest grows and changes the quality of the habitat. Therefore, I do not discuss the ramifications of model predictions regarding regeneration greater than 50%, and I present 75% and 100% forest regeneration model results as points of comparison only. Due to the stochastic nature of the model I report average times until regeneration. Finally, because of the sheer volume of computing time required to run multiple analyses, minimum, median and maximum values were averaged based on 6 runs each.

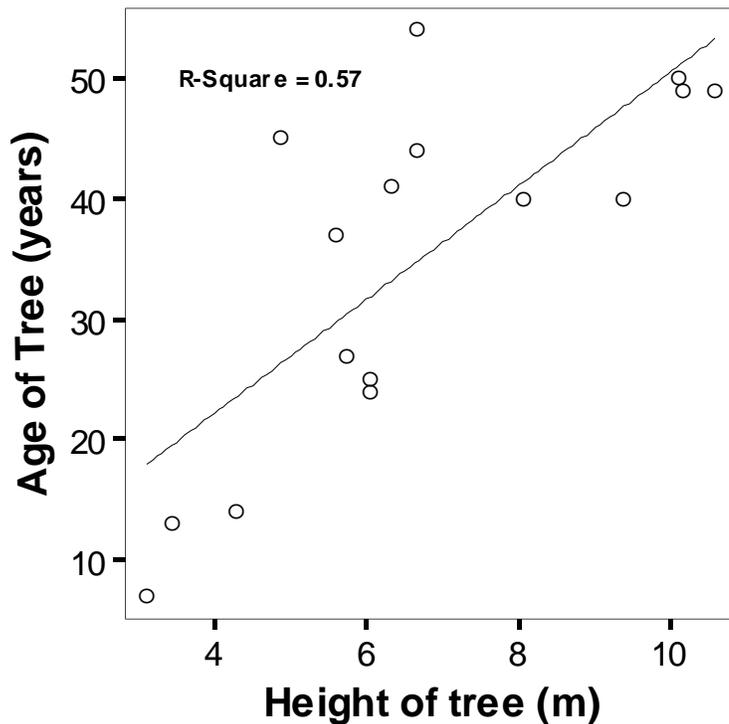


Figure 12. Correlation between the age of *Drymis winterii* (as determined by coring) and tree height.

### Management Scenarios

I applied the model to three management scenarios; a high cost, medium cost, and a do-nothing scenario. The high cost scenario assumes that the land owner has sufficient

labor and money available to add dead wood to the field, plant saplings, and perhaps even burn back some of the *Baccharis* and *Sphagnum*. In this scenario, non-forest cover types were reduced by 5% each, CWD cover was increased by 5%, and 25 saplings are planted each year. The medium cost model assumes that the farmer has an active interest in restoring the old-field, but has little resources to do so. This farmer may plant a few trees when the time is right, but will not be able to burn back the shrubs and lichen or drag abundant logs or cut pieces of CWD into the field. In this scenario CWD cover is increased by 1% and 10 saplings are planted annually. The do-nothing, or low cost, scenario assumes that the landowner lacks either resources or interest, and leaves the land as it is. Each management scenario was run with 3 starting conditions – poor, medium, and high quality fields. These three field types represent points along the continuum from very low quality fields (no trees, a lot of *Baccharis* and *Sphagnum* cover, no CWD), to very high quality fields (many trees remaining, no *Baccharis* or *Sphagnum* cover, good CWD coverage, Table 3). In all, 9 starting conditions (3 cost by 3 starting condition scenarios) were run 5 times each.

## **Results**

### **Initial Conditions**

#### **Coarse woody debris**

On average, increasing the amount of dead wood has a positive impact on the rate of forest regeneration (Fig. 13). However, as more CWD is added, diminishing returns occur, particularly after 1-2% cover of CWD. In fields with zero initial trees, the impact of CWD is more pronounced (Fig. 14).

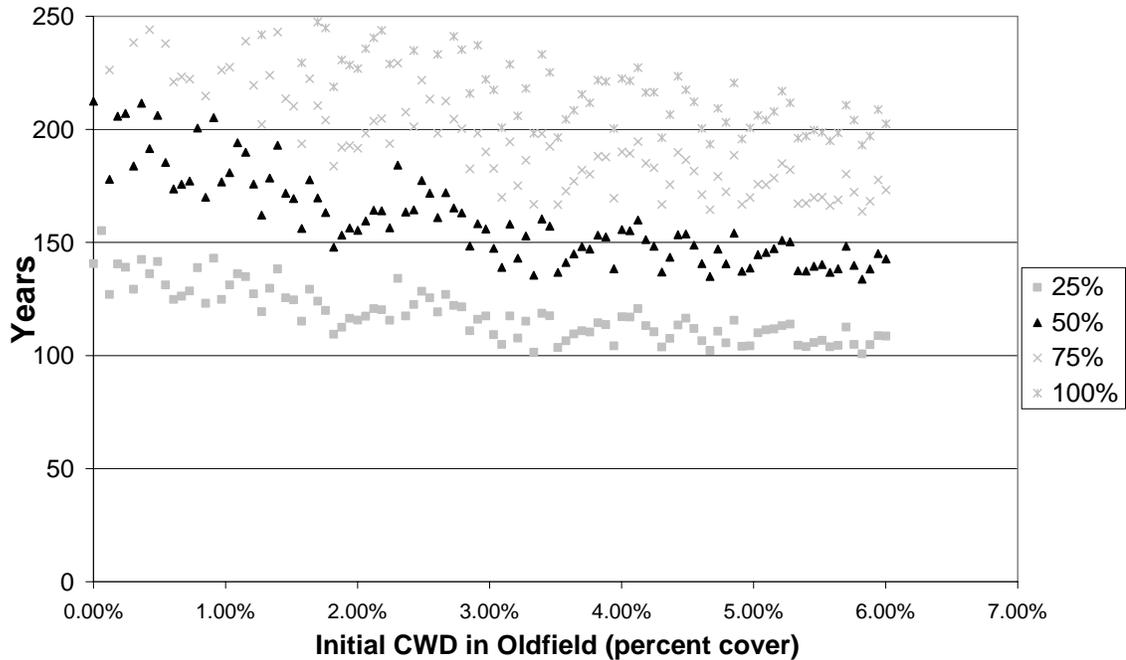


Figure 13. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial amount of coarse woody debris (CWD) is increased.

### *Baccharis*

As the initial coverage of *Baccharis* increases, the time required for forest regeneration increases (Fig. 15). In fields with less than 30% *Baccharis* cover, little effect is seen, but this is because I am measuring time until 50% regeneration, and at these low values there is little obstacle to regeneration of 50% of the old-field. Above 30% *Baccharis* cover, the impact is drastic, but is dependent on the values chosen for the rate at which forest “shades out” *Baccharis* (see below).

### *Sphagnum* and grass

Changes in the initial coverage of *Sphagnum* and of ferns and grasses show a similar pattern to that exhibited by changes in the coverage of *Baccharis* (Fig. 16 and Fig. 17). However, the percent cover required to slow forest growth corresponds with the rate

at which forest is able to out-compete either cover type. Thus, *Sphagnum* has less impact than *Baccharis*, and grass less than *Sphagnum*.

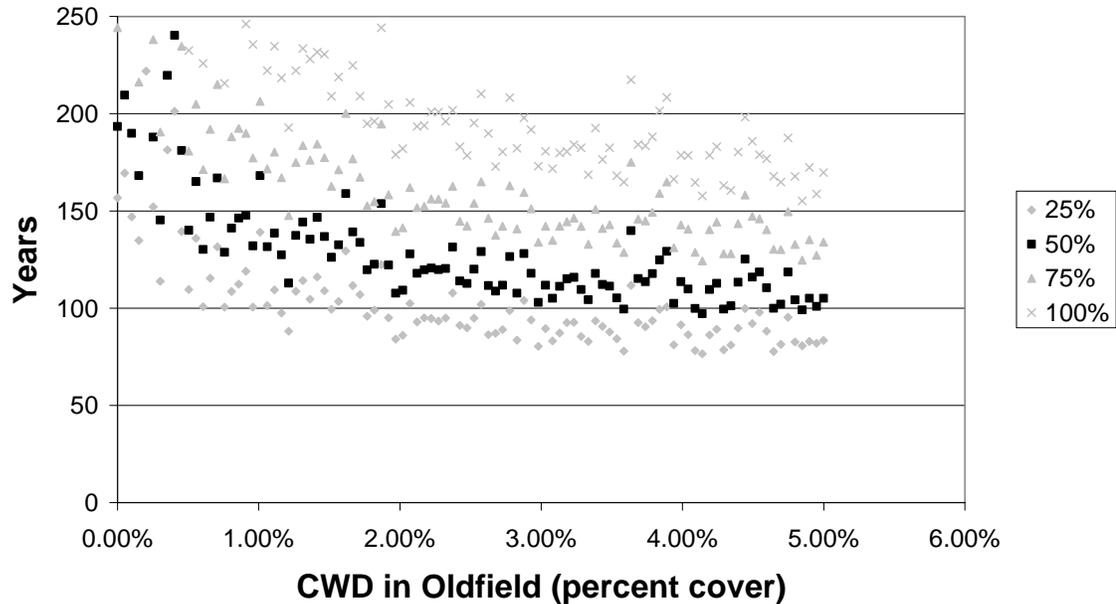


Figure 14. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial amount of coarse woody debris (CWD) is increased with zero initial trees in the old-field.

### Tree cover

Initial tree cover has some effect on rates of subsequent forest regeneration (Fig 18). The time required for 25% and 50% forest regeneration is somewhat reduced by adding more trees.

### Length of edge

Increasing the length of the border with adjacent forest proportionately decreases the time required for forest regeneration because of the increased availability of seed dispersers and seeds. For example, the difference between 125 and 225 meters of edge is far less than the difference between 25 and 125 meters of edge (Fig. 20).

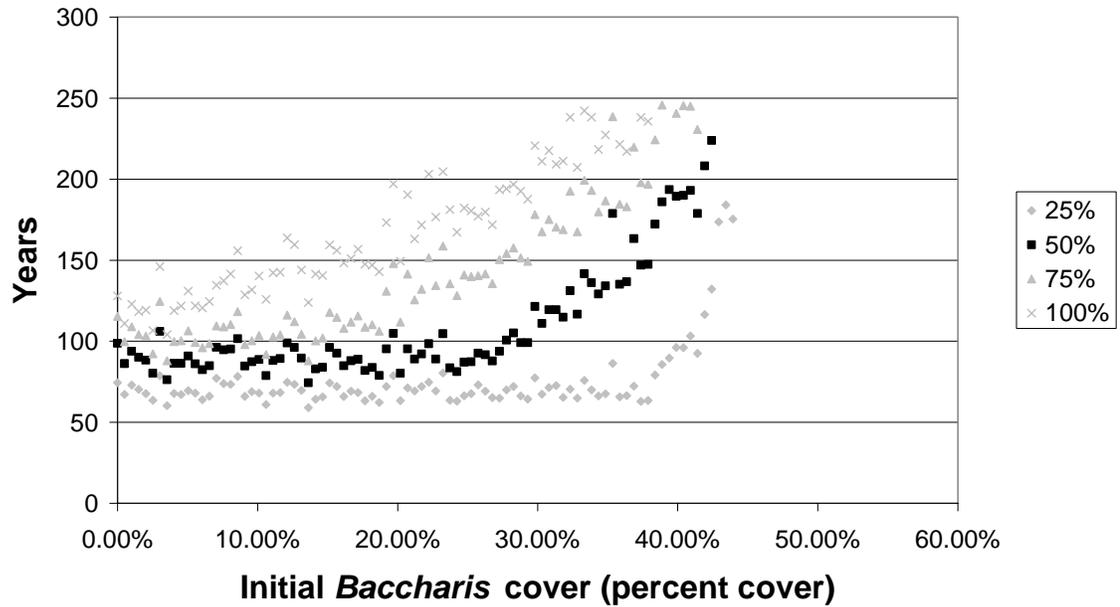


Figure 15. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial coverage of *Baccharis* is increased.

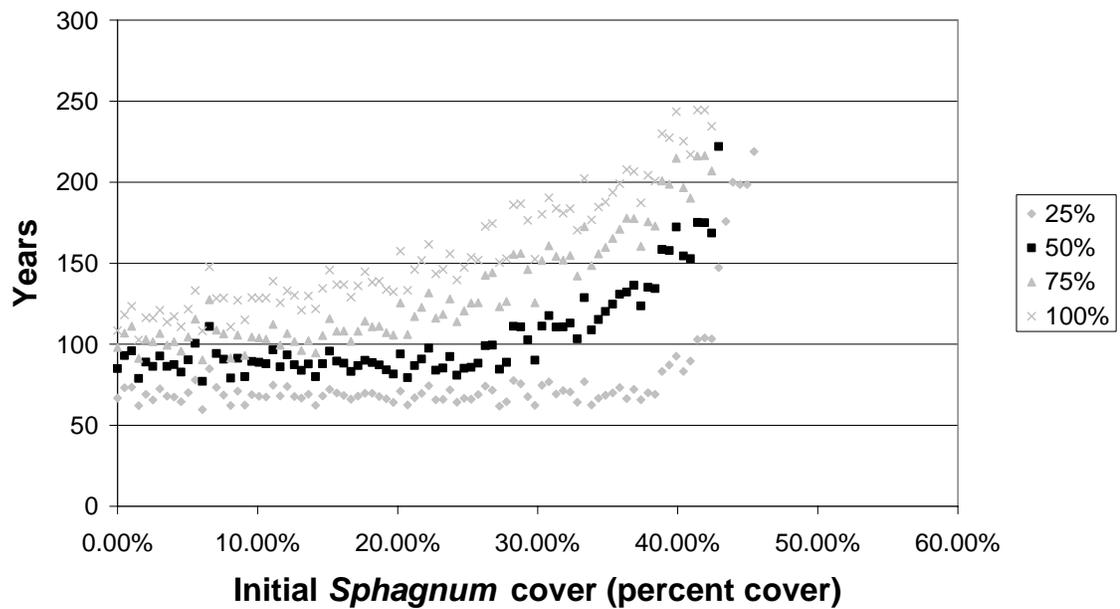


Figure 16. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial coverage of *Sphagnum* is increased.

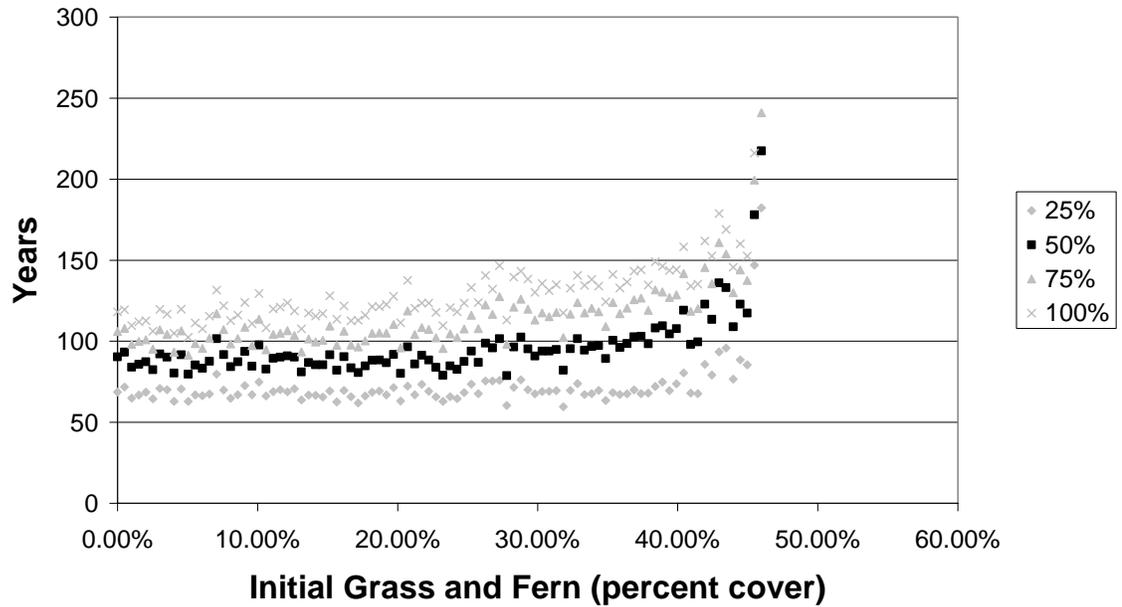


Figure 17. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial coverage of grasses and ferns is increased.

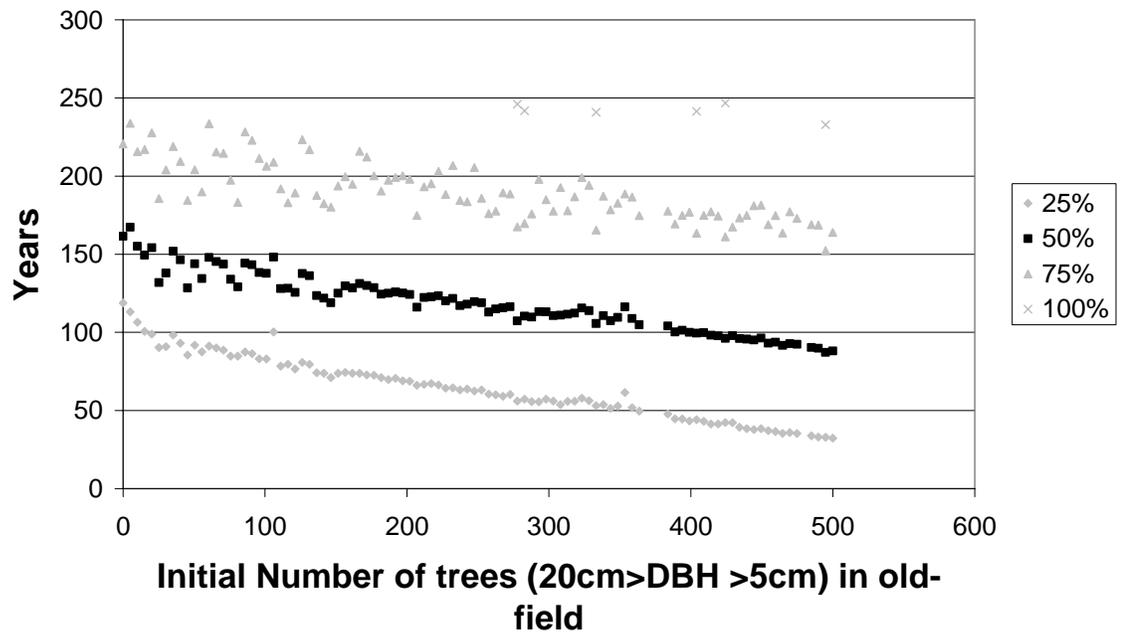


Figure 18. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial number of trees is increased.

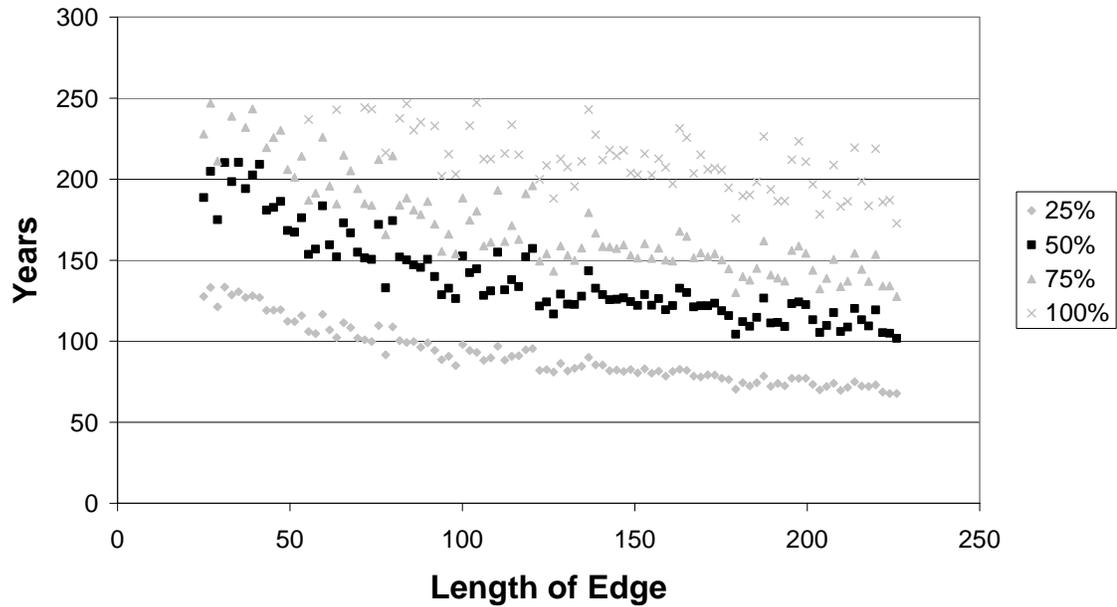


Figure 19. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the length of adjacent edge is increased.

### Bird density

As expected, forest regeneration rate is positively correlated with bird density (Fig. 20). The range in bird density values correspond with roughly 150 years in forest regeneration times.

### Sensitivity Analyses

#### Germination and tree growth rate

The variation among rates lower than 20% is much greater than among rates between 20 and 70% (Fig. 21). The value for the germination rate was difficult to obtain, and additional research is needed before the model should be used to make predictions. Field observations (Chapter 1) revealed a low germination rate of 0.98%. Conversely, controlled experiments (Figueroa & Lusk 2001; Figueroa 2003) found a germination rate for the same tree species of 75%. A reasonable compromise would return a germination rate of 35.49%, but as the model demonstrates, this is too high because at such high

germination rates, forest regenerates much faster than historical observations suggest. I conservatively chose a 6% rate of germination for the model. When subjected to sensitivity analysis, little change was seen for germination rates above 1% (Fig. 21). There is a ~125 year variation in time until 50% regeneration between 0% and 1% (Fig. 21). This extreme variation demonstrates that getting more accurate estimates of this value is critical to the successful prediction of forest regeneration. As seen in Figure 22, regeneration times vary proportionately to tree growth rates.

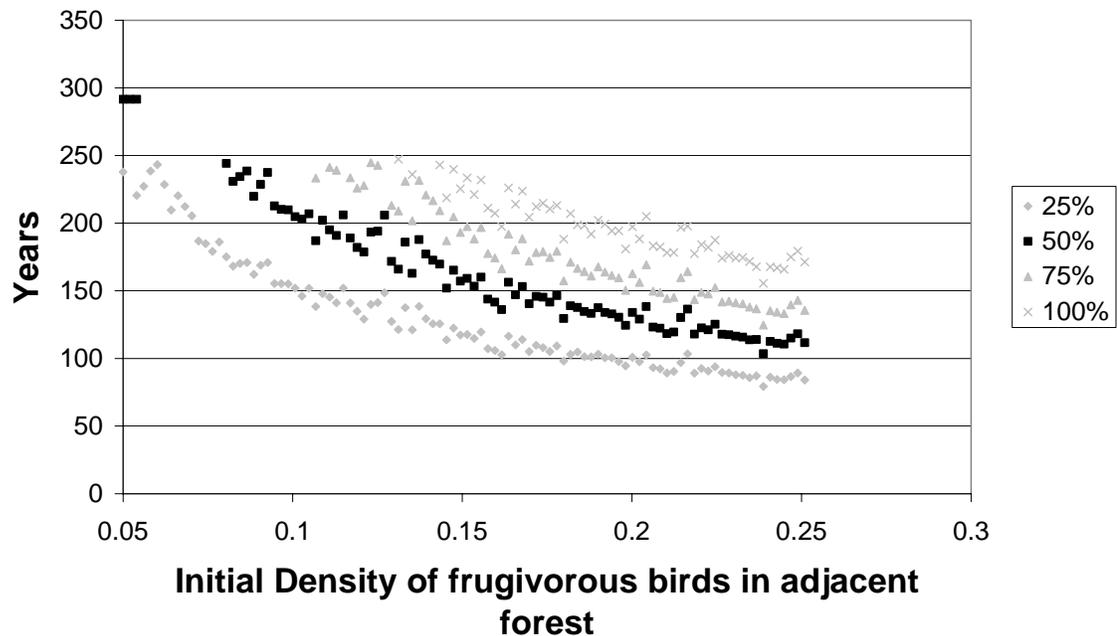


Figure 20. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the initial number of frugivorous birds is increased.

### Survival rate of seedlings on dead wood

According to Pasic and Armesto (2000), survival of seedlings is 12 times higher on CWD than on adjacent ground. However, variation in this variable had no impact on the outcome of the model (Fig. 23). Overall seedling mortality had a minor impact on time

until forest regeneration (Fig. 24). The higher the seedling mortality the longer the time required until forest regeneration.

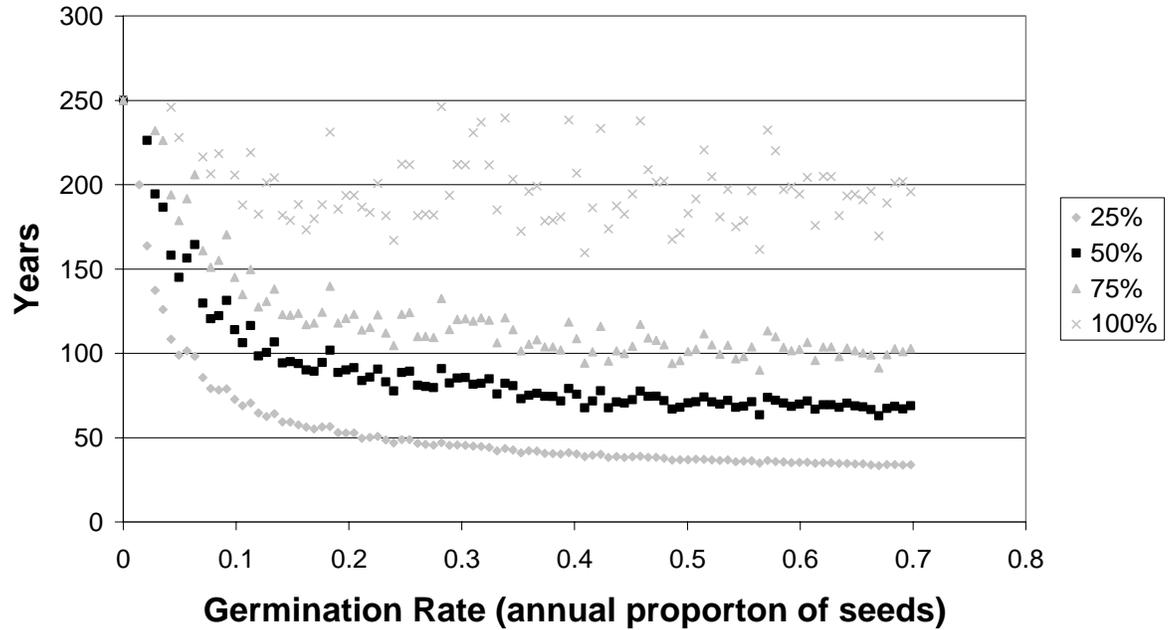


Figure 21. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the germination rate is increased.

### Rate of cover loss to forest

I parameterized the model to allow for the possibility that forest trees modify the microclimate such that it becomes unsuitable for *Baccharis*, *Sphagnum*, or grasses. However, at high rates of competition with other substrate types, the forest does not grow fast enough to take advantage of the improved habitat conditions (Figs. 25-27). On the other hand, if the time required for forest tree species to out-compete cover types such as *Sphagnum* and *Baccharis* is very high (i.e. very low rates of cover loss), it has profound effects on the model, therefore, this relationship could dictate whether or not old-fields are in a state of arrested succession. For example, if *Baccharis* is lost any faster than 0.008m<sup>2</sup> per month, there is no corresponding increase in forest cover because forest

does not grow any faster to take advantage of the increased *Baccharis* loss (Fig. 25). At a value of 0.008 m<sup>2</sup> for *Baccharis* reduction, it takes roughly 12 years for a tree to shade out 1 m<sup>2</sup> of adjacent *Baccharis*. Although these rates of loss have no effect on time until 50% regeneration in the sensitivity analyses (i.e. average levels), if a particular field has a very large area covered with *Baccharis* or *Sphagnum*, changes in competition rates can be very important.

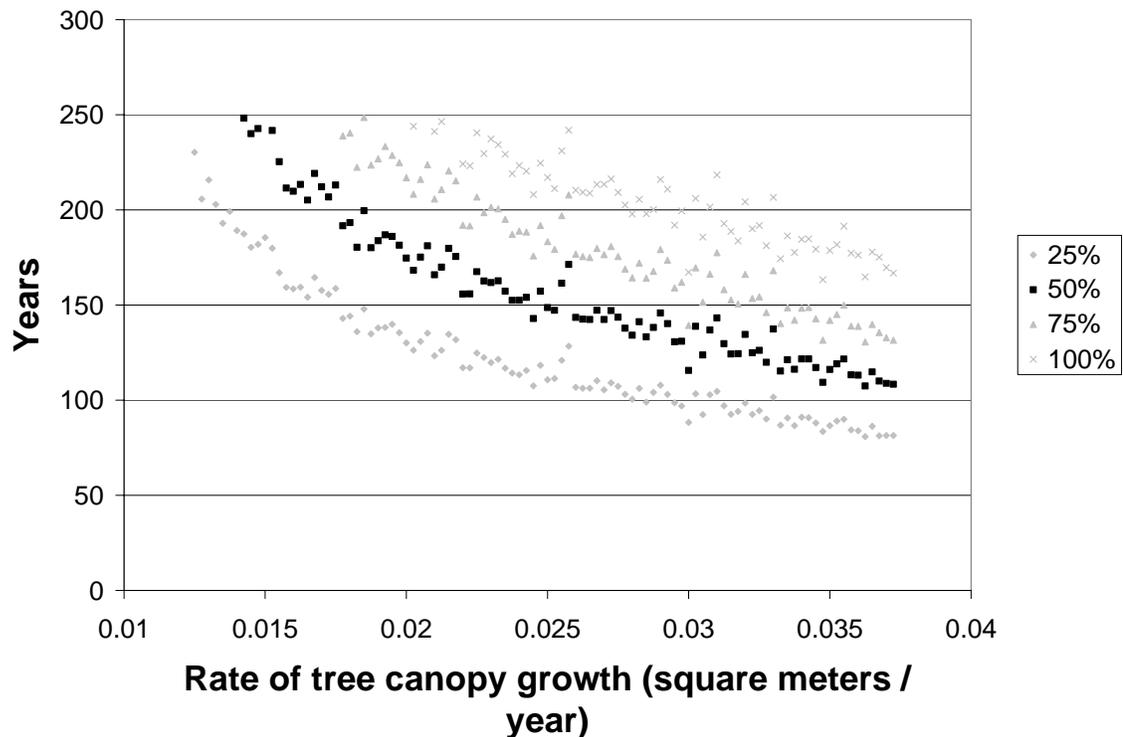


Figure 22. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the rate of tree growth is increased or decreased.

### Rarity of new recruitment-foci formation

For the model runs I chose an  $r$  (rarity of new focus formation) value of 0.1. As this value was chosen purely to keep the model estimations conservative, it is important

to subject it to sensitivity analyses. Figure 28 demonstrates that this value directly influences the rate of forest regeneration, especially at lower values.

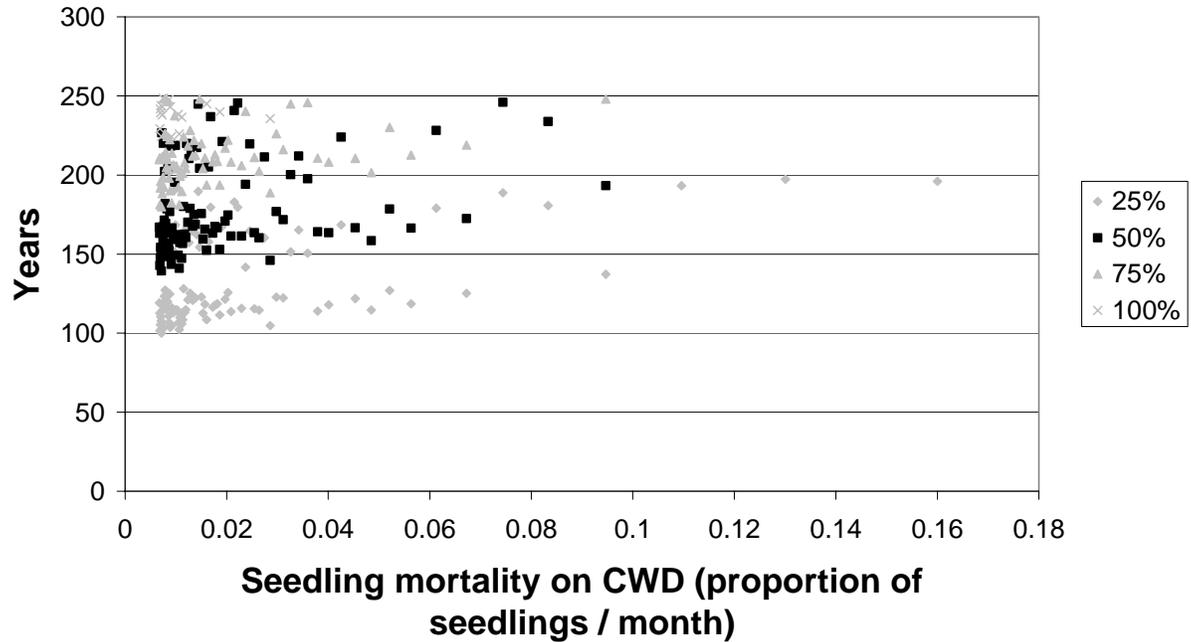


Figure 23. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the mortality of seedlings on dead wood is increased. Default mortality of seedlings is 0.16% seedlings / month.

### Management scenarios

High quality fields with high cost input (additions of both CWD and saplings) show the fastest regeneration times, followed by medium quality fields with high-cost input. All field types show significant benefits from increasing the cost of input, however low quality fields require high-cost inputs to achieve any significant regeneration at all (Table 3).

## Discussion

### Relative Importance of Seed Dispersal and Germination Limitation

When either seed dispersal or suitable germination microsites were set to very low values (limiting), the outcomes suggest that germination site availability is potentially

more limiting of forest regeneration. At very low rates of seed dispersal forest regenerates significantly faster with adequate availability of suitable germination sites than in situations with very few germination sites. My results suggest that during the initial stages of reclaiming established *Baccharis* fields, germination sites may be the more important limiting factor (Fig. 29). My results agree generally with similar studies in that both dispersal and germination are limiting factors (Costa Rican abandoned pasture – Holl et al, (2000); Puerto Rico - Zimmerman et al. (2000). Unlike these studies, however, my modeling effort allowed me to explore the relative importance of one factor versus the other over a range of realistic values of starting conditions.

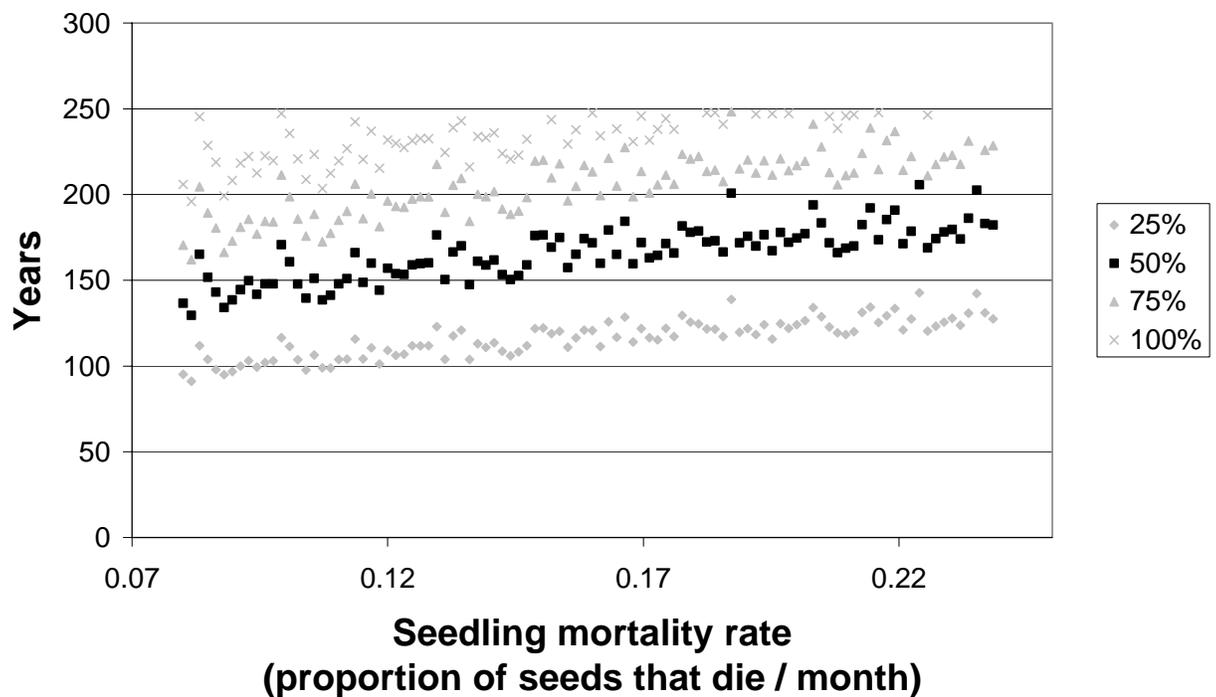


Figure 24. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the rate of seedling mortality increases.

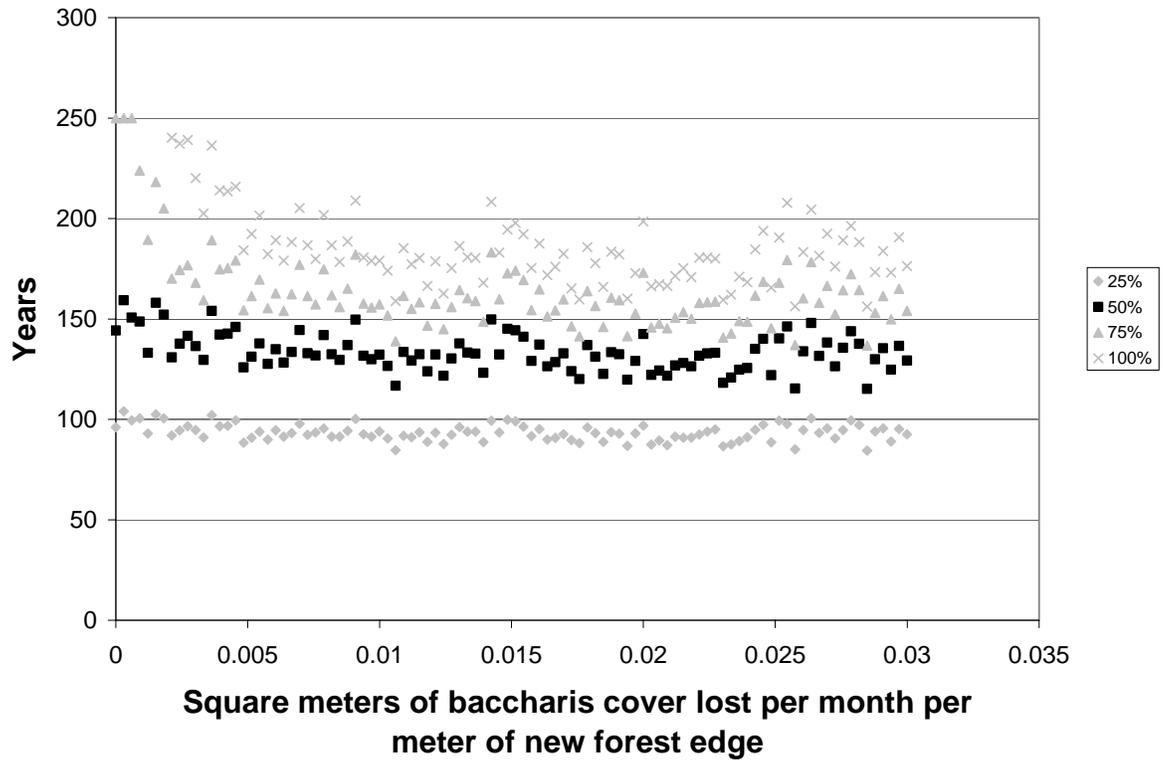


Figure 25. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the rate of out-competition of *Baccharis* is increased.

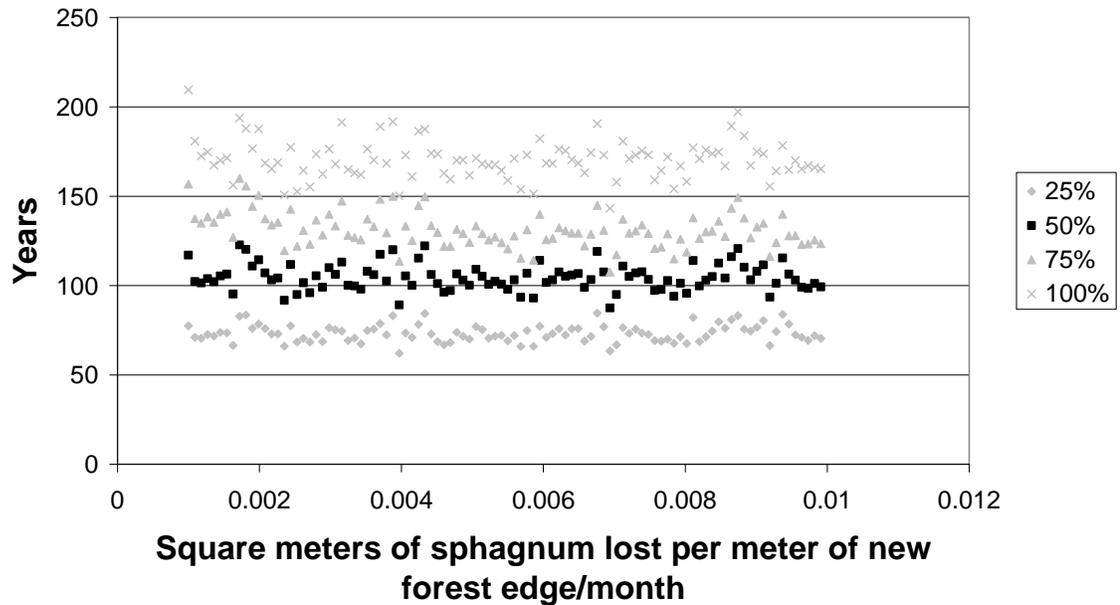


Figure 26. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the rate of out-competition of *Sphagnum* is increased.

Table 3. Field conditions, input, and time required for 50% regeneration under 3 different management scenarios and three different starting conditions. (HC= High Cost, MC= Medium Cost, LC = Low Cost, HQ = High Quality, MQ = Medium Quality, LQ = Low Quality).

	High Cost			Medium Cost			Low Cost		
	HQ	MQ	LQ	HQ	MQ	LQ	HQ	MQ	LQ
<i>Sphagnum</i> (% cover)	0%	5%	14.5%	1%	10%	19.5%	1%	10%	19.5%
<i>Baccharis</i> (% cover)	0%	10%	25%	1%	15%	30%	1%	15%	30%
Grass (% cover)	1%	10%	0%	1%	10%	0%	1%	10%	0%
Dead Wood (% cover)	10%	6%	5%	6%	2%	1%	5%	1%	0%
Saplings Planted/yr	25	25	25	10	10	10	0	0	0
Initial trees	100	50	0	100	50	0	100	50	0
Average time until 50% forest cover (years)	42	43	65	48	53	no regen	103	140	No regen

I found avian frugivores to be critical for sustaining regeneration of old-fields throughout the progression of forest accretion to recruitment foci (Fig. 20). In this way, the model suggests that the most rapid regeneration will not be achieved without constant, ample seed inputs from birds visiting the sites. As fragmentation, forest loss, and degradation of remnant forest patches intensifies, inadequate seed rain could become limiting as frugivore density and activity declines. Currently, however, the high abundance of *Elaenia albiceps* (et al. 2005) and the species' apparent tolerance for disturbance, ensure they are likely to be available at sites I studied (and most disturbed sites in Chiloé) to provide seed input, as long as there are recruitment foci available to

attract them into fields. In the case of reliable dispersal, the importance of both germination rate and availability of germination substrates (Figs. 15-17) including coarse woody debris (Fig. 13), may be relatively higher in determining variations in observed regeneration rate. But if seed dispersal ceases, then reclamation of *Baccharis* fields is unlikely to occur without intense and costly manipulations (see below).

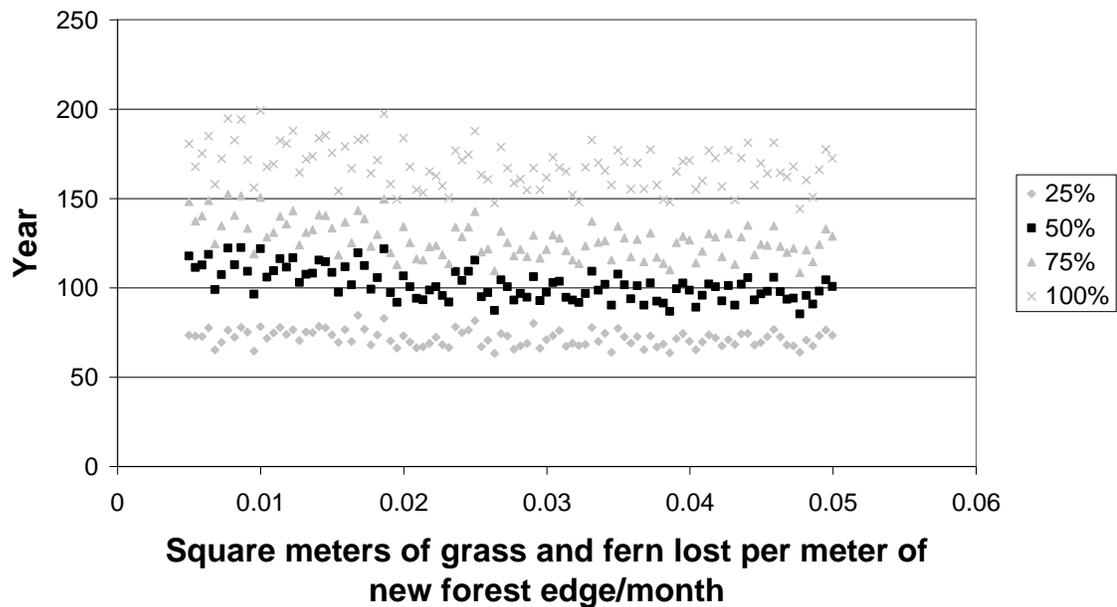


Figure 27. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the rate of out-competition of grass and fern is increased.

## Restoration Methods / Management Scenarios

### Assessment of model scenarios

Recommendations for restoring old-fields will vary somewhat according to the management scenario involved. The three field types modeled represent points along the continuum from very low quality fields (no trees, a lot of *Baccharis* and *Sphagnum* cover, no CWD), to very high quality fields (many trees remaining, no *Baccharis* or *Sphagnum* cover, good CWD coverage). Very high and very low quality fields require a different approach to ensure regeneration (Table 3). High quality fields (i.e. fields not fully

cleared or burned, or already undergoing succession) can be essentially left alone, and regeneration will still occur, although according to the model it will still require roughly 100 years. In other words, high quality fields would represent fields in which succession is not arrested. On the other hand, in low-quality fields, no regeneration occurs without significant input, including a high level of sapling planting (Table 3). The model suggests that the initial starting conditions have a large impact on the outcome of restoration efforts. Whereas increasing the input from a medium cost scenario to a high cost scenario has little impact on regeneration times for high and medium quality fields (5 or 10 year improvements), 50% regeneration does not occur within 250 years in poor quality fields without high cost inputs. Therefore, if a farmer has no resources, and wants to accelerate regeneration, he needs to avoid burning when clearing for pasture and leave fruiting tree species scattered throughout the field. Whereas, if a farmer has sufficient resources, quick regeneration can be obtained in a low quality field if labor and money are expended to plant trees and drag wood into the field (as long as it is close to forest with dense bird populations).

### **Recommendations for efficient reclamation of *Baccharis* fields**

Based on this modeling effort and exploration of scenarios derived from discussions with landowners regarding their experiences, an effective restoration strategy would need to concentrate in the following areas in the order that I consider them here.

**(1) Site location.** Areas selected for forest regeneration should be adjacent to mid-successional or old growth forest stands in order to ensure sufficient visitation and seed dispersal by *Elania albiceps* (Díaz et al. 2005). Seed dispersal into old-fields clearly helps sustain any attempts at restoration, whether a landowner is relying principally on manipulations (additions of CWD and plantings) or natural processes (Figs. 19 and 20).

A landowner without resources for restoration, but with a variety of potential sites and flexibility in choosing which sites can be allowed to go back to forest is not without recourse. A high quality field (with trees and CWD) near a proper forest edge can be set aside for forest regeneration and has a high likelihood of becoming a forest without any manipulation, though even a small number of plantings could help speed the process considerably (Table 3).

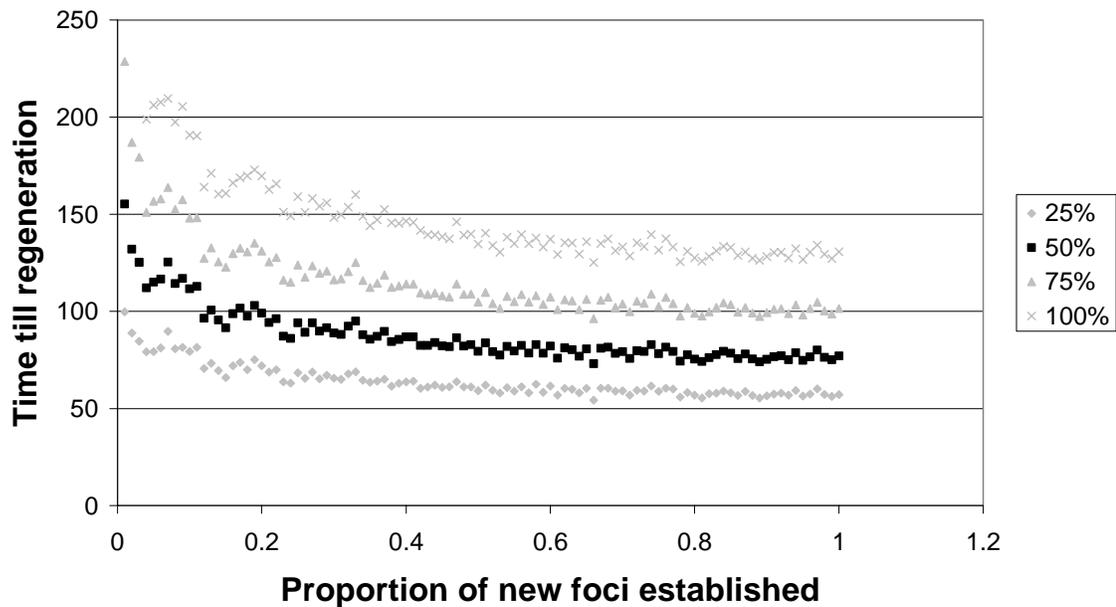


Figure 28. Model prediction of the number of years required to achieve 25, 50, 75 and 100% regeneration of degraded old-field habitat as the value of “r” (additional rarity of new recruitment foci establishment) is increased.

The best time to make the decision regarding placement of a potential regeneration site is before complete forest clearing occurs. If, for example, only partial clearing and no burning was done, followed by an observation period of a year; an assessment of a site’s best use could be accomplished while the site was still of high quality (in terms of regeneration potential). If the physical conditions of the cleared site proved to foster *Baccharis* rather than drier land use options (e.g., pasture) then the site should be left to regenerate to forest while the landowner assessed other sites for non-forest land uses.

This kind of assessment would save a great deal of wasted labor; as landowners we work with relate that certain *Baccharis*-dominated sites (apparently, the most mesic ones) can be cleared and burned repeatedly without successful establishment of pasture or cropland. After repeated burning and complete clearing, these sites rapidly reach states of stable *Baccharis-Sphagnum* cover. My work suggests this occurs because such sites are devoid of suitable germination substrates. Thereafter, these sites remain in an unproductive stable state of no, or only marginal, use to humans and wildlife (Darnell and Sieving, in press, Díaz et al. 2005). Therefore, intensive clearing and burning of such sites, without timely assessment of future use, leads directly to more forest clearing and the spread of *Baccharis*. To my knowledge, there is no way of determining, prior to beginning forest clearing, what post-clearing site characteristics will be with respect to *Baccharis* formation, although some research is beginning to address this idea in other systems (Chanasyk et al. 2003). Therefore, I put forward the recommendation to partially clear and then wait to see what the site tendencies appear to be.

**(2) Germination sites.** Given a proper location close to forest to insure adequate dispersal, then the next focus should be on providing sufficient germination substrates. Depending on the number of trees, amount of CWD, and shrub cover of the old-field, this could entail the addition of CWD and/or the removal of *Baccharis* and *Sphagnum*. The positive impacts of CWD are significant (Papic & Armesto 2000, suggested by model). However, the degree of benefit obtained from adding dead wood to a site depends on initial condition of the field. Fields show a slight benefit from an increase in the initial amount of dead wood, likely because any impact that dead wood might have as sites for new foci is swamped by positive germination conditions provided by existing recruitment

foci. However, in fields with no trees initially, the impact of CWD as nurse logs is profound (Fig. 14). For example, with 0 trees, the time required for regeneration of 50% forest cover decreased from 200 years with no dead wood, to roughly 100 years when 2% of the field is covered with CWD. The importance of CWD in ecosystem function is no longer underestimated (Carmona et al. 2002), especially in facilitation of recruitment of new trees (McGee & Birmingham 1997; Slocum 2000).

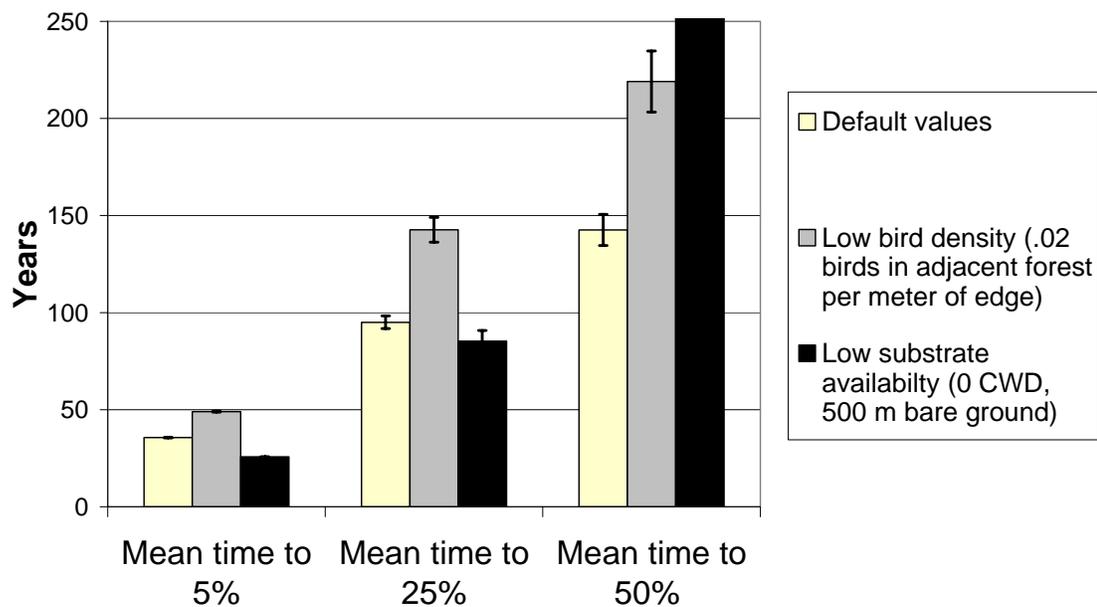


Figure 29. Time predicted for regeneration of forest (to 5, 25, and 50% forest cover) with low densities of seed dispersers, compared with time required for regeneration with very few micro-sites suitable for germination, compared to default values of each (see text). Error bars represent 1 SD.

**(3) Shrub and *Sphagnum* management.** Even though, in some cases, shrubs can act as facilitators to forest regeneration (Duncan & Chapman 2003; Holl 2002; Li & Wilson 1998; Zahawl & Auspurger 1999), they often have the opposite effect. Shrubs inhibit seedling growth in Appalachian canopy gaps (Beckage et al. 2000). Similarly, Denslow et al. (1991) found evidence for inhibition of tree seedling establishment by broad-leaved understory plants in the tropics. Finally, Hill et al. (1995) found that shrub canopies

along utility rights of way in New York were very resistant to invasion. Therefore, in the context of restoring *Baccharis* fields given the presence of both avian seed dispersers and suitable microsites for germination, the single most important deterrent to forest succession is the presence of *Sphagnum* and *Baccharis*. This is because seeds simply cannot germinate and survive in direct competition with these two cover types (Table 3, Figs. 15 and 16). Instead of burning away the shrub and moss layer - which can only be done during the two driest summer months and may destroy CWD and seedlings - perhaps the most parsimonious approach is to reduce competition with these cover types at the edges of recruitment foci by physical means (cutting shrubs and trampling at the perimeter of recruitment foci). Providing a modest sized open buffer of suitable germination substrate (e.g., bare ground, or modest CWD) around trees and tree clusters would release one of the main inhibitors of the rate of regeneration suggested by the model; competitive effects at the edges of recruitment foci (Figs. 15, 16, and 17), and may be less labor-intensive than manipulations at the scale of whole fields.

**(4) Planting trees.** Finally, I would suggest actively planting new trees in old-fields.

The model demonstrates that planting just a few trees each year can have a large impact on forest regeneration (Fig. 30). Reay and Norton (1999) found that without plantings, restoration in a New Zealand temperate forest proceeded at a much slower pace.

According to the model, an average field (as defined above; see Methods: Sensitivity Analyses) will require 157 years to reach 50% tree canopy cover. Planting 10 trees per ha per year will reduce the time to 83 years, as predicted by my model. Further increasing the rate of tree planting does little to decrease the regeneration rate (Fig. 30), likely due to limitations on the growth rate of trees, and competition from *Baccharis* and

*Sphagnum*. However, as discussed in Chapter 1, there may be a threshold value for the number of trees required to lure avian seed dispersers into old-fields. Further research is required before this can be incorporated into the model. Although this model overlooks potential differences between species, planting trees of a variety of forest species and paying attention to the facilitative effects of various species may be very important (Jansen 1997).

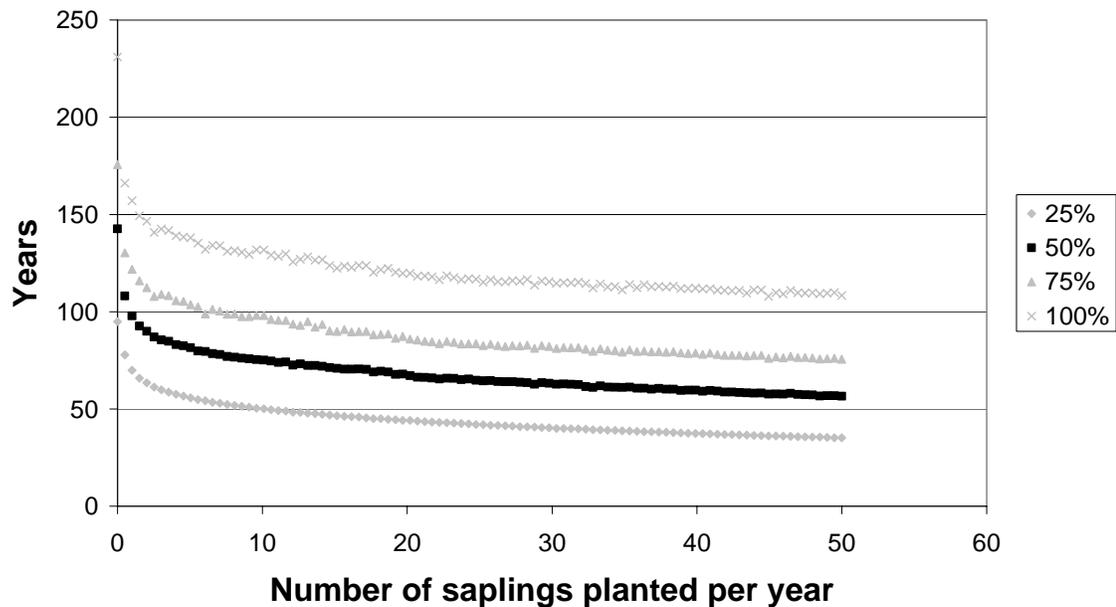


Figure 30. Model prediction of the effect of the number of saplings planted annually on the rate of forest regeneration (to 25, 50, 75, 100% forest cover).

Finally, another type of planting, not addressed by my work, is of the native bamboo (*Chusquea valdiviensis*), which is very attractive to native understory birds (Reid et al. 2004). Large patches of bamboo occur naturally associated with all seral stages of south-temperate rainforest (Donoso 1996). It would be worthwhile investigating the influence of bamboo on tree establishment in these fields due to its potential to provide habitat immediately. However, the benefits of bamboo as a disperser attractant may be offset by its negative impact on seedling establishment (Donoso & Nyland 2005).

## **Assessment of the Model**

### **Complexity**

While it is far from a complete description of the south temperate rainforest ecosystem, this model acts as a good starting point for future research and hypothesis generation. By necessity the model is far simpler than the ecosystem that it represents. All tree-related data were obtained regarding only one species (*Drimys winterii*). This species is not a poor choice, however, because it is one of the most common bird dispersed colonizers of old-fields (Armesto et al. 2001a) and occurs in all seral stages of forest in this region (Lusk & Del Pozo 2002). Models of greater complexity are in use for similar studies. For example, LANDIS – a spatially explicit landscape model (Mladenoff et al. 1996) - could incorporate a variety of tree and understory species with unique demographic characteristics into regeneration scenarios. Additionally, a more accurate (and much more complex) model might factor in such variables as carbon, other nutrient and water cycles and energy flows (Kirschbaum 1999). However, by maintaining simplicity, I was able to focus on parameters relevant to my original research question concerning the relative importance of seedling establishment and seed dispersal. Moreover, there is some merit in keeping the model simple and utilizing statistical methods (e.g., Monte Carlo method) to model the stochastic properties inherent in complex systems (Young et al. 1996).

### **Relevant scales**

Because most key ecological processes of forest regeneration at edges take place within 50 meters of the forest, the effects of larger spatial scales were ignored, even though seed dispersers, for example, operate at larger scales. While I was constrained in my field approaches (Chapter 1) to work on processes relevant to field-forest ecotones, I

do not think my conclusions concerning restoration of old-fields in general are inaccurate because forest regeneration in old fields tends to occur through accretion at edges of recruitment foci and remnant patches (Debussche & Isenmann 1994). In order to incorporate larger-scale site characteristics, like attenuation in seed dispersal with distance from forest, further study of avian frugivore movements would have been required. I deemed this unnecessary because in the landscape where I worked, most *Baccharis* fields were not more than 250-300 m wide. Frugivorous birds readily and quickly crossed these open areas between patches of forest, so it is unlikely that dispersal was dramatically different throughout the fields. In order to select sites that were equivalent in proximity to forest patches and other land use types, the plot size I used to collect data was easy to standardize from a design perspective. Perhaps the greatest caution in using the model is relevant to the combined effects of the long time scales involved and the potential that (over such long times) factors originating beyond the spatial scale of the site could be significantly involved in determining final outcomes (Parker 1997).

### **Model improvement**

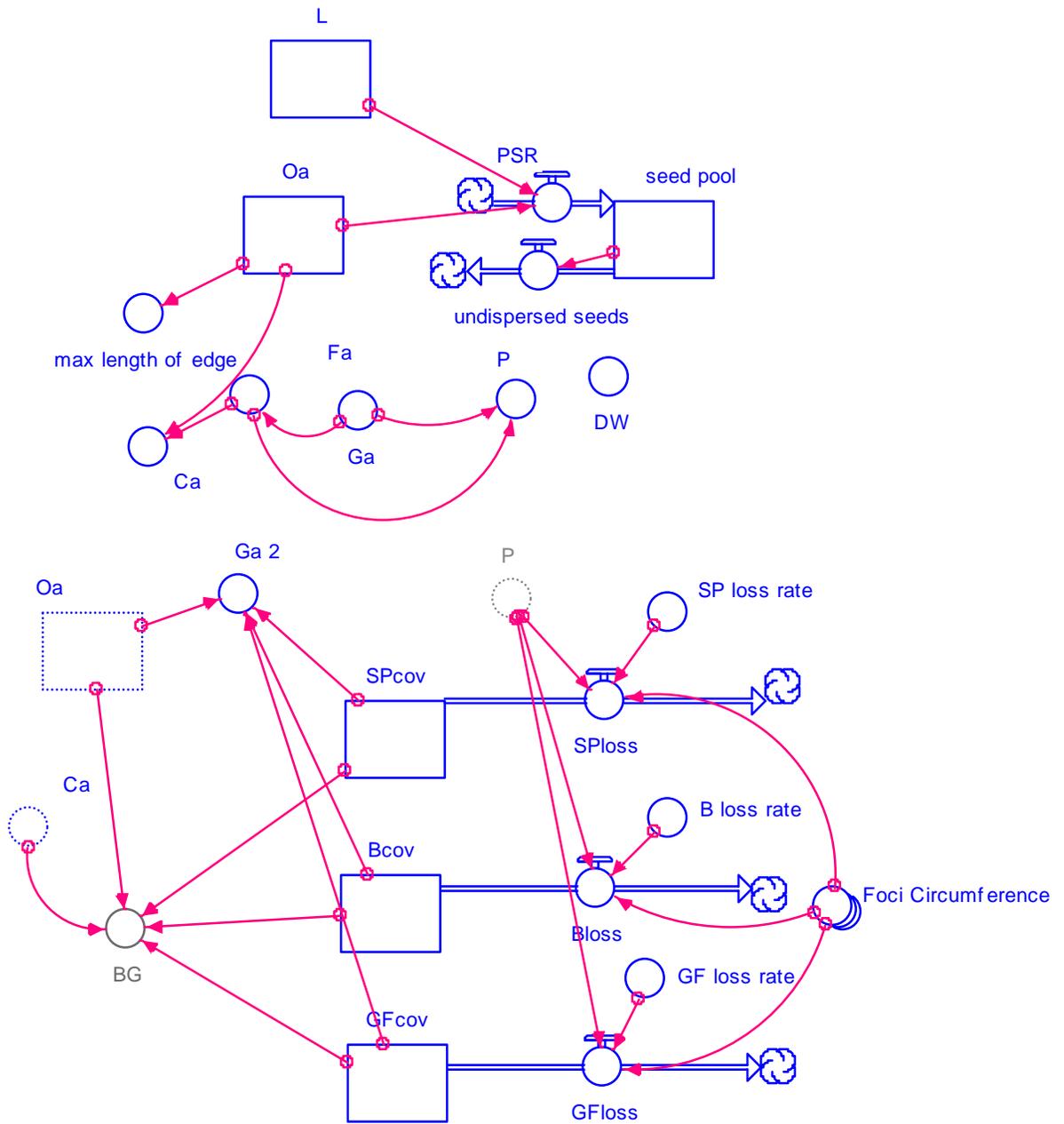
One major assumption of the model is that *Baccharis*, *Sphagnum* and grass are static features of the old-field (i.e. they do not increase in area). In reality they are likely to increase in cover area when not in direct competition with trees, but including this dynamic was not feasible. However, this simplification could overlook important dynamics of the system (Duncan & Chapman 2003; Holl 2002), and is deserving of further work.

Finally, I suggest that the influence of standing water be incorporated into modeling efforts, and that greater understanding of the hydrology of these sites is

necessary. Currently, standing water is assumed to be a factor leading to the increased survival rate of seedlings on CWD. However, an analysis of historic weather trends, combined with study of germination rates of immersed seeds may better illuminate the role that the hydrology of the system plays in forest regeneration. Moreover, it also seems important to establish the validity of a central assumption we make, based in part on observations, that the water table is affected by forest clearing. We assume that one of the reasons landowners clear so many areas that become wet and shrub-dominated is that a high water table is not evident prior to clearing, but that the water table often rises following clearing (e.g., Sun et al. 2000). This could occur in sites dominated by tree species with high transpiration rates. Other sites, with lower rates of transpiration, may be more easily assessed as to post-clearing hydrology. Further knowledge is needed regarding site characteristics that can predict the outcome of forest clearing (e.g., Chanasyk et al. 2003). If arrested succession can be avoided by informed choices before forest clearing, this would reduce the overall impact on an already fragmented ecosystem. For fields already in an arrested state, it is hoped that this research and further research will shed some light on returning old fields to forests that provide benefits to both humans and wildlife.

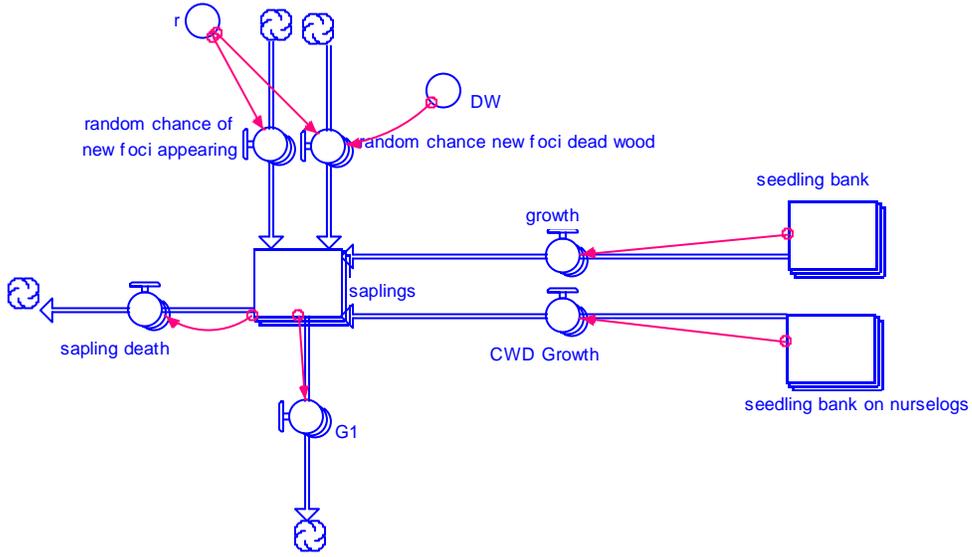
APPENDIX A  
 ICONOGRAPHIC REPRESENTATION OF MODEL

OLD-FIELD CHARACTERISTICS

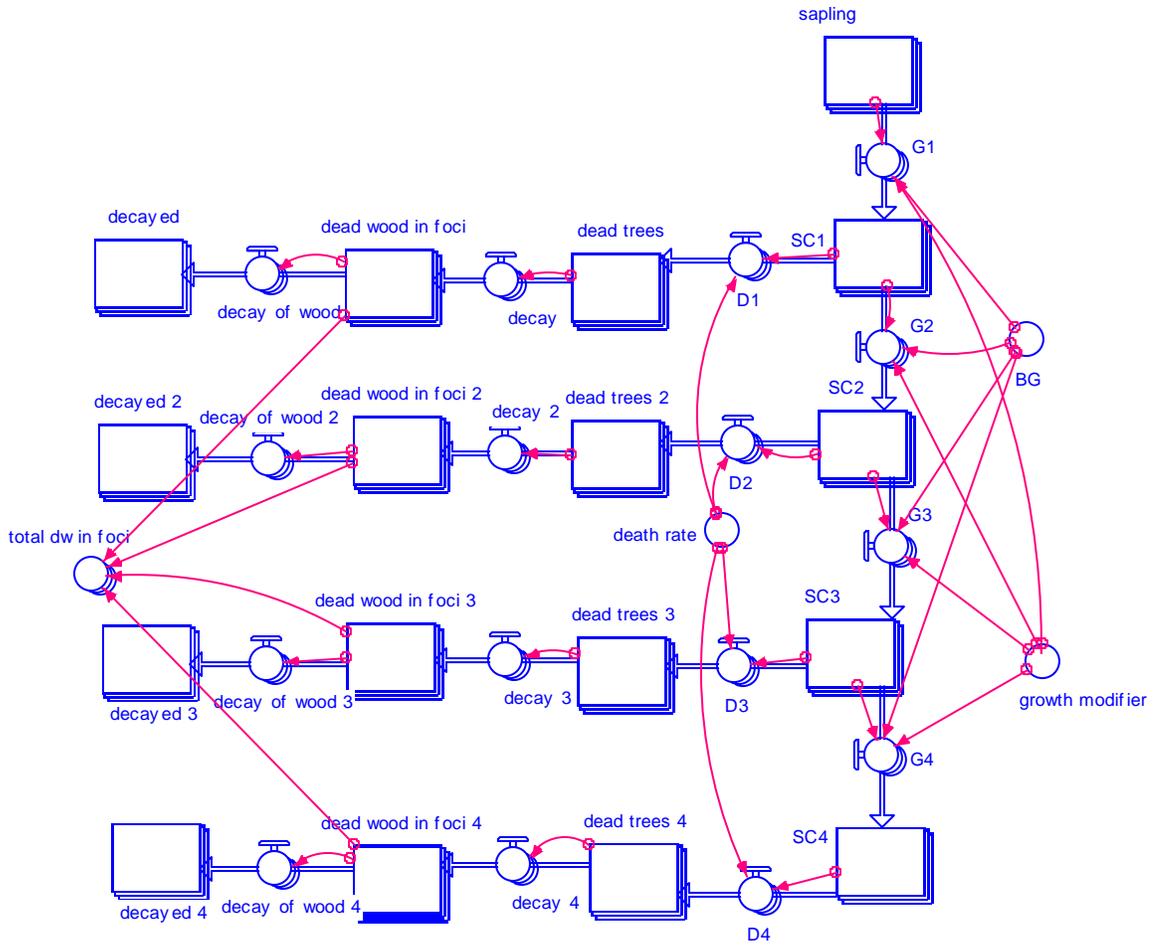




### CREATION OF NEW RECRUITMENT FOCI



### TREE GROWTH AND SURVIVAL





APPENDIX B  
MODEL EQUATIONS

**OLD-FIELD CHARACTERISTICS**

$$L(t) = L(t - dt)$$
$$\text{INIT } L = 0$$

$$Oa(t) = Oa(t - dt)$$
$$\text{INIT } Oa = 0$$

$$Ca = Fa/Oa$$

$$Db = .15625$$

$$Fa = \text{IF } (\text{total\_attractive\_trees} + .0000000000001) * 1.68 > Ga \text{ THEN } Ga \text{ ELSE } (\text{total\_attractive\_trees} + .0000000000001) * 1.68$$

$$\text{max\_length\_of\_edge} = (\text{SQRT}(Oa)) * 4$$

$$Bcov(t) = Bcov(t - dt) + (- Bloss) * dt$$

$$\text{INIT } Bcov = 0$$

OUTFLOWS:

$$Bloss = \text{IF } P > 0.999 \text{ THEN } \text{ARRAYSUM}(Fc[*]) * (B\_loss\_rate) \text{ ELSE } 0$$

$$GFcov(t) = GFcov(t - dt) + (- GFloss) * dt$$

$$\text{INIT } GFcov = 0$$

OUTFLOWS:

$$GFloss = \text{IF } P > 0.999 \text{ THEN } \text{ARRAYSUM}(Fc[*]) * GF\_loss\_rate \text{ ELSE } 0$$

$$SPcov(t) = SPcov(t - dt) + (- SPloss) * dt$$

$$\text{INIT } SPcov = 0$$

OUTFLOWS:

$$SPloss = \text{IF } P > 0.999 \text{ THEN } \text{ARRAYSUM}(Fc[*]) * (SP\_loss\_rate) \text{ ELSE } 0$$

$$BG = Oa - (Bcov + SPcov + GFcov + (Ca * Oa))$$

$$B\_loss\_rate = 1/288$$

Ga = IF (Oa-(Bcov+GFcov+SPcov)) <= 0 THEN .000000001 ELSE (Oa-(Bcov+GFcov+SPcov))

GF\_loss\_rate = 1/48

SP\_loss\_rate = 1/180

### SEED RAIN

seed\_pool(t) = seed\_pool(t - dt) + (PSR - ASR[1] - ASR[2] - ASR[3] - ASR[4] - ASR[5] - ASR[6] - ASR[7] - ASR[8] - ASR[9] - ASR[10] - ASR[11] - ASR[12] - ASR[13] - ASR[14] - ASR[15] - ASR[16] - ASR[17] - ASR[18] - ASR[19] - ASR[20] - ASR[21] - ASR[22] - ASR[23] - ASR[24] - ASR[25] - ASR[26] - ASR[27] - ASR[28] - ASR[29] - ASR[30] - ASR[AllFoci] - undispersed\_seeds) \* dt  
INIT seed\_pool = 0

INFLOWS:

PSR = (Sr\*Oa)\*(L/100)\*(Db/.15625)

OUTFLOWS:

ASR[AllFoci] = (seed\_pool\*((Af[AllFoci]/Oa)))\*Fg[AllFoci]

undispersed\_seeds = seed\_pool-(ARRAYSUM(ASR[\*]))

Sf[AllFoci](t) = Sf[AllFoci](t - dt) + (ASR[AllFoci] - G[AllFoci] - seed\_death[AllFoci]) \* dt

INIT Sf[AllFoci] = 0

INFLOWS:

ASR[AllFoci] = (seed\_pool\*((Af[AllFoci]/Oa)))\*Fg[AllFoci]

OUTFLOWS:

seed\_death[AllFoci] = (Sf[AllFoci]-G[AllFoci])

Af[AllFoci] = trees\_in\_foci[AllFoci]\*1.68

Fg[AllFoci] = (Af[AllFoci]- (((SQRT(Af[AllFoci]/PI))- 0.5)^2)\*PI)/(Af[AllFoci]+.0000000000000001)

Sr = GRAPH(total\_attractive\_trees)

(0.00, 1.82), (36.6, 1.82), (73.2, 1.82), (110, 1.79), (146, 1.76), (183, 1.73), (220, 1.70), (256, 1.67), (293, 1.64), (329, 1.61), (366, 1.58), (402, 1.55), (439, 1.52), (476, 1.49), (512, 1.46), (549, 1.43), (585, 1.40), (622, 1.37), (659, 1.34), (695, 1.31), (732, 1.28), (768, 1.25), (805, 1.22), (841, 1.19), (878, 1.16), (915, 1.13), (951, 1.10), (988, 1.07), (1024, 1.04), (1061, 1.01), (1098, 0.98), (1134, 0.95), (1171, 0.92), (1207, 0.89), (1244,

0.86), (1280, 0.83), (1317, 0.8), (1354, 0.77), (1390, 0.74), (1427, 0.71), (1463, 0.68), (1500, 0.65)

### **SEED GERMINATION AND SEEDLING SURVIVAL**

seedlings[AllFoci](t) = seedlings[AllFoci](t - dt) + (G[AllFoci] - transition[AllFoci] - transition\_dw[AllFoci]) \* dt  
 INIT seedlings[AllFoci] = 0

INFLOWS:

G[AllFoci] = IF BG < 1 THEN 0 ELSE ((Sf[AllFoci]\*Gr))

OUTFLOWS:

transition[AllFoci] = ((seedlings[AllFoci]\*non\_dead\_wood\_proportion[AllFoci]))

transition\_dw[AllFoci] = seedlings[AllFoci]\*dw\_proportion[AllFoci]

seedling\_bank[AllFoci](t) = seedling\_bank[AllFoci](t - dt) + (transition[AllFoci] - growth[AllFoci] - Dseedling[AllFoci]) \* dt

INIT seedling\_bank[AllFoci] = 0

INFLOWS:

transition[AllFoci] = ((seedlings[AllFoci]\*non\_dead\_wood\_proportion[AllFoci]))

OUTFLOWS:

growth[AllFoci] = (IF BG < 1 THEN 0 ELSE  
 seedling\_bank[AllFoci]/12)+(Dseedling[AllFoci]\*0)

Dseedling[AllFoci] = (seedling\_mortality)\*seedling\_bank[AllFoci]

seedling\_bank\_on\_nurselogs[AllFoci](t) = seedling\_bank\_on\_nurselogs[AllFoci](t - dt) + (transition\_dw[AllFoci] - DCWDseedling[AllFoci] - CWD\_Growth[AllFoci]) \* dt

INIT seedling\_bank\_on\_nurselogs[AllFoci] = 0

INFLOWS:

transition\_dw[AllFoci] = seedlings[AllFoci]\*dw\_proportion[AllFoci]

OUTFLOWS:

DCWDseedling[AllFoci] =  
 ((seedling\_mortality/CWD\_death\_rate))\*seedling\_bank\_on\_nurselogs[AllFoci]

CWD\_death\_rate = 12

dw\_proportion[AllFoci] = total\_dw\_in\_foci[AllFoci]\*2/(Af[AllFoci] + .000000000001)

Gr = 0

non\_dead\_wood\_proportion[AllFoci] = (1-dw\_proportion[AllFoci])

seedling\_mortality = .04

### **CREATION OF NEW RECRUITMENT FOCI**

random\_chance\_new\_foci\_dead\_wood[AllFoci] = (IF Af[AllFoci] = 0 THEN  
MONTECARLO((0.103/12)\*DW\*0.23\*((L/100)\*(Db/0.15625)\*r)) ELSE 0)

INFLOW TO: sapling (IN SECTOR: Tree Growth and Survival)  
random\_chance\_of\_new\_foci\_appearing[AllFoci] = (IF Af[AllFoci] = 0 THEN  
MONTECARLO((0.063/12)\*BG\*0.02\*((L/100)\*(Db/0.15625)\*r)) ELSE 0)

INFLOW TO: sapling (IN SECTOR: Tree Growth and Survival)  
DW = 0  
r = .1

### **TREE GROWTH AND SURVIVAL**

dead\_trees[AllFoci](t) = dead\_trees[AllFoci](t - dt) + (D1[AllFoci] - decay[AllFoci]) \* dt  
INIT dead\_trees[AllFoci] = 0

INFLOWS:  
D1[AllFoci] = death\_modifier\*.89\*SC1[AllFoci]

OUTFLOWS:  
decay[AllFoci] = dead\_trees[AllFoci]/120

dead\_trees\_2[AllFoci](t) = dead\_trees\_2[AllFoci](t - dt) + (D2[AllFoci] -  
decay\_2[AllFoci]) \* dt  
INIT dead\_trees\_2[AllFoci] = 0

INFLOWS:  
D2[AllFoci] = death\_modifier\*.94\*SC2[AllFoci]

OUTFLOWS:  
decay\_2[AllFoci] = dead\_trees\_2[AllFoci]/120

dead\_trees\_3[AllFoci](t) = dead\_trees\_3[AllFoci](t - dt) + (D3[AllFoci] -  
decay\_3[AllFoci]) \* dt  
INIT dead\_trees\_3[AllFoci] = 0

INFLOWS:  
D3[AllFoci] = death\_modifier\*1.06\*SC3[AllFoci]

OUTFLOWS:  
decay\_3[AllFoci] = dead\_trees\_3[AllFoci]/120

$dead\_trees\_4[AllFoci](t) = dead\_trees\_4[AllFoci](t - dt) + (D4[AllFoci] - decay\_4[AllFoci]) * dt$   
 INIT  $dead\_trees\_4[AllFoci] = 0$

INFLOWS:

$D4[AllFoci] = (death\_modifier) * 1.11 * SC4[AllFoci]$

OUTFLOWS:

$decay\_4[AllFoci] = dead\_trees\_4[AllFoci]/120$

$dead\_wood\_in\_foci[AllFoci](t) = dead\_wood\_in\_foci[AllFoci](t - dt) + (decay[AllFoci] - decay\_of\_wood[AllFoci]) * dt$   
 INIT  $dead\_wood\_in\_foci[AllFoci] = 0$

INFLOWS:

$decay[AllFoci] = dead\_trees[AllFoci]/120$

OUTFLOWS:

$decay\_of\_wood[AllFoci] = dead\_wood\_in\_foci[AllFoci]/120$

$dead\_wood\_in\_foci\_2[AllFoci](t) = dead\_wood\_in\_foci\_2[AllFoci](t - dt) + (decay\_2[AllFoci] - decay\_of\_wood\_2[AllFoci]) * dt$

INIT  $dead\_wood\_in\_foci\_2[AllFoci] = 0$

INFLOWS:

$decay\_2[AllFoci] = dead\_trees\_2[AllFoci]/120$

OUTFLOWS:

$decay\_of\_wood\_2[AllFoci] = dead\_wood\_in\_foci\_2[AllFoci]/120$

$dead\_wood\_in\_foci\_3[AllFoci](t) = dead\_wood\_in\_foci\_3[AllFoci](t - dt) + (decay\_3[AllFoci] - decay\_of\_wood\_3[AllFoci]) * dt$

INIT  $dead\_wood\_in\_foci\_3[AllFoci] = 0$

INFLOWS:

$decay\_3[AllFoci] = dead\_trees\_3[AllFoci]/120$

OUTFLOWS:

$decay\_of\_wood\_3[AllFoci] = dead\_wood\_in\_foci\_3[AllFoci]/120$

$dead\_wood\_in\_foci\_4[AllFoci](t) = dead\_wood\_in\_foci\_4[AllFoci](t - dt) + (decay\_4[AllFoci] - decay\_of\_wood\_4[AllFoci]) * dt$

INIT  $dead\_wood\_in\_foci\_4[AllFoci] = 0$

INFLOWS:

$decay\_4[AllFoci] = dead\_trees\_4[AllFoci]/120$

## OUTFLOWS:

$$\text{decay\_of\_wood\_4}[\text{AllFoci}] = \text{dead\_wood\_in\_foci\_4}[\text{AllFoci}]/120$$

$$\text{decayed}[\text{AllFoci}](t) = \text{decayed}[\text{AllFoci}](t - dt) + (\text{decay\_of\_wood}[\text{AllFoci}]) * dt$$

$$\text{INIT decayed}[\text{AllFoci}] = 0$$

## INFLOWS:

$$\text{decay\_of\_wood}[\text{AllFoci}] = \text{dead\_wood\_in\_foci}[\text{AllFoci}]/120$$

$$\text{decayed\_2}[\text{AllFoci}](t) = \text{decayed\_2}[\text{AllFoci}](t - dt) + (\text{decay\_of\_wood\_2}[\text{AllFoci}]) * dt$$

$$\text{INIT decayed\_2}[\text{AllFoci}] = 0$$

## INFLOWS:

$$\text{decay\_of\_wood\_2}[\text{AllFoci}] = \text{dead\_wood\_in\_foci\_2}[\text{AllFoci}]/120$$

$$\text{sapling}[\text{AllFoci}](t) = \text{sapling}[\text{AllFoci}](t - dt) + (\text{growth}[\text{AllFoci}] + \text{input}[\text{AllFoci}] +$$

$$\text{CWD\_Growth}[\text{AllFoci}] + \text{random\_chance\_new\_foci\_dead\_wood}[\text{AllFoci}] +$$

$$\text{random\_chance\_of\_new\_foci\_appearing}[\text{AllFoci}] - \text{G1}[\text{AllFoci}] -$$

$$\text{sapling\_death}[\text{AllFoci}]) * dt$$

$$\text{INIT sapling}[\text{AllFoci}] = 0$$

## INFLOWS:

growth[AllFoci] (IN SECTOR: Seed Germination and Seedling Survival)

$$\text{input}[1] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[2] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[3] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[4] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[5] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[6] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[7] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[8] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[9] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[10] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[11] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[12] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[13] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[14] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[15] = \text{annual\_sapling\_addition}/180$$

$$\text{input}[16] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[17] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[18] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[19] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[20] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[21] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[22] = \text{annual\_sapling\_addition} * 0$$

$$\text{input}[23] = \text{annual\_sapling\_addition} * 0$$

input[24] = annual\_sapling\_addition\*0  
 input[25] = annual\_sapling\_addition\*0  
 input[26] = annual\_sapling\_addition\*0  
 input[27] = annual\_sapling\_addition\*0  
 input[28] = annual\_sapling\_addition\*0  
 input[29] = annual\_sapling\_addition\*0  
 input[30] = annual\_sapling\_addition\*0

CWD\_Growth[AllFoci] (Not in a sector)

random\_chance\_new\_foci\_dead\_wood[AllFoci] (IN SECTOR: Chance of new foci appearing)

random\_chance\_of\_new\_foci\_appearing[AllFoci] (IN SECTOR: Chance of new foci appearing)

OUTFLOWS:

$G1[AllFoci] = (IF\ BG < 1\ THEN\ 0\ ELSE\ sapling[AllFoci]/292.75)*growth\_modifier$

$sapling\_death[AllFoci] = .0083*sapling[AllFoci]$

$SC1[AllFoci](t) = SC1[AllFoci](t - dt) + (G1[AllFoci] - G2[AllFoci] - D1[AllFoci]) * dt$   
 INIT SC1[AllFoci] = 0

INFLOWS:

$G1[AllFoci] = (IF\ BG < 1\ THEN\ 0\ ELSE\ sapling[AllFoci]/292.75)*growth\_modifier$

OUTFLOWS:

$G2[AllFoci] = (IF\ BG < 1\ THEN\ 0\ ELSE\ SC1[AllFoci]/342.75)*growth\_modifier$

$D1[AllFoci] = death\_modifier*.89*SC1[AllFoci]$

$SC2[AllFoci](t) = SC2[AllFoci](t - dt) + (G2[AllFoci] - G3[AllFoci] - D2[AllFoci]) * dt$   
 INIT SC2[AllFoci] = 0

INFLOWS:

$G2[AllFoci] = (IF\ BG < 1\ THEN\ 0\ ELSE\ SC1[AllFoci]/342.75)*growth\_modifier$

OUTFLOWS:

$G3[AllFoci] = (IF\ BG < 1\ THEN\ 0\ ELSE\ SC2[AllFoci]/687.5)*growth\_modifier$

$D2[AllFoci] = death\_modifier*.94*SC2[AllFoci]$

$SC3[AllFoci](t) = SC3[AllFoci](t - dt) + (G3[AllFoci] - G4[AllFoci] - D3[AllFoci]) * dt$   
 INIT SC3[AllFoci] = 0

INFLOWS:

$$G3[\text{AllFoci}] = (\text{IF BG} < 1 \text{ THEN } 0 \text{ ELSE } \text{SC2}[\text{AllFoci}]/687.5) * \text{growth\_modifier}$$

OUTFLOWS:

$$G4[\text{AllFoci}] = (\text{IF BG} < 1 \text{ THEN } 0 \text{ ELSE } \text{SC3}[\text{AllFoci}]/1075) * \text{growth\_modifier}$$

$$D3[\text{AllFoci}] = \text{death\_modifier} * 1.06 * \text{SC3}[\text{AllFoci}]$$

$$\text{SC4}[\text{AllFoci}](t) = \text{SC4}[\text{AllFoci}](t - dt) + (G4[\text{AllFoci}] - D4[\text{AllFoci}]) * dt$$

$$\text{INIT SC4}[\text{AllFoci}] = 0$$

INFLOWS:

$$G4[\text{AllFoci}] = (\text{IF BG} < 1 \text{ THEN } 0 \text{ ELSE } \text{SC3}[\text{AllFoci}]/1075) * \text{growth\_modifier}$$

OUTFLOWS:

$$D4[\text{AllFoci}] = (\text{death\_modifier}) * 1.11 * \text{SC4}[\text{AllFoci}]$$

$$\text{annual\_sapling\_addition} = 0$$

$$\text{death\_modifier} = 0.00181$$

$$\begin{aligned} \text{number\_of\_foci} = & (\text{IF trees\_in\_foci}[1] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[2] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[3] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[4] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[5] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[6] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[7] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[8] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[9] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[10] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[11] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[12] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[13] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[14] \\ & > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[15] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF} \\ & \text{trees\_in\_foci}[16] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[17] > 0 \text{ THEN } 1 \text{ ELSE } 0) + \\ & (\text{IF trees\_in\_foci}[18] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[19] > 0 \text{ THEN } 1 \text{ ELSE } 0) \\ & + (\text{IF trees\_in\_foci}[20] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[21] > 0 \text{ THEN } 1 \text{ ELSE} \\ & 0) + (\text{IF trees\_in\_foci}[22] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[23] > 0 \text{ THEN } 1 \\ & \text{ELSE } 0) + (\text{IF trees\_in\_foci}[24] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[25] > 0 \text{ THEN} \\ & 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[26] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[27] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[28] > 0 \text{ THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[29] > 0 \\ & \text{THEN } 1 \text{ ELSE } 0) + (\text{IF trees\_in\_foci}[30] > 0 \text{ THEN } 1 \text{ ELSE } 0) \end{aligned}$$

$$\text{total\_dw\_in\_foci}[\text{AllFoci}] =$$

$$((\text{dead\_wood\_in\_foci}[\text{AllFoci}] * .5) + \text{dead\_wood\_in\_foci\_2}[\text{AllFoci}] + (\text{dead\_wood\_in\_foci\_3}[\text{AllFoci}] * 2) + (\text{dead\_wood\_in\_foci\_4}[\text{AllFoci}] * 3))$$

$$\text{trees\_in\_foci}[\text{AllFoci}] =$$

$$((\text{dead\_trees}[\text{AllFoci}] + \text{dead\_wood\_in\_foci}[\text{AllFoci}] + \text{SC1}[\text{AllFoci}] + \text{decayed}[\text{AllFoci}]) * .5) + ((\text{dead\_trees\_2}[\text{AllFoci}] + \text{dead\_wood\_in\_foci\_2}[\text{AllFoci}] + \text{decayed\_2}[\text{AllFoci}] + \text{SC2}[\text{AllFoci}])) + ((\text{dead\_trees\_3}[\text{AllFoci}] + \text{dead\_wood\_in\_foci\_3}[\text{AllFoci}] + \text{decayed\_3}[\text{AllFoci}]))$$

]+SC3[AllFoci])\*2)+((dead\_trees\_4[AllFoci]+dead\_wood\_in\_foci\_4[AllFoci]+decayed\_4[AllFoci]+SC4[AllFoci])\*3)

Not in a sector

decayed\_3[AllFoci](t) = decayed\_3[AllFoci](t - dt) + (decay\_of\_wood\_3[AllFoci]) \* dt  
INIT decayed\_3[AllFoci] = 0

INFLOWS:

decay\_of\_wood\_3[AllFoci] (IN SECTOR: Tree Growth and Survival)

decayed\_4[AllFoci](t) = decayed\_4[AllFoci](t - dt) + (decay\_of\_wood\_4[AllFoci]) \* dt  
INIT decayed\_4[AllFoci] = 0

INFLOWS:

decay\_of\_wood\_4[AllFoci] (IN SECTOR: Tree Growth and Survival)

CWD\_Growth[AllFoci] = (IF BG < 1 THEN 0 ELSE  
seedling\_bank\_on\_nurselogs[AllFoci]/12)+(DCWDseedling[AllFoci]\*0)

OUTFLOW FROM: seedling\_bank\_on\_nurselogs (IN SECTOR: Seed Germination and Seedling Survival)

INFLOW TO: sapling (IN SECTOR: Tree Growth and Survival)

Fc[AllFoci] = (2\*PI)\*(SQRT(Af[AllFoci]/PI)

growth\_modifier = 1

P = (Fa/Ga)

total\_attractive\_trees = (ARRAYSUM(SC1[\*])\*0.5)+ ARRAYSUM(SC2[\*]) +  
(ARRAYSUM(SC3[\*])\*2) + (ARRAYSUM(SC4[\*])\*3) +  
(ARRAYSUM(dead\_trees[\*])\*0.5) + ARRAYSUM(dead\_trees\_2[\*]) +  
(ARRAYSUM(dead\_trees\_3[\*])\*6) + (ARRAYSUM(dead\_trees\_4[\*])\*9) +  
(ARRAYSUM(dead\_wood\_in\_foci[\*])\*0.5) + ARRAYSUM(dead\_wood\_in\_foci\_2[\*]) +  
(ARRAYSUM(dead\_wood\_in\_foci\_3[\*])\*2) +  
(ARRAYSUM(dead\_wood\_in\_foci\_4[\*])\*3) + (ARRAYSUM(decayed[\*])\*0.5) +  
ARRAYSUM(decayed\_2[\*]) + (ARRAYSUM(decayed\_3[\*])\*2) +  
(ARRAYSUM(decayed\_4[\*])\*3)

year = TIME/12

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## BIOGRAPHICAL SKETCH

Michael was born amongst the suburban sprawl that is otherwise known as West Palm Beach, Florida. It was there that his father, a wetland biologist, helped to instill a great love of the natural world in his young son. After 18 years of life in a drained wetland, Michael moved to Gainesville, Florida, to attend the University of Florida and become a rabid fan of Gator football. Despite his interests in writing and philosophy, as well as his steadfast desire not to follow in his father's footsteps, Michael graduated in 1999 with a B.S. in wildlife ecology and conservation. A love of Gainesville, a great advisor, a noble research goal, and a chance to do research in Southern Chile all conspired to keep Michael in Gainesville to write this thesis. Now that this thesis is finally done, Michael hopes to pursue a career integrating ecological research with information technology, spend a lot of time thinking about as much as possible, have lots of fun, and continue learning amazing things.