A thesis submitted to the Department of Environmental Sciences and Policy of Central European University in part fulfilment of the Degree of Master of Science

Vegetation Biodiversity Survey and Seed Rain Assessment as Part of Longterm Reforestation Monitoring at the Cloud Forest School in Monteverde, Costa Rica

Lisa LAMB

May, 2012

Budapest

Erasmus Mundus Masters Course in Environmental Sciences, Policy and Management





This thesis is submitted in fulfillment of the Master of Science degree awarded as a result of successful completion of the Erasmus Mundus Masters course in Environmental Sciences, Policy and Management (MESPOM) jointly operated by the University of the Aegean (Greece), Central European University (Hungary), Lund University (Sweden) and the University of Manchester (United Kingdom).



Notes on copyright and the ownership of intellectual property rights:

(1) Copyright in text of this thesis rests with the Author. Copies (by any process) either in full, or of extracts, may be made only in accordance with instructions given by the Author and lodged in the Central European University Library. Details may be obtained from the Librarian. This page must form part of any such copies made. Further copies (by any process) of copies made in accordance with such instructions may not be made without the permission (in writing) of the Author.

(2) The ownership of any intellectual property rights which may be described in this thesis is vested in the Central European University, subject to any prior agreement to the contrary, and may not be made available for use by third parties without the written permission of the University, which will prescribe the terms and conditions of any such agreement.

(3) For bibliographic and reference purposes this thesis should be referred to as:

Lamb, L. 2011. Vegetation biodiversity survey and seed rain assessment as part of long-term reforestation monitoring at the Cloud Forest School in Monteverde, Costa Rica. Master of Science thesis, Central European University, Budapest.

Further information on the conditions under which disclosures and exploitation may take place is available from the Head of the Department of Environmental Sciences and Policy, Central European University.

Author's declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Lisa Lamb

Lisa LAMB

CENTRAL EUROPEAN UNIVERSITY

ABSTRACT OF THESIS submitted by:

Lisa LAMB

for the degree of Master of Science and entitled: Vegetation biodiversity survey and seed rain assessment as part of long-term reforestation monitoring at the Cloud Forest School in Monteverde, Costa Rica

May, 2012.

Monteverde, Costa Rica has extremely high conservation value because of its high biodiversity and endemism, especially in its cloud forests. Reforestation monitoring programs at the Cloud Forest School (CEC) in Monteverde are important for understanding which reforestation strategies work best and to raise conservation awareness through environmental education. Restoration monitoring programs should measure at least one component of diversity, vegetation structure, or ecological processes. This research measures ecosystem interactions (seed dispersal) and more extensive diversity assessments (plant identification) to evaluate the suitability of existing monitoring protocols and to assess the feasibility of adding a new component to the monitoring program. Vegetation sampling of a larger sampling area revealed that Inga plots have significantly higher total and seedling biodiversity than Mixed plots, but the existing monitoring protocol's small sample size is too small to detect these differences. The seed rain assessment showed no significant differences between Inga and Mixed plots, but this must be treated with caution because this research is only valid for seeds visible to the naked eye. It is recommended that in the future the CEC monitoring program management should: a) organize and manage the monitoring data in a database, b) expand the role of monitoring in the curricula, c) increase the vegetation sampling area and create reference plots, d) choose an appropriate component of ecosystem processes to monitor, and e) change the vegetation identification protocols so that students only identify larger flowering saplings and trees instead of seedlings.

Keywords: ecological monitoring, reforestation, biodiversity, conservation, vegetation survey, seedling, seed dispersal, cloud forests, Costa Rica, Monteverde, Cloud Forest School

Acknowledgements

Above all, I would like to thank the people, land, forests, and wildlife of Monteverde, whose love and pulsing life reminded me every day what conservation and community are really about. I cannot express enough thanks to my mother and the Zuñiga family for all their support, love, patience, and faith. I am deeply thankful to my advisor Brandon Anthony for all his advice, constructive feedback, patience, and invaluable insight as I went through the research process. I am also sincerely thankful to Patricia Townsend for the idea for this thesis, for reviewing this thesis, and for all her helpful suggestions. I am extremely indebted to Willow Zuchowski and William A. Haber, who generously gave their time and expertise to identify the plants. I am sincerely grateful to Debra Hamilton, who also gave her time and knowledge in the interview, which corrected a significant mistake and assumption about the *Inga* trees.

This research project would not have been possible without the help and cooperation of the CEC staff and management, and I thank them for supporting reforestation monitoring and environmental education on their campus. I greatly appreciate Milton Brenes for help with identifying some of the plant and seed species to common names and for his interest in this project. I am also grateful to Viviana Abarca Ovares for helping me construct over 135 seed traps and to the 10th grade students and teacher for participating in this monitoring program.

I am extremely thankful for the Lydia Press Memorial Foundation and the CEU Foundation for assisting me with greatly needed research funds for this project. MESPOM has been a truly life-changing experience for me in terms of the people I have been privileged to meet and the holistic integration of ideas during the coursework, so I am grateful to the MESPOM Consortium for the opportunity to be part of this amazing program.

Table of Contents

Chapter 1: Introduction	1
1.1 Background: Deforestation in Costa Rica	1
1.2 Monteverde, Costa Rica	2
1.3 Reforestation and monitoring at CEC: a local conservation strategy	3
1.4 Motivation and objectives	6
Chapter 2: Global, regional, and local threats and conservation strategies for cloud forests	9
2.1 Global threats to cloud forests	9
2.2 Global conservation strategies for cloud forests	. 12
2.3 The Mesoamerican Biological Corridor (MBC): a regional conservation strategy	. 13
2.4 Restoration as a regional and local conservation strategy	. 14
2.4.1 Seed dispersal	. 16
2.5 Reforestation in the greater Monteverde region	. 17
Chapter 3: Research Design	. 19
3.1 Specific research questions	. 19
3.1.1 Vegetation biodiversity monitoring	. 19
3.1.2 Ecosystem interactions assessment: Seed rain	. 19
3.1.1 Interview	. 21
3.2 Methodology	. 22
3.2.1 Plant diversity sampling design	. 22
3.2.1.1 Sample size and counting methods	. 23
2.2.1.2 Identification and classification	. 24
3.2.1.5 Italiping	. 20
3.2.2 Seed rain sampling design	. 20
3.2.2.3 Identification and classification	. 27
3.2.3.5 Identification and classification	30
3.2.5 Sutistical power	31
Chapter 4. Results and analysis	32
4.1 Seedling and vegetation recruitment	. 32
4 1 1 Combined total vegetation data	32
4.1.2 Tree (seedling and sapling) data	. 35
4.1.3 Combined total vegetation data from a smaller sample size	. 38
4.1.3 Tree (seedling and sapling) data from a smaller sample size	. 41
4.2 Seed trap design and pilot studies	. 44
4.2.1 Seed trap data	. 45
4.3 Interview results	. 48
4.3.1 Inga punctata was not planted above its range	. 49
4.3.2 Community support for conservation in Monteverde	. 50
4.3.3 Montoring in the greater Monteverde region	. 51
Chapter 5: Discussion	. 54
5.1 Vegetation biodiversity sampling	. 54
5.1.1 Difficulties in plant identification	. 56
5.1.2 Limitations of using only two quadrats	. 57
5.1.3 Conclusions	. 57
5.2 Seed rain	. 58
5.2.1 Difficulties in seed identification: problems with detectability	. 58
5.2.2 Dispersal mechanism	. 60
5.2.3 Conclusions	. 60
5.3 Interview	. 61
Chapter 6 Recommendations for the CEC Monitoring Program	. 63
6.1 Managing monitoring data	. 63
6.2 Expanding monitoring in the curricula.	. 63
6.5 Increasing sample size and creating reference plots	. 64
6.4 Include another component of ecosystem processes	. 65
6.6 Conclusion	. 03
0.0 COnclusion	. 08
Appandix: Detential Animal Disparsors	. 09 75
Appendix, rotential Animal Dispersets	. 13

List of Tables

Table 1 Comparison of plant biodiversity indices between Inga and Mixed plots	33
Table 2 Student's T-test for significance between Inga and Mixed plots - all vegetation	35
Table 3 Comparison of biodiversity indices for species between Inga and Mixed plots	37
Table 4 T-test for significance between Inga and Mixed plots- tree species only	38
Table 5 T-test for significance between Inga and Mixed plots - two quadrats per plot	41
Table 6 T-test for significance between Inga and Mixed plots- tree species, two quadrats per plot	43
Table 7 Comparison of biodiversity indices for seed species between Inga and Mixed plots	47
Table 8 T-test for significance between Inga and Mixed plots – seeds	48

List of Figures

Figure 1 Monteverde, Costa Rica	3
Figure 2 CEC reforestation monitoring plots	5
Figure 3 Global distribution of tropical montane cloud forests	10
Figure 4 Mesoamerican Biological Corridor	14
Figure 5 Seed traps	28
Figure 6 Cumulative and mean plant species and family richness	32
Figure 7 Cumulative and mean tree species and family richness	36
Figure 8 Cumulative and mean plant species and family richness, two quadrats	39
Figure 9 Mean tree species and family richness, large and small samples	42
Figure 10 Animal dispersed seeds	45
Figure 11 Cumulative and mean species and family richness- seeds	46
Figure 12 Reforestation plots-Mixed and Inga	55

List of Abbreviations

CEC= Centro de Educación Creativa (Cloud Forest School) MBC= Mesoamerican Biological Corridor SER= Society for Ecological Restoration

Chapter 1: Introduction

1.1 Background: Deforestation in Costa Rica

In Costa Rica, 50-90% of the original tropical forests were cleared from the 1950s-1980s, mostly for cattle pastures to provide cheap beef for American fast food chains (Myers 1981; Koll *et. al.* 1995; Hall *et. al.* 2000). Despite government subsidies and funding from the World Bank and USAID, many of these pastures were abandoned after soil degradation or falling international prices for beef (Calvo-Alvarado *et. al.* 2009; Leopold *et. al.* 2001; FAO 2001). These land use changes have had significant negative impacts on many local communities because forest plant species provide timber, medicine, food, and other ecosystem services (Kappelle et. al. 2000). Widespread soil erosion, habitat destruction, and biodiversity loss led to changes in conservation and forest policies through the Forestry Law of 1996, which restricts forest clearing, introduced a Payment for Environmental Services scheme, and promotes sustainable forest management (Calvo-Alvarado *et. al.* 2009; Declerck *et. al.* 2010).

Although some of the abandoned pastures and other degraded habitat will naturally regenerate into forest, this process of succession can take decades or even centuries and is unlikely in many locations, given the extent of the deforestation and soil degradation (Carpenter *et. al.* 2004). This is especially true for cloud forests, which are fragile ecosystems that often show slow rates of recovery and can take 200-300 years to develop into mature forest if the disturbance is large (Foster 2001). Invasive exotic grasses were usually planted for livestock grazing, and even when pastures are abandoned, a variety of abiotic and biotic conditions can make it difficult or impossible for native forest species to re-colonize the areas

(Kuusipalo *et. al.* 1995). This state of "arrested succession" highlights the long-term negative impacts of deforestation and invasive exotic species in the tropics, especially considering the valuable ecosystem services these forests provide to local communities (Janzen 1990; Zahawi and Augspurger 1999).

1.2 Monteverde, Costa Rica

The Monteverde region of Costa Rica (Figure 1) is located at 84.8° W longitude, 10.3° N latitude in the Tilarán Mountains, which span the Continental Divide (Foster 2001; Guswa *et. al.* 2007). The Pacific Slope of the greater Monteverde region consists of seasonal forests (premontane moist forest and premontane wet forest), cloud forests (lower montane wet forest, lower montane rain forest, and elfin forest), and coffee farms and pastures (Haber et. al. 2000). These different life zones are compressed due to narrow altitudinal and climatic requirements of tree species, which results in high community turnover rates for trees, epiphytes, and other taxa. For example, the Monteverde region has over 400 bird species and 3000 plant species, including 750 trees, 870 epiphytes, 400 orchids, and 180 ferns (Haber et. al. 2000; Young and McDonald 2000). Thus, the region has an extremely high conservation value in terms of its alpha, beta, and gamma biodiversity.



Figure 1 Monteverde, Costa Rica (Source: Guswa et. al. 2007)

1.3 Reforestation and monitoring at CEC: a local conservation

strategy

The Cloud Forest School (Centro de Educación Creativa, or CEC) is a bilingual Spanish and English K-11 school in Monteverde, Costa Rica that was founded to create a multicultural setting where local children can study in an environmentally focused program (Mello *et. al.* 2010). The CEC was established in 1991 by purchasing 42 hectares of land from the Nature Conservancy, which contained primary forest, secondary forest, and abandoned cattle pasture. Part of CEC's charter was to conserve existing primary and secondary forests and to restore 9 ha of abandoned pasture, and over 10,000 seedlings planted since 1999 (Mello *et. al.* 2010). Although the school children, staff, parents, and volunteers have been participating in these intensive reforestation programs for over a decade, little to no records were kept of the success of these efforts (Townsend, pers. comm.).

Restoration has been difficult because the pastures were used for cattle grazing for approximately 50 years and are dominated by invasive exotic grasses,

such as African star grass (*Cynodon nlemfuensis*) and *Digitaria abyssinica*. When reforested trees died, new trees were planted to replace them, so it is difficult to know the age of the trees and the effectiveness of the tree planting in specific locations (Townsend, pers. comm.). These restoration efforts obviously require considerable financial and human resources and it is important to learn which reforestation techniques produce the best results. Therefore, in 2009 the school began a monitoring program involving high school students assessing the effectiveness of two restoration strategies – one with an even mixture of native species and one with predominantly one species of guaba (*Inga punctata*) (Townsend, pers. comm.). The location of the experimental reforestation monitoring plots in one of the abandoned pastures is shown below in Figure 2. Each monitoring plot is 5mx10m, and there are five Inga plots and five Mixed plots for a total of ten permanent monitoring plots, each of which contains two permanent 1mx1m subplots for detailed ground cover and seedling recruitment monitoring.



Figure 2. CEC reforestation monitoring plots (Townsend, pers. comm.)

Guabas (*Inga*) are fast-growing, nitrogen-fixing trees, and are thought to aid in natural forest regeneration by shading out grasses, enhancing soil nutrients, and providing appropriate vegetation structure for animal dispersers (Mello *et. al.* 2010). *I. punctata* has a natural range of 900-1400m and is native to the Tilarán Mountains, so this species has been planted along with other native tree species as part of reforestation, corridor, and windbreak programs in the Monteverde region (Haber et. al. 2000; Hamilton, pers. comm.). The elevation of the CEC school and forests ranges from approximately 1400m-1580m, according to recent trail maps on the campus. Thus, part of the CEC falls within the natural habitat range of *I. punctata* and other areas are above its upper range limit. The reforestation monitoring areas

are approximately 1400-1450m in elevation, which is at the upper limit or slightly above the natural range of *I. punctata.* Species planted above their range may be able to survive but not necessarily reproduce, which over time can lead to changes in forest community composition as other species gradually recruit in the forest (Hamilton, pers. comm.). *I. punctata* may potentially serve as nurse trees for more biodiverse understory tree species that may eventually replace the initial reforested vegetation. Since these *Inga* plots have predominantly one species (and hence low initial biodiversity), this trend of replacement may be desirable, but only long-term monitoring data will tell if this is in fact what happens. Thus, experimental planting and monitoring of *I. punctata* at the upper limit of its natural range can provide information about its effectiveness as a reforestation and wildlife corridor species, and perhaps its potential for range shifts into higher elevations.

1.4 Motivation and objectives

Given the limited financial, temporal, and human resources available to most conservation programs, it is extremely important to be efficient and thus to know which reforestation strategy performs better. I wanted to research which reforestation strategy (Inga or Mixed) worked better at the CEC in terms of: a) vegetation structure, b) plant biodiversity, and c) ecosystem processes (SER 2004). Most monitoring programs measure at least one component of diversity, vegetation structure, or ecological processes, but only 38% of monitoring programs measure components from all three categories (Ruiz-Jaen and Aide 2005a). The existing monitoring protocols at the CEC measure several parameters of vegetation structure (DBH, tree height, canopy width, percent ground cover) and a few components of diversity (number of seedlings, percent ground cover, some plant identification). Therefore, my overarching goal for this research was to do a pilot study to measure

ecosystem interactions (seed dispersal) and more extensive diversity assessments (plant identification). Additionally, I wanted to evaluate the feasibility of expanding the CEC's monitoring program to incorporate measurements from at least one component each of diversity, vegetation structure, and ecological processes (Ruiz-Jaen and Aide 2005a).

Monitoring programs are notoriously difficult to design, expensive to maintain, and do not usually last more than five years (Mattfeldt *et. al.* 2009). Furthermore, many monitoring programs have been criticized for using protocols that are not statistically rigorous and for not defining research goals prior to collecting data (Lindenmayer and Likens 2010). These flaws can make it difficult or impossible to detect change in ecosystem health over time or inform management about the success or failure of management actions (e.g. reforestation strategies). Therefore, one of objectives of this research project was to evaluate the existing monitoring program at the CEC to see if the program needs to be improved or changed.

At the onset of this research, I understood that the *I. punctata* trees were planted about 100-300m above their natural range at the CEC and were planted extensively in the Monteverde region. Some of the *I. punctata* in the plots have shown signs of wind damage (e.g. fallen branches, fallen trees), and I was not sure if this was natural or if the species was not adapted to the strong winds higher in elevation. I did not know if it was the intention of the reforestation programs to use tree species from lower down the mountain for assisted colonization, if the Inga trees were only used because they grow fast, if the Inga are mainly being used for wildlife corridors, a combination of these reasons, etc. This was especially interesting in the context of climate change induced range shifts and the controversy surrounding the theoretical and practical applications of assisted range shifts

(Williams and Jackson 2007; Williams *et. al.* 2007; Keith et. al. 2009; Hewitt *et. al.* 2011; Loss et. al. 2011). Therefore, I was curious about: a) why this species was used so frequently for reforestation and windbreak programs, b) why it was planted above its natural range, and c) how successful it was in the areas above its range in terms of survivorship, growth, and reproduction.

Chapter 2: Global, regional, and local threats and conservation strategies for cloud forests

2.1 Global threats to cloud forests

Cloud forests are centers of endemism and speciation, covering less than 0.26 percent of the Earth's land yet hosting a vast array of biodiversity, including 20 percent of the world's range-restricted bird species (Bubb *et. al.* 2004; Foster 2001). These fragile ecosystems are found between 500-3500m elevation, receive between 500-6000 mm/year rainfall, and are characterized by trees covered in a vast array of epiphytes. Since cloud forests can only grow in the narrow altitudinal bands where clouds form on mountains, they are often fragmented and isolated in patches at the top of mountains (Bubb *et. al.* 2004). This is shown in Figure 3, which illustrates that cloud forests are usually found in patches along major mountain ranges or on island mountains. Indeed, cloud forests have been compared to island archipelagoes in terms of their endemism, explosive speciation, and sensitivity to changes in climate (Foster 2001).



Figure 3 Global distribution of tropical montane cloud forests (Aldrich *et. al.* 1997)

These unique ecosystems not only support a variety of species, but the ecosystem services they provide are also critically important to surrounding communities. For example, cloud forest vegetation intercepts orographic precipitation (fog and mist), which is critical to local water resources, especially in dry seasons (Guswa et. al. 2007). Epiphytes in cloud forest trees are important for capturing moisture directly from clouds and fog, and they can store 3000-50000 liters/hectare of water (Richardson et. al. 2000; Sugden 1981). Cloud forests have also been shown to harbor wild relatives of several crop species, including papaya, tomato, passion fruit, avocado, beans, blackberry, cucumber, pepper, and potato (Bubb et. al. 2004). Cloud forests are thus globally important sources of genetic

diversity for important crops, in addition to providing timber, firewood, medicine, and water. Therefore, cloud forests are biodiversity rich ecosystems that supply a variety of direct and indirect ecosystem services to nearby communities and should be considered high priority conservation areas (Bubb et. al. 2004).

Cloud forests are threatened worldwide by a variety of local and global factors, including conversion to cropland, conversion to grazing land, over-hunting, fire, timber harvesting, fuelwood harvesting, roads, mining, drug cultivation, alien species, habitat fragmentation and disturbance, and climate change (Bubb et. al. 2004). The frequency and intensity of these threats vary across regions, but perhaps one of the most ominous threats is climate change because future temperature and precipitation trends are predicted to shift cloud layers up in elevation (Pounds et. al. 1999; Foster 2001). These changes in temperature and orographic precipitation could drastically reduce or even eliminate the existing habitat ranges of cloud forests, especially in mountaintops where cloud forests cannot expand to higher elevations (Gasner et. al. 2010). Epiphytes are especially sensitive to changes in cloud or fog cover because they do not have an extensive root system, but instead obtain water directly from the surrounding moisture-laden air (Foster 2001). Epiphytes provide habitat, nesting material, and water for a variety of invertebrates, birds, frogs, and some primates in addition to contributing significant inputs of nitrates and other nutrients to the cloud forest ecosystem (Benzing 1998; Richardson 2000). Therefore, the local or global extinction of epiphytes could have significant yet unknown impacts to the cloud forest ecosystem as a whole due to changes in water, light, and nutrient cycling (Foster 2001). This potential reduction or elimination of cloud forests would have serious negative impacts to biodiversity conservation and water resources, amongst other ecosystem services.

The potential synergistic effects of deforestation, habitat fragmentation, and climate change are not well understood, but the negative impacts to cloud forests could be multiplied by these intersecting threats. Habitat destruction and isolation leads to small populations, restricted metapopulation flows, and stochastic processes that may lead to local, regional, or global extinctions of species (Opdam and Wascher 2004). Due to the natural patchiness and the high rates of endemism of most cloud forests, there may be few source populations of species to support small or declining populations (Foster 2001). Furthermore, climate change may result in disappearing climates (especially in tropical montane forests) and no-analog community assemblages as species react individualistically to novel climates, which could disrupt ecosystem functioning (Williams et. al. 2007; Williams and Jackson 2007). Although there will be certain unavoidable changes in global temperatures and precipitation in the future due to time lags in the global cycles and feedback systems, the magnitude and impacts of these changes on specific locations is difficult to predict (Gasner et. al. 2010).

2.2 Global conservation strategies for cloud forests

In order to ensure survival of the cloud forest ecosystem as a whole, it is necessary to protect existing areas of cloud forest, reduce or eliminate deforestation in unprotected cloud forests, reforest areas that previously contained cloud forests, and reduce global greenhouse gas emissions (Foster 2001). Protected areas embedded in a landscape with wildlife corridors and forested private land are much more likely to allow cloud forest species to move into other nearby areas with suitable habitats than an isolated reserve would, especially in a changing climate with shifting ranges (Toledo-Aceves et. al. 2011; Townsend 2011). Climate change mitigation strategies for cloud forests need to incorporate the needs of local

communities, since they often create deforestation or fragmentation pressures on the ecosystem yet rely on the water resources and other ecosystem services provided by cloud forests (Bubb et. al. 2004). Thus, the fate of many cloud forests is inextricably linked with the fate of nearby mountain communities at the local level, connectivity through reserves and corridors at the regional level, conservation policies at the national level, and reductions in greenhouse gas emissions at the global level (Bubb et. al. 2004; Toledo-Aceves et. al. 2011).

2.3 The Mesoamerican Biological Corridor (MBC): a regional

conservation strategy

Many affected communities, NGOs, private landowners, and governmental agencies have tried to reverse the worrisome deforestation and biodiversity loss by establishing protected areas, implementing new policies, starting reforestation programs, and organizing outreach campaigns. For example, the Mesoamerican Biological Corridor (MBC) (see Figure 4) is an important international attempt to protect the Mesoamerican biodiversity hotspot by establishing protected areas, increasing connectivity between protected areas through corridors, and supporting sustainable land use in the intervening land matrix (Corrales and Zuñiga 2001; Herrera 2003; Miller et. al. 2001). The overarching goal of the MBC is to conserve regional biodiversity while meeting the poverty alleviation and rural development needs of local communities in Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and five southern states of Mexico (Miller et. al. 2001; Ray et. al. 2006). However, many of the proposed corridors were previously deforested, which has led to more intense dry seasons, which in turn changes the community composition of regenerating forests by favoring drier forest species. This

deforestation-induced regional climate change may ultimately diminish the ecological utility of the planned corridors and illustrates how land-use change can have farreaching consequences (Ray et. al. 2006). Furthermore, this situation emphasizes the importance of preventing land degradation whenever possible and highlights the need for actively restoring degraded lands in the MBC and elsewhere.



Figure 4 Mesoamerican Biological Corridor. Dark green shows existing protected areas, light green indicates proposed connecting corridors, red denotes proposed protected areas, and light tan indicates other land uses. (Corrales and Zuñiga 2001; Herrera 2003)

2.4 Restoration as a regional and local conservation strategy

Restoration strategies vary according to the types of plant species used, the

area reforested, the growth stage of the plants (e.g. seeds or seedlings), and the financial and human resources available (Doust *et. al.* 2008). Some reforestation programs use only native plant species, others use exotics (especially valuable timber species), or a combination of both (Cusack and Montagnini 2004). The most common restoration strategy is to reforest continuous tracts of land, but some research shows that reforesting smaller patches of vegetation might be more cost effective, as the patches eventually spread outward to become continuous forest (Corbin and Holl 2012). Although many financial and human resources have been allocated to tree-planting or direct seeding efforts, far fewer resources are spent monitoring the success of these reforestation programs (Ruiz-Jaen and Aide 2005a). Time and budget limitations are often cited as the main barriers to implementing long-term monitoring programs, but it is crucial to understand which restoration strategies produce the best results so that limited resources can be used wisely (Townsend 2011).

According to the Society for Ecological Restoration (SER), the overarching goal of restoration is to create a self-propagating ecosystem resistant to perturbations and similar in community structure and biodiversity to reference sites (SER 2004). The SER *Primer on Ecological Restoration* suggested nine ecosystem attributes for monitoring programs to assess the efficacy of restoration efforts, but a recent review of monitoring programs shows that no study measured all of SER's suggested attributes (SER 2004; Ruiz-Jaen and Aide 2005a). In practice, most monitoring programs measure at least one component of diversity, vegetation structure, or ecological processes, but only 38% of monitoring programs measure components from all three categories (Ruiz-Jaen and Aide 2005a). Vegetation structure provides information about habitat suitability, diversity can predict future community

CEU eTD Collection

assemblages or exotic species invasions, and ecosystem interactions can assess the stability of the restored ecosystem (Ruiz-Jaen and Aide 2005b). Thus, these three major categories of restored ecosystem attributes are important for monitoring programs to evaluate the potential for the restored ecosystem to regenerate independently of human intervention.

2.4.1 Seed dispersal

Reforestation success is highly dependent on survival of seeds and seedlings, self-regeneration of the planted vegetation, and seed dispersal of species from nearby primary or secondary forest. Seed dispersal is one the major factors limiting natural regeneration and reforestation efforts in tropical rainforests, so many monitoring studies measure various components of seed rain1, germination, seedling recruitment, predation, and persistence in the seed bank (Drake 1998; Farwig and Berens 2012). Mobile animal species such as birds, bats, and mammals are vitally important for dispersing seeds of tropical forest species, either through endozoochory, synzoochory, or epizoochory₂ (Wunderle 1997; Mori and Brown 1998). These animals are unlikely to spend much time in hostile environments without refuge (e.g. abandoned pastures), which is why seed rain dramatically drops off several meters from forest edge (Melo et. al. 2006). Larger seeds may require larger animal dispersers, but habitat loss and destruction can eliminate larger vertebrates at a faster rate than smaller animal dispersers (Costa et. al. 2012; Cramer et. al. 2007). This means that certain size classes of seeds may have a higher or lower dispersal rate, which over time can alter the species composition and

¹ Seed rain is the amount and type of seeds that are delivered to a given area, either by wind, gravity, animals, water, etc.

² Endozoochory is when seeds are carried inside the digestive tract of an animal; synzoochory is when seeds are carried inside the mouth; epizoochory is when seeds are transported outside the animal on its fur or feathers, usually via hooks, barbs, etc. (Wunderle 1997; Mori and Brown 1998)

structure of a forest (Costa *et. al.* 2012; Farwig and Berens 2012). Those seeds that do enter unsheltered sites in pastures often have high predation rates and may not germinate or establish successfully due to unfavorable microclimates (Garcia-Orth and Martínez-Ramos 2008). Additionally, the persistence of seeds is highly dependent on species and local environmental factors, with alien species often producing seeds that survive for long periods of time in a given seed bank (Drake 1998). This lack of seed and seedling availability severely limits natural forest regeneration, so reforestation often attempts to speed up the process of succession by artificially enhancing dispersal and eventually creating suitable habitat for animal dispersers (Pejchar *et. al.* 2008).

2.5 Reforestation in the greater Monteverde region

The cloud forests of Monteverde are world-renowned for their biodiversity and the region experiences high levels of ecotourism, hosting over 200,000 visitors per year (Guswa *et. al.* 2007; Townsend 2011). Although the income from ecotourism has benefitted the nearby communities of Santa Elena, Monteverde, Cerro Plano, Canitas, etc., the large numbers of tourists have also put stress on the local water resources, especially because the peak tourist season coincides with the dry season (Guswa *et. al.* 2007). The Monteverde area has several private biological reserves, university ecology programs, and research centers, so overall there is support for conservation and monitoring efforts. Restoration programs in the Monteverde region have planted almost a million trees from the 1970s to restore abandoned agricultural fields and create windbreaks (Harvey and Haber 1999; Townsend 2011). Despite the large amount of human and financial resources invested in the region, the success of the various reforestation strategies and programs has not been systematically monitored. However, interviews and surveys of local landowners,

researchers, and students have shown that monitoring is an important priority for these stakeholders (Townsend 2011).

Although reforested areas may be suitable for cloud forest species to colonize, it can take hundreds of years to fully regenerate cloud forest and climate change may alter the suitability of these areas (Foster 2001). Several species from lower elevations have already moved into the cloud forest (e.g. keel-billed toucans, which prey on the eggs of the endangered resplendent quetzal), so perhaps increasing habitat connectivity through corridors or assisted migration will bring corresponding lower montane predators (Pounds *et. al.* 1999; Townsend 2011; Loss *et. al.* 2011). The existing cloud forest species don't have anywhere further up the mountain to colonize and the feasibility, effectiveness, and outcome of purposefully introducing new species through assisted migration are unknown (Keith et. al. 2009). Thus, the current conservation strategy in the greater Monteverde region is to protect areas with cloud forests, encourage private landowners to keep forests on their land, prevent further deforestation, and reforest to increase habitat areas and create wildlife corridors (Hamilton, pers.comm.).

Chapter 3: Research Design

3.1 Specific research questions

3.1.1 Vegetation biodiversity monitoring

The annual monitoring data is important for evaluating the short-term and longterm effectiveness of the two reforestation strategies and the appropriateness of using *Inga* at or slightly above its natural range. This monitoring also allows the students to learn about abiotic and biotic interactions, plant competition, ecology, and the effectiveness of different restoration strategies. An overarching goal of the CEC's monitoring program is to involve students at a young age in citizen science so they understand the importance of careful monitoring in achieving biodiversity conservation objectives and to train them for monitoring efforts in other parts of the Monteverde region (Mello *et. al.* 2010; Townsend 2011). Furthermore, the seedling recruitment data are vital for answering the following research questions, which will be addressed in this thesis:

Vegetation diversity monitoring research questions

1. What are the density, richness, evenness, and biodiversity of the vegetation in the Inga and Mixed plots?

2. What are the density, richness, evenness, and biodiversity of the seedlings recruiting in the Inga and Mixed plots?

3. Are the current identification monitoring protocols sufficiently able to detect differences in vegetation biodiversity in Inga and Mixed plots?

3.1.2 Ecosystem interactions assessment: Seed rain

Measuring seed rain provides information about seed density, size, richness,

and diversity falling in a reforested area, which can give an indication of restoration success and future trends in community structure (Alvarez-Buylla and Martinez-Ramos 1990). If the seed rain lacks certain kinds of seeds in sufficient densities, it may indicate that further restoration efforts are necessary. For example, if large seeds are not found in the seed rain, it may mean that large-bodied animal dispersers do not yet consider the reforested area to be suitable habitat, so further direct seeding or seedling planting may be necessary to reintroduce those tree species (Melo *et. al.* 2006). Similarly, seedling species establishing naturally (without human intervention) but not found in the seed rain may indicate the contribution of seeds in the seed bank (Alvarez-Buylla and Martinez-Ramos 1990). The natural seedling recruitment can be considered the subset of the seed rain and/or seed bank that is able to survive in the local microhabitat. Comparing seed rain with natural seedling establishment is a useful method to evaluate which seeds fall in a restored area but do not germinate or recruit successfully because of predation, competition, and/or adverse environmental conditions (Chabrerie and Alard 2005).

This information is important to show if seed-dispersing animals are being attracted to the reforested plots and if so, how many seeds they are bringing into the plots. Differences in the amount, composition, and size of the seed rain between the plots can reveal which restoration strategy (using an even mixture of native species or using mostly *I. punctata*) attracts more seed-dispersing animals at this stage in the reforestation process. This information is crucial for testing the validity of the *nucleation reforestation theory*, which proposes that small clumps of trees expand outwards until they eventually close the gaps between them and become continuous forest (Corbin and Holl 2012). Nucleation will only be possible at the CEC if the reforested clumps are able to compete with invasive grasses and eventually expand

outward through self-regeneration, which requires animal dispersers, germination, and seedling survival. Although it is beyond the scope of this project to experimentally determine why some seeds fall but do not germinate or recruit, comparing the seed rain data to the seedling establishment still provides valuable information about seed dispersal. Furthermore, this information addresses the following research questions:

Seed Rain Research Questions

1. What are seed density, richness, size, and diversity of the seed rain in the *Inga* and Mixed native tree plots?

2. What is the contribution to the seed rain from existing vegetation within the plots and from animal dispersed and wind dispersed seeds?

3. Which species (if any) are deposited in the seed rain that are not found in the seedlings recruiting the plots and which recruiting seedling species are not found in the seed rain?

4. Is seed rain monitoring a feasible future component for detecting changes in ecosystem interactions in the plots as part of the CEC's long-term student monitoring program?

3.1.1 Interview

My motivation for interviewing the director of the Fundacion Conservacionista Costarricense (Costa Rican Conservation Foundation) stemmed from my desire to better understand the reforestation and monitoring program at the CEC in the context of the conservation efforts in the wider region. Additionally, I wanted to learn more about the range of *I. punctata* and other tree species planted at the CEC, because initially I was led to believe that the tree species had been planted above its range. It was important to know if this was accidental through lack of knowledge of

the species' range or intentional, perhaps with the purpose of testing assisted migration. I also was curious if *I. punctata* or other species had been planted above their ranges in reforestation and living fence programs, and if so, whether or not it was intentional. This directly related to my research because the Inga plots appear to be achieving greater reforestation success than the Mixed plots in terms of structure and diversity, at least in the short-term. However, if the Inga plots largely consisted of *I. punctata* trees planted above their range, then this would have been a questionable reforestation method. Thus, my goal for the interview with the director was to confirm and clarify the following research questions and issues:

Interview Research Questions

1. Why was *I. punctata* used so frequently for reforestation and windbreak programs in the Monteverde region?

2. Why was it planted above its natural range?

3. How successful was it in the areas above its range in terms of survivorship, growth, and reproduction?

3.2 Methodology

This research consisted of data collection for the CEC's long-term monitoring program, a short-term assessment of seed rain, and an interview with a key informant familiar with reforestation and monitoring at the study site and in the greater Monteverde region.

3.2.1 Plant diversity sampling design

I coordinated the 2012 data collection for the CEC annual reforestation monitoring program as part of this research. Specifically, I explained basic ecological concepts and research protocols to students, teachers, staff, etc. and guided data

CEU eTD Collection

collection and analysis for the 10 Inga and Mixed native tree experimental plots. This year's data collection used similar monitoring methods and protocols to those that have been used since the monitoring program's inception in 2009 to maintain continuity in the data. Each plot's two permanent 1mx1m subplots (quadrats) were used for ground cover and plant and seedling richness data.

3.2.1.1 Sample size and counting methods

Previous years' vegetation monitoring had a sample size which was quite small relative to the total area of the plots, since two permanent 1mx1m quadrats per ten 5mx10m plot results in only 20m² sampled out of 500m² total. Using a minimum sample size calculator (Creative Research Solutions 2012), 95% confidence level, confidence intervals of +/- 10, and an area population of 500, the minimum sample size should be 81 m², or roughly 8 m² per plot. Therefore, I could not assume that the initial monitoring results yielded significantly representative estimates of the population parameters, and this is especially important given that each plot has unique microclimatic conditions. Thus, the potential variability among Inga plots and among Mixed plots were such that a larger sample size was needed to detect any real differences between them.

The Inga and mixed plot were sampled using a random sample design and 8m² per plot were surveyed for all vegetation. A random number generator was used to select quadrats to sample, and a 1mx1m PVC quadrat marker subdivided into 16 squares was used to simplify counting and identification. Species were counted and identified whenever possible using plant and tree field guides from Costa Rica and Monteverde (Haber et. al. 2000; Zamora 1993; Zamora *et. al.* 2004; Zuchowski 2005). Some plots were overgrown with very dense vegetation and it was difficult and time-consuming to accurately count all the individual plants of a given species.

Since the quadrat marker was subdivided into 16 squares, the abundance for dense grasses or shrubs was estimated by counting individuals in representative squares and then multiplying the totals by the appropriate number of squares in order to extrapolate to the entire quadrat. Although this method of sampling introduces error into the data collection, it still provides a good estimate of the overall abundance of a given species.

Some plots were covered so densely with grasses and *V. arborescens* that it was impossible to know which blades were from separate individual plants, especially since several grass species produce roots at each node. Indeed, most of the stems and blades may have belonged to only a few individual plants, but that does not provide data about the way these invasive grasses dominate the plots by forming dense mats that outcompete other plant species. For these species, the number of blades or stems was counted, since that provides a measure of dominance and density and was more feasible than trying to ascertain which stems belonged to each individual plant. Dense stands of vegetation made it difficult to identify smaller plants that grow low to the ground, especially in plots and quadrats dominated by invasive grasses and shrubs. This may have resulted in underestimating the true plant biodiversity in some of the quadrats, but this limitation was unavoidable without removing the dominant vegetation.

3.2.1.2 Identification and classification

Unknown species were described, photographed, and coded until identification was possible. The CEC's land steward and a local nature guide assisted with some of the plant identification on site. To my knowledge, technical dichotomous keys for local species were not available and most of the weedy herbaceous species or fern species were not included in the local plant books. Samples of unknown species

CEU eTD Collection

were eventually taken for identification to two local botanists who have studied Monteverde's flora and ecology for over 30 years and have published several books describing plant species in Costa Rica and Monteverde (Haber et. al. 2000; Zuchowski 2005). A few species (four ferns and 2 vines) were left unidentified because I had assumed the initial identification from previous monitoring years was correct and didn't bring samples to the local botanists. Later I discovered that the ferns were probably identified incorrectly the first time. However, this did not affect the species richness calculations because as long as the species can be distinguished (which they were), then the biodiversity indices can be used. For the family richness calculations with plots containing these unknown species, I counted only one family for all the unknown ferns even though the fern species most likely belonged to different families. For situations where two or more species were unknowingly counted as one species, both families were counted because it was highly likely that there were individuals of both species present in the quadrats. Thus, there were some unintentional inaccuracies in the species identification, but conservative yet realistic methods were used to count species and family richness, which were then used in composite biodiversity indices.

The plant species were classified as herbaceous, shrub, tree (seedling and sapling), or fern and were compiled into 'total vegetation' (herbaceous + shrub + tree (seedling and sapling) + ferns). The total plant diversity data were then converted into biodiversity indices such as the Shannon-Weiner and Evenness Indices, since the vegetation richness, evenness, and density were each relevant to this research and these indices incorporate these variables. Since the number and diversity of seedlings and saplings recruiting in the plots is important for evaluating the effectiveness of the two reforestation strategies, the tree species data were also

analyzed separately as a subset of the total vegetation. Adult trees were not included in the analysis because they were most likely planted in the reforestation program and thus do not represent naturally recruiting vegetation. The differences in mean values between Inga and Mixed plots were tested for significance using total vegetation data and only tree species (seedling and sapling) data.

3.2.1.3 Trampling

There is an important tradeoff between sampling a representative area versus trampling the vegetation in order to sample the plots sufficiently. This trampling effect was especially noticeable after the students monitored the canopy structure and percent ground cover in all the plots. Ideally, the monitoring program should have protocols that maximize this tradeoff by determining the optimum number of quadrats that will be able to sufficiently detect changes in seedling biodiversity over time while minimizing the number of quadrats needed, but this is difficult to estimate without knowing the population parameters.

3.2.2 Seed rain sampling design

There are many different types of seed traps and each design provides different information about seed dispersal and seed rain (Chabreri and Alard 2005). Although funnel traps placed at ground level are the most efficient for catching seeds, many of the reforestation plots are overgrown with tall African star grass and *Vernonia arborescens* that intercept seed rain. Furthermore, this design would entail unearthing large amounts of soil in reforestation areas, which could potentially disturb the seed bank and recruiting vegetation, thus affecting the monitoring results in future years. Pot traps for germination and identification were not feasible for this short-term assessment and the natural seedling recruitment data from the long-term
seedling monitoring would likely provide similar information (Chabreri and Alard 2005). Hanging traps were not practical for the Mixed plots because they did not have the vegetation structure (e.g. branches) necessary to support this kind of trap. Therefore, two seed trap designs (PVC traps and bucket/box traps) were considered suitable for this site based on the literature review. These two trap designs were constructed and placed randomly in one randomly selected plot (plot 10) and checked for seeds one week later.

3.2.2.1 Pilot study of two seed trap designs

The PVC traps were constructed of mosquito netting, PVC connector pieces, PVC pipe cut into 8 equal sections for the frame, and PVC pipe cut into 4 pieces to support the frame off the ground. The bucket traps were made of plastic buckets and mosquito netting cut clipped onto the rim of the buckets. The PVC traps had an area of 0.5 m², whereas the bucket traps only had an area of 0.053 m², so initially the PVC trap design seemed preferable to the bucket traps. Unfortunately, the PVC traps were unable to withstand the notoriously strong winds and they blew over, so this seed trap design was not suitable for this site. Therefore, bucket traps made from heavy-duty plastic pots lined with fine-mesh (1-2mm) netting were used for initial pilot data collection, as it has been employed successfully in previous research (Chabreri and Alard 2005; Drake 1998; Pejchar et. al. 2008). Additional seed traps were made from cardboard boxes lined with thin cloth (see Figure 5 below) so that a greater area could be sampled using a similar seed trap design to the bucket traps. The cloth had a finer mesh than the initial netting (1-2mm), and small seeds could not pass through the cloth or be washed away in the rain, yet the cloth was able to dry relatively quickly. The final seed trap sampling design consisted of 30 plastic buckets with an area of 1.59m² and 138 cardboard box traps with an area of

18.80m² for a total sample area of 20.40m², which was roughly 2m² per plot. This seed rain sample area was initially chosen to complement the CEC monitoring protocol's vegetation diversity sample area (two 1mx1m quadrats per plot) before it was realized that this vegetation sample area was four times smaller than the minimum sample area based on statistical calculations. However, 80m² of seed trap area proved to be impractical given the financial, temporal, and material resources available. Furthermore, a literature review of common sample sizes in other seed rain studies showed a much smaller number of seed traps and/ or smaller seed trap size per area sampled (Alvarez-Buylla and Martinez-Ramos 1990; Chabrerie and Alard 2005; Costa *et. al.* 2012; Cramer *et. al.* 2007; Drake 1998; Melo et. al. 2006; Stevenson and Vargas 2008).



Figure 5 Seed traps. A total of 30 bucket traps and 138 box traps were constructed from plastic buckets, cardboard boxes, cloth, and clothespins

3.2.2.2 Simple random sample design

Seed rain is notoriously clumped and many seed rain studies continue to find new seeds even after sampling a very large area. Thus, although a larger sampling area would have probably improved the results of this research, the sampling area of the seed traps is most likely sufficient for the size of the study site. Seed rain usually has high spatial variability and clumped distributions, especially under trees that arboreal mammals and birds use for perches, so random stratified sampling below trees is appropriate for many seed rain studies (Alvarez-Buylla and Martinez-Ramos 1990; Chabrerie and Alard 2005; Costa *et. al.* 2012; Cramer *et. al.* 2007; Drake 1998; Melo et. al. 2006; Stevenson and Vargas 2008). However, bats are also important dispersers for some local plant families (*Piperaceae*) and since bats defecate in flight, they could potentially disperse seeds in open pastures or areas of the plots without dense canopy (Haber *et. al.* 2000). Thus, seed traps were set up in the permanent monitoring plots using simple random sampling to measure the seed density, size, richness, and diversity of the seed rain in each plot. Many tree species in the Monteverde Pacific slope flower and produce fruit in the dry season, so this seed rain assessment was conducted in the dry season (Haber *et. al.* 2000).

3.2.2.3 Identification and classification

There were few resources readily available to help with identification of tropical seeds, especially local Monteverde plant species, so this was the most challenging part of the research project. Originally, I planned to identify the seeds collected in the seed traps by taking them to a local scientific institute that had an extensive collection of local seed species. However, I found out in the course of the research that this seed collection that had been so painstakingly identified and assembled had actually been discarded (Zuchowski, pers.comm.). This made it significantly more difficult to identify the seeds, especially since technical dichotomous keys were not readily available. The CEC's land steward was able to identify all the seed species collected except one, but he knew the local common names rather than the scientific names. Although several plant identification books (Haber et. al. 2000; Zuchowski 2005) and Costa Rica's INBio (2007) have scientific

species names cross-referenced with common names, I was not able to find the common names in any of these resources and thus was not able to determine the scientific names for the seed species. However, some seed species could be identified by checking the nearby vegetation for fruit and seeds. Furthermore, since I was able to distinguish the seed species, I was able to calculate composite biodiversity indices without knowing the scientific names. I used the same methodology of conservatively counting plant families with the unknown seed species as I did with the unknown plant species.

Seeds dispersed in animal droppings were recorded separately from seeds falling from overhead trees and wind-dispersed seeds. This sample design accounts for endozoochory and synzoochory, as most animal dispersers typically perch when they regurgitate or defecate seeds. However, this design did not account for epizoochory, so this research excludes that form of dispersion.

3.2.3 Statistical power

Initially, I attempted to calculate power of the monitoring design to detect true differences in tree and total plant species richness, abundance, evenness, and biodiversity indices between the Inga and Mixed plots. However, this requires assumptions about the population parameters, which in this case were the mean and standard deviation of the Inga and Mixed plots. Since the initial monitoring design had a small vegetation sample size, I could not assume that the initial monitoring results yielded accurate estimates of the population parameters. In summary, both the population parameters and the minimum effect size were not known, so the a priori power calculations were not possible. Therefore, the ability of the experimental design to correctly confirm valid differences in vegetation diversity and seed rain diversity between the Inga and Mixed plots is not known.

CEU eTD Collection

3.2.4 Formal interview

A semi-structured interview was conducted with the director of Fundacion Conservacionista Costarricense (Costa Rican Conservation Foundation) to explore questions relating to reforestation and monitoring trends in the greater Monteverde region. This relates to the overall research goal of trying to identify which reforestation strategy is most effective. The director of this nonprofit organization has been involved extensively with several conservation programs in the Monteverde area. I knew that the director also manages several native tree nurseries for reforestation efforts in the region and that seedlings from her nurseries were planted at the CEC. Thus, the director of Fundacion Conservacionista Costarricense had detailed, first-hand knowledge of the quantity of species planted and their range limits and was considered to be a key informant for exploring these topics.

Chapter 4: Results and analysis

4.1 Seedling and vegetation recruitment

4.1.1 Combined total vegetation data

Vegetation data from each quadrat were compiled for each plot and averaged to compare the differences between Inga and Mixed plots as well as the variability between plots from the same category (Inga or Mixed). Vegetation data from the five Inga plots were compiled to show the cumulative Inga plant biodiversity data, and the same was calculated with data from the five Mixed plots. Total vegetation includes trees (seedlings and saplings), shrubs, grasses, and other herbaceous vegetation.

The cumulative species and family richness for Inga plots and Mixed plots is shown below in Figure 6, along with the mean species and family richness. Figure 6 shows that Inga plots had a higher mean species and family richness than Mixed plots.



Figure 6 Cumulative and mean plant species and family richness for Inga and Mixed plots. Error bars show standard deviation.

Although species richness is the most frequently used and perhaps the most intuitive biodiversity indicator, it does not account for species evenness or phylogenetic distinctiveness, which is why other measures of biodiversity are also important to consider (Gibbs 2004). For example, Figure 4 indicates that Inga plots have greater species and taxonomic diversity than Mixed plots, but richness alone does not account for the community dominance of a few common species. Thus, the data were converted into other biodiversity indicators, including the Shannon-Weiner Index and the Evenness Index. The cumulative data for the Inga and Mixed plots (see Table 1 below) shows that the Inga plots have higher plant biodiversity than the Mixed plots. The Inga plots have a greater Shannon-Weiner Index, greater Evenness, in addition to the greater species and family richness previously discussed. The total plant abundance in Mixed plots is over three times greater than the total Inga plant abundance, but the Mixed plots are dominated by relatively dense stands of invasive exotic grasses and shrubs, which lowers biodiversity indices for the Mixed plots.

Table 1 Comparison of plant biodiversity indices between Inga and Mixed plots

	Inga	Mixed
Total Abundance	13541	40766
Density (Plants/m ²)	339	1019
Total Species Richness (S)	46	30
Total Family Richness	24	19
Shannon-Weiner Index (H)	1.60	1.04

Evenness (H/In(S)	0.42	0.30

The indices in Table 1 were calculated with the total cumulative data from the five Inga and five Mixed plots rather than the averaged data. Although Table 1 presents the overall differences between the two types of plots, it does not show whether or not the differences are caused by true differences between the plots or just random variability within the Inga and Mixed data. Although confidence intervals would be more useful than p-value rejection-support testing for comparing differences between mean Inga and Mixed data, this research involves small sample sizes and independent samples, therefore certain statistical procedures are not appropriate if underlying assumptions are false (Beaver *et. al.* 2006).

Therefore, student's T-tests were performed in order to test for significant differences in mean species and family richness, evenness, and composite biodiversity indices between the Inga and Mixed plots, assuming small samples, and $\alpha = 0.05$ (two tails). The results of the student t-tests are summarized in Table 2, which shows that all of the t-tests were statistically significant. Therefore, the null hypothesis of no differences between average Inga and Mixed plots can be rejected and the alternative hypothesis can be accepted for richness, evenness, and the composite biodiversity index. The Mixed plots had significantly higher plant abundance and plant density, which is to be expected, given the dense grass and shrub cover in the Mixed plots.

Table 2 Student's T-test for significance between Inga and Mixed plots - all vegetation (* = p<.05; ** = p<.01)

		Plant Abundance	Density (Plants/m ²)	Species Richness (S)	Family Richness	Shannon- Weiner Index (H)	Evenness (H/In(S)
ga	Mean	2708.20	338.53	24.20	16.80	1.85	0.58
lnç	s.d.	3424.25	428.03	3.49	0.84	0.65	0.19
Mixed	Mean	8203.80	1025.48	17.40	12.00	0.92	0.32
	s.d.	1858.18	232.27	1.67	1.87	0.35	0.13
	T- value	-3.15	-3.15	3.93	5.24	2.83	2.48
	df	6.17	6.17	5.74	5.54	6.19	7.15
	Р	0.0190*	0.0190*	0.0084**	0.0025**	0.0289*	0.0413*

4.1.2 Tree (seedling and sapling) data

Although the vegetation data show that the Inga plots have a greater plant biodiversity than Mixed plots, this does not necessarily mean that the plant species identified are associated with restored forest ecosystems. Figure 7 below shows the cumulative and mean tree species and tree family richness for Inga and Mixed plots, with roughly the same trends as in Figure 6. The Inga plots had greater mean and cumulative tree species and family richness, indicating a higher species and taxonomic diversity of recruiting trees (seedlings and saplings).



Figure 7 Cumulative and mean tree (seedling and sapling) species and family richness for Inga and Mixed plots. Error bars show standard deviation.

The cumulative tree species data were also converted into the same composite biodiversity indices used for the total vegetation data and are summarized in Table 3. The Inga plots had over ten times more seedlings than the Mixed plots and therefore a much higher seedling density. Those seedlings that are surviving in the Mixed plots are found in more even proportions than the seedlings in the Inga plots, but there is a very low abundance and richness. Although the Inga plots had greater tree species and family richness, they were also dominated by one species (*Viburnum costaricanum*) and thus had lower composite biodiversity indices, which may indicate that Inga plots have lower tree biodiversity than Mixed plots. However, given the very low tree abundance, density, and species and family richness in the Mixed plots, this does not mean that the Mixed plots have higher seedling recruitment rates or reforestation success.

	Inga	Mixed
Tree Abundance	247.00	19.00
Tree Density (seedlings/m ²)	6.18	0.48
Tree Species Richness (S _t)	20.00	9.00
Tree Family Richness	15.00	8.00
Shannon-Weiner Index (H _t)	1.77	2.09
Evenness (H _t /In(S _t)	0.59	0.95

 Table 3 Comparison of biodiversity indices for tree (seedling and sapling)

 species between Inga and Mixed plots

Table 3 shows that the Inga plots had lower values for the Shannon-Weiner Index and the Evenness Index, but once again the data used to calculate these indices was cumulative and not averaged. The differences between the mean Inga and Mixed plot tree data were tested using the same equations, methodology, and critical values as previously explained for the total vegetation data. Specifically, a student's T-test was performed for tree species and family richness, composite biodiversity indices, tree density, etc. assuming small samples, $\alpha = 0.05$, two tails, and unequal variances.

The composite biodiversity indices did not perform well with the low tree species abundance and richness in the Mixed plots. For example, there were two Mixed plots (plot 6 and 7) with only 'singletons', which are species only represented by one individual. Furthermore, there was one Mixed plot (plot 4) that only had one seedling, so the Shannon-Weiner Index was 0, the species richness was 1, and since ln(1)=0, the Evenness Index was also 0/0. These data were excluded from calculations in order to facilitate statistical and mathematical software processing, but this reduced the degrees of freedom in an already small sample.

The results of the t-tests for differences between means in Inga and Mixed plots are summarized in Table 4. The differences in the Inga and Mixed tree Shannon-Weiner and Evenness index were not statistically significant, so there is insufficient evidence to reject the null hypothesis of no differences between mean plot values. However, the t-test statistics were significant for tree abundance, tree density, and tree species and family richness, so the null hypothesis can be rejected and the alternative hypothesis accepted for these data categories. Although the differences between the mean composite biodiversity and Evenness indices may be due to chance alone, the Inga plots have significantly greater tree abundance, density, species and family richness.

Table	4 Stud	dent's T-test	for signific	ance betw	een Inga a	nd Mixed	plots- tree
specie	es only	[,] (seedlings a	nd saplings	s) (** = <i>p</i> <.0	1; *** = <i>p</i> <.	001)	
		Ŧ		Ŧ	Ŧ	0	-

			. V		/		
		Tree	Density	Tree	Tree	Shannon-	Evenness
		Abundance	(Trees/m ²)	Species	Family	Weiner	(H/In(S)
				Richness	Richness	Index (H)	
				(S)			
ga	Mean	49.40	6.18	8.20	7.60	1.17	0.56
Ĩ	s.d.	18.45	2.31	1.30	1.14	0.70	0.33
Mixed	Mean	3.80	0.48	2.60	2.40	0.67	0.79
	s.d.	2.05	0.26	1.14	0.89	0.52	0.35
	T- value	5.49	5.49	7.23	8.02	1.27	-1.00
	df	4.10	4.10	7.86	7.57	7.39	6.43
	Р	0.0050**	0.0050**	0.0001***	0.0001***	0.2419	0.3551

4.1.3 Combined total vegetation data from a smaller sample size

The CEC's existing plant diversity monitoring program used two permanent quadrats for a total of 20 m^2 vegetation monitored instead of the eight quadrats (80

m² vegetation) that were studied in this research. Surveying a greater area of vegetation can yield more accurate monitoring results but also requires more time. In order to evaluate the effectiveness of the current vegetation monitoring protocols (e.g. surveying two 1-m² quadrats), the data from the two permanent quadrats were calculated separately and compared to the data from all eight quadrats. Figure 8 shows that the mean species and family richness are lower when only using data collected from the two permanent quadrats (which is not surprising, given the smaller sampling area). However, the mean Mixed and the mean two quadrat Mixed family richness have overlapping standard deviations, so the differences in means may not be significant.



Figure 8 Cumulative and mean plant species and family richness for Inga and Mixed plots using total data and data only from the two permanent quadrats. Error bars show standard deviation.

Perhaps more important than the ability of the two quadrats to detect a mean number of plant and family species equal to the larger sample is the ability to detect differences between Inga and Mixed plots. The mean species richness from the smaller samples are similar to each other and their standard deviations overlap, suggesting no real differences between the species richness in Inga and Mixed plots. The family richness from the small sample data shows the same results. Clearly, there are significant differences in species and family richness between Inga and Mixed plots, as presented in Figure 7, Table 2, and Table 4. This demonstrates that the data from the two quadrats is insufficient to detect differences in mean species or family richness between Inga and Mixed plots.

The vegetation data from the small sample (two quadrats per plot) were compiled and calculated into the same biodiversity indices as the total sample data (eight quadrats per plot), and student's T-tests were performed to compare differences between the mean values from Inga and Mixed plot data. The results are summarized in Table 5, which shows that the differences between plant abundance and plant density were statistically significant. This demonstrates that this smaller sample can detect true differences between Inga and Mixed plots for these variables. However, the differences between species richness, family richness, the Shannon-Weiner Index, and species evenness were not statistically significant. This shows that the smaller sampling area is unable to detect real differences in these variables between Inga and Mixed plots.

Table 5 Student's T-test for significance between Inga and Mixed plots - using vegetation data from only two permanent quadrats per plot

		Abundance	Shannon- Weiner (H)	Species Richness (S)	Family Richness	Density (Plants/m ²)	Evenness (H/In(S)
Ø	Mean	719.80	1.13	13.20	10.80	359.90	0.44
ŭ	s.d.	784.79	0.39	2.59	2.77	392.39	0.16
Mixed	Mean	2308.00	0.76	11.20	8.80	1154.00	0.32
	s.d.	721.18	0.48	0.84	1.64	360.59	0.20
	T- value	-3.33	1.32	1.64	1.39	-3.33	1.12
	df	7.94	7.73	4.83	6.50	7.94	7.71
	Р	0.0105	0.2246	0.1632	0.2112	0.0105	0.2947

4.1.3 Tree (seedling and sapling) data from a smaller sample size

Tree data were isolated from the permanent quadrat vegetation data in order to assess the ability of smaller samples to detect differences in tree recruitment between Inga and Mixed plots. Tree species and tree family richness from the small sample data (2 quadrats per plot) and larger sample data (8 quadrats per plot) are shown below in Figure 9. The smaller sample sizes from the permanent quadrats show significantly lower tree species and tree family richness than the larger sample sizes. However, the data from two quadrats were sufficiently able to detect differences between Inga and Mixed plots, although this may be due to the very low tree richness (and abundance) in the Mixed plots.



Figure 9 Mean tree species (seedling and sapling) and family richness for Inga and Mixed plots using all tree data and only tree data from the two permanent quadrats. Error bars show standard deviation.

All of the tree species in the small sample (2 quadrats) of the Mixed plots were singletons, and one individual from one species was found in each plot. This made it impossible to use Evenness Index, since an abundance of 1 results in dividing by 0/0, as discussed previously. Since all four small samples (2 quadrats) of the Mixed plots had only singletons, it was not possible to use these indices, comparing differences in mean values, or perform a Student's T test. However, the tree abundance, species richness, family richness, Shannon-Weiner Index, and tree density were able to be averaged, compared, and Student's T-tests were performed for these variables, as summarized below in Table 6.

Table 6 Student's T-test for significance between Inga and Mixed plots- using tree species (seedlings and saplings) using data from only two permanent quadrats per plot

		Tree Abundance	Shannon- Weiner (H)	Tree Species Richness (S)	Tree Family Richness	Density (Plants/m ²)	Evenness (H/In(S)
	Mean	11.00	1.31	3.60	3.40	6.88	0.88
Inga	s. d.	8.37	0.16	2.07	1.95	3.28	0.05
							NA
	Mean	0.80	0.00	0.80	0.80	0.40	(#DIV/0)
							NA
Mixed	s. d.	0.45	0.00	0.45	0.45	0.22	(#DIV/0)
							NA
	T- value	2.72	18.03	2.95	2.91	4.41	(#DIV/0)
							NA
	df	4.02	4.00	4.37	4.42	4.04	(#DIV/0)
							NA
	Р	0.0525	0.0005**	0.0375*	0.0388*	0.0286*	(#DIV/0)

The differences between the mean tree values using only the two permanent quadrats' data were statistically significant for all variables except tree abundance. However, there were several singletons in the plot data, which can lead to misinterpretation of the results of the calculations and Student's t-test. For example, four of the Mixed plots had only one individual tree, one Mixed plot had no trees, and one Inga plot had no trees. The difference between the mean Shannon-Weiner Index for the Inga and Mixed trees is highly significant, but this is because Mixed plots had an mean value of 0 for the index. When only one individual tree (singleton) is found in a plot, the calculation for the Shannon-Weiner Index is: $-\sum p(x)\ln(p(x)) = -\sum 1 \ln(1) = 0$

Thus, the Student's T-test for differences between mean Mixed and Inga Shannon-Weiner Index scores is significant but simply indicate a lack of sufficient data and are not truly meaningful for interpreting reforestation monitoring results. This result indicates that even using only two quadrats per plot is sufficient to detect significant differences between tree species and tree family richness as well as tree density. However, the results of the T-tests from the smaller samples should be treated with some caution because of the small number of tree seedlings found in the small sample size. This limited tree data can render some of the differences between Inga and Mixed plots. This difficulty with analyzing the tree data is an indication of the limitations involved in only using two quadrats per plot to monitor for vegetation and seedling recruitment.

4.2 Seed trap design and pilot studies

All of the seeds appeared to have been either wind-dispersed or gravity dispersed, as there were no signs of regurgitated or defecated seeds in the seed traps. Some of the seeds were still in pods or encased in protective layers, further indicating that they came from nearby vegetation instead of from animal dispersers. Several grass and herbaceous species were found in the traps, which are usually wind dispersed. I observed clumps of seeds and fruit pulp (Figure 10) on the ground in one of the plots (plot 1), which contained two species (*Eugenia guatemalensis* and *Myrsine coriacea*), but unfortunately this clump did not fall into any of the seed traps. This clump of seeds was most likely regurgitated by a vertebrate, but I was unable to determine whether it was from a bird, arboreal mammal, or terrestrial mammal.



Figure 10 Animal dispersed seeds (*Eugenia guatemalensis* and *Myrsine coriacea*) in plot 1

4.2.1 Seed trap data

The larger seed trap sampling area resulted in a greater species richness and hence biodiversity than previously detected in pilot studies. The cumulative number of seed species and seed family species was larger in Inga plots than Mixed plots, but these differences were small. As illustrated below in Figure 11, the Inga plots only had one more seed species and seed family than the Mixed plots. Although the mean values for seed species and seed family richness was higher in Inga plots than Mixed plots, the standard deviation was high and overlapped. This indicates that any differences in mean seed species and family richness could be due to variability in the data instead of true differences in seed rain between plot types.



Figure 11 Cumulative and mean species and family richness for seeds in Inga and Mixed plots. Error bars show standard deviation.

The cumulative seed data for the Inga and Mixed plots (Table 7) shows that the Inga plots have higher total seed biodiversity than the Mixed plots. The Inga plots have a slightly larger Shannon-Weiner Index, and higher seed species and family richness. The cumulative seed abundance in Mixed plots, however, is over three and a half times greater than the cumulative Inga seed abundance, but the Evenness Index is approximately equal for the two types of plots. This indicates that although the Mixed plots had more total seeds in the seed traps, the seeds were in roughly similar proportions in both types of plots. However, the Evenness Index does not differentiate species compositions between the Mixed and Inga plots, and the seed species were not identical between Inga and Mixed plots. Furthermore, this data is cumulative and not averaged, so it conceals the variability among Inga plots and Mixed plots.

	Inga	Mixed
Seed Abundance	912.00	3428.00
Seed Density (seeds/ m ²)	89.19	334.62
Total Seed Species Richness	8.00	7.00
Total Seed Family Richness	5.00	4.00
Shannon-Weiner (H)	0.48	0.44
Evenness (Shannon) (H/In(S)	0.23	0.23

 Table 7 Comparison of biodiversity indices for seed species between Inga and

 Mixed plots

The differences between the mean Inga and Mixed plot seed data were tested using the same equations, methodology, and critical values as previously explained for the vegetation data. The results of the t-tests for differences between means in Inga and Mixed plots for the seed data are summarized below in Table 8. The mean differences between seed species richness and seed family richness were not significant, which was consistent with the trend shown in Figure 11. All other variables showed significant differences for mean values between Inga and Mixed plots, including the Evenness Index. This shows that the cumulative seed data from Table 7 may conceal variability within the two types of plots and that testing for differences between means is more useful for comparing genuine differences in Inga and Mixed plot data.

Table 8 Student's T-test for significance between Inga and Mixed plots – seeds (* = p<.05; ** = p<.01)

		Abundance	Density (Plants/	Species Richness	Family Richness	Shannon- Weiner	Evenness (H/In(S)
			m²)	(S)		(H)	
		182.40	89.49	4.80	3.40	0.88	0.58
ga	Mean						
luĉ		158.26	78.03	1.48	0.89	0.24	0.17
	s.d.						
_		685.60	335.24	3.60	2.40	0.35	0.30
(ec	Mean						
Αi		326.11	158.98	0.89	0.55	0.20	0.20
	s.d.						
	T-	-3.10	-3.10	1.55	2.13	3.76	2.44
	value						
		5.79	5.82	6.57	6.63	7.73	7.69
	df						
		0.0220*	0.0219*	0.1680	0.0726	0.0059**	0.0420*
	Р						

4.3 Interview results

The director of Fundacion Conservacionista Costarricense (Costa Rican Conservation Foundation) started and manages two main nurseries in the Monteverde region, which produce 74 species from 34 plant families. Her goal is to establish several nurseries down the mountain so that native trees can be donated or planted along the Bellbird Corridor. The demand for seedlings for reforestation has been fairly steady throughout the last decade, but it's only in recent years that the nurseries are finally able to supply enough trees to meet this demand. The total amount of trees produced between the two nurseries fluctuates from year to year; last year her nurseries produced 40,000 trees and this year they produced 26,000 trees. Her nursery has provided 7000 *I. punctata* throughout the region from 1997-2010, and *I. punctata* accounted for 7.7% of all trees produced.

4.3.1 *Inga punctata* was not planted above its range

The interview revealed that none of the trees from her nurseries, including *l. punctata*, were purposefully planted above their range limits because she asks the location where each tree is going to be planted prior to giving out seedlings to people. *I. punctata* grows from 900-1400m in pasture edges and secondary forest and the CEC reforestation plots reach elevations up to 1450m, so this is the upper limit of *I. punctata*, but not really above its range. In terms of the wind damage to some of the trees, she said that tree damage is a natural part of the forest life cycle here, especially because winds can be really intense and can catch branches of the wide canopy trees like *I. punctata* or dama [*Citharexylum costaricense*]. She also mentioned that damage to these trees is probably not because of higher winds at higher elevations, since upper elevations have more intact forest, so the existing vegetation blocks the wind more than in the deforested lower elevations.

According to the director, *I. punctata* actually was not used extensively in the windbreak program and overall it has not been overplanted in reforestation programs throughout the Monteverde region. At the CEC it has been overplanted because it survives well in the old pastures, so the CEC staff liked using this species. Thus, the use of *I. punctata* was not as extensive as I was previously led to believe and more importantly, the species was not planted above its range. However, tubu (*Montanoa guatemalensis*) was planted extensively above its upper elevation range limit (1200m) during the windbreak program of the 1970s. "Tubu was chosen for the windbreak project because it is a strong, fast growing tree that keeps its leaves. People didn't intentionally plant tubu above its range but they didn't know its range limit, and in general tubu is not reproducing by itself above its range, was not

done so intentionally or as part of climate change mitigation strategies, but simply because it survives and grows well.

4.3.2 Community support for conservation in Monteverde

When asked about her thoughts on the motivations for reforestation throughout the region and the potential use of assisted migration as part of reforestation efforts throughout the region, she answered,

"The major reasons for reforestation in the region are: 1. natural love of forests, 2. greater perceived value of trees for sustainable tourism on property or farms, and 3. windbreaks. Overall, nobody wants to try assisted migration because it is too risky and there is too much we don't know about the phenology of the trees. It's a bit presumptuous to think we can know where to move plant communities when we don't what each species needs to survive. For example, we do not know if certain species are limited in their distribution by rain, soil nutrients, temperature, etc., so without this detailed knowledge we cannot accurately know where to move each species. Some species do better at the middle of their elevation range, whereas other species show fewer differences in survival and growth throughout their ranges. If anything, we could put more emphasis on reforesting at the upper ranges of the life zone."

This suggests that communities in the region support conservation and reforestation of forests for intrinsic values, potential sources of income, and soil conservation for farms. Her response also shows that reforestation efforts in the region are not attempting assisted range shifts because there are still many species and ecosystem interactions that are poorly understood. In addition, her response

indicates that researching tree species survival and seed dispersal at the end of their range could provide useful information for conservation and reforestation programs.

She advised that regional reforestation monitoring programs should define their objectives prior to data collection and try to balance "data quality, time management, and quality management". Thus, monitoring programs need to maximize their financial, time, and human resources to obtain the highest quality data possible for the given inputs. For community based monitoring programs, Debra stated, "It is important to know if the overall goal is to take accurate data or if the goal is to involve students in monitoring and conservation. A lot of work goes into programs that work with people, and these programs need to be well thought out in terms of feasibility and organization." Thus, even when monitoring programs are based on volunteer data, they still require human and financial resources to coordinate and organize volunteers, and it is crucial to know what the monitoring goals are from the beginning.

4.3.3 Montoring in the greater Monteverde region

She has also monitored the tree species in different reforestation treatments on her own properties, and hopefully over time the results will show which strategy works the best. The tree species chosen for reforestation monitoring should depend on the life zone and elevation of the site, and the overall proportion should be roughly representative of the families and species replanted, which hopefully match the proportion of families and species found in nature. The monitoring plots are set up, trees are tagged or marked, staked, and the survival and growth rate data are collected. One of the important areas of reforestation research for the nurseries is to determine "the minimum investment of maintenance for the maximum regrowth."

and others do not. The monitoring results for survivorship are used to adjust the amount or percentage of a given species that is planted. The nurseries try to match the percentage of reforested plant families with what is found naturally in the forests, so if a certain species has low survivorship, they will start to plant higher percentages of it.

Comparing the differences in survival and growth rates between reforested areas and areas that were just allowed to regenerate naturally is important information for the nursery. As she described,

"The best way to regenerate forest is to fence off an area because the Monteverde area has good seed banks, good soil, and when we reforest areas we are only trying to speed up the process of succession. There have not been studies on nucleation, but nucleation depends on which tree species can compete and survive in the pasture grasses. Guajava [*Psidium guajava*] survives and competes with the grasses, and initially I thought it would be good to have the shade and canopy structure from these trees, but we have noticed that no other tree species can grow underneath guajavas. It's in the same family as *Eucalyptus*, so maybe it produces toxins or oils that inhibit growth of other seedlings. Soil, erosion, and slope also make a difference in the survival of reforested stands."

Thus, one of the biggest barriers to natural regeneration is competition with invasive exotic pasture grasses, such as African star grass (*C. nlemfuensis*), although microhabitat factors are also important. This indicates that biotic interactions are often more important determinants of seedling survival at reforestation sites than abiotic factors. This also shows that the nucleation reforestation theory has not been explicitly tested throughout the reforested areas but implies that it is only valid when

species can overcome these biotic interactions. Her statement underscores the importance of monitoring the reforested areas because sometimes the initial assumptions are incorrect, such as with the effect of guajavas on other seedlings.

Chapter 5: Discussion

5.1 Vegetation biodiversity sampling

Overall, the Mixed plots had a significantly greater plant density and abundance and a lower species richness, taxonomic diversity (family richness), evenness, and biodiversity indices than the Inga plots. When the seedling data were analyzed separately from the total plant data, the Inga plots had significantly greater tree abundance, density, species richness, and taxonomic diversity (family richness) but the biodiversity indices and evenness were not significantly different between Inga and Mixed plots. This is because Inga plots had much more seedlings than Mixed plots, but they were mostly dominated by a few tree species. Furthermore, the biodiversity indices do not perform well with singletons, so the low seedling richness and abundance in the Mixed plots influenced the outcome of the t-tests for these parameters. This shows that after almost 10 years from the initial reforestation (2004-2005), the Mixed plots still lack the vegetation diversity and structure of forest and have few seedlings.

The goal of reforestation is to have a forest similar in biodiversity composition, structure, and ecosystem processes to reference sites. Although this research did not include reference sites, it is obvious (see Figures 12) that Inga plots more closely resemble forest than the Mixed plots in terms of vegetation structure, canopy development, and seedling recruitment. Thus, perhaps the Inga plots have a better short-term reforestation success than Mixed plots, but there is a strong chance that over time the Inga forest could be dominated by a few tree species.



Figure 12 Reforestation plots with students measuring vegetation structure. The first image is a Mixed plot; note the lack of canopy cover and the tall grasses and shrubs. The second image is an Inga plot; note the developed canopy structure and the large number of recruiting seedlings.

5.1.1 Difficulties in plant identification

When the species were identified, I discovered that two species I had coded differently (Unknown O and Unknown BB) were actually the same species (Elephantopus mollis). In addition, some species were very similar in morphology to other species and grow together in the same habitat, so some of the plants I identified as one species were actually more than one species. For example, Fleischmannia pycnocephala [family: Compositae (Asteraceae)] is very similar in appearance to Ageratum conyzoides [family: Compositae (Asteraceae)], so some of the plants I identified as F. pycnocephala may have been A. conyzoides. I was not aware of this similarity until after the two local botanists helped me with the identification. Similiarly, Hydrocotyle sp. [family Araliaceae] may have been mistaken for Centella asiatica [family: Apiaceae], and Tripogandra serrulata [family: Commelinaceae] may have been misidentified as Oplismenus burmannii [family: Poaceae]. Some of these species are related at least at the family level (e.g. F. pyconocephala and A. conyzoides), but several species were not closely related and it is impossible to know which species was present in the field, as most likely both of them were. This highlights the difficulties in identifying vegetation without access to a technical key, especially for species not flowering or producing fruit. However, none of these species were seedlings, which was the primary reason for the vegetation identification. Since this research sample design includes a much greater overall sampling area (80m²) than the initial monitoring program (20m²), it is possible that new species were encountered that were not identified in previous years.

5.1.2 Limitations of using only two quadrats

The two quadrats were able to detect statistically significant differences in some biodiversity indices, plant abundance, and plant density but were unable to detect significant differences between species richness, family richness, the Shannon-Weiner Index, and species evenness. This shows that the smaller sampling area had a mixed performance for detecting real differences in these variables between Inga and Mixed plots. When the data from the two quadrats was separated into tree data, the results of Student's t-tests became less meaningful because the seedling richness and abundance were low in both types of plots, especially in the Mixed plots. This difficulty with analyzing the tree data from the small sample indicates that using only two quadrats in the existing monitoring program is insufficient for true differences in biodiversity indices for tree (seedling and sapling) data. Thus, the CEC's reforestation monitoring program may benefit from changing the vegetation identification monitoring protocols, depending on the program goals.

5.1.3 Conclusions

Although the vegetation data show that the Inga plots have a greater plant biodiversity than Mixed plots, this does not mean that the plant species identified are associated with restored forest ecosystems. Biodiversity indices do not distinguish early successional species or invasive species from secondary forest species, so only continued monitoring will show if the community composition of the reforested plots begins to resemble the adjacent secondary forests. For example, there were many fruiting *Viburnum costaricanum* trees in the nearby secondary forests, which most likely explains the large abundance of *Viburnum costaricanum* seedlings in the

Inga plots. This may eventually result in community dominance by this species, but many of the seedlings were quite small and may not survive to become adult trees. Therefore, only continued long-term monitoring will show trends in succession in the reforestation plots.

5.2 Seed rain

The process of designing the seed rain sampling protocol and re-evaluating the minimum vegetation sampling area for the plots has highlighted the complexities involved in designing monitoring protocols that allow for rigorous data collection yet are balanced with needs for environmental education.

5.2.1 Difficulties in seed identification: problems with detectability

The interview with the director of Fundacion Conservacionista Costarricense resulted in the recommendation to ask for seed identification help from a local nature tour guide who has extensive experience identifying seeds. I was able to contact this scientist and although he did not have time to help identify the seeds, he was able to point out a significant flaw in my sample design: the 'detectability' of the seeds in the seed traps. I had unintentionally assumed that the seeds would be small but visible with the naked eye, especially because the few resources for tropical seed identification that I managed to find were related to plant species with larger seeds (Vozzo 2010). Most of the seeds I found on the ground on the CEC campus and other nearby forests were larger than 1-2mm, and I did not find any seeds on the bottom of the buckets and boxes. Furthermore, local plant guides frequently describe fruit but not seeds and experimental research on local seed species often involved plant species with larger seeds (Haber *et. al.* 2000; Townsend 2011; Wenny 2000a; Wenny 2000b; Zamora 1993; Zamora *et. al.* 2004;

Zuchowski 2005). However, this seed scientist informed me that over 80% of the seeds in the area are so small that they need to be identified with a microscope under high (~100X) magnification. Apparently, this applies to many of the tree species as well epiphytes, hemiepiphytes, ferns, grasses, etc., especially in disturbed areas like the study site.

Although the CEC does have microscopes, they are several years old and not meant for professional laboratory research, as they are meant for primary and secondary students. Even if powerful microscopes were available and I had had sufficient time to search every cm² of the 20.40 m² seed trap cloth for seeds, I would still not have been able to identify the seeds without a technical dichotomous key for local seeds, which I was not able to obtain, or weeks of assistance from a seed biologist, which was not realistic for this project's time frame and budget. Thus, the seed trap data refer only to larger seeds (1-2mm or larger) that I was able to observe visually in the traps, which may only represent 20% of the seeds that actually fell in the plots, according to the local scientist. Unfortunately, I was only informed of this serious limitation in my sample design after all other data had been collected and when I was trying to find the scientific names of the seeds previously identified by common names. Given more time, laboratory space, dichotomous keys, and a powerful microscope, I would have tried to search the seed traps more thoroughly for smaller seed species.

It was also especially frustrating to discover the that extensive seed collection I thought was housed in one of the local scientific institutes had actually been discarded, since I had been hoping to use the collection for identifying seeds to species level. Although the CEC's land steward knew the common names of most seeds, most of the names were not cross-listed with any plants in the INBio website

or in the local tree field guide (Haber *et. al.* 2000). Since the scientific names of most seeds were unknown, the seed species found in the plots could not be compared to the vegetation recruiting in the plots as originally intended, so this part of the research questions remains unanswered.

5.2.2 Dispersal mechanism

Originally, I wanted to compare bird seed rain with bat seed rain, but I have since realized that subsampling the seed traps in the mornings or evenings would very likely yield no detectable seed rain at all, since even after almost two weeks most of the seed traps were dominated by one wind-dispersed species (*V. arborescens*). Birds are the most important animal seed dispersers in the Monteverde region, although arboreal mammals and bats are also important dispersers (Haber et. al. 2000). Furthermore, terrestrial mammalian seed rain could also be very important for secondary seed dispersal, especially given the high numbers of agoutis on the campus (Wenny 2000a&b). All the seeds collected in the seed traps appeared to have been gravity dispersed or wind dispersed, since there were no signs of animal dispersed (e.g. regurgitated or defecated) seeds. However, the difficulties in detecting common small seeds means that no conclusions can be made about the ability of the seed traps to sample the small seeds that animals disperse.

5.2.3 Conclusions

Designing an appropriate seed rain sampling protocol and methodology has been an enlightening experience combining information gathered from literature review and the process of trial and error, as tailoring seed trap sampling design to the local conditions was much more complicated than originally anticipated.

CEU eTD Collection

Although one of the original research goals was to compare the seedling data to the seed rain, the inability to detect and identify small seeds severely limits the inferences that can be made about the composition of the seed rain. This is especially problematic if the majority of the seed rain is composed of these small seeds. Therefore, the seed rain was not compared to the recruiting vegetation or analyzed for seed size, and this part of the vegetation research question is unanswered.

The seed trap data showed no significant differences in the species richness and phylogenetic distinctiveness (family richness) between the Mixed plots and Inga plots, but these results must be treated with caution given the limited detectability of the seeds and the inability to identify all seeds found in the traps. The seed trap data showed significant differences in mean seed density and biodiversity between Inga and Mixed plots because *V. arborescens* dominated most of the seed traps in Mixed plots. Based on this limited data, no inferences can be made about the true seed species richness, diversity, or dispersal mechanism of the majority of the seeds, since most of the seeds were most likely not detected.

5.3 Interview

At the outset of this research project, I was under the impression that the *I. puncata* species in the CEC reforestation plots were planted above their natural range, but this interview and subsequent research revealed otherwise. Thus, the use of *I. punctata* was not as extensive as I was previously led to believe and more importantly, the species was not planted above its range. This changed the whole dynamic of the way I had been thinking about the reforestation strategies at the CEC because I had thought of *I. punctata* as an exotic but noninvasive species from lower down the mountain. This also shows the importance of regional context because the

CEU eTD Collection

species had only been overplanted at the CEC and not in the greater Monteverde region.

Furthermore, the interview revealed that reforestation may not always be able to speed up the rate of natural succession, especially because many abandoned pastures exhibit strong interspecific plant competition, leading to arrested succession. This is evident in most of the Mixed plots, especially those further away from remnant forest fragments, such as plot 6 and 7. It is important to note that these permanent monitoring plots are no longer maintained (e.g. no grass cutting) as they were when they were initially reforested. In addition, it takes many years of monitoring data to determine whether or not reforestation has been more effective than natural succession. Thus, the interview with Debra yielded a wealth of information relevant to the reforestation and monitoring at the CEC and in the wider context of the Monteverde region.
Chapter 6 Recommendations for the CEC Monitoring Program

6.1 Managing monitoring data

One of the most important improvements the CEC could make for its monitoring program would be to set up a digital database for managing all the monitoring data, monitoring protocols, and photos of the plots and plants. The monitoring data is currently kept in several separate files with different formatting and it is difficult for the management to interpret the results of the monitoring. Organizing and managing the data is especially important to maintain continuity of the monitoring program and to illustrate long-term trends. Furthermore, new teachers may not be familiar with the monitoring goals, data, or protocols, so compiling all the data and media in one central database would be very helpful for teachers as well as the management. An excellent idea presented by the CEC management was to build an information center presenting the results of the reforestation and monitoring and perhaps housing plant specimens. Thus, physical and digital information databases would greatly improve the utility of the monitoring program by making it more accessible and streamlined.

6.2 Expanding monitoring in the curricula

The CEC's reforestation monitoring program has dual goals of detecting changes in reforestation success over time while providing an opportunity for environmental education, and monitoring protocols should ideally meet both of these goals sufficiently. The student monitoring program provides excellent opportunities for the 10th grade students to learn about succession and the outcome of different

reforestation strategies. Furthermore, students hone their vegetation identification, mathematical, and analytical skills when they measure vegetation structure, ground cover, and diameter at breast height (DBH). The CEC could further its environmental education goals by including more grade levels in the monitoring program and by involving the students in more of the calculations, thus incorporating monitoring into more than one subject. Independent student research projects should be encouraged and fostered, since this would involve them in conservation and allow them to learn the scientific method first-hand. Hence, there are several options for the CEC to expand the role of this reforestation monitoring program into their curricula.

6.3 Increasing sample size and creating reference plots

The permanent monitoring plots and permanent quadrats are also meant to detect changes and differences in reforestation success over time and inform the monitoring program about which reforestation strategy works better. In order to fulfill this goal, the sampling design should be statistically rigorous enough to detect valid differences between Inga and Mixed plots despite inherent variability within the data. This is especially important given the fact that the plots are each unique sites that have potential differences in aspect, slope, soil type, etc. and that some natural variability within plots is to be expected. Therefore, in future years it may be prudent to include more quadrats within each plot. Furthermore, it would be very informative if the CEC set up monitoring plots in former pasture areas that have not been reforested since the school's inception. There are several small patches like this along the trails on campus, and setting up five permanent monitoring plots in these areas would serve as a control to compare the effectiveness of reforestation and simply "fencing off" land, as Debra discussed. Furthermore, including five more

permanent monitoring plots would increase the total number of treatments and would facilitate the use of other statistical methods, such as Curtis-Bray ordination, Chi square tests, etc. by serving as reference sites.

6.4 Include another component of ecosystem processes

Seed dispersal is an important ecosystem process for reforestation, but the existing sampling design is apparently unable to detect the vast majority of seeds. Therefore, incorporating seed rain monitoring does not seem to be a feasible future component of the CEC's long-term student monitoring program unless specific large seeded tree species are chosen for monitoring. Unfortunately, this means that the current monitoring protocols only measure two out of three monitoring categories (e.g. vegetation structure and diversity) but not ecosystem processes. Seed dispersal, plant competition, nutrient cycling, and other biotic interactions are all important ecosystem processes. Perhaps future research at the school could be focused on finding a feasible way to measure one or several of these ecosystem processes to evaluate restoration success.

6.5 Change the student vegetation identification protocols

Although the vegetation identification is important for informing the monitoring program about which species are recruiting, it is extremely difficult to identify every species even within a quadrat. Furthermore, the several plant identification books that are readily available (Haber *et. al.* 2000; Zamora 1993; Zamora *et. al.* 2004; Zuchowski 2005) often do not have full scientific technical dichotomous keys, and I was unable to find a hard copy or an electronic version for the local species. In addition, some tree species change leaf morphology as they grow (e.g. *Hampea appendiculata*). Even if the CEC was able to find such a resource, it would have

been extremely difficult and time consuming to identify all the vegetation and I do not think it is appropriate for high school students. Saplings and seedlings that are not yet producing flowers or fruit are notoriously difficult to identify to species or even family level, and it would not have been able to identify the plants without the generous assistance of the two local botanists. Thus, I think it would be more appropriate to change the student-monitoring program so that the students no longer try to identify seedlings, as it can be time-consuming, frustrating, and could potentially detract from students' appreciation of conservation efforts.

Although it could be argued that it is important for students to learn the local species and that the seedling identification should remain a part the protocols, I would argue that trying to identify seedlings and saplings that are not flowering or fruiting without detailed scientific knowledge available (e.g. assistance from a botanist or dichotomous key) will likely lead to misidentifications. This not only wastes everyone's time, but also is also worse than not identifying any seedlings because students start to memorize and identify species incorrectly. Furthermore, the large amount of people and time spent in the plots trying to identify seedlings also results in a lot of vegetation trampling, which could affect future monitoring data and reforestation efforts by compacting soil, killing vegetation, increasing erosion, and changing the vegetation structure. Students interested in plant identification should learn to identify flowering or fruiting trees or larger saplings in the plots instead of small seedlings (Haber, pers.comm.; and Zuchowski, pers.comm.). Thus, I recommend that the annual student monitoring data consist of ground cover, DBH, tree canopy width, tree height, total seedling abundance, and perhaps identification of larger flowering/ fruiting saplings and trees if possible.

If the CEC does decide to continue the annual seedling vegetation

identification for education purposes, then one possibility to assist identification is to create a collection of pressed dried plant samples for the students to use as an onsite herbarium. However, this would require assistance from a local biologist to identify the initial samples as well as space in a dry, secure location on the campus to store the plant samples. Although I tried to press and preserve some of the samples already identified by the local botanists, the high humidity degraded the specimens. Thus, creating an on-site herbarium to help with the vegetation identification may be difficult given the CEC's resources and the local climate, especially during the rainy season. I photographed many plant species that were later identified, but this does not constitute a fool-proof way to identify the species, since many plant species look similar to each other and technical expertise is needed to distinguish them. Additionally, there may be new species recruiting in the plots that were not identified in this research project, so further help with identification may be necessary anyway.

Costa Rica has the world's highest species richness per unit area, and the species turnover is especially high in the greater Monteverde region, which means that plant identification data for this monitoring program needs to be based on detailed scientific expertise specific to the region (Haber et. al. 2000). Therefore, I recommend the full vegetation identification surveys be conducted once in five years with a professional botanist familiar with species found in abandoned pastures and secondary forests in Monteverde, or at least a researcher with access to a technical dichotomous key for the local vegetation. Five years would be frequent enough to track changes in vegetation composition over time while allowing the plots to recover from the additional trampling inherent in sampling a larger area of the plots (minimum 8 quadrats per plot). This may require the school to obtain technical

dichotomous keys (if they are available) or perhaps more realistically, hire local botanists to complete the monitoring surveys once in five years.

6.6 Conclusion

If the CEC incorporates some or all of these recommendations, then hopefully the data accuracy and environmental education value of this monitoring program will improve and the school will be able to meet both of its monitoring goals better. It is my sincere hope that the information researched and presented in this thesis will be practical and useful for the CEC management and other reforestation monitoring programs in the greater Monteverde region. Monteverde is a truly magical place resplendent in biodiversity, and it needs to be conserved, reforested, monitored, and protected to benefit present and future generations.

References

- Aldrich, M., Billington, C., Edwards, M. and Laidlaw R. A. 1997. Global directory of tropical montane cloud forests Draft. Cambridge: *UNEP-WCMC*.
- Alvarez-Buylla, E. R. and Martinez-Ramos, M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84:314-325.
- Beaver, R. J., Beaver, B. M., and Mendenhall, W. 2006. *Introduction To Probability And Statistics*, 12th ed. Belmont, USA: Thomson Brooks/Cole.
- Benzing, D.H., 1998. Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climatic Change* 39: 519–540.
- Bubb, P., May, I., Miles, L., Sayer, J. 2004 Cloud Forest Agenda. Cambridge: UNEP-WCMC.
- Calvo-Alvarado, J., McLennan, B., Sanchez-Azofeifa, A., and Garvin, T. 2009. Deforestation and forest restoration in Guanacaste, Costa Rica: Putting conservation policies in context. *Forest Ecology and Management* 258: 931– 940.
- Carpenter, F. L., Nichols, J. D., and Sandi, E. 2004. Early growth of native and exotic trees planted on degraded tropical pasture. *Forest Ecology and Management* 196: 367–378.
- Chabrerie, O. and Alard, D. 2005. Comparison of three seed trap types in a chalk grassland: toward a standardized protocol. *Plant Ecology* 176:101-112.
- Corbin, J. D. and Holl, K. D. 2012. Applied nucleation as a forest restoration strategy. *Forest Ecology and Management* 265: 37–46.
- Corrales, L. and Zuñiga, T. 2001. Análisis de Representatividad Ecológica del Corredor Biológico Mesoamericano [Analysis of the ecological representativeness of the Mesoamerican Biological Corridor]. Managua, Nicaragua: Corredor Biológico Mesoamericano (CBM).
- Costa, J. B. P., Melo, F. P. L. de, Santos, B. A., Tabarelli, M. 2012. Reduced availability of large seeds constrains Atlantic forest regeneration. *Acta Oecologica* 39: 61-66.
- Cramer, J. M., Mesquita, R. C. G., Williamson, G. B. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation* 137: 415–423.
- Creative Research Systems 2012. Sample size calculator. http://www.surveysystem.com/sscalc.htm. Accessed March and April 2012.

Cusack, D. and Montagnini, F. 2004. The role of native species plantations in

recovery of understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and Management* 188: 1–15.

- DeClerck, F.A.J., Chazdon, R., Holl, K.D., Milder, J.C., Finegan, B., Martinez-Salinas, A., Imbach, P., Canet, L., Ramos, Z., 2010. Biodiversity conservation in human- modified landscapes of Mesoamerica: Past, present, and future. *Biological Conservation* 14: 2301–2313.
- Doust, S. J., Erskine, P. D., and Lamb, D. 2008. Restoring rainforest species by direct seeding: Tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *Forest Ecology and Management* 256:1178–1188.
- Drake, D. R. 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science* 9: 103-112.
- Farwig, N. and Berens, D.G. 2012. Imagine a world without seed dispersers: A review of threats, consequences and future directions. *Basic and Applied Ecology* 13: 109–115.
- Food and Agricultural Organization (FAO) 2001. *Global Forest Resources* Assessment 2000 (Main Report). Rome: FAO Forestry Paper 140.
- Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55: 73–106.
- Garcia-Orth, X. and Martínez-Ramos, M. 2008. Seed dynamics of early and late successional tree species in tropical abandoned pastures: Seed burial as a way of evading predation. *Restoration Ecology* 16: 435-443.
- Gasner, M. R., Jankowski, J. E., Ciecka, A. L., Kyle, K. O., Rabenold, K. N. 2010. Projecting the local impacts of climate change on a Central American montane avian community. *Biological Conservation* 143: 1250–1258.
- Gibbs, J. 2004. What is Biodiversity? A comparison of spider communities. *Connexions* Updated 13 July 2004. http://cnx.org/content/m12179/1.1/. Accessed 26 February 2012.
- Guswa, A. J., Rhodes, A. L., and Newell, S. E. 2007. Importance of orographic precipitation to the water resources of Monteverde, Costa Rica. *Advances in Water Resources* 30: 2098–2112.
- Haber, W. A., Zuchowski, W., and Bello, E. 2000. *An Introduction to Cloud Forest Trees Monteverde, Costa Rica* 2nd ed. Monteverde de Puntarenas, Costa Rica: Mountain Gem Publications.
- Hall, C.A.S., Hall, M., Aguilar, B., 2000. A brief historical and visual introduction to Costa Rica. In: Hall, C.A.S. (Ed.), *Quantifying Sustainable Development. The Future of Tropical Economies.* San Diego and London: Academic Press 19– 42.

- Harvey, C.A., Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. *Agroforestry Systems* 44: 37-68.
- Herrera, J. C. G. 2003. Mesoamerican Biological Corridor: regional initiative for the promotion of forest conservation. Invited paper at XII World Forestry Congress, Québec City, Canada.
- Hewitt, N., Klenk, N., Smith, A.L., Bazely, D.R., Yan, N., Wood, S., MacLellan, J.I., Lipsig-Mumme, C., and Henriques, I. 2011. Taking stock of the assisted migration debate. *Biological Conservation* 144: 2560–2572.
- Instituto Nacional de Biodiversidad (INBio) [National Biodiversity Institute of Costa Rica]. 2007. Especies de Costa Rica. Nombres comunes [Plant species common name and scientific name search function.] <u>http://darnis.inbio.ac.cr/ubis/FMPro?-DB=Grupos&-lay=W_SubGrupo&-</u> <u>error=norec.html&-Format=comun.html&-Max=30&-SortField=subgrupo&-</u> <u>Op=eq&grupo_id=1&-Find</u>. Accessed March, April, and May 2012.
- Kappelle, M., Avertin, G., Juárez, M. E., and N. Zamora. 2000. Useful Plants within a Campesino Community in a Costa Rican Montane Cloud Forest. *Mountain Research and Development* 20:162-171.
- Keith, S. A., Newton, A. C., Herbert, R. J., Morecroft, M. D., and Bealey, C. E. 2009. Non-analogous community formation in response to climate change. *Journal for Nature Conservation* 17: 228—235
- Koll, K.D., Daily, G.C., Ehrlich, P.R. 1995. Knowledge and perception in Costa Rica. *Conservation Biology* 9: 1548-1558.
- Kuusipalo, J., Goran, A., Jafarsidik, Y., Otsamo, A., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded Imperata cylindrica grassland: understory development in forest plantations. *Journal of Vegetation Science* 6: 205–210.
- Janzen, D. H. 1990. An abandoned field is not a treefall gap. *Vida Silvestre Neotropical* 2: 64-67.
- Leopold, A. C., Andrus, R., Finkeldey, A., Knowles, D. 2001. Attempting restoration of wet tropical forests in Costa Rica. *Forest Ecology and Management* 142: 243-249.
- Lindenmayer, D. B. and Likens, G. E. 2010. The science and application of ecological monitoring. *Biological Conservation* 143: 1317–1328
- Loss, S. R., Terwilliger, L. A., and Peterson, A. C. 2011. Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation* 144: 92–100.

Mattfeldt, S. D., Bailey, L. L., Grant, E. H. C. 2009. Monitoring multiple species:

Estimating state variables and exploring the efficacy of a monitoring program. *Biological Conservation* 142: 720-737.

- Melo, F. P. L. de, Dirzo, R., and Tabarelli, M. 2006. Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. *Biological Conservation* 132: 50– 60.
- Mello, A. J., Townsend, P. A., and Filardo, K. 2010. Reforestation and restoration at the cloud forest school in Monteverde, Costa Rica: learning by doing. *Ecological Restoration* 28:2.
- Miller, K., Chang, E. & Johnson, N. 2001. Defining Common Ground for the Mesoamerican Biological Corridor. Washington, DC: *World Resources Institute (WRI)*.
- Mori, S. and Brown, J. 1998. Epizoochorous dispersal by barbs, hooks, and spines in a lowland moist forest in central French Guiana. *Brittonia* 50 (2): 165-173.
- Myers, N. 1981. The hamburger connection: How Central America's forests become North America's hamburgers. *Ambio* 10:2-8.
- Opdam, P. and Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117: 285–297.
- Pejchar, L., Pringle, R. M., Ranganathan, J., Zook, J. R., Duran, G., Oviedo, F., and Daily, G. C. 2008. Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. *Biological Conservation* 141: 536-544.
- Pounds, A. J., Fogden, M. P. L., and Campbell, J. H. 1999. Biological response to climate change on a tropical mountain. *Nature* 389: 611–614.
- Ray, D. K., Welch, R. M., Lawton, R. O., and Nair, U. S. 2006. Dry season clouds and rainfall in northern Central America: Implications for the Mesoamerican Biological Corridor. *Global and Planetary Change* 54: 150–162.
- Richardson, B. A., Richardson, M. J., Scatena, F. N., and McDowell, W. H. 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology* 16: 167-188.
- Ruiz-Jaen, M. C. and Aide, T. M. 2005a. Restoration Success: How Is It Being Measured? *Restoration Ecology* 13 (3): 569–577.
- Ruiz-Jaen, M. C. and Aide, T. M. 2005b. Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. *Forest Ecology* and Management 218: 159–173.
- Society for Ecological Restoration International Science & Policy Working Group (SER). 2004. The SER International Primer on Ecological Restoration.

www.ser.org & Tucson: Society for Ecological Restoration International.

- Stevenson, P. R. and Vargas, I. N. 2008. Sample size and appropriate design of fruit and seed traps in tropical forests. *Journal of Tropical Ecology* 24: 95-105.
- Sugden, A. M. 1981. Aspects of ecology of vascular epiphytes in two Colombian cloud forests: II. Habitat preferences of Bromeliaceae in the Serrania de Macuira. *Selbyana* 5: 264-273.
- Toledo-Aceves, T., Meave, J. A., González-Espinosa, M., Ramírez-Marcial, N. 2011. Tropical montane cloud forests: Current threats and opportunities for their conservation and sustainable management in Mexico. *Journal of Environmental Management* 92: 974-981.
- Townsend PA. 2011. Conservation and restoration for a changing climate in Monteverde, Costa Rica. Doctoral dissertation, Department of Biology, University of Washington, Seattle, WA.
- Vozzo, J. A., ed. 2010. *Manual de semillas de árboles tropicales* [Seed manual of tropical trees]. *Departamento de Agricultura de los Estados Unidos Servicio Forestal.*
- Wenny, D.G. 2000a. Seed Dispersal of a High Quality Fruit by Specialized Frugivores: High Quality Dispersal? *Biotropica* 32 (2): 327-337.
- Wenny, D.G. 2000b. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. *Ecological Monographs* 70 (2): 331–351.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.
- Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy* of Sciences USA 104: 5738–5742.
- Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forestry Ecology and Management* 99: 223–235.
- Young, B. E. and McDonald, D. B. 2000. Birds. In: *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*, eds. N. M. Nadkarni and N. T. Wheelwright. New York: Oxford University Press.
- Zahawi, R. A., and Augspurger, C. K. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* 31: 540-552.
- Zamora, N. 1993. *Flora arborescente de Costa Rica* [Arborescent flora of Costa Rica]. Cartago, Costa Rica: Editorial Technológica de Costa Rica.

- Zamora, N., Jiménez, Q., and Poveda, L. J. 2004. *Árboles de Costa Rica, Trees of Costa Rica*, 3rd ed. Santo Domingo de Heredia, Costa Rica: Instituto Nacional de Biodiversidad (INBio), Centro Científico Tropical, and Conservación Internacional
- Zuchowski, W. 2005. *A guide to tropical plants of Costa Rica*. Miami: Zona Tropical Publications.

Personal Communications

- Haber, William A. Plant biologist and entomologist; co-author of local tree species book. Identification help and informal interview. Monteverde, April 14, 2012.
- Hamilton, Debra. Director and coordinator of native tree nurseries in the Monteverde region. Formal interview. Santa Elena, Costa Rica, April 19, 2012.
- Martinez, Rolando. Nature guide. April 9, 2012. Identification help and informal interview. CEC, April 6, 2012.
- Solano, Rodrigo. Nature guide and seed identification expert. Telephone communication, May 3, 2012.
- Townsend, Patricia. Researcher and previous CEC monitoring coordinator. Email communication, February-May 2012.
- Zuchowski, Willow. Plant biologist; author and co-author of tree and plant species books. Identification help, email communication, and informal interview. Monteverde, April 14, 2012.

Appendix: Potential Animal Dispersers

Note: bats are also important seed dispersers, but I was unable to photograph any at the CEC.



³ Blue-crowned motmot (Momotus momota) with what appears to be a *Myrsine coriacea* fruit. This species is one of many seed-dispersing animals found on the Cloud Forest School campus.



 ⁴ White-faced capuchin monkey (*Cebus capucinus*)
⁵ Central American agouti (*Dasyprocta punctata*) These are very common on the CEC campus.