CHAPTER 1

Two surrogates for wildfire, prescribed burning and mechanical clearing, differentially affect demography of a rare, endemic plant

ABSTRACT

Alteration of historic disturbance regimes is one of the biggest threats to species' persistence. This is particularly true for species adapted to frequent, low-intensity fires. When restoration via prescribed fire is not an option, surrogate methods of clearing vegetation are needed. We use an observational study of fire effects and an experimental study of mechanical clearing to test how restoration techniques affect individual vital rates and population growth rate of a rare, endemic plant *Croton linearis*. We found that survival rates one-year post-disturbance were similar across mechanical clearing, prescribed fire, and control plots. Two-years post treatment, however, survival in burned plots was much higher than that in either mechanically cleared plots or controls. Both fire and mechanical treatments stimulated a flush of recruitment in the first-year post disturbance but not in the second year, and we saw very little recruitment in control plots in either year. These vital rates combined to produce stable populations two years post treatment in the fire plots and shrinking populations in both mechanically cleared and control plots. Our results suggest that when possible, prescribed fire should be used to manage *C. linearis* populations. Because mechanical clearing increases recruitment, it is potentially a better alternative than no action. By focusing on vital rates instead of community level responses, we were able to calculate population growth rates and therefore predict how management will affect the trajectories of species of interest in the future. This mechanistic approach is especially important for maintaining and restoring rare species populations in an era of rapid change.

INTRODUCTION

Fire adapted ecosystems are among the world's most endangered (Noss et al. 1995). Loss of fire-dependent ecosystems is highest near human development, as people restrict or eliminate fire near their homes, cities, and farms. Loss of natural fire regimes remains a threat even within protected areas. In many cases, this is a legacy of historical management, in which fire was viewed as a neutral or even negative process in maintaining habitat. Without fire, however, succession fundamentally alters the competitive landscape for plants and animals, changing habitat structure and species composition, ultimately leading to extirpation of species adapted to historic fire regimes (Leach & Givnish 1996; Bond & Keeley 2005; Ratajczak et al. 2011).The preferred management strategy in these systems is prescribed fire. However, lighting fires can be difficult due to high costs, narrow prescription windows, and the threat of escape (Miller & Wade 2003). This results in the need for habitat management that replicates the effects of fire such as mechanical understory removal. Mechanical methods mimic the effects of fire on vegetation structure but have different effects on below ground processes and litter dynamics (Moghaddas & Stephens 2007; Youngblood et al. 2008; Stephens et al. 2012); differences that could result in altered population dynamics for fire-adapted species. We test how prescribed fire and a surrogate, mechanical understory removal, affect survival, recruitment, and population growth rates of a rare plant.

The success of fire management and its surrogates, in terms of rare species restoration, will be determined by the effects a management strategy has on population size and growth rates of target species. Efforts to understand how fires and their surrogate management strategies affect populations should, therefore, focus on estimating responses of vital rates. The differential effects of restoration strategies have been examined in many fire prone systems, however, these

comparisons focus on community responses or changes in species cover rather than individual vital rates (Perchemlides et al. 2008; Steen et al. 2013a; 2013b). Studies that do focus on vital rates generally only examine the effects of fire and do not compare fire to other management strategies (Liu et al. 2005; Menges 2007, but see Gross et al. 1998). The advantage of focusing on vital rates is that it allows for estimation of population growth rates, and therefore, of the future trajectory of the population. This information is especially important for land managers tasked with the job of ensuring the survival of threatened and endangered plants and animals. Understanding the likely trajectory of a population following a specific management action feeds into the decision-making process. With this information, land managers can consider the full range of costs, benefits, and risks when deciding between different management strategies (van Wilgen 2013).

By focusing on how vital rates are affected by different management strategies, we can begin to tease apart the mechanisms that underlie species responses to habitat management. As an example that is particularly relevant to our study, plants that are adapted to frequent fires generally fall into one of two categories, seeders and sprouters (Keeley 1977). This distinction between seeders and sprouters is generally based on the vital rate that contributes the most to a plant's population growth rate following a fire. Seeders are killed by fires, but have extensive seed banks, the germination of which is stimulated by heat or chemical cues, such as smoke or charcoal (Keeley et al. 2011). For these species, conditions that promote germination from the seedbank are most important for population recovery post-fire. Sprouters lose their above-ground biomass as a result of fires but survive and re-sprout following the fire. Re-sprouting often depends on resources stored underground in carbohydrate rich lignotubers or other structures which are unaffected by the fire (Bond & Midgley 2001). Unlike germination, re-sprouting post-

fire does not rely on specific environmental cues but is instead a response to the loss of above ground biomass. The goal of mechanical fire surrogates is to replicate the vegetation structure of frequently burned systems by removing standing above ground biomass and reducing canopy cover, thereby increasing the amount of sunlight reaching the ground (Stephens et al. 2009). These methods differ from fires in that they leave a layer of mulch and debris behind, plant material that would be consumed and recycled in a fire (Youngblood et al. 2008). This key difference between mechanical treatments and fires has the potential to interact with species life history, potentially promoting a specific set of adaptations over others. For example, we might expect mechanical treatments to favor sprouters that respond to biomass loss over seeders that rely on heat or chemical cues for germination. If this is the case, we predict mechanical surrogates and prescribed fires to have similar effects on sprouter vital rates, but very different effects on seeder vital rates. We might also expect these two restoration treatments to differentially effect animal species through differential effects on key resources such as nesting sites or food. This kind of detailed information about vital rates will allow us to better design fire surrogates to promote target species and potentially predict how different species may respond to a given treatment based on life history traits.

We test the effects of fire and mechanical restoration treatments on vital rates of pineland croton (*Croton linearis* [Euphorbiaceae], hereafter referred to as croton), a rare plant endemic to fire-adapted pine rocklands in South Florida. Although not listed as endangered itself, croton is the only host for two endangered butterflies, Bartram's scrub-hairstreak (*Strymon acis bartrami*) and Florida leafwing (*Anaea troglodyta*). After habitat loss, loss of disturbance regime is the primary reason for declines in these species. Most of the remaining pine rockland fragments are surrounded by people in Miami-Dade county and on Big Pine Key, making fire difficult to

implement and mechanical treatments an attractive alternative. Working in an experimental study of mechanical clearing and an observational study of fire effects, we ask: do fire and mechanical clearing result in similar survival and recruitment responses and population growth rates? This research is essential for understanding population level responses of this rare plant to habitat restoration and has implications for restoration of other species, specifically the butterflies that rely on croton.

METHODS

Study system

Pine rocklands are found only in south Florida, The Bahamas, and Turks and Caicos where they grow directly out of the limestone substrate. These forests are characterized by open stands of South Florida slash pines (*Pinus ellioti* var. densa) and an open shrub/palm subcanopy, below which a rich herbaceous community thrives. In south Florida, pine rocklands once extended along the Miami rock ridge, from North Miami Beach to Everglades National Park, and a few islands in the Florida Keys. Ninety percent of the pine rockland on mainland south Florida and much of the habitat in the Keys has been cleared for development in the last 100 years. The largest remaining pine rocklands are protected within Everglades National Park, Navy Wells – a Miami-Dade County Natural Area, and the National Key Deer Refuge on Big Pine Key. Given this large decline of pine rockland habitat, croton populations have declined and become increasingly fragmented. Pine rockland habitat loss affects not only croton, but the butterflies that rely on it, Bartram's scrub-hairstreak and Florida leafwing. Declines in these butterfly populations are closely linked with the fragmentation and loss of croton populations in the landscape.

Remaining pine rocklands are vulnerable to lack of disturbance and subsequent forest succession, which excludes croton, this is true even within protected areas. Historically, pine rocklands burned frequently, maintaining the forest in an early successional state. Croton is well adapted to fire; based on anecdotal data, it appears to both seed and re-sprout following fires (C. Anderson unpublished data). Without fire, pine rocklands convert to hardwood hammocks, and croton eventually disappears from the ecosystem. Since 1951, croton has gone from being one of the 10 most common plants in pine rocklands on Big Pine Key (Alexander 1972) to covering less than 0.01% of pine rocklands in 2014 (Bradley 2009); this decline has occurred simultaneous with decline in fire across the island.

Fire is the preferred management strategy for maintaining croton and habitat for Bartram's scrub-hairstreaks and Florida leafwings; however, there exist multiple obstacles to implementing prescribed fire, especially at the wildland-urban interface and in instances where fuels have accumulated to levels that make it unsafe to burn. In these areas, mechanical clearing through mowing, brush hogging, etc. has been proposed as a possible habitat maintenance strategy. This is motivated by anecdotal observations of croton plants sprouting and thriving in newly cleared fire breaks. While these observations are encouraging, evidence-based data are necessary for making informed management decisions.

Mechanical clearing experiment

To test the effects of mechanical clearing on croton demography, we implemented a clearing experiment on Big Pine Key. In July 2015, we established four, half-hectare replicates each of two treatments, mechanical clearing and a no treatment control. US Fish and Wildlife Service fire staff implemented clearing treatments by haphazardly driving a skid steer with a

masticating head through the treatment unit. The prescription for the treatment was to clear and mulch the understory vegetation in a mosaic pattern covering 50% of the plot with the goal of mimicking the mosaic burn patterns that might result from a prescribed fire.

Prior to treatments, we tagged all croton plants in 15 subplots in each replicate. To ensure that we tagged croton plants across the replicate, we identified croton sampling plots by establishing a grid of parallel 50-meter transects spaced 10 meters apart in all treatment units (total of 10 transects). In each unit, we randomly selected five transects and established three, permanent 2.5m-radius subplots on each one, in the middle and each end of each transect. We marked subplots by hammering a 25cm galvanized spike at the subplot center and attached a numbered, metal plant tag to identify the subplot number. In each subplot, we tagged all croton plants by wiring metal plant tags around the base of each plant. If we did not reach our goal of 30 plants tagged in the first five transects, we randomly sampled additional transects until we reached at least 30 plants. We tagged plants in 5-10 subplots in each unit, depending on croton density.

We first tagged plants in July 2015 and implemented mechanical treatments in August of the same year. We re-sampled the croton plots in July 2016 and July 2017. Each time we re-sampled we located all previously tagged plants and recorded if they were alive or dead. We also tagged new seedlings as well as plants that we missed in the previous round of sampling. New seedlings were easily distinguished from missed plants by their orange-colored stems that were not noticeably woody. From these data, we estimated annual survival and recruitment in the two years following mechanical treatments. To quanitfy recruitment, we divided the number of seedlings tagged after the disturbance by the number of tagged plants in the year prior to disturbance.

Prescribed fire monitoring

To test the effects of fire on croton demography, we used long-term croton monitoring data that has been collected over the last decade in Everglades National Park. There are four different fires represented in this data set, in 2006, 2007, 2013, and 2016. The 2006, 2007, and 2013 fires occurred in three different fire units within the park, and the 2016 fire burned the same unit as the 2006 fire. In each of these fire units, Everglades National Park monitors fire effects on croton in one 20m X 50m plot. Every croton plant within the monitoring plot was tagged with a metal plant tag and its location within the plot was mapped prior to burning, the number of croton plants in each fire unit ranged from 7-84. Following each fire, plants were re-surveyed monthly and, in three of the four fires, new seedlings were mapped and tagged as they were discovered. Only two of these fire units were monitored two years post-fire, one of which had new recruits that were tagged. To estimate annual survival we compared the croton surveys from the month before each fire to the same month in subsequent years in which data were available. We standardized recruitment as detailed above.

Statistical analyses

All statistical analyses were done in R version 3.3.1 (R Core Team, 2016).

Survival: To test for differences in overall survival, we used a generalized linear model with a binomial response variable and fixed effects of treatment (mechanical, fire, control) and year (one year and two years post treatment) using the glm function and Anova function from the car package (Fox & Weisberg 2011).

Recruitment: We tested for differences in recruitment between the three treatments with a linear model, using our standardized recruitment estimates as the response variable, and post-hoc tests with the TukeyHSD function.

Recruit vs. established plant survival: We compared survival of new recruits to survival of previously established plants in the second year post-treatment in our mechanical experiment only (we did not have these data in our prescribed fire dataset). To do this we used a two-way ANOVA with main effects of age (recruit vs. established) and treatment (mechanical vs. control).

Population growth rate: We calculated count-based population growth rates for the two years following treatments as N(t+1)/N(t). Because we did not have recruitment data for year two post-fire, we assumed there was no additional recruitment in that second year. This was based on our observations of very little (almost no) recruitment following mechanical treatments, and results in the most conservative estimate possible. We then used a linear model and post-hoc Tukey test to test for differences between population growth rates across treatments and years.

RESULTS

We tagged a total of 588 croton plants, 161 in control plots, 292 in fire plots, and 135 in mechanically cleared plots.

Overall survival by treatment depended on year (interaction: Wald's chi-square=24.74, df=2, $p<0.0001$). In the first year post-treatment, survival was similar across all treatment types. In the second year post-treatment, survival in both disturbance treatments increased, while survival in control plots showed the opposite trend (Figure 1a).

Recruitment was highest in mechanically cleared plots and was significantly higher in mechanical plots than controls ($F_{2,8}$=5.85, p=0.027). Recruitment in fire plots was intermediate between control and mechanical treatments, and not statistically different from either, although it was marginally significantly greater than controls (p=0.075; Figure 1b). Survival of new recruits was not different from survival of already established plants (Wald's chi-square=0.059, df=1, p=0.81). However, there was a trend in mechanically cleared plots of survival being higher for new recruits (0.85±0.084) than previously established plants (0.77±0.059), and a trend suggesting that recruit survival was higher in mechanically cleared plots (0.85±0.084) than controls (0.64±0.17). The interaction between plant age and treatment was not significant (Wald's chi-square=1.12, df=1, p=0.29; Figure 2).

Differences in survival and recruitment across treatments combined to produce differences in population growth rates. There was a significant treatment effect ($F_{2,,18}$=4.33, p=0.033), with population growth rate in the fire treatment significantly higher than controls, mechanical treatment fell between the two and was not statistically different from either (Figure 1c). Growth rates were higher in the first year following disturbance than the second ($F_{1,19}$=8.04, p=0.013). Mean growth rates were above 1 in both disturbance treatments one year post treatment, but fell below 1 in mechanically cleared plots two years post-clearing. Fire treatment was the only one in which population growth did not fall below one, and thus was the only treatment that resulted in a stable population.

DISCUSSION

We demonstrated that mechanical surrogates for fire are a useful restoration strategy, but are unable to replace fire completely. Mechanical understory removal results in similar patterns

of vital rate responses as found after prescribed fire, however, the magnitude of the response differed between treatments. These differences do not yield growing populations in mechanical clearing treatments as are found after prescribed fire. In mechanically cleared plots survival declines quickly to a rate that is similar to controls. It is this vital rate that appears to have the greatest influence on population growth rate. Recruitment is also important to increase population growth, and thus conditions should be maintained in which croton seeds can readily sprout post disturbance. Because mechanical clearing leads to more recruitment than no action, it is better restoration strategy than doing nothing, but efforts should be made to use fire as a restoration tool when possible.

Like many shrubs in fire-adapted landscapes, croton relies heavily on re-sprouting post disturbance to maintain extant populations. Eighty and seventy percent of croton plants survived and re-sprouted following fires and mechanical clearing, respectively. There are tradeoffs associated with sprouting and seeding, such that plants that invest heavily in below-ground carbohydrate stores for re-sprouting invest less in reproduction (Bond & Keeley 2005). Because of this, sprouters are expected to be good competitors, but poor dispersers (Higgins et al. 2008). Although we documented post-treatment recruitment, it only occurred in plots where croton was present prior to treatment, suggesting that croton seeds do not disperse far from natal patches (as far as we know, croton dispersal is limited to dehiscence, although animals may disperse seeds further). These results highlight the importance of promoting the survival of existing croton patches. Once patches are extirpated, they are unlikely to be re-colonized rapidly.

A key question can be answered by focusing on demographic responses to disturbance: which vital rate contributes most to the overall population growth rate, or has the highest elasticity? For many organisms, the vital rate with the highest elasticity is the one that is least

variable (Pfister 1998). Of the two vital rates we measured, survival was half as variable as recruitment (Figure 1), suggesting that survival has higher elasticity. This is yet another line of evidence that highlights the importance of using management strategies that promote survival of existing plants. If this is the goal of management and restoration efforts in these habitats, fire is the best method to accomplish that goal; mechanical clearing did not increase survival above controls in either year post-disturbance. We acknowledge that there are additional vital rates that could have even higher elasticities than recruitment and survival, such as fecundity and seed survival. However, for other plants that resprout at high rates following disturbance, survival and growth of existing plants generally have the highest elasticities (Menges & Quintana-Ascencio 2004; Liu et al. 2005; Altwegg et al. 2014).

Even vital rates with low elasticity contribute to overall population growth rates. Without restoration, croton populations on Big Pine Key are shrinking at a rate of 20-30% per year. Mechanical clearing abated this trend as it was followed by a flush of recruitment (Figure 1b). These new recruits had slightly higher survival than established plants in both cleared and control plots (Figure 2). If this trend continues, these new recruits could have a positive impact on long term population persistence (Pascarella & Horvitz 1998). Since there was no recruitment and low overall survival in control plots in both years, mechanical clearing, while not as effective a restoration tool as prescribed fire, is better than no restoration at all.

Regardless of life-history strategy, too frequent and too long of a disturbance return interval leads to declining populations of disturbance-adapted species (Altwegg et al. 2014). To understand the optimal disturbance return interval, we would ideally estimate all vital rates in populations at different years post-disturbance and then simulate the effects of varying disturbance return intervals on long-term population growth rates (Gross et al. 1998; Menges &

Quintana-Ascencio 2004; Liu et al. 2005; Menges et al. 2006). For croton, this will require more information than we currently have. One of the mechanisms through which altered disturbance return intervals affect populations is by altering the variability of vital rates between disturbance phases (Morris et al. 2006). For example, for many disturbance-adapted species, including croton, the variability of recruitment between disturbance phases is high, with high recruitment immediately following disturbance and almost no recruitment between disturbances (Figure 1B). If disturbance frequency was to increase, it is possible that post-disturbance recruitment would decrease, due to insufficient time for mature plants to replenish the seedbank. This would in effect decrease the between-phase variability of this vital rate, and negatively affect the long-term population growth rate. On the other end of the disturbance frequency spectrum, long return intervals allow succession to reduce the survival of fire adapted plants by increasing vegetation structure and therefore competition for light. Based on the population declines we measured in our control plots on Big Pine Key that have not burned in 15 years, we can infer that a 15 year disturbance return interval is too long to maintain growing croton populations. In addition to increasing competition, long fire return intervals increase the threat of catastrophic wildfires. Unlike the frequent, low intensity fires that native species are adapted to, these catastrophic fires are generally much hotter and may result in population declines or even extinction. Hot fires can kill seeds in the seedbank and consume below ground resource stores thus limiting the probability that fire adapted plants survive (Moreno & Oechel 1993; Odion & Davis 2000; Pausas & Keeley 2014). The catastrophic fires that result from fire suppression and long fire return intervals also have the ironic consequence of threatening homes and other valuable infrastructure. Understanding optimal fire return intervals is therefore important for both maintaining rare species populations and reducing threats to human development.

We measured a plant's response to two different types of disturbance-based management, but the question remains: what happens when disturbances interact? Mechanical clearing has been proposed as a pre-fire treatment in this system to reduce vertical fuels and therefore the risk of prescribed fire escape. What we do not yet understand is how this would affect the responses that we measured. Given that we saw very little recruitment in the second year following both disturbance treatments, we might hypothesize that the two disturbances in sequence act antagonistically, with the first disturbance, mechanical clearing, stimulating germination and thus depleting the seed bank such that there are few seeds left to germinate following the second disturbance, prescribed fire. Additionally, mechanical clearing is likely to alter fire behavior since it concentrates fuels on the ground, thus increasing ground fire temperature and duration. This could have the unintended consequence of killing seeds present in the seedbank (Busse et al. 2005) or burning up the underground resource stores necessary for re-sprouting post-fire. In this case, the two responses again act antagonistically by reducing recruitment and/or survival. Conversely, if the prescribed fires occurred before seeds germinate, they could act synergistically with the mechanical clearing, further enhancing germination rates by increasing the amount of bare ground and providing additional chemical cues that may be necessary to stimulate germination.

Understanding how interacting disturbances affect vital rates is necessary to predict how communities will be shaped in the future. This is true both in the management context described above, and in the context of climate change. Systems like the pine savannahs in the SE US are subject to fire disturbances as well as hurricanes, both of which are projected to shift in frequency with a changing climate. This is especially the case in south Florida that is exposed to near annual hurricanes, and to hurricanes that are increasing in intensity due to climate change.

Beckage et al. (2006) used simple Lotka-Volterra competition models to demonstrate that the return intervals of both fires and hurricanes interact to maintain pine savannas, and alteration of either return interval has the ability to shift the system to an alternative state; more frequent disturbance of either kind leads to grassland, and less frequent disturbance to closed canopy forest. This model predicts that these disturbances act synergistically to accelerate habitat shifts over time, but this has yet to be tested empirically. As global change accelerates, it is more likely that disturbance events simultaneously shift in their intensity and frequency, increasing the probability of interactions between multiple disturbances.

We have shown that mechanical disturbance is not a perfect surrogate for fire, but is a better alternative than no action. Our experimental test of the demographic effects of both prescribed fire and its mechanical surrogate on a rare plant provides a framework for understanding the mechanisms underlying population level responses to these restoration strategies. These mechanisms are important to include into predictions of species responses to global change (Gilman et al. 2010; Buckley et al. 2010). In the face of changing climate, it may become even more difficult to meet the environmental conditions necessary for prescribed burning (Terando et al. in prep), therefore other habitat maintenance and restoration strategies may become increasingly important in fire adapted systems. By focusing on vital rates instead of community level responses, we acquire the data needed to predict how disturbance will affect the trajectories of species of interest, and thus establish ecologically-based management strategies to recover rare species.

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FIGURES

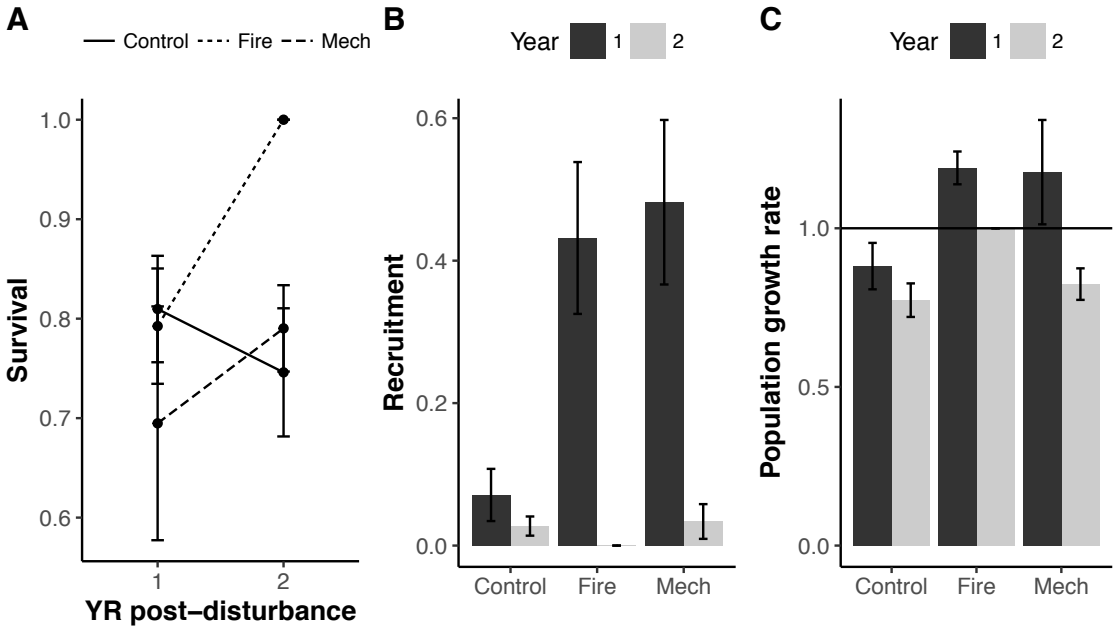

Figure 1.1. Survival, recruitment, and population growth rates across treatments. A) Proportional survival following fire (dotted line), mechanical clearing (dashed line), and no treatment control (solid line). B) Standardized recruitment and C) population growth rates in year one (black bars) and year two (grey bars) post-treatment. Error bars are standard error in all panels. Population growth rates >1 indicate growing population.

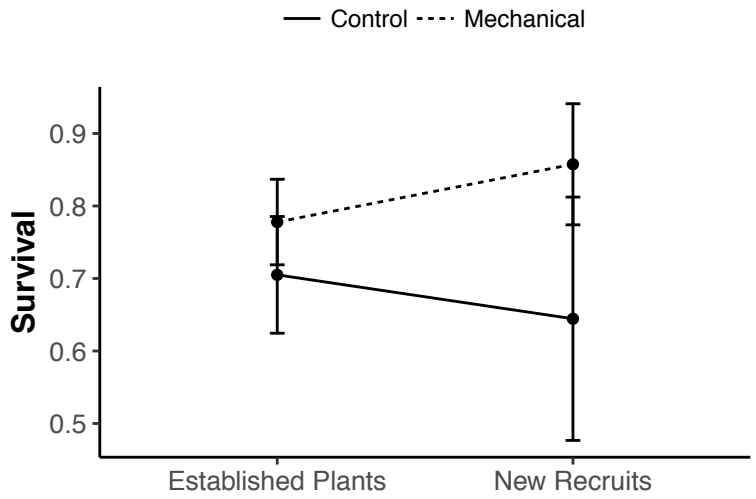

Figure 1.2. Survival of previously established plants and new recruits in mechanically cleared plots (dotted line) and controls (solid line), error bars are standard error.