

TESTING PREDICTIONS OF ISLAND BIOGEOGRAPHY THEORY IN TROPICAL
PREMONTANE FOREST FRAGMENTS

by

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(Under the Direction of Chris J. Peterson)

ABSTRACT

Habitat fragmentation is a major threat to biodiversity and a prevalent disturbance in tropical premontane forest landscapes, yet fragmentation impacts in premontane forests are poorly understood. To understand plant responses to fragmentation, I examined fragmentation impacts using a traditional conceptual framework, island biogeography theory, along with more recent concepts about fragmentation impacts, edge effects and matrix influences. In my first study, I tested island biogeography theory predictions for herbaceous plant and tree species richness in fragments of varying in size and isolation distance from 1 to 209 hectares, and 0.5 to 6.7km, respectively. Contrary to predictions of the theory, I found that there was no relationship between species richness and fragment size or species richness and isolation distance. Examination of the plant community composition revealed an increase in pioneer tree species in small size classes indicating a possible shift of the forest fragment community to a more successional and less mature forest after fragmentation. In my second study, I address the impact of the surrounding matrix on the microclimate and plant composition from the edge to the forest interior. I observed a narrow edge effect in microclimate and species composition extending 10m into the forest fragment. Within 10m from the edge and into the fragment I

observed more weedy herbaceous species and a greater proportion of pioneer trees, indicating a shift in plant composition near edges as a result of fragmentation. My final study examines fragmentation using a landscape approach to understand the relationship between matrix (landscape) characteristics and plant composition in fragments. I used spatial analysis software to characterize the matrix surrounding the focal fragments of this study. The influence of matrix characteristics and configuration on species composition data was determined using principle components analysis. The landscape was described a patchy landscape made of irregular patches of primary and regenerating forest, pasture and croplands, based on landscape metric analysis. Principle components analysis demonstrated that landscape metrics such as fragment shape and isolation are highly correlated with both tree species diversity and species component, particularly the proportion of pioneer tree species. These studies demonstrate that plant community responses to fragmentation can be better understood in the context of the landscape than by examination of the fragment in isolation.

INDEX WORDS: Biogeography, island biogeography, fragmentation, edge effects, microclimate, matrix, tropical forest, premontane forest;

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DEDICATION

This dissertation is dedicated to my parents and sisters, who though thousands of miles away, were always present through their support and encouragement.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Habitat fragmentation is considered a major threat to biodiversity (Murcia, 1995; Collinge, 1996; Collinge and Forman, 2009; Laurance et al., 2011). Fragmentation describes the breaking up of once continuous habitat into smaller patches (fragments) which are surrounded by a matrix – an area of alternative landuse. Fragmentation impacts can be biotic and abiotic and can affect both the landscape, as a whole, and an individual fragment. Abiotic impacts can be structural, functional and climatic. Structural changes include changes in the landscape configuration, such as size and shape, and changes to the forest architecture within fragments, such as reducing the number of canopy layers (Collinge and Forman, 2009). Functional changes describe the quality of the both the matrix and the fragment, including the availability of resources suitable for forest species such as fruits and nesting habitat (Kupfer et al., 2006). Climatic changes often result in a more open habitat. For example, due to loss of canopy, light levels and temperature of the matrix and within the fragment may increase (Laurance et al., 2002).

Within each fragment, biotic changes include shifts in the suites of species as fragments may lose species that are interior dwellers while species that can utilize the non-forest habitat increase. Fragmentation may lead to the introduction of exotic species into fragments which may also amplify this shift in species composition (With, 2002). Species diversity may also change

after fragmentation. For example, the loss of primates and birds has been reported in forest fragments in Amazonian lowland forests after fragmentation, whereas frog species have increased (Schwarzkopf and Rylands, 1989; Bierregaard et al., 1992; Laurance et al., 2002). For some taxa, including butterflies, the results can be dependent on species characteristics. Post fragmentation, forest interior butterflies decreased in fragments while generalist species increased (Brown and Hutchings, 1997). Biotic changes for plant taxa are also dependent on their life history characteristics such as dispersal mode or shade tolerance. Additionally, plant-animal interactions, for instance pollination, dispersal and predation can alter regeneration and mortality of plant species and may lead to changes in plant community composition.

However, not all fragmentation consequences are as obvious as these demographic changes. Fragments may experience loss of genetic diversity as a result of altered species interaction following fragmentation. Dispersal into isolated fragments as a result of restricted disperser habitat can lead to genetic bottle necks for fragment populations (Aldrich and Hamrick, 1998; Mech and Hallett, 2001).

Efforts to conceptualize the various impacts of patchy or isolated habitats have been underway since the development of species area curve models (Arrhenius, 1921; Gleason, 1922). However, renewed interests in biogeography theory and its implication for conservation occurred with the publication of MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography (ETIB). The ETIB provided researchers with a broad conceptual framework that could be used to study not just ocean islands but habitat islands of all kinds. The theory predicts an increase in species richness as island area increases and island isolation decreases. These changes in species richness are driven by changes in the colonization and extinction rates of islands. Colonization rates decrease on islands experiencing greater isolation while extinction

rates increase in smaller islands. Modifications to the theory have recognized the dependence of extinction rate on isolation as well as area as small island populations can be rescued by colonization from nearby sources (Brown and Kodric-Brown, 1977). The theory also predicts an increase in turnovers due to local extinction of small populations in small islands.

Predictions of island biogeography theory when interpreted in the context of conservation biology argue for the protection of large reserves or at least smaller reserves with considerable connectivity. This idea was heatedly disputed in the SLOSS (Single Large Or Several Small Reserves) debate (Diamond, 1975; May, 1975; Terborgh, 1976; Simberloff and Abele, 1982). However, the debate had limited direct influence on conservation practice as fragmentation results in a mosaic of smaller habitat patches which are restricted to less favorable locations on the landscape, such as steep slopes (Saunders et al., 1991; Vitousek et al., 1997).

Island biogeography theory, despite being a useful stepping stone towards understanding fragmentation, has limitations. The theory does not account for characteristics of the matrix, which the theory treats as an inhospitable background throughout which hospitable patches are interspersed. However, the matrix is now recognized as being heterogeneous. Variations in disturbance, edge effects and differences in matrix suitability as a habitat or for movement of certain taxa have been shown to drive processes within forest patches (Saunders et al., 1991; Laurance et al., 2011). The theory also considers the fragment itself to be a homogenous suitable habitat which may not be the case in fragments experiencing influences of the matrix near edges.

IBT is neutral and therefore does not take into consideration the differences among functional groups or species occupying islands (Bush and Whittaker, 1993). However, compositional differences have been reported in newly colonized of islands (Bush and Whittaker, 1991) and in fragments after isolation (Nascimento, 2006).

To address the limitations of island biogeography theory, new approaches have been pursued to study fragmentation. Edge effects and matrix impact have been very informative for understanding species responses to fragmentation. Species differ in their niches and interactions and may respond differently to the quality and extent of the matrix (Ricketts, 2001; Tabarelli et al., 2004).

At the forest-matrix boundary, abiotic conditions from the matrix may encroach into the forest fragment for a considerable distance, creating an edge which varies distinctly from the interior. As a result, the core area of suitable habitat for forest-interior specialists may be reduced. Changes in temperature, water availability, and light levels can affect regeneration near the forest edge (Nascimento et al., 2006). Forest interior animals also avoid the use of edges, effectively diminishing the habitat and resources available to their populations (Ewers and Didham, 2007). The extent of the edge influences varies greatly among abiotic factors. For example, changes in microclimate 50m into the interior and wind disturbances to 300m have been reported in lowland tropical forest fragments (Kapos, 1989; Laurance et al., 2002).

Matrix impacts extend beyond abiotic edge effects. Species viability in and mobility through the matrix may be equally important for fragment diversity and community composition. The quality of the matrix may determine whether it poses a barrier to the movement of pollinators and seed dispersers and affects plant regeneration and genetic diversity (Gascon et al., 1999; Ricketts, 2001). Thus, the presence of fragments in the landscape may increase the connectivity of the matrix.

This dissertation examines premontane tropical fragments in the vicinity of the Las Cruces Biological Station, Coto Brus canton, in southern Costa Rica. These premontane landscapes have been cleared over the last half century at a very rapid rate for agriculture

including cattle pasture and coffee production. Cattle pastures composed primarily of disturbance adapted grass species are drastically different from the original forest in both vegetation and microclimate. Cattle pastures also experience constant disturbance by grazing and soils compaction by cattle. Coffee is an important crop in premontane landscapes, particularly in Costa Rica. Other crops such as caña de india (*Costus guanaiensis*), sugar cane (*Saccharum officinarum*) and vegetable crops are also under cultivation in these landscapes.

Forest fragments are part of the countryside landscapes that dominate much of the tropics (Daily, 2001), particularly at mid-elevations. These landscapes are composed of a mosaic of forest fragments, croplands, pasture and developed areas. Fragments may serve as the key component in maintaining biodiversity (Daily et al., 2003) and ecosystem services such as pollination and carbon sequestration (Brosi et al., 2008). As a result these regions are currently being identified for conservation. For example, corridors are proposed and underway to connect the Las Cruces reserve to the Guyamí reserve, a 7000 hectare forest approximately 6km away. The creation of corridors can be facilitated by including smaller fragments already in the landscape as part of corridors, reducing the need for extensive restoration projects. Thus, it is important to understand fragment properties in order to identify suitable fragments for conservation measures. This dissertation is focused on understanding plant responses to fragmentation in these premontane fragments. I employ three approaches, an island biogeography theory framework, investigation of local edge effects and a landscape analysis of matrix influence.

In chapter 2, I address whether island biogeography theory can be used as a model for plant species response to fragmentation. Specifically, I examine species area and species

isolation relationships. I also determine the impact of fragmentation on plant community composition.

The research in chapter 3 examines fragmentation influences on a very local scale. I examine microclimate conditions within a 120m transect from the surrounding pasture into the forest. Air temperature, relative humidity (vapor pressure deficit) and canopy openness are measured along this transect to establish the microclimatic gradient. I also measure the distance that edge effects penetrate into the forest interior and the response of plants along that gradient.

The edge effect and other responses to fragmentation can be influenced by the surrounding landuse. Therefore, in chapter 4 I address how the surrounding matrix affects plant richness, diversity and composition. I conduct a landscape analysis using geographic information systems and spatial analysis software to characterize the matrix. Additionally, I examine the impact of these matrix characters on plant community composition.

The intent of this research is to develop a more thorough understanding of fragmentation impacts on plant biodiversity through the application of different conceptual frameworks. Furthermore, the findings of this research can be applied to conservation efforts in fragmented landscapes.

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CHAPTER 2

ISLAND BIOGEOGRAPHY THEORY AS A PREDICTOR OF SPECIES DIVERSITY IN TROPICAL PREMONTANE FOREST FRAGMENTS¹

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ABSTRACT

Forest fragmentation is prevalent in tropical landscapes where once continuous forests now persist as isolated patches in a matrix of other land use such as pasture and croplands. The Equilibrium Theory of Island Biogeography provides a conceptual framework within which the effects of fragmentation can be examined. Specifically, the theory predicts an increase in the number of species with increasing area and decreasing isolation distance of the island. We tested these predictions in fragmented premontane tropical landscapes in southern Costa Rica which have been fragmented for approximately 50 years. We measured diversity of trees and herbaceous plants in fragments of varying sizes from 1- 209 hectares in area. We did not find a significant positive relationship between species richness and fragment area or species richness and isolation distance for either tree or herbaceous species. Additionally, observed patterns of dominance were similar among fragments, again suggesting no effect of island size or isolation on community structure. Our results indicate that fragment area is a poor predictor of species diversity of premontane Costa Rican forest after 50 years of fragmentation. This may be a result of prolonged relaxation time, the time taken for species to regain equilibrium after disturbance. Our results have implications for the role of small fragments in conservation practices. Small fragments may serve as refugia of species diversity for a considerable time after disturbance and harbor individuals which could provide propagules for reforestation. Small fragments may also serve as stepping stones for dispersers which could maintain connectivity among fragments. Long relaxation times may also serve as a buffer period during which conservation measures can be implemented to mitigate biodiversity loss.

INTRODUCTION

Naturally fragmented habitats occur in many landscapes due to natural disturbances such as wind and fire. Over the last 6000 years, deforestation and habitat fragmentation by human activities in temperate regions, such as Europe has been well documented (Williams, 2006). However, over the past half-century, forest fragmentation in the tropics has accelerated and poses a major threat to tropical biodiversity (Skole and Tucker, 1993; Whitmore, 1997; Sanchez-Azofeifa et al., 2001). Forest fragmentation describes a landscape change from continuous forest cover to a mosaic consisting of isolated forest patches surrounded by non-forest land use such as pasture or crop lands. Responses of plants and animals to forest fragmentation often have been explained in the context of island biogeography theory (MacArthur and Wilson, 1967b).

Island biogeography theory predicts a positive relationship between island area and species richness, and a negative relationship between species richness and island isolation (distance from the nearest mainland or continuous forest). Such patterns stem from the trend that smaller islands can support small populations of species which may be more vulnerable to extinction. Thus, smaller islands are expected to have higher extinction rates compared to large islands. Isolated islands are more difficult to reach and would therefore have lower immigration rates compared to near islands. These changes in immigration and extinction rates would result in lower species richness in small isolated islands.

Based on the equilibrium theory of island biogeography, we expect fragments to show decreasing species richness in response to decreasing size (area) and increasing isolation. Disproportionate loss of rare (or low frequency) species may lead to dominance by a few species in fragmented forests compared to low abundance of most species that is typical of continuous tropical forest (Benítez-Malvido and Martinez-Ramos, 2003a). Thus relative abundances of

species in fragments may be more uneven than in continuous forest. Such changes in species abundance and distribution have been reported as early as ten to twenty years after fragmentation (Laurance et al., 1998; Gascon 2000; Laurance et al., 2000).

Several of the above patterns have been reported in low elevation forests such as those of the central Amazon. The Biological Dynamics of Forest Fragment Project, a well studied fragmented system in central Amazonia, has documented a decline in species richness of many taxa in smaller and more isolated fragments compared to continuous forest (Bierregaard et al., 1992), including mammals (Schwarzkopf and Rylands, 1989), insects (Powell and Powell, 1987), insectivorous birds (Stouffer and Bierregaard, 1995a), and palms (Scariot, 1999). For plant taxa, species richness has been shown to decrease and tree mortality increase in forest fragments (Benítez-Malvido and Martinez-Ramos, 2003; Laurance et al., 2006).

However, not all species in lowland forests are negatively impacted by fragmentation. In Amazonian forests, some butterfly species showed no change in species richness, but butterfly populations in fragments showed more variability over time (Leidner et al., 2010). Hummingbird (Stouffer and Bierregaard, 1995b) and liana (Laurance et al., 2001) species richness has been reported to increase with fragmentation as they inhabit the forest/matrix edge created by fragmentation.

Patterns observed in lowland forest may not generalize to higher elevation forests. For example, loss of species richness within small or more isolated fragments is not always observed in montane environments (1500m in elevation). Fragment size and isolation had little effect on species richness while edge effects influenced species richness and diversity in the Chiapas Highland of Mexico (Cayuela et al., 2006) . In Costa Rican cloud forest, research has focused on the change in plant composition and structure after fragmentation. For example, increased

abundance pioneer and gap tree seedlings and saplings were found near fragment edges (Oosterhoorn and Kappelle, 2000). This shift in plant composition near the fragment edge may result from a gradual loss of mature species due to expansion of the fragment by colonization of pioneer nears at or near the fragment edge (Sizer and Tanner, 1999; Gascon et al., 2000). Alternatively, the fragment edge may recede due to increased mortality of mature trees near the edge, and subsequent colonization of pioneers (Gascon et al 2000, Laurance et al 2006a, Laurance et al 2006b).

Despite widespread deforestation and fragmentation in mid-elevation forests, few studies have examined fragmentation impacts on plant diversity in mid elevation forests. It is unclear whether plant communities in these landscapes respond to fragmentation similar to low elevation or montane forests. We test the predictions of island biogeography in Costa Rican mid-elevation landscapes. Specifically, by examining the species richness and diversity of herbaceous and woody plant species in fragments of varying sizes and degree of isolation. We also examine other measures of plant diversity, such as community similarity and composition, which may change in response to fragmentation but are not accounted for by island biogeography theory.

METHODS

Study Sites

This study was conducted in the premontane region on the Pacific slope of Costa Rica: the vicinity of the Las Cruces Biological Station in southern Costa Rica. The Las Cruces Biological Station is located within the canton of Coto Brus near the Panama border about 6km south of the town of San Vito (8°47'N, 82°57'9W). The elevation in this region ranges from 1000 to 1500 m. Forests in the study area are classified as premontane wet forest (Holdridge et

al., 1971). The climate of the region is slightly seasonal with average annual precipitation of 3820 mm, most of which falls between the months of April and November. Average annual temperature is 20.7°C with a mean diurnal temperature from 13-26° C. Extensive clearing for cattle pasture in the 1950s and 1960s has left a predominantly agricultural landscape with scattered forest remnants (Juarez, 1994). Current forest cover is estimated at 27% (Daily et al., 2001).

Sampling design

Eight fragments ranging from 1 to 209 hectares located within an area with a 7km radius in the Las Cruces region were included in this study. Herbaceous species were sampled in six fragments and tree species sampled in seven fragments (Table 1). Three 20m x 20m randomly located plots were surveyed during the months of June-August of 2006, 2008 and 2010. Within each plot, the number and abundance of all herbaceous plants and trees greater than 10cm in diameter at breast height were recorded. Specimens were identified to recognizable taxonomic units (RTU) - family and genus, and species when possible (Mayfield & Daily, 2005). We will use the term 'species' to mean RTU unless otherwise indicated. We recorded the number of individuals of each species and measured the diameter at breast height of the trees. Tree species were assigned to small (<20cm DBH), medium (20 – 40cm DBH) and large (> 40cm DBH) diameter size classes. Trees were also classified according to their life history patterns as pioneer, intermediate or mature-forest species. Vouchers were submitted to Las Cruces Biological Station Herbarium.

Analytical Procedures

We determined species richness by constructing species-individual accumulation curves using EstimateS 8.2.0 biodiversity estimation program (Colwell, 2010). We also used jackknife-2, a nonparametric incidence-based coverage estimator of the EstimateS program, to generate true species richness (Colwell and Coddington, 1994; Colwell, 2010). Species diversity (Simpson's Reciprocal Diversity Index $1/D$ where $D = \sum n(n-1)/N(n-1)$, n = the total number of individuals of a species and N = the total number of individuals of all species) was also determined for each fragment. Fragment area (the fragment size, not the area sampled) and species richness were log-transformed and regression analysis was used to determine the relationship between species richness and area. We estimated community similarity, the proportion of species shared between site pairs, using Jaccard's coefficient of similarity. Jaccard's Index is calculated as $CJ = c / (a + b + c)$, where c is the number of species common to both communities and a and b are the number of species occurring only in communities A and B, respectively. Communities that are entirely similar in floristic composition have a Jaccard's index of 1, while communities with no overlapping species have an index of 0 (Magurran, 2004). To determine factors that contribute to community similarity, including fragment size ratios, proximity and elevational difference between fragments, we used multiple regression (SAS Institute Inc., 2001). To determine community structure, we constructed rank abundance plots for species within each fragment. Analyses of covariance were used to compare species proportions for life history and diameter size classes with area and distance as covariates. Differences among diameter size classes for pioneer and mature-forest species were then tested using G-tests.

RESULTS

Diversity

In the Las Cruces fragments, 150 herbaceous recognizable taxonomic units (RTUs) from 18 families and 187 tree RTUs from 33 families were collected. Trees of the Clusiaceae, Euphorbiaceae, Melastomataceae and Moraceae were most abundant in the Las Cruces region fragments (Table 2a). The most abundant herbaceous families were the Araceae, Arecaceae, Cyclanthaceae and Marantaceae (Table 2b). Species diversity was high among fragments as indicated by Simpson's Diversity Index ranging from 11.0-35.1 and 26.8-62.7, for Las Cruces herbs and trees respectively.

Species – Area and Species-Isolation Relationships

Regression analysis showed a non-significant positive relationship between species richness and fragment size for both herbaceous or tree species ($r^2=0.12$, $p = 0.5003$ and $r^2=0.16$, $p=0.3774$, respectively (Figure 2). No significant relationship was detected between species richness and isolation distance for either herb or tree species ($r^2=0.11$, $p=0.5226$ and $r^2=0.03$, $p=0.7257$).

Species Distributions

All fragments had similar species relative abundances. A few species were relatively common, but most species were represented by one or a few individuals (Figure 3).

Community Similarity

Similarity among fragments was low. Jaccard's indices for herbaceous species ranged from 0.12 to 0.343, indicating that even the most similar fragments shared only about a third of their species. Similarity among tree species was slightly higher ranging from 0.045-0.391; however, less than 40% of the species were shared between fragments. Elevational similarity explained approximately 12 % and 18% of the variation in herbaceous and tree species community similarity, respectively (Figure 4b, d). However, proximity and fragment size similarity did not explain the patterns of community similarity.

Pioneer and Mature-Forest Species

Tree species were classified by life history as pioneer or mature forest species (Table 3). No relationship was observed between proportion of pioneer or mature-forest tree species in small (<20cm in diameter at breast height), medium (20- <40cm) or large (\geq 40cm) trees and fragment area (analysis of covariance, $p= 0.3680$) or distance (analysis of covariance, $p= 0.2705$). A greater proportion of pioneer species were found in small size classes compared to large size classes while, more mature-forest species were represented by larger trees (>40cm in diameter) than as small or medium trees (G-tests, $p=0.0023$).

DISCUSSION

Our results demonstrate that the area-richness and isolation-richness relationships predicted by island biogeography theory were not supported for herbaceous or tree species in this Costa Rican premontane landscape. Species richness was similar among all fragments, even small and isolated fragments. Thus, in the Las Cruces region, mid-elevation plant diversity

patterns are more similar to patterns observed in fragments in montane (Oosterhoorn and Kappelle, 2000; Cayuela et al., 2006) than to low elevation landscapes (Laurance et al., 2011). This absence of a significant positive relationship between fragment size or isolation and species richness has been observed for other taxa that are tolerant of, or adapted to, disturbances like fragmentation. For example, small mammals which are able to find suitable habitat in fragments have maintained species richness in fragments of various sizes after fragmentation (Malcolm, 1997). In the Las Cruces region, Schlaepfer and Gavin (2001) did not find an effect of fragment area or distance, but observed temporal and edge effects on frog and lizard distribution. Research on the impact of edge effects on plant diversity can illustrate whether similar patterns are observed for herbaceous and tree species.

The degree of fragmentation in the surrounding landscape may also influence species richness in fragments. Some researchers propose a threshold of deforestation in a landscape above which fragment size and isolation become important (Andren, 1994; Fahrig, 1998). For birds and mammals, Andren (1994) estimated significant loss of species and changes in population sizes due to fragmentation in habitats with 30% or less of their original forest cover. For plant species, the threshold may be even lower. Arroyo et al (2009) found significant species area relationships in a landscape with only 4 % forested land cover while fragment area was not an important predictor of diversity in landscapes with 11% and 24% forest cover. With approximately 27% of its original forest cover, fragments in the Las Cruces area may not be sufficiently isolated to disrupt dispersal and colonization events that limit species richness and affect species composition (Arroyo-Rodriguez and Mandujano, 2006). In fragmented landscapes, as well as continuous forests, medium to long distance events by bats, birds, monkeys and other animal dispersers can account for approximately half or more of seedling or sapling

establishment dispersal among fragments (Hardesty et al., 2006; Hanson et al., 2007; Fuchs and Hamrick, 2010). In the Las Cruces region, pedigree analysis of a mature-forest tree *Symphonia globulifera* demonstrated that dispersal responses to fragmentation may be complex. Long distance seed dispersal into forest fragments was observed for *S. globulifera* species, but only a few pasture trees contributed to these dispersal events (Aldrich and Hamrick, 1998).

We observed high plant diversity in all fragments regardless of fragment size. Thus, even small patches can be reservoirs of high plant diversity. The apparent stability of species richness and diversity after fragmentation we observed for plant species has been reported for other taxa in the Las Cruces area. For example, Daily et al. (2001) estimated a loss of fewer than 10% of bird species in the area, while Brosi et al (2008) reported that bee communities in the Las Cruces area remain diverse after fragmentation, though there were changes in the community composition. High species diversity in small patches has also been reported for trees and shrubs in fragmented landscapes (dos Santos et al., 2007; Arroyo-Rodriguez et al., 2009), insects (Benedick et al., 2006; Brosi et al., 2008) and birds (Fischer and Lindenmayer, 2002). Despite this diversity, most species occurred in only 1 or 2 fragments indicating the importance of conservation on a landscape scale, suggesting that preservation of high levels of biodiversity can be possible through protection of several smaller fragments with complementary species composition. Thus our study demonstrates the importance of examining species composition as well as richness. We note that the equilibrium theory of island biogeography does not take into account community composition and when the theory is applied to fragmented landscapes, important differences among fragments may be overlooked.

Maintenance of high post-fragmentation diversity indicates a long relaxation period for plant communities in pre-montane landscapes. The relaxation effect (Brown, 1971; Diamond,

1972) describes the decline in species richness due to local extinction in patches due to habitat isolation. Fifty years after fragmentation, small fragments showed similar plant diversity to large areas of forest. Much of the research on community relaxation after fragmentation has focused on birds (Brooks et al., 1999; Ferraz et al., 2003) and has shown rapid decline in bird populations 50 years after fragmentation. Few studies have focused on plants (Leach and Givnish, 1996). The slow decline in species diversity in plant communities may be due to the life span of plants or to recolonization events among fragments (Brown and Kodric-Brown, 1977; Turner and Corlett, 1996). We do see some evidence of a change in species composition in Las Cruces fragments with time. The larger proportion of pioneer species in small trees may indicate a change in the future tree community. Further examination of tree turnover can confirm these observations.

Forest fragments can act as sources for natural recolonization and restoration of adjacent landscapes (Janzen, 1988; Turner and Corlett, 1996). Birds, bats and other seed dispersal agents may move among fragments or between fragments and larger tracts of forest, and in doing so may disperse seeds into the surrounding matrix (Galindo-González and Sosa, 2003; Sekercioglu et al., 2007). Dispersal and recolonization events have been supported by pedigree and spatial genetic analyses of seeds and seedlings (Céspedes et al., 2003; Hardesty et al., 2006). Animal seed dispersers and pollinators may also facilitate gene flow among distant individuals or populations using isolated trees in the matrix as stepping stones (Fuchs and Hamrick, 2011). Dispersers that can persist in or favor fragment edges such as some monkeys (Chaves et al., 2010) and small mammals (Malcolm, 1997) can also disperse seeds into the matrix. These dispersal events can result in recolonization of the matrix, provided that the matrix abiotic environment does not prohibit germination or establishment. Restoration efforts by land managers and researchers may also utilize fragments to provide seeds or seedlings for

reforestation. Fragments in the vicinity of reforestation projects can provide easy access to propagules reducing the labor or transportation efforts for reforestation. Locally adapted propagules from nearby fragments may have higher survival rates, given that there is sufficient genetic diversity to prevent inbreeding depression (McKay et al., 2005).

Our study is one of the few to examine responses of both tree and herbaceous species to fragmentation. Our results demonstrate that post-fragmentation, forest fragments can maintain diverse plant communities for several decades. Small fragments can serve as sources of propagules for reforestation and recolonization of the adjacent matrix, thus providing a temporal buffer during which conservation efforts can be undertaken. Conservation of small forest patches in fragmented landscapes can be important to preserving plant diversity in mid-elevation tropical landscapes.

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Table 2.1a Characteristics of fragments in which tree species were sampled.

Fragment	Area (ha)	Distance (km) from Las Cruces fragment	Species Richness	Simpson's Diversity
2	4	0.5	32	26.8
3	16	0.5	39	50.3
4	19	6.7	22	59.5
5	20	1.4	13	42.8
6	27	4.9	33	59.9
7	33	1.5	26	61.8
8	209	0.0	55	62.7

Table 2.1b Characteristics of fragments in which herbaceous species were sampled.

Fragment	Area (ha)	Distance (km) from Las Cruces fragment	Species Richness	Simpson's Diversity
1	1	1.5	36	11.0
2	4	0.5	38	31.8
3	16	0.5	34	25.0
4	19	6.7	30	28.9
6	27	4.9	37	18.9
7	33	1.5	35	35.1

Table 2.2a. Most common tree species in forest fragment in the vicinity of the Las Cruces Biological Station, Coto Brus canton, Costa Rica

Species	Family	Individuals per 0.1 hectare	Life History
<i>Pseudolmedia mollis</i>	Moraceae	16.7	Mature-forest species
<i>Alchornea latifolia</i>	Euphorbiaceae	16.7	Pioneer
<i>Guarea bullata</i>	Meliaceae	14.2	Mature-forest species
<i>Alchornea glandulosa</i>	Euphorbiaceae	14.2	Pioneer
<i>Dsyrovomita paniculata</i>	Clusiaceae	13.3	Mature-forest species
<i>Conostegia icosandra</i>	Melastomataceae	13.3	Mature-forest species

Table 2.2b. Most common herbaceous species in forest fragment in the vicinity of the Las Cruces Biological Station, Coto Brus canton, Costa Rica

Species	Family	Stems per 0.1 hectare
<i>Asplundia isabelina</i>	Cyclanthaceae	38.0
<i>Pavonia schiedeana</i>	Malvaceae	35.8
<i>Chamaedorea sp.</i>	Arecaceae	29.2
<i>Geonoma sp.</i>	Arecaceae	22.1
<i>Cyclanthus bipartitus</i>	Cyclanthaceae	21.3
<i>Peperomia lancifolioideae</i>	Piperaceae	20.3

Table 2.3. Life history for common tree species in the Las Cruces region

Life History	
Pioneer	Mature Forest Species
<i>Alchornea glandulosa</i>	<i>Calophyllum brasiliensis</i>
<i>Allophylus psilospermus</i>	<i>Dendropanax sessiliflorus</i>
<i>Cecropia obtusifolia</i>	<i>Dstovomita paniculata</i>
<i>Cecropia peltata</i>	<i>Ficus tonduzii</i>
<i>Hampea appendiculata</i>	<i>Guarea bullata</i>
<i>Inga punctata</i>	<i>Guarea montana</i>
<i>Jacaratia dolichaula</i>	<i>Lacistema aggregatum</i>
<i>Miconia trinervia</i>	<i>Ocotea sp. 1</i>
<i>Mollinedia viridiflora</i>	<i>Otoba novogranatensis</i>
<i>Piper arboreum</i>	<i>Pseudolmedia mollis</i>

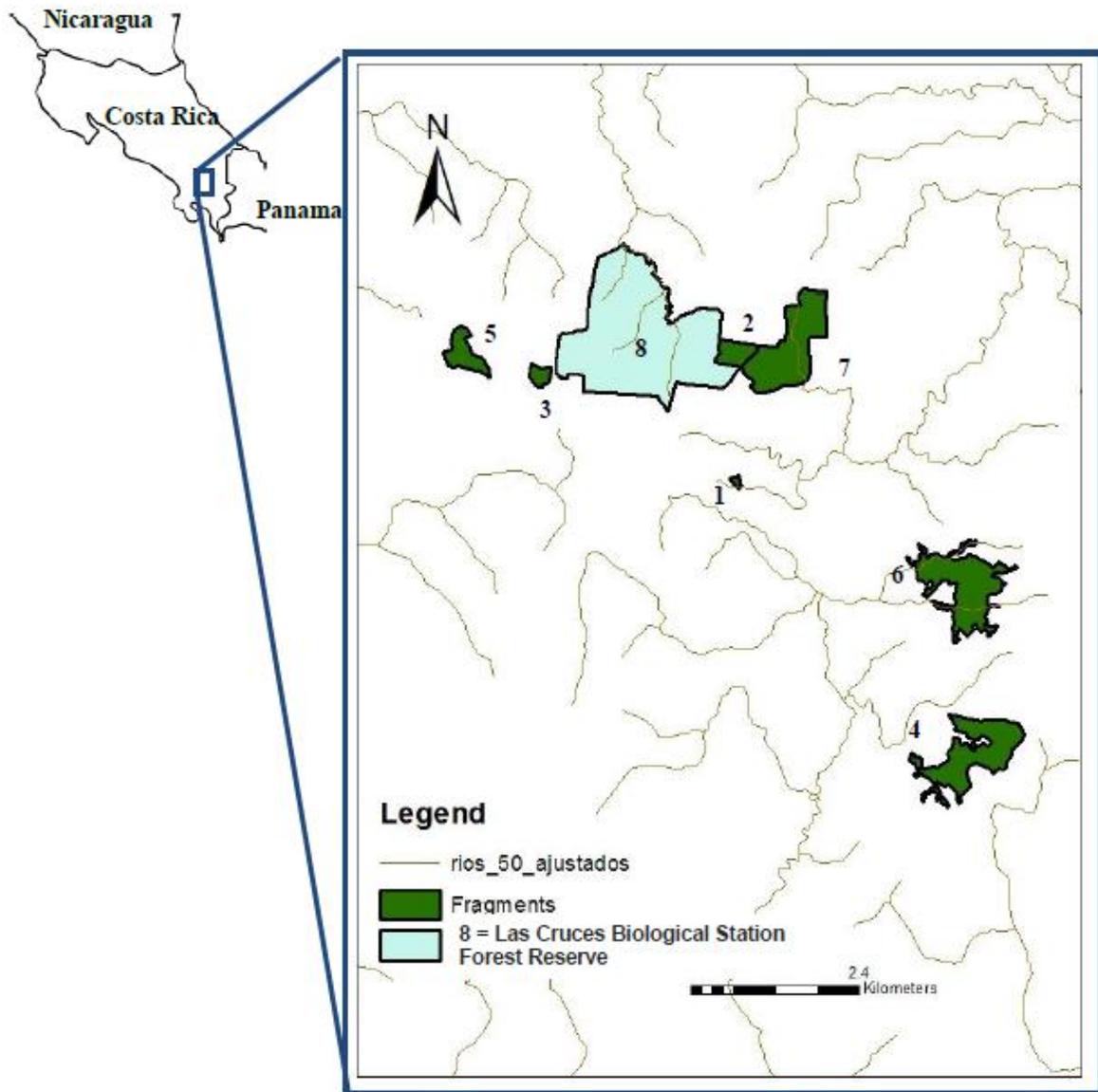


Figure 2.1. Map of fragments in the vicinity of Las Cruces Biological Station, Coto Brus, Costa Rica. LCSBS=Las Cruces Biological Station 209ha fragment

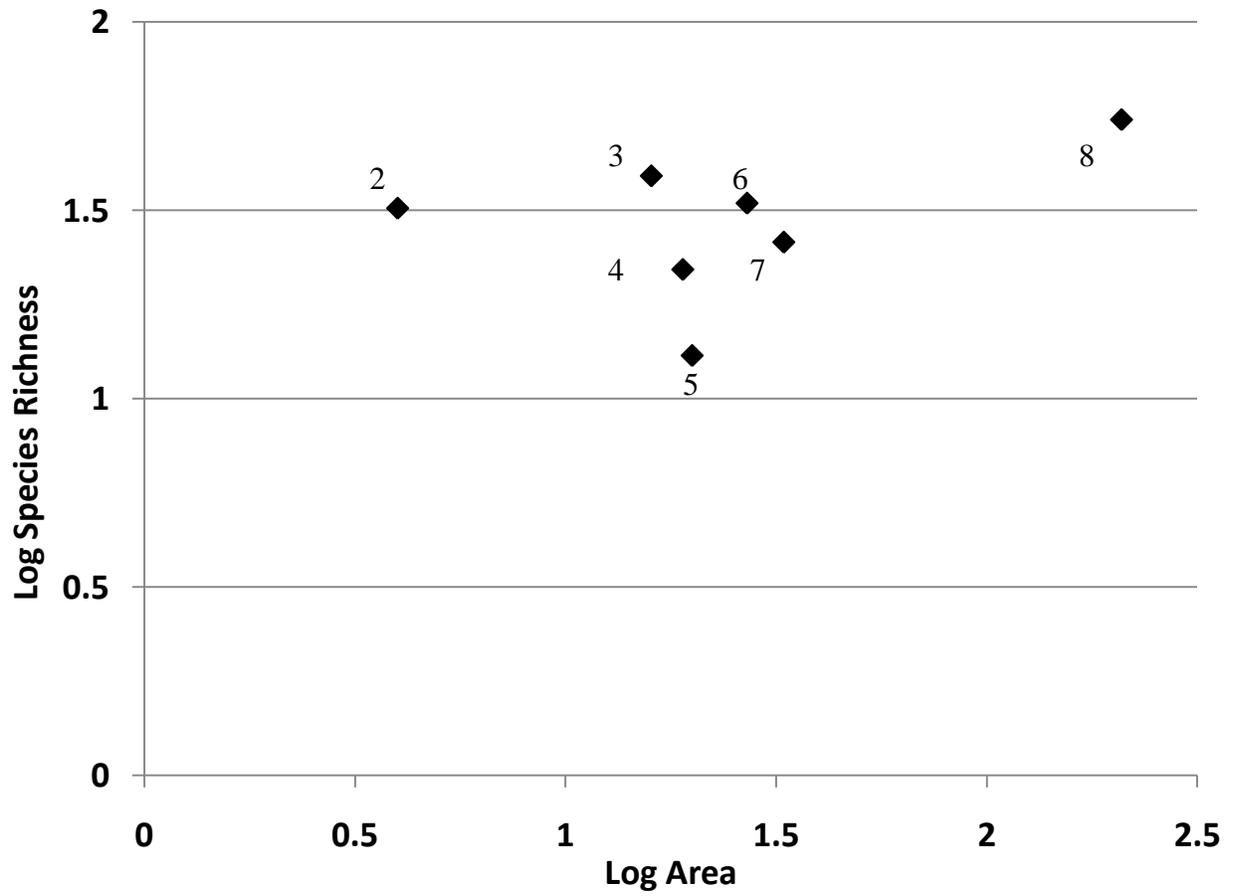


Figure 2.2a. Regression of log of species richness against log of fragment area (size) curve for tree species in Las Cruces Fragments. ($r^2=0.16$, $p = 0.3774$)

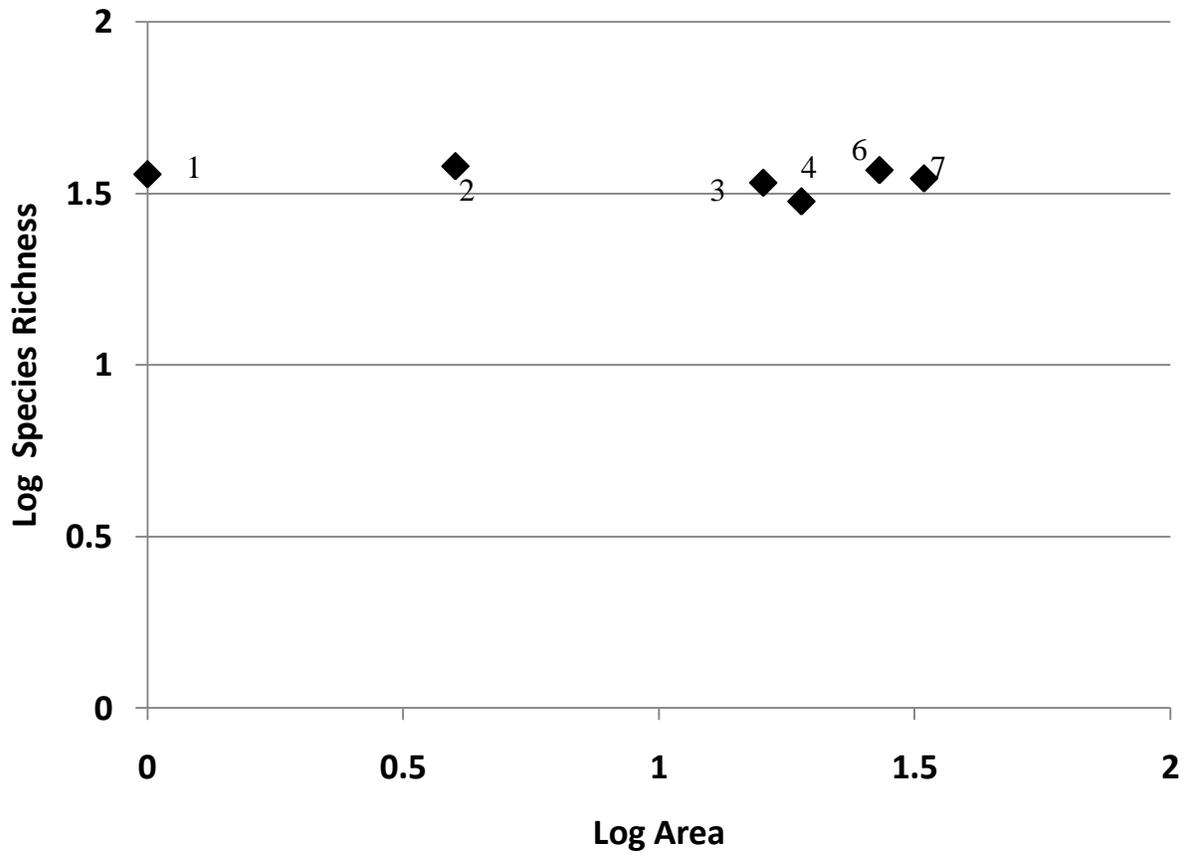


Figure 2.2b. Regression of log of species richness against log of fragment area (size) curve for herbaceous species in Las Cruces fragments ($r^2=0.12$, $p = 0.5003$)

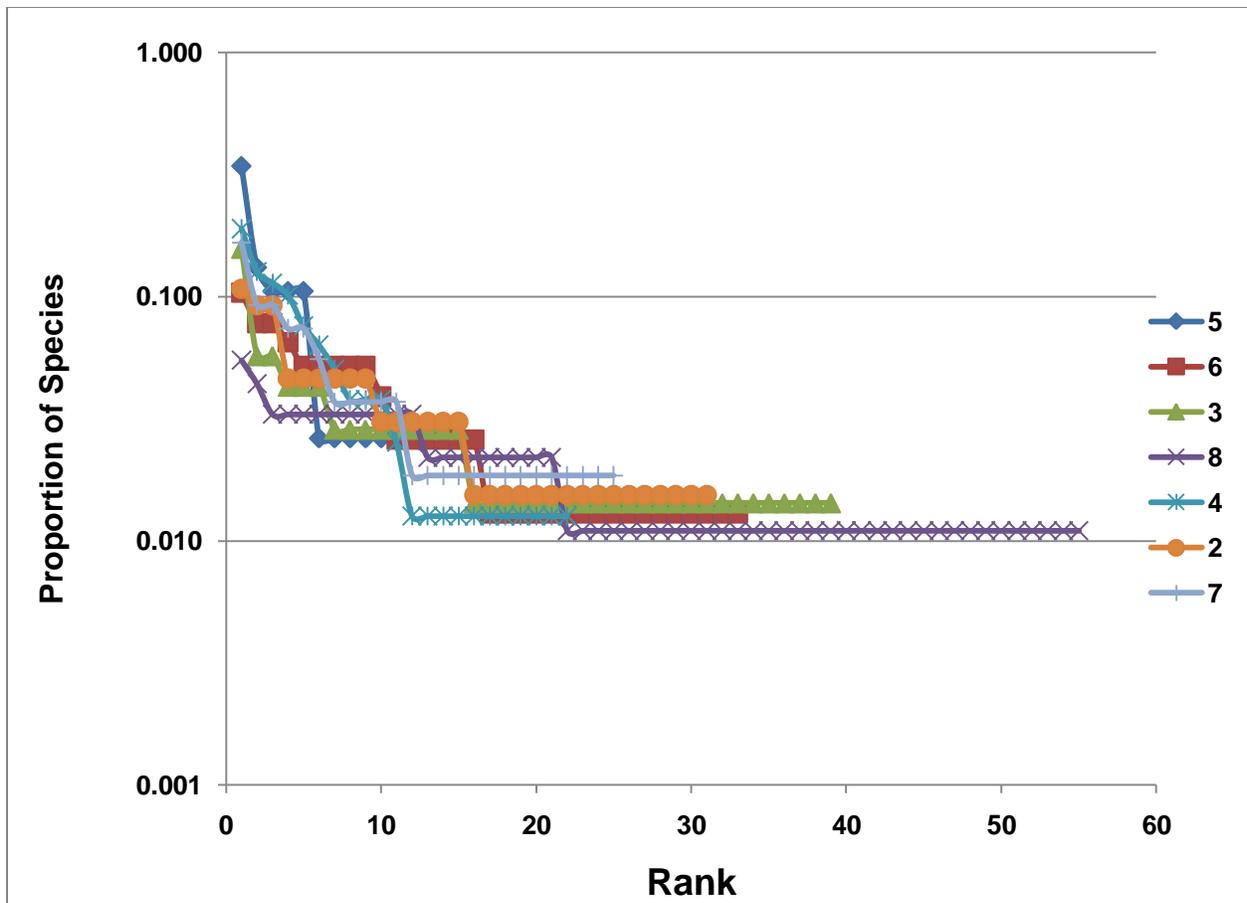


Figure 2.3a. Rank abundance curve for tree species in Las Cruces fragments

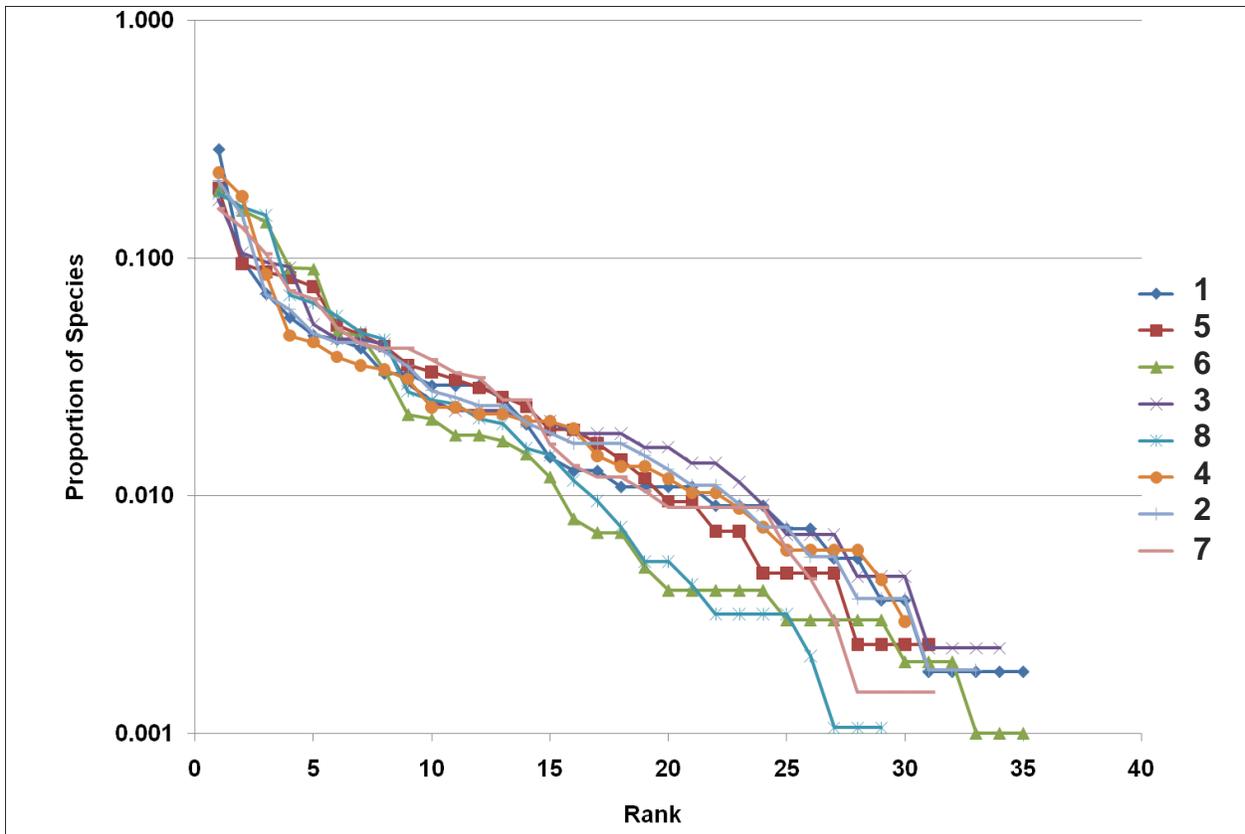


Figure 2.3b. Rank abundance curve for herbaceous species in Las Cruces fragments

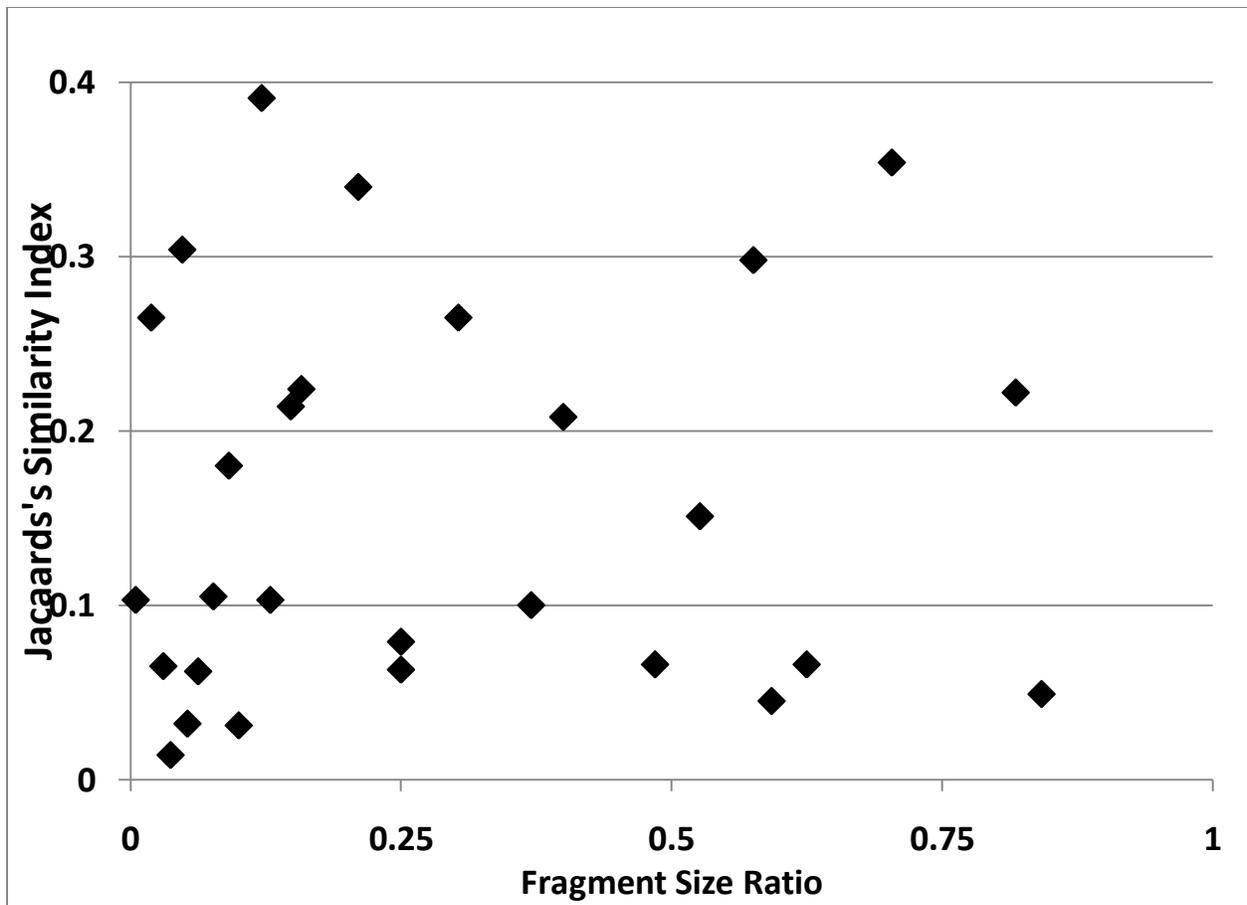


Figure 2.4a. Fragment size ratio regressed against community similarity for herb species.

($r^2=0.004$, $p= 0.4667$)

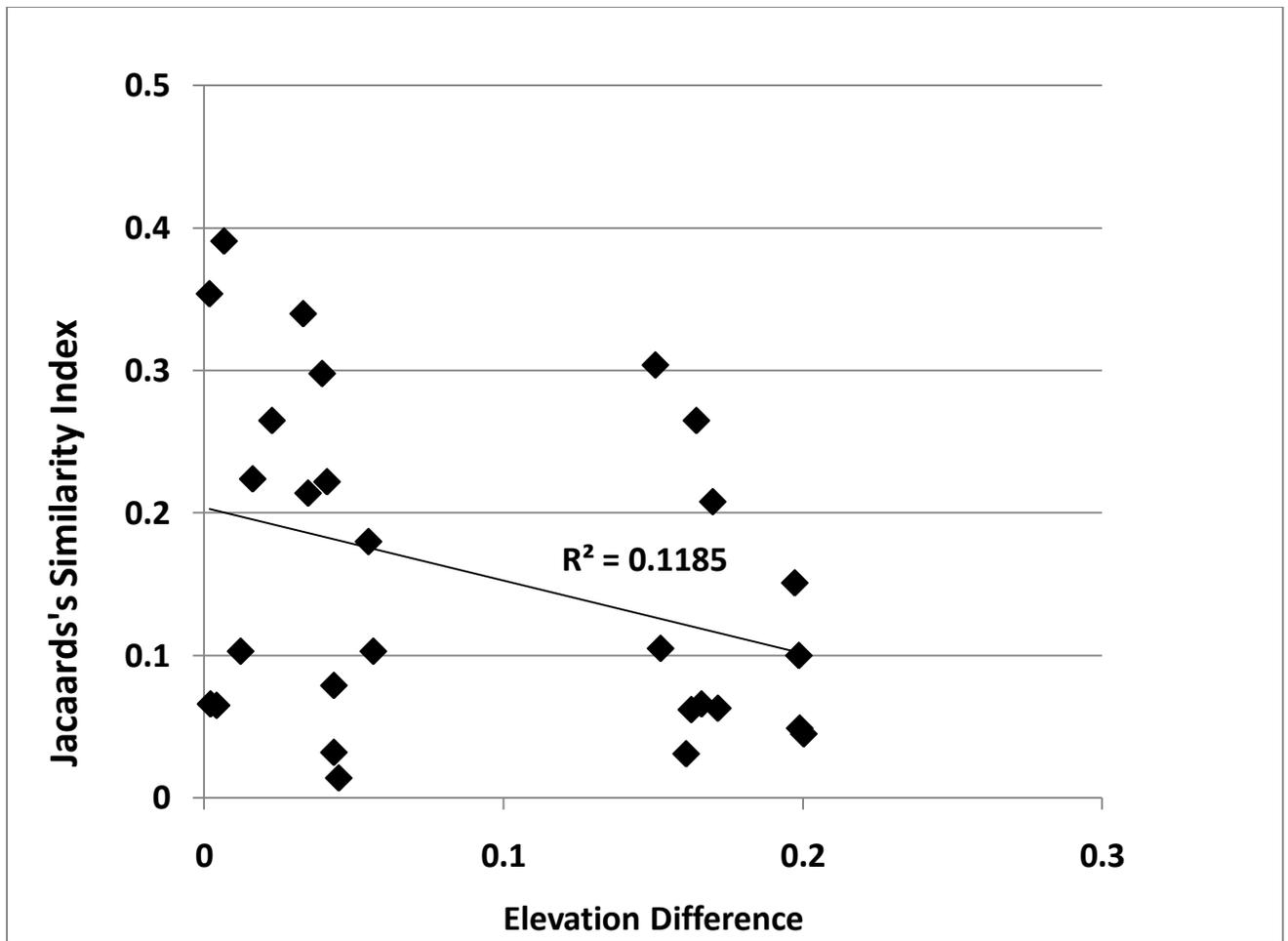


Figure 2.4b. Elevational difference regressed against community similarity for herb species.

($r^2=0.12$, $p=0.0068$)

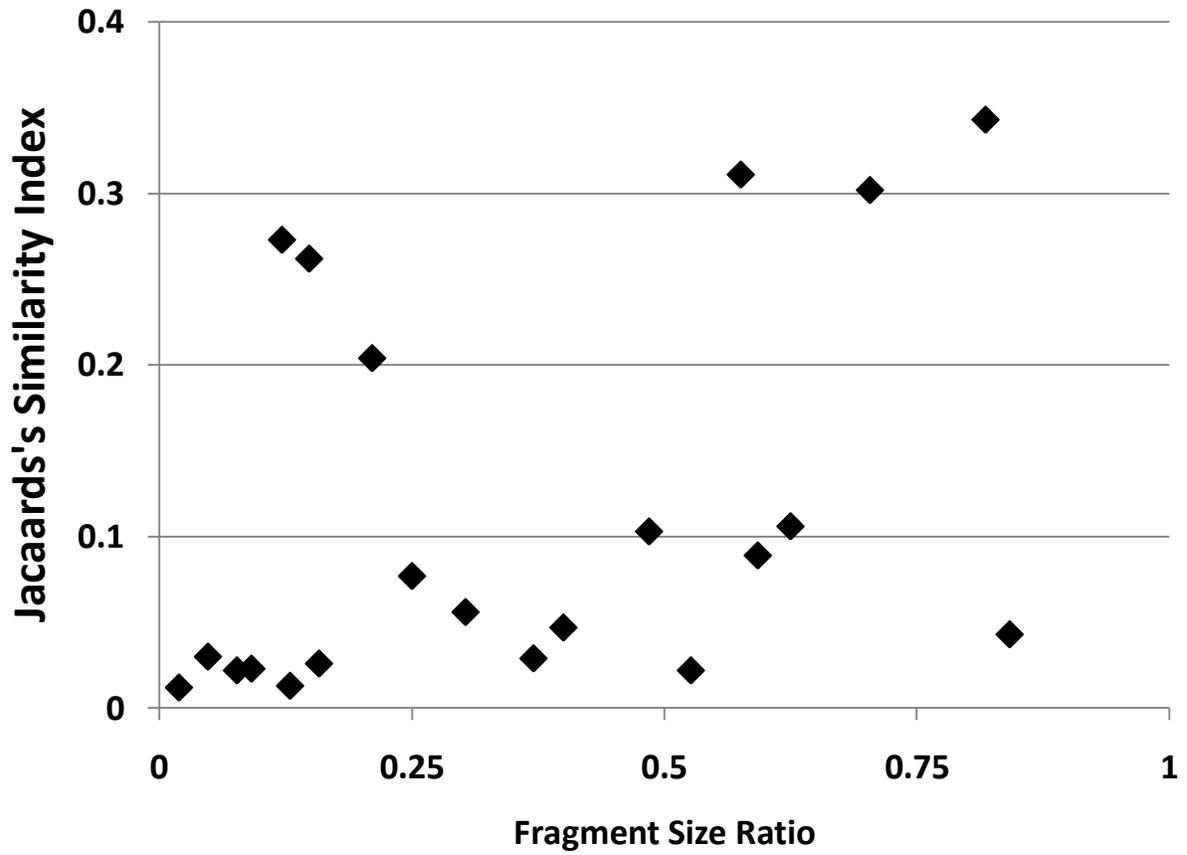


Figure 2.4c. Fragment size ratio regressed against community similarity for tree species. ($r^2=0.14$, $p=0.093$)

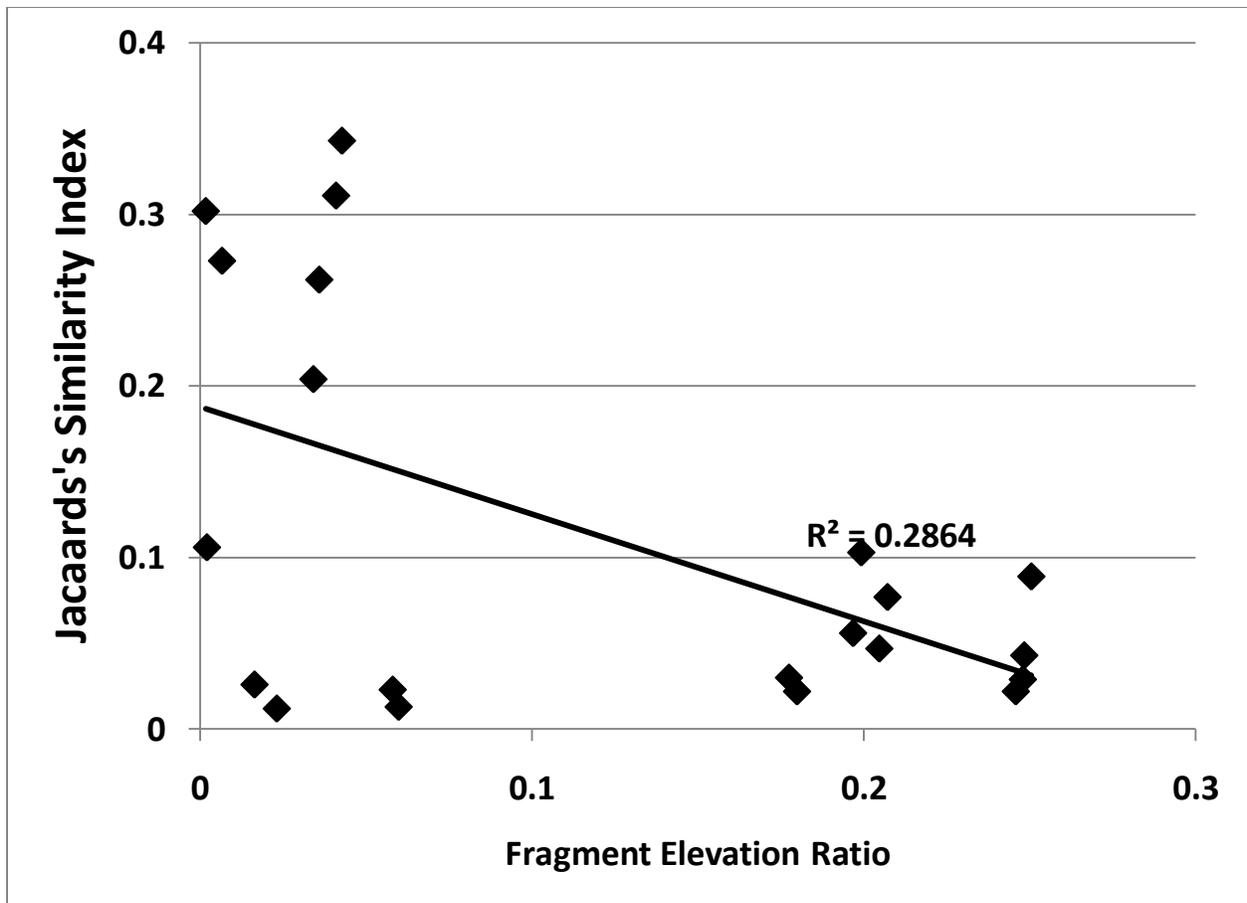


Figure 2.4d. Elevational difference regressed against community similarity for tree species.

($r^2=0.29$, $p=0.0023$)

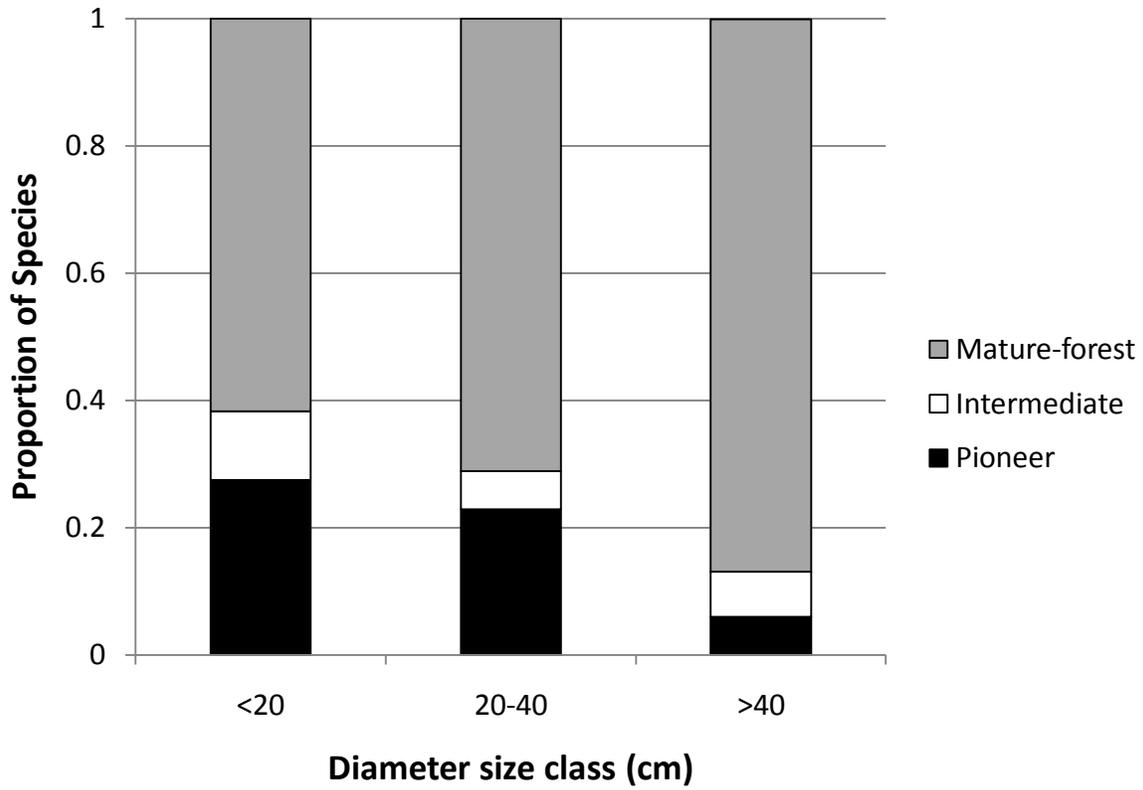


Figure 2.5. Proportion of pioneer, intermediate and mature-forest tree species in small, medium and large size-classes in Las Cruces fragments (G-test, $p=0.0023$)

CHAPTER 3

MICROCLIMATIC EDGE EFFECTS AND PLANT COMMUNITY COMPOSITION IN TROPICAL PREMONTANE FOREST FRAGMENTS²

² Prevost, L.B. and C. J. Peterson. To be submitted to *Biological Conservation*

ABSTRACT

Research on fragmented tropical landscapes has shown strong edge effects immediately after fragmentation. However few studies have examined long term edge effects in microclimate or plant composition, particularly in the tropics. Additionally, very little is known about edge effect responses in premontane regions which have undergone recent and rapid fragmentation in the last half-century. Understanding microclimate gradients near edges and corresponding shifts in plant communities is important for identifying fragments of high conservation value. We examined air temperature, vapor pressure deficit and canopy openness along edge-interior gradients in 3 premontane forest fragments in southern Costa Rica. We also surveyed the tree and herbaceous species community along this gradient. An edge effect to 10m was detected for average and maximum air temperature. Vapor pressure deficit increased up to 20m into the forest fragment interior. The canopy openness edge effect extended to 10m in two of our fragments and to the forest-pasture border in the third fragment. The plant community displayed an edge effect pattern similar to that observed in microclimate. Pioneer trees and trees of smaller diameter were more abundant within the first 10 m of the fragment edge. Herbaceous species composition of the herbaceous layer displayed a parallel change with more disturbance-tolerant species occurring within 10m of the edge. We also report the presence of one non-native herb, *Impatiens walleriana* at the forest edge. The gradient in microclimate and plant composition from the pasture/fragment edge up to 10m into the fragment suggests a shift from mature forest to an early successional plant community within these premontane fragments, as a result of disturbance.

INTRODUCTION

In the tropics, landscapes once covered with forest now exist as a mosaic of remnant forest fragments interspersed among non-forest landuse. The environment surrounding fragments may experience abiotic conditions considerably different from the fragment interior, which may influence abiotic conditions and biotic responses near the forest-nonforest boundary. As forest fragmentation and habitat loss threatens biodiversity, researchers have taken varied approaches to understand the underlying factors driving changes in biodiversity including island biogeography theory (Collinge, 1996; Benedick et al., 2006), population and community dynamics (Laurance et al., 2002; Driscoll, 2008), and microclimate and edge effects (Kapos, 1989; Murcia, 1995). Edge effects is a broadly defined term that includes several patterns and processes, both biotic and abiotic, that show a gradient or threshold from forest fragment boundaries to forest interiors. The interaction of the forest and non-forest habitat creates conditions at the edge that may differ from conditions in the fragment interior or in continuous forest. These edge effects may be abiotic, direct biotic responses (e.g. changes in species composition) or indirect biotic effects due to species interactions (Murcia, 1995). In this study we focus on abiotic effects of microclimate and direct biotic edge effects on plant composition.

Studies of microclimatic edge effects have focused primarily on lowland forest fragments (elevations below 500m). In Amazonian lowland fragments, edge effects have been reported in the first 100m inward from the forest edge. Some exceptions are wind disturbance and tree mortality which extend up to 300m into the interior, but most changes in species composition and abiotic conditions occur closer to the forest/matrix boundary. Strong but short-lived gradients in microclimate variables were found immediately following fragmentation. For example, Kapos (1989) reported a higher vapor pressure deficit, increased temperature and

increased photosynthetic radiation near edges within the first six months after fragmentation in lowland Amazonian forest. Air temperatures cooled as far as 60m into the forest of a 100ha forest reserve. High levels of photosynthetically active radiation penetrated the first 20m into the forest before stabilizing. Soil moisture levels however, showed no response to distance from edge. One year after fragmentation, Sizer and Tanner (1999) reported elevated vapor pressure deficit and temperature extended 50m into the same 100ha fragment. Four years after fragmentation, however, the gradients in abiotic conditions from the forest edge were no longer detected (Camargo and Kapos, 1995). These early effects of fragmentation were confirmed in other lowland fragments. Stevens and Husband (1998) report soil moisture, temperature and relative humidity gradients extended 40 to 80m into fragments, shortly after fragmentation. Additionally, the disappearance of the edge effect after a few decades has been supported by research in lowland Costa Rica forests (Schedlbauer et al., 2007). This loss of edge effect over time is thought to be due to 'sealing' or closing of the forest edge due to regrowth of the dense understory (Murcia, 1995).

Most of the studies that have examined edge effects in tropical fragments above 1000m have been limited to comparisons of vegetation structure and composition near the edge to that in the forest interior (Restrepo et al., 1999; Oosterhoorn and Kappelle, 2000; Lawes et al., 2005). In contrast, only one study has determined the distance that edge conditions persist into the forest interior and found that edge effects extending more than 60m into the forest (Newmark et al., 2001). However, microclimate variables were measured along forest trails which may be more open and permeable to conditions in the agricultural lands surrounding fragments, and this study design may overestimate the distance into the forest fragment that edge effects permeate. A study designed to quantify microclimate within the forest understory along transects from the

fragment edge to interior is needed to provide a more accurate measure of edge effects in forest fragments at elevations above 1000m.

Accurate assessment of microclimate gradients can be used to estimate the proportion of the forest fragment that provides habitat suitable for forest-interior species. This is important in premontane and other mid-elevation tropical forests which have experienced high levels of deforestation and fragmentation in the past half century (Sanchez-Azofeifa et al., 2001). We anticipate that edge effects in premontane fragments may persist for longer periods than in lowland fragments because of the mild temperature and open forest structure found at this higher elevation. Research in temperate forest fragments, which experience milder temperatures and have more open vegetation (similar to premontane fragments), has shown that the edge vegetation may not completely seal the interior from conditions in the surrounding matrix (Matlack et al., 1993). Many plant species, being long-lived and sessile, cannot avoid climatic changes near the edge. Thus plant communities may change after fragmentation due to differential mortality and recruitment in response to changing microclimate near forest edges. In this study, we investigate the microclimate patterns in microclimate along an edge to interior gradient in premontane tropical forest fragments in Costa Rica 50 years after fragmentation. Specifically, we determine the change in microclimatic variables and the width of the edge effect. We also examine how herbaceous and tree species composition track microclimate from pasture to fragment interior.

METHODS

We conducted this study in the vicinity of the Las Cruces Biological Station of the Organization for Tropical Studies in southern Costa Rica in June and July 2010. In a 7km radius,

we selected 3 forest fragments ranging in size from 16 to 27ha. We selected fragments with a northern border adjacent to pasture and facing the direction of the oncoming winds. All fragments were created in 1950s when the region first began to experience intense deforestation for pasture and crop lands. Elevation ranged from 1190 to 1460m in elevation. In each fragment 3 transects were established extending from 20 meters in the surrounding pasture and continuing 120m into the fragment interior, for a total of 9 transects. Transects were oriented to the north in the direction of wind currents to account for maximum influence of pasture conditions into the fragment. Measurements were taken at 9 points along each transect: -20, 0, 10, 20, 30, 40, 50, 75, 100m. We selected this design to have greater resolution near the edge, as previous fragmentation studies (Kapos, 1989; Laurance et al., 1997; Laurance et al, 2002; Delgado et al., 2007) report edge effects (with the exception of wind disturbance) extended up to 100m into the forest fragment.

We measured air temperature and relative humidity using Onset HOBO[®] H-8 and U-12 data loggers mounted 1m above the ground and shaded from rainfall and direct sunlight. From these measurements we calculated vapor pressure deficit (VPD) using the formula $VPD = VP_{sat} * (1 - \text{relative humidity}/100)$ where VP_{sat} (vapor pressure at saturation temperature) = $0.6108 * e^{17.27T/(T + 237.3)}$ and T = temperature in degrees Celsius). Air temperature and VPD were measured along one transect for the duration of the study and for two 1 week periods along the remaining eight transects. To determine whether the time measurements were taken influenced our findings, means were compared among time periods and no significant differences were found. We determined average, maximum and minimum daily temperatures at each transect point.

Canopy openness was used as a proxy for light availability because it gives a more comprehensive estimate of light availability throughout the day and year compared to instantaneous measurements taken with light meters. Canopy openness was measured using hemispherical photographs taken at 1m above the ground using a Nikon Coolpix880 digital camera and a fish-eye lens (Nikon FC-E8). Photographs were analyzed with Gap Light Analyzer software to quantify openness (Frazer et al. 2000).

We sampled the canopy tree stratum using the point quarter method. Each point along the transect was divided into quadrants, and in each quadrant the distance to and diameter of the nearest tree above 10cm diameter at breast height (DBH) was measured. Tree diameter was classified into three size classes: small (≤ 20 m), medium (20 to ≤ 30 m) and large (> 30 m). Trees were classified according to life history pattern as either pioneer or mature forest species. We also surveyed the herbaceous vegetation within a 1m x 1m plot centered at the transect point.

Data Analysis

Microclimate variables were transformed when necessary to meet requirements for normality prior to analysis. Percent canopy openness was log transformed and vapor pressure deficit was arcsine transformed. We used ANOVA with Helmert contrast statements to compare distances for a given microclimate variable (Delgado et al., 2007) and Bonferroni corrections for multiple comparisons. The Helmert procedure compares all distances to the reference distance which was located in the pasture (-20m). The point at which no statistical difference was observed indicated the threshold at which edge effects were no longer detected and stable interior abiotic conditions were found.

RESULTS

Microclimate

Both average and maximum daily temperatures showed an overall decline from edge to forest interior in all fragments (Figure 1). Maximum daily temperatures declined approximately 8 °C while average daily temperatures showed a smaller decline of about 2°C. Analysis of variance with Helmert contrasts indicated that average and maximum daily temperatures stabilized at 10m into the forest fragment for all fragments ($p < 0.05$). Average minimum temperature, did not show any variation with distance from fragment edge ($p = 0.2385$).

Vapor pressure deficit (VPD) was lower and more stable in fragment interiors than near the edge (Figure 2, $p < 0.05$). A significant decrease in VPD from 0.175 ± 0.068 in the pasture to 0.055 ± 0.005 at 20m into fragment interiors was observed.

There was a significant interaction between distance from forest edge and site for canopy openness ($p = 0.03$). Canopy openness, our proxy for light availability, declined from pasture to forest interior in fragments (Figure 3). Fragment CP experienced a 39% decline in canopy openness from the pasture to 10m into the forest interior ($p < 0.05$). Fragments LL and DC experienced a 23% and 19% decline respectively from the pasture to the pasture-fragment boundary (0m) ($p < 0.05$).

Plant Community Composition

The proportion of pioneer trees was significantly higher closer to the fragment edge than in the forest interior (Figure 4; G-test, $p < 0.0001$), while mature forest species were more

prevalent in the forest interior. Over 80% of trees in the matrix and on the forest-matrix boundary were pioneers. Pioneer species were represented disproportionately as smaller trees (<20cm DBH) and mature forest species were more common as larger trees (Figure 5; G-test, $p < 0.0001$).

Herbaceous species richness remained constant along the edge-interior transect (Figure 6a) - analysis of variance, Kruskal-Wallis test $p = 0.536$). However, the density of stems was higher at the forest edge compared to the forest interior (Figure 6b) - analysis of variance, Kruskal-Wallis test $p = 0.0048$). We noted a change in the suite of species observed within the first 10m into fragment compared to the fragment interior (20m-100m) which corresponds to the 10m edge effect for microclimate (Table 1). Species of the Asteraceae family were most common at edges. *Impatiens walleriana*, the only non-native identified in our study, grew within the first 10m of the fragment. Araceae species are more common in the forest interior.

DISCUSSION

Fifty years after fragmentation we detected edge effects as microclimatic and plant community composition gradients in premontane forests in the Las Cruces region in Costa Rica. We observed a gradient of decreasing average and maximum temperature, decreasing canopy openness and increasing relative humidity from the surrounding pasture extending 10 to 20m into the forest fragment interior. Our findings differed from those for lowland Amazonian forests where microclimate edge effects showed strong gradients immediate after fragmentation, but those gradients disappeared within four years. The architecture of the forest edge may play an important role in determining the ability of matrix microclimatic conditions to penetrate into the forest fragment (Murcia, 1995). Matlack (1993) and Murcia (1995) have described “sealed”

edges as having a multi-layer dense understory vegetation that gradually decreases from the created fragment-pasture edge and into the pasture, providing a denser and wider buffer between the matrix and fragment interior. On the other hand, abrupt edges provide little lateral protection for the fragment interior. Forest edges in the Las Cruces area typically contain large tree trunks present at the forest –pasture border with a single layer of understory 1-1.5m tall, and can be classified as abrupt. These abrupt edges in our study fragments may allow the penetration of pasture conditions into the forest decades after fragmentation in these premontane landscapes.

Although edge effects persist approximately fifty years after fragmentation, the edge effect detected is fairly moderate. This may be due to the difference in climate between premontane and lowland habitats. In the Las Cruces area, the climate is very moderate with mean temperatures around 20°C and high annual rainfall (approximately 3800mm) with considerable rainfall in the dry season. The landscape is periodically covered with mist during the day, creating a much more humid and mild climate than in lowland forests which experience several months without rainfall. Unlike lowland Amazonian forests, the Las Cruces region does not experience fires. Our results demonstrating a narrow but persistent edge effect is most similar to the findings of Delgado et al (2007), temperate forests edges in the Canary Islands which also experience mild temperature around or below 20°C.

Corresponding to the gradient in microclimate, we observed a greater proportion of pioneer tree species (predominantly *Miconia*, *Allophylus*, *Cecropia*, *Alchornea* and *Inga* species) at the forest edge. Our results support a pattern of increased recruitment of *Cecropia* and other disturbance-adapted species from the edge to 10m into the forest interior (Bierregaard et al., 1992; Sizer and Tanner, 1999). This change in species composition coincides with an increase in the proportion of smaller trees (<20cm DBH), suggesting a shift from mature forest trees to early

successional habitat near the forest edge after fragmentation. We recommend further study of trees species germination, establishment, mortality and turnover to determine whether succession will progress to the mature forest stage at the edge or whether the edge persists as early successional habitat (Laurance et al, 2002; Laurance, 2002).

The potential for increased fluctuations in population and communities dynamics, referred to as hyperdynamism, (Laurance, 2002), has been reported <100m from fragment edges in lower Amazonian forests. Pioneer recruitment increased with the number of nearby edges, and tree mortality increased near edges, leading to shifts in edge community composition from large-seeded old growth forest species to early disturbance-adapted and abiotically-dispersed species (Laurance, Nascimento, Laurance, Andrade, Fearnside, et al., 2006).

Along with a shift tree composition, we observed a change in herbaceous community composition from the pasture/fragment boundary into the forest interior. Species typical of open or disturbed habitats, such as *Erechtites sp.*, *Impatiens walleriana* and *Rubus sp.* appear near the edge but are absent from the forest interior. *Impatiens walleriana*, a non-native species, is of particular interest as it been reported to escape from cultivation and spread to disturbed areas and stream sides (Zuchowshki, 2005; Gargiullo et al., 2008). Growing *Impatiens* populations occur in disturbed areas in the nearby Las Cruces reserve along the banks of creeks in secondary forest (LBP personal observation).

The microclimate edge effect and corresponding change in plant composition near edges that we observed may also influence the animal community and alter plant-animal interactions. Edges may provide insufficient habitat cover or lack food resources for some animal species. For example, understory birds may experience increase predation near edges (Newton and Heske, 2001) and thus modify their behavior to restrict use of edge habitat to only lowlight periods when

predation risk is reduced and limit movement across open areas (Rodriguez et al., 2001).

Changes in the distribution of bird populations may, in turn, affect plant reproduction through the restricted movement of dispersers and pollinators across deforested habitat (Bierregaard et al., 1992; Brosi et al., 2009; Ruiz-Gutierrez et al., 2010). Thus, understanding edge effects is important for conservation both plant and animal diversity tropical forest fragments

Our findings of moderate microclimatic and plant community composition edge effects from the edge to 10m into the forest fragment indicate that fragments in the Las Cruces area may be valuable for conservation. With previous reports of an edge effect of 40-50m in lowland Amazonian tropical forests, small fragments of approximately 1 hectare would support little or no forest interior habitat. Based on these reports of 40m edge effects, Young and Mitchell (1994) have proposed that regularly-shaped reserves require areas of at least 9 hectares to provide more than fifty percent interior habitat compared to edge habitat. In the Las Cruces area, few fragments are regularly shaped. Nevertheless, with edge effects extending only 10m into the forest interior, even fragments 1 hectare and smaller may provide considerable proportions of interior habitat with a microclimate suitable for mature forest trees and herbaceous species. However, in addition to abiotic conditions, biotic factors such as the ability of dispersers and pollinators to persist in fragments, and population sizes necessary to support high genetic diversity should also be taken into consideration in selecting fragments for conservation.

We conclude that moderate but long term microclimatic edge effects occur in fragments in the Las Cruces region. Fragment edges are dominated by early successional and disturbance adapted plant species. Future studies will be needed to determine whether this community shift is the result of increased fluctuation in community dynamics.

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Table 3.1. Herbaceous species and families and their distribution along edge-interior transects in Las Cruces fragments.

Restricted to first 10 m		Restricted to forest interior (distances $\geq 20\text{m}$)		Distributed throughout	
Family	Species	Family	Species	Family	Species
Araliaceae	<i>Sanicula liberta</i>	Araceae	<i>Philodendron verrucosum</i>	Araceae	<i>Dieffenbachia orestedii</i>
Asteraceae	<i>Melampodium sp.</i>	Araceae	<i>Spathyphyllum wendlandi</i>	Arecaceae	<i>Chamaedorea costaricana</i>
Asteraceae	<i>Bidens reptans</i>	Araceae	<i>Philodendron sp.</i>	Arecaceae	<i>Chamaedorea pinnatifrons</i>
Asteraceae	<i>Elephantopus sp.</i>	Arecaceae	<i>Geonoma congesta</i>	Arecaceae	<i>Chamaedorea pygmaea</i>
Asteraceae	<i>Erechtites sp.</i>	Arecaceae	<i>Geonoma sp.</i>	Arecaceae	<i>Chamaedorea sp.</i>
Balsamiaceae	<i>Impatiens walleriana</i>	Bromeliaceae	<i>Bromelia sp.</i>	Commelinaceae	<i>Tradescantia sp.</i>
Euphorbiaceae	<i>Acalypha arvensis</i>	Cyclanthaceae	<i>Asplundia isabelina</i>	Commelinaceae	<i>Commelina sp.</i>
Malvaceae	<i>Pavonia sp.</i>	Marantaceae	<i>Pleistachya sp.</i>	Costaceae	<i>Costus sp.</i>
Rosaceae	<i>Rubus sp.</i>			Costaceae	<i>Renalmea sp.</i>
				Cyclanthaceae	<i>Cyclanthus bipartitus</i>
				Fabaceae	<i>Desmodium axillare</i>
				Gesneriaceae	<i>Columnea sp.</i>
				Marantaceae	<i>Calathea crotalifera</i>
				Poaceae	<i>Pharus sp.</i>

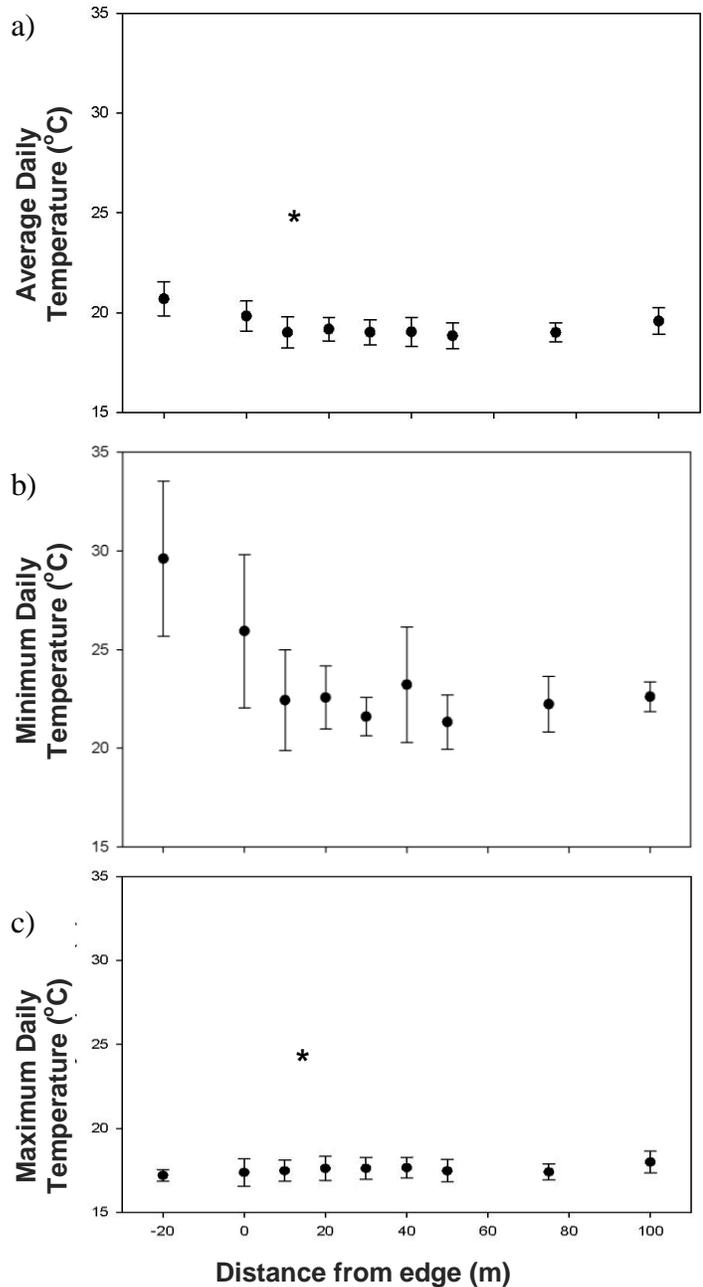


Figure 3.1. a) Average, b) Maximum and c) Minimum Daily Temperature along transects extending from pasture (negative value) into the forest interior (positive values). Mean values plotted with error bars representing the standard deviation. Asterisk denotes the distance-from-edge beyond which no significant effect is detected using analysis of variance with Helmert contrasts. average temperature, maximum temperature $p < 0.05$; minimum temperature $p=0.238$

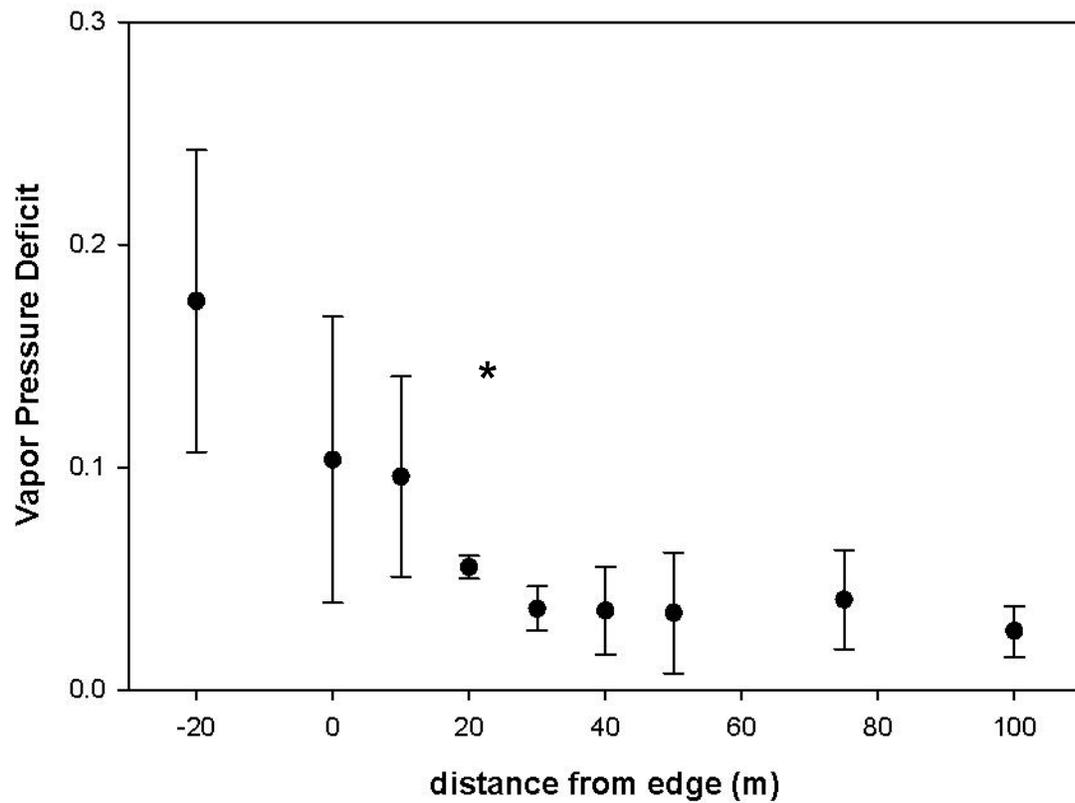


Figure 3.2. Average vapor pressure deficit along transects extending from pasture (negative value) into the forest interior (positive values). Mean values plotted with error bars representing the standard deviation. Asterisk denotes the distance-from-edge beyond which no significant effect is detected using analysis of variance with Helmert contrasts, $p < 0.05$

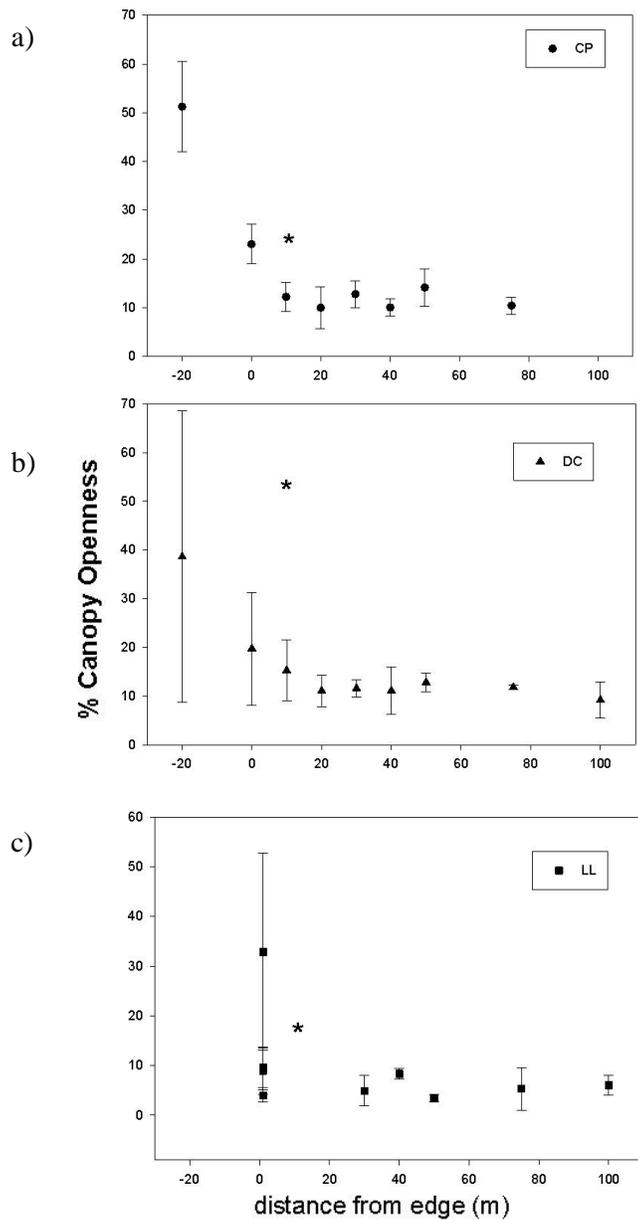


Figure 3.3. Percent Canopy Openness for fragments a) CP, b) DC and c) LL along transects extending from pasture (negative value) into the forest interior (positive values). Mean values plotted with error bars representing the standard deviation. Asterisk denotes the distance-from-edge beyond which no significant effect is detected using analysis of variance with Helmert contrasts, $p < 0.05$.

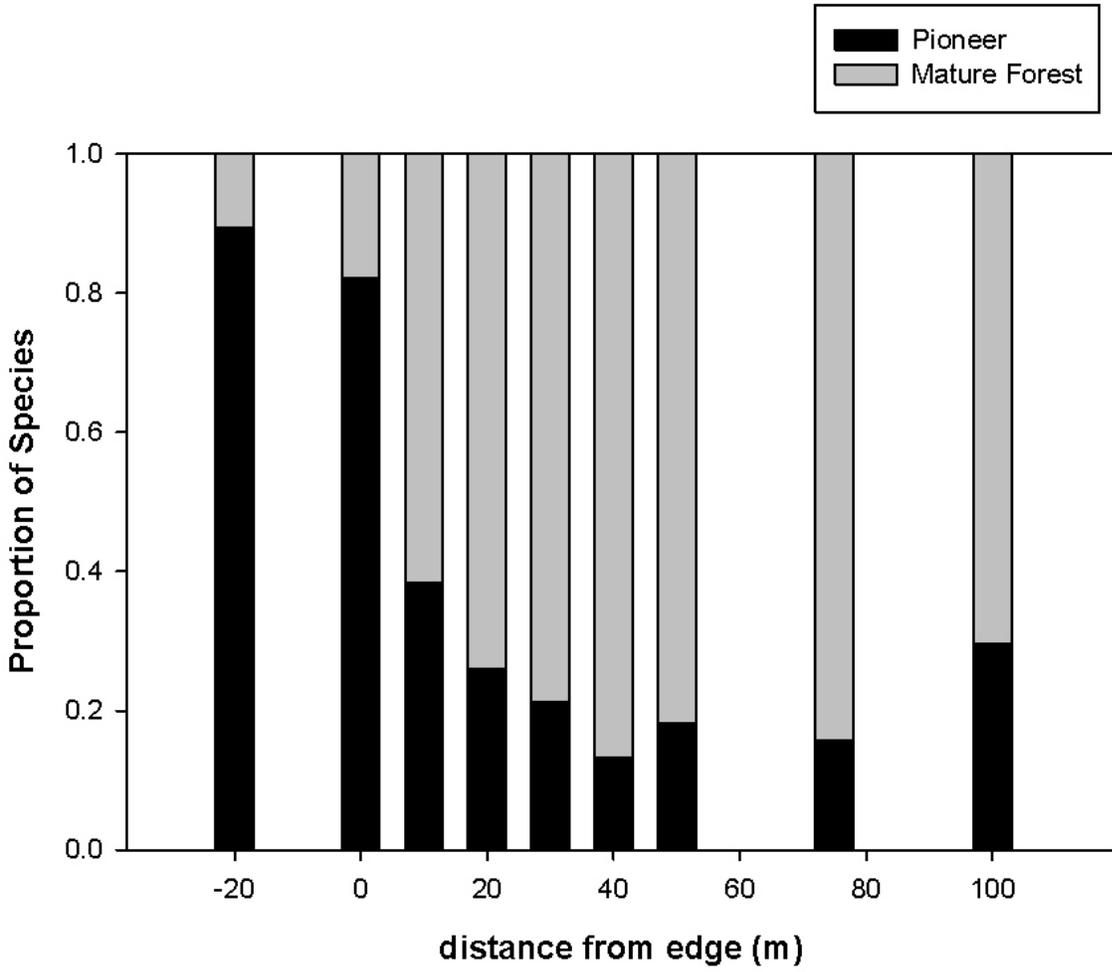


Figure 3.4. Proportion of pioneer and mature forest species along transects extending from pasture to forest interior.

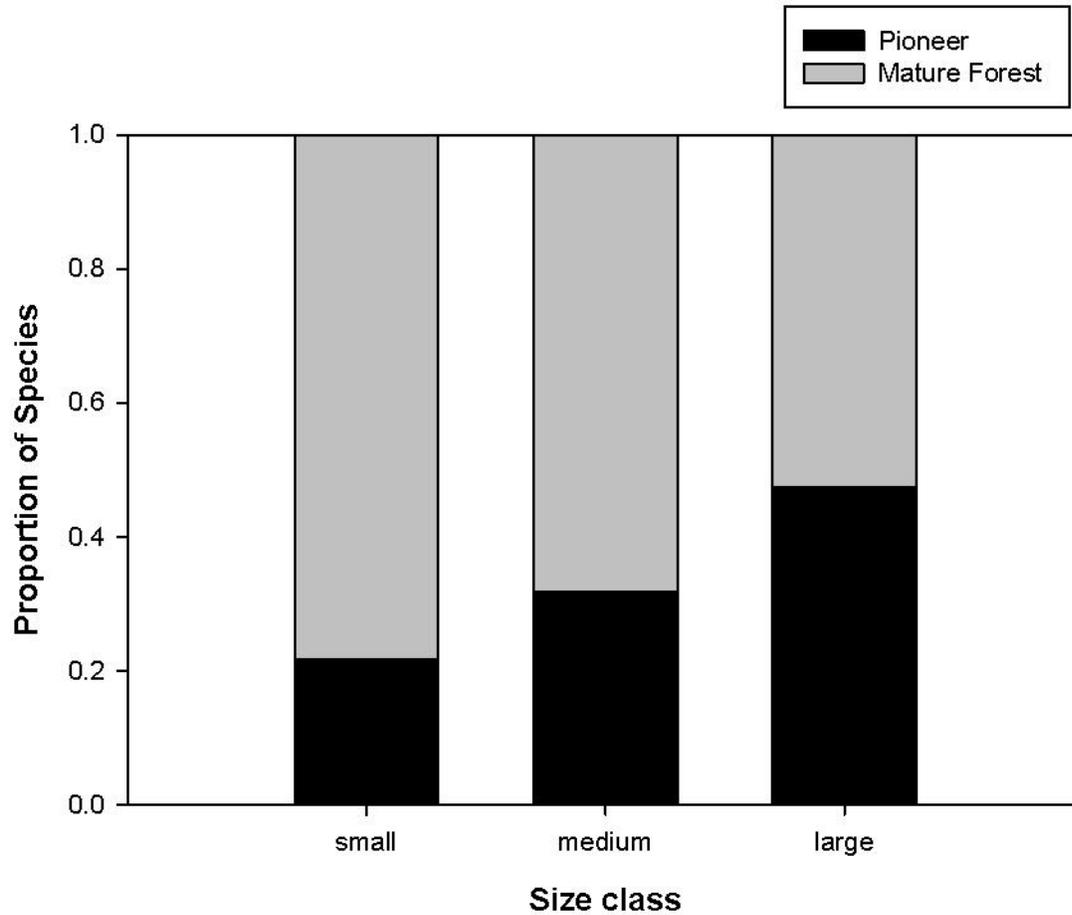


Figure 3.5. Proportion of pioneer and mature forest species belong to different life history groups within 3 diameter size classes. Small included trees with a diameter at breast height < 20cm; medium 20-30cm; large > 30cm.

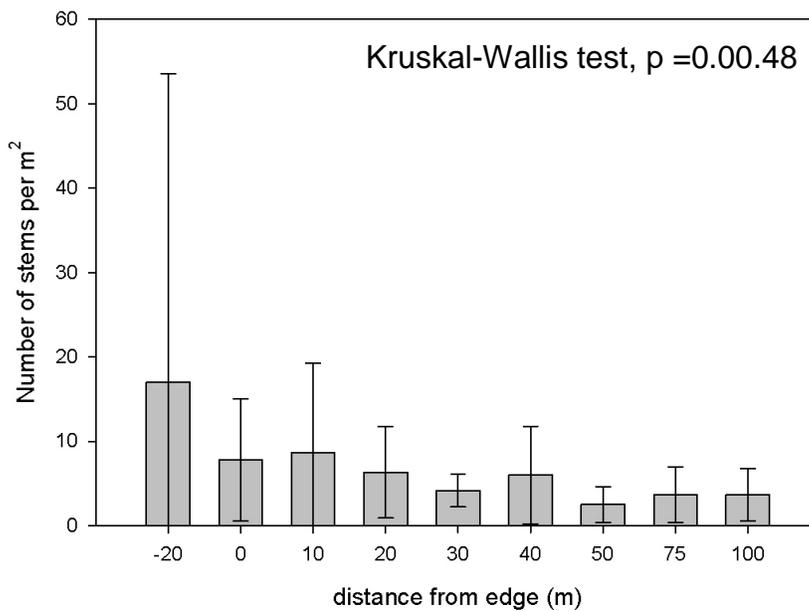
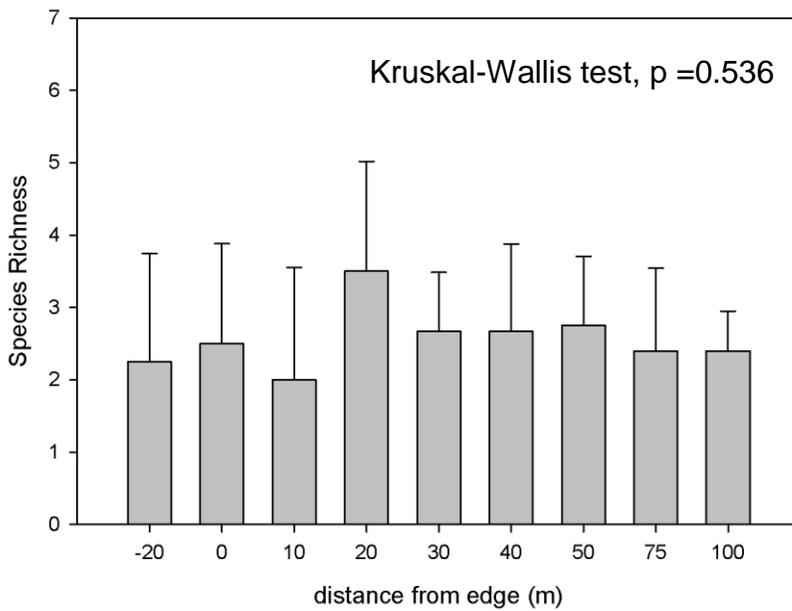


Figure 3.6. a) Species Richness and b) Stem Density per square meter of herbs along transects extending from pasture (negative value) into the forest interior (positive values). Mean values plotted with error bars representing the standard deviation.

CHAPTER 4

MATRIX INFLUENCES ON SPECIES COMPOSITION IN A PREMONTANE FOREST LANDSCAPE³

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ABSTRACT

Although island biogeography theory has been an influential model for understanding species diversity in fragmented habitats, recent approaches are providing more insight into species responses. Island biogeography theory does not take into account the heterogeneity of the matrix which represents important variables that can influence species persistence in and movement among fragments. We hypothesize that landscape heterogeneity and configuration influence plant composition in forest fragments. We examined the heterogeneity of the matrix in a fragmented premontane landscape using spatial analysis applications. We also examined the influence of the matrix composition and configuration on plant species composition within fragments using principal components analysis (PCA). Fragment configuration metrics classified the landscape as patchy with many irregularly shaped fragments. Landuse in the matrix was dominated by pasture but also contained crop gardens, regenerating forest and primary forest patches. Species richness increased with the amount of primary forest in the habitat within a radius of 500m from the focal fragments. Tree species composition was also correlated with forest cover along with metrics for fragment shape, number and edge. PCA results showed that pioneer species were strongly clustered with metrics describing irregularly shaped fragments. Our findings demonstrate that matrix type and configuration analyses can be used to understand tree composition in fragments.

INTRODUCTION

Fragmentation has been shown to have diverse influences on plant communities (Lovejoy et al., 1983; Murcia, 1995) and multiple approaches have been adopted to understand floristic composition in fragments. Although island biogeography theory has provided an underlying

conceptual framework for understanding the ecology and biogeography of forest fragments (Harris, 1984; Collinge and Forman, 2009), more recent studies of matrix influences have provided further insight into how remnant forest communities respond to fragmentation (Kupfer et al., 2006; Watling et al., 2011). The term matrix is used to describe areas no longer covered in primary forest and includes landuse such as pasture, crop lands, and roads (Lindenmayer and Franklin, 2002; Kupfer et al., 2006). The matrix influences the plant and animal communities in fragments through direct effects and indirect effects mediated by species interactions. Matrix structure and composition can influence the magnitude of the microclimatic gradient experienced near the edge of the fragment. For example, a matrix composed of regenerated forest with several vertical layers can reduce edge effects within fragments compared to a more open matrix, such as pastureland (Matlack, 1993). The composition of the matrix may also influence the species composition trajectory (Nascimento et al., 2006).

Matrix influences can be much more complex, particularly for fragmented plant communities. Matrix quality can be very heterogeneous making the matrix hospitable to some species and hostile to others (Rodewald, 2003; Umetsu and Pardini, 2007). The extent of the matrix also can vary among landscapes (Andren, 1999). Even small patches of hospitable matrix, such as isolated trees in pastures, may act as stepping stones for movement of animal seed dispersers among fragments. Thus the matrix quality and extent affects tolerance of and movement through the matrix for animal species (Gascon et al., 1999; Baum et al., 2004). The matrix composition can change with time causing a subsequent change in the suite of species that can tolerate the matrix (Chazdon, 2003).

Most studies on the influences of the matrix on plant communities focus on impacts mediated through interactions with animal species. Positive interactions such as dispersal and

pollination can be influenced by the persistence of birds and other animals in the matrix. Seed dispersal by frugivorous birds has been reported to increase when the adjacent habitat is more similar to the native vegetation (Zamora et al., 2010). Toucans may disperse seeds less frequently across landscapes with little forest habitat and fruit resources (Graham, 2001). The ability to traverse the matrix may vary considerably among insect pollinators (Cane, 2001; Ricketts, 2001). Interactions with competitors and herbivores may also affect forest plant composition. Seed predation may increase in fragments if the density of predators increases due to limited emigration into the surrounding matrix (Herrera et al., 2011), slowing regeneration. Invasive species may show contrasting responses to the matrix compared to native forest species. Invasive species are often wind dispersed and have high mobility across the matrix compared to large seeded mature forest species (With, 2002). They may also be able to tolerate more frequent disturbances that may occur in the matrix (With, 2002; Kupfer et al., 2006). In areas with agricultural and residential landuse, invasive species may be more likely to be introduced and spread into nearby forests (Allen et al., 2006; Kupfer et al., 2006).

The previously mentioned studies have focused primarily on animal populations and plant species richness and diversity with little examination of the impact of the matrix on plant community composition. However, there is some evidence that matrix composition can influence plant community succession in gaps (Janzen, 1983; Grau, 2004) and, in one case, forest fragments (Nascimento et al., 2006). In our study, we characterize the matrix around fragments in tropical premontane landscapes and examine the influence of the matrix on plant diversity and composition. We hypothesize that the landscape is heterogeneous and plant composition will differ depending on the type of landuse in the matrix.

METHODS

Eight fragments from 1 to 209 hectares were identified for study in the vicinity of the Las Cruces Biological Station, Coto Brus canton, southern Costa Rica (Figure 4.1). Aerial photos (1:60000), a baseline map of forest cover, and ground truthing were used to determine landuse within a 1km radius or buffer zone of all focal fragments. Aerial photos and baseline maps were obtained through the Las Cruces Biological Station Geographical Information Systems and Remote Sensing Database of the Organization of Tropical Studies. From these baseline maps, we created a landuse map of the focal fragments and surrounding landscape in the vicinity of the Las Cruces Biological Station. The matrix landuse was classified into 4 categories; primary forest, regenerating forest, pasture and croplands. We used the spatial analysis applications FRAGSTATS (McGarigal et al., 2002) and Patch Analyst (Elkie et al., 2010) to assess fragmentation metrics in the region. For each focal fragment, four concentric buffer zones were constructed extending 50m, 100m, 500m and 1000, from the fragment border into the surrounding landuse. Matrix characteristics were measured for each buffer zone. We also determined landscape metrics for each of the four landuse categories. The type of landuse was designated as the class variable.

Landscape metrics included measures of landscape configuration, patch shape and isolation. Landscape configuration metrics described the size and number of patches in the matrix and include Class Area in hectares (CA), area covered by primary forest; the number habitat patches (NumP), the mean patch size of all the habitat patches in the matrix (MPS, hectares); the standard deviation of the patch sizes (PSSD, hectares); the coefficient of variation of the size of habitat patches (PSCov). Patch shape metrics described the amount of edge present in the matrix and include the total edge distance (TE, km), the mean distance of edge per patch

(MPE, km). The shape index was calculated as the amount of edge in a fragment divided by the minimum edge found in a regularly shaped fragment. For the FRAGSTATS and Patch Analyst programs, a regular fragment was considered a square as the measurement was based on raster (square-grid) representation, where circular features cannot be exactly drawn in the program. Mean shape index (MSI) is the mean for all patches. Area-weighted mean shape index (AWMSI) was calculated as the total shape index for a patch type multiplied by the proportional abundance of the patches.

We sampled the plant community using three 20m x 20m randomly located plots in each fragment. Within each plot, the number and abundance of all herbaceous plants and trees greater than 10cm in diameter at breast height was recorded. Specimens were identified to recognizable taxonomic units (RTU) - family and genus, and species when possible (Mayfield and Daily, 2005). In the following text, we will use the term 'species' to mean RTU unless otherwise indicated. We recorded the number of individuals of each species and measured the diameter at breast height of the trees. Vouchers were submitted to Las Cruces Biological Station Herbarium.

Statistical Analysis

We estimated species richness and diversity within fragments using EstimateS biodiversity analysis software (Colwell, 2010). To determine the distance at which matrix type influences plant species richness and diversity, we used analysis of covariance with distance as a covariate. Within this distance, principal components analysis (PCA) was performed to investigate the relationships between species composition and matrix characteristics. The PCA was conducted using PC-ORD version 5.31 (McCune and Mefford, 2006). We performed the PCA using matrix (landscape) characters as the primary matrix overlain with log-transformed

data on species richness as the secondary matrix. We determined the relationship between the proportion of pioneers and the first two ordination scores using regression analysis.

RESULTS

We observed that within each buffer zone around the fragment the landscape consisted of many relatively small habitat patches as indicated by the number of patches and the mean patch size. The mean patch size ranged from 0.6 to 22.1 hectares (Table 4.1). Table 4.1 also shows the metric values at the landscape level for the buffer zones at 50m, 100m, 500m and 1000m from the fragment edge. The mean patch size decreased with the buffer zone distances of 50m to 500m indicating that the landscape is becoming increasingly fragmented around focal fragments. This trend did not continue 1000m outside the fragment edge as most fragments were within 1km of each other and buffers tended to overlap. Fragments in all buffer zones vary greatly in size as indicated by the large coefficients of variations ranging from 100 to 300%.

Fragments are highly irregular in shape as indicated by mean patch shape values that are all greater than 1 (range 1.71-4.28). This relation between fragment size and edge is confirmed by values greater than 1 when area was statistically controlled for, as seen with average weighed mean shape indices from 1.39 to 2.59.

Comparison of landuse metrics across four buffer distances around the fragment, with plant richness and diversity measures showed significant increase for tree diversity ($p < 0.05$, analysis of covariance, Figure 4.2) with increased primary forest cover. Simpson's index of diversity significantly increased with the proportion of primary forest surrounding the fragment up to a 500m radius. Tree species richness and herbaceous species richness and diversity of focal

fragments were not significantly correlated with the amount of non-primary forest habitat ($p > 0.05$).

The first two axes of the principal components analysis explained 58% and 49% of the variation among species for trees and herbs, respectively (Table 4.2). The regression of PCA also indicated that species community composition was strongly correlated with landscape metrics (Figure 4.3, Table 4.2). For trees, eigen values and loadings indicated that the first axis was strongly influenced by cover area, edge and shape feature and the second axis by the shape metric area weighted mean shape index. The proportion of pioneer species was correlated with vectors for matrix shape ($r^2 = 0.45$, $p < 0.05$). For herbaceous species, the first two axis had strong loading for area weighted mean shape index.

DISCUSSION

The matrix configuration of the premontane landscape surrounding the Las Cruces Biological Station is irregular and patchy as indicated by landuse metrics. Though the landscape is dominated by pasture, near the Las Cruces Biological Station large fragment reserve we observed a cluster of fragments with increased non-forest habit as we travel outward in the landscape. This clustering of patches suggests that fragmentation is a non-random process. Deforestation is more likely to occur in accessible areas near roads and other cleared areas, and forest patches are left behind on steep slopes or poor soils which are difficult to access or poor for agriculture (Nason et al., 1997; Laurance, 2008).

Premontane fragments in our study were embedded in a matrix of various landuses. Agriculture encompassed cultivation of a variety of crops including coffee, banana, caña de india (*Costus guanaiensis*), and vegetables. Matrix heterogeneity was driven by the large number of

patches and high patch shape covariance at the 500m and 1000m scale. Heterogeneity of the landscape is important, as it influences the movement and survival of both plant and animal species through the matrix and among fragments (Collinge and Forman, 2009). This heterogeneity is not accounted for in island biogeography models and therefore examination of the matrix can identify unique factors that influence diversity within fragments (Kupfer et al., 2006; Collinge and Forman, 2009). We identified metrics quantifying patch shape and landscape cover as important correlates with species composition in fragmented landscapes. The influence of patch shape, a function of the amount of edge, on species composition is supported by findings in our study on microclimate edge effects (chapter 3). Near the fragment edge, increased light and temperature support the growth of pioneer species compared to the fragment interior.

Within a 500m buffer zone, we observed a correlation of tree species diversity with primary forest cover. Tree species abundance and diversity can be heavily dependent on recruitment and mortality rates. Pioneer species regeneration and composition has been shown to vary with the nature of the surrounding matrix in lowland tropical forests (Nascimento et al., 2006). Both the structure and composition of the surrounding matrix may influence species richness within fragments (Kupfer et al., 2006; Kennedy et al., 2010). Many forest interior species are sensitive to changes in the matrix and may avoid use of the matrix (Mech and Hallett, 2001; Lindenmayer and Franklin, 2002; Cordeiro and Howe, 2003). However, some generalist species may be unaffected by changes in the matrix as they are able to obtain resources from various habitats (Cane, 2001). Still other suites of species, such as invasive and pioneer species which prefer high light environment, may thrive in the non-forest matrix (Saunders et al., 1991; With, 2002). In our study, pioneer species were positively correlated with patch non-regularity, i.e. more abundant in patches with greater edge relative to patch area. This is consistent with life

history patterns of pioneers which are shade-intolerant and are more abundant in disturbed forest and other high-light habitats (Laurance et al., 2006).

One limitation of our study was that analysis was confined to a 1km radius from fragments and may not extrapolate to a wider scale. However, our analysis of landscape metrics suggests that within a 500m radius landscape attributes may be useful for determining plant responses to fragmentation. Specifically, tree species diversity and composition may be influenced by the type of matrix cover and the configuration of the matrix.

Our findings have important implications for the development of conservation practices and concept models to understand fragmentation. Much of the conservation literature has emphasized the need for managing plant and animal populations within fragments or creating corridors for animal movement (Laurance and Gascon, 1997; Laurance and Laurance, 1999; de Lima and Gascon, 1999). However, the results of our study suggest that management of the landscape (fragments and matrix) would be beneficial for the preservation of mature forest trees in the fragment plant community. Our results suggest that management practices increasing forest cover and regularity of fragment shape can lead to increased diversity and greater abundance of mature forest trees in fragments. Additionally, our results also compliment conceptual fragmentation model proposed by Kupfer et al (2006). In this model, the matrix is included as a filter with moderates the resource base, disturbance, microclimate and other conditions experienced within fragments which in turn, influence species diversity, species interactions and ecosystem services (Zuidema et al., 1996; Lindenmayer and Franklin, 2002). The correlations between matrix characteristics and species composition obtained from our principal components analysis can be used to further developed conceptual models.

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Table 4.1. Landscape structural metrics for focal fragments in near the Biological Station. Landscape is compared at four buffer distances around the focal fragment; 50m, 100m, 500m, 1000m. Metrics were derived using the Patch Analyst software. Metric codes: CA class area- the area covered by primary forest; NumP number of patches; MPS mean patch size; PSSD patch size standard deviation; PSCov patch shape coefficient of variation; TE total edge; MPE mean patch edge; MSI mean shape index; AWMSI Area Weighted Mean Shape Index.

Fragment	CA	NumP	MPS	PSSD	PSCoV	TE	MPE	MSI	AWMSI
<i>50m buffer</i>									
COP	5.4	8	0.7	0.8	121.96	2.7	0.33	2.50	1.53
CP	33.9	4	8.5	8.8	103.55	9.0	2.26	3.59	2.48
GAM	13.6	5	2.7	4.0	148.15	3.5	0.71	2.83	1.46
LCBS	241.9	11	22.0	59.7	271.59	28.7	2.61	4.53	2.09
LL	74.6	8	9.3	18.0	192.70	14.3	1.78	3.01	2.72
PC	10.5	3	3.5	2.5	70.79	3.1	1.03	1.71	1.86
WG	69.7	11	6.3	14.2	224.61	18.2	1.66	4.28	2.55
<i>100m buffer</i>									
COP	10.6	17	0.6	0.9	148.29	4.9	0.29	3.38	1.45
CP	48.1	9	5.3	7.7	144.41	10.2	1.13	2.39	1.94
DC	82.5	16	5.2	10.5	203.75	17.9	1.12	3.11	2.25
GAM	21.4	21	1.0	2.8	273.79	7.2	0.34	2.71	1.58
LCBS	278.4	43	6.5	30.7	473.37	36.6	0.85	3.34	1.61
LL	93.3	15	6.2	14.0	224.53	15.6	1.04	2.38	2.06
PC	17.2	10	1.7	2.4	136.46	4.8	0.48	1.83	1.44
WG	95.2	25	3.8	11.4	300.66	21.3	0.85	3.01	2.13

Table 4.1 continued

Fragment	CA	NumP	MPS	PSSD	PSCoV	TE	MPE	MSI	AWMSI
<i>500m buffer</i>									
COP	108.8	40	2.7	6.4	235.49	22.2	0.56	3.03	1.48
CP	215.3	57	3.8	10.1	266.21	40.0	0.70	2.94	1.62
DC	291.2	36	8.1	18.4	227.85	44.3	1.23	4.16	2.08
GAM	140.3	82	1.7	3.5	204.58	39.1	0.48	2.95	1.51
LCBS	610.1	117	5.2	20.5	392.72	85.8	0.73	3.47	1.53
LL	297.9	71	4.2	12.2	291.30	53.4	0.75	2.97	1.92
PC	127.8	61	2.1	4.5	215.57	30.5	0.50	2.35	1.47
WG	337.8	107	3.2	12.2	385.03	63.7	0.60	2.60	1.85
<i>1000m buffer</i>									
COP	372.5	57	6.5	20.9	320.16	43.2	0.76	2.81	1.39
CP	576.8	133	4.3	10.4	239.23	103.5	0.78	2.78	1.68
DC	685.4	54	12.7	34.8	274.10	78.2	1.45	4.05	1.98
GAM	429.8	118	3.6	8.4	230.91	80.4	0.68	2.96	1.56
LCBS	1150.8	260	4.4	14.3	324.04	178.3	0.69	3.19	1.56
LL	692.3	125	5.5	15.3	275.98	102.4	0.82	3.25	1.86
PC	407.6	134	3.0	7.9	259.70	84.1	0.63	2.73	1.61
WG	768.3	184	4.2	13.9	332.30	127.2	0.69	2.59	1.64

Table 4.2. Eigen Values and Pearson Correlations for metric vectors with the first two ordination axes for PCA of herbaceous and tree communities

Axis	Tree species		Herbaceous Species	
	1	2	1	2
Eigen Value	59.069	36.689	32.446	20.406
% variance	36.332	22.566	29.845	18.771
Metric	r^2	r^2	r^2	r^2
CA	.903	.020	.079	.042
NumP	.041	.196	0.223	0.001
MPS	.905	.006	0.064	0.062
PSSD	.942	0.071	.046	0.037
ED	.991	.001	.003	0.063
MSI	.498	.370	0.174	0.136
AWMSI	0.010	0.512	0.677	.350

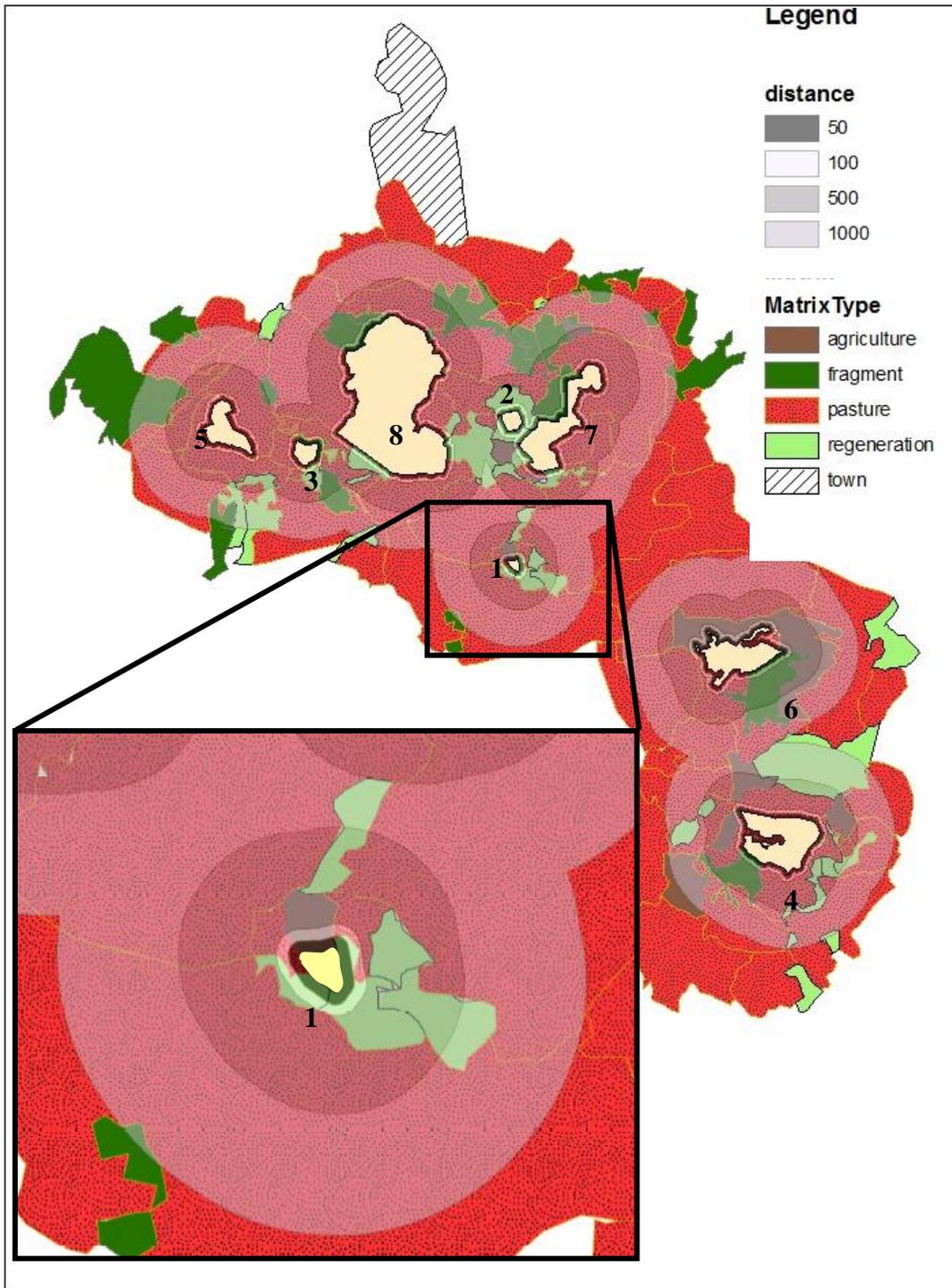


Figure 4.1. Landscape map of the Las Cruces Biological Reserve (fragment8) and surrounding focal fragments showing landscape buffer zones at 50m, 100m, 500m, 1000m. The inset shows Fragment 1a view of fragment 1 and its buffer zones in more detail.

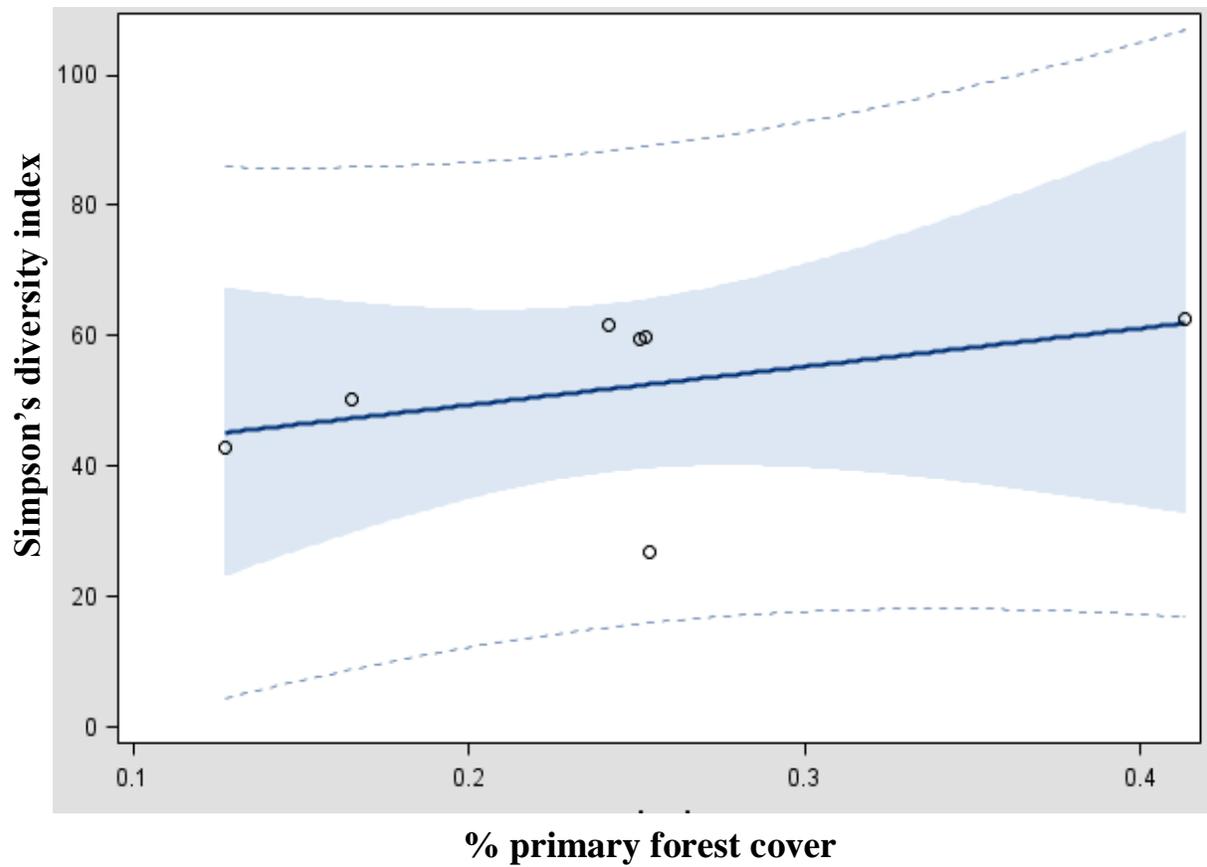


Figure 4.2. Species diversity of trees increases with primary forest cover. This graph represents the relationship for the 500m buffer zone. Similar significant relationship are observed at 50m and 100m ($p < 0.005$, analysis of covariance).

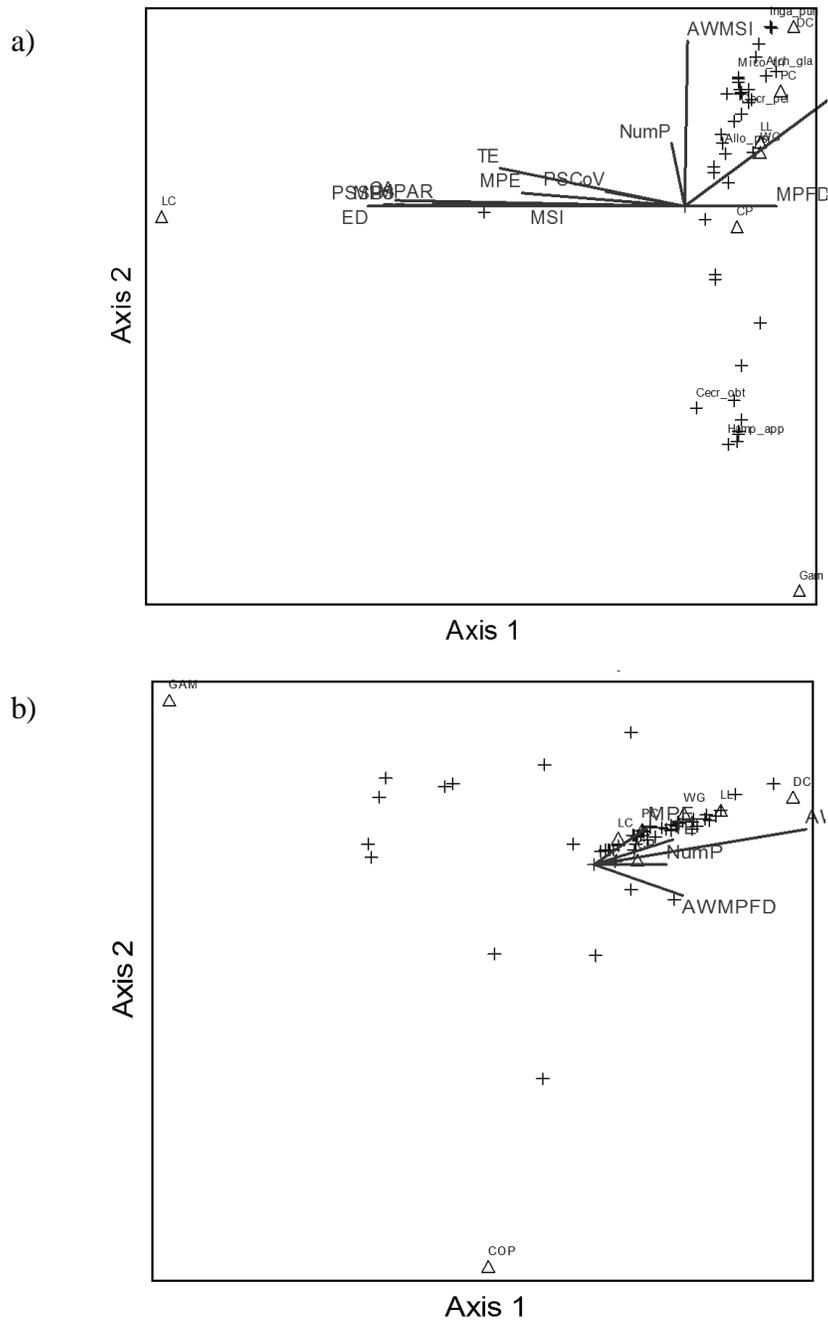


Figure 4.3. Principle components analysis biplot for a) tree and b) herbaceous species in focal fragments. Symbols represented: + species, Δ focal fragments, — landscape metrics. Full descriptions of metric variables are detailed in Table 2.

CHAPTER 5

CONCLUSIONS

This dissertation examined fragmentation impacts using the traditional conceptual framework of island biogeography theory, along with more recent concepts about fragmentation impacts, edge effects and matrix influences. Premontane forests have experienced high rates of deforestation in the later twentieth century (Sanchez-Azofeifa et al., 2001) and continue to be threatened by habitat loss for agriculture, road building and development. Currently, the typical landscape at premontane elevations in Costa Rica, and elsewhere in the tropics, is a mosaic of smaller forest remnants or fragments surrounding by non-forest landuse (Daily et al., 2001). Although fragmentation has been shown to alter diversity and dynamics in lowland forests (Bierregaard et al., 1992; Laurance et al., 2011), it is unclear whether these findings generalize to higher elevation forests. Climate and the plant composition differ between lowland and premontane forests, and extensive drought and fire common to lowland forests are generally absent in premontane forests. Thus, there is a need for better understanding of premontane forest plant community responses to fragmentation, particularly as anthropogenic pressures continue to threaten habitat and biodiversity in premontane forests.

I first examined fragmentation impacts in premontane forest using a traditional framework – island biogeography theory (MacArthur and Wilson, 1967). In chapter 2, I investigated fragmentation responses predicted by island biogeography theory. Although island biogeography has been a key concept in predicting species richness on oceanic islands and

lowland Amazonian fragments (McArthur and Wilson, 1967; Bierregaard et al., 1992), my study found that island biogeography theory predictions for species richness were not supported for herbaceous or tree species in the premontane habitat studied. Species richness did not show a significant relationship to fragment size or degree of isolation in the Las Cruces Region. Instead, results showed that approximately fifty years after fragmentation, current plant communities may still reflect the high richness and diversity of pre-fragmentation continuous forest.

My study also observed very low similarity among fragments, indicating that each fragment is unique sharing only a few species with other fragment. This high diversity is typical of tropical forests. Many species have rare distributions and are represented by one or a few individuals of per hectares. Although, diversity remains high among fragments, plant community composition varies greatly among fragments. Pioneer tree species, typically more common gaps and near forest edges, dominate the smaller tree sizes classes. This foreshadows a shift in composition from dominance by mature forest species to a greater abundance of pioneer tree species in a few generation. As observed in lowland tropical forests, both increased mortality of mature forest species and high regeneration rates of pioneer contribute to this compositional change (Laurance et al., 2006a, Laurance et al., 2006, Nascimento et al., 2006). Thus, although smaller and more isolated fragments in the Las Cruces area appear highly diverse (contrary to predictions of island biogeography theory), premontane forests fragments may lose more mature-forest species in the future. However, protracted relaxation over several decades, allows time for conservation measures such as restoration and protection of mature forest species which can moderate fragmentation impacts and biodiversity loss.

Species compositional changes within fragments can be driven by abiotic factors which affect recruitment and growth (Kapos, 1989; Sizer and Tanner, 1999). Fragment edges exposed

to the surrounding matrix may experience conditions that differ greatly from the forest interior. The matrix is often more open, and experiences greater irradiation, higher temperatures and greater moisture stress than forest interior. These contrasting conditions, termed edge effects, can penetrate into the fragment reducing the amount of forest interior available to interior-dwelling species. In chapter 3, I quantified the magnitude and distance of edge effects in the Las Cruces region and determined accompanying species composition changes from the surrounding pasture into the fragment interior. A moderate edge effect extending 10m into the forest interior persisted even fifty years post fragmentation. This persistent edge effect may be due to the abrupt edge of fragments, with less sealing or closing of the vegetation at the fragment/pasture boundary. An increase in pioneer trees and more weedy herbs was observed closer to the fragment boundary than in the forest interior which corresponded with an increase in temperature, vapor pressure deficit and light availability within 10m of the forest edge. The greater abundance of pioneer trees near fragment edges compare to fragment interior support the idea that the shift in plant composition shift observed in chapter 2 is a result of more open edge or gap –like habitat found in forest fragments than in continuous forest.

In addition, to providing information of the response of plant communities to fragmentation, the results of chapter 2 and 3 can inform conservation practices, specifically in reserve design. I found in chapter 2 that small fragments experience high diversity and maintain conservational value. The edge effects in these fragments extend only a short distance into the fragment (chapter 3), leaving even small fragments with predominantly interior habitat. A one hectare square fragment (100m x 100m), for example, will contain more than 60% interior habitat compared to edge and provide a microclimate suitable for interior species. These findings recognize the value and potential several small fragments (and not just one large fragment) for

conservation (Diamond, 1975; Arroyo-Rodriguez et al., 2009). One caveat, however, is that small fragments may not provide sufficient resources (e.g. food and nest-sites) to support animal populations, even when microclimate is optimal.

The final data chapter of this dissertation takes a landscape approach to understanding plant diversity in fragments, and focuses on the configuration of the matrix rather than solely on the fragment interior. Both matrix quality (landuse) and configuration (edge, shape, and patchiness) can influence fragment species composition (Lindenmayer and Franklin, 2002). Using spatial analysis software, I described a patchy landscape made of irregular patches of primary and regenerating forest, pasture and agricultural crops. This study demonstrated that landscape metrics correlate with both tree species diversity and composition. This is a novel approach to understanding fragment plant composition and corroborates the findings of chapter 3 that matrix can affect plant species composition. In both chapters, edge plays an important role determining plant composition; the amount of edge (chapter 4) and the distance from the edge (chapter 3) are both associated with increased pioneer abundance. Thus landscape quality and edge parameters can be used to build or improve fragmentation models (Kupfer et al., 2006).

The matrix may act as a barrier or conduit to movement of seeds and pollen among fragments, particularly for animal dispersed species (Ricketts, 2001; Watling et al., 2011). In chapter 4, spatial analysis demonstrated that tree species richness was greater in fragments surrounded by other patches of primary forest. In this way fragments may serve as stepping stones for the movement of animal dispersers. Thus, management practices that increase the amount of forested habitat in the landscape may aid conservation in fragmented landscape.

In summary, my studies demonstrate that a more complete understating of fragmentation impacts on plant composition can be obtained via evaluation of the fragment in the context of its

surrounding rather than by analysis of the fragment in isolation. This dissertation also suggests that small premontane fragments in a heterogeneous landscape can maintain high levels of biodiversity for at least a few decades, allowing some time for the implementation of conservation practices to ameliorate the loss of biodiversity.

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