Tropical Forest Restoration on Cattle Pastures in the Guanacaste Province of Costa Rica

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Among the scenes which are deeply impressed on my mind, none exceed in sublimity the primeval forests undefaced by the hand of man; whether those of Brazil, where the powers of Life are predominant, or those of Tierra del Fuego, where Death and Decay prevail. Both are temples filled with the varied productions of the God of Nature: no one can stand in these solitudes unmoved, and not feel that there is more in man than the mere breath of his body.

– Charles Darwin
The Voyage of the Beagle

The biodiversity crisis represents the greatest challenge humans have ever faced. To the extent that this generation *will continue to fail, it will represent our greatest failure as a species, and the one for which we are least likely to be forgiven by the generations to come. To the extent that we at least partly succeed (in spite of ourselves), it will be our species' greatest achievement. Conservation biology in the short-term and restoration ecology in the long-term are the complementary activities that will form the basis of our belated (but not hopeless) attempt to salvage the disaster.*

– Professor Truman Young
"Restoration ecology and conservation biology"
Biological Conservation, 2000

Permitting Information

Field research was conducted under Costa Rican research permit number ACG-PI-042-2014. Invertebrates were exported from Costa Rica under permit DGVS-019-2014, authorized by Roger Blanco Segura, the Director of Research at Área de Conservación Guanacaste, Guanacaste Province, Costa Rica. They were brought into the US under eDeclaration 2014CH1544975 through the US Fish and Wildlife Service. The invertebrates are housed at the Field Museum of Natural History in Chicago, IL.

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I have had the great fortune of working with a tremendous number of talented people to create this senior thesis. This thesis, as you will see, has been divided into multiple different chapters, each with their own unique story under the overarching theme of the restoration and regeneration of tropical forests in Costa Rica. I have worked with a unique set of collaborators for each of these sections with the exceptions of Tim Treuer and Professor David Wilcove, who have served as advisors for the entirety of this thesis. I am indebted to their grace, goodwill, and wisdom.

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I was also going to include the results of an experiment involving extensive DNA sequencing of beetles. I was unable to prepare this section in time, but I would still like to recognize the help I received. Thank you to Professor Bridgett vonHoldt for offering to help me make sense of the data. Thank you to Katherine Sullivan and the EEB lab technicians, Mary McLaughlin and Craig Marshall, for letting me use the dissecting microscope and camera. Professors Paul Hebert and Daniel Janzen and Dr. Evgeny Zakharov helped me tremendously in navigating the barcoding process. The specimens themselves are currently being held at the Field Museum, where I was assisted by Joe Rowlett and Rebekah Baquiran in properly documenting and archiving the specimens.

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Finally, thank you to my father, my mother, and my sister, for supporting me during my 4 years at Princeton. From the random emails of encouragement to the endless kimchi every time I've gone home, you guys have always been there for me and for that I will forever be grateful. Thank you for loving me enough to always look out for me and to stop me from running off of cliffs, as fun and exciting as they may have seemed at the time. Nothing that I have ever done could have been possible without you.

FOREWORD

The complexity and beauty of tropical forests have long drawn scientists and tourists alike. Unfortunately, numerous stressors and shifting economic realities are causing their rapid destruction and unique species are lost every day. In the face of this stark reality, there is a bastion of hope. In northwestern Costa Rica, a massive restoration and regeneration project is underway. It aspires to connect a patchwork of ecosystems and conserve them into perpetuity so that everyone may come to learn from the forests. It is here in Área de Conservación Guanacaste (ACG), that this thesis took form.

This senior thesis explores various aspects of the restoration and regeneration of the forests of northwest Costa Rica. I have written this foreword as an attempt to provide context for each of the chapters presented in the ensuing pages.

Chapter 1 provides a review of the vast literature on the regeneration and restoration of cattle pastures in the Neotropics and the various factors that play a role in succession. Given the volume of available literature, the review here is necessarily abridged. Readers familiar with the field will find the first few pages of this chapter to be superfluous and should skip immediately to the discussion of Mesoamerican tropical forests.

Chapter 2 focuses on the field work that I conducted in Costa Rica, where I examined the restoration of a cattle pasture in ACG through the application of 1,000 truckloads of orange peels. This chapter is the nucleus upon which the rest of my thesis revolves.

Chapter 3 provides a game theoretic model for succession on cattle pastures. The work presented here is tentative due to the paucity of data with which we could have parameterized our model and due to the lack of other literature specifically dealing with succession dynamics and game theory.

My thesis ends with my own thoughts about conservation and restoration, as inherently limited, tentative, and exploratory as they will be. I hope that you will enjoy reading a piece of work that I honestly do believe represents the capstone of my Princeton education and experience.

I authorize the Princeton University Library to deposit a copy of this thesis in the online digital archive, such that users on the Princeton computing network may access my research. I hope it does them some service.

I conclude with a final variation of a phrase that I have written many times before:

This *senior thesis* represents my own work in accordance with University Regulations.

Jonathan Choi
Princeton Class of 2015

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CHAPTER 1

TROPICAL FORESTS, REGENERATION, AND RESTORATION IN MESOAMERICA: A REVIEW OF THE LITERATURE

God has cared for these trees, saved them from drought, disease, avalanches, and a thousand tempests and floods. But he cannot save them from fools.

- *John Muir*

ABSTRACT

New trends in urbanization and globalization in Mesoamerica have presented promising opportunities for forest regeneration on cattle pastures. However, numerous barriers to passive regeneration, including land use history, fire management, cattle ranching, the lack of seed sources, soil nutrient limitations, and microclimatic conditions have stalled the regrowth of forests. Plantation planting and applied nucleation, though promising, is expensive and difficult to implement. Bird and bat perch construction may help to disperse seeds, but they do not ameliorate soil conditions. Additional methods from the mine restoration literature have been proposed, but there is much left to research.

Keywords: cattle pastures, plantations, applied nucleation, seed dispersal, conservation

CONSERVATION BIOLOGY AND RESTORATION ECOLOGY

We face an environmental crisis. The next century will be spent struggling to meet the ethical imperative to cloth, feed, nourish, and educate billions of people. This imperative will direct us to take many actions, some of which will have permanent ecological consequences. We will cut down forests and replace them with fields and cement jungles in our attempt to deal with both demographic and climatic changes. Each day, we witness the disappearance of numerous species as ecosystems are lost.

Conservation biology operates in the face of these challenges and seeks to answer the question of how to protect species and ecosystems, while understanding the needs of developing and developed economies. The field is necessarily interdisciplinary using knowledge from philosophy to phylogenetics to provide insight to questions that range from the sustainable development of Sub-Saharan Africa to the protection of American Elms on Washington Road.

In the words of Richard Primack, conservation biology has three goals: "To document the full range of biological diversity on Earth, [to] investigate [the] human impact on species, communities, and ecosystems [and to] develop practical approaches to prevent the extinction of species … and protect and restore biological communities and their associated ecosystem functions" (2008).

With its first goal, conservation faces an uphill battle. Humans have always altered the ecosystems they inhabit. The end of the Pleistocene Era and the retreating of the glaciers, approximately 12,000 years ago, also heralded the human-assisted extinction of American megafauna (Pearson 2005). This era has witnessed changes that will remain for millennia to come. Evolutionary lineages that have existed for millions of years are being destroyed in a second on the geological clock. The impact that we have had on the composition of the atmosphere itself has changed every corner of the Earth. The magnitude of these changes was expressed by Soulé & Kohm in 1989, who write that:

> This ubiquity of human disturbance and destruction is dramatized by the modern convention of putting quotation marks around such words as "pristine," and "natural." Biologists are painfully aware that there are virtually no unpolluted, unperturbed *sanctum sanctori* left on the planet. Nature, as we observe it today, merely manifests degrees of disturbance … Indeed, there are few sites left, both marine and terrestrial, where one can observe something very close to pre-human nature.

What do we do from here? Primack's third goal provides our answer and our starting point for the rest of this thesis. Though we recognize that we will never be able to return nature to a pre-human state, we endeavor to protect and restore the populations, communities, and landscapes that we still can. Ultimately, this is the goal of restoration ecology. By addressing the challenges presented by conservation biology and incorporating the tools of restoration ecology, we may be able to stem the tide of the inexorable extinctions happening around the world.

A paper written at the turn of the millennium by Professor Truman Young from the University of California at Davis provides a broad contextualization of restoration ecology as a sub-discipline to conservation. In particular, Young optimistically predicts the future ascent of restoration ecology, working in concert with conservation biology, human demographic changes, and new cultural trends, to eventually stem the hemorrhaging of species from the planet. He notes that while conservation biology has necessarily been focused on short term species loss prevention to both slow the rate of species loss and to prevent the extinction of species with small populations, restoration asks the question of how to generate long-term recovery. Underscoring the vital importance of the role of conservation biology in ensuring that there is something left to restore, he writes:

> ***Conservation biology and implementation as they are practised today are nothing less than the most important human activities in the history of the planet.*** It is my optimistic hope that one day they can take a back seat to the great restoration

> opportunities that are already being seized, and that will increase dramatically in the future. [Emphasis in original]

Young's conviction and optimism about the potential of restoration ecology is not his alone. A paper by Andy Dobson, A D Bradshaw and A J M Baker in Science in 1997 outlines the opportunities that terrestrial restoration ecology has to supplement conservation biology in terrestrial biospheres. They note that land use change and habitat destruction follow a pattern, whereby pristine forest is initially converted to agriculture, used for some time, and then abandoned, allowing for regeneration and recovery. By modeling this system in a manner similar to the susceptible, infected, recovering model (SIR) of disease ecology, the authors were able to demonstrate that increasing the recovery rate of abandoned land would have a significant impact on reducing deforestation by reducing the pressure to log new pristine forests. Though their paper foresees major challenges, they ultimately conclude that "there is a need for restoration to become a standard part of the conservation biologist's armory" (Dobson et al. 1997).

Restoration ecology has also been characterized as a potential acid test for our current understanding of ecological theory and as a means to explore ecological ideas in the context of a controlled experiment (Young et al. 2005). Its intellectual underpinnings, which lie squarely in traditional ecological concepts like niches, competition, facilitation, and mutualism, can be employed to assemble restored ecosystems. The task of reconstructing these ecosystems tests our working knowledge of the rules of community structure and assembly. This thesis, situated within this burgeoning field of research, specifically focuses on restoring and reassembling the processes of ecological succession on the abandoned cattle pastures of Mesoamerica.

THE ECOLOGY AND CONSERVATION OF TROPICAL FORESTS

Tropical ecology is the study of the interactions between species and their biotic and abiotic environments in the Tropics. Due to the sheer diversity of tropical forests, it is difficult to establish broad generalizations. I will now attempt to do exactly that. Tropical forests are some of the most biologically diverse ecosystems in the world. Though they comprise only around 7% of the surface of the Earth, they are home to over 50% of the world's biological diversity (Primack 2008). They also provide vital ecosystem services such as fire wood, water, and animal protein to communities in and around them (Wright 2010; Kricher 2011). Tropical forests are also characterized by their high net primary productivity, their relatively poor soils, and their rapid nutrient cycling (Kricher 2011).

There are also differences in the ecologies of tropical rain forests and tropical dry forests. Tropical rain forests are the more abundant variant and the type that is most celebrated in popular culture. It is from these types of forests that we get images of dazzling orchids, beautiful invertebrate life, lush greenery and exotic birds. They are characterized by heavy, consistent rainfall, high temperatures with little variability, and a predominance of non-deciduous tropical trees (World Wildlife Fund 2014).

The second, less common variant of tropical forests is tropical dry forests (TDF), which are chronically understudied when compared to their wet forest cousins (Janzen 1988a; Hardwick et al. 2000; Sánchez-Azofeifa et al. 2005a, 2005b). They are defined by the Inter-American Institute for Global Change's TROPI-DRY initiative as forests that receive between 700 and 2500 mm of rain per year, have a pronounced dry season and have a mean annual temperature ≥ 25° C (http://tropi-dry.eas.ualberta.ca/). Though they are not as biologically diverse as the tropical rain forest, they are still home to a wide variety of organisms (Murphy & Lugo 1986; Janzen 1988a; Mittermeier et al. 1998; Linares-Palomino et al. 2011).

Both of these forest types are home to many species with innumerable interactions between them. Work by researchers at numerous field stations like those at La Selva and Santa Rosa in Costa Rica and Barro Colorado Island in Panama have discovered interactions at numerous trophic levels ranging from the internal biota of individual insects to the dispersal of seeds across the vast expanse of tropical forests. These autoecological stories have shaped our understanding of many foundational ecological principles including predation, mutualisms, and competition (Ghazoul & Sheil 2010; Mittelbach 2012). However, the value of these forests extends far beyond their research value. These forests provide a host of valuable ecosystem services including carbon sequestration, biological controls for pest organisms, and the retention of water within ecosystems and ground soil (Primack 2008; Thompson et al. 2011). They also serve as vast reservoirs for genetic information and diversity, allowing them to adapt to changing climates and circumstances.

Unfortunately, tropical forests and the species that inhabit them are disappearing at an astonishing rate. As of 2008, 150,000 km^2 of forest were being lost annually, roughly equivalent to an area the size of Tennessee or Guatemala every year (Primack 2008). Much of this loss has been the result of slash and burn agricultural systems that move between patches of cleared forests. Commercial logging, cattle ranching, and cash crop production have also contributed to the destruction of tropical forests. Wood extraction, hunting, and climate change also threaten tropical forests and the animals that inhabit them (Turner 1996; Dirzo & Raven 2003; Dunn 2004; Primack 2008; Ghazoul & Sheil 2010; Wright 2010; Kricher 2011; Gibson et al. 2011; Thompson et al. 2011). This continued stress on tropical forests will eventually undermine their ability to provide the numerous life-sustaining benefits they provide (Foley et al. 2005).

Mesoamerican Tropical Forests

For this thesis, we will focus on the tropical forests of Mesoamerica, roughly defined as southern Mexico to northern Colombia. This region is particularly noteworthy due to its role in the Great American Interchange after the rise of the Isthmus of Panama approximately 3 million years ago (Miura et al. 2010; Futuyma 2013). In this exchange, the South American marsupials moved north across the isthmus while the North American placental mammals traveled south (Futuyma 2013). This interchange, coupled with the arrival of humans approximately 12,000 years ago and the end of the Pleistocene era, ultimately saw the demise of many American megafaunal species including mastodons, ground sloths, and the American "cheetah" (Janzen & Martin 1982; Kricher 2011; Futuyma 2013).

The arrival of humans to Mesoamerica changed the ecology of the region drastically. The first migration, known as the Pre-Clovis culture, came as hunter gatherers from northeast Asia, crossing the Bering Land Bridge around 18,000 years ago, and eventually migrating down the Pacific coast into Central America (Cooke 2005; Fagundes et al. 2008; Cooke et al. 2013). The second migration is known as, unsurprisingly, the Clovis culture, a hunter-gatherer society characterized by the presence of specific fluted spear tips known as Clovis points (Cooke 2005; Kricher 2011).

These groups quickly formed more complex societies, some of which adopted agriculture. Charcoal deposits both in soil layers and in lake sediments appear approximately 7,000 years before present and suggest that fire was employed for small-scale slash and burn agriculture throughout the Neotropics (Pearson 2005; Piperno 2011; Cooke et al. 2013).

Many plant cultivars were domesticated around this time, including squash, maize, peanuts, manioc, potatoes, and chili peppers (Kricher 2011; Piperno 2011). After the domestication of these various cultivars, many societies transitioned from small scale cultivation to true agriculture (Kricher 2011; Piperno 2011).

The scale of this agriculture is non-negligible and the idea of the "noble savage" living as one with nature is probably not accurate (Denevan 1992, 2011). While there are certainly groups of hunter gatherers who do live relatively lightly off the land, the societies that had developed in Central America by 1492 were incredibly complex and were supported by large agricultural complexes. One of the most famous of these groups was the Maya, whose extensive silviculture, agriculture, animal domestication, and hill terracing techniques were able to support large and complex metropolises throughout Central America (Kricher 2011; Thornton et al. 2012).

All of this came at a price. The settlement of these large societies disproportionately occurred in tropical dry forests (TDF), probably due to their more-predictable seasonality, the relatively fewer number of biting insects and their higher soil fertility relative to tropical wet forests (Murphy & Lugo 1986; Griscom & Ashton 2011). The land clearing that these societies undertook, particularly as development grants from organizations like the World Bank poured in the 1950s, resulted in the reduction of Mesoamerican TDF to 1.7% of its former range (Figure 1, Trejo & Dirzo 2000; Calvo-Alvarado et al. 2009; Wright 2010; Griscom & Ashton 2011; Cooke et al. 2013).

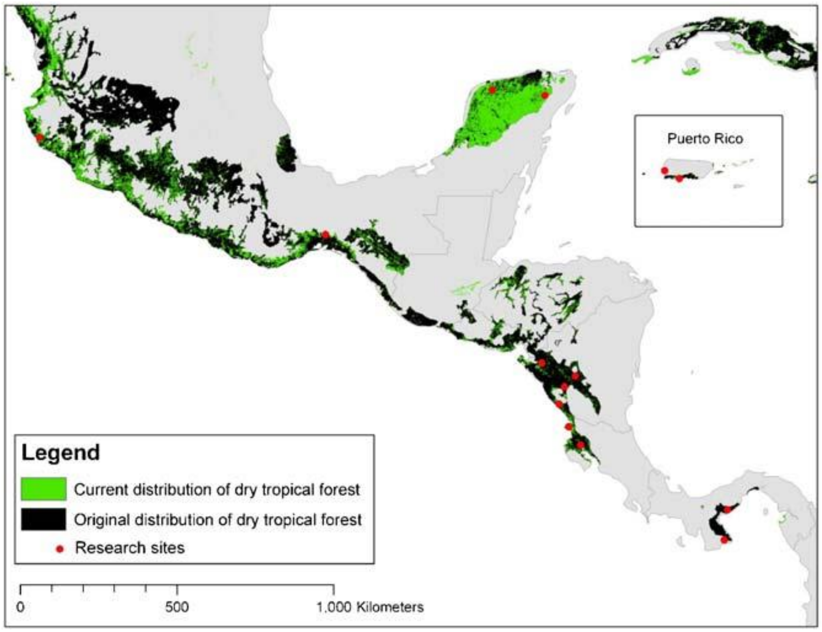


Figure 1 – Current and original distribution of tropical dry forest. From Griscom and Ashton 2011.

In spite of the massive reduction in tropical dry forest, a concerted effort to protect and conserve them has allowed for a modest recovery (Moline 1999; Griscom & Ashton 2011). It is, however, insufficient to protect TDF in isolation. Research has suggested that many TDF species use refugia in moist and wet forest to survive between seasons and that wet forest species may occasionally migrate into the dry forest during the wet season to escape predation and take advantage of leaf flush (Janzen 1988a; Allen 2001; Srygley et al. 2010). The examples of these species show that active steps must also be taken to restore and conserve patchworks of different ecosystems.

BARRIERS TO TROPICAL FOREST REGENERATION

The localized abandonment of agricultural activities throughout the Neotropics as a result of globalization and the acquisition of lands for conservation has resulted in numerous opportunities for the regrowth and regeneration of tropical forests from old fields (Griscom & Ashton 2011). Programs including the subsidization of forest regrowth in Panama and the payment for ecosystem services model in Costa Rica, along with better paying jobs in cities and increases in land prices, have encouraged landowners to give up agriculture (Daniels et al. 2010; Griscom & Ashton 2011).

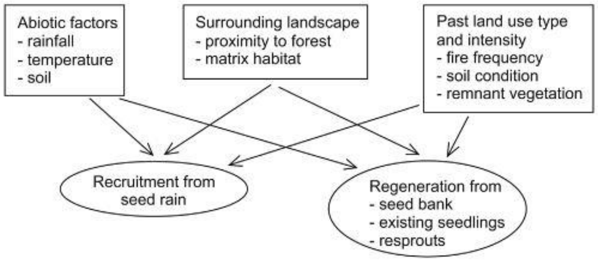


Figure 2 – Barriers to regeneration on tropical forests, as described by Holl 2007.

Unfortunately, in spite of these opportunities, researchers have noted arrested succession on many cattle pastures throughout the Neotropics. Studies have pointed to numerous barriers to regeneration, including previous land use, seed rain and dispersal limitation, seed survival and predation, poor soil conditions, and competition from other vegetation (Figure 2, Holl 2007). Though an exhaustive literature review is outside of the scope of this senior thesis, I will summarize and highlight a few studies of various different barriers to regeneration on cattle pastures within the Neotropics.

Previous Land Use

Previous land use has a significant effect on the capacity for an abandoned agricultural field to regenerate (Janzen 2002). The successional trajectory of a field that has gone through one year of non-intensive farming will be drastically different from that of a field that has been cultivated for centuries (Grau et al. 2003; Holl 2007; Cramer et al. 2008).

For example, lands under fire management, such as in the case of slash and burn agriculture or pasture management, will have extremely low levels of soil nutrients due to the volatilization of minerals due to fire exposure (Neary et al. 1999; Ravi et al. 2010). The challenge remains to determine which of a multitude of different factors allow for the relatively rapid regrowth of forests in certain settings while other areas remain in a state of arrested succession.

Cattle Ranchers and Their Cattle

An important barrier can be posed by agricultural interests who have used the land for decades. Though sometimes the abandonment of old pastures may be voluntary, sometimes governments may simply set aside large areas of land for conservation, without an active attempt to enforce the mandate of conservation. This may lead to conflicts between the park and the people that live around it, complicating conservation efforts (Allen 2001; Primack 2008).

The effect of cattle grazing itself has a largely negative effect, but it can sometimes be used to actively support conservation efforts. One of the most successful examples of cattle management to advance the interests of forest restoration occurred at Área de Conservación Guanacaste (ACG) in Costa Rica. In ACG, cattle were used to reduce the amount of grass on fields, thus reducing the fuel load in the park and reducing the risk of a catastrophic fire. On the other hand, if cattle are allowed to graze for too long, they will prevent succession by trampling and eating saplings (Allen 2001; Griscom et al. 2009). In general, cattle exclusion seems to be accepted as the best management program possible if fires can be controlled without needing to reduce the fuel load or if the fuel load can be otherwise removed in an effective manner (Griscom & Ashton 2011).

Fire

Fires, whether they are natural or manmade, also pose a significant risk to tropical forest regeneration (Janzen 1988b; Calvo-Alvarado et al. 2009). Frequent and intense fires in the past land use of a particular plot will destroy seed banks and volatize soil nutrients (Brown et al. 2004). Fires will also destroy trees if sufficiently hot enough and will encourage the growth of fire-adapted grasses (Hart et al. 2005; Griscom & Ashton 2011).

Fire, at a larger community and landscape level, will select against fire-intolerant species and select for fire-tolerant species. The forest that subsequently regenerates will then be very different from the original community (Janzen 1988b; Griscom & Ashton 2011). Though the task of fire suppression on a large national park may be monumental, it is necessary to consider if tropical forests are to stand a chance at regeneration. Chapter 3 of this thesis explores the frequency of fires in relation to succession in further depth through the use of a game theoretic model.

Seed Dispersal & Survival

Seed dispersal presents one of the most serious barriers to regeneration and has been the focus of research efforts. The barrier at a landscape scale is fairly dramatic – if an entire forest is logged and the seeds in the soil are destroyed from predation, fire, or agriculture, then it is highly unlikely that a forest will regrow on the site, simply because there are no more seeds.

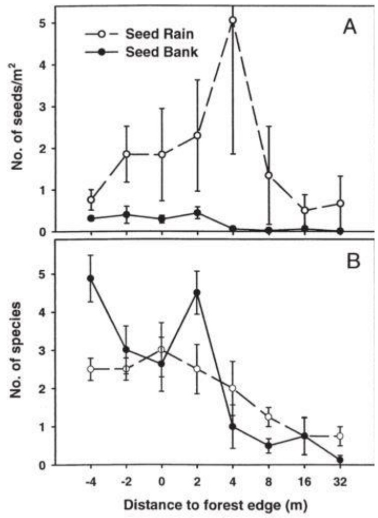


Figure 3 – Pronounced decreases in seed quantity as distance from the forest edge increases. From Zimmerman et al 2000.

At the plot level, studies of individual pastures have compared seed dispersal to a variety of other factors that might prevent growth. The work of Karen Holl at the University of California Santa Cruz has shed a considerable amount of light on the seed dispersal barrier in the forests of Costa

Rica. Her 1999 study demonstrated that in a seasonal montane forest, seed rain in the forest was much higher than the seed rain in an abutting cattle pasture. Her studies demonstrated that the differences in soil nutrients between the two sites did not have as dramatic of an effect on the growth rate of seedlings (Holl 1999). Her follow up study in 2000 demonstrated again that seed dispersal had a significant limiting effect on regeneration, but that competition from pasture grasses was also having an effect. At her site, she reported that while 1,670 seeds per meter squared per year were falling in traps 250m into the forest, only 190 seeds fell into a similar trap 250m into the pasture. She also reported that the only animal dispersed seed to be dispersed beyond 5m of the forest border were seeds of the shrub genus *Solanum*, and that even then, there were only 3 such seeds per meter squared per year (Holl et al. 2000).

These dramatic results have been corroborated by other researchers. The work of Zimmerman et al. (2000) found that the diversity and density of seed rain declined precipitously as distance from the forest edge increased (Figure 3). Their study, conducted in a recently abandoned cattle pasture in Puerto Rico, also highlighted the role of seed predation in preventing succession.

In addition, it has generally been established that wind dispersed species disperse much more readily into pastures than do animal dispersed species (Janzen 1988c; Wunderle 1997; Vieira & Scariot 2006; Griscom & Ashton 2011). It has been hypothesized that this is due to the fact that there are very few incentives for seed dispersing animals to venture into an open pasture. In addition to the fact that there are fewer areas to hide in an open pasture, the drastic differences in heat and the lack of structural complexity to allow for birds to perch prevents animal-assisted seed dispersal (Janzen 1988b). This is compounded by the fact that if a cattle pasture is seeded only with wind dispersed trees, subsequent generations of animals will still have little incentive to enter the cattle pasture due to the lack of a viable food source (Janzen 1988b, 2002; Wunderle 1997). This difference in dispersal tendency is particularly problematic, given that the vast majority of tropical plant species are animal dispersed (Howe & Smallwood 1982; Janzen 1988b).

Even if seeds, whether wind or animal dispersed, do reach cattle pastures, there are additional hurdles to seed germination and survival. An opinion piece by Reid & Holl (2013) highlighted numerous ways in which seeds may still fail to germinate after arriving in a pasture. They highlight the role that seed predation, desiccation, rot, and competition from other herbaceous plants can play in preventing the effective establishment of trees.

Soil Conditions and Microclimate

The literature regarding soil conditions and microclimatic environment in pastures and abutting forests is not as extensive as that regarding seed dispersal, but the data that does exist is dramatic. Cycles of cattle grazing and fire management can denude nutrients from cattle pasture soils (Brown & Lugo 1990; Reiners et al. 1994; Davidson et al. 2004). Work done by Aide & Cavelier (1994) in lowland Colombia demonstrated that pasture soils can be highly degraded and that the severe nutrient leaching from the soil posed the most significant barrier within their study. They found that erosion had stripped soil horizons A and B from the pasture, leaving bare rocks exposed at the surface. They also demonstrated that the destruction of the soil seed bank, the lack of seed dispersal, and the presence of fire also restricted regeneration.

Karen Holl's previously mentioned 1999 survey also surveyed soil microclimatic conditions and identified significant differences between pastures and forests. She showed that air temperature, vapor pressure deficit, and sunlight were much higher in the cattle pasture but much lower in the forest when measured 1m from the ground. A subsequent seed germination and growth project on the soils in the forests and pastures noted that soil nutrients did not have an effect on growth rates.

Ultimately, the studies that I have seen do not directly reference the role of soil conditions as being a direct barrier to the regeneration of tropical forests. What has been established is that soil properties change drastically during the process of forest conversion (Guariguata & Ostertag 2001; Griscom & Ashton 2011). As the intensity of use continues to increase, soils typically lose fertility and it may take a long time for those soils to recover (Brown & Lugo 1990; Guariguata & Ostertag 2001). This finding suggests a potential mechanism by which soil conditions might be a barrier to regeneration.

Competition from Existing Vegetation

Even if seeds manage to disperse successfully and even if soil conditions allow seeds to germinate and establish, the young saplings must deal with competition from both native and invasive grasses which will compete directly for available nutrients and light(D'Antonio & Vitousek 1992; Guariguata et al. 1995; Sarmiento 1997; Holl 1998; Allen 2001; Hoffmann & Haridasan 2008; Griscom & Ashton 2011). This fierce competition is particularly true in pastures with invasive African C4 grasses that were initially planted for use in cattle pastures (Calvo-Alvarado et al. 2009; Griscom & Ashton 2011).

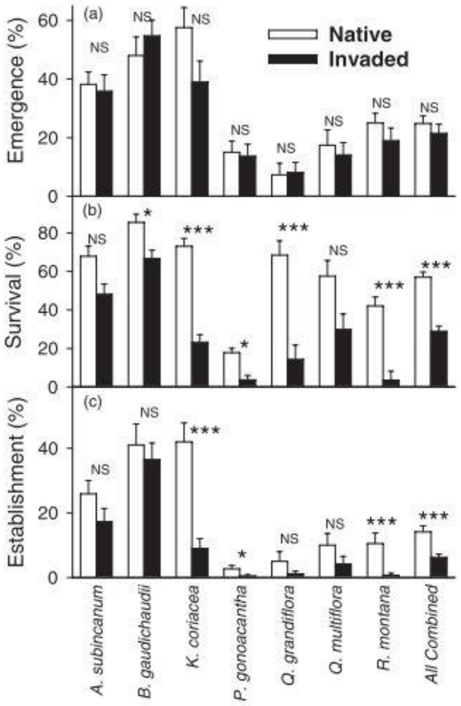


Figure 4 – Species-specific differences in emergence, survival, and establishment in invasive and non-invasive pastures. Figure from Hoffman and Haridasan 2008.

The effect of these C4 grasses has been documented throughout the Neotropics. An extensive survey of seeds falling on cattle pastures in the tropical Andes demonstrated that in a patchwork landscape with varying levels of seed rain, the best predictor for whether seeds will successfully survive and germinate is the presence or absence of the invasive African tussock grass *Setaria sphaceleta* (Sarmiento 1997). A different study in the Brazilian cerrado found that when sowing seven different tree seeds in pastures of native grasses and the invasive grass *Melinis minutiflora*, invasive grass pastures had half of the seedling survival of native pasture, though this effect was species specific among the 7 different species (Figure 4, Hoffmann & Haridasan 2008). A third study, conducted in Costa Rica found that the presence of invasive grasses, like *Axonopus scoparius* and *Melinus minutifloria*, and early colonizing shrubs had a negative effect on the growth of seedlings of the species *Calophyllum brasiliense* and that above ground clearing had a positive effect on growth, suggesting that the biggest factor was competition for light (Holl 1998).

This review of the barriers to regeneration presents a clear picture of how growth may by slowed, with the understanding that the extent to which each barrier is at play will depend on local conditions. The unique combinations of land use history, local tree communities, soil conditions, and the communities of seed disperser communities will result in a wide variety of different outcomes.

RESTORATION EFFORTS

Given the numerous and significant barriers that exist to regeneration, many different methods for restoration have been proposed. This has been reviewed in depth in the work of Griscom and Ashton (2011). Their summary figure is reproduced below.

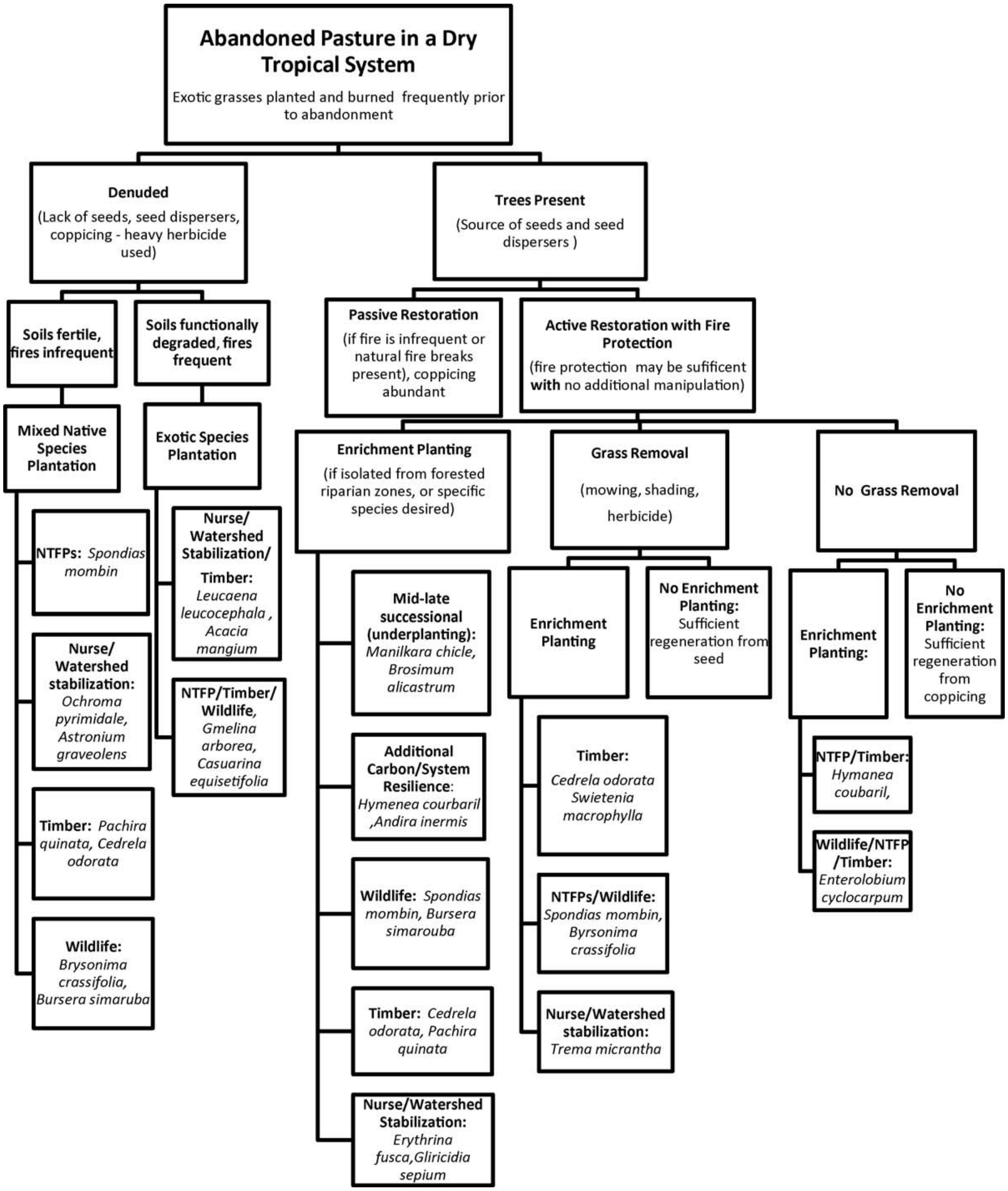


Figure 5 – A summary of different methods for restoring cattle pastures to forest. Recommendations for more denuded landscapes are on the left, while methods in the presence of native trees are on the right. From Griscom and Ashton (2011)

Previous land use history is an important predictive factor for determining how successful certain interventions will be. On the left hand branch of the figure, areas that are severely denuded due to extensive agriculture will need to be actively restored. Decades of intensive land use will destroy nearby seed sources and will wipe the seed bank available for forests to regenerate from (Griscom & Ashton 2011).

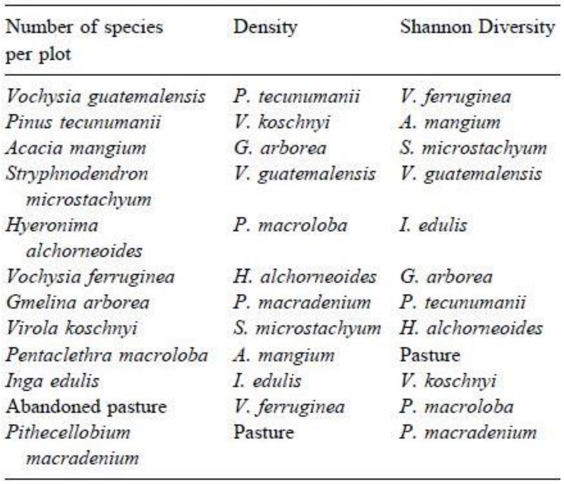
On the right hand branch, those communities with sufficient seed sources and adequate disperser communities will be able to undergo either passive or active restoration. The different restoration methods, be it native plantation planting, exotic plantation planting, or enrichment planting with or without grass removal, will have different efficacies dependent on abiotic and biotic factors, and will generate different services, whether they provision non-timber forest products, stabilize the watershed, act as nurse plants, provide timber, or provide food for wildlife (Griscom & Ashton 2011).

Passive Regeneration

The oldest, cheapest, and most prevalent method for tropical forest regeneration is passive regeneration, whereby pastures are left to their own devices. This method of passive restoration can either result in arrested succession given nearly insurmountable barriers to regeneration (Aide & Cavelier 1994; Sarmiento 1997; Zimmerman et al. 2000) or can lead to eventual regrowth (Aide et al. 2000; Grau et al. 2003; Gilroy et al. 2014). The most obvious shortcoming to this approach are the highly variable results (Griscom & Ashton 2011; Corbin & Holl 2012). Some studies report the regeneration of significant carbon stocks in as little as thirty or forty years (Grau et al. 2003; Gilroy et al. 2014) while others show no immediate signs of regrowth (Sarmiento 1997)

Plantations

Table 1 – Plantation species and pasture across ranked according to different potential measures of restoration success. From Haggar et al. 1997.



Number of species per plot	Density	Shannon Diversity
Vochysia guatemalensis	*P. tecunumanii*	*V. ferruginea*
Pinus tecunumanii	*V. koschnyi*	*A. mangium*
Acacia mangium	*G. arborea*	*S. microstachyum*
Stryphnodendron microstachyum	*V. guatemalensis*	*V. guatemalensis*
Hyeronima alchorneoides	*P. macroloba*	*I. edulis*
Vochysia ferruginea	*H. alchorneoides*	*G. arborea*
Gmelina arborea	*P. macradenium*	*P. tecunumanii*
Virola koschnyi	*S. microstachyum*	*H. alchorneoides*
Pentaclethra macroloba	*A. mangium*	Pasture
Inga edulis	*I. edulis*	*V. koschnyi*
Abandoned pasture	*V. ferruginea*	*P. macroloba*
Pithecellobium macradenium	Pasture	*P. macradenium*

One of the earliest proposed restoration methods was to simply grow plantations of trees. It was though that these trees would help to retain and conserve local wildlife, sequester carbon, and pay for themselves when they were logged for timber or their fruits were sold. Unfortunately, it appears that the conservation benefits of these plantations are specific to the type of trees planted Guariguata et al. (1995) found vastly different results in understory species composition from plantations of two different species. Though they conclude that plantation planting may be useful for encouraging tree recruitment, they note that there is a need for information on how individual species affect understory community growth and establishment. Another study in 7 year old plantations for 7 different species found that each individual plantation had had different effects on biomass accumulation and species richness (Powers et al. 1997). The effectiveness of plantations also depends on the goal in mind. Depending on whether one chooses to look at the number of woody species within each plot, the density of stems in each plot, or the Shannon diversity of all of the regenerating species within the plots, the results of plantation farming can differ drastically (Table 1, Haggar et al. 1997).

The effect of plantation planting is thus incredibly varied. Two examples, both from Costa Rica, demonstrate both the potential benefit and potential harm of plantation-based restoration. The benefits of plantation-based restoration were demonstrated through the partnership between ACG and a *Gmelina* forester. *Gmelina* is a species of commercially useful tree used for its timber. *Gmelina* growers will often purchase tracts of forest, plow it over, and plant *Gmelina* instead. However, *Gmelina* growers are also willing to plant plantations on cattle pastures. In ACG, growers were allowed to use cattle pastures to grow a plantation of these trees. The growth of *Gmelina* trees shaded out pasture grasses and introduced thick understory vegetation. When the *Gmelina* plantation was harvested, profits were shared and herbicide was applied to the *Gmelina* roots. This process, pioneered at ACG, successfully demonstrated that plantations can successfully and cost effectively encourage restoration (Janzen 1999).

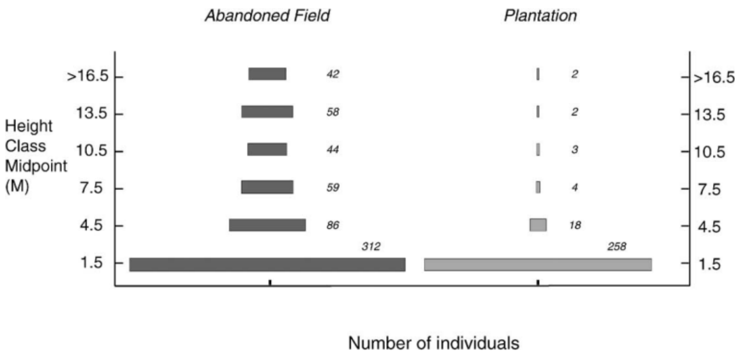


Figure 6 – Reduction in height of trees in plantations relative to abandoned fields. From Healey and Gara 2003.

However, relying on regrowth from plantations may also be counterproductive. Studies of teak (*Tectona grandis*) plantations in Costa Rica revealed that plantation growing had a net negative impact on tree growth relative to abandoned fields nearby. Native trees were less abundant, shorter, and less diverse within the teak plantation than next to it (Figure 4, Healey & Gara 2003).

Ultimately, it must be remembered that plantations are planted with the goal of profit maximization in mind, with the conservation and regeneration of forests as a nice added bonus. Establishing plantations for the explicit goal of restoration often runs into issues of cost effectiveness and over which types of trees to plant. Though the experience of the ACG points towards a method by which active restoration may be accomplished in a cost effective way, additional information about which species of plantations will be the most effective at catalyzing regeneration is needed.

Bird Perches and Bat Boxes

Recognizing the severe limitation to regeneration posed by the lack of seed dispersal, various researchers have installed bird perches and bat boxes in the hopes that these will attract birds and bats into fields (Wunderle 1997; Holl et al. 2000; Reid & Holl 2013). An experiment conducted by Holl et al. (2000) found that the use of 5m tall branches in pastures was able to recruit birds, but that this ultimately had no effect on seed germination and survival. Without successfully ameliorating soil conditions, seeds will inevitably be predated, desiccate, or rot. Still, given the need to have higher structural complexity to successfully recruit seed dispersers (Wunderle 1997), this provides an important first step in increasing the structural complexity of pastures.

Applied Nucleation and Nurse Shrubs

In response to ideas of facilitation, nucleation, and mutualism, restorationists began to plant "nurse plants" in the middle of abandoned pastures to encourage seed dispersal and to ameliorate soil conditions. Applied nucleation typically involves the planting of a few native shrubs and trees in small clusters, in the hopes that local seed dispersing animals will be attracted and disperse more seeds. The shrubs and trees also reduce the competition from pasture grasses by shading them out. Studies of nucleation in primary succession predict that these small islands of vegetation will grow into each other and create a continuous canopy (reviewed in Corbin & Holl 2012).

The method of applied nucleation has two major advantages over plantation-based restoration. First, we have seen that plantations can result in either the suppression of recruitment or in the recruitment of a specific guild of trees. Nucleation is typically done by planting a small but diverse community of plants that will encourage diverse recruitment from the nearby forest matrix. Second, nucleation is cheaper than a plantation, given that a smaller number of trees have to be planted. The effectiveness of plantations versus applied nucleation remains to be determined. A comparison study between nucleation, plantations and passive regeneration found that there was increased seedling recruitment inside of islands compared to plantations and that seedling recruitment was twice as high in nucleated islands when compared to passive regeneration (Zahawi et al. 2013). A similar study, however, found that there was greater seedling damage and slower growth in nucleated islands vis-à-vis plantations (Holl et al. 2011).

The reduced cost of nucleation and its efficacy makes nucleation an attractive potential method for restoration. Though the method is slower than direct plantation planting, it is better able to mimic long-term processes of seed dispersal and nucleation (Gómez-Aparicio et al. 2004).

Other Interesting Methods

There are two more methods that appear within the literature that have had little follow up but show very interesting possibilities. Both examples come from the literature about the restoration of sand pits used for industrial mining. The first method involves the use of paper de-inking sludge, which helped to increase water retention and other elements of soil fertility in Quebec (Fierro et al. 1999). The second method involves the use of hydrogels on a sandpit in Venezuela to help regrow tropical dry forest (Fajardo et al. 2012). The hydrogels operated by slowly releasing water over time, as opposed to a normal pattern of watering, where water is not retained for long periods of time. Additional insights from the mine restoration literature should be kept in mind as the field progresses in the future.

CONCLUSION

Land use changes in Mesoamerica have exacted a heavy toll on tropical forests, particularly with the rise of the beef industry in the latter half of the 20th century. Recent demographic changes have led to the abandonment of cattle pastures throughout Mesoamerica, presenting an opportunity to restore tropical forests.

However, extensive and numerous barriers to regeneration exist. Previous land use can destroy nearby seed sources, cattle may trample or graze young seedlings, and fire can kill saplings and destroy soil nutrients. Seeds may not be able to disperse effectively due to the lack of seed dispersing agents and even if they do arrive, poor soil conditions and competition from existing vegetation may prevent them from seeding.

Numerous approaches to regeneration have been proposed to overcome these barriers, each with their own sets of advantageous and disadvantages. Passive regeneration may face insurmountable biological barriers but is by far the cheapest. Plantation planting has variable effects on the recruited plant community and is costly. Bird and bat perches may help to disperse seeds, but do not address soil microclimate conditions and competition from nearby vegetation. Applied nucleation may provide an answer to these methods by planting a small area with forest to encourage eventual succession, but this method still ultimately costs money. Additional methods are being explored in the mine restoration literature, but have not been explored extensively. Ultimately, though there is much promise in these various methods, much is left to discover.

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CHAPTER 2

ORANGE IS THE NEW GREEN: ACCELERATING TROPICAL FOREST REGENERATION IN COSTA RICA USING CITRUS WASTE

I grew up in this town, my poetry was born between the hill and the river, it took its voice from the rain, and like the timber, it steeped itself in the forests.

– *Pablo Neruda*

Author's Note – The research presented here will be submitted for publication in a peer-reviewed journal with the following co-authors: Tim Treuer (Princeton University), Daniel Perez Aviles (University of Minnesota), Guillermo Funes (Universidad de El Salvador), Joseph Rowlett (Field Museum of Natural History, Chicago), Laura C. Shanks (Beloit College), Bonnie Waring (University of Minnesota), Leland Werden (University of Minnesota), Jennifer Powers (University of Minnesota), David Wilcove (Princeton University), Winnie Hallwachs (University of Pennsylvania), and Daniel Janzen (University of Pennsylvania).

Choi designed the 2014 surveys, gathered and analyzed the data, and drafted the entirety of this chapter. Treuer and Wilcove contributed greatly to study design and implementation in the field. Aviles, Funes, and Rowlett, contributed their taxonomic expertise to identify the trees, birds, and insects from the survey. Shanks conducted the 2000 soil survey and graciously allowed me to reproduce her unpublished data. Waring, Werden, and Powers contributed to the 2014 analysis of soils. Hallwachs and Janzen began the entire project in 1998. Without them this project would have never started. We also acknowledge the contributions of Maria Marta Chavarria and Roger Blanco Segura, key administrators at ACG who were instrumental in negotiating the initial 1998 project.

ABSTRACT

Ecological restoration has demonstrated huge potential in slowing and ultimately reversing the tide of species extinction and land use change. Trends in urbanization and globalization have led to the widespread abandonment of cattle pastures which have the potential to be restored to forest. Unfortunately, the perception of restoration as expensive and contrary to economically "useful" land use has precluded efforts to regrow forests. The use of agricultural waste generated from orange juice manufacturing, namely pulp and peels, in Área de Conservación Guanacaste offers a unique opportunity to explore the restoration of tropical forests from cattle pastures in Mesoamerica.

After the supervised application of 1,000 truckloads of orange peels in 1998, soil surveys in 2000 and 2014 recorded large scale differences in soil properties. Vegetation surveys in 2014 recorded a 3 fold increase in species richness for trees larger than 5 cm in DBH and a 2 to 4 fold increase in aboveground biomass. Invertebrate pitfall traps revealed a large difference in number of individuals between the two sites, but was unable to discern a difference in family-level diversity. Vertebrate audio surveys using passive audio recorders provide a hint into the vertebrate community using the restored habitat, including howler monkeys (*Alouatta palliata*) and white-faced capuchin monkeys (*Cebus capucinus*).

The potential for the use of orange peel-based restoration is immense. Studies of the exact mechanisms for orange-peel catalyzed regeneration and the potential for the use of other agricultural waste would help to improve policy recommendations for restoration. The uniquely cost-effective nature of this restoration method makes it a particularly attractive method for further research.

Keywords: restoration, cattle pastures, soil nutrients, vegetation, pitfall trapping, invertebrates, audio monitoring

INTRODUCTION

Given the rapid loss of tropical forests, policy makers and scientists have proposed numerous methods for overcoming barriers to restoration on abandoned cattle pastures in the Neotropics including passive regeneration (Hardwick et al. 2000; Griscom & Ashton 2011), plantation planting (Haggar et al. 1997; Healey & Gara 2003) and the planting of small tree islands to encourage nucleation (Holl et al. 2011; Corbin & Holl 2012; Zahawi et al. 2013). A novel approach to catalyzing growth was attempted in Área de Conservación Guanacaste (ACG) in 1998 through the application of orange peels (Escofet 2000; Allen 2001). In this chapter, we examine the land use history of Guanacaste Province and the history of this orange peel project. We then analyze data from a field study comparing the site and an adjoining abandoned cattle pasture to look at the effects of this orange peel deposition.

The Land Use History of Guanacaste Province

The Guanacaste province of northwestern Costa Rica is home to a large remnant of the tropical dry forest that used to run along the Pacific Coast of Mesoamerica (Allen 2001; Palmer 2003). The province is one of the most sparsely populated within the country and has a long history of agriculture and cattle ranching (Calvo-Alvarado et al. 2009). The original Chorotega people had been subsistence farmers for thousands of years within the region. When the Spanish arrived in the early 16th century, cattle were introduced to the area and ranching began. This expanded significantly in the middle of the 20th century, as post-WWII development subsidies from organizations like the World Bank helped to make cattle ranching more profitable. By the 1970s, economic pressures had eliminated much of the forest within the province (Allen 2001; Calvo-Alvarado et al. 2009). The new ranching methods and changes that occurred within Guanacaste are described in depth by Calvo-Alvarado et al. 2009:

> Land used for subsistence agriculture was also converted to pasture as the thin soils became degraded and unable to sustain crop production (Gregersen 1994). In the Northeast, deforestation intensified on the already existing haciendas as new farming techniques enabled farmers to increase the size of cattle herds. New techniques included, fencing, the expansion of fire resistant exotic grasses such as Jaragua (*Hyparrhenia rufa*), and the introduction of Brahman cattle breed that had a much higher output than the European Creole cattle (Hall 1984; Edelman 1985; Jiménez & González 2001; Peters 2001). The new fire resistant grasses also led to the widespread use of fire as a method for establishing and 'cleaning' pasture. Fire proved to be a very efficient method for expanding and maintaining pastures in Guanacaste's dry climate (Parsons 1983).

The leaching of vital nutrients from the soil due to decades of grazing and burning and the introduction of exotic grasses has prevented many forests from returning to abandoned cattle pastures throughout the Neotropics (e.g. D'Antonio & Vitousek 1992; Aide & Cavelier 1994; Sarmiento 1997; Hoffmann & Haridasan 2008; Griscom et al. 2009; Griscom & Ashton 2011; Fajardo et al. 2012). Damage to seed banks and the severe reduction in seed rain associated with deforestation has also hamstrung regeneration. Inadequate wind dispersed seeds and dwindling populations of animal seed dispersers from nearby forest fragments place considerable constraints on regeneration (Janzen 1988; Skoglund 1992; Holl 1999; Zimmerman et al. 2000; Khurana & Singh 2002; Griscom & Ashton 2011). Finally, desiccation, seed predation, and herbivory provide a final hurdle that many young seedlings are unable to overcome (Guariguata & Ostertag 2001; Reid & Holl 2013).

History of Parque Nacional Santa Rosa and Área de Conservación Guanacaste

In response to the massive destruction of forests in Guanacaste Province and these barriers to regeneration, biologists and government officials set about protecting areas within the province (Janzen 1999; Allen 2001; Arroyo-Mora et al. 2005; Calvo-Alvarado et al. 2009). In 1966, the first plans for a park within Guanacaste province were drawn up by Kenton Miller, then a forestry officer at the United Nations Food and Agricultural Organization, with input from Joe Tosi and Leslie Holdridge. The park would be centered on La Casona de Santa Rosa, the site of multiple historically and culturally significant battles in which the Costa Rican militia repeatedly repulsed invaders entering the country from Nicaragua. Using land sold to the Costa Rican government by the brother of former Nicaraguan President Luis Somoza in 1968, the Costa Rican Legislative Assembly established Santa Rosa National Park in 1971 as one of the nation's first national parks (Allen 2001).

When the park was first established, much of the park and the surrounding landscape were comprised of pastures with interspersed old growth and secondary forest. Lack of effective fire control and the presence of the invasive jaragua grass (*Hyparrhenia rufa)* stalled the regrowth of many parts of the forest (Janzen 1988; Allen 2001). Resources were scarce: the most important tools for fire suppression often were buckets of water, wet brooms, and shovels. Squatters and hunters plagued the parks and killed many of the wildlife that were necessary for seed dispersal. Yet conservationists still envisioned a large scale conservation area to link various different ecosystems within the park (Allen 2001).

Over time the park grew to become one of the most successful examples of restoration in the world. The heroic fundraising efforts by University of Pennsylvania Professor-Emeritus Daniel Janzen and his wife, Dr. Winnie Hallwachs, brought money in for land purchases. The election of conservation-minded President Óscar Arias in 1986 was a major boon to the fledgling park as he legally protected much of the land proposed for later integration into Santa Rosa. An additional 1987 donation of $3.5 million USD from the Swedish government allowed for the establishment of a $17 million USD endowment through a debt-for-nature exchange. Additional efforts by Alvaro Umaña, Alvaro Ugalde, Mario Boza and Rodrigo Gámez contributed significantly to the success of the park (Allen 2001).

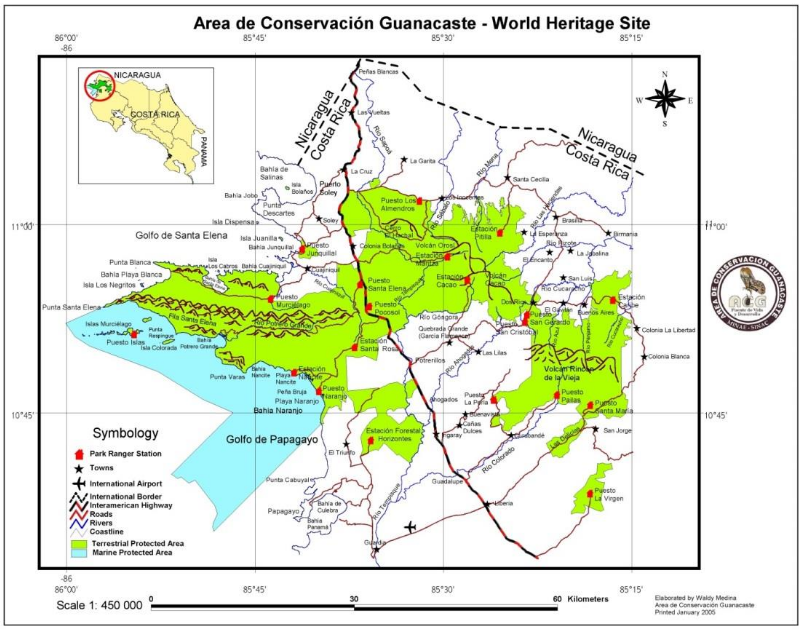

Figure 1 – Map of the Área de Conservación Guanacaste in northwest Costa Rica. All of the green territory represents areas under formal protection as part of the ACG. Image from Waldy Medina of the ACG, taken from the ACG Research website.

Through consistent firefighting, limitations on cattle ranching, and fundraising, the 10,400 ha Santa Rosa National Park has expanded into a sprawling 147,000 ha UNESCO World Heritage Site known as Área de Conservación Guanacaste (ACG, Figure 1). Land has gradually been incorporated into the conservation area and now spans from a marine protected area along the Pacific shoreline for nesting Leatherback and Olive Ridley sea turtles, up three volcanoes and down into the wet forests of the Caribbean watershed (Janzen 1999; Allen 2001; Palmer 2003; Área de Conservación Guanacaste 2014; UNESCO 2014). ACG is now home to over 7,000 species of plants, 900 vertebrate species including 500 bird species, and an estimated 20,000 species of Coleopterans, 13,000 species of Hymenopterans and 8,000 species of Lepidopterans (UNESCO 2014). In total, ACG represents 2% of the land area of Costa Rica and 13% of Guanacaste Province, but its estimated 335,000 terrestrial species represents approximately 2.6% of the world's biodiversity: more biodiversity than Northern Mexico, the US, and Canada combined (Área de Conservación Guanacaste 2014).

As part of its founding goal, ACG aims to not only conserve tropical dry forest and adjoining ecosystems, but also to promote the active restoration of degraded ecosystems.

This is particularly pressing, given the extent of cattle pastures and degraded lands adjoining the park. In order to further this goal, ACG has consistently sought out projects that would both promote restoration and allow the park to make money to cover operating costs (Janzen 1999; Escofet 2000; Allen 2001; Palmer 2003).

The 1998 Del Oro-ACG Agreement

One of the most controversial of these restoration projects was the 1998 Del Oro-ACG Agreement. Del Oro is an orange juice company that has extensive orange groves and juicing operations to the north of the park (delorocr.com). It also owns extensive patches of old secondary forests that abut ACG. In order to acquire these lands and to help restore cattle pastures that had been purchased by ACG, Professor Janzen helped to negotiate a deal between the two organizations. On August 24, 1998 the Minister of the Ministry of Energy and the Natural Environment of Costa Rica (MINAE) on behalf of ACG and the President of the Board of Directors of the Del Oro Group signed a contract in which Del Oro would agree to pay ACG for ecosystem services, ecological consulting, and waste removal services.

This was a novel contract through which a company would actively be paying for ecosystem services from a national park. The contract was worth approximately $480,000 USD (approximately $700,000 USD adjusted for inflation to 2014) and paid for natural pest control, water provision, land for orange breeding experiments and ecological consulting. The bulk of the contract covered the biodegradation of orange peel waste generated from the juicing of orange peels at Del Oro's plant. Del Oro was given rights to apply 1,000 truckloads of processed orange juice waste per annum on persistent pastures within ACG for 20 years at a cost of $11,930 USD per year ($17,440 USD adjusted) or $238,600 USD total ($348,750 USD adjusted) (Escofet 2000; Allen 2001; Rojas & Aylward 2003).

The agreed area for dumping was on La Guitarra, a ranch between Cerro el Hacha and Volcán Orosí that was formerly owned by Luis Roberto Gallego in Sector El Hacha of

ACG (11.028 N, -85.523 W). The site is situated within the transition zone between wet and dry tropical forest, with nearby forest fragments featuring aspects of the species composition of both types of forest. An access road running north to south was cut through a former cattle pasture and a seasonal river feeds a small forest fragment to the north.

The first deposition occurred in early 1997 with a test deposit of 100 truckloads at a site called Modulo I (Module I). Scientists from ACG, MINAE, and local universities conducted a variety of surveys and tests. The data suggested that the process of biodegradation, though smelly, did not pose a major threat to water quality or human health (Jimenez 1997, 1999; Universidad Nacional 1999). Plant surveys conducted in 1997, show that the area was largely dominated by pasture trees and invasive pasture grass, primarily jaragua grass (*Hyprrhenia rufa*) which was introduced from Africa for the purposes of cattle ranching (Jimenez 1997, 1999; Calvo-Alvarado et al. 2009).

The first application occurred in 1998 at a site known officially as Modulo II (Module II). Due to the unprecedented and large nature of this project, it attracted national attention (Janzen 1999; Escofet 2000; Allen 2001; Palmer 2003). The attention brought a lawsuit in 1999 which was founded on allegations that the improper use of orange peels was contaminating nearby waters and attracting citrus pests to the area (Escofet 2000). The Supreme Court eventually found that due to improper pilot studies and improper review of the contract, Del Oro and ACG needed to cancel their contract (*Ticofruit Sociedad Anonima v. Ministerio de Ambiente y Energia, El Ministerio de Salud, y Del Oro Sociedad Anonima* 1999). The Supreme Court decision, along with the associated negative press and changes in management, at Del Oro ultimately precludes the further possibility of applying additional orange peels within ACG.

Nonetheless, plant surveys conducted in 1997, 1999 and 2003 found that plant biodiversity had increased dramatically as a result of dumping (Jimenez, unpublished data). Before the treatment, there were 23 species of plants in the plot. In 2003, 53 months after the treatment, there were 123 species. Pastures directly abutting the site of dumping had shown no major changes in succession or forest species composition.

In order to examine the differences in soil properties since the deposition and the changes in the plant community since 2003, we conducted a variety of soil analyses and vegetation surveys. We also conducted invertebrate pitfall trapping and bird audio analysis to determine whether the deposition of the orange peels had also succeeded in recruiting different sets of animal species to the site.

METHODS

Study Site and Dump

In 1998, 1000 truckloads of peels, seeds, and pulp, weighing approximately 12,000 tons total, were applied on a 3 hectare plot on the eastern side of a specially constructed access road at Modulo II. The organic material was spread into a layer approximately 30 cm thick (Mata 1998), weighing approximately 400 kg/m^2 of which 320 kg/m^2 was water and 80 kg/m^2 was organic waste (Universidad Nacional 1999). Chemical analyses determined that the distributed organic waste was 13% cellulose, 8% protein, 68% carbohydrate, 4% fats and 5% ash (Universidad Nacional 1999). Nutrient surveys of the remnant orange peels found 14.0 g Ca/kg waste, 0.9 g Mg/kg waste, 9.7 g K/kg waste, and 1.2 P/kg waste (Del Oro 1998). Four months after initial deposition, there was still a layer of 10-20 cm of organic matter at the site (Mata 1998). In 1999, the area was tilled to a depth of approximately 15 cm using a tractor. The organic material was further incorporated after the larvae of the fly families Stratiomyidae and Syrphidae consumed the decaying plant material (Jimenez 1999).

No other major management has occurred in the area since 1999. Three horses that are owned by the ACG are occasionally allowed to graze in the area, but the grazing does not seem extensive (pers obs). The site was particularly dry during the time of the study (Segura 2014) and the river that would normally flow along the northern border was almost always dry (pers. obs).

Soil Sampling

Soil samples were collected and analyzed in 2000 and 2014. The sampling and nutrient analysis in 2000 were conducted by Laura Caspar Shanks who was then an undergraduate at Beloit College The data from her work is reproduced here with her permission (See Appendix B). A second set of soil samples was taken in 2014 by Jonathan Choi and was imported into the US under the permit of Professor Jennifer Powers at the

University of Minnesota. Tests for total nitrogen, total carbon, and Mehlich III extractions for exchangeable cations were conducted at the Research Analytical Lab at the University of Minnesota. Particle size distribution tests were conducted by Leland Werden, a graduate student at the University of Minnesota working at the Estación Experimiental Forestal Horizontes in ACG (The Horizontes Experimental Forestry Station).

Soil Sampling and Analysis in 2000

Samples in 2000 from the fertilization site were taken by overlaying a 20 cell grid of 40m by 12m cells over the 3 ha plot and sampling 6 times within each cell to create 6 samples for analyses. Thus each of the 6 analyzed samples was comprised of 20 cores taken from each of the cells in the grid. Samples from outside the treatment area were taken by walking perpendicular to the edge of the deposition site for 100 paces (approx. 67 m) in 4 different directions. Then, walking parallel to the deposition, 5 cores were taken approximately 25 paces apart (approx. 17 m). This procedure was repeated 6 times, thus creating a sample of 6 composite samples of 20 cores.

Each core was taken to a depth of 20 cm with a diameter of approximately 3 cm using a screw-type auger. pH was measured by mixing the samples in deionized water and in a solution of KCl before being analyzed with a pH probe. Percent moisture was measured as the difference in mass of a 100g sample of soil after 24 hours in an oven at 100C. Organic matter was measured by firing a 10g sample in a crucible at 600C for 4 hours. Al^{3+} was measured by titrating a KCl solution with phenothalyne with 0.01M NaOH until the solution turned light purple. Phosphorous was measured using sequential extraction. Concentrations of Ca, Mg and K were determined by Mehlich III extractions and Cu, Fe and Zn were determined using a DTPA method (Canadian Society of Soil Science 2008). The data from inside Modulo II and from the surrounding area were compared using single-tailed Student's t-tests in Statgraphics (Rockville, MD).

Soil Sampling and Analysis in 2014

In July 2014, 9 stakes were planted in each treatment every 25 m to create a 50 x 50 m grid. Soil color was determined using a field guide published by Visual Color Systems (www.visualcolorsystems.com). Samples for texture analysis were taken from the top 10 cm to the east of each stake. Texture was determined using a ribbon test (Colorado Master Gardener Program 2014) and a subsequent confirmatory hydrometer test (Bouyoucos 1962). Soil moisture was determined by air drying soils at room temperature for 5 days. Measurements of mass 24 hours apart on the 4th and 5th days showed that soil moisture changed by less than 5% (mean = 2.57% ± 0.07 SE). This was interpreted to mean that the soils were dry.

Soil samples for nutrient analysis were subsampled 9 times at 10 cm depth within a 1m x 1m grid on the western side of each stake, before being mixed, dried, crushed, and sieved for transportation and later analysis. In sites that were too rocky for grid-based sampling, samples were subsampled within a 2 m radius to the west of the stake. Analyses of the samples for minerals extractable by Mehlich III, nitrogen, and carbon were conducted at the University of Minnesota.

Before comparing any set of data from 2014 a Shapiro-Wilks test for normality was run. If both sets of data were shown to be normal, a Welch's unequal variances t-test was used. This test assumes that both data sets are normally distributed, but assumes that the variances are unequal in size, making this test more appropriate than the more common Student's t-test. If one of the datasets was not normally distributed, a Wilcoxon rank-sum test was applied, which is better able to deal with non-normal data. All data analyzed as part of the 2014 surveys were analyzed using R (R Core Team 2013). All 2014 data was visualized using the R package ggplot2 (Wickham 2009)

Vegetation Surveys

Three 100m transects were established in each plot at a distance 50m, 75m and 100m from the access road in June of 2014. Transects were laid over the course of a morning with a team of collaborators from the University of Minnesota. All DBH data was measured in the field over the course of 2 weeks. All trees within 3m of the transect that were larger than 5 cm diameter at breast height (DBH) and taller than 1.3m were tagged, measured, and identified by Daniel Perez Aviles, a plant taxonomist employed by the University of Minnesota. All saplings smaller than 5 cm DBH and taller than 1.3m and all lianas greater than 5cm DBH that were growing within 3m of the transect were measured, but were not tagged or identified.

Solar radiation indices, proportion of visible sky, and leaf area indices were determined using HemiView software and images taken with a fisheye lens on 11 July 2014 (Rich et al. 1998). Photos (n = 66) were taken 1.3m off the ground every 10m along each transect within each treatment group. A tripod was used to stabilize the camera and a spherical level was used to ensure that the camera was level. The sky was largely overcast with intermittent showers and high winds when the photos were taken. Threshold for leaf obstruction was determined visually. Given that all of the sets of data were not normally distributed, Wilcoxon rank sum tests were used to compare the solar radiation indices, proportion of visible sky, and leaf area indices between the unfertilized and fertilized sides.

Macroinvertebrate Surveys

Three pitfall traps were installed in the middle of each of the transects within each treatment. Pitfall traps were created by installing two 16 oz plastic cups flush to the soil surface(Greensdale 1964; Ward et al. 2001; Madryn 2010). Ethanol (80%) was used as a killing and preservative agent. Wooden trap covers were installed to prevent the cups from flooding with rainwater and were checked every 3 to 4 days. Ethanol preserved samples were identified by Joe Rowlett at the Field Museum of Natural History in Chicago, IL. Insects were identified, when possible, to family or subfamily. If specimens were not identified to subfamily, the next largest available taxon was used.

Since the samples obtained from the pitfall samples were all aggregated into single containers before transportation, we are unable to determine whether there is spatial or temporal variation in the families of invertebrates captured. We are also unable to determine what the average number of families obtained by a trap in a single week might be.

Vertebrate Audio Surveys

Vertebrate species composition was explored using a SM2+ Audio Recording Device (wildlifeacoustics.com). The recording device was placed approximately 1.5m off the ground along the transects that were furthest from the other treatment. Audio was recorded between 0500 to 0800 and 1600 to 1900 each day. Five minute portions every 30 minutes were sampled to roughly simulate the sampling of a point count. All of the bird calls were identified by Guillermo Funes, a biology student and avid birder at the Universidad de El Salvador. Those calls that could not easily be identified even after comparisons with audio databases were marked as unknown for later review.

We assume that this dataset is only able to give us data on the presence or absence of species and is not able to tell us anything about relative abundance. This is because it is impossible to distinguish between a single bird calling for 3 hours on a given sample, and 15 birds calling one time each. Subsequent surveys using either point counts or more advanced bird audio monitoring could improve our understanding of the bird community.

Quantifying Biomass from Vegetation Surveys

Allometric equations were used to estimate aboveground biomass (AGB). Since the study site was in a transition area between dry and wet forests, equations were sought that either explicitly looked at "moist" forest or that were derived from sites similar to Modulo II. To that end, 4 equations from 3 different papers were used.

The first and second equations were for dry and moist tropical forests based on a meta-analysis by Chave et al. 2005. We chose these equations due to their robust dataset of 2,410 trees and their frequency in the literature (e.g. Malhi et al. 2006, Gibbs et al. 2007, Phillips et al. 2009, Goetz et al. 2009, Lewis et al. 2009, Baccini et al. 2012). The parameters for the equations from Chave et al. 2005 include trunk diameter in cm (DBH) and wood specific gravity in g/cm^3 (ρ). The equations are listed below.

$$AGB_{Dry} = \rho * \exp(-0.667 + 1.784\ln(DBH) + 0.207\,(\ln(DBH))^2 - 0.0281(\ln(D))^3)$$

$$AGB_{Moist} = \rho * \exp(-1.499 + 2.148\ln(DBH) + 0.207\,(\ln(DBH))^2 - 0.0281(\ln(D))^3)$$

All of the wood specific gravity measures were derived from the Global Wood Density Database (Zanne et al. 2009; Chave et al. 2009). Those values that could not be taken directly from the database were derived in other ways based off of existing data (Table 1). All saplings were assigned a wood specific gravity value of 0.645 g/cm^3 which was the average wood specific gravity value from a survey of 2456 Neotropical tree species (Chave et al. 2006).

Table 1 – Wood specific gravity constants used for calculating aboveground biomass from the Global Wood Density "Dryad" Dataset.

Tree Species Name	Wood Specific Gravity	Extraction/Derivation from Dryad Dataset
Apeiba tibourbou	0.2	Only 1 Available Value
Ardisia revoluta	0.62	Value for *Apeiba guaiensis* from S. America
Bursera simaruba	0.335	Average of Central American values
Byrsonima crassifolia	0.59	Central American value
Cecropia peltata	0.295	Average of Central American values
Cochlospermum vitifolium	0.165	Central American value
Cordia alliodora	0.473	Average Central American values
Cordia panamensis	0.524	Average of all American values for genus *Cordia*
Curatella americana	0.65	Only 1 Available Value
Ficus spp	0.397	Average of all American values for genus *Ficus*
Genipa americana	0.66	Average of Central American values
Gliricidea sepium	0.585	Average of Mexican and S. American values
Guazuma ulmifolia	0.535	Average of Central American values
Luehea seemannii	0.417	Only 1 Available Value
Muntingia calabura	0.3	Only 1 Available Value
Piper spp	0.394	Average of all American values for genus *Piper*
Sapium glandulosum	0.415	Average of South American values
Schefflera morototoni	0.454	Average of South American values
Simaruba glauca/ amara	0.423	Average of Central American values
Spondias mombin	0.36	Central American value
Tabebuia rosea	0.48	Central American value
Trichilia martiana	0.47	Only 1 Available Value
Vacchellia collinsii	0.8	Only 1 Available Value
Vernonia patens	0.540	Available value (synonym *Vernonanthura patens)*
Xylopia frutescens	0.593	Average of South American values

We note that these models, given that they do not include a height-of-tree component, do not fit quite as well as others available. We have decided, however, to include these models due to their widespread use within the literature.

We also used a model developed by Sierra et al. 2007 to estimate total carbon stocks within an ecosystem that resembles the one in our study. Their study focused on the Porce region of Colombia, which receives slightly more rain than a true dry forest but in a similarly seasonal manner. The equation is listed below.

$$\ln(Tree\ Biomass) = -2.232 + 2.422\ln(DBH)$$

The convention among studies like ours has been to assume that carbon biomass can be roughly approximated as being half of the aboveground biomass (Brown & Lugo 1982; Malhi et al. 2004). Though this generally tends to overestimate the carbon biomass of tropical trees, we have decided to keep this generalized way of calculating carbon biomass for simplicity (Chave et al. 2005).

The final method used to analyze our data are a set of equations suggested by collaborators at the University of Minnesota. The equations of van Breugel et al. (2011) were originally formulated to examine differences in errors between plots of different compositions. As part of this analysis, they created a set of allometric equations that suit the dry forests of Panama, including a set of species-specific equations and an adjusted equation that better incorporates wood specific gravity. The equations generally take one of the two following forms, depending on whether a species-specific allometric equation is available.

$$\ln(AGB) = a + b * \ln(DBH)$$

$$\ln(AGB) = a + b_1 * \ln(DBH) + b_2 * \ln(Wood\ Specific\ Gravity)$$

A modified version of the first equation was used for the saplings that we did not have species specific information available for. The parameters for a, b_1, and b_2 are specified in the van Bruegel et al. paper.

Quantifying Species Richness

Species richness remains a tried and true method for comparing differences between two different sites. Species richness is defined as the total number of individual species found in a given location and ignores differences in relative abundance in species (Magurran 1988). An easy way to visualize these differences is through the use of rarefaction curves (Gotelli & Colwell 2001; Colwell et al. 2012). This method has been used elsewhere as a way to compare richness between different ecosystems and provides a simple way to visualize differences in diversity (e.g. Barlow et al. 2007). In this approach, individuals are randomly sampled without replacement from a given population. As the number of individuals that are sampled increases, the number of unique species encountered is tallied. We can then estimate how many species should be represented within a population assuming that a certain number of individuals have been sampled. In this regard, rarefaction curves are similar to species area curves. Rarefaction analysis with both interpolation and extrapolation was conducted using the iNEXT package (Colwell et al. 2012; Hsieh et al. 2014).

Quantifying Species Diversity

Though species richness has been used extensively and is a relatively easy metric to measure, species richness ignores the relative abundance of each species, such that a forest with 97 trees of species a, 1 tree of species b, 1 tree of species c and 1 tree of species d will be as species rich as a forest with 4 equally abundant tree species. Other calculations of biodiversity are able to take both species richness and their relative abundances into account. This chapter uses both the Shannon Index and the Simpson Index to examine the diversity between the two treatments.

The Shannon Index or Shannon Entropy (H') is a measure of the uncertainty with which one can predict the next item in a given set (Shannon 1948). It is calculated as the summation of the ratio of individuals of a given species (s) to all individuals of all species (p_i) times the natural log of this ratio (Nangendo et al. 2002). This index is thus sensitive to the relative abundance of species within a given sample. The index is typically written and calculated as follows:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

The Simpson Index (λ) is used to quantify species dominance and represents the probability that two individuals selected randomly from a population will be from the same group (Simpson 1949; Nangendo et al. 2002). It is calculated using the following formula.

$$\lambda = \sum p_i^2$$

The variable p_i is the same as that used above for the Shannon Index. Due to the fact that this index decreases as biodiversity increases, we will use the complement of this index ($1 - \lambda$), also known as the Gini-Simpson Index, along with the Inverse Simpson Index ($1/\lambda$), for our analysis and discussion (Nangendo et al. 2002).

In order to calculate these indices and to plot rarefaction curves, different levels of classification were used for each data set. Biodiversity on the level of vegetation was limited to those trees that were larger than 5 cm DBH. This necessarily excluded all types of grasses, lianas and herbs, biasing the sample towards being more similar. Invertebrates were grouped by subfamily regardless of obvious visual differences at the genus level. In the event that subfamily information was not available, the next largest taxon was used, though often this was simply the family level. Biodiversity indices for plants and invertebrates were calculated using the vegan package in R (Oksanen et al. 2013).Rarefaction was not performed on the vertebrate audio data.

RESULTS

Soil Color, Moisture, Texture, and Nutrients

Table 2 – Soil properties from samples taken in 2000 at Module II and the surrounding area, as analyzed by Laura Shanks in 2000.

	Module II (Mean ± SD) (2000)	Surrounding Area (Mean ± SD)(2000)	p-value
pH (H_2O)	6.1 ± 0.3	5.5 ± 0.3	0.006
pH (KCl)	4.7 ± 0.2	4.5 ± 0.3	0.36
Moisture %	17.8 ± 0.8	22.0 ± 2.0	< 0.001
Organic material %	4.66 ± 0.65	3.56 ± 1.09	0.06
Al^{3+} (mL/100 g soil)	0.2 ± 0.2	0.9 ± 0.3	< 0.001
Ca (ppm)	1840 ±480	1160 ± 180	0.003
Mg (ppm)	564 ± 122.4	556.8 ± 32.2	0.88
K (ppm)	1657.5 ± 386.1	425.1 ± 300.3	< 0.001
P (ppm)	21.3 ± 10.8	13.8 ± 2.1	0.13
Cu (ppm)	4.8 ± 0.9	2.2 ± 0.3	< 0.001
Fe (ppm)	557 ± 293	181 ± 60	0.01
Zn (ppm)	1.5 ± 0.6	0.5 ± 0.2	0.004

Table 3 – Soil properties from samples taken in 2014 at Module II and an adjoining control pasture.

	Module II (Mean ± SD) (2014)	Control Pasture (Mean ± SD) (2014)	p-value
Soil Moisture	23.28 ± 2.09	24.21 ± 1.58	0.019
Carbon (%)	5.313 ± 0.55	5.038 ± 1.00	0.48
Nitrogen (%)	0.422 ± 0.04	0.329 ± 0.05	< 0.001
C:N Ratio	12.58 ± 0.56	15.23 ± 0.78	< 0.001
Ca (ppm)	2109 ± 521.6	739.5 ± 245.5	< 0.001
Mg (ppm)	392.2 ± 98.3	240.8 ± 64.7	0.001
K (ppm)	321.4 ± 97.4	147.86 ± 38.5	< 0.001
P (ppm)	7.409 ± 4.66	2.874 ± 0.86	< 0.001
Cu (ppm)	7.019 ± 0.76	4.004 ±0.89	< 0.001
Fe (ppm)	223.1 ± 78.6	128.61 ± 46.5	0.001
Zn (ppm)	1.714 ±0.40	1.039 ± 0.37	0.005
Mn (ppm)	164.6 ± 53.0	93.02 ± 53.5	0.012
Na (ppm)	20.63 ± 5.01	21.93 ± 3.31	0.52

Soil color was typically more heterogeneous in the unfertilized area than in the fertilized area. Color was typically darker and browner (Munsell Color Code 7.5YR 2.5/2) in the fertilized area while unfertilized soils were redder (Munsell Color Code 5YR 2.5/2, Appendix B). Soil texture, which was clay dominated in 2000, remained clay in 2014 (Appendix B). Soil moisture in was significantly higher in the control than in the fertilized treatment in the 2000 survey (Student's t-test, *n* = 6 per treatment, *p* < 0.001, Table 2) and in the 2014 survey (Wilcoxon rank-sum, *n* = 45 per treatment, *p* = 0.020, Figure 2, Table 3).

The soil nutrient survey in 2014 (Table 3) confirms the findings of the 2000 survey (Table 2); the application of orange peels led to a significant increase in a variety of nutrients. In 2000, surveys found an increase in pH (Student's one-tail t-test, *n* = 6, p = 0.006), higher moisture (Student's, p < 0.001), higher concentrations of K (Student's, p < 0.001), Ca (Student's, p = 0.003), Cu (Student's, p < 0.001), Fe (Student's, p < 0.01), and Zn (Student's, p = 0.004) and lower concentrations of Al (Student's, p < 0.001). The data for Ca, Mg, and

K are presented here in ppm, but were originally reported in units of mEq/ 100 g soil. Data for Mn and Na are not available because those nutrients were not surveyed in 2000.

The 2014 survey (Figure 2, Table 3) found significant increases in N (Welch t-test, *n* = 18, $p < 0.001$), K (Welch, $p < 0.001$), Ca (Wilxocon, $p < 0.001$), Cu (Wilcoxon, $p < 0.001$), Fe (Welch, $p < 0.001$), Zn (Wilcoxon, $p = 0.006$), Mg (Welch, $p = 0.002$), Mn (Welch, $p = 0.012$) and P (Wilcoxon, $p < 0.001$) and decreases in the C:N ratio (Welch, $p < 0.001$) with no information available on pH, Al^{3+} and organic material. Data for Al^{3+} and pH are unavailable due to the methods for analysis used in 2014.

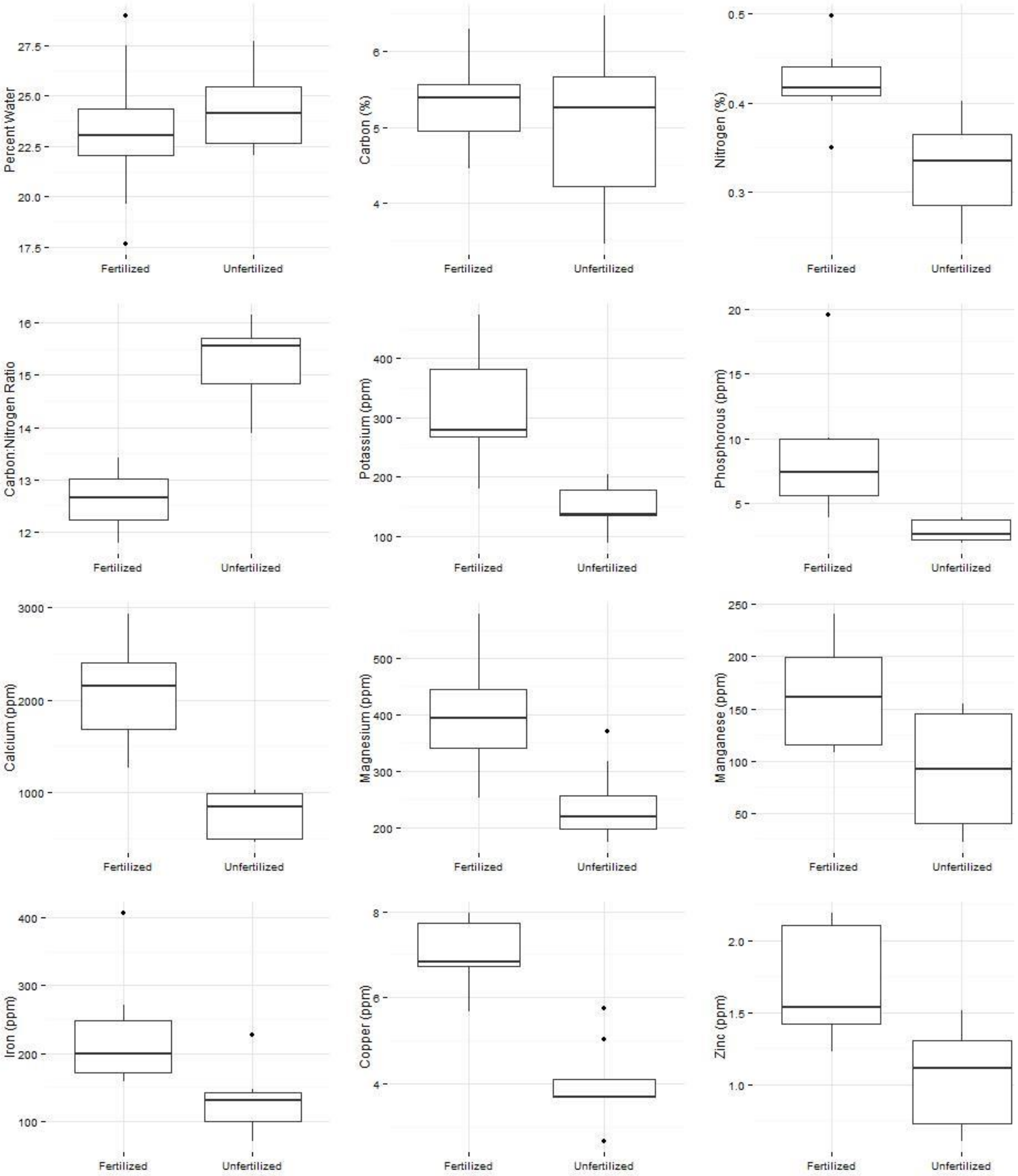

Figure 2 – Differences in soil fertility metrics between the fertilized and unfertilized treatments in the 2014 samples. All differences, except for differences in carbon and sodium, are statistically significant.

Vegetation

Community Composition

Within an observed area of 1800 m^2 on the unfertilized side, there were 149 trees with a DBH greater than 5 cm representing 8 different species from 7 different families (Tables 4 and 5). Only 3 of the species were unique to the unfertilized side. In an equal area on the fertilized side, there were 133 trees with a DBH greater than 5 cm representing 24 different species from 20 different families of which 18 species were unique (Tables 4 and 6). These differences were statistically significant based on the plotted rarefaction curves and are visualized in pie charts ($p < 0.05$, Figures 3 and 4). When using rarefaction, the lack of overlap at the 95% confidence interval is taken as a conservative estimate for significant differences at $p < 0.05$ (Colwell 2013).

Table 4 – Diversity indices for tree species between the two treatment groups

	Treatment	
Index	Unfertilized	Fertilized
Species Richness	8	24
Unique Species	3	19
Shannon Index	0.960	2.820
Gini-Simpson Index	0.470	0.927
Inverse Simpson Index	1.886	13.701

Table 5 – Species list for trees larger than 5 cm DBH in the unfertilized treatment, sorted by abundance. Asterisks indicate species not found in the other treatment.

Family	Species	Number of Individuals
Dilleniaceae	*Curatella americana*	104
Malpighiaceae	*Byrsonima crassifolia*	30
Cochlospermaceae	*Cochlospermum vitifolium*	5
Fabaceae – Papilionoideae	*Gliricidia sepium* *	5
Myrsinaceae	*Ardisia revoluta* *	2
Euphorbiaceae	*Sapium glandulosum* *	1
Urticaceae	*Cecropia peltata*	1
Fabaceae – Mimosoidea	*Vachellia collinsii*	1

Table 6 – Species list for trees larger than 5 cm DBH in the fertilized treatment, sorted by abundance. Asterisks indicate species not found in the other treatment.

Family	Species	Number of Individuals
Urticaceae	*Cecropia peltata*	16
Malvaceae – Byttnerioideae	*Guazuma ulmifolia* *	15
Cochlospermaceae	*Cochlospermum vitifolium*	13
Meliaceae	*Trichilia martiana* *	12
Annonaceae	*Xylopia frutescens* *	11
Dilleniaceae	*Curatella americana*	11
Asteraceae	*Vernonia patens* *	6
Malvaceae – Grewioidea	*Apeiba tibourbou* *	6
Boraginaceae	*Cordia alliodora* *	5
Piperaceae	*Piper spp* *	4
Malpighiaceae	*Byrsonima crassifolia*	4
Malvaceae – Grewioidea	*Luehea seemannii* *	3
Boraginaceae	*Cordia panamensis* *	3
Anacardiaceae	*Spondias mombin* *	3
Araliaceae	*Schefflera morototoni* *	2
Muntingiaceae	*Muntingia calabura* *	2
Fabaceae – Mimosoideae	*Vachellia collinsii*	2
Moraceae	*Ficus spp 1 (Ficus tonduzzi)* *	1
Moraceae	*Ficus spp 2* *	1
Rubiaceae	*Genipa americana* *	1
Simaroubaceae	*Simaruba glauca aka amara* *	1
Burseraceae	*Bursera simaruba* *	1
Bignoniaceae	*Tabebuia rosea* *	1

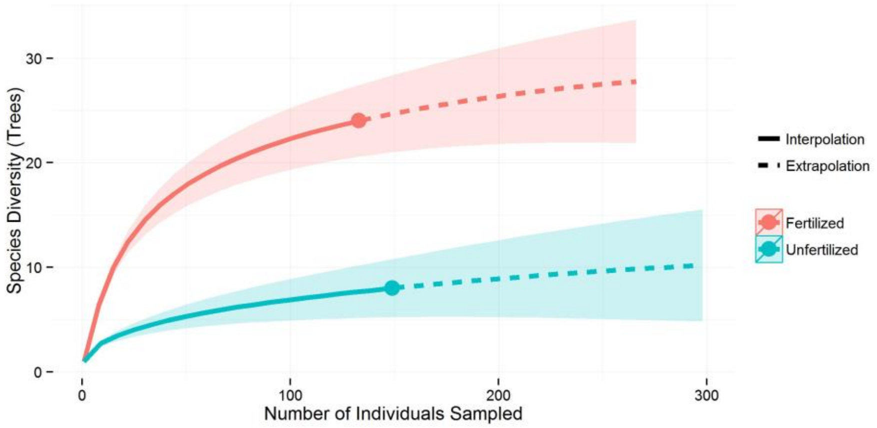

Figure 3 – Non-overlapping rarefaction curves imply a statistically significant difference in tree community species richness.

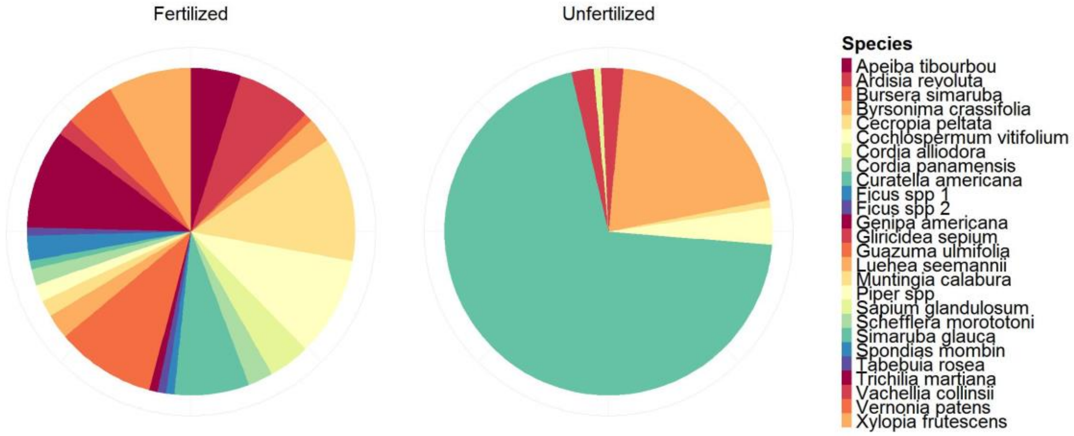

Figure 4 – Relative abundance of individual species as a portion of the entire community. The unfertilized side is dominated by *Curatella americana* in light green and *Byrsonima crassifolia* in orange.

Analysis on the basis of seed dispersal mechanism showed that the vast majority of the seeds on the unfertilized side were dispersed by birds (Figure 5, Table 7). This may be due to the fact that both dominant species on the unfertilized side, namely *Curatella americana* and *Byrsonima crassifolia*, are both bird dispersed. There were numerous trees whose exact dispersal syndrome were indiscernible from the literature and were simple classified as being “animal” dispersed, though this may range from birds and bats to monkeys and horses. We are aware that mammals and birds, are in fact “animals,” but we submit this as a semi-casual petition for further autecological studies on seed dispersal mechanisms of Neotropical trees for the purposes of restoration.

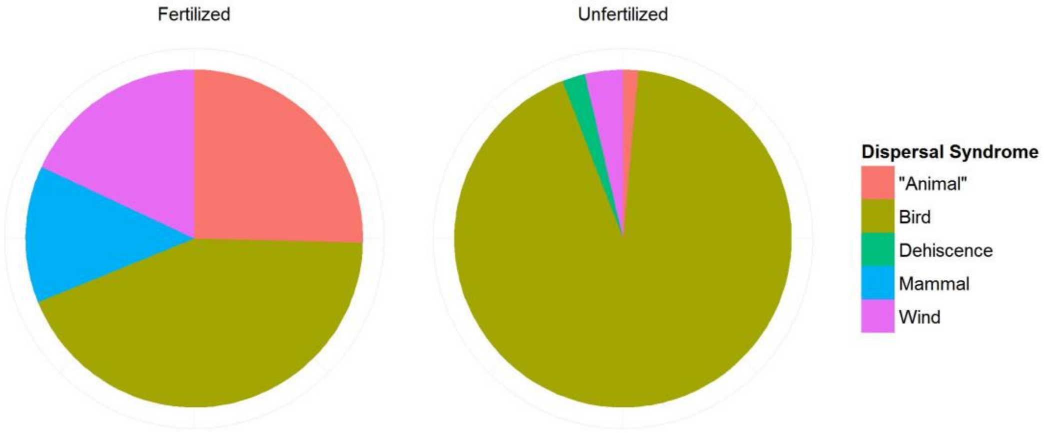

Figure 5 – Large differences in the dispersal syndrome of trees larger than 5 cm DBH between the two treatments.

Table 7 – The typical habitat of individual tree species found within Santa Rosa National Park, a park within the larger ACG, according to Janzen 1983 (excludes 3 species, *Schefflera morototoni*, *Xylopia frutescens* and *Vernonia patens*) and their dispersal syndromes. List in alpha order sorted by Treatment group.

Species Name	Treatment	Community Level	Rarity	Habitat	Dispersal Syndrome	Syndrome Source
Ardisia revoluta	Unfertilized	Understory	Frequent	Riparian, Alluvial	Animal	Powers et al. 2009
Gliricidia sepium	Unfertilized	Subcanopy	Occasional	Plateau, Slope, Open	Animal, Dehiscence	Janzen 1983; Powers et al. 2009
Sapium glandulosum	Unfertilized	Canopy	Occasional	Alluvial, Slope	Bird, Monkey	Norconk et al. 1998; Link & Stevenson 2004
Byrsonima crassifolia	Both	Canopy	Occasional	Plateau, Slope, Open	Bird, Small Mammal	Janzen 1983; Powers et al. 2009
Cecropia peltata	Both	Canopy	Frequent	Secondary	Bird, Bat	Griscom et al. 2009; Powers et al. 2009
Cochlospermum vitifolium	Both	Subcanopy	Occasional	Plateau, Slope	Wind	Janzen 1983; Griscom et al. 2009; Powers et al. 2009; López-Martínez et al. 2013
Curatella americana	Both	Canopy	Frequent	Plateau, Open	Bird	Barbosa et al. 2012
Vachellia collinsii	Both	Understory	Common	Open, Plateau, Slope, Ridge, Secondary	Bird, Bat	Griscom et al. 2009
Apeiba tibourbou	Fertilized	Subcanopy	Occasional	Plateau, Slope	Animal	Link & Stevenson 2004
Bursera simaruba	Fertilized	Canopy	Frequent	Slope, Ridge	Animal	Janzen 1983; Griscom et al. 2009
Cordia alliodora	Fertilized	Subcanopy	Frequent	Plateau, Slope	Wind, Bird	Opler et al. 1975; Janzen 1983; Griscom et al. 2009
Cordia panamensis	Fertilized	Understory	Frequent	Plateau, Slope	Bird	Opler et al. 1975; Griscom et al. 2009
Ficus spp	Fertilized	Various	Common	Various	Animal	Janzen 1983; Link & Stevenson 2004
Genipa americana	Fertilized	Subcanopy	Occasional	Plateau, Slope	Mammal, Bird	Griscom et al. 2009
Guazuma ulmifolia	Fertilized	Subcanopy	Common	Plateau, Slope, Open	Large Mammal	Janzen 1983; Powers et al. 2009
Luehea seemannii	Fertilized	Canopy	Occasional	Swamp, Alluvial	Wind	Muller-Landau et al. 2008; López-Martínez et al. 2013
Muntingia calabura	Fertilized	Subcanopy	Frequent	Open	Bird, Bat	Griscom et al. 2009
			Rare	Plateau, Slope		
Piper		Treelet	Common	Plateau, Ridge	Bird, Bat	Janzen 1983
Schefflera morototoni	Fertilized				Animal	Link & Stevenson 2004
Simaruba glauca	Fertilized	Canopy	Occasional	Plateau, Slope	Animal, Primate	Chapman 1989
Spondias mombin	Fertilized	Canopy	Frequent	Slope, Open	Bird, Large Mammal	Griscom et al. 2009; Powers et al. 2009
Tabebuia rosea	Fertilized	Canopy	Frequent	Plateau, Slope	Wind	Griscom et al. 2009
Trichilia martiana	Fertilized	Subcanopy	Frequent	Plateau, Slope	Bird	Powers et al. 2009
Vernonia patens	Fertilized				Wind	Griscom et al. 2009
Xylopia frutescens	Fertilized				Animal	Zahawi & Augspurger 2006

Aboveground Biomass and Allometry

Analysis using all 4 of the allometric equations suggests dramatic increases in aboveground biomass (Figure 6). The most conservative estimation was the Chave et al. dry forest equation, which estimated an increase in aboveground biomass by a factor of 2.29. The output of the equations of van Bruegel et al. estimated an increase by 2.33, Chave et. al's moist forest equation estimated an increase of 3.27 and the Sierra et al. equation estimated an increase of 4.20. It should be noted that even with these dramatic trends across 4 different models, incorporating the error generated by taking DBH measurements, diurnal variations in DBH as a result of water uptake and weather, and the uncertainty generated by the models, discourages a more rigorous or confident statement about the amount of aboveground biomass in the system. The uncertainty of these measurements also discourages us from conducting any analysis of the potential carbon sequestration and carbon pricing implications for orange peel-catalyzed forest regeneration.

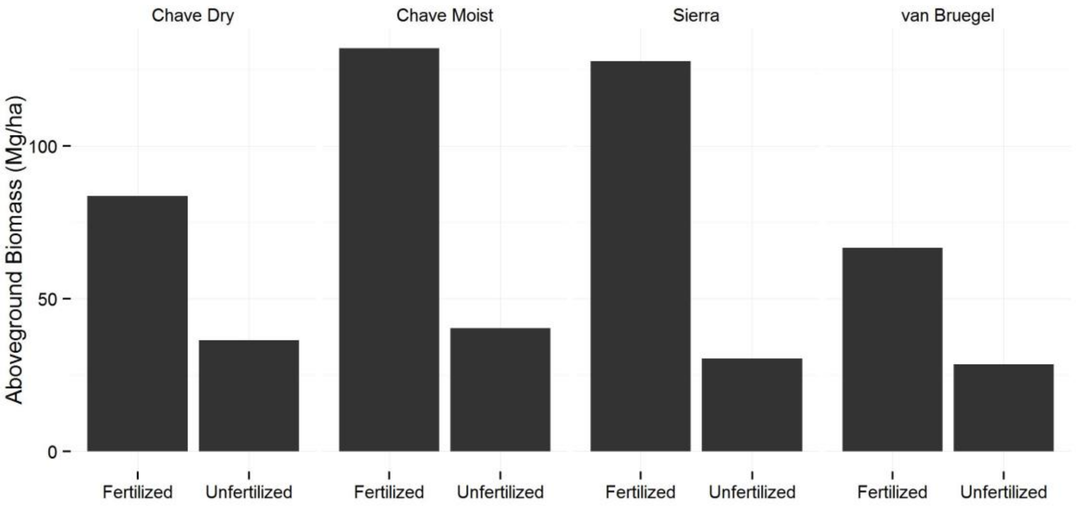

Figure 6 – Differences in aboveground biomass between the fertilized and unfertilized treatments across 4 different equations.

Canopy Cover and Solar Radiation

The proportion of visible sky in each image (Wilcoxon, p < 0.001), the direct site factor (Wilcoxon, p < 0.001) and indirect site factor (Wilcoxon, p < 0.001) were all significantly higher in the control than in the treatment. The leaf area index, defined as the leaf area per unit ground area, was also significantly higher in the treatment group (Wilcoxon, $p < 0.001$, Figure 7).

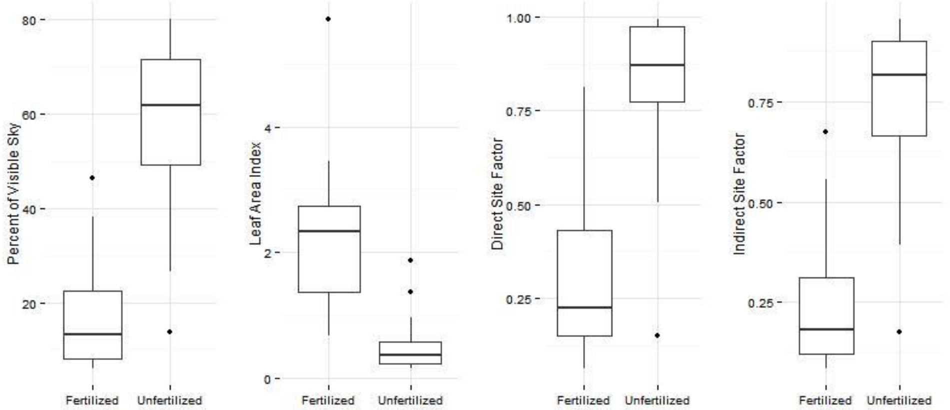

Figure 7 – Significant differences in percent of visible sky, leaf area index, direct site factor, and indirect site factors between the two sites.

Invertebrates

Pitfall traps yielded a total of approximately 1936 arthropod specimens of which 258 were from the unfertilized treatment (Table 9) and the remaining 1678 were from the fertilized treatment (Table 10). Approximately 1000 of these were from a single genus of ant from the family Ponerinae and were excluded from the analysis. Both samples have 17 orders represented, though the fertilized side had 47 subfamilies to the unfertilized side's 42 subfamilies (Table 8). Analysis using various diversity indices found that there was slightly greater diversity in families on the fertilized side than on the unfertilized side. When both

Table 8 – Diversity indices and species richness in both unfertilized and fertilized treatments.

	Treatment	
Index	Fertilized	Unfertilized
Subfamily Richness	47	42
Unique Subfamilies	23	17
Shannon Index	2.928	2.852
Gini-Simpson Index	0.927	0.900
Inverse Simpson Index	13.660	10.011
Coleoptera		
Subfamily Richness	16	10
Unique Subfamilies	13	6
Shannon Index	1.847	2.119
Diptera		
Subfamily Richness	6	6
Unique Subfamilies	4	4
Shannon Index	0.842	1.193

beetles (Coleoptera) and flies (Diptera) were analyzed individually, it was found that the unfertilized treatment was more diverse, though these differences may be attributable to insufficient sample size.

Table 9 – Family list for macroinvertebrates found in the pitfall traps of the unfertilized treatment. Asterisks indicate subfamilies not found in the other treatment.

Families and Subfamilies by Order	Number of Individuals	Families and Subfamilies by Order	Number of Individuals
Acari	~ 60	Hemiptera	
Araneae		Naucoridae	42
Pholcidae *	6	Reduviidae	2
Linyphiidae	3	Unidentified	2
Lycosidae	3	Cydnidae *	1
Oonopidae *	3	Hymenoptera	
Salticidae	1	Formicidae – Ponerinae	22
Blattodae	1	Formicidae – Myrmicinae	11
Coleoptera		Formicidae – Formicinae	1
Curculionidae – Scolytinae	6	Chalcidoidea *	1
Anthicidae *	4	Isoptera *	2
Elateridae *	4	Lepidoptera *	2
Geotrupidae – Bolboceratinae *	4	Opiliones	1
Staphylinidae – Aleocharinae	4	Oribatida	2
Nitidulidae	4	Orthoptera	
Latridiidae – Corticariinae *	1	Gryllidae	6
Curculionidae	1	Polydesmida *	1
Mycetophagidae *	1	Scorpiones	2
Tenebrionidae – Alleculinae *	1	Scutigeromorpha	1
Dermaptera	24	Spirobolida	2
Diptera		Thysanura	
Drosophilidae	23	Lepismatidae	1
Sciaridae	10		
Milichiidae *	3		
Cecidomyiidae *	2		
Platystomatidae *	1		
Sphaeroceridae *	1		

Table 10 – Family list for macroinvertebrates found in the pitfall traps of the fertilized treatment. Asterisks indicate subfamilies not found in the other treatment.

Families and Subfamilies by Order	Number of Individuals	Families and Subfamilies by Order	Number of Individuals
Acari	~ 60	Diptera	
Araneae		Drosophilidae	70
Linyphiidae	18	Phoridae *	14
Lycosidae	8	Sciaridae	4
Salticidae	3	Mycetophilidae *	3
Thomasiidae *	1	Sphaeroceridae – Sphaerocerinae *	1
Blattodea	2	Tipulidae *	1
Coleoptera		Hemiptera	
Curculionidae - Scolytinae	54	Naucoridae	61
Nitidulidae	23	Reduviidae	12
Staphylinidae – Aleocharinae	22	Anthocoridae *	1
Staphylinidae – Staphylininae *	19	Unidentified	1
Corylophidae *	4	Hymenoptera	
Staphylinidae – Philonthini *	3	Formicidae - Ponerinae	~ 1050
Scarabidae – Scarabinae *	3	Formicidae – Myrmicinae	~ 55
Anobiidae – Ptininae *	2	Formicidae – Formicinae	1
Endomychidae *	2	Apoidea *	1
Histeridae *	2	Opiliones	
Lampyridae *	2	Laniatores *	4
Scarabidae – Aphodiinae *	2	Unidentified	4
Carabidae – Harpalinae *	1	Oribatida	5
Curculionidae	1	Orthoptera	
Curculionidae – Platypodidae *	1	Gryllidae	2
Passalidae *	1	Psocoptera *	2
Silvanidae *	1	Scorpiones	1
Unidentified	9	Scutigeromorpha	5
Collembola *	~ 75	Spirobolida	2
Dermaptera	~ 70	Symphyla *	8

Rarefaction, whether it sorts families from the entire sample or from individual orders, displays differences with very large margins of error which are difficult to interpret (Figure 8). Rarefaction for the entire sample did not include the 1,000 ants from a singular genus. Overall there appears to be a general trend for the unfertilized sample to accumulate families at a faster rate than the fertilized side.

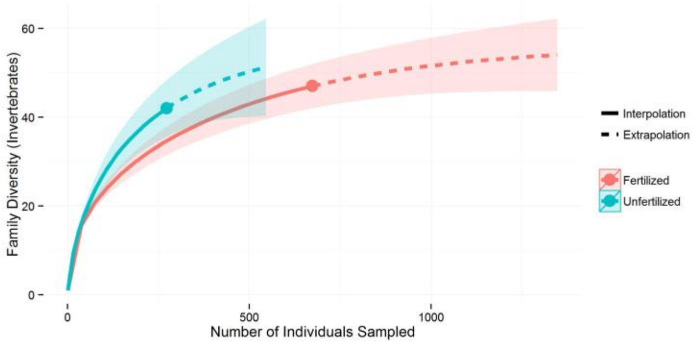

Figure 8 – Differences in family diversity across all different orders, excluding 1,000 ants in the family Ponerinae.

Vertebrate Audio

Given the limitations in our methodology, we are only able to report the presence of species and not their relative abundance. Over the course of 144, 5-minute simulated "point counts," 34 bird species and 2 monkey species were detected (Table 11). White faced capuchin monkeys (*Cebus capucinus*) and howler monkeys (*Alouatta palliata*) were found within the 78 point counts in the fertilized treatment and the 66 point counts in the unfertilized treatment. Twenty bird species were shared between the two treatments, with 9 bird species unique to the fertilized treatment, and 5 bird species unique to the unfertilized treatment. Of the 20 shared species, 15 were Mesoamerica-restricted. Within the bird species unique to either treatment, 5 of the species found in the unfertilized treatment and 4 of the species found in the fertilized treatment were Mesoamerica-restricted. There were 17 unidentifiable calls in the fertilized treatment and 19 in the unfertilized treatment. Many of these were identified as parakeets, amazons, or toucans but further species-level determination was unavailable.

Table 11 – Vertebrate species observed in the audio recordings, ordered by which treatment they were found in and alphabetically by common name. Restricted refers to whether the species was restricted in range to Mesoamerica.

Common Name	Species Name	Treatment	Guild	Restricted	Most Disturbed Habitat	Least Disturbed Habitat	Source
Howler Monkey	*Alouatta palliata*	Both	Folivore	No			Glander 1977
White-Faced Capuchin	*Cebus capucinus*	Both	Omnivore	Yes			Wainwright 2002; Rylands et al. 2006
Banded Wren	*Thryophilus pleurostictus*	Both	Insectivore	Yes	Secondary	Gaps	Kroodsma & Brewer 2005a
Black Headed Trogon	*Trogon melanocephalus*	Both	Omnivore	Yes	Secondary	Gallery	Collar 2001
Blue-crowned Motmot	*Momotus lessonii*	Both	Omnivore	Yes	Plantation	Primary	del Hoyo et al. 2014a
Cinnamon Hummingbird	*Amazilia rutile*	Both	Nectarivore	Yes	Savanna	Secondary	Weller et al. 2015
Collared Aracari	*Pteroglossus torquatus*	Both	Omnivore	Yes	Secondary	Late Secondary	Short & Kirwan 2014
Golden-olive Woodpecker	*Colaptes rubiginosus*	Both	Insectivore	No	Plantation	Secondary	Winkler & Christie 2002a
Great Kiskadee	*Pitangus sulphuratus*	Both	Omnivore	No	Savanna	Early Secondary	Mobley 2004a
Hoffmann's Woodpecker	*Melanerpes hoffmannii*	Both	Insectivore	Yes	Plantation	Secondary	Winkler & Christie 2002b
Keel-billed Toucan	*Ramphastos sulfuratus*	Both	Omnivore	Yes	Savanna	Late Secondary	Short & Sharpe 2014
Lineated Woodpecker	*Hylatomus lineatus*	Both	Insectivore	No	Savanna	Gallery	Winkler & Christie 2002c
Long-tailed Manakin	*Chiroxiphia linearis*	Both	Frugivore	Yes	Early Secondary	Gallery	Snow 2004
Montezuma Oropendola	*Psarocolius montezuma*	Both	Omnivore	Yes	Savanna	Secondary	Fraga 2011
Plain Wren	*Thryothorus modestus*	Both	Insectivore	Yes	Savanna	Secondary	Kroodsma & Brewer 2005b
Scrub Euphonia	*Euphonia affinis*	Both	Omnivore	Yes	Savanna	Gallery	Hilty 2011a
Social Flycatcher	*Myiozetetes similis*	Both	Omnivore	No	Savanna	Gallery	Mobley 2004b
Thicket Tinamou	*Crypturellus cinnamomeus*	Both	Omnivore	Yes	Secondary	Primary	Cabot et al. 2014
White-fronted Amazon	*Amazona albifrons*	Both	Herbivore	Yes	Secondary	Late Secondary	Collar & Boesman 2014
White-throated Magpie jay	*Calocitta formosa*	Both	Omnivore	Yes	Savanna	Gallery	dos Anjos 2009
White-tipped Dove	*Leptoptila verreauxi*	Both	Insectivore	No	Early Secondary	Secondary	Baptista et al. 2013a
Yellow-naped Amazon	*Amazona auropalliata*	Both	Herbivore	Yes	Savanna	Secondary	del Hoyo et al. 2014b
Barred Antshrike	*Thamnophilus doliatus*	Fertilized	Insectivore	No	Secondary	Gallery	Zimmer et al. 2012
Boat-biller flycatcher	*Megarynchus pitangua*	Fertilized	Omnivore	No	Savanna	Late Secondary	Mobley 2004c
Common Pauraque	*Nyctidromus albicollis*	Fertilized	Insectivore	No	Plantation	Secondary	Cleere 1999
Dusky Capped Flycatcher	*Myiarchus tuberculifer*	Fertilized	Insectivore	No	Plantation	Late Secondary	Joseph 2004
Masked Tityra	*Tityra semifasciata*	Fertilized	Omnivore	Yes	Savanna	Gaps	Mobley & de Juana 2014a
Piratic Flycatcher	*Legatus leucophaius*	Fertilized	Omnivore	No	Savanna	Late Secondary	Mobley 2004d
Rufous-and-white Wren	*Thryothorus rufalbus*	Fertilized	Insectivore	Yes	Early Secondary	Gallery	Kroodsma & Brewer 2005c
Rufous-naped Wren	*Campylohynchus rufinucha*	Fertilized	Insectivore	Yes	Savanna	Secondary	Kroodsma & Brewer 2005d
White-lored Gnatcatcher	*Polioptila albiloris*	Fertilized	Insectivore	Yes	Early Secondary	Secondary	Atwood & Lerman 2006
Gray-headed Chachalaca	*Ortalis cinereiceps*	Unfertilized	Herbivore	Yes	Savanna	Gallery	del Hoyo & Kirwan 2013
Lesser Ground Cuckoo	*Morococcyx erythropygus*	Unfertilized	Omnivore	Yes	Savanna	Secondary	Payne 1997
Red-billed Pigeon	*Patagioenas flavirostris*	Unfertilized	Herbivore	Yes	Savanna	Gaps	Baptista et al. 2013b
Silver-throated Tanager	*Tangara icterocephala*	Unfertilized	Omnivore	Yes	Gaps	Late Secondary	Hilty 2011b
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Unfertilized	Omnivore	Yes	Savanna	Secondary	Mobley & de Juana 2014b

DISCUSSION

There is a core assumption that is made by this study that must be addressed before beginning the rest of the analysis. This study assumes that the fertilized treatment and the control pasture located approximately 25 m away were functionally equivalent up until the deposition of orange peels in 1998. That is to say, we assume that both sites had the same land use history, that they were both under the same pattern of management when the area was used as a cattle pasture, that they had the same access to seed dispersing communities, that they were affected similarly by climatic variables, and that they rest upon the same type of soil. In short, we assume that had the orange peels not been added, our fertilized plot would have looked the same as our control pasture. Given the close proximity of the two sites, we believe that this is a reasonable assumption to make. We thus attribute any changes in soil nutrients, plant community, invertebrate community, and vertebrate communities, to changes that have occurred due to the 1998 deposition of orange peels.

Soil Properties and Nutrients

It is worth highlighting that the sampling and laboratory analysis methods between 2000 and 2014 were different. These differences, coupled with the inherent heterogeneity of soil, can make comparisons between the 2000 and 2014 values difficult at best and inappropriate at worst. However, making comparisons about the differences within a year are still valid, given that they were collected and analyzed in very similar fashions. That is to say, the statistical comparison in soil nutrients between the fertilized treatment and the unfertilized control in 2014 is valid based on the shared methodology for analysis, but that the comparison of the fertilized treatment in 2000 to the fertilized treatment in 2014 is less legitimate due to differences in soil sampling protocol and lab techniques. With this in mind, we proceed with caution.

Soil Color, Moisture, and Texture

Differences in soil color may have arisen from the addition of orange peels, but the extreme heterogeneity in soil color makes generalizing difficult. Texture analysis revealed that all of the soils were still dominated by clay particles, a finding that is consistent with previous texture analyses in the area (Jimenez 1999).

Soil moisture was found to be lower on the fertilized side than in the area surrounding Modulo II in the 2000 survey and in the control pasture in the 2014 survey. This may be due to the increased growth of trees in the plots. It is well known that trees have a higher capacity for extracting water from systems than grass, suggesting a possible mechanism by which soil moisture will be lower on the fertilized side (Bond et al. 2008). Additionally, the natural history of *Hyparrhenia rufa* suggests that the grass is able to modify the microclimate at the soil surface level, thus potentially encouraging the conservation of soil moisture (Daubenmire 1972).

Soil Acidity

Soil acidity plays a critical role in the leaching or retention of soil nutrients through the process of cation exchange. Soil particles, or colloids, are typically negatively charged and will attract various different nutrients that are free-floating in soil water as ions (e.g. NH_4^+, Ca^{2+}, K^+). These ions will adsorb to colloids and are therefore resistant to removal and leaching from the passing of water. The ability for cations to move in the soil is referred to as the cation exchange capacity of the soil and it is critically important to retaining soil nutrients in the soil. In acidic soils, H^+ ions are plentiful in the soil and will compete with other positively charged nutrient ions, such as Ca^{2+}, Mg^{2+}, K^+, and Na^+, for the binding sites to these negatively charged soil particles. The nutrients that have been bumped out of these sites by the H^+ are susceptible to being washed out of the system as a result of rainfall and subsequent leaching (Gardiner & Miller 2008).

Increased soil acidity also has two other important negative effects for soil fertility. High soil acidity is unfavorable to plant growth because highly acidic soils break down Al^{3+}, which can then be incorporated into soil roots at nearly toxic levels (Brenes & Pearson 1973; Gardiner & Miller 2008). Aluminum which has been solubilized as a result of high acidity, much like the H^+ ions discussed previously, will interfere with the adsorption of other positively charged nutrients to soil colloids, thus contributing to problems of nutrient retention in acidic soil (Juo & Franzluebbers 2003). Increased soil acidity also suppresses the activity of Nitrogen fixing and organic matter decomposing bacteria, thus slowing the rate of nutrient fixation by an ecosystem (Gardiner & Miller 2008).

The reduction in soil acidity observed in 2000, as initially suggested by the unpublished work of Shanks, implies that the incorporations of Ca^{2+} and K^+ cations may have increased the pH of the soil by competing with H^+ ions for adsorption sites. In alfisols, which underlay much of the soils in the region, Ca^{2+} and K^+ are the dominant forces in cation exchange (Lathwell & Grove 1986). Their dominant return in 2000 and the retention of these nutrients in 2014 suggest that the cation exchange capacity of the soils in general have improved.

Additional pH measurements would be able to confirm whether or not pH had indeed stabilized as a result of the orange peel addition. The significant differences in Ca^{2+}, Mg^{2+}, and K^+ in 2014 is suggestive of a decrease in acidity and in increase in cation exchange capacity, but we cannot confirm this finding.

Macronutrients (Nitrogen, Potassium, Phosphorus)

There are notable differences in the 2000 and 2014 surveys in the analysis of N, P and K. Nitrogen analysis conducted in 2014, absent in the 2000 survey, found that there was more N in the fertilized treatment when compared to the unfertilized pasture. N is often a critical and limiting nutrient for plant development and growth and it is often incorporated into fertilizers used in agriculture (Davidson et al. 2004; Menge et al. 2009). N is unique in that it must be incorporated into plants either as nitrate or ammonium and cannot be efficiently incorporated as soluble nitrogen. Given that N plays a critical role in the development of cell walls, plant proteins, chlorophyll, and nucleic acids, it is not surprising that N cycling is well studied (Gardiner & Miller 2008).

There are numerous potential mechanisms by which N could have been incorporated into the system, each of which should be explored further. The most obvious mechanism is from the mineralization of N from the orange peels themselves. One of the largest sources for N in an unfertilized system is the mineralization of soil organic matter (Gardiner & Miller 2008). In this case, it was likely the rapid mineralization of orange pulp which provided the largest direct source of N (Correia Guerrero et al. 1995).

The orange peels may have also provided better microclimatic conditions to encourage the growth and establishment of nitrogen fixing bacteria or trees of the nitrogen fixing family Fabaceae. Though this is not apparent from looking at the tree diversity data, there were substantially more members of *Vachellia collinsii,* a nitrogen fixing tree, on the fertilized side, though many of them were less than 5 cm DBH, thereby excluding them from our tree analysis (pers. obs). This may have primed a feedback loop, by which the introduction of nitrogen fixing organisms lead to the incorporation of more N, which allows for the recruitment of additional nitrogen fixing organisms, until there has been an overall increase in N in the system (Brown & Lugo 1990; Batterman et al. 2013).

Potassium was found in considerable amounts in the initial orange peel dump and was also found to be significantly more prevalent in the treatment soils in both the 2000 and 2014 surveys. Potassium is second only to nitrogen in terms of its use in plants and is an incredibly important nutrient for enzyme activity. Most K^+ available for plant use is found attached to soil particles as participants in cationic exchange. The decomposition of additional plant material may be further incorporated into soils through cation exchange, but free-floating K is readily lost as a result of leaching during heavy rains (Gardiner & Miller 2008). The addition of K^+ in previously acidic soil is particularly important, considering that highly acidic soils will likely not have high cation exchange capacity (due to the incorporation of H^+ ions), and are thus more prone to losing K^+ (Gardiner & Miller 2008). This makes the addition of orange peels particularly beneficial for the dystrophic and acidic soils in our site.

Potassium also is particularly interesting due to its conspicuous differences between 2000 and 2014. In spite of all of the red flags that such a comparison might raise, the dramatic decrease in potassium between 2000 and 2014 in both the treatment and the control are worth discussing. The most conservative explanation is simply that the differences in sampling and analysis methods resulted in strange artifacts in the data. Another possible explanation is that the extremely high quantity of potassium in 2000 is a lingering artifact of the orange peel fertilization, given the high concentrations of K^+ in the orange peels (Del Oro 1998). The subsequent decreases in both the fertilized and unfertilized treatments could possibly be due to leaching. Longitudinal studies would be able to document these changes in much better detail.

Phosphorus is also often a limiting nutrient and is vital for its role in energy transfer as part of adenosine triphosphate (ATP) and in the formation of nucleic acids (Davidson et al. 2004). The biggest limiting factor with the incorporation of P into plants is due to problems with converting P into a readily soluble form that can then be incorporated into plants (Gardiner & Miller 2008). The lack of significant differences in 2000 suggests that P was not a major nutrient that was incorporated into the soil as a result of the orange peel deposition. This is corroborated by findings from Portugal, whereby orange waste had an insignificant impact on soil phosphorus (Correia Guerrero et al. 1995). However, the shift by 2014 implies that additional phosphorus was incorporated into the system through unknown means. Speculation would point to the mineralization of P from falling vegetation from young trees by bacteria (Rodríguez & Fraga 1999), contributing to nutrient accumulation in trees (Brown & Lugo 1990), though the exact mechanisms of this would need to be elucidated in a more detailed longitudinal study.

The results of the phosphorus analysis in general give us reason to pause. When directly comparing the levels of phosphorus in the 2000 survey and in the 2014 survey, we find large differences that seem rather counterintuitive. It seems odd that the area outside of the treatment area (i.e. the control) in 2000 had 13.8 ppm of P while the treatment area in 2014 only had 7.409 ppm and the control only had 2.874. We believe that this difference is attributable to differences in analysis methods (sequential extraction of P in 2000 versus Mehlich III extraction in 2014). This begs the question as to whether substantial differences would have been observed had phosphorus been analyzed using Mehlich III extractions in 2000. As it stands, the considerable uncertainty regarding phosphorus precludes us from discussing further.

Secondary Nutrients (Calcium, Magnesium)

Calcium, though not normally a limiting nutrient, can be limiting in highly acidic soils that have experienced extensive leaching. This is because in soils with low pH, the strength and number of H^+ ions may simply displace calcium ions, making them more susceptible to leaching and making them generally more scarce (Lathwell & Grove 1986; Gardiner & Miller 2008). In this study, the orange peels were noted for their high concentration of calcium. There was also significantly higher calcium on the fertilized side than in the control in 2000 and 2014. It is possible that the application of additional calcium was able to displace the hydrogen ions from the soil, thus improving the pH and increasing the cation exchange capacity of the soil.

Magnesium occupies a similar role in cation exchange, but plays a different biological role as an enzyme activator. The newly statistically significant differences in 2014, compared to the lack of differences in 2000, may potentially be attributed to subsequent processes of accumulation in the intervening 15 years. The most likely of potential sources would be the activity of bacteria weathering the parent rock, thus generating new minerals and soil (Schlesinger 1997).

Micronutrients (Copper, Iron, Manganese, Zinc)

Micronutrients as a whole are characterized as being essential to life, but not necessarily in large quantities. Each micronutrient plays critical roles in cellular pathways and deficiencies in any of them can stunt plant growth (Gardiner & Miller 2008). Of the micronutrients analyzed, all of them had significantly higher levels after the deposition by 2000. These differences have persisted till 2014. The exception to this trend is manganese, which was not analyzed in 2000 but also demonstrated significant differences in the 2014 analysis.

Potential Mechanisms for Observed Nutrient Differences

It is obvious that the effect of the orange peel deposition was dramatic. Numerous metrics of soil fertility improved dramatically both 2 years and 16 years after the deposition. Though it is difficult to discuss with certainty the exact mechanisms by which soil fertility improved as a result of the orange peel deposition, there are numerous factors that we speculate may have had an effect. The amount of calcium, magnesium, and potassium in the orange peels may have ameliorated soil acidity by adsorbing to soil colloids and precluding H^+ binding. These improved pH conditions would allow microfauna to begin fixing nitrogen (Gardiner & Miller 2008). The increased biotic activity may have also encouraged the secretion of organic acids by microbes and decomposers, thus contributing to the weathering of parent rock and an improvement in the rate of micronutrient release and accumulation (Schlesinger 1997). There is still considerable uncertainty regarding the kinetics of this reaction as information on the parent material is lacking. Additionally, the decay of orange peels into soil organic matter would have increased the capacity of the soil to retain water (Gardiner & Miller 2008). The slow process of decay would have also reduced the rate at which nutrients were put into the system relative to pure fertilizer application. This delayed release may have increased the orange peel applications' efficiency relative to a traditional application of fertilizer (Gardiner & Miller 2008).

There is evidence that some of the nutrients may have been leached from the system. In spite of the difficulties in making comparisons across the years, the obvious reduction in potassium between 2000 and 2014 seems to be too large to ignore. However, it is still telling that even in the face of the leaching since 2000, the biotic community still has recovered significantly. We suspect that there may have been a priming effect, whereby the initial input of orange peels jump-started a system of nutrient cycling and accumulation that would not have started without it. Even in the face of nutrient leaching, which is expected due to the amount of rain the system receives, the newly bolstered biological community seems to be able to retain nutrients, potentially encouraging further steps in succession.

Vegetation

Species Richness and Diversity

The dramatic increase in species richness and diversity as a result of the fertilization event is unmistakable. The non-overlapping confidence intervals in the rarefaction curves confirm that there are significantly more tree species on the fertilized side than on the unfertilized side. We expect that this difference will only increase with the sampling of liana species, herbaceous species, and grass species. This expectation is supported by the presence of physically taller trees which might be able to better support lianas (pers obs.), and by dramatic increases in nutrients, as discussed above. When the rarefaction curves are extrapolated further, we see that while the fertilized side is projected to continue accumulating new species at a relatively fast rate, the unfertilized side is beginning to level off. Shannon indices and Simpson indices also reveal a general increase in species diversity. That is to say that the community on the fertilized side is less dominated by individual species and that the fertilized side has a generally more even distribution of species.

Species Composition and Natural History

When evaluating the value of secondary forests for restoration, special attention must be paid to whether the forest is able to facilitate further development towards later stages of succession, and not just with respect to the diversity of trees alone (Brown & Lugo 1990). This might be evaluated by measuring fluxes nutrient pools or in the type of tree species that have grown in the recovering forest. Given our analysis of nutrient pools in the previous section, we now turn to the natural histories of the community assemblages in both treatments, with a particular emphasis on the capacity of the community to catalyze later succession.

On the unfertilized side, the tree community is dominated by two species, *Curatella americana*, a pasture tree found in the "driest savannahs" of Costa Rica and Panama, and *Byrsonima crassifolia*, a fire adapted pasture tree that is almost never found in forest (Condit et al. 2014). These 2 species alone comprise 89% of the species found on the unfertilized side. The remaining 11% were largely trees found within the first 40 meters of one transect which ran relatively close to a riparian gallery forest. The heavy dominance of these two species, particularly within Guanacaste province, is attributed to the acidity of the soil and the high winds in the area (Vargas Ulate 2000). The presence of these two species is reflective of a long history of fire-management for cattle pastures.

This fire-adapted community differs greatly from the much more species rich community found in the fertilized treatment. The abundance of *Cecropia peltata* is particularly noteworthy, given that it is known to support at least 28 different vertebrate species in the Guanacaste region alone (Fleming & Williams 1990). The presence of *C. peltata* not only serves as an attractant for seed dispersing animals but also as evidence for previous dispersal into the area. The two individuals of the *Ficus* species lend further support to the idea that vertebrate seed dispersers have dispersed seeds into the area. The uncertainty of which exact *Ficus* species has established itself makes it difficult to determine exactly whether these are early or late successional fig trees, but they still act as potential attractants for seed dispersers (Condit et al. 2014).

An analysis of the tree communities on the basis of dispersal syndrome shows an increase in dispersal syndrome diversity for trees on the fertilized side. This may be due to real differences in the survival rates of seeds with different dispersal syndromes in different ecosystems or it may be a statistical and graphical artifact of the sheer dominance of *C. americana* and *B. crassifolia*, which are both bird dispersed species. Though some species were indeterminately animal dispersed (e.g. *Xylopia frutescens*), other species were clearly dispersed by mammalian agents (e.g. *Guazuma ulmifolia* and *Spondias mombin*), suggesting that the fertilized side in particular is being utilized by larger mammals, even if only as a movement corridor.

Aboveground Biomass

Aboveground biomass increased by a factor of 2.29 to 4.20 between the fertilized and unfertilized treatments. This dramatic increase is reflective of the large differences in height and size of the trees between the two treatments. These differences reflect the hypothesis that previously limiting nutrients, soil conditions, and competition from vegetation have been removed as a result of orange peel fertilization. Though the error within the models and other errors with the measurement prevent rigorous statistical analysis and any further estimates on carbon pricing, we believe that it is obvious that orange peel fertilization can catalyze regrowth and regeneration.

Invertebrates

The most striking result from the pitfall trap analysis is the large difference in number of individuals present. Though biomass was never measured, the specimens from the fertilized side are both more numerous and weighed more collectively (pers. obs). Though one could speculate for a long while about this result, an obvious explanation might be that higher primary productivity has driven a subsequent increase in number and biomass of insects (Mittelbach 2012). This is supported by the large differences in aboveground biomass between the two treatments. The differences in sheer numbers are potentially suggestive of recovery.

The diversity analysis is somewhat difficult to interpret. The extent with which the confidence intervals of the rarefaction curves overlap suggests that there are no significant differences in family richness between the two treatments. This seems counter-intuitive, due to the increase in niches that might be expected by the increase in diversity of habitats after restoration. This result might be explained in a number of ways. First, the control pitfall traps were located in a larger continuous area which may have been able to support a greater diversity of families, as might be predicted by the species-area relationship. Second, the lack of surveys for flying insects and tree-dwelling insects may have hidden a more drastic difference in general diversity in the invertebrate community. Finally, it is entirely possible that additional data need to be collected.

Analyzing the different taxonomic families in terms of ecological significance and function is difficult due to the myriad life strategies that can be found within individual families and subfamilies and due to the small sample size in this study. Without individual species identification and additional autecological information, we cannot say much more. It is worth, however, highlighting the presence of beetles in the family *Scarabidae* on the fertilized side, which is a family typically associated with dung. This suggests that there might be a large enough vertebrate population to support non-negligible communities of dung beetles. Unfortunately, without further species or genus level identification, it is difficult to make further concrete claims. The beetles collected in this survey are currently being sequenced for mitochondrial DNA as part of the Barcode of Life Database (BOLD) at the University of Guelph in Ontario in the hopes that further information might be obtained. Unfortunately, at the time of binding this data was unavailable.

Vertebrate Audio

The presence of larger bodied mammals and birds suggests that the area has a large amount of seed dispersal potential. The proximity of the two treatment sites, in addition to the loud volume of many of the calling animals present makes it difficult to discern which animals are situated on the fertilized side and which are situated on the unfertilized side. This is demonstrated in particular by howler monkeys (*Alouatta palliata*), which were detected by the recorders on both sides of the experiment. It seems unlikely that this exclusively folivorous mammal would descend to a habitat dominated by short, shrubby trees, but it is very difficult to exclude that possibility from the recordings alone (Glander 1977). Furthermore, the presence of a nearby gallery forest further complicates the issue; without the ability to discern whether an animal was in the fertilized side or in the gallery forest we cannot say that the detected species is utilizing the restored habitat. Additional data would greatly contribute to our understanding of how different species are utilizing the two different habitats. A subsequent survey with equipment that will allow us to determine where calls are coming from has been scheduled for the summer of 2015.

As it stands, because our current data on animal vocalizations do not enable us to pinpoint the locations of loud species, we are unable to discriminate between two alternative hypotheses that ultimately tell two very different but interesting stories about the orange peel project. The first potential hypothesis is that the bird communities utilizing these two habitats differ. This would imply that the restoration was successful and that a new assemblage of species has returned to the regenerated forest. This would also tell us that the addition of orange peels affected every trophic level. The alternative hypothesis is that the vertebrate communities are the same between the two sites. Though this certainly weakens our claim that the restoration was resoundingly successful from a faunal perspective, it does shed considerable light on the barriers to forest regeneration. Such a finding would suggest that seed dispersal is not the primary barrier within this ecosystem and that other barriers including soil microclimate and nutrient limitation might play a more significant role. The reality of the situation undoubtedly lies somewhere in the middle – the vertebrate communities probably do differ to an extent, reflecting successful restoration, but the overlapping species suggest that seed dispersal is not the only barrier in this ecosystem.

Restoration Implications

The potential restoration implications are enormous. Given the evidence for rapidly accelerated succession and the fact that this method was able to generate revenue for ACG, additional research efforts should be directed towards the use of agricultural waste for forest restoration on tropical pastures. It remains to be seen whether there was anything unique about citrus waste or whether other agricultural wastes, such as coffee fruits or guava peels, might be able to be used in a similar fashion. The use of agricultural waste is particularly noteworthy because it avoids the problem of high costs that plague other active restoration methods like plantation planting. Further research exploring the exact mechanisms of this citrus waste-accelerated succession and the reproducibility of our results would drastically improve the strength of our study and any subsequent policy recommendations.

CONCLUSIONS AND FUTURE STUDIES

The addition of orange peels has dramatically catalyzed the regeneration of the forest. Soil nutrient surveys confirm that the nutrient chemistry of the site has changed dramatically and suggests that nutrient priming and its subsequent feedback loops may have been the mechanism for the dramatic differences observed in plant community. The invertebrate data suggest a large difference in the number of primary consumers being supported by the changed habitat, though it yields little interpretable data on changes in family richness. The vertebrate audio surveys provide a tantalizing look into the possible differences in vertebrate community between the sites, but the data are unable to identify clear differences between the two treatments.

There is great potential for future work at this site. With respect to soils, analysis for bulk density, other soil physical properties, and for soil microbial activity would answer further questions about the exact reasons for the observed differences in soil quality. Surveys of sapling survival, seedling survival, seed rain, seed bank, and surveys for lianas, shrubs, and grasses would allow us to better understand the larger biological community. More extensive pitfall trapping including pitfall traps using meat or dung for carrion beetle and dung beetle diversity and abundance respectively, along with flying insect traps and transects would greatly supplement our pilot data regarding invertebrates. More sophisticated audio survey instruments, point counts, camera traps, and sand track traps would greatly expand our knowledge of which vertebrate species are utilizing which habitats. Finally, additional replicates of orange peel fertilization, direct comparisons to plantation planting and applied nucleation, and comparisons to other agricultural waste fertilization would help us to determine the exact mechanisms by which succession can be accelerated and would help inform future potential policy recommendations. Given the potential for this research and our university's strong attachment to all things orange, the primary author believes that future research efforts should be directed towards the topics outlined briefly above.

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APPENDIX A – SOIL ANALYSES

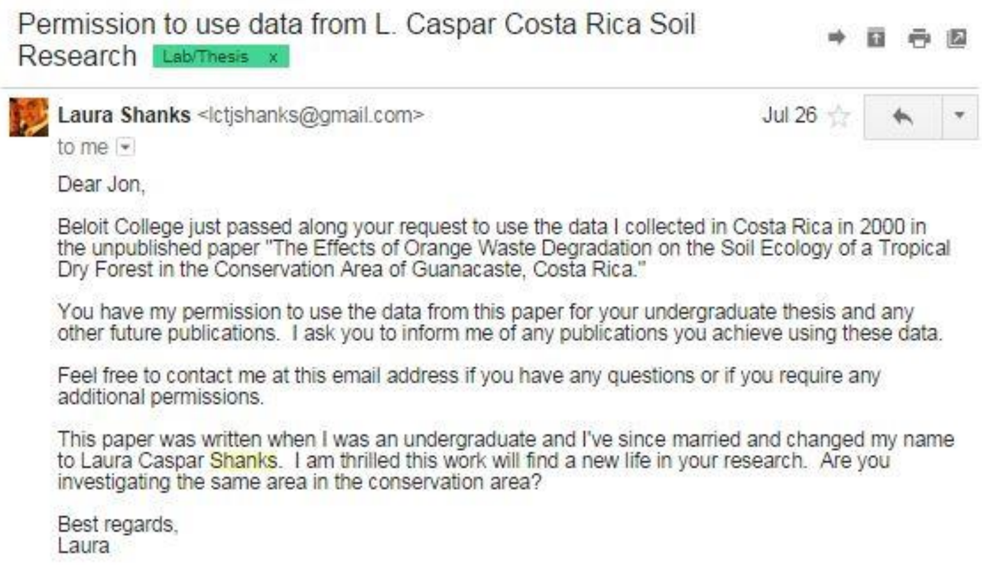
Table A – Color codes of soils within the site with north facing the top of the page

Unfertilized Side			Fertilized Side		
2.5 YR 2.5/3	2.5 YR 4/6	5 YR 4/4	7.5 YR 2.5/2	7.5 YR 2.5/2	7.5 YR 2.5/2
7.5 YR 3/2	5 YR 3/3	7.5 YR 2.5/2	7.5 YR 2.5/2	7.5 YR 2.5/2	5 YR 2.5/1
5 YR 2.5/2	5 YR 2.5/2	2.5 YR 3/2	5 YR 2.5/2	5 YR 2.5/2	7.5 YR 2.5/2

Table B – Soil texture within the site with north facing the top of the page

Unfertilized Side			Fertilized Side		
Clay	Silty Clay	Clay	Clay	Silty Clay	Sandy Clay
Sandy Clay	Silty Clay	Silty Clay	Clay	Sandy Clay	Silty Clay
Clay	Silty Clay	Silty Clay	Silty Clay	Silty Clay	Silty Clay

APPENDIX B – PERMISSION FOR DATA FROM LAURA CASPAR CHANKS



Permission to use data from L. Caspar Costa Rica Soil Research

Laura Shanks <lctjshanks@gmail.com> Jul 26

to me

Dear Jon,

Beloit College just passed along your request to use the data I collected in Costa Rica in 2000 in the unpublished paper "The Effects of Orange Waste Degradation on the Soil Ecology of a Tropical Dry Forest in the Conservation Area of Guanacaste, Costa Rica."

You have my permission to use the data from this paper for your undergraduate thesis and any other future publications. I ask you to inform me of any publications you achieve using these data.

Feel free to contact me at this email address if you have any questions or if you require any additional permissions.

This paper was written when I was an undergraduate and I've since married and changed my name to Laura Caspar Shanks. I am thrilled this work will find a new life in your research. Are you investigating the same area in the conservation area?

Best regards,
Laura

APPENDIX C – SPECIES LISTS FROM PREVIOUS SURVEYS

Table A – Plant List of Species Present in "Modulo II" Prior to the Deposition of Orange Peels

Authored by Guillermo Jimenez in 1997, Transcribed by Jonathan Choi
From Corrales, M Gustabo. 1997. Proyecto de Manejo y Tratamiento de Cascaras de Naranja Provenientes de la Planta Procesadora Del ORO SA. Evaluacion del Sitio Dentro del Area de Conservacion Guanacaste (Sector El Hacha Destinado a Recibir las Cascaras de Naranja. Documento ACG, MINAE, p.29.

Asterisks denote the most common species

Family	*Species*
Polygonaceae	*Securidaca* spp
Dilleniaceae	*Diolocarpus dentatus*
	Curatella americana
Tiliaceae	*Apeiba tibourbou*
Sterculiaceae	*Waltheria indica* *
	Waltheria glomerata
	Helicteres guazumaefolia *
Malvaceae	*Malachra alceifolia*
Flacourtiaceae	*Zuelania guidonia*
	Xylosma spp
Cochlospermaceae	*Cochlospermum vitifolium*
Fabaceae	*Chamacaecriste dephyla*
	2 unidentified spp
Myrtaceae	*Psidium guineense*
Melastomataceae	*Miconia argentea*
	1 unidentified spp
Rhamnaceae	*Guoania polygama*
Sapindaceae	*Serjania schiedeana*
Malphighiaceae	*Byrsonima crassifolia* *
Verbenaceae	*Stachytarpheta jamaicensis*
Bignoniaceae	*Tabebuia rosea*
Rubiaceae	*Alibertia edulis*
	Genipa americana
Poaceae	*Hyparrhenia rufa* *
Apocynaceae	2 unidentified spp
Labiaceae	*Hyptis suaviolens* *
Asteraceae	2 unidentified spp
Boraginaceae	*Cordia guanacastensis*

Table B – Inventory of Plants from "Modulo II" in November of 1999

Author Unknown, Research Program, ACG, Translated and Transcribed by Jonathan Choi

Family	*Species*
Acanthaceae	*Dyschoriste valeriana*
Amaranthaceae	*Amaranthus spinosus*
	Iresine diffusa
Araceae	*Syngonium* spp
Asclepiadaceae	*Asclepia curassavica*
Asteraceae	*Bidens pilosa*
	Chromolaena odorata
	Conyza bonariensis
	Emilia fosbergii
	Erechtites hieracifolia
	Eupatorium collinum
	Fleischmannia sideritides
	Hebeclinium macrophyllum
	Mikania spp
	Stevia aff tephrophylla
	Tridax procumbens
Bignoniaceae	*Tabebuia rosea*
Caryophyllaceae	*Drymaria cordata*
Cecropiaceae	*Cecropia obtusifolia*
Convolvulaceae	*Ipomoea carnia*
Cucurbitaceae	*Cayaponia racemosa*
	Melothria pendula
Cyperaceae	*Cyperus luzulae*
	Cyperus odoratus
	Eleocharis nigrescens
	Fimbristylis dichotoma
	Kyllinga pumila
	Rhynchospora eximia
	Rhynchospora brevirostris
	Rhynchospora nervosa spp ciliate
	Unidentified spp
Dilleniaceae	*Curatella americana*
Euphorbiceae	*Chamaesyce hyssopifolia*
	Croton trinitatis
Fabaceae	*Chamaecrista desvauxii*
	Desmodium barbatum
	Indigofera lespedezioides
	Rhynchosia reticulata
Fabaceae – Caesalpinioideae	*Aeschynomene sensitiva*
Fabaceae – Mimosoideae	*Aeschynomene americana*
	Chamaecrista nictitans
	Mimosa pigra
	Mimosa pudica
Fabaceae – Faboideae	*Crotalaria pilosa*
	Crotalaria sagittalis
	Desmodium barbatum
	Erioxema diffusum
	Sesbania emerus
Hydrophyllaceae	*Hydrolea spinosa*
Lamiaceae	*Hyptis capitata*
	Hyptis verticillata
Malvaceae	*Malvaceae* spp
	Sida linofolia
	Sida rhombifolia
	Urena lobata
Melanthiacea	*Thypha* spp
Melastomataceae	*Miconia argentea*
Moraceae	*Ficus* spp
Nymphaeaceae	*Nymphea aff glandulifera*
Onagraceae	*Ludwigia nervosa*
	Ludwigia octovalvis
Phytolaccaceae	*Phytolacca icosandra*
Poaceae	*Eleusine indica*
	Hyparrenia rufa
	Panicum cayennense
	Paspalum spp (x3)
	Setaria parviflora

Ponteridaceae	*Heteranthera limosa*
	Heteranthera reniformis
Portulaccaceae	*Portulaca oleracea*
Pteridaceae	*Pityrogramma calomelanos*
Rubiaceae	*Richardia scabra*
	Spermacoce calomelanos
Scrophulariaceae	*Mazus pumilus*
Solanaceae	*Physalis angulata*
	Physalis nicandroides
	Solanum spp 1
	Solanum adhaerens
	Solanum americanum
Sterculiaceae	*Helicteres gauzumifolia*
	Melochia villosa
	Waltheria glomerulata
	Walterhia indica
Tiliaceae	*Muntingia calabura*
Verbenaceae	*Lantana camara*
Vitaceae	*Cissus pseudosicyoides*
	Cissus verticillata

CHAPTER 3

A GAME THEORETIC FIRE-MEDIATED SUCCESSION MODEL OF A NEOTROPICAL PASTURE

Essentially, all models are wrong, but some are useful.

\- *George E. P. Box*
Empirical Model-Building and Response Surfaces (1987)

Author's Note: Adapted with permission from Professors Tarnita and Wilcove from a final paper for EEB 325: Mathematical Modeling for Biology and Medicine, taught by Professor Tarnita.

ABSTRACT

With the shift away from cattle ranching in certain areas of the Neotropics, the regeneration of forests from cattle pastures has become a focus of research for ecologists and conservationists. This paper proposes the use of a game theoretic model to examine the dynamics of forest regeneration in the face of different fire regimes. Building on the work of Robert van Hulst, our model simplifies vegetation dynamics and incorporates fire as a repetitive disastrous event relative to the work of van Hulst. The model predicts the existence of two stable states between pasture and forest depending on fire frequency and severity. The model also predicts that fire suppression can encourage the return of forest if suppression occurs before the loss of large amounts of forest. Our model also demonstrates a state of arrested succession, where dramatic losses in forest cover from fire cycles dramatically reduce the rate of forest recovery. Additional empirical studies are needed to parameterize this model with field data.

Keywords: regeneration, restoration, invasion, evolutionarily stable strategy, forest, conservation

INTRODUCTION

Forest succession is difficult to model due to the multitude of different pathways and variables involved including nutrient availability, grazing, fire, and competition (Connell & Slatyer 1977; Brown & Lugo 1990; Glenn-Lewin & Maarel 1992; van Hulst 1992; Kennard 2002; Holl 2007). However, predictions made by models of succession from old agricultural lands and cattle pastures are of interest within restoration ecology (Sánchez-Azofeifa et al. 2005; Holl 2007; Griscom et al. 2009; Calvo-Alvarado et al. 2009). This is particularly true of the Neotropics, where incentives for cattle ranching have declined, thus allowing for passive regeneration towards secondary forest in various cattle pastures (Arroyo-Mora et al. 2005; Calvo-Alvarado et al. 2009). However, passive regeneration is unpredictable and can appear to be arrested due to numerous factors (Sarmiento 1997; Aide et al. 2000), including nutrient limitation (Davidson et al. 2004; Menge et al. 2009), competition between grasses and later successional species (Hoffmann & Haridasan 2008) and insufficient seed rain (Holl 1999; Zimmerman et al. 2000).

Given that we do not have access to the data and understanding necessary for a fully parameterized, generalizable model of succession, this paper proposes a simplified game theoretic model of competition dynamics between grasses, early successional trees, and late successional trees on a cattle pasture and aims to provide insight into succession and regeneration. In this model, we summarize the net effect of all competitive interactions into one variable, rather than individually enumerate the myriad of different factors which might contribute to competition. The paucity of autecological data that exists for individual species and their interactions limits the amount of parameterization possible. We also utilize this simplified model due to its ease of interpretation and manipulation.

In addition, we aim to incorporate insights from fire ecology. A growing body of theoretical, field, and model-based research suggests that differences in climate and fire act to regulate forest cover. Areas with little precipitation will have grasslands while areas with more precipitation will have forests. In areas of intermediate precipitation, the presence of fire will shift the system towards grassland, and fire suppression will shift the system towards forest (Staver et al. 2011; Staver & Levin 2012). We use this knowledge to model the impact of persistent fire and suppressed fire on a hypothetical plant community that might exist within an area of intermediate precipitation.

Ecologists have published very few studies using game theory to predict succession (e.g. Hulst 1987, 1992), and thus the results of this paper are necessarily tentative and exploratory. Most of the research on the topic matter of plant ecology and game theory has thus far focused on the evolution of characters rather than on successional dynamics (McNickle & Dybzinski 2013). Further contributions of various theorists, field biologists, and mathematical biologists will be necessary to understand the implications of using game theory to model succession across different ecosystems.

Game Theory and Ecology

In order to make this paper more broadly accessible, we attempt to summarize the relevant aspects of evolutionary game theory here. The review article written by McNickle and Dybzinski (2013) provides a much more detailed, non-mathematical introduction to evolutionary game theory and plant ecology. Work by van Hulst in 1987 and 1992 in exploring succession and invasion through game theory is also useful and is presented with a more in-depth mathematical approach. Additional reviews by Geritz et al. in 1998 and McGill and Brown in 2007 are also good resources that summarize evolutionary game theory.

Though game theory was used initially to inform economics, many of the ideas have been incorporated into studies of evolution. Evolutionary game theory has been used to predict Evolutionarily Stable Strategies (ESS), or life strategies that are resistant to invasion by new strategies (Margalef 1968; Maynard Smith 1982; McNickle & Dybzinski 2013). A famous example of this is a model constructed by Smith and Price in 1973 that explained the existence of limited, non-lethal intraspecific competition rather than extreme, lethal competition. Thus, evolutionary game theory has been used in the past to help describe possible explanations for various biological phenomena.

In the world of forest succession modeling, the use of evolutionary game theory differs from traditional linear successional models and Markov models in that the interactions modeled through a game theoretic approach are non-linear and the role of density dependent interactions between different individuals playing different strategies is explicitly included in the model (van Hulst 1992; McNickle & Dybzinski 2013). Traditional linear models with systems of differential equations or stochastic Markov models are typically created such that changing initial conditions does not change the ultimate behavior of the model (van Hulst 1992). This is intuitively inconsistent with current understanding of plant succession dynamics; for example, the ultimate community structure in a nutrient-leached cattle pasture that is filled with coarse silicate grass will differ vastly from that of an aerated, fertilized, and plowed field.

Game theoretic models are unique in that the success of each actor is dependent on the strategy played by other actors; that is the frequency of other strategies in a system will directly impact the payout of each individual. This addresses the problem of differing initial conditions – a model that is initially dominated by coarse silicate grasses will have a different end result than a model that is initially dominated by old growth forest. It is for this reason that game theoretic models are unique and may provide additional insight into the process of succession on cattle pastures.

METHODS

Model Description

The model was crafted in a manner very similar to the succession model described by van Hulst in 1987 and 1992. This model assumes a population of individuals who are randomly interacting with each other. Though this does not reflect the dynamics of seed rain and colonization in the real world, we use this rough approximation as the model is greatly complicated by the incorporation of species specific competition in a spatially explicit manner. Our model is comprised of a vector **x** of relative frequencies of *n* ecological guilds, such that $\sum_i x_i = 1$, and an *n* by *n* matrix **A**. This matrix is known in game theory as the payoff matrix, where any given element, $a_{i,j}$, of matrix **A** is proportional to the relative fitness of an individual of guild *i* invading or colonizing a community comprised of members of guild *j* (van Hulst 1992). In practice, these parameters can be estimated from chronosequences or long-term monitoring studies by looking at growth rates of certain species within different community compositions (i.e. van Hulst 1987).

The replicator equation that is commonly used in evolutionary game theory was applied to the frequency vector and the payoff matrix (van Hulst 1987; Nowak 2006). These equations have been shown by others to be equivalent to a Lotka-Volterra competition model accounting for proportional abundances of different guilds (van Hulst 1992). The generalized replicator equation is as follows:

$$\frac{dx_i}{dt} = x_i[f_i(x) - \varphi(x)];$$

$$\text{where} \quad f_i(x) = \sum_{j=1}^{n} a_{i,j}\, x_j \qquad \text{and} \qquad \varphi(x) = \sum_{j=1}^{n} x_j f_j(x)$$

In words, this differential equation represents the change in relative frequency of guild x_i. It is calculated as its relative frequency x_i multiplied by its own fitness, $f_i(x)$, which is given by the second equation, subtracted by the average fitness of the population $\varphi(x)$, which is given by the third equation (Maynard Smith 1982; van Hulst 1987, 1992; Nowak 2006).

A simplistic fire model was used by simulating a regular catastrophic event on the population. Each fire was set to occur with a certain frequency and with a certain severity. The fire was initially assumed to eliminate 30% of grasses, 70% of early successional trees and 30% of late successional trees. These parameters were chosen because while fire-adapted grasses would be able to recover reasonably quickly and old-growth trees would shade out the grasses near each tree to prevent strong fires, early successional trees would be too small to shade out grasses or to successfully survive fires, thus leading to their increased relative mortality. These parameters were later adjusted to reflect the effect of different fire control regimes on the model's end behavior.

Model Parameterization

Initial frequencies of the populations were set to be 97% bare ground and 1% grass, early successional forest, and late successional forest respectively. This was done to ensure that the populations would succeed each other in the generally accepted order of bare ground to grass to early successional trees to late successional trees (Rees et al. 2001). The initial frequencies for this model must remain non-zero, as setting a parameter value to zero would result in no change in the population.

Bare ground can be imagined as a completely fallow area that lacks any vegetation what so ever but has the conditions necessary to support plant life. Grass represents an area that has been invaded by a tall, fire-adapted grass like *Hyparrhenia rufa* and *Melinis minutiflora* (Daubenmire 1972; Baruch & Jackson 2005; Hoffmann & Haridasan 2008). Early successional forests would not have an enclosed canopy, allowing significant light penetration to the forest floor, and would be comprised of shade-intolerant species like

Cecropia peltata or *Byrsonima crassifolia* (Janzen 1983). Finally, late successional forests are defined by shade-tolerant species with a closed canopy and a humid microclimate which reduces the possibility of fires.

The payoff matrix was created so as to simulate reasonable succession. The main diagonal of this matrix was reduced to zero as it is in the model of van Hulst 1987. This is because the reduction of each element in a column by the same constant will not change the relative payoffs and the deterministic end behavior of the model.

The actual parameters inserted into the payoff matrix can either reflect general interactions between different guilds or it can be constructed using detailed information about facilitation, competition, and inhibition between different species (Connell & Slatyer 1977; van Hulst 1992). Due to the lack of relevant data, the parameters here only reflect broad interactions and there was no attempt to individually quantify the effects of facilitation, competition, and inhibition among different guilds. The model parameters used are shown below.

$$\begin{array}{l|cccc|} & 1 & 2 & 3 & 4 \\ 1.\,\mathit{Bare\ Ground} & 0 & -0.1 & -0.05 & -0.01 \\ 2.\,\mathit{Grass} & 0.5 & 0 & -0.1 & -0.2 \\ 3.\,\mathit{Early\ Succesional} & 0.2 & 0.1 & 0 & -0.01 \\ 4.\,\mathit{Late\ Succesional} & 0.05 & -0.2 & 0.5 & 0 \end{array}$$

The justification for the chosen parameters is as follows going across by rows before proceeding down columns. Bare ground as a category will fail to increase in size in the face of any form of vegetation, but will be more unsuccessful against grasses than against late successional trees. This is because while tree fall events may clear up new bare ground, there are few regularly occurring events that will strip off an entire layer of grass or shrubby secondary growth. Grass will very quickly colonize bare ground, but will be unable to persist in a community of any other form of vegetation due to its shade intolerance. It will have a more difficult time against late successional forest than early successional forest as late successional forests will have more shade. Early successional trees will colonize bare ground more readily than they will grass, but they will be overgrown by late successional forest. Finally, late successional forest will very slowly colonize bare ground, such as within forest gaps, and it will be unable to colonize grass due to the harsh microclimate, but it will successfully colonize early successional forest.

This payoff matrix thus predicts that the only evolutionarily stable strategy is that of late successional forest. This is the state that we would expect in areas with high precipitation and in places that do not experience fire on a regular basis (Staver et al. 2011). This means that fire should be the factor that will regulate and drive conversion to grassland.

RESULTS

The game theoretic model was able to recreate a simplistic successional model similar to those described by van Hulst (Figure 1). The simulation of frequent and intense fires was able to simulate an alternative stable state dominated by grasses (Figure 2). This reflects a fairly common phenomenon in Central America, whereby ranchers will light their pastures on fire at the end of the dry season every year to encourage the growth of new shoots at the onset of the rainy season (Griscom et al. 2009; Calvo-Alvarado et al. 2009; Griscom & Ashton 2011). Increasing the time between fires and the survival of early successional trees by 2 successfully allows for the return of old growth forest (Figure 3). This simulates an aggressive fire suppression regime that is able to successfully fight fires until the successful establishment of old growth forest to shade out fire-feeding grasses. Choosing different amounts of time between fires and adjusting the effect of fire in different

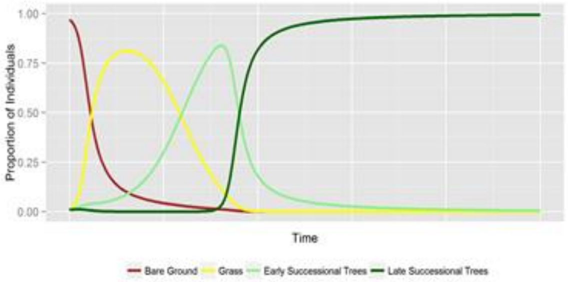


Figure 1 - Forest recovery demonstrated by a model without fire.

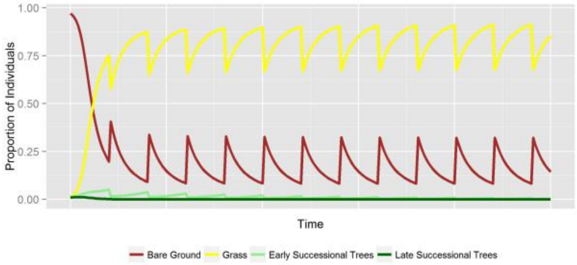


Figure 2 - Grassland stable state in a model with persistent, severe fires.

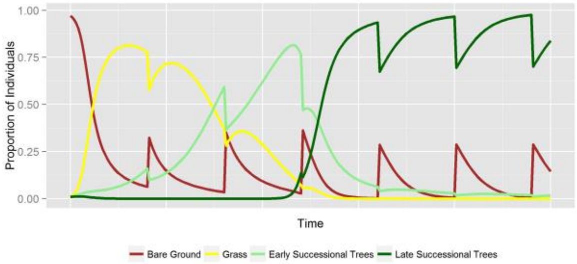


Figure 3 - Eventual forest recovery in a scenario with reduced fire intensity, increased time between fire events and the end of fire after the recruitment of sufficient early successional trees.

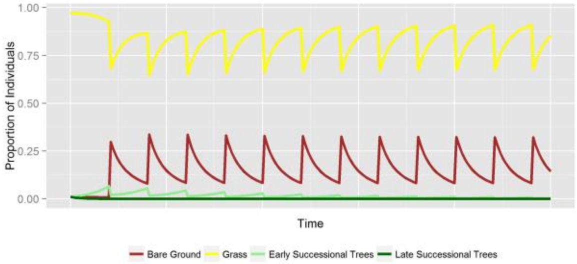


Figure 4 - Continued grass dominance in a scenario with frequent fires and an initial grass-dominated community.

ways created different, but predictable, results. The shorter the time between fires or the more intense the fires, the longer it took to establish additional forests. Changing the initial community to one that is grass dominated demonstrates similar patterns, whereby frequent fires allow grasslands to persist (Figure 4) while fire suppression allows succession to continue (Figure 5). Finally, the cessation of fires after a certain number of fire cycles resulted in a state similar to arrested succession, whereby succession seems to stall completely. Though the model predicts that the system will eventually return to late successional forest, this succession will take much longer than a system without fire (Figure 6).

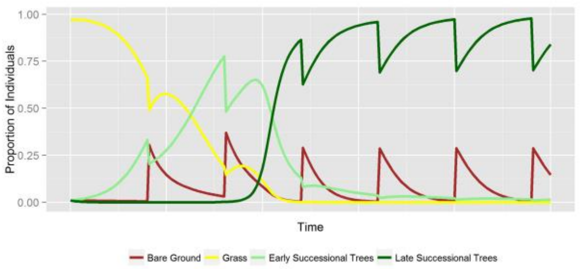


Figure 5 - Eventual succession from a grass dominated ecosystem in a scenario with suppressed fires.

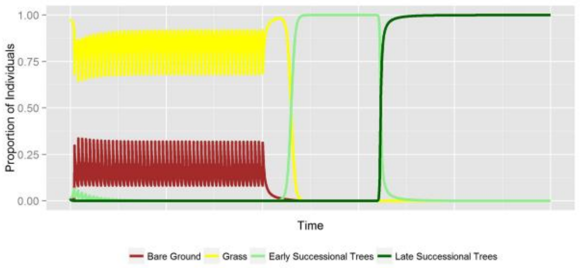


Figure 6 - Delayed succession in a scenario where fires were ended after numerous fire events. The time scale here is 10 times longer than previous graphs.

DISCUSSION

Our results demonstrate that the game theoretic model of van Hulst 1987 can potentially be used to explore fire dynamics in pastures. The model suggests that in the absence of severe barriers to succession such as the local extirpation of seed sources and dispersers or extreme nutrient leaching, pastures should eventually grow into forests (Figure 1). The repeated fire cycles and subsequent grass dominance demonstrated in Figures 2 and 4 is corroborated by other theoretical and empirical work (Staver et al. 2011; Staver & Levin 2012; Whelan et al. 2013).

Figures 3 and 5 demonstrate that if fires are limited and local seed sources have not been destroyed by multiple fire cycles, then forests under aggressive fire control may recover. Such an approach to fire suppression was able to successfully encourage the regeneration of forests throughout Central America, perhaps most famously in Área de Conservación Guanacaste (ACG) (Janzen 1999; Allen 2001). Notably, in ACG this regime of fire suppression and subsequent regeneration was only possible due to the proximity of patches of remnant old growth forest with sufficient numbers of seed dispersers to encourage the colonization and dispersal of early successional trees.

Figure 6 suggests a possible mechanism by which arrested succession might occur, a phenomenon in which abandoned pastures appear to not regenerate, which has been documented throughout the Neotropics (Aide & Cavelier 1994; Sarmiento 1997; Holl 1999; Zimmerman et al. 2000; Fajardo et al. 2012). This could occur through the destruction of the soil seed bank (D'Antonio & Vitousek 1992; Skoglund 1992) or through the volatilization of nutrients after harsh fires (Debano 1990; Johnson & Wedin 1997; Holl 1999). The destruction of fruit-bearing trees within the pastures would also prevent additional succession as seed dispersing birds would not have perches to land on (Janzen 1988;

Wunderle 1997; Holl et al. 2000) and other seed-dispersing animals would not have incentives to travel out of the forest (Norconk et al. 1998; Dalling et al. 2002). However, this model suggests that forest might return eventually if early successional forest was finally able to disperse from its reduced extent and was able to successfully shade out grasses and facilitate the return of old growth forest. .

The relative rapidity with which this model transitions from different states may be worth noting. Some of this rapidity is certainly due to the numerous simplifying assumptions inserted into this model. On the other hand, literature does exist talking about the possibility of abrupt changes from grassland to forest, particularly in areas that receive sufficient rainfall to support forests but where fire is sufficiently frequent to prevent woody growth (Staver et al. 2011; Staver & Levin 2012). Research on alternative stable states from theoretical population ecology also predicts potentially rapid changes between stable states (Beisner et al. 2003), though field data is needed to corroborate these predications.

Importantly, this model should not be taken as evidence that old growth forest will always return in all instances or that the conservation of forests should not be a paramount concern to ecologists. Losses in biological diversity as a result of the destruction of old growth forests are often irreplaceable and the payoff matrix may change as a result of those losses, preventing the return of forests (Wright 2010; Gibson et al. 2011). Nutrient limitation and changes in hydrology may also prevent the recruitment of additional forest (Davidson et al. 2004; Menge et al. 2009). Finally, grasses even without fire, may be too dominant of a competitive force to allow for the succession of other species (D'Antonio & Vitousek 1992; Sarmiento 1997).

The biggest limitations of this model are its lack of species-specific data and parameterization and its inability to account for highly destructive, stochastic events such as hurricanes, war, the introduction of new invasive species or the extirpation of keystone species. Species-specific data, including species' survival in the face of fire, might be able to further elucidate potential underlying mechanisms in forest succession and tropical species coexistence. Understanding rates of leaf or seed predation by certain animal species and their role in seed dispersal and germination would provide additional detail to this model, allowing for simulations with plant-animal interactions. In addition, the lack of minor stochastic disturbance events prevents the current model from being used to model the potential for these disturbances to allow for the coexistence of different species (Horn 1974; Rees et al. 2001; Kennard et al. 2002).

More speculatively, the game theoretic succession model may also be appropriate for use in aquatic succession and the study of coral reefs. Coral species compete with each other and there are various different types of coral cover that may inhibit the growth of other corals. In addition, corals are known to send propagules out to create additional corals in a fashion similar to the ways that trees disperse their seeds. The effects of grazing, overfishing, and mass-bleaching events might be incorporated into such a model, though catastrophic events would have different impacts on different classes of corals, much like the fires in this model.

Though van Hulst 1987 was able to use these game theoretic succession models to model primary succession in a Californian intertidal zone and on sand flats in the Netherlands, it remains to be seen whether such an approach is possible within the tropics or when modeling secondary succession. Additional empirical data for numerous systems, particularly from autecological studies and longitudinal succession monitoring would be able to vastly improve the quality of these models. Experiments involving addition and removal experiments to determine invasion and persistence strength would be particularly valuable as this type of data would be the easiest to integrate into the current model.

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APPENDIX – CODE IN R

Appendix A – Set Up, Initial Parameters, and Succession Model

```
library('deSolve')
library('ggplot2')
library('reshape2')
library('RColorBrewer')

#### Setting Initial Parameters for the Model ####
lengthsim <- 20000

### Initial Starting Populations as Proportions ###
Grass = 0.01
Early = 0.01
Late = 0.01
Bare = 0.97

inits <- c(xB = Bare, # Proportion of Bare Ground
           xG = Grass, # Proportion of Grasses
           xE = Early, # Proportion of Early Secondary
           xL = Late) # Proportion of Late Secondary

dt <- seq(0, lengthsim, 1)      # set the time points for evaluation

### Interaction Matrix ###
parms <- c(AlphaBB <- 0, AlphaBG <- -0.01, AlphaBE <- -0.05, AlphaBL <-
-0.1,
           AlphaGB <- 0.5, AlphaGG <- 0, AlphaGE <- -0.1, AlphaGL <- -
0.2,
           AlphaEB <- 0.2, AlphaEG <- 0.1, AlphaEE <- 0, AlphaEL <- -
0.01,
           AlphaLB <- 0.05, AlphaLG <- -0.2, AlphaLE <- 0.5, AlphaLL <-
0)

### Succession Model/Game Theory Model/Replicator Equation ###
GameTheorySuccessionModel <- function(t, y, parms){
  with(as.list(c(parms, y)), {
    fB <- (AlphaBB * xB + AlphaBG * xG + AlphaBE * xE + AlphaBL * xL)
    fG <- (AlphaGB * xB + AlphaGG * xG + AlphaGE * xE + AlphaGL * xL)
    fE <- (AlphaEB * xB + AlphaEG * xG + AlphaEE * xE + AlphaEL * xL)
    fL <- (AlphaLB * xB + AlphaLG * xG + AlphaLE * xE + AlphaLL * xL)
    AvgFitness <- fB * xB + fG * xG + fE * xE + fL * xL

    dxB <- fB * xB - AvgFitness * xB
    dxG <- fG * xG - AvgFitness * xG
    dxE <- fE * xE - AvgFitness * xE
    dxL <- fL * xL - AvgFitness * xL

    der <- c(dxB, dxG, dxE, dxL)
    return(list(der))  # the output must be returned
  }) # end of 'with'
}  # end of function definition
```

Appendix B – Figure 1, Simulation without Fire

```
sim <- as.data.frame(lsoda(y = inits,
                           times = dt,
                           func = GameTheorySuccessionModel,
                           parms = parms))

sim.melt <- melt(sim, measure.vars = c("xB", "xG", "xE", "xL"))
simgg <- ggplot(data = sim.melt,
                aes(x = time, y = value))

simgg + geom_line(aes(color = variable), size = 1.25) +
  scale_color_manual(values = c("brown", "yellow",
                                "lightgreen", "darkgreen"),
                     labels = c("Bare Ground", "Grass",
                                "Early Successional Trees",
                                "Late Successional Trees")) +
  labs(x = "Time", y = "Proportion of Individuals") +
  theme(axis.title = element_text(size = 12),
        axis.text.x = element_blank(),
        axis.ticks.x = element_blank(),
        axis.text.y = element_text(size = 11),
        legend.position = "bottom",
        legend.title = element_blank()) +
  scale_x_continuous(limits = c(0, 250))

ggsave(file = "NoFireSimulation.jpg")
```

Appendix C – Figure 2, Code for Simulation with Regular/Man Made Fires.

The initial populations were modified and the same code was run again for Figure 4.

```
firefreq <- 20
firedamagegrass <- 0.7
firedamageearly <- 0.3
firedamagelate <- 0.7
firevector <- seq(firefreq, lengthsim, by = firefreq)

regfireevent <- function(t, y, parms){
  with(as.list(c(parms, y)), {
    xG <- xG * firedamagegrass
    xE <- xE * firedamageearly
    xL <- xL * firedamagelate
    xB <- 1 + (-1)*xG + (-1)*xE + (-1)*xL
    return(c(xB, xG, xE, xL))
  })
}

regfiresim <- as.data.frame(lsoda(y = inits,
                                  times = dt,
                                  func = GameTheorySuccessionModel,
                                  parms = parms,
                                  events = list(func = regfireevent,
                                                time = firevector)))

regfire.melt <- melt(regfiresim, measure.vars = c("xB", "xG", "xE",
"xL"))
regfiregg <- ggplot(data = regfire.melt,
                    aes(x = time, y = value))

regfiregg + geom_line(aes(color = variable), size = 1.25) +
  scale_color_manual(values = c("brown", "yellow",
                                "lightgreen", "darkgreen"),
                     labels = c("Bare Ground", "Grass",
                                "Early Successional Trees",
                                "Late Successional Trees")) +
  labs(x = "Time", y = "Proportion of Individuals") +
  theme(axis.title = element_text(size = 12),
        axis.text.x = element_blank(),
        axis.ticks.x = element_blank(),
        axis.text.y = element_text(size = 11),
        legend.position = "bottom",
        legend.title = element_blank()) +
  scale_x_continuous(limits = c(0, 250))
ggsave(file = "ManMadeFireSimulation.jpg")
```

Appendix D – Figure 3, Code for Simulation with Fire Suppression

The initial populations were modified and the same code was run again for Figure 5.

```
suppfirefreq <- 40
suppfiredamagegrass <- 0.7
suppfiredamageearly <- 0.6
suppfiredamagelate <- 0.7
suppfirevector <- seq(suppfirefreq, lengthsim, by = suppfirefreq)

suppfireevent <- function(t, y, parms){
  with(as.list(c(parms, y)), {
    xG <- xG * suppfiredamagegrass
    xE <- xE * suppfiredamageearly
    xL <- xL * suppfiredamagelate
    xB <- 1 + (-1)*xG + (-1)*xE + (-1)*xL
    return(c(xB, xG, xE, xL))
  })
}

suppfiresim <- as.data.frame(lsoda(y = inits,
                                   times = dt,
                                   func = GameTheorySuccessionModel,
                                   parms = parms,
                                   events = list(func = suppfireevent,
                                                 time =
suppfirevector)))

suppfire.melt <- melt(suppfiresim, measure.vars = c("xB", "xG", "xE",
"xL"))
suppfiregg <- ggplot(data = suppfire.melt,
                     aes(x = time, y = value))

suppfiregg + geom_line(aes(color = variable), size = 1.25) +
  scale_color_manual(values = c("brown", "yellow",
                                "lightgreen", "darkgreen"),
                     labels = c("Bare Ground", "Grass",
                                "Early Successional Trees",
                                "Late Successional Trees")) +
  labs(x = "Time", y = "Proportion of Individuals") +
  theme(axis.title = element_text(size = 12),
        axis.text.x = element_blank(),
        axis.ticks.x = element_blank(),
        axis.text.y = element_text(size = 11),
        legend.position = "bottom",
        legend.title = element_blank()) +
  scale_x_continuous(limits = c(0, 250))
ggsave(file = "SuppressedFireSimulation.jpg")
```

Appendix E – Figure 6, Code for Simulation with Fires Ended

```
firefreq <- 20
firedamagegrass <- 0.7
firedamageearly <- 0.3
firedamagelate <- 0.7
lengthsim <- 1000
firevector <- seq(firefreq, lengthsim, by = firefreq)

regfireevent <- function(t, y, parms){
  with(as.list(c(parms, y)), {
    xG <- xG * firedamagegrass
    xE <- xE * firedamageearly
    xL <- xL * firedamagelate
    xB <- 1 + (-1)*xG + (-1)*xE + (-1)*xL
    return(c(xB, xG, xE, xL))
  })
}

regfiresim <- as.data.frame(lsoda(y = inits,
                                  times = dt,
                                  func = GameTheorySuccessionModel,
                                  parms = parms,
                                  events = list(func = regfireevent,
                                  time = firevector)))

regfire.melt <- melt(regfiresim, measure.vars = c("xB", "xG", "xE",
"xL"))
regfiregg <- ggplot(data = regfire.melt,
                    aes(x = (time), y = value))

regfiregg + geom_line(aes(color = variable), size = 1.25) +
  scale_color_manual(values = c("brown", "yellow",
                                "lightgreen", "darkgreen"),
                     labels = c("Bare Ground", "Grass",
                                "Early Successional Trees",
                                "Late Successional Trees")) +
  labs(x = "Time", y = "Proportion of Individuals") +
  theme(axis.title = element_text(size = 12),
        axis.text.x = element_blank(),
        axis.ticks.x = element_blank(),
        axis.text.y = element_text(size = 11),
        legend.position = "bottom",
        legend.title = element_blank()) +
  scale_x_continuous(limits = c(0, 2500))
ggsave(file = "EndFireSimulation.jpg")
```

CHAPTER 4

RESTORATION ECOLOGY AND THE END OF NATURE: CONCLUSIONS AND REFLECTIONS

We shall never achieve harmony with the land, anymore than we shall achieve absolute justice or liberty for people. In these higher aspirations the important thing is not to achieve but to strive.

\- *Aldo Leopold*

Round River: From the Journals of Aldo Leopold

In this thesis, I have done three things. First, I have surveyed the literature about the barriers to tropical forest regeneration and the various restoration methods which have been tested. I have attempted to demonstrate the way that methods like plantation planting and applied nucleation have been used to overcome seed dispersal barriers, soil nutrient limitations, and competition from other vegetation.

Second, I have shed light on a unique method for restoration involving the use of citrus waste. This method, pioneered at Área de Conservación Guanacaste (ACG), showed the potential for innovative restoration methods to benefit local business and advance the goals of restoration. The orange peel project was able to drastically change the soil nutrient profile and subsequently the plant community, all while disposing of a waste product from a major agricultural operation. This collaboration of industry, conservation, and restoration represents a new way forward in how environmental protection can be conceived.

Finally, I used game theory to look at frequency dependent succession in a simplified cattle pasture/forest regeneration system. The simplistic replicator equation-based model was able to show that fire management could determine the fate of regenerative growth in grass-dominated ecosystems.

This thesis has demonstrated to me that the efforts to restore, conserve, and understand tropical ecosystems will ultimately require new ways of thinking. Traditional methods of erecting fences and fortresses and giving guards guns are limited in their efficacy. If biologists are to be successful in protecting what they find beautiful in the natural world, we will have to think of ways to shape the culture around us, to help them see what we see when we look out the window in wonder.

In the face of misunderstandings on the side of conservationists and the people living in the areas around the park, the orange peel project was shut down. Now, with poison in the political climate, changes in management, and scars from old legal battles, it is unlikely that such a partnership will occur again in ACG. Still, it is this innovative way of thinking about the challenge of restoration and integration of the park within the larger community that will help us shape the future of our natural heritage.

During the process of writing this thesis, I grappled with an idea that I originally encountered in the book *The End of Nature* by Bill McKibben (1989). In it, McKibben writes that:

> An idea, a relationship, can go extinct, just like an animal or a plant. The idea in this case is "nature," the separate and wild province, the world apart from man to which he adapted, under whose rules he was born and died… We never thought that we had wrecked nature. Deep down, we never really thought we could … But, quite by accident, it turned out that carbon dioxide and other gases we were producing in our pursuit of a better life … *could* [sic] alter the power of the sun, could increase its heat… We have produced the carbon dioxide—we are ending nature.

Reading his words 26 years later, I can concede that he was right to some extent. We have altered the world; we have cut down the forests, overfished the oceans, and treated the reefs like a garbage dump. The gases that we have thrown into the atmosphere at an accelerating rate will have long-lasting effects on the world. Nearly every single ecological community that exists on the planet has been affected by the industrial machinations of humanity.

In the face of this crisis, McKibben grapples with the question of what the environmental movement might do. He writes:

> "If nature were about to end, we might muster endless energy to stave it off; but if nature has already ended, what are we fighting for? Before any redwoods had been cloned or genetically improved, one could understand clearly what the fight against such tinkering was about. It was about the idea that a redwood was somehow sacred, that its fundamental identity should remain beyond our control. But once that barrier has been broken, what is the fight about, then? … how can there be a mystique of the rain now that every drop … bears the permanent stamp of man?"

And perhaps here too, he is correct. Perhaps the idea of "nature" has been throttled and perhaps killed by the persistent efforts of humanity, be it through climate change or through genetic engineering.

Yet McKibben does not clearly answer the question of what we should do at the end of nature. He concludes that perhaps we can find that sense of awe and majesty that we used to attribute first to God and then to nature, by looking into the night sky and drawing from it a sense of wonder. Though it would certainly be disingenuous to say that he has given up on protecting the environment, I still found his answer to the end of nature to be unsatisfactory.

These were the thoughts that floated in my head as I stared at the dim bulb that flickered against the Costa Rican night during the summer of 2014. And it was through the course of writing my thesis, learning more about ACG, and becoming part of the story of one of the most improbable and hard fought stories of restoration, that I think I came to find my answer to the question of what to do at the end of nature.

McKibben's point about CO_2, though well taken, missed our obligation to all that continues to breathe, feed, and live in that "nature" that we have killed. It has missed our obligation to open the eyes of our children, our neighbors, and ourselves, to the world that exists outside of our manicured gardens. Though we may have touched every corner of the Earth through climate change, this does not change the fact that species continue to live here, continue to propagate and interact in beautiful ways that we are only now beginning to appreciate. To say that there is no point to discovery simply because humanity has already touched it is to deny that there is something wonderful about seeing a forest return from the ashes of an ecological nightmare or something enlightening to understanding how Darwin's finches evolved. It is to deny that there is beauty in crafting a model that explores sociality or joy in receiving interpretable results from a Western blot. It is to deny the exquisite intricacy of the mating rituals of the red-capped manakin or the raw power of a swarm of army ants tearing through a forest. Sure, humanity is omnipresent in all that we see and observe of the biology of this planet, but to give up on discovering more about nature, protecting nature, and restoring nature, is to miss the point. While nature may have intrinsic value as a monolithic unknown, as McKibben suggests, the work that scientists have done has shown that behind every unknown lies a rich and complex labyrinth of secrets, beckoning, tempting, and imploring us to search further. It is the job of biologists to ensure that this doorway to discovering the "natural" world remains open for every generation that will ever come to walk on this Earth.

Perhaps one day society will feel no pang of regret if we realize that concrete and smoke stacks have covered the forests of Costa Rica, the last patches of plains in Illinois, or the forests of New Jersey. And perhaps one day, economic efficiency will have us replacing bees with nanobots or mangrove trees with cement levees. And perhaps one day our own folly will have us creating clouds to blot out a sun that burns too bright or have us dumping calcium into an ocean whose acidity has corralled the coral reefs into the scattered corners of the sea. And perhaps one day all of the mystery of the natural world will have been distilled into a cost-effective drug that can be taken for some kind of cheap high; that wonder and wander will be replaced with potions and pills.

But my answer to Bill McKibben's end of nature is that it is too early. It is too early to give up on the elkhorn coral, the African wild dog, or the Bengal tiger. It is too early to deny future generations their time to explore outside, to play in the dirt, to see what there is out there. It is too early to say that there is no mystery, no joy, no majesty in nature. And so long as a biologist draws breath, it is our responsibility to study, protect, and preserve those wild places that first drew us into the discipline.