Landscape effects on insect pests of *Dracaena marginata* and their associated natural enemies in Costa Rica

by

Mildred Linkimer

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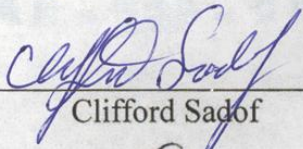**2012**

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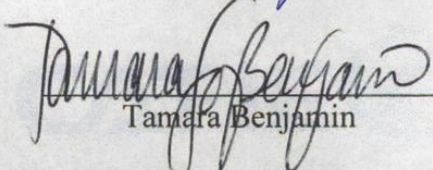
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Student name

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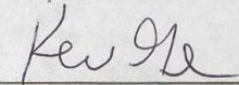Has been reviewed in final form and approved, as indicated by the signatures and dates
given below:

Major Co-Advisors: Date: 2/29/12
                    Fernando Casanoves

                                                                           Date: 4/17/12
                    Clifford Sadof

Committee Members: Date: 2/29/12
                    Tamara Benjamin

                                                                           Date: April 17, 2012
                    Jeffrey Holland

                                                                           Date: 4-18-12
                    Kevin Gibson

Area Head: Date:
                    John Beer

Dean, Graduate School: Date:
                    Thomas Dormody

DEDICATION

To Heiner and Ariel, happiness and strength of my life.

To my mom and dad who never stopped fighting for us.

A Heiner y Ariel, la felicidad y Fortaleza de mi vida.

A mi papá y mamá que nunca dejaron de luchar por nosotros.

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CONTENTS

SUMMARY

Ornamental production is one of the most important economical sources of income for Costa Rica (CR) and a significant part of their agricultural landscape. Within the ornamental plants, *Dracaena marginata* Lam. (Rusaceae) provides an opportunity to study the population dynamics of three families of herbivorous arthropods which differ importantly in terms of their biology: Cicadellidae (leafhoppers), Tettigoniidae (katydids) and Diaspidiidae (armored scales) (Colpetzer 2005). This study examined how the landscape in which *D. marginata* is embedded affected the abundance and distribution of these three insect pest groups and their associated natural enemies.

In order to evaluate the effect of the macro landscape on crop pest abundance, different landscape metrics were evaluated at six spatial scales from local to broad scale. Insect groups showed different responses at different spatial scales. While leafhopper egg abundance was more sensitive in terms of their correlations with different land uses and metrics; katydid egg abundance showed only some isolated correlations at specific spatial scales, metrics and land uses. On the other hand, armored scale abundance practically showed no correlation with any land use and metric at the spatial scales set in this study.

We also tested the hypothesis that forest patches may provide ecosystem services for *D. marginata* fields, acting as a source of natural enemies and predators that can reduce insect pest populations. We found that forest may provide ecosystem services for *D. marginata* fields, reducing leafhopper populations through bottom up and top down effects. Leafhopper eggs and nymph populations were lower in plots near forest patches, while katydid egg presence was not affected by the presence of forest but their abundance increased at the field edge. Levels of parasitism also played an important role of regulating leafhopper and katydid populations when conditions were appropriate. Armored scale abundance was not affected by the adjacency of forest, however we identified that the presence and distribution of natural enemies was a key factor, which seemed to suppress their populations at the field edges.

Finally, the effect of the landscape at the local scale was evaluated through the response of pest populations and their natural enemies to the presence of weeds from

selective functional groups in the ground cover of *D. marginata* production fields. Leafhoppers were more sensitive to changes in weed cover composition and females seemed to prefer to concentrate their oviposition on Dracaena plants, which are a suitable host to produce offspring, increasing egg density on grassy treatments. Predatory insects also played an important role regulating leafhopper populations. Vegetation composition and structure strongly influenced katydid distribution as they were never found in areas lacking their preferred hosts. For armored scales other factors, such as dispersal capacity and management practices, are more important for their distribution in the fields.

We concluded that the differences in the response among our insect pest groups to the landscape, from broad to local scales, are mainly attributed to a combination of factors that influenced their capacity to disperse, colonize Dracaena fields, and escape from natural enemies.

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LIST OF ACRONYMS

APHIS: Animal and Plant Health Inspection Service

CNP: Consejo Nacional de la Producción

CSP: Clean Stock Program

MAG: Ministerio de Agricultura y Ganadería

USDA: United State Department of Agriculture

CHAPTER 1. INTRODUCTORY CHAPTER

Ornamental production is one of the most important economical sources of income for Costa Rica (CR), exporting more than US$85 million in ornamental plants and flowers to different countries around the world (Arce *et al.* 2009). In the past few years the development of the ornamental sector has become almost as important as coffee production. The principal trading partner is the United States of America (USA), which imports 56% of Costa Rican ornamental production, representing more than US$31 million (CSP 2005). Currently, ornamental production supports small producers and their families as well as medium and large enterprises. It provides a steady source of income, and creates jobs in vulnerable rural areas and surrounding urban sites. Specifically for the genus *Dracaena*, an important ornamental plant in CR, there are more than 40 firms who export to the USA involving more than 500 small and medium farmers (CSP 2005).

However, Costa Rican's ornamental market with the USA is at risk due to a possible market closure. A Pest Risk Analysis (PRA) developed by the Costa Rican Ministry of Agriculture of Costa Rica (MAG) and the United States Department of Agriculture (USDA) showed a high percentage of pest interceptions in *Dracaena* at USA entry ports. Between 1984 and 2011, there were more than 11,000 interceptions in Dracaena plants from CR, representing 30% of all interceptions of Costa Rican agricultural products (Colpetzer *et al.* 2011). These interceptions have a negative economic impact on everyone in the production chain (farmers, packing houses and exporters) due to costs incurred from fumigation or disposal, and also create a loss of image for Costa Rican agricultural products at the world level.

In order to minimize the phytosanitary risk associated with *Dracaena* exportations to the USA, a Clean Stock Program (CSP) has been implemented in CR. This program includes a series of best agricultural practices (BAP) that are carried out to reduce the risk of quarantine insect introductions in the USA. To develop these BAP's it is necessary to identify and characterize the quarantine pests and their natural enemies associated with the crop, as well as to evaluate how they respond to different agricultural practices and

landscape variables. As far as the landscape effects are concerned, it has been demonstrated that landscape patterns can have an effect on insect ecological and spatial processes such as dispersion, distribution, movement, population size and richness (e.g. Kareiva 1983, Turner 1989, Fahrig and Merriam 1985, Harrison and Tomas 1991, Dunning *et al.* 1992, Coll and Bottrell 1994, Hanski, 1994, Jonsen and Fahrig 1997, With *et al.* 1999, 2002, Chust *et al.* 2004). The purpose of this study is to evaluate the effect of the landscape context on the *Dracaena marginata* pest complex and to find possible alternatives to pest control related to landscape management in Dracaena fields.

1.1 Objectives

General objectives

To evaluate the effect of the landscape, in which the *D. marginata* is embedded, on the abundance and distribution of three insect pest groups with different biology traits (leafhoppers, armored scales and katydids) and their associated natural enemies.

Specific objectives

1) To evaluate the effect of the macro landscape context, in which *D. marginata* is embedded, on insect pest groups with different biology traits.

2) To evaluate the response of insect pest groups to different spatial scales within the macro landscape context.

3) To determine the effect of the presence of forest near *D. marginata* fields on pest abundance, natural enemies abundance and parasitism levels.

4) To evaluate the response of pest populations and their natural enemies to the presence of weeds from selective functional groups in the ground cover of *D. marginata* production fields.

1.2 Hypotheses

The landscape patterns where *Dracaena marginata* is grown are characterized by its spatial heterogeneity and diversity of land uses, typical of the tropics. These patterns may have an influence on insect pest distributions and abundance, oftentimes converting this crop into a prime host plant, consequently increasing the pest pressure on the crop.

1) Macro landscape context, in which *D. marginata* is embedded, have an influence on the insect pest abundance and this landscape effect can differ between insect groups depending on their biological traits.

2) Insect pest groups respond at different spatial scales depending on their dispersal capacities.

3) Forest provides ecosystem services for *D. marginata* fields, acting as a source of natural enemies and predators that can reduce the abundance of at least one insect pest group.

4) Insect pest groups and their natural enemies respond differently to weeds in *D. marginata* production fields from different functional groups.

1.3 Literature review

Generalities of Dracaena marginata

Dracaena belongs to the Dracaenacea family in the order Lilials. It originates from Asia and Africa, but is able to grow throughout the world. There are more than 40 *Dracaena* species described, but only six of them are produced commercially: *D. deremensis*, *D. fragrans*, *D. godseffiana*, *D. marginata*, *D. reflexa* y *D. sanderiana* (Salas *et al.* 1991, Chen *et al.* 2002) (**Figure 1.1**).

Figure 1.1.   Different species and varieties of Dracaena: (A) Dracaena deremensis 'Warneckii', (B) Dracaena deremensis 'Lemon Lime', (C) Dracaena deremensis 'Compacta', (D) Dracaena fragrans 'Massangeana', (E) Dracaena sanderiana, (F) Dracaena reflexa. Source: Sánchez de Lorenzo (2003).

Dracaena marginata, known as Madagascar Dragon Tree or Red Edged Dracaena, originated from Madagascar and is considered a slow-growing shrub, eventually reaching heights of 2-5 meters with linear leaves that are 30-90 cm long and 2-7 cm wide. The color of the plant varies from strong olive green with red margins to magenta (Huxley 1992, Lötschert and Beese 1983). In Costa Rica, six varieties are produced commercially: green, bicolor, tricolor, colorama, tigra or kiwi and purple or magenta (**Figure 1.2**). These varieties are mainly commercialized as tips but, over the past few years, the increase in demand has diversified the market and new forms are being produced such as straights, candelabras, multiples, character and stumps. Different sizes are also produced from small individual plants (4-5") to plants with canes larger than 18" (Acuña *et al.* 1992).

Figure 1.2.   Some of the most commonly produced varieties of *D. marginata* in Costa Rica. Green (A), Magenta (B) and Bicolor (C).

D. marginata is mainly cultivated in sunny conditions; however it is possible to produce it under shade between 6 and 14 moles/day. Plant development is improved when temperatures fluctuate between 23.9 ℃ and 32.2 ℃, soil pH is between 5.5 and 6.3, average relative humidity ranges from 90 to 95% and annual precipitation is around 3000 mm. These conditions are generally found in the tropics at altitudes from 0 to 700 m (PROEXANT 2007).

Principal quarantine pests associated to *Dracaena marginata*

Based on the number of interceptions that have been registered between 1984 and 2004 in the port of Miami, Florida, 74.5 % of the interceptions belonged to four quarantine pest groups: leafhoppers from the family Cicadellidae (41 %); katydids from the family Tettigonidae (23.2%); snails or mollusks, mainly *Succinea costaricana*, (6.5%); and armored scales (3.7%) (PIN 2006).

Leafhoppers. Homoptera: Cicadellidae

The Cicadellidae family, commonly known as leafhoppers, belongs to the Order Homoptera. They are known for their colorful patterns, elongated shape and large size, which can be between three and 15 mm in length. There are more than 50 subfamilies in the world, of which at least 16 have been reported in Costa Rica. Leafhoopers uses their stiletto to feed exclusively on sap from the leaves and stems of different types of plants. They

develop rapidly and can produce six generations or more each year. Nymphs feed on the same plants and in the same way as adults. They pass through five nymphal stages before becoming adults, which can live from a few weeks to months (Godoy 2006).

In *D. marginata* fields in Costa Rica, more than 60 different morphotypes of cicadellids and delphacids have been found and identified (**Figure 1.3** and **Figure 1.4**). Six types of eggs, which have quarantine importance, have been recognized. Some of the most important species include: *Calweliolla reservata*, *Empoasca* sp. and *Oncometopia clarior*. *Empoasca* sp., mainly found in green and magenta varieties, is characterized for laying cryptic eggs, which make them difficult to detect in Dracaena leaves (CSP 2007). Studies have been also found (Prado 2006) that leafhopper eggs can be parasitized by insects from the following families: Trichogrammatidae, Chalcididae, Encyrtidae, Dryinidae, Pipuneulidae, Epipyropidae, Eulophidae, Platygastridae, Mymaridae, and Strepsiptera.

The economical importance of leafhoppers lies in that they are known to be vectors of diseases that impact other agricultural crops around the world. For example, *Scaphoideus titanus* Ball is the phytoplasma agent of Flavescence doreé (*Candidatus Phytoplasma vitis*, 16Sr-V) a persistent disease of grapevines (Boudon-Padieu 2000), first found in Europe, but is now widespread throughout the world. *Homalodisca coagulata* has been associated with outbreaks of plant diseases induced by the bacterium *Xylella fastidiosa* Wells in grapevines (Pierce's disease), oleander (oleander leaf scorch) and almonds (almond leaf scorch) (Blua and Morgan 2003, Purcel *et al.* 1999, Almeida and Purcell 2003) in the United States. *Oncometopia nigricans* has also been found to be a vector of Citrus Variegated Chlorosis, an economically important destructive disease in Brazil that is caused by the same bacterium, *Xylella fastidiosa* Wells (Brlansky *et al.* 2002).

Figure 1.3.   Different morphotypes of nymphs and adults of Cicadellidae and Delphacidae found in Dracaena fields in Costa Rica. Photos by E. Hidalgo.
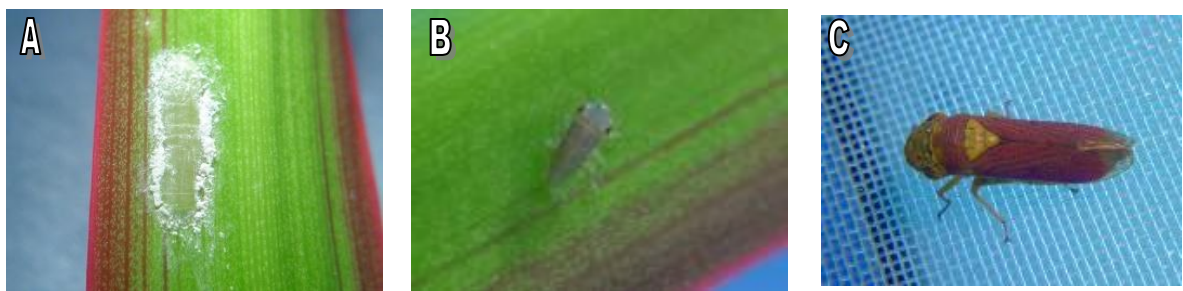
Figure 1.4   *Oncometopia clarior* one of the most commonly found cicadellids in Costa Rica Dracaena fields. (A): egg mass, (B): nymph, (C): adult. Photos by E. Hidalgo.

Tettigoniids. Orthoptera: Tettigoniidae

Insects known as katydids belong to the Tettigonidae family. This family has more than 6800 species and is distinguished from other families of the Order Orthoptera by its large antennae which are longer than their body, reaching lengths of 5 to 6.4 cm (Davies 1991). Their colors vary from green to brown and are characterized for being nocturnal. One of the most important quarantine katydid found in *Dracaena* fields in Costa Rica is *Microcentrum* sp. (**Figure 1.5**). They are associated with a variety of plants, but are mainly found in crops and weeds related to the Poaceae family (Squitier and Capinera 2002). Katydids do not feed on *D. marginata*, however interceptions occur because they lay their eggs on the ornamental plants. Unlike many other groups of insects, currently there are no exotic or introduced orthopteran species among the state of Florida in the USA, one of the principal destinations of CR ornamentals (University of Florida 1999). The nymphal stages feed on grasses within the fields and once they become adults migrate to other areas (CSP 2007). Temperature and humidity are related positively with species richness, composition and abundance of orthopterans (Kemp *et al.* 1990). As such, when temperature and humidity increase, orthopterans growth speeds up.

Figure 1.5.   Different stages of the commonly found Katydid, *Microcentrum* sp. (A): eggs, (B): nymph and (C): adults in Dracaena fields in Costa Rica. Photos by E. Hidalgo.

Chemical control is the most traditional method used to reduce orthopteran populations. However, due to their great mobility; other individual grasshoppers migrate into the areas that have been vacated by mortality. Biological control includes the use of biopesticides and natural enemies. *Nosema locustae* Canning, which is a protozoan (microsporidian) that infects orthopterans has been used to control a great diversity of orthopterans throughout western North America (Evans 1990). *Metarhizium anisoplae* has

also been used as a biopesticide to control orthopterans in their first stages. *Nosema* and *Metarhizium* do not kill or harm other insects, wildlife, or humans (Lomer *et al.* 2001). Some tettigonid species are also susceptible to *Leidyana* sp., and *Hentschelia* sp. Natural enemies such as *Isodantia harrisi* (Fernald), *Centrodora xiphidii* (Perkins) and *Bracnistella lutea* (Fullaway) have also shown high levels of parasitism in Tettigonids (Senthilkumar 2004).

Scales. Homoptera: Coccoidea

Scales are a large group of plant feeding insects. Adult female scales are wingless and legless and spend their lives pressed against their hosts. Males are winged so they can fly to mate with wingless females. This group is commonly divided into soft scales (Coccididae) and armored scales (Diaspididae). Soft scales have a waxy film secreted over their body wall, while armored scales are protected with a hard separate cover secreted over their bodies. Female scale insects lay their eggs under their scale covers. In their first stage, young scales have legs and are fairly active. Known as crawlers, they are able to disperse by walking or blowing in the wind to, colonize new feeding sites. They become immobile when they change to adults. The waxy coating or cover gives adult scales a barrier or protection against most insecticides (Foldi 1990).

Armored scales are generally smaller than soft scales, but sometimes their abundance is higher, and can seriously affect or even kill their host plants. Effective control can require repeated foliar insecticidal sprays timed to coincide with the crawler stage of each generation (Virginia Cooperative Extension 2007). Some of the most important scale insect genres associated with *D. marginata* in Costa Rica include: *Aspidiotus* sp., *Chrysomphalus* sp. and *Pinnaspis* sp. (**Figure 1.6**) (CSP 2007).

Figure 1.6. Scale insects of the genres: (A)Aspidiotus, (B) Crysomphalus and (C) Pinnaspis. Source: Prado (2006). Photos by E. Hidalgo.

Scale insects often increase in warm and humid environments (Buss and Turner 2006). When temperatures rise, the life cycle is shortened and the nymph numbers increase (McClure 1990). An increase in airflow or a decrease in plant density in crop areas has been recommended to change environmental conditions and reduce their numbers (Buss and Turner 2006). Dispersal of scales depends upon the movement of crawlers, but can also be moved by wind, birds or other insects. The most important means of dispersal is the movement of infested plants by man (University of Florida 2007).

Natural controls, such as parasitoids, predators, pathogens and environmental conditions usually maintain scale populations below damaging levels in undisturbed habitats (Hank and Denno 1993). However, under certain circumstances, scale populations can increase and become injurious (Wawrzynski and Ascerno 2007). An increase in the frequency of pesticide use has been associated with thriving scale populations due to a probable decrease in natural enemy abundance (Raupp *et al.* 2001, Prado 2006).

Landscape ecology

Landscape ecology is often defined as the study of the effect of landscape patterns on ecological processes in ecosystems. Landscape ecology considers the development and dynamics of spatial heterogeneity, including interactions and exchanges across heterogeneous landscapes, the influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity (Turner 1989). Landscape ecology addresses the importance of the spatial pattern or configuration on the ecological processes. Since it is not only related to how much there is of a particular element but also with how it

is arranged, it is necessary to apply the concept across a wide range of scales. Landscape ecology does not define *a priori*, specific spatial scales that can be applied; as such it is necessary to identify scales that best characterize relationships between spatial arrangements and the process of study (Turner *et al.* 2001).

Landscape Concept

The term landscape is referred to as the landform of a region in the aggregate, or to the land surface and its associate habitats at different scales (Turner 1989). Most simply, it is an area that is spatially heterogeneous in at least one factor of interest (Turner *et al.* 2001). Landscapes are the result of a number of factors, variability in abiotic conditions such as climate and landform; biotic interactions; patterns of human settlement and land use; and the dynamics of natural disturbance and succession (Turner *et al.* 2001).

Climate and landform establish the pattern on which the soils and biota of a region are developed. Climate influences biogeography patterns through the distribution of energy and water. Landforms are determined by the landscape patterns, particularly the distribution of moisture, nutrients, and resources in that landscape. They are also impacted by the disturbance regimes and are constrained by the pattern and rate of geomorphic processes. In this sense, climate and landform are determinant in the development of landscapes.

Even in a homogeneous space, interactions among organisms may lead to diverse spatial structure. In fact, theoretical population ecology explains how interactions, such as competition and predation within and among populations, can generate diverse spatial patterns and how these patterns influence the outcome of interactions (Ives *et al.* 1998). Humans also have a strong effect on landscape patterns, altering the rate and direction of natural processes. Land-use patterns form the abiotic templates that determine the environment in which organisms live, reproduce, and disperse (Turner *et al.* 2001).

Characteristics of the landscape

The landscape can be characterized in three aspects: structure, function, and change (Forman and Godron 1986). Structure refers to the spatial relationships between each ecosystem, including the distribution of energy, materials, and species in relation to the size, shapes, numbers, kinds and configurations of the components. Function concerns the

interactions between the spatial elements: the flow of energy, resources, and organisms among the components of the ecosystems. Change refers to the variation in the structure and function of the ecological mosaic through time (Turner 1989).

Concept of scale

Scale refers to the spatial or temporal dimension of an object or a process. It is used by ecologists to refer both to the magnitude of a study or extent of the processes, and also to the spatial and temporal resolution of the data or the degree of detail (Fortin and Dale 2005). In other words, it is characterized by its grain, the finest spatial resolution within a given data set; and its extent, which refers to the size of the overall study area (Turner *et al.* 2001, Quattrochi and Goodchild 1997). Therefore, an area might be considered homogeneous in a smaller extent (e.g. one forest stand), or heterogeneous in a larger extent (e.g. a mosaic of forest stands) (Fortin and Dale 2005). If landscapes are considered spatially heterogeneous areas, the structure, function, and change of landscapes will be scale-dependent. For that reason, to explain this concept, landscape changes with the grain or the extent of the measurement (Turner 1989) as such spatial and temporal scale effects must be taken into account in studies of landscape ecology.

Some studies have focused on defining how species perceive their landscape at different scales. For example, Wiens and Milne (1989) determined how beetles respond to the mosaic patterns found at a micro-landscape scale, and developed models that predict random movements through landscapes under various constraints. However, depending on the system studied, the physical distances that influence local vs. global can be different (Fortin and Dale 2005). Thus, the scale will not be the same from the perspective of a beetle in comparison to a wolf.

Quantifying landscape patterns

Analyzing spatial patterns using different methodologies and scales of observations become a necessary strategy in order to understand the ecological complexity. Thus, because landscape ecology studies the interactions between spatial patterns and ecological processes, it is necessary to identify and quantify the landscape structures. As such,

quantitative methods are required to compare the different landscape patterns so that measurable links to ecological processes can be determined.

A "pattern" is defined as "the way in which the elements of something are arranged" (Merriam-Webster 2005), implying that it is possible to find it and describe it. It is also defined as "the perfect embodiment of something" (Merriam-Webster 2005) and therefore "pattern" is sometimes used as the opposite of "random". Taking into account that patterns in ecological systems are dynamic, evolving and changing, a spatial pattern is usually a single realization of snapshot of a process or of a combination of processes at one given time (Fortin *et al.* 2003).

There are a number of terms that describe patterns found within a landscape: diversity, dominance, contagion, fragmentation, and patch shape complexity (Frohn 1998). Diversity, often referred to as landscape richness, is defined as the total number of landcover types (Forman 1995). Landcover is defined as *"the observed (bio) physical cover on the earth's surface"* including vegetation and man-made features (Gregorio and Jansen 2000). Dominance is defined as the degree to which one or a few landcover types dominate the landscape in terms of proportion. Contagion is the tendency of landcovers to cluster or clump into a few large patches (Wickham *et al.* 1996). Fragmentation is the tendency of landcover types to break up into many small patches (Forman 1995). Both terms are opposite of one another. The last term, patch shape complexity, refers to the relationship between the perimeter of a patch and the area of the patch. In general, complex patches have greater scaled perimeter-to-area ratios, and simple patches have lower scaled perimeter-to-area ratios. The last three terms are relative to both spatial resolution and ecological processes.

Landscape patterns and ecology of the insects

Spatial patterning and changes in landscape structure (e.g. habitat fragmentation) can have an effect on insect ecological processes such as dispersion, distribution, movement, persistence (Turner 1989), population size, and richness. For example, Jonsen and Fahrig (1997) determined that the landscape has a dynamic spatial structure and can have an influence over the distribution of both local and regional populations of organisms.

Changes in landscape structure, such as the reduction of the proportion of one or more patch types or the increase in patch isolation, can alter the ability of organisms to disperse (Fahrig and Merriam 1985). The size of populations can also be altered by the effects of spatial and temporal patch structure. Specifically, three factors of habitat patch structure have been demonstrated to have an influence on insect population size: patch size and patch age, which have a positive effect on population size; and frequency of disturbance, which has a negative effect (Kareiva 1990, Harrison and Tomas 1991, Fahrig 1992). In addition, density and species diversity of vegetation have shown to influence herbivore movement (Kareiva 1983) and insect population size because they are able to alter the capability of natural enemies to attack herbivores (Coll and Bottrell 1994, Tscharntke and Kruess 1999).

It is important to take into account that landscape context does not influence all species equally (Kareiva 1990, With *et al.* 1999, 2002). Insects, that are able to obtain necessary resources to survive by using more than one habitat type, rise when landscape diversity increases (Dunning *et al.* 1992). There are some effects that lead to an increase in the species richness and abundances of generalist insects at the landscape level. For example, when the connectivity becomes greater, dispersal rates will increase and the rate of local extinctions will decrease due to increased immigration. Also, faster recolonization of local extinctions can occur due to increased dispersal rates (Fahrig and Merriam 1985, Hanski 1994). However, specialist populations seem to be affected by the amount of crops on the landscape. Size and abundance of specialists increase with the proportion of crops, since susceptibility to extinction will increase in larger populations; and the tendency to go extinct at local populations will have less impact on a high number of local populations (Jonsen and Fahrig 1997).

To understand how the organisms perceive their landscape and to obtain results more realistically, it is essential, previous to any landscape analysis, to identify all the biological and ecological features of the organisms involved.

Landscape context on insects at different spatial scales

Different species respond to their environment at different spatial and temporal scales (Wiens and Milne 1989, With 1994a, b). In addition, the interactions among

communities are made up of species with different spatial strategies (Kareiva 1990, With *et al.* 1999, 2002). Thus, it is important to consider how different organisms perceive their landscape, to understand the links between the species-specific use of the space and the spatial scale experienced with population dynamics and ecological processes.

Wiens and Milne (1989) and Wiens (1992) suggested that there is a link between the scale of landscape perception and the mobility and activity of organisms within local habitats. He indicated that populations of highly mobile organisms would be less sensitive to the spatial configuration of local habitat patches than those less mobile. In this sense, it is expected that less mobile species would respond at finer scales than would a higher mobile group. For example, Chust *et al.* (2004) studied the scale at which forest spatial patterns cause changes in richness and abundance of Homopteran. They demonstrated that the relative abundance of these species show an association with the vegetative cover at local spatial scales (optimal scale: 0.36-2.25 ha) and that 62% of their richness variation could be identified at an optimal local scale of 6.25 ha (250 × 250 m). Conversely, predators and parasitoids of the Dipteran groups, respond to landscape patterns at broader scales (250-272 ha) and this could be explained by the greater mobility of Dipteran groups in comparison to most Homopteran species. As a consequence, developing the appropriate scale has become a challenge for ecologists because there is no single correct scale at which all organisms respond to the landscape, or at which investigators may expect to analyze their data. Actually, it has been affirmed, "ecologists must recognize that identifying the right scale still requires combining art with science, because satisfactory algorithms do not currently exist" (Turner *et al.* 2001).

Cicadellids and their relation with the macro and micro landscape

Cicadellids have been associated with specific land uses, which provide food, reproduction sites or shelter areas. As such, some landscape variables are important factors in insect dispersion and disease spread. For example, *Citrus* plants have been identified as an excellent reproductive and overwintering host for *Homalodisca coagulates* (Blua and Morgan 2003). Other habitats, such as riparian vegetation, have been related to *Graphocephala atropunctata* (Signoret), the blue-green sharpshooter (Purcell 1975), and irrigated pasture and other habitat supporting grasses have been linked with

Draeculacephala minerva Ball, the green sharpshooter, and *Xyphon fulgida* (Nottingham), the redheaded sharpshooter (Purcell and Frazier 1985). Other studies suggest that the surrounding landscape plays a major role in the population dynamics of the leafhoppers *Empoasca vitis* and *Scaphoideus titanus* (Decante and van Helden 2006). They found that the forests bordering vineyards could increase adult influx and could also induce accumulation of migrating adults either, by 'turbulence' effects placing them behind such borders, or by a 'natural barrier' effect intercepting the highly mobile adults, emigrating from the other plots. Conversely, Chust *et al.* (2004) deduced that Homopteran species richness was affected negatively with the amount of surrounding forest. Richness increased in a landscape is characterized by scattered forest patches within a matrix of agricultural and fallow land .At the micro landscape level, the relationships between cicadellids and their host plants are scarce. In general, it has been shown that cicadellids commonly inhabit grasses (Godoy 2006), although other authors have failed to find this association (Lamp *et al.* 1994). Due to their great mobility, leafhoppers are able to migrate from crops to wild plants and conversely without overlap between habitats (Hidalgo *et al.* 1999). In addition, it has been determined that leafhoppers required different plant species to complete their life cycle. For example, Sauer and Maurer (2001) found that the cicadellid *Attenuipiga Vanduzeei* prefers *Sporobolus heterolepis* as shelter and *Bouteloua curtipendula* for oviposition. *Lantana camara* has been associated as an important host plant for the development of the *Oncometopia* life cycle (Milanez *et al.* 2003, CSP 2007). Weeds such as *Laportea aestuans, Phyllanthus amarus* and *Cyathula prostata* have also been found to be host plants for feeding the leafhopper *Oncometopia clarior* (Perez 2007). The preference for the host plant has also been associated with season. For example *Draeculacephala crassicornis* Van Duzee lays its eggs on grasses in pastures at the beginning of summer and on *Bromus carinatus* at the end of the season (Purcell 1985).

Related with the effect of landscape over the spatial distribution of leafhoppers' natural enemies Cerutti *et al.* (1991) and Bosco *et al.* (1997) determined that the proximity of mixed forests was associated with an increase in the presence of natural enemies, and thus a decrease in the overall populations of *E. vitis*. However, other studies (Böll and Hermann 2004) have not shown any effect of such surroundings on population levels of these cicadellid parasitoids. These results suggest that there is no single response of

organisms to the landscape. Each organism, even of the same family, could perceive and could be affected by the landscape in different ways. Thus, studies in this topic should be considered carefully, trying to focus on the study area and trying to avoid generalizations.

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CHAPTER 2. EFFECTS OF MACRO LANDSCAPE CONTEXT ON PESTS OF QUARANTINE IMPORTANCE ASSOCIATED WITH *DRACAENA MARGINATA* IN COSTA RICA

2.1 Introduction

Local ecological pattern and processes, including the occurrence of species, population densities and dynamics, trophic interactions and community structure, have been determined to be influenced by the landscape matrix in which the species are embedded (Turner 1989, Kareiva 1990, Menalled *et al.* 1999, Thies and Tscharntke 1999, 2003, Tischendorf and Fahrig 2000, Ricketts 2001, Turner and Gardner 2001, Chust *et al.* 2004). Particularly for insects, different characteristics landscape elements, including those related to the habitat fragments or patches, such as size, geometry, spatial arrangement, isolation, and quality of habitats have demonstrated to affect occurrence and population density of insect communities (Tscharntke and Brandle 2004 and references therein).

For example, Jonsen and Fahrig (1997) determined that landscape has a dynamic spatial structure and can have an influence over the distribution of generalist and specialist insect herbivores. Changes in landscape structure, such as the reduction of the proportion of one or more patch types or the increase in patch isolation, can alter the ability of organisms to disperse (Fahrig and Merriam 1985). Some other landscape metrics, including those related to patch size, patch density, patch shape and spatial arrangement of host patches have also been demonstrated to have an influence on insect population size (Kareiva 1990, Fahrig 1992, Beckler *et al.* 2004, Grilli 2008). In addition, density and species diversity of vegetation have been shown to influence herbivore movement (Kareiva 1983) and insect population size because they are able to alter the capability of natural enemies to attack herbivores (Coll and Bottrell 1996, Tscharntke and Kruess 1999).

On the other hand, landscape context, also called "matrix" (i.e., the nonhabitat surrounding the native habitat patches of interest, Ricketts 2001), does more than simply define and isolate the patches, as it was assumed by the two classical paradigms of island

biogeography and metapopulation dynamics (MacArthur and Wilson 1967, Hanski 1998). Landscape matrices can also have an influence on the organism processes. As such, depending on the nature of the landscape component, grain size (*i.e.* the smallest spatial scale at which an organism recognizes spatial heterogeneity according to its perceptual range, Wiens 1989), and the degree of contrast on the other side of the patch boundary (Baguette and van Dyck 2007), the intervening habitat (matrix) may facilitate (functioning as breeding or foraging habitat) or impede the movements of insects among habitat patches (Ricketts 2001, Cronin 2003, Tscharntke and Brandl 2004, Haynes and Cronin 2006, Jonsen *et al.* 2007, Chin and Taylor 2009).

However, as interactions among communities are made up of species with different biological traits including body size, resource specialization and spatial strategies (Kareiva 1990, With *et al.* 1999, 2002), the landscape context does not influence all species equally (Kareiva 1990, With *et al.* 1999, 2002). For instance, generalist insects, that are able to obtain necessary resources to survive by using more than one habitat type, rise when landscape diversity increases (Dunning *et al.* 1992). Additionally, when the connectivity becomes greater, dispersal rates of generalist insects will increase and the rate of local extinctions will decrease due to increased immigration. Also, faster recolonization of local extinctions can occur due to increased dispersal rates (Fahrig and Merriam 1985, Hanski 1994). On the other hand, size and abundance of specialist populations increase with the proportion of the host crop. Other studies (Wiens and Milne 1989, Wiens 1992, Chust *et al.* 2004) have also suggested that there is a link between the scale of landscape perception and the mobility and activity of organisms. They indicated that populations of highly mobile organisms would be less sensitive to the spatial configuration of local habitat patches than those less mobile. In this sense, it is expected that less mobile species would respond at finer scales than would a higher mobile group.

In Costa Rica, where the production of ornamental plants is a significant part of the agricultural landscape, *Dracaena marginata* Lam. (Rusaceae) provides an opportunity to study the population dynamics of three families of herbivorous arthropods which differ importantly in terms of their biology: Cicadellidae (leafhoppers), Tettigoniidae (katydids) and Diaspidiidae (armored scales) (Colpetzer 2005). Leafhoppers have a wide range of

hosts in crops and non-crop habitats and are obligate sucking herbivores (Nault and Rodriguez 1985, Denno and Perfect 1994). Katydids are chewing insects and some species are strict herbivores while other species are facultative predators. They have a diverse range of diets, and are mostly present in grasslands and weedy areas, and typically feed on either grasses or forbs, although some species feed on both (Joern 1979, Squitier and Carpintera 2002). Armored scales have also a wide range of host plants and are sap-feeding insects (Culik *et al.* 2008, Magsig-Castillo *et al.* 2010). While leafhoppers and katydids have high dispersal capacities, armored scales are sedentary for most of their life cycle.

In this study, we test the hypothesis that the macro landscape context in which *D. marginata* is embedded can influence insect pest populations and its effects will depend on specific insect biology. We asked the following questions: (1) Do pest populations respond to the macro landscape context at different spatial scales? (2) How does the macro landscape context influence insect pests with different dispersion abilities? (3) Does insect pest abundance differ depending on the land use type at the macro landscape level? (4) Do insect pest responses differ depending on the landscape metric at the macro landscape level?

2.2   Materials and methods

Study area

The study area was located in an agricultural landscape of ornamental production in the Northern zone of Costa Rica in La Tigra, San Carlos (**Figure 2.1**). This area has an elevation ranging from 160 to 340 m, with temperatures between 26 and 30 ℃, solar radiation on average of 5 light hours, annual average precipitation of 3000 mm and relative humidity between 80 and 90%. Predominant vegetation in this zone includes forests (primary and secondary), pastures, forest plantations, scrublands, and annual and perennial crops (mainly plantain, heart of palm, and pineapple) (MAG 2007, IMN 2006).

Figure 2.1. Localization of study area (red circle) in Costa Rica. Source: http://www.govisitcostarica.co.cr.

Insect Pest Database

We evaluated the effect of the macro landscape context on the abundance of three pests of quarantine importance on *D. marginata* fields. The selection of pests was based on the results from the study carried out by Prado *et al.* (2008), which studied the population dynamics of quarantine pests found in *Dracaena marginata* agroecosystems in Costa Rica bound for export to the US market. We used the data from Prado´s study which included information about the abundance of leafhoppers (mainly *Caldwelliola* sp. (Subfamily: Cicadellinae; Tribe: Cicadellini) and *Oncometopia* sp. (Subfamily: Cicadellinae; Tribe: Proconiini) and katydid eggs (mainly from the genus *Microcentrum* and *Conocephalus*), as well as armored scale population (primarily Florida red scale, *Chrysomphalum aonidum*

(L.)). Leaves with armored scales were used as an indicator of scale abundance (Prado 2006).

Data on pest abundance were taken previously in 2006 during the dry and rainy season (Prado 2006). In that study they used a sampling grid of 10×10 m for a total of 32 sampling points per 2500 m^2 plot. At each point a total of nine commercial tips from plants were selected randomly: 3 tips in the lower stratum (from 0 to 50cm), 3 tips in the medium stratum (50 to 100cm) and 3 tips in the highest stratum (more than 100cm). In each tip, the total number of each pest was recorded; corresponding to the X and Y grid coordinates (see more details in Prado *et al.* 2008) (**Figure 2.2**).
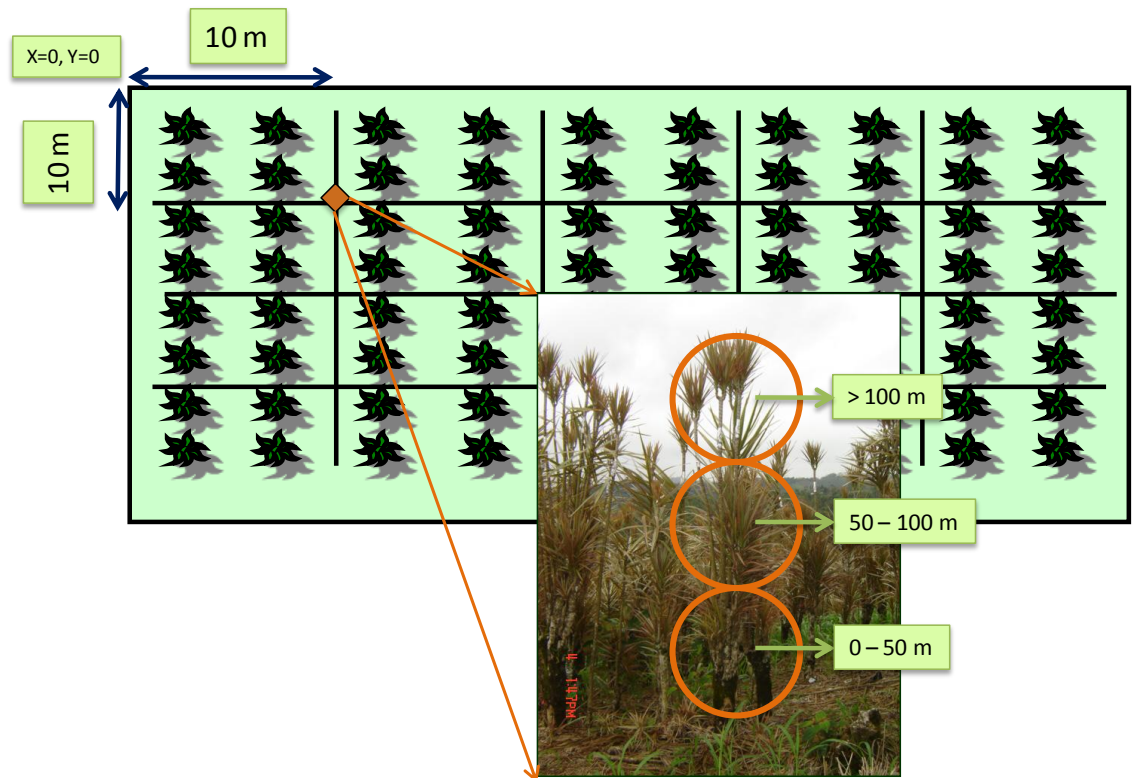
Figure 2.2.   Illustration of the systematic sampling of quarantined pests in a 10 × 10 m grid in a *Dracaena marginata* field established by Prado *et al.* 2008. In the photo the three strata can be seen on the Dracaena plant.

Land use mapping

To determine landscape structure, habitat patches in the study site were identified on 1:40,000 scale aerial photos from 2005. Maps with the main land uses for each landscape were drawn. Land use was assigned to the following categories: pastures with and without trees, forests (including primary and secondary), riparian forests, crops (including annuals and perennial), ornamental crops, scrublands, water (including rivers and lakes) and others (including urban areas and other land covers) (**Table 2.1**). These categories were included because they have been described as the dominant land uses in the study zone (MAG 2006).

In order to digitize the maps, the minimum mapping unit (MMU) was established at 1 ha. As such, areas smaller than the MMU were included with other adjacent land uses

types and were not shown as separate entities on the map. This area was chosen because it approximates the minimal area of the *Dracaena* farms.

Table 2.1.   Categorical descriptions for land uses found in the landscape of La Tigra, Costa Rica. Modified from Pinedo 2006 and the U.S. National Vegetation Classification System.

Land use	Description
Pasture	Areas devoid of forests and currently cultivated with grasses or pastures mainly dedicated to extensive cattle raising.
Pasture with trees	Areas devoid of forests and currently cultivated with grasses or pastures mainly dedicated to cattle raising and silvopastoral areas containing more than 40% of trees.
Forest	This category is formed by evergreen forests, in which evergreen species generally contribute more than 75% of total tree cover, and mixed evergreen-deciduous closed canopy, in which evergreen and deciduous species each generally contribute 25-75% of total tree cover.
Riparian forest	Conformed of the remaining forests established along the margins of water masses such as rivers, lakes and streams.
Agricultural crops	Includes all traditional and technical agriculture with subsistence and commercial purposes. This category incorporates annual as well as perennial crops.
Ornamental crops	Consists of all types of ornamental production including flowers and foliage.
Scrubland	Areas currently occupied by vegetation of low bearing such as shrubs and weeds. These are generally agricultural terrains which are left to rest in fallow.
Water	Rivers, lakes and streams areas
Others	Areas covered by urbanized areas, industrial zones, bare soil and others.

Quantifying landscape structure

In order to evaluate the effect of landscape context and structure on crop pest abundance at different spatial scales, we selected 15 fields of *Dracaena marginata* (five of each variety: bicolor, green and magenta) in the study area (Prado *et al.* 2008). Using the land use map, a circular area three kilometers in diameter around each farm was buffered with the software ArcGIS 9.0. Within each of these landscapes, structure was estimated at six different spatial scales constructed with circular sectors or distances: Ø 0.5 km, Ø 1 km, Ø 1.5 km, Ø 2 km, Ø 2.5 km, Ø 3 km, representing a nested set of landscape sectors at different spatial scales (**Figure 2.3**). For each distance, different landscape metrics were evaluated and quantified using the Patch Analyst extension in ArcGIS 9.0. Patch Analyst consists of several scripts written in Avenue and C code (Elkie *et al.* 1999), which calculate spatial statistics using the Fragstats Spatial Pattern Analysis program (McGarigal and Marks, 1995).

Landscape metrics included those related with the following categories: area metrics (percent of landscape, ZLAND); patch shape (Area-Weighted Mean Shape Index, AWMSI); spatial arrangement of patches (Mean proximity index, MPI) and diversity metrics (Shannon's diversity index, SHDI). AWMSI, MPI and SHEI were measured at the landscape level; while ZLAND, AWMSI and MPI were calculated at the patch level for each of the land types selected. A detailed description of the metrics used in this study can be found in McGarigal and Marks (1995). We selected these metrics as they have been identified as independent metrics that might characterize spatial heterogeneity of landscape patterns (Cushman *et al.* 2008, Li and Reynolds 1994, 1995, McGarigal and Marks 1995) as well as having been shown to have an association with insect populations (Beckler *et al.* 2004, Grilli 2008, Jonsen and Fahrig 1997, Overgaard *et al.* 2003).

Percent of landscape (ZLAND), also known as buffer distance, occupied by each land use type is a measure of landscape composition in relative terms; specifically, how much of the landscape consists of a particular patch type. ZLAND equals the percentage of landscape comprised of the corresponding patch type (McGarigal and Marks 1995) and was calculated at the landscape level (Ø 3 km), which represents the broader spatial scale, in order to preliminary characterize the different landscapes in which *D. marginata* fields are

located. ZLAND helped us to understand better the composition and proportion of land use types across the study area, as well as to identify groups of farms with similar landscape composition. For our study, ZLAND metrics were also computed at each of the six circular distances in order to evaluate if the proportion of the most important land use types presented in the landscape have an influence on insect pest population at the different scales.

Area-Weighted Mean Shape Index (AWMSI) is computed at the class and landscape level by weighting patches according to their size. Then, larger patches are weighted more heavily than smaller patches in calculating the average patch shape for the class or landscape. AWMSI is used as a measure of shape complexity, AWMSI equals one when all patches of the corresponding patch type are simple and compact, and increases without limit as the patch shapes become more irregular and convoluted (McGarigal and Marks 1995).

Mean proximity index (MPI) is a measure of the degree of isolation and fragmentation of each patch type within a specified neighborhood of the focal patch (Gustafson and Parker 1994). The proximity index was developed by Gustafson and Parker (1992) and takes into account the size and proximity distance of all patches (in our case from each land use type) whose edges fall at least partially within some specified distance of the focal patch (Bender *et al.* 2003). It quantifies the spatial context of a habitat patch in relation to its neighbors. MPI equals the average proximity index for patches in the class. MPI equal zero if all patches of the corresponding patch type have no neighbors of the same type within the specified search radius. MPI increases without limit as patches of the corresponding patch type become less isolated and less fragmented in distribution (McGarigal and Marks 1995).

Diversity metrics were used to assess the effect of landscape diversity on specific insect pest abundance. The Shannon-Wiener Diversity Index (SHDI) measured the landscape diversity, in terms of the diversity of patch types within each landscape, by combining the number of different patch types with their relative proportions (O'Neill *et al.* 1988, Mladenoff 1993). SHDI equals zero if the landscape contains only one patch (i.e., no diversity). SHDI increases as the number of different patch types increases and/or the

proportional distribution of area among patch types becomes more equitable (McGarigal and Marks 1995).
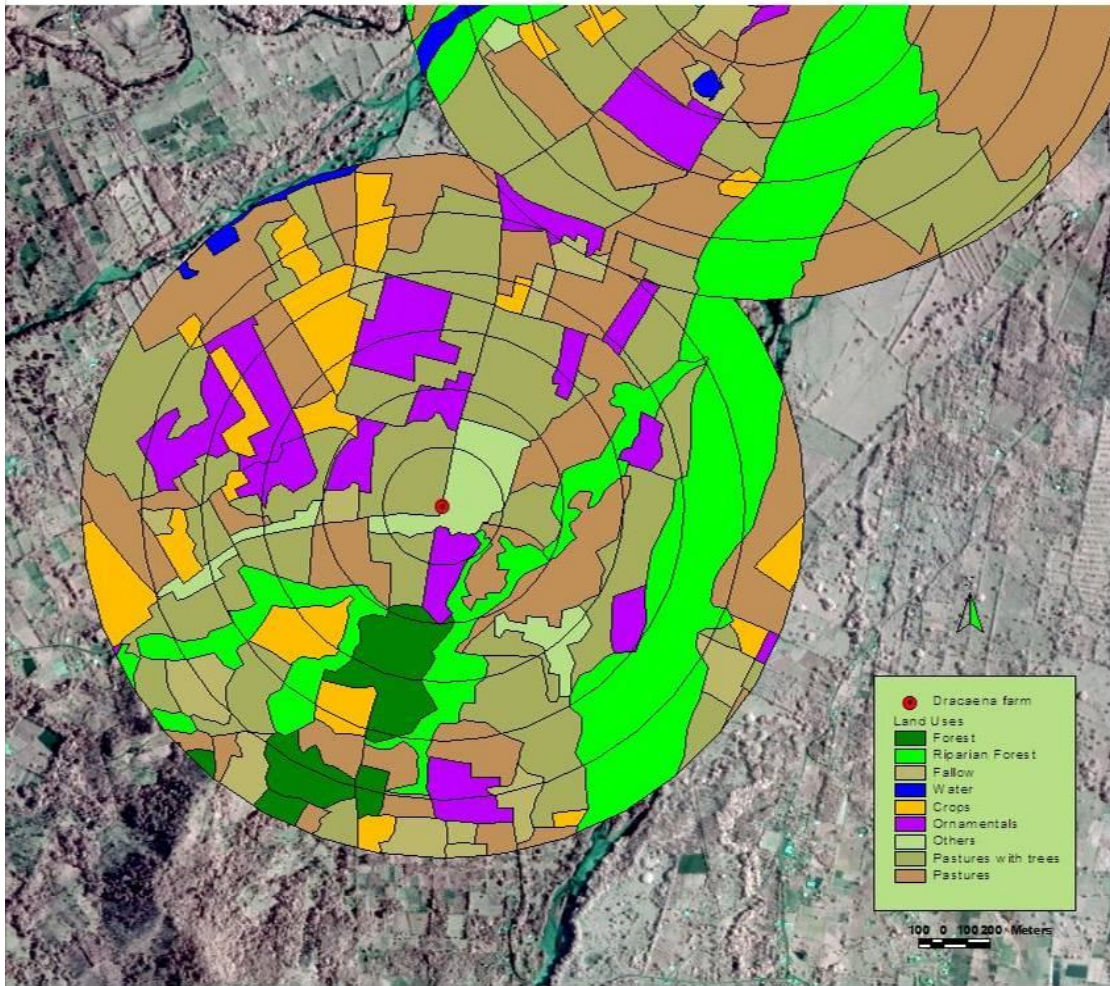
Figure 2.3. Map showing a Dracaena farm and its surrounding land uses. Rings are displayed every 0.125 km.

Statistical methods

Multivariate analysis was performed to explore the structure of the landscape in terms of composition; as well as to identify the natural grouping of the observations (Dracaena fields), because data structure is not known "a priori". Using the nine class areas, we used Cluster analysis to create groups of farms whose similarity is a maximum at the criterion of land use area. A dendrogram was built from a hierarchical cluster analysis using the Average Linkage method and the Euclidean distance. Principal component analysis

was used to create bi-plots graphics (Gabriel 1971), in order to identify the main relations between landscape components and fields.

In order to determine the effect of different landscape metrics on the average number of pests, Pearson correlations were conducted using the software InfoStat Professional (Di Rienzo *et al.* 2010). Pest abundance was averaged for each field, and then, Pearson correlations were run for each of the insect pests (leafhopper eggs, katydid eggs, and leaves infested with armored scales) and each landscape metrics. We used metrics at both landscape level and at the class level for the three most important land use categories (Ornamental, Pasture, Forest). These steps were repeated at the six distances to determine how different spatial scales within the landscape context influence insect pest abundance. When correlation was significant at any spatial scale, we plotted the correlation coefficients (*r*) for each of the six scales to illustrate scale-dependence effects of landscape structure on pest abundance at the analyzed spatial scales.

2.3   Results

Landscape Characterization

Ornamental class was the predominant land use across the 15 landscapes, covering an average area of 25.6% out of the Ø 3 km (≈ 707 Ha). Pastures, forests, pastures with trees and riparian forest were also important categories within the *D. marginata* landscape. Remaining categories present in the circular landscapes comprised an average proportion less than 10% (**Table 2.2**; **Annex 2.3**).

Table 2.2.   Composition of the landscape surrounding Dracaena fields (n=15) at circular sectors of Ø 3 km in the Northern zone of Costa Rica, 2006.

Land use type	Area (Ha) Mean ± S.E.	Min (Ha)	Max (Ha)
Ornamentals	180.6 ± 24.6	84.8	335.0
Pastures	141.4 ± 18.2	60.9	253.8
Forests	132.9 ± 30.2	20.3	306.1
Pasture w/trees	113.3 ± 11.0	56.5	194.6
Riparian forest	70.3 ± 14.6	28.3	180.5
Crops	30.6 ± 4.7	6.9	71.7
Other	20.7 ± 4.1	1.5	61.5
Water	7.8 ± 1.8	0.0	19.7
Shrubland	6.9 ± 1.9	0.0	17.4

When landscapes surrounding *Dracaena* fields were characterized by their composition, we identified different groups of similarity through the cluster analysis. When a reference cut line was drawn to a distance equal to 50% of the maximum distance (2.67) we found three well defined groups (1, 6, 2) and three remaining fields (3, 4, 5) which were not grouped (**Figure 2.4**). According to the Principal component analysis, 95% of the variability between the landscape compositions of different *D. marginata* fields was explained by the first four components. The first component (PC1), which explained the 56.3% of the variability area, was mostly comprised of forest and pasture with trees. The second PC (which accounted for 23.6% of the variability) was comprised by the amount of area of Riparian forests and Ornamental use (**Figure 2.5**; **Annex 2.1**). Fields from cluster 6 were more associated with areas of Ornamentals, Shrubland and Water. Fields in cluster 1 had larger areas of pastures and riparian forests; and those in cluster 2 were related to forest areas. Three fields were not clustered but were related to other land use variables, *e.g.* number 4 was associated with larger areas of pasture with trees (**Figure 2.5**).
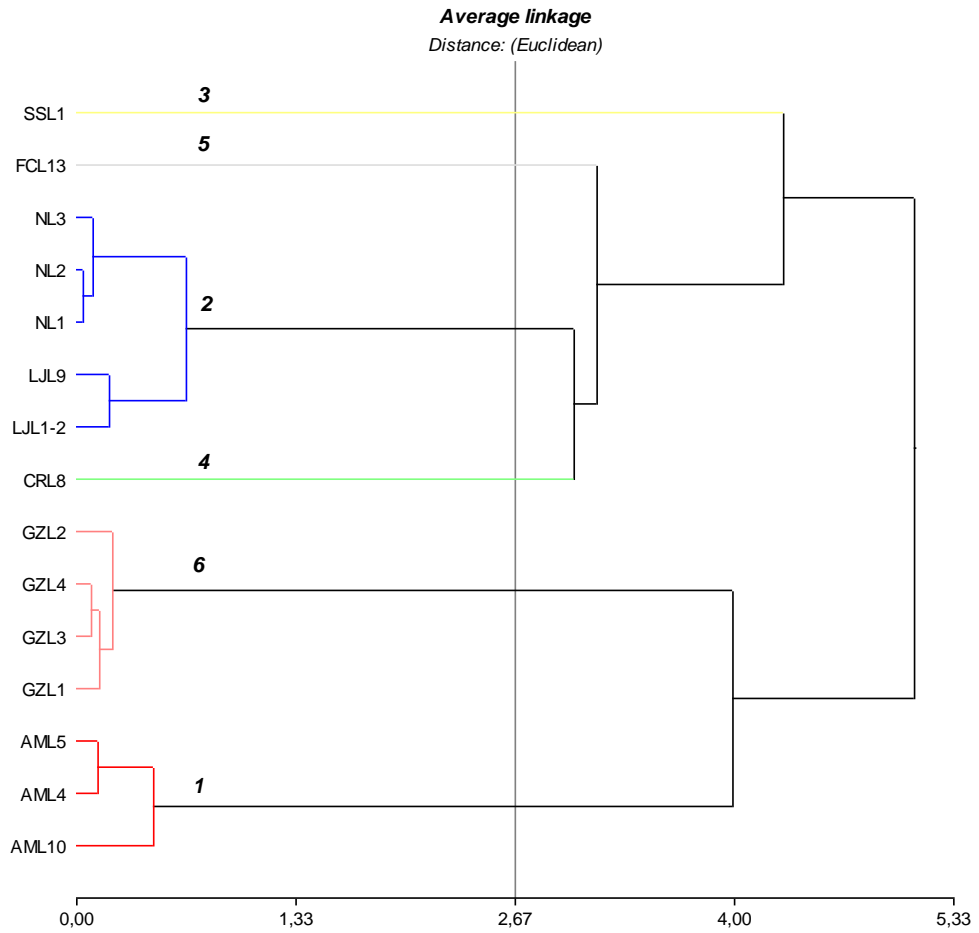
Figure 2.4. Dendrogram (Cluster Analysis) obtained by the Average Linkage method and Euclidean distance to describe groups of farms with similarity landscape usage in 3 km circular areas around *D. marginata* plantations in Costa Rica, 2006. Bold numbers (1-6) identified the clusters of farms created. A reference cut line was drawn to a distance equal to 50% of the maximum distance (2.67). Cophenetic correlation coefficient: (0.988)
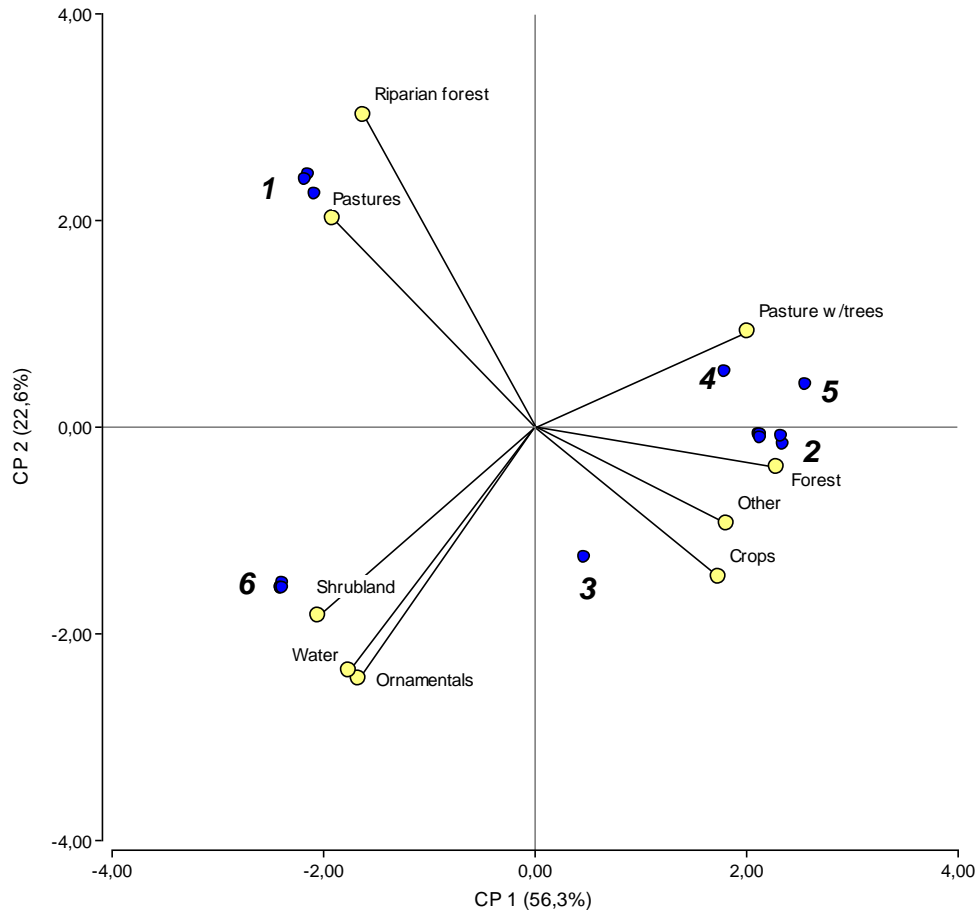
Figure 2.5. Biplot obtained through principal component analysis for the relation between area of land use categories (yellow circles) within a 3 km diameter circular area surrounding *D. marginata* fields, Costa Rica, 2006. PC1 is primarily comprised of forest and pasture with trees whereas PC2 is mostly represented by riparian forests and ornamental land use (See table 2.1 for explanation of land use areas). Numbers indicate the groups of farms (blue circles) obtained in the cluster analysis.

Effect of landscape metrics on insect pest abundance at the landscape level

Landscape level metrics are summarized in **Table 2.3**. Average AWMSI index increased with the spatial scale from the distance 0.5 km to 3.0 km. Correlation coefficients between AWMSI and leafhopper egg and katydid egg number increased from Ø 0.5 km to Ø 1.5 km, showing an increase of the AWMSI effect at the first three distances. After the distance of 1.5 km, the AWMSI effect on these two insect pests drops off (**Figure 2.6a**). However, we only found a significant positive correlation between AWMSI and katydid egg abundance at the landscape sector of 1.5 km diameter ($r_p(30)= 0.37$, *p*=0.0444).

Armored scale population was not correlated with AWMSI metric at any spatial scale (**Annex 2.2**).

MPI index also increased as the landscape diameter increased. At the Ø 2.5 km distance we found a reduction in the index value in comparison to the Ø 2.0 km, however this reduction is not important because at that distance (Ø 2.0 km) we found the highest standard errors (*i.e.* the highest variations of MPI among fields) (**Table 2.3**). The strongest effects of MPI on insect pest abundance were found at the smallest spatial scales (**Figure 2.6b**). We found significant correlations between MPI metric and leafhopper egg ($r_p(30)$= 0.50, p=0.0049) and katydid egg number ($r_p(30)$= 0.52, p=0.0031) at the distance of Ø 0.5 km; and with armored scale populations at Ø 1.0 km ($r_p(30)$= 0.46, p=0.0103).

SHDI index increased from Ø 0.5 km to Ø 1.5 km, from that distance the index value is rather similar up to Ø 3.0 km. Correlation coefficients between SHDI and insect pests were higher for katydid eggs across the distances in comparison with the other insect pests. We only found a significant positive correlation ($p<0.05$) between SHDI and katydid egg abundance at 0.5 km distance $r_p(30)$= 0.38, p=0.0383), although after this distance correlations were mostly in the positive range and significant at a $p < 0.10$. (**Figure 2.6c**).

Table 2.3. Landscape level metrics (average ± SE) in 15 *D. marginata* fields of the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Landscape metrics include: Area-Weighted Mean Shape Index (AWMSI), Mean Proximity Index (MPI) and Shannon's diversity index (SHDI). Landscape metrics with no units.

Spatial scale	AWMSI ± SE	MPI ± SE	SHDI ± SE
0.5 km	1.41 ± 0.05	6.62 ± 3.61	0.53 ± 0.09
1.0 km	1.63 ± 0.06	16.88 ± 5.04	0.67 ± 0.07
1.5 km	1.88 ± 0.04	59.95 ± 29.71	0.75 ± 0.03
2.0 km	2.13 ± 0.06	111.19 ± 50.05	0.77 ± 0.02
2.5 km	2.28 ± 0.06	81.57 ± 7.40	0.76 ± 0.02
3.0 km	2.34 ± 0.05	145.97 ± 30.80	0.78 ± 0.02
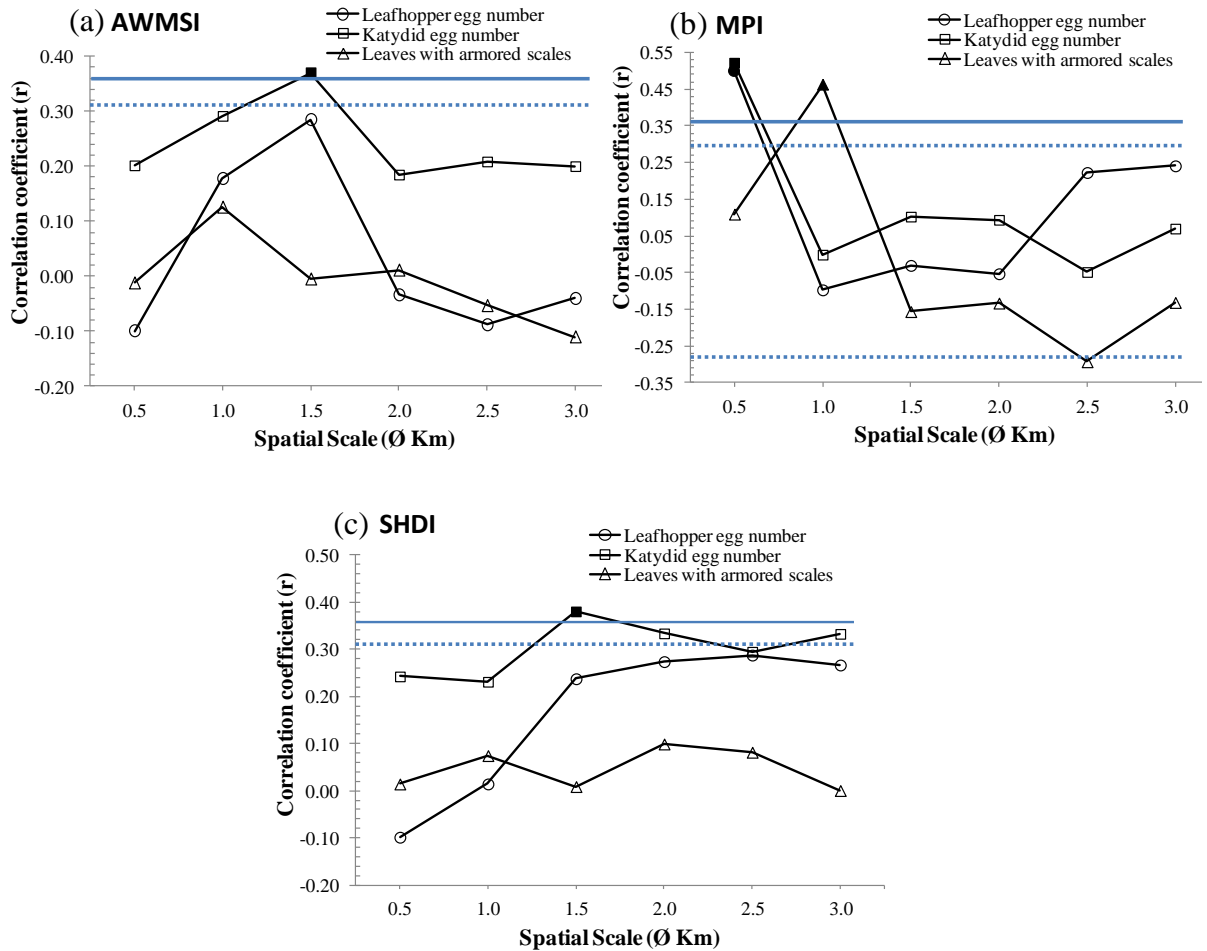
Figure 2.6. Correlation coefficients ([r]) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and different landscape level metrics in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Landscape metrics include: (a) Area-Weighted Mean Shape Index (AWMSI), (b) Mean Proximity Index (MPI) and (c) Shannon's diversity index (SHDI). Solid symbols represent significant Pearson correlations (*p<0.05*). Horizontal lines represent the statistical limits for *p<0.05* (solid line) and *p* < 0.10 (dotted line). See statistics in **Annex 2.2**.

Effect of landscape metrics on insect pest abundance at the class level

A summary of the effect of landscape metrics on the average abundance of the insect pests for the three most important land uses is shown in **Annex 2.3**. Our index of shape complexity (AWMSI) showed that all our land uses types are characterized for having irregular patch shapes, as they have average index values higher than one. (**Annex 2.3**). On the other hand, our values for the MPI index showed that, on average, the highest fragmentation or isolation was found for pastures (low MPI values), while the lowest was

identified for the ornamental patches (high MPI values). High MPI values were also recorded for forest patches, but high MPI differences were found among fields, as the standard error was high (**Annex 2.3**). We found a negative Pearson correlation between the MPI index of ornamentals and MPI index of pastures from Ø 1.5 km to Ø 3.0 km distance (Ø 1.5 km: $r_p(30)=-0.41$, $p=0.0238$; Ø 2.0 km: $r_p(30)=-0.45$, $p=0.0115$; Ø 2.5km: $r_p(30)=-0.61$, $p=0.0003$; Ø 3.0 km: $r_p(30)=-0.60$, $p=0.0004$).

Our measure of landscape composition (ZLAND) showed us that the proportion of ornamental land use was not related to any of our insect pest groups (**Figure 2.7a**). However, the shape and isolation of ornamental patches showed a significant relationship with leafhopper egg abundance. Ornamental MPI correlated positively with leafhopper egg abundance showing a scale-dependence effect at the smallest spatial scales (0.5 km: $r_p(30)=0.37$, $p=0.0431$; 1.0 km: $r_p(30)=0.42$, $p=0.0201$; 1.5 km: $r_p(30)=0.58$, $p=0.0008$). Then, these associations disappeared at the larger spatial scales (**Figure 2.7c**). On the other hand, the AWMSI index for ornamental land use did not show association with leafhopper egg at the smallest spatial scales but recorded positive significant correlations from the Ø 2.0 km distance (Ø 2.0 km: $r_p(30)=0.44$, $p=0.0142$; Ø 2.5 km: $r_p(30)=0.47$, $p=0.0088$; Ø 3.0 km: $r_p(30)=0.43$, $p=0.0173$) (**Figure 2.7b**).

Katydid egg abundance was only associated with the shape index for ornamental patches. We identified a similar tendency of that found with leafhopper eggs, the magnitude of the correlation increased with the spatial scale. From the distance of Ø 1.5 km, the correlation coefficients remained over the confidence limit at a $p < 0.10$ level, but is only significant (*p<0.05*) at Ø 2.0 km ($r_p(30)=0.39$, $p=0.0342$). We did not find an effect of any of the ornamental metric on armored scale population at any spatial scale.
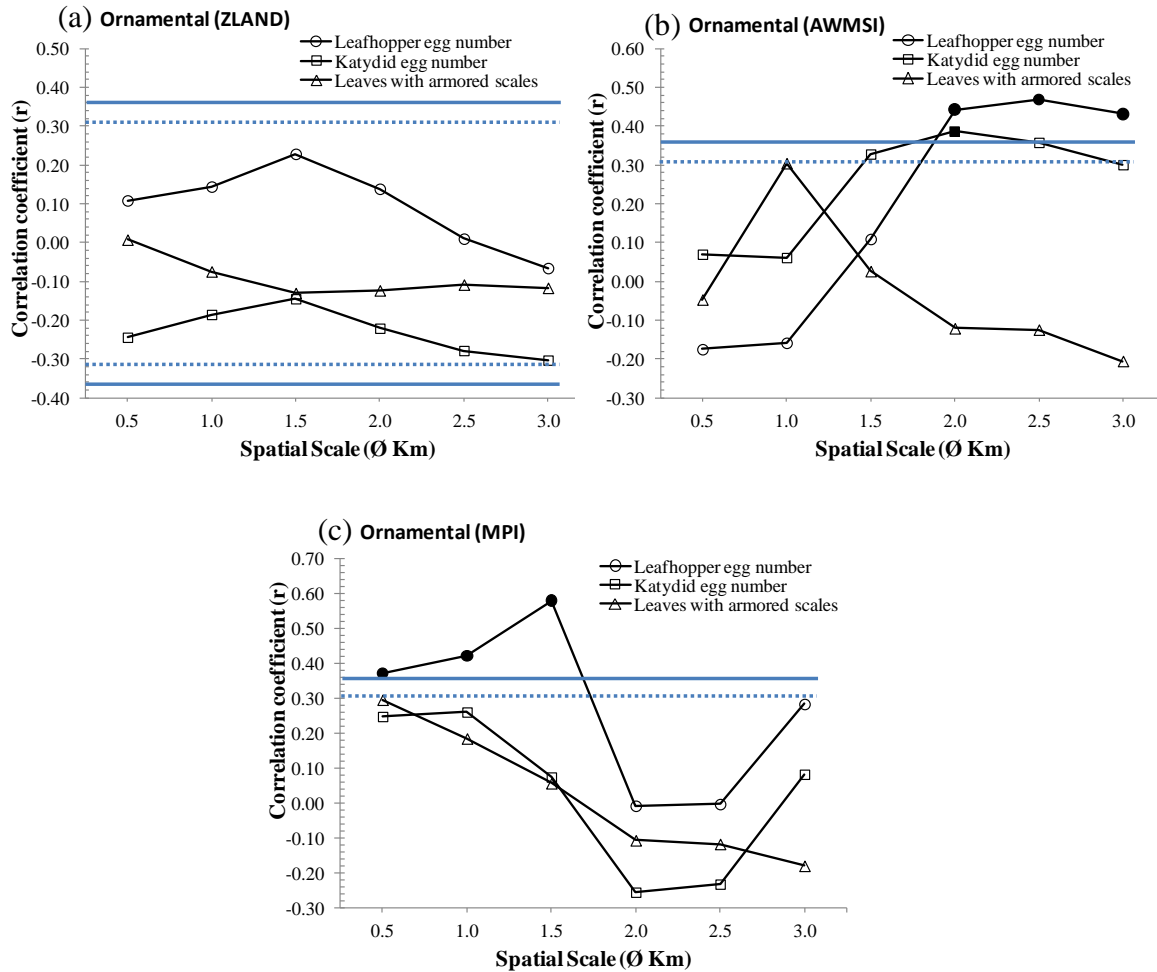
Figure 2.7. Correlation coefficients ([r]) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and ornamental landscape metrics in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Solid symbols represent significant Pearson correlations (*p<0.05*). Horizontal lines represent the statistical limits for *p<0.05* (solid line) and *p < 0.10* (dotted line). See statistics in **Annex 2.4**.

The proportion of pasture was only associated with leafhopper egg abundance. The magnitude of the correlation between the proportion of pasture and leafhopper egg abundance increased negatively as the spatial scale became greater and was significant (*p<0.05*) at Ø 1.5 and Ø 2.0 km ($r_p(30)=-0.41$, *p=0.0253*; $r_p(30)=-0.41$, *p=0.0263*), from that distance correlations remained in the negative range and within the confidence limit of *p < 0.10* (**Figure 2.8a**). At these distances, as the percent of pasture increases, the number of leafhopper egg decreases. Our indices of shape complexity (AWMSI) and isolation

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(MPI) for pastures also showed negative significant correlation with leafhopper eggs but only at Ø 1.5 km (AWMSI: $r_p(30)= -0.47$, $p=0.0092$ and MPI: $(r_p(30)= -0.37$, $p=0.0463$) (**Figure 2.8b,c**).

Patch complexity (AWMSI) was the only metric related to pasture that was associated with katydid egg abundance. The magnitude of the correlation increased negatively with the spatial scale but is only significant at a distance of Ø 2.0 km $(r_p(30)=-0.36$, $p=0.0476$) (**Figure 2.8b**). Pasture MPI index was the only metric that influenced armored scale population. A positive significant association was found at the higher spatial scale (Ø 3.0 km: $r_p(30)=0.43$, $p=0.0177$) but we did not identified any tendency through the different distances (**Figure 2.8c**).

Percent of forest was only related to katydid egg abundance. We identified a scale-dependent effect of the forest proportion which increased with the spatial scale and showed a significant positive correlation ($p<0.05$) at the highest distance (Ø 3.0 km: $(r_p(30)=0.38$, $p=0.0381$) (**Figure 2.9a**). Shape complexity of forest patches was not related to any insect pest group. On the other hand, the degree of isolation of forest patches was associated to leafhopper egg abundance. We found a negative significant correlation between the forest MPI index and leafhopper egg abundance at the two lowest spatial scales (Ø 0.5 km: $r_p(30)= -0.35$, $p=0.0458$ and Ø 1.0 km: $r_p(30)= -0.37$, $p=0.0454$) (**Figure 2.9c**).
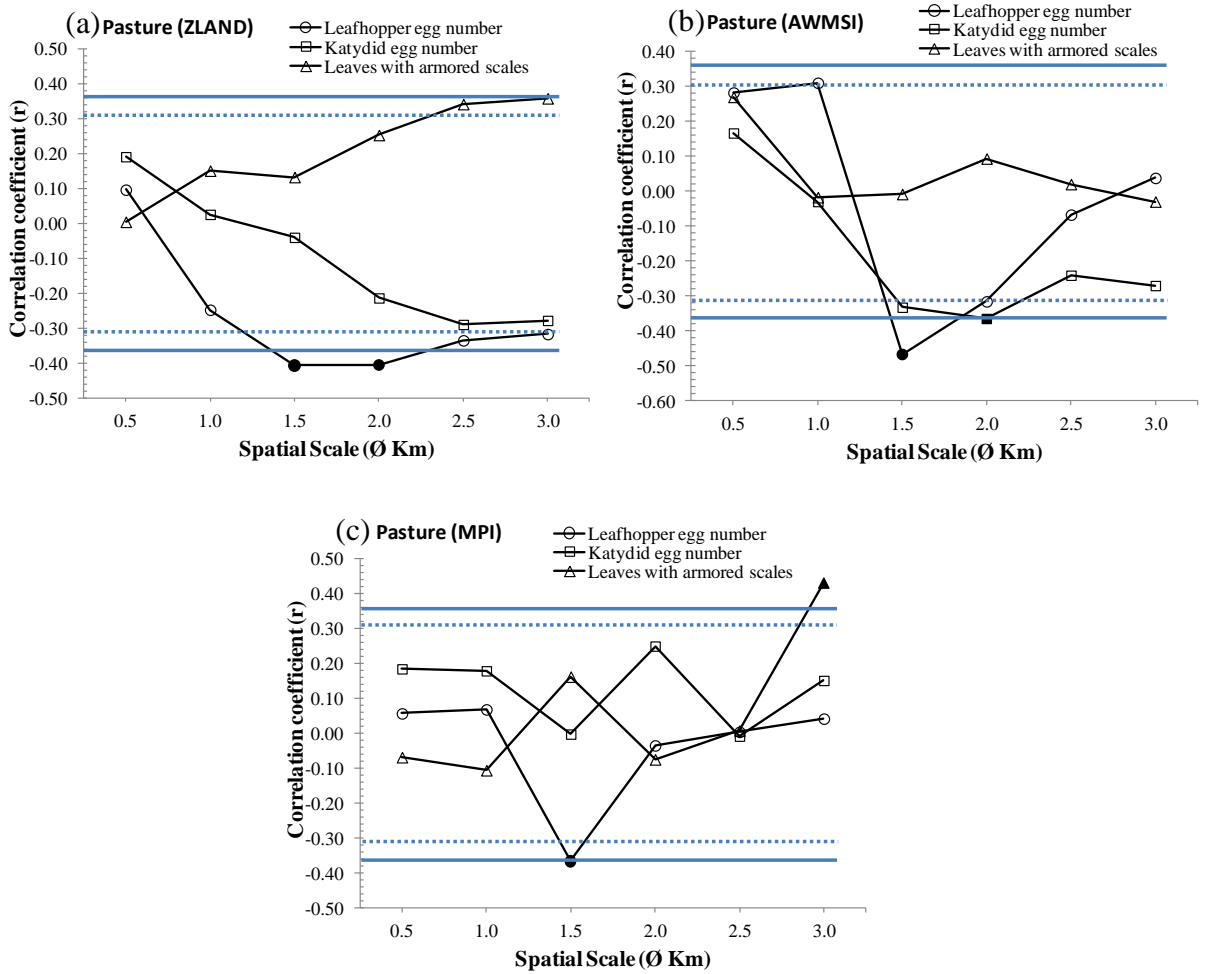
Figure 2.8. Correlation coefficients ([r]) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and pasture landscape metrics in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Solid symbols represent significant Pearson correlations (*p<0.05*). Horizontal lines represent the statistical limits for *p<0.05* (solid line) and *p* < 0.10 (dotted line). See statistics in **Annex 2.5**.
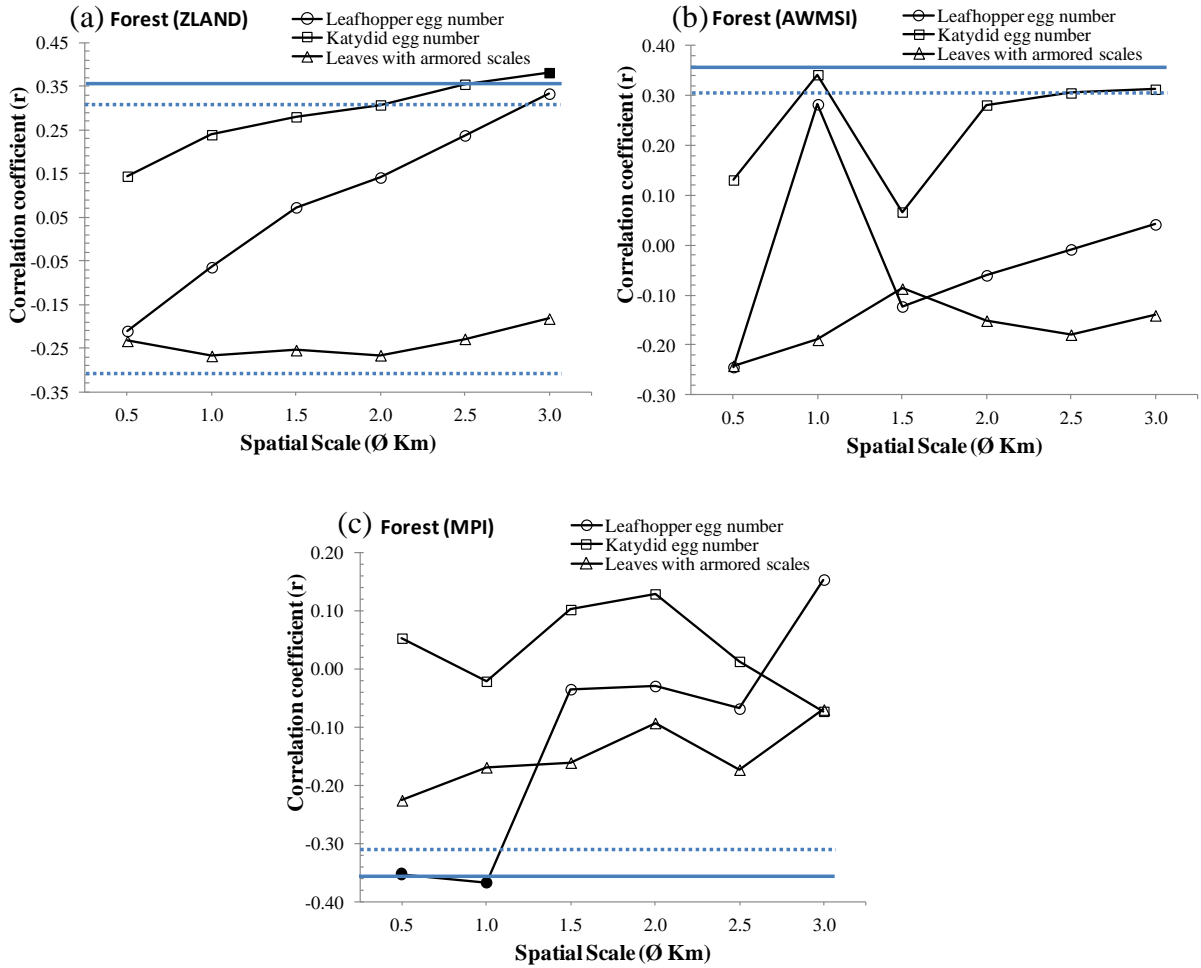
Figure 2.9. Correlation coefficients ([r]) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and forest landscape metrics in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Solid symbols represent significant Pearson correlations (*p<0.05*). Horizontal lines represent the statistical limits for *p<0.05* (solid line) and *p* < 0.10 (dotted line). See statistics in **Annex 2.6**.

2.4 Discussion

D. marginata fields were characterized as being embedded in an agricultural matrix dominated by ornamental and pastures lands. Forest was also an important category within the Ø 3.0 km buffer with a percentage of cover of 18.84±4.28, although is considered as highly fragmented under McIntyre and Hobbs (1999) terminology. Three well defined groups were identified through the cluster analysis. One group was mainly associated with

ornamental lands, while the other two groups were related to pastures, forests and riparian forests. Forest land uses can be an important component of the landscape to evaluate because of their capacity to provide ecosystem services on farms (e.g. Janzen 1987, Marino and Landis 1996, Klein *et al.* 2003a,b, De Marco and Coelho 2004, Kremen *et al.* 2004, Ricketts 2004, Chacoff *et al.* 2006, Bianchi *et al.* 2006, Banks *et al.* 2007, Benevides *et al.* 2009, Brosi 2009, Thomson *et al.* 2010).

Effect of landscape level metrics on insect pest abundance

Responses of insect pests at the macro landscape level were scale-dependent and differed among insect pests, land uses and evaluated landscape metrics. While at the landscape level insect pests responded to landscape metrics at smaller scales (from Ø 0.5 to Ø 1.5 km); at the class level (land use type) insect responses occurred at different spatial scales (from Ø 0.5 to Ø 3 km) depending on the insect species, landscape metric and land use type. Other studies have also found that different species groups respond to the landscape at distinct spatial scales (e.g. Wiens and Milne 1989, Wiens 1992, Dauber *et al.* 2003, Thies *et al.* 2003, Chust *et al.* 2004, Tews *et al.* 2004, Aviron *et al.* 2005). Furthermore, responses to landscape structure, including landscape metrics and landscape composition are species specific (e.g. Taylor *et al.* 1993, Jonsen and Fahrig 1997, Wiens *et al.* 1997, Kruess 2003, Thies *et al.* 2003, Chust *et al.* 2004).

Idiosyncrasies of the insect groups, mainly differences in dispersal and colonization abilities (Fahrig, 2001, Tscharntke and Brandl 2004) have been used to explain the different responses of insects to the macro landscape. Generalist insect abundance within agricultural fields have been reported to increase as the number of patch types in the landscape increase and/or their proportions became more equal (Jonsen and Farigh 1997). We only found a significant (*p<0.05*) positive effect of landscape diversity (SHDI index) on katydid egg abundance at Ø 1.5 km, although from that distance the correlation coefficients were always positive and tended to remain within the $p < 0.10$ limit level. Katydids are generalist insects with a wide range of hosts and high dispersal capacities. Factors such as host plant abundance, diversity, taxonomic composition and physical structure of the vegetation have been reported for other orthopterans as keys for their habitat selection and distribution (Vestal 1913, Otte and Joern 1977, Joern 1979, 1982, Kemp *et al.* 1990, Fielding and

Brusven 1992, Cuningham and Sampson 2000, Squitier and Capinera 2002). As such, a high landscape diversity increase the likelihood of katydids to find more suitable resources, as they can easily migrate to new areas looking for their preferred hosts, and increase their population.

Despite the fact that many leafhopper species are generalist insects, we could not find the effect of landscape diversity on egg abundance we expected. We could explain this lack of effect for two possible reasons. First, unlike katydids, other factors such as host plant availability and nutritional quality (Park *et al.* 2006, Mizell *et al.* 2008, Northfield *et al.* 2009) of agricultural crops have been reported to play a determinant role on the resurgence of leafhoppers in fields. For instance, leafhoppers must feed frequently to meet their nutritional requirements, and prefer to feed when xylem tension and plant nutrient content, including amino acid presence in the xylem fluid, are highest (Andersen *et al.* 1992, Broadbeck *et al.* 1993, Pérez 2007). Adult females also have a marked preference for host plants with higher contents of amides, and they are very likely to oviposit on these plants (Andersen *et al.* 1989, 1992, 2005). Consequently, leafhopper adults may have been more discriminating in terms of the categories of host selection and the spatial extent and land use classifications defined in our study. This would limit the ability of our analysis to identify specific habitat patches with the most suitable host plants. Second, it could be possible that the landscape diversity effect may occur at smaller spatial scales than those we measured.

In the case of armored scale insects, even though they are able to survive on a broad range of plant hosts (Culik *et al.* 2008, Hanks and Denno 1994, Magsig-Castillo *et al.* 2010); their dispersal capacity is limited. Only their wingless first instar, known as crawlers, can disperse. Long distance dispersal to new host plants is passive and mainly achieved through the wind, although other phoretic means such as insects, birds, animals, other insects and humans (e.g. Beardsley and Gonzalez 1975, Magsig-Castillo *et al.* 2010) have been also reported. Passive dispersal does not allow them to easily select their preferred host plant or migrate to other areas looking for new suitable hosts. Hence, we expected to find an effect of the landscape pattern on insect scale abundance at the smallest scale (Ø 0.5 km), which cover an area of approximately 19 ha. However we did not find an

effect of landscape diversity at any spatial scale. Instead, other factors have been reported to play a determinant role on the patchy distribution pattern of armored scales insects on crops (Hanks 1991, Hanks and Denno 1993), including the presence and distribution of natural enemies, host plant-water relation (Hanks and Denno 1993) and management practices (Prado *et al.* 2008). In terms of the management practices, Jonsen and Fahrig (1997) explained that the large anthropogenic disturbances generally occur at scales of the field (from 1 to 10 Ha), so armored scale insects may be responding to the landscape pattern at finer scales that those set in our study.

Effect of landscape patch metrics on insect pest abundance

Additionally to the landscape level metrics, which are measured taking into account the landscape as a whole, we also evaluated the effect of specific land uses (ornamental, forest and pastures) on insect pest abundance computing three different metrics (ZLAND, MPI and AWMSI) for each land use class. Insect pest groups showed different responses to each land use and metrics at the different spatial scales. While leafhopper egg abundance was more sensitive in terms of their correlations with different land uses and metrics and responded to spatial scales up to Ø 1.5 km; katydid egg abundance showed only some isolated correlations at specific spatial scales (including the highest: Ø 3.0 km), metrics and land uses. On the other hand, armored scale abundance practically showed no correlation with any land use and metric at the spatial scales set in this study. According to Tscharntke and Brandl (2004) local population dynamics may be influenced by the ratio of the foraging range and/or dispersal ability to the distance between landscape elements. Factors including the position in trophic level and insect traits such as body size, dispersal abilities, resource specialization, rarity, and population size variability have been used to explain the spatial scale experienced by a species. In this sense, insect groups with large body size and/or higher dispersal abilities, such as leafhopper and katydids, may respond to the landscape pattern at broader spatial scales than would a less-mobile insect group such as the armored scales (Chust *et al.* 2004).

Our results indicated that *D. marginata* fields are a source of leafhoppers and katydids as we found a positive association between our indexes of isolation and shape complexity of ornamentals and egg abundance. In the same way, we also found that large

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areas of pastures, or a higher connectivity between patches of this land use, resulted in the reduction or fragmentation of ornamental patches, affecting negatively the egg abundance of these two insect pests as less suitable resources are available in *D. marginata* fields.

Following this trend, we found a negative correlation between our index of isolation (MPI) in pastures and leafhopper egg abundance, as when pastures connectivity decreases ornamental patches becomes more connected in distribution. According to Taylor *et al.* 1993, when patch isolation decreases and connectivity becomes greater, the amount of habitat patch types on a landscape available for generalist species, such as leafhoppers, increases. Consequently, immigration increases as a result of a rise in the dispersal rates while the rate of local extinctions decreases (Brown and Kodric-Brown 1977). The increment in dispersal rates is also a consequence of the faster re-colonization of local extinction (Fahrig and Merriam 1985). These effects have been also used by Hanski (1994) to explain an increase in the species richness and abundance of generalist insects at the landscape level.

Additionally, we also observed an association of the shape complexity in ornamentals and pastures with leafhopper and katydid egg abundance. According to Bender *et al.* 2003, patch characteristics such as patch shape and size may be a key factor on population dynamics because larger, irregular shaped patches may "intercept" more immigrants than small, regular patches. The complexity of ornamentals patches may increase the possibility to intercept more leafhoppers and katydids rising egg abundance in *D. marginata* fields. On the other hand, more irregular pasture patches may intercept more of these insect pests acting as a barrier, and then reducing the pest pressure on *D. marginata* fields. Other studies have also found that species diversity and abundance may be affected positively (Hamazaki 1996, Grez and Prado 2000, Louzada 2000, Collinge and Palmer 2002, Cobbold and Supp *in press.*) or negatively (Santos 2004) by the patch shape complexity; while others species do not respond to patch shape (Sobrinho and Schoereder 2007, Cobbold and Supp *in press.*) as was the case for armored scale populations. Stamps *et al.* (1987) have explained these differences among group of species as the effect of boundary shapes on organism movement is context dependent, and influenced by the structural and functional relationships between patches and their surrounding matrix, as

well as the idiosyncrasies of the species, such as differences in dispersal and colonization abilities, and habitat requirements (Fahrig, 2001).

On the other hand, it is important to highlight that connectivity between forest patches seems to be providing important ecosystem services on leafhopper egg abundance, as we found that connectivity between forest patches was negatively correlated with leafhopper abundance at the smaller scales. One possible mechanism could explain this negative association. Even though we did not evaluate the effect of the landscape context on natural enemies' populations, we could expect that forest is providing a 'top-down' effect through the enhancement of natural enemy populations, which can lead to leafhopper suppression. It has been demonstrated that forests may have a strong effect on natural enemy and herbivore trophic levels (Dyer and Stireman 2003, Sperber *et al.* 2004). They support higher biodiversity, providing alternative non-prey foods, shelter and alternative prey, but also offer a greater diversity of microclimates for natural enemies (Fernandes and Price 1991, Landis *et al.* 2000, Bianchi *et al.* 2006. Kruess and Tscharntke (2000) suggested that large undisturbed habitats are necessary to preserve large populations of natural enemies. An increase in the connectivity of forest patches increases the possibility of natural enemies to move to other areas of the landscapes searching for new preys. Thus, the decision of leafhoppers adults to leave a suitable host patch and move between forest patches may be accompanied by a higher risk of predation (Mizell *et al.* 2008). This risk is augmented if we take into consideration that our results showed the higher forest effects at the smaller scale and another study in *D. marginata* fields (see chapter 3) showed us that the higher number of natural enemies occurred at the edges of fields near forest. Other studies have also suggested that it is more likely to find an effect of parasitism on herbivores in landscape characterized by a high proportion of large and undisturbed habitats (Thies and Tscharntke 1999, Kruess 2003); and this effect is most successful at scales ranging from 0.3 to 72 Ha (Roland and Taylor 1997), which coincides with the smallest scales of our study. However it should be necessary to carry out separate experiments under controlled conditions to test this hypothesis.

In the case of katydids, our measure of landscape composition showed us that only the amount of forest had a positive effect on egg abundance at the highest distance (Ø 3.0

km). As they have high dispersal abilities and larger bodies, katydids may be moving within the landscape at larger scales (Tscharntke and Brandl 2004) to use alternative habitats, in this case forest lands, to make use of additional available resources which supplement those found in *D. marginata* fields. Dunning *et al.* (1992) describe supplementation as the capacity of an organism to utilize more than one habitat within a landscape in order to supplement their resource intake.

Specifically for armored scale populations, MPI for pastures was the only metric that had a statistical effect on armored scales population at the highest spatial scale. It is difficult to find a logical biological explanation for this behavior as we did not find any significant effect on the evaluated land uses and metrics used at the different spatial scales. Furthermore, we could have expected to find effects on armored scale insects at the smaller scales taking into account their limited dispersal abilities and small body size (Chust *et al.* 2004, Tscharntke and Brandl 2004); as well as other factors (mentioned above) that have been used to explained their spatial distribution, and that are known to occur at smaller spatial scales (Jonsen and Farigh 1997). As such, it would be necessary to carry out new experimental studies to validate these results and determine if the effect was real or random.

2.5   Conclusions

The response of insect pests to the macro landscape characteristics was scale-dependent and differed among insect groups, land uses and landscape metrics selected in this study. Idiosyncrasies of the insect groups, mainly differences in dispersal and colonization abilities and habitat requirements, have been used to explain the different responses of insects to the macro landscape.

Katydids are generalist insects with a wide range of hosts and high dispersal capacities which allow them to easily migrate to new areas across the landscape looking for their preferred hosts. They mainly respond to factors such as host plant abundance, diversity, taxonomic composition and physical structure of the vegetation for their habitat selection and distribution, as such landscape diversity played an important role on katydid egg distribution and abundance.

On the other hand, the distribution and abundance of leafhopper eggs, which are also insects with high dispersal capabilities and a broad number of host plants, respond principally to other factors including host plant availability and nutritional quality of the agricultural crops As such, landscape diversity did not have an effect on their oviposition. Instead, egg abundance was attributed to other metrics such as abundance and connectivity of ornamental lands which are known to meet their nutritional requirements. In this sense, *D. marginata* fields were considered a source of leafhoppers as well as katydids as we found a positive association between our indexes of isolation and shape complexity of ornamentals and egg abundance.

In the particular case of armored scale insects, their limited dispersal capacity does not allow them to easily select or migrate to other areas looking for new suitable hosts. Other factors, including the presence and distribution of natural enemies, host plant-water relation and management practices, which are known to occur at smaller spatial scales, have been used to explain their patchy distribution pattern on crops. Hence, we were not able to find an effect of the landscape context on armored scale population at the spatial scales set in our study.

Connectivity between forest patches played an important role on leafhopper egg abundance as it seemed to be providing ecosystemic services via 'top-down' effects through the enhancement of natural enemy populations which lead to leafhopper suppression.

As our buffer distances were set arbitrarily, because the average dispersal distances of our specific insect pests was unknown, it would be necessary to carry out new studies to validate our results and determine if leafhoppers, katydids, and specially armored scale insects, are responding to the landscape context at local or finer scales than those reported in this study. It would be also recommended to establish field experiments under controlled conditions to validate our results with the specific land uses classes, which showed responses in our study.

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2.7 Annexes

Annex 2.1. Principal component analysis identifying the main relations between landscape components and *Dracaena marginata* fields, Costa Rica.

Standardized data

Eigenvalues

Lambda	Value	Proportion	Acumulated proportion
1	5,07	0,56	0,56
2	2,03	0,23	0,79
3	0,90	0,10	0,89
4	0,54	0,06	0,95
5	0,43	0,05	1,00
6	0,02	2,3E-03	1,00
7	2,7E-03	3,0E-04	1,00
8	1,4E-03	1,5E-04	1,00
9	4,6E-05	5,1E-06	1,00

Eigenvectors

Variables	e1	e2
Ornamentals	-0,29	-0,43
Pastures	-0,34	0,36
Riparian forest	-0,29	0,53
Pasture w/trees	0,36	0,16
Crops	0,31	-0,26
Shrubland	-0,36	-0,32
Water	-0,31	-0,42
Forest	0,40	-0,07
Other	0,32	-0,16

Cophenetic correlation = 0,905

Annex 2.2. Pearson correlation coefficients (*r*) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and different landscape level metrics in 15 *D. marginata* fields at six spatial scales (from Ø 0.5 to Ø 3 km). Landscape metrics include: Area-Weighted Mean Shape Index (AWMSI), Mean Proximity Index (MPI) and Shannon's diversity index (SHDI). Costa Rica, 2006. Significant correlations with $p<0.05$.

Landscape Metric	Leafhopper egg number		Katydid egg number		Leaves with armored scales	
	R	*P*	*R*	*P*	*R*	*P*
AWMSI						
0.5 km	-0.10	0.6025	0.20	0.2875	-0.01	0.9492
1.0 km	0.18	0.3476	0.29	0.1193	0.13	0.5084
1.5 km	0.28	0.1272	0.37	**0.0444**	-0.01	0.9791
2.0 km	-0.03	0.8593	0.18	0.3308	0.01	0.9530
2.5 km	-0.09	0.6429	0.21	0.2707	-0.05	0.7795
3.0 km	-0.04	0.8320	0.20	0.2912	-0.11	0.5622
MPI						
0.5 km	0.50	**0.0049**	0.52	**0.0031**	0.11	0.5653
1.0 km	-0.10	0.6094	0.00	0.9948	0.46	**0.0103**
1.5 km	-0.03	0.8730	0.10	0.5900	-0.16	0.4089
2.0 km	-0.05	0.7795	0.09	0.6218	-0.13	0.4824
2.5 km	0.22	0.2366	-0.05	0.7992	-0.29	0.1157
3.0 km	0.24	0.1994	0.07	0.7134	-0.13	0.4882
SHDI						
0.5 km	-0.10	0.6051	0.24	0.1964	0.01	0.9395
1.0 km	0.01	0.9390	0.23	0.2187	0.07	0.6948
1.5 km	0.24	0.2059	0.38	**0.0383**	0.01	0.9624
2.0 km	0.27	0.1429	0.33	0.0713	0.10	0.6017
2.5 km	0.29	0.1229	0.30	0.1135	0.08	0.6675
3.0 km	0.27	0.1541	0.33	0.0722	0.00	0.9974

Annex 2.3. Class level metrics (average ± SE) for the three most important land uses in 15 *D. marginata* fields of the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Landscape metrics include: Area-Weighted Mean Shape Index (AWMSI), Mean Proximity Index (MPI) and Percent of Land (ZLAND). AWMSI and MPI with no units; ZLAND (%).

Land use	AWMSI ± SE	MPI ± SE	ZLAND ± SE
Ornamental			
Spatial scale			
0.5 km	1.40 ± 0.07	4.96 ± 4.07	62.92 ± 6.92
1.0 km	1.62 ± 0.09	27.89 ± 11.39	46.06 ± 7.59
1.5 km	1.89 ± 0.07	91.72 ± 21.50	36.28 ± 5.28
2.0 km	2.01 ± 0.10	222.27 ± 63.35	30.91 ± 4.17
2.5 km	2.10 ± 0.08	278.53 ± 41.36	27.93 ± 4.00
3.0 km	2.11 ± 0.09	593.44 ± 113.15	25.65 ± 3.51
Pasture			
Spatial scale			
0.5 km	0.79 ± 0.20	2.05 ± 1.94	6.44 ± 3.58
1.0 km	1.60 ± 0.13	6.40 ± 3.91	9.96 ± 2.62
1.5 km	1.73 ± 0.03	20.90 ± 9.87	14.42 ± 2.39
2.0 km	2.00 ± 0.05	31.87 ± 12.20	17.26 ± 1.97
2.5 km	2.05 ± 0.06	41.79 ± 11.14	18.83 ± 2.23
3.0 km	2.08 ± 0.09	38.01 ± 12.67	20.07 ± 2.58
Forest			
Spatial scale			
0.5 km	0.33 ± 0.18	0.09 ± 0.05	4.03 ± 2.19
1.0 km	1.13 ± 0.30	2.45 ± 2.07	9.83 ± 3.76
1.5 km	1.87 ± 0.15	115.74 ± 102.98	12.11 ± 3.80
2.0 km	1.90 ± 0.17	526.62 ± 517.08	16.39 ± 4.43
2.5 km	2.09 ± 0.20	82.00 ± 32.55	18.52 ± 4.58
3.0 km	2.26 ± 0.19	270.55 ± 176.51	18.84 ± 4.28

Annex 2.4. Pearson correlation coefficients (*r*) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and ornamental land use metrics for the three most important land uses in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Significant correlations with $p<0.05$.

Landscape Use	Leafhopper egg number		Katydid egg number		Leaves with armored scales	
	R	**P**	**R**	**P**	**R**	**P**
Zland						
0.5 km	0.11	0.5669	-0.24	0.1940	0.01	0.9674
1.0 km	0.14	0.4458	-0.19	0.3275	-0.07	0.6969
1.5 km	0.23	0.2236	-0.14	0.4459	-0.13	0.4939
2.0 km	0.14	0.4641	-0.22	0.2413	-0.12	0.5174
2.5 km	0.01	0.9571	-0.28	0.1367	-0.11	0.5695
3.0 km	-0.07	0.7311	-0.30	0.1039	-0.12	0.5399
AWMSI						
0.5 km	-0.1747	0.3558	0.0702	0.7126	-0.0466	0.8069
1.0 km	-0.1582	0.4038	0.0616	0.7466	0.3049	0.1014
1.5 km	0.1095	0.5646	0.3285	0.0764	0.0266	0.8889
2.0 km	0.4432	**0.0142**	0.3878	**0.0342**	-0.1208	0.5249
2.5 km	0.4697	**0.0088**	0.3585	0.0517	-0.1242	0.5131
3.0 km	0.4314	**0.0173**	0.3011	0.1059	-0.2051	0.2769
MPI						
0.5 km	0.3718	**0.0431**	0.2483	0.1857	0.2964	0.1117
1.0 km	0.4221	**0.0201**	0.2611	0.1634	0.1853	0.3269
1.5 km	0.5801	**0.0008**	0.0749	0.6942	0.0570	0.7648
2.0 km	-0.0075	0.9685	-0.2550	0.1738	-0.1064	0.5759
2.5 km	-0.0026	0.9890	-0.2319	0.2175	-0.1169	0.5384
3.0 km	0.2841	0.1282	0.0828	0.6635	-0.1795	0.3424

Annex 2.5. Pearson correlation coefficients (*r*) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and pasture land use metrics for the three most important land uses in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Significant correlations with $p<0.05$.

Landscape Use	Leafhopper egg number		Katydid egg number		Leaves with armored scales	
	R	*P*	*R*	*P*	*R*	*P*
Zland						
0.5 km	0.10	0.6130	0.19	0.3127	0.00	0.9825
1.0 km	-0.25	0.1867	0.03	0.8936	0.15	0.4267
1.5 km	-0.41	**0.0253**	-0.04	0.8324	0.13	0.4856
2.0 km	-0.41	**0.0263**	-0.21	0.2564	0.25	0.1777
2.5 km	-0.34	0.0700	-0.29	0.1202	0.34	0.0649
3.0 km	-0.32	0.0875	-0.28	0.1364	0.36	0.0522
AWMSI						
0.5 km	0.2834	0.1291	0.1675	0.3763	0.2709	0.1476
1.0 km	0.3113	0.0940	-0.0289	0.8794	-0.0164	0.9314
1.5 km	-0.4673	**0.0092**	-0.3316	0.0735	-0.0074	0.9691
2.0 km	-0.3148	0.0902	-0.3646	**0.0476**	0.0944	0.6196
2.5 km	-0.0664	0.7272	-0.2400	0.2015	0.0211	0.9121
3.0 km	0.0388	0.8386	-0.2695	0.1499	-0.0289	0.8795
MPI						
0.5 km	0.0571	0.7643	0.1848	0.3283	-0.0683	0.7199
1.0 km	0.0686	0.7188	0.1792	0.3433	-0.1057	0.5782
1.5 km	-0.3666	**0.0463**	-0.0021	0.9912	0.1625	0.3909
2.0 km	-0.0346	0.8561	0.2500	0.1826	-0.0746	0.6954
2.5 km	0.0043	0.9822	-0.0080	0.9665	0.0083	0.9653
3.0 km	0.0421	0.8253	0.1516	0.4240	0.4301	**0.0177**

Annex 2.6. Pearson correlation coefficients (*r*) between the average number of insect pests (leafhopper eggs, katydid eggs and leaves infested with armored scales) and forest land use metrics for the three most important land uses in 15 *D. marginata* fields in the northern of Costa Rica at six spatial scales (from Ø 0.5 to Ø 3 km). Metrics include: (a) Percent of landscape (ZLAND) (b) Area-Weighted Mean Shape Index (AWMSI) and (c) Mean Proximity Index (MPI). Significant correlations with *p* < 0.05.

Landscape Use	Leafhopper egg number		Katydid egg number		Leaves with armored scales	
	R	*P*	*R*	*P*	*R*	*P*
Zland						
0.5 km	-0.21	0.2642	0.14	0.4474	-0.23	0.2149
1.0 km	-0.06	0.7349	0.24	0.2030	-0.27	0.1525
1.5 km	0.07	0.7026	0.28	0.1338	-0.25	0.1748
2.0 km	0.14	0.4570	0.31	0.0984	-0.27	0.1548
2.5 km	0.24	0.2061	0.35	0.0544	-0.23	0.2243
3.0 km	0.33	0.0719	0.38	**0.0381**	-0.18	0.3351
AWMSI						
0.5 km	-0.2441	0.1937	0.1310	0.4902	-0.2416	0.1984
1.0 km	0.2828	0.1299	0.3421	0.0642	-0.1895	0.3159
1.5 km	-0.1227	0.5183	0.0667	0.7261	-0.0868	0.6483
2.0 km	-0.0602	0.7519	0.2813	0.1321	-0.1511	0.4254
2.5 km	-0.0082	0.9656	0.3055	0.1006	-0.1792	0.3434
3.0 km	0.0420	0.8255	0.3129	0.0923	-0.1405	0.4588
MPI						
0.5 km	-0.3529	**0.0458**	0.0527	0.7820	-0.2260	0.2298
1.0 km	-0.3680	**0.0454**	-0.0214	0.9105	-0.1692	0.3713
1.5 km	-0.0350	0.8542	0.1019	0.5921	-0.1612	0.3947
2.0 km	-0.0295	0.8770	0.1288	0.4977	-0.0931	0.6245
2.5 km	-0.0684	0.7195	0.0128	0.9465	-0.1733	0.3597
3.0 km	0.1534	0.4184	-0.0731	0.7011	-0.0700	0.7134

CHAPTER 3. EFFECT OF FOREST AND DISTANCE FROM FIELD EDGE ON PEST POPULATIONS AND THEIR NATURAL ENEMIES IN *DRACAENA MARGINATA* IN COSTA RICA

3.1 Introduction

The landscape context can have an important effect on insect ecological and spatial processes such as population size, richness, biodiversity, dispersion, distribution and movement (e.g. Kareiva 1983, Turner 1989, Fahrig and Merriam 1985, Harrison and Tomas 1991, Dunning *et al.* 1992, Coll and Bottrell 1994, Hanski, 1994, Jonsen and Fahrig 1997, With *et al.* 1999, 2002, Chust *et al.* 2004, Chacoff and Aizen 2006, Arellano *et al.* 2008, Gaines and Gratton 2010, Werling and Gratton 2010). Its influence can be particularly important in agroecosystems, where landscape composition and diversity can either have negative effects, e.g. providing conditions for the development and spreading of insect pest populations; or positive effects, e.g. supplying habitats for natural enemies, which in turn reduce pest populations.

Changes in composition and diversity of landscapes in agricultural areas have been related to intensification of agricultural activities (Robinson and Sutherland 2002). Currently, it is common to find agricultural landscapes dominated by large areas of crop fields scattered with small fragments of unmanaged patches of native vegetation. Management practices in these crop habitats often provide sub-optimal conditions for the development of populations of herbivorous pests and especially their arthropod natural enemies (Kruess 2003, Schmidt and Tscharntke 2005). As a consequence, colonization of natural enemies after disturbances in cropping system may depend on surrounding natural habitats (Wissinger 1997, Tscharntke *et al.* 2005b). Non-crop habitats such as forests, hedgerows, field margins, edges and fallow fields can play an important role providing alternative prey, plant food resources, an optimal microclimate, and refuge and hibernation areas for natural enemies (Landis *et al.* 2000, 2005). These conditions may not only improve the conservation of biodiversity but also act as sources of beneficial arthropods,

which have the potential to reduce pest outbreaks (Thies and Tscharntke 1999, Schmidt *et al.* 2005, Bianchi *et al.* 2006, Issacs *et al.* 2009, Lundgren 2009, Thomson and Hoffmann 2009).

Forests in temperate climates have been noted for their capacity to provide ecosystem services on farms such as biodiversity, biological control and pollination (e.g. Marino and Landis 1996, Klein *et al.* 2003a,b, De Marco and Coelho 2004, Kremen *et al.* 2004, Chacoff *et al.* 2006, Bianchi *et al.* 2006, Benevides *et al.* 2009, Thomson *et al.* 2010). Ecosystem services provided by tropical forests in Costa Rica have also been highlighted for their important contribution to nearby agricultural lands providing habitat conservation for increasing arthropod diversity (Janzen 1987, Banks *et al.* 2007) and enhancing pollination services (Ricketts 2004, Brosi 2009).

In Costa Rica, where the production of ornamental plants is a significant part of the agricultural landscape, *Dracaena marginata* Lam. (Rusaceae), provides an opportunity to study population dynamics of herbivorous arthropods in three families Cicadellidae (leafhoppers), Tettigoniidae (katydids) and Diaspididae (armored scales) in specific landscape contexts. These arthropods differ importantly in terms of their biology. Leafhoppers are obligate sucking herbivores with a wide range of hosts in crops and non-crop habitats (Nault and Rodriguez 1985, Denno and Perfect 1994). Katydids are chewing insects with a diverse range of diets. Some species are strict herbivores whereas other species are facultative predators. They are mostly present in grasslands and weedy areas, and typically feed on either grasses or forbs, although some species feed on both (Joern 1979, 1982, Squitier and Carpinera 2002). Armored scales are sap-feeding insects with a wide range of host plants (Culik *et al.* 2008, Magsig-Castillo *et al.* 2010). While leafhoppers and katydids have high dispersal capacities; armored scales are sedentary for most of their life cycle.

In Costa Rica most of *D. marginata* agroecosystems are embedded in areas with a broad diversity of land uses including crop habitats such as pineapple and other ornamental plants; and non-crop habitats such as pastures, scrublands and forests. In Costa Rica, over 48% of the land is covered by some type of tree cover forest. At least 60% of the coverage has been classified as disturbed forest or mature secondary forests with similar structure to

the undisturbed natural forests with the remainder classified as intermediate or early secondary forests (Calvo-Alvarado 2009). In the Atlantic and Northern areas of Costa Rica it is common to find patches of secondary forests near *D. marginata* production fields. For instance, based on aerial photos we found that forest is the third most important land use, representing an 18.9% of the landscape associated with *D. marginata* in the Northern zone of Costa Rica (see Chapter 2 for details).

In this study, we tested the hypothesis that forest patches provide ecosystem services for *D. marginata* fields, acting as a source of natural enemies and predators that can reduce insect pest populations. In particular we asked the following questions: (1) Do the levels of insect pest abundance and parasitism differ between ornamental fields when an adjacent forest is present or absent?; (2) Do pest abundance, natural enemies abundance and parasitism levels change with increasing distance from field edge in the presence or absence of an adjacent?; (3) Do leafhoppers, katydids and armored scales show the same responses to forest and distance from field edge?; (4) Is there movement of pests and natural enemies from the forest to the field and back?; (5) Does the season has an effect on insect populations and parasitism in plots near forests?

3.2 Material and methods

Study area

The study was carried out in three areas of ornamental production in Costa Rica: San Carlos and Sarapiquí in the Northern zone, and Siquirres in the Atlantic zone. San Carlos has an elevation ranging from 160 to 340 m, with temperatures between 26 and 30 ℃; Guápiles is located at 262 m, the average temperature is 27 ℃; Sarapiquí has an average elevation of 37 m, its annual temperatures are between 19.5 and 31.5 ℃. Atlantic zone (Siquirres) has an annual average precipitation between 3500-4500 mm, while in the North zone (San Carlos and Sarapiquí) is 3200 mm (IMN 2010).

Effect of forest on insect pest population and parasitism

In order to evaluate the effect of adjacent forest on insect pest population, 14 plots distributed among six farms which grew four commercially produced varieties of *D.*

marginata (green, magenta, bicolor and pamella) were selected. Six plots were located in the Atlantic Zone near Siquirres and eight in the Northern Zone near Sarapiquí and San Carlos. Eight of the plots were adjacent to a secondary forest and six were located at distances of at least 1 km away.

Forests in the study area were mostly secondary forest types. According to Chokkalingam and De Jong (2001), these are forests that have regrown after significant human and/or natural disturbance of the original forest vegetation. The selected forests in this study encompassed a minimum of three hectares and were at least nine years old, exceeding the minimum standards for forest classification (FAO 1998). In this part of Costa Rica, forests consist of primarily of plants in three families Melastomataceae, Piperaceae and Malvaceae (Finegan 1996). Upon visual inspection of a 10 m transect along the forest edge we found these plants to be present in the forests adjacent to our eight study plots. In addition we also encountered species from the families: Urticaceae, Fabaceae, Bignoniaceae, Euphorbiaceae, Vochysiaceae, Salicaceae, Boraginaceae, Araliaceae, and Hypericaceae. Some scattered species with a larger size and longevity belonging to families such as Simaroubaceae and Moraceae were also identified. In general, non-forest field plots belonged to farms of larger producers, while plots with contiguous forest (forest fields) were located in farms of small producers.

Sampling

The experiment was carried out between September 2008 and August 2009. Three distances were selected (0, 10, 20 m) to determine how abundance of insect pests and parasitism varied with the distance from the field edge adjacent to a forest (**Figure 3.1**). Plot sizes of forested plots ranged between 50 m × 50 m to 100 × 80 m. Non-forest plots were taken from unforested areas ranging from 4500 m^2 to 7500 m^2 in size. At each distance from the plot edge, plant tips were sampled from 15 points, 0.67 m apart; along a 10 m transect parallel to field edge. At each sampling point one plant tip was selected from the lower (0 - 50 m), middle (50 - 100 m) or upper (more than 100 m) strata of plant height (**Figure 3.1**). Five samples were collected along each transect.

Each tip was visually inspected for numbers of leafhopper nymphs, spiders and other predacious insects. Then each tip was removed, placed into a plastic bag and then into a cooler and taken to the laboratory where they were dissected to count leafhopper and katydid eggs under a dissecting microscope. Parasitism level was determined as the number of parasitized eggs. The abundance of armored scale insects (*Chrysomphalus* sp.) per tip was measured by counting the number of infested leaves. In previous work, Prado *et al.* (2008) found that the number of leaves with scales were a reliable indicator of their presence.

The first census occurred during the rainy season between October and December in 2008 (average monthly precipitation = 677.0 mm). A second census was taken on plots near forests during the dry season between March to May in 2009 (average monthly precipitation = 264.1 mm). The objective was to evaluate if seasonality had an influence on the effect of forest on insect pest population and natural enemies abundance.
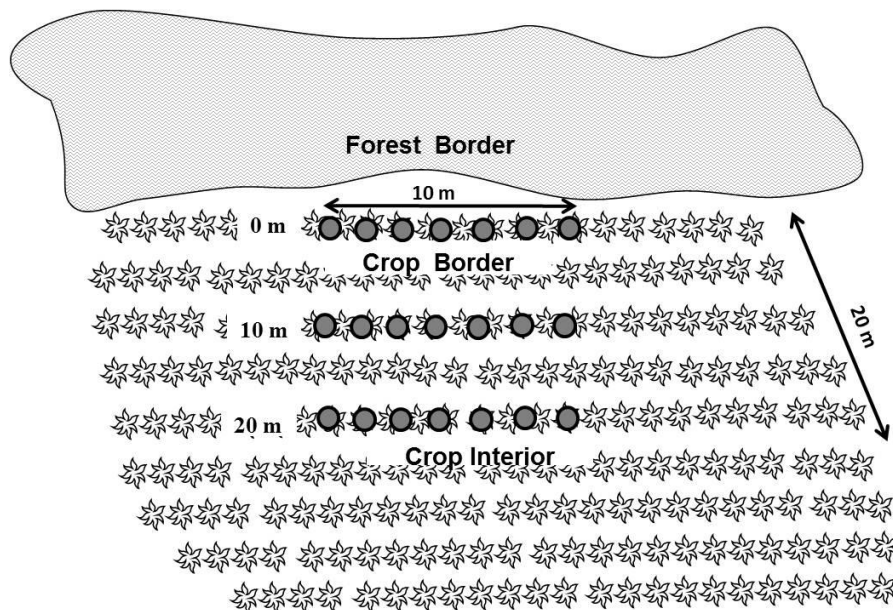
Figure 3.1.   Schematic diagram the sampling methodology used to collect quarantine insects in a *D. marginata* plot adjacent forested areas (not to scale). Gray circles represent examples of sampling sites at 0, 10 and 20 meters from field edge.

Statistical analysis

The total number of leafhopper nymphs, leafhopper parasitism, *Caldwelliola* sp. parasitism, katydid eggs, and katydid parasitism were analyzed with analysis of variance

(ANOVA) under the general and mixed model framework using the restricted maximum likelihood method (REML) (Di Rienzo *et al.* 2010). To analyze the effect of forest and distance on pest population and parasitism level in the 10 m transect, the model assumed the effect of forest, distance to the edge and their interaction as fixed factors. Plot and forest were considered random effects. When analyzing the effect of season and distance in the transect sampling, we assumed season, distance and their interaction as fixed factors, whereas that plots and season were considered random.

For each response variable a series of models were run with different error variance structures and function error correlations to determine the appropriate model for analysis. We used the Akaike's Information Criterion (AIC) and the Bayesian information criterion (BIC) to select the best-fitted model (smaller is better for both criteria). In the cases where the model values for these criteria were close, we used likelihood ratio test (LRT) to test hypothesis to decide which model provided the best fit. Means of significant effects were separated using a Fisher protected least significant difference (LSD) at a significance of *p*= 0.05.

Data were analyzed to test the data normality assumption. When populations were not normal, proportional data was transformed to arcsine square root. Leafhopper, *Caldwelliola* sp. and *Oncometopia* sp. eggs, number of leaves with scales and predatory insects were analyzed with generalized linear models (Agresti 1990) because they did not meet the normality assumption after transformation. In this case, counts were transformed using a log linear link canonical function prior to analysis with a mixed model procedure using InfoStat Professional (Di Rienzo *et al.* 2010). For variables related to proportions or with a large number of zeros we used generalized linear models procedure using a binomial distribution for presence and absence, considering values higher than zero to indicate an organism was present. In both cases we used distance as a covariate.

For variables analyzed with mixed models, F value, numerator and denominator degrees of freedom and p value (F = value, df= num, den, *p*= value) are provided. For generalized linear models analysis, the test hypothesis for variables was calculated from the Chi square statistic (χ^2= value; df= num, den; *p*= value). Degrees of freedom for the factors, model and p-values are shown.

Movement of leafhoppers and natural enemies in fields adjacent to forest

To determine the potential directionality of movement from adjacent forest to Dracaena field and vice versa, migration Malaise traps (Walker 1978) were used (Irwin *et al.* 2000). Two traps were placed next to each other along the field edge of each of the Dracaena plots that were adjacent to forests. Distance from field edge to forest was not more than 4 m (**Figure 3.2**). Malaise traps were left in the field for 8 days. Insects were collected on the each side of the Malaise traps and taken to the laboratory for identification. Total number of insects, leafhopper and natural enemies (Mymaridae families) were recorded for each field. A paired t-test was conducted to determine significant differences between trap sides of the migration Malaise trap at each edge (Di Rienzo *et al.* 2010).

Figure 3.2.   Picture showing the position of Malaise traps to evaluate the movement of leafhoppers and natural enemies from adjacent forest to Dracaena field and vice versa.

3.3 Results

Pests were found from each of the four targeted groups in all of the study plots (**Table 3.1**). Identification of leafhopper eggs revealed that there were four morphospecies from the following genera: *Caldwelliola*, *Oncometopia*, *Diestostemma*, and *Gypona*. The two most important leafhoppers in terms of abundance, registering 80.2% of total of eggs found in the field, were *Caldwelliola* sp. (Subfamily: Cicadellinae; Tribe: Cicadellini)

(46.70%) and *Oncometopia* sp. (Subfamily: Cicadellinae; Tribe: Proconiini) (33.50%). The 73.7% of the nymphs identified in the field belonged on the genus *Empoasca,* while the rest were identified as *Caldwelliola* sp. (16.2%) and *Oncometopia* sp. (10.2%). Most of the nymphs found during this study belonged to the genus *Empoasca*, for which it was not possible to evaluate egg abundance due to their small size (0.5mm) and cryptic location inside the Dracaena leaves. Based on the high population of adult *Empoasca* and the high egg abundance reported by Hidalgo (2012) the leafhopper egg counts reported in this study underestimate the egg total population but gives a good estimation for those eggs large enough to be counted using simple inspection methods.

Katydid eggs were less abundant, but eggs from 18 morphospecies were found including some in the genus *Microcentrum* and *Conocephalus*. The highest average for the insects was found for the number of leaves infested with armored scales, primarily Florida red scale, *Chrysomphalum aonidum* (L.). Parasitism proportion was higher for leafhopper eggs in comparison to katydid eggs (**Table 3.1**). Leafhopper eggs were parasitized by *Gonatocerus* spp. (Hymenoptera: Mymaridae). We found parasitism mainly on *Caldwelliola* spp. (57.14%) and *Oncometopia* sp. (31.75%) eggs, but we also identified at least one parasitized egg on the others six types of leafhoppers eggs found in the fields. We also found predatory insects such as spiders (order Araneae); lacewings (Chrysopidae), preying mantids (Mantidae); ladybird beetles (Coccinellidae) and Assassin bug (Reduviidae).

Table 3.1.   Means and SE of measures of insect pest abundance and proportion of selected pest parasitized per tip of *D. marginata* in 14 plots in Costa Rica during, 2008-2009. Armored scale abundance was registered as the number of leaves infested with armored scales.

Insect	mean $\pm$ SE
Leafhopper eggs	0.31 ± 0.10
Leafhopper eggs parasitized	0.34 ± 0.08
Leafhopper nymphs	0.17 ± 0.04
Katydid eggs	0.21 ± 0.05
Katydid eggs parasitized	0.19 ± 0.07
Leaves with armored scales	0.39 ± 0.08
Predatory insects	0.20 ± 0.03

Leafhopper and parasitism level

Effect of forest and distance

Presence of forest significantly affected leafhopper egg abundance (χ^2=4.31; df=1, 36; p=0.378) and leafhopper nymph population (F = 5.31; df = 1,12; p= 0.0399). Leafhopper eggs and nymph abundance were higher in absence of forest than in its presence. Similarly, the number of *Caldwelliola* sp. and *Oncometopia* sp eggs per tip was lower in plots near forest (χ^2=4.30; df = 1, 36; p= 0.0382 and χ^2=8.52; df = 1, 38; p= 0.0035; respectively) (**Table 3.2**). This difference was particularly important for *Oncometopia* sp. where, in plots surrounded by forests, average abundance was almost nil (**Table 3.2**). Overall, distance had no impact on populations of total leafhopper eggs (χ^2=0.07; df = 2, 36; p= 0.9679), *Caldwelliola* sp. eggs (χ^2=1.01; df = 1, 36; p= 0.3147), *Oncometopia* sp. (χ^2=0.0001; df = 1, 36; p= >0.9999) or nymphs (F = 0.63; df = 2, 24; p= 0.5390).

Table 3.2. Effects of the presence of forest on the average abundance of total leafhopper eggs, nymphs and the quarantine leafhopper eggs of *Caldwelliola* sp. and *Oncometopia* sp. per tip on *D. marginata* plants in 14 production plots in Costa Rica, 2008-2009.

Forest	N	Total eggs	*Caldwelliola* sp. eggs	*Oncometopia* sp. eggs	Nymphs
Absent	6	0.53 ± 0.21[a]	0.25 ± 0.12 [a]	0.24 ± 0.11 [a]	0.26 ± 0.06 [a]
Present	8	0.15 ± 0.05 [b]	0.07 ± 0.03 [b]	0.003 ± 0.003 [b]	0.10 ± 0.04 [b]

Means within the same column followed by different letters indicated significant differences (p<0.05, Fisher LSD).

We did not find a significant effect of the presence/absence of forest or distance for the proportion of total leafhopper eggs that were parasitized (F = 0.23; df = 1, 10; p= 0.6415; F = 0.02; df = 2, 16; p= 0.9814, respectively). However, looking at the parasitized proportion of leafhopper eggs by species, we found a significant interaction between forest and distance on the proportion on *Caldwelliola* sp. eggs that were parasitized (F = 4.69; df = 2, 11; p= 0.0336). The highest proportion of parasitism was found in forested plots at 20 meters from the field edge (0.76 ± 0.19), which differed significantly from non-forest plots at the same distance (0.16 ± 0.19) (**Figure 3.3**). We did not detect any parasitism of *Oncometopia* sp. eggs in forested plots (**Table 3.3**).

Table 3.3. Average parasitism proportion of total leafhopper, *Caldwelliola* sp. and *Oncometopia* sp. eggs per tip on *D. marginata* plants in 14 production plots in Costa Rica, 2008- 2009.

Factor	N	Proportion parasitized (Mean ± SE)		
		Total parasitized leafhopper eggs	*Caldwelliola* sp.	*Oncometopia* sp.
No Forest	6	0.31 ± 0.06	0.39 ± 0.15	0.36 ± 0.15
Forest	8	0.38 ± 0.15	0.58 ± 0.19	0.00 ± 0.00
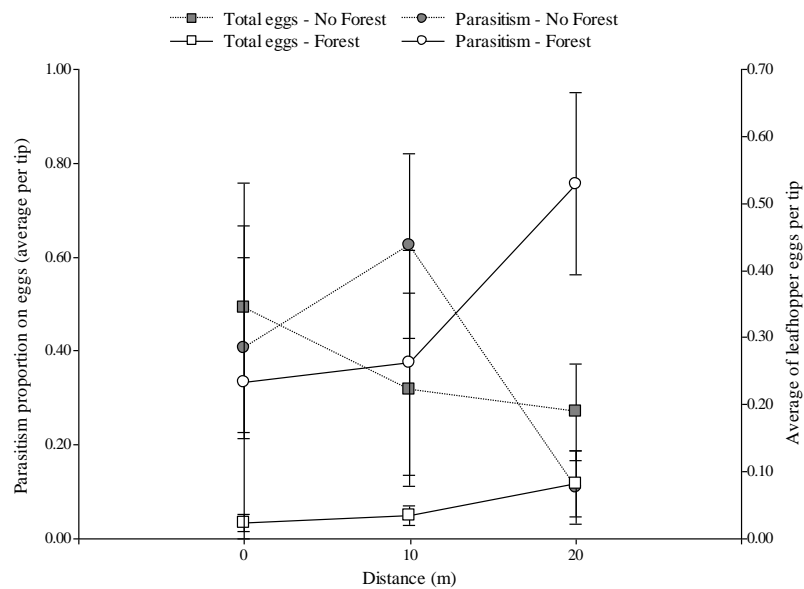
Figure 3.3. Average number per tip (± SE) of *Caldwelliola* sp. eggs (square symbol) and parasitism proportion (circle symbol) found in *Dracaena marginata* fields adjacent to forest (white symbol) and in absence of forest (gray symbol) sampled at 0, 10 and 20 m from the edge of the plot, Costa Rica, 2008-2009.

Effect of season on forested fields

Evaluations of Dracaena fields near forest showed that season had a significant effect on the abundance of leafhopper nymphs (χ^2=5.15; df=1,41; *p*=0.0234). The leafhopper nymph population was higher during the rainy season (**Table 3.4**). Season also influenced *Caldwelliola* sp. egg parasitism (χ^2=3.95; df=1,10; *p*=0.0468) with a higher parasitism proportion during the dry season (**Table 3.5**). In the rainy season we only found *Caldwelliola* sp. parasitism in one forested plot at 20 meters from field edge. We also found a significant effect of distance from field edge in the forest fields (χ^2=4.50; df=1,10;

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p=0.0339). The proportion of parasitized *Caldwelliola* sp. eggs was higher at 20 meters (0.72±0.20; n=5) than at 0 and 10 meters from the field edge (0.25±0.25; n=4 and 0.30±0.20; n=5; respectively). This coincided with what we found comparing fields in presence and absence of forest; we found the highest parasitism proportion in forested plots at 20 meters from the field edge (**Figure 3.3**).

Table 3.4. Effects of season on the average per tip abundance of quarantine insect pests on *D. marginata* plots in Costa Rica, 2009.

Factor	N	Total eggs	*Caldwelliola* sp. eggs	Nymphs	Leaves infested with armored scales	Katydid eggs
Rainy	8	0.18 ± 0.07[a]	0.04 ± 0.03 [a]	0.04 ± 0.01 [a]	0.14 ± 0.08 [a]	0.07 ± 0.03 [a]
Dry	7	0.35 ± 0.20 [a]	0.04 ± 0.02 [a]	0.008 ± 0.005 [b]	0.37 ± 0.14 [a]	0.22 ± 0.06 [b]

Means within the same column followed by different letters indicated significant differences (p<0.05< Fisher LSD).

Table 3.5. Effects of season on the average per tip abundance of leafhopper egg parasitism and the abundance of predatory insects on *D. marginata* plots in Costa Rica, 2009.

Factor	N	Predatory insects	Leafhopper parasitism	*Caldwelliola* sp. parasitism	Katydid parasitism
Rainy	8	0.26 ± 0.06 [a]	0.30 ± 0.14 [a]	0.10 ± 0.10 [a]	0.42 ± 0.17 [a]
Dry	7	0.19 ± 0.06 [a]	0.48 ± 0.18 [a]	0.62 ± 0.24 [b]	0.24 ± 0.17 [a]

Means within the same column followed by different letters indicated significant differences (p<0.05< Fisher LSD).

We did not find differences between the rainy and dry season on leafhopper egg abundance (χ^2=0.48; df=1,41; p=0.4863), leafhopper parasitism (χ^2=0.01; df=1,28; p=0.9306), nor *Cadwelliola* sp. eggs (χ^2=0.24; df=1,41; p=0.6237) in forested plots. *Oncometopia* sp. eggs were present just on four plants of the forested plots with an average of 0.001 ± 0.001 (n = 15; min = 0.00; max = 0.22 very few to examine effects of season on parasitism.

Katydid eggs and parasitism level

Effect of forest and distance

Forest had no significant influence on the abundance of katydid eggs (F = 0.62; df = 1, 12; p= 0.4467) or the proportion of parasitized katydid eggs (F = 0.08; df = 1, 11; p= 0.7806). Conversely, distance from field edge significantly affected the katydid abundance (F = 3.81; df = 2, 24; p= 0.0364). Number of katydid eggs was higher at the field edge (0.29 ± 0.05) than at 10 and 20 meters into the field (0.17±0.05 and 0.16±0.04;

respectively) (**Figure 3.4**). In the case of katydid parasitism, distance from field edge had a marginal effect on parasitism ($F = 3.38$; df = 2, 15; $p= 0.0616$). A tendency was identified showing a lower proportion parasitized at the field edge compared to 10 and 20 meters. Comparing the patterns of parasitism and katydid abundance at the different distances, we determined that the highest katydid abundance found at the field border coincided with the lowest parasitism proportion at the same distance (**Figure 3.4**). However, we did not find a significant Pearson correlation between katydid eggs and proportion parasitized ($r_p(42)=0.09$, $p=0.64$).
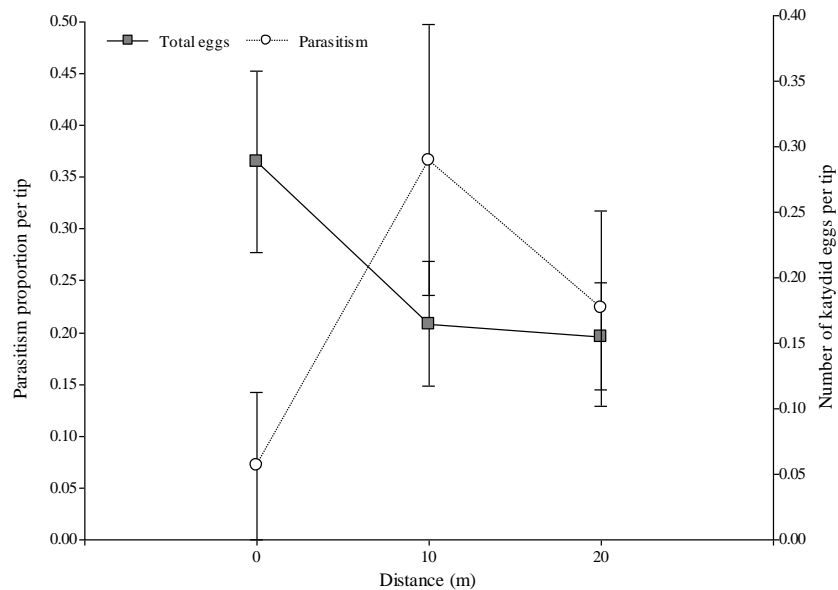
Figure 3.4.   Effect of distance from field edge on the average abundance of katydid eggs (square symbol) and parasitism proportion (circle symble) per tip on *D. marginata* plots in Costa Rica, 2008-2009.

Effect of season on forested fields

When evaluating the effect of season on forested fields, we found significantly more katydid eggs in forested plots during the dry season (**Table 3.4**) ($F = 6.58$; df=1,6; $p=0.0427$). We did not find an effect of season on katydid egg parasitism ($F = 0.68$; df=1,5; $p=0.4487$); however we found a marginal effect on the interaction between distance and season on parasitism proportion on katydid eggs ($F = 3.55$; df = 2, 13; $p= 0.0587$). A higher proportion of parasitized eggs was observed in the rainy season at 0 meters from the field edge (0.60 ± 0.24) compared to the dry season (0.14 ± 0.14) at the same distance (**Figure 3.5**).
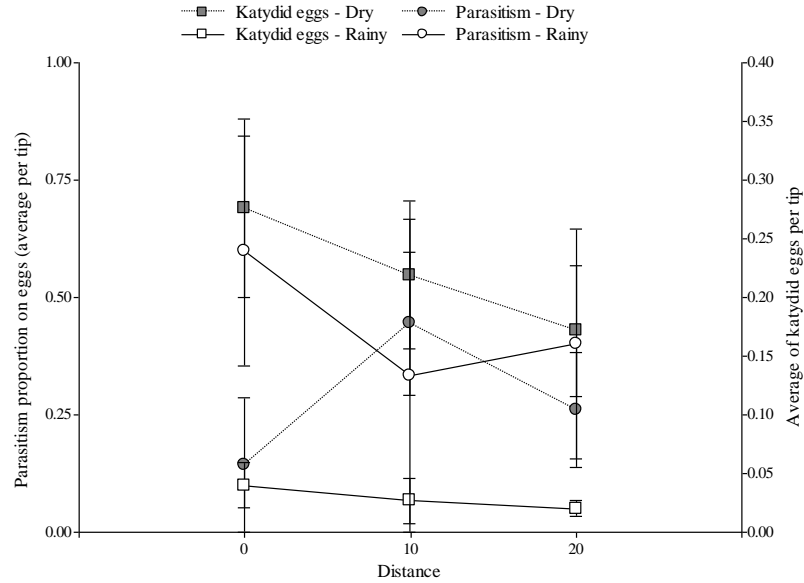
Figure 3.5.   Effect of the interaction of dry (gray color) and rainy (white color) seasons with distance from field edge on the average per tip of katydid eggs (square symbol) and parasitism proportion (circle symbol) on *D. marginata* plots in Costa Rica, 2008-2009.

Armored scale population

Effect of forest and distance

The presence of forest had no impact on populations of armored scales (χ^2=0.85; df=1,38; *p*=0.3570). Distance from field edge significantly affected armored scale population (χ^2=8.65; df=1,38; *p*=0.0033). Lower numbers of leaves infested with armored scales were found at the field edge, (0.29 ± 0.08) than at 10 and 20 meters (0.44 ± 0.12 and 0.43 ± 0.12, respectively).

Effect of season on forested fields

We did not find an effect of season on the number of leaves infested with armored scales (*F*=3.62; df=1,6; *p*=0.1060); however the interaction between season and distance from field edge had a significant impact on leaves infested with armored scale populations (*F* = 4.56; df = 2, 26; *p*= 0.0201) (**Figure 3.6**). We determined that at 20 meters from field edges, there were more leaves infested with armored scales in the dry season than during the rainy season.
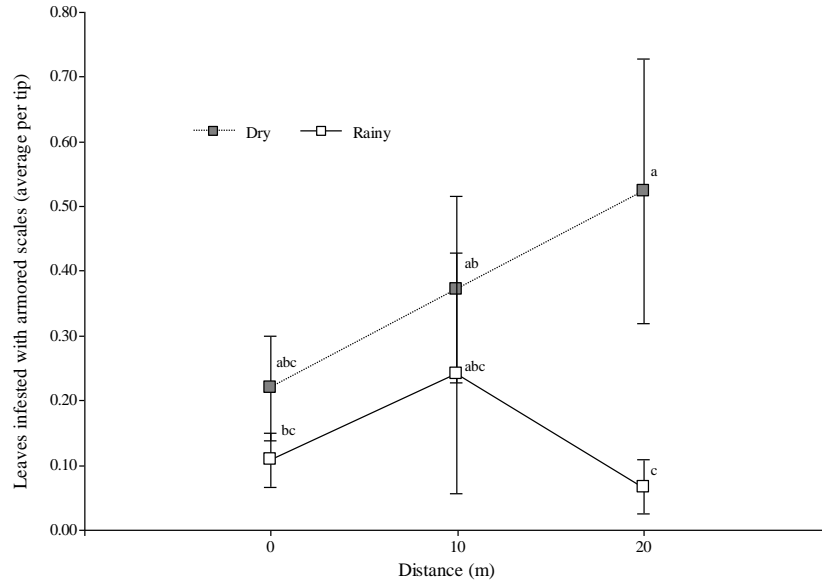
Figure 3.6. Number of leaves infested with armored scales per tip (average ± SE) sampled in a 10 meter transect in *D. marginata* fields during dry (gray symbol) and rainy (white symbol) seasons at three distances from field edge in Costa Rica, 2008-2009. Different letters indicated significant differences ($p<0.05<$ Fisher LSD).

Predatory insect population

Effect of forest and distance

We did not find a significant effect of the presence/absence of forest or distance on predatory insect population ($\chi^2=0.003$; df=1,38; $p=0.9545$ and $\chi^2=0.02$; df=1,38; $p=0.8860$, respectively). When we compared the number of predatory insects with the different pest insects, we found a positive significant Pearson correlation with *Oncometopia* sp. eggs ($r_p(42)=0.38$, $p=0.01$) and a negative correlation with the number of leaves infested with scales ($r_p(42)=-0.49$, $p=0.001$). For leafhopper egg abundance we found a positive Pearson correlation in plots away forest ($r_p(42)=0.74$, $p<0.001$) but a negative correlation in forest plots ($r_p(42)=-0.55$, $p=0.01$).

Effect of season on forested fields

We did not find an effect of season on predatory insect abundance ($F=0.77$; df=1,6; $p=0.4154$); however the interaction between season and distance from field edge was significant ($F = 4.52$; df = 2, 26; $p= 0.0207$). A higher population was found during the rainy season at the field edge compared with dry season at the same distance. A tendency

was also observed in the rainy season showing that the number of predatory insects decreased as the distance from the field edge decreased (**Figure 3.7**).
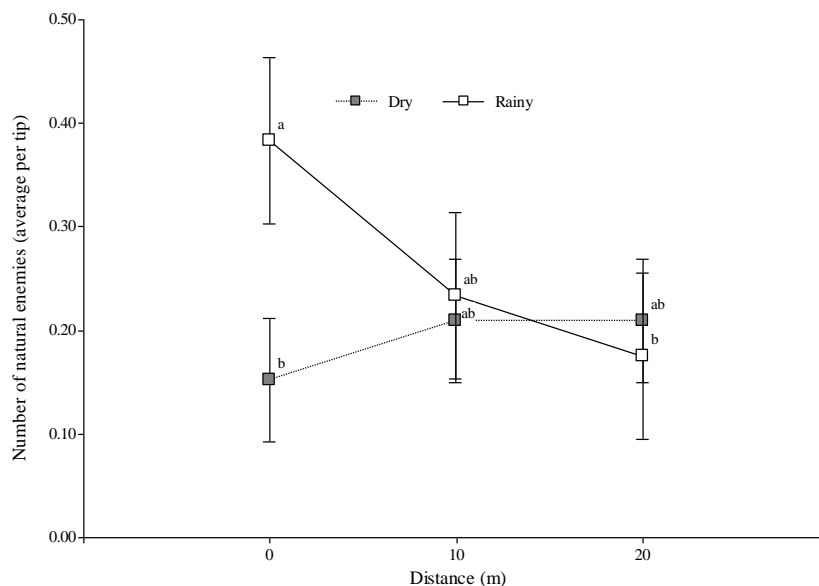
Figure 3.7. Number of predatory insects per tip (average ± SE) sampled in a 10 meter transect in *D. marginata* fields during dry (gray symbol) and rainy (white symbol) seasons at three distances from field edge in Costa Rica, 2008-2009. Different letters indicated significant differences ($p<0.05<$ Fisher LSD).

Movement of leafhoppers and natural enemies in fields adjacent to forest

A total of 2646 insects were collected in the malaise traps belonging mainly to the Noctuidae and Vespidae families. The 32.31% (855) of the individuals belonging to Mymaridae family are considered potential parasitoids of leafhopper eggs. Only the 1.62% (43) of the individuals collected were leafhopper adults.

The paired t-test results demonstrated that the abundance of natural enemies we collected from the two Malaise trap sides was significantly different ($p=$ 0.0056). Mymarids appeared to move from *D. marginata* fields to forest sites. Average for Mymarid abundance was higher at the field edge (97.00 ± 18.95) than at the forest edge (25.14 ± 4.49). We did not find differences in the abundance of leafhopper adults moving in the two directions ($p=$ 0.2808).

3.4 Discussion

Abundance of leafhoppers, katydids and armored scales showed different responses to presence of forest and distance from the edge of the field. These differences were mainly attributed to a combined influence of the biology and life history of each group and the presence of natural enemies that may affect suppress pest populations.

Leafhopper abundance and parasitism level

Effect of forest and distance.

We found a lower number of leafhopper eggs and nymph populations in plots near forest patches. The shaded conditions of our forested plots may provide one possible explanation for the decreased incidence of leafhoppers species found in our study. Some studies have demonstrated that sap flow content is reduced in crops under shaded conditions, mainly the sap flow peaks during midday (Alarcón *et al.* 2006, van Kanten and Vaast 2006). Due to its impact on photosynthesis and transpiration rates, shade can reduce the xylem feeding resources for leafhoppers. Leafhoppers have been reported to be very sensitive in terms of their nutritional needs (Park *et al.* 2006, Mizell *et al.* 2008, Northfield *et al.* 2009). For instance, they must feed frequently to meet their nutritional requirements, and prefer to feed when xylem tension and plant nutrient content; including amino acid presence in the xylem fluid, are highest (Andersen *et al.* 1992, Broadbeck *et al.* 1993, Pérez 2007). Adult females also consume more on host plants with higher content of amides, and they are very likely to oviposit on these plants (Andersen *et al.* 1989, 1992, 2005). On the other hand, nymphs develop faster on host plants whose amino acid composition have a with lower percentage of amides) (Brodbeck *et al.* 1995, 1996, 1999).

In this way, and taking into account that shade can decrease temperature and light in parts of the field up to 14 meters from the forest edge (González-Montagut 1996), forests may provide ecosystem services via "bottom up", factors that alter plant physiology by its impact on microclimate, and which provide unsuitable conditions for the development of leafhopper populations. Ramos (2008) also found that shade effect may depend on the species and landscape context. In her study, shade negatively affected the abundance of most of the leafhopper species, including *Fusigonalia lativitatta* and *Graphocephala*

permagna, although also positively affected the abundance of other few species (e.g. *Ladoffa* sp. and *Beirneola anita*). Other studies have also reported forests as a source of leafhoppers (Irwin *et al.* 2000, Chust *et al.* 2004, Giustolin *et al.* 2009).

Forest shade may also provide optimal conditions, which can lead to leafhopper suppression via 'top-down' effects through the enhancement of natural enemy populations. On Dracaena we found a higher parasitism level with respect to the total egg numbers in forested plots while the opposite response was found in non-forest plots. It has been demonstrated that shade structure and overstory density and richness may have a strong effect on natural enemy and herbivore trophic levels (Dyer and Stireman 2003, Sperber *et al.* 2004). Canopy cover maintains a suitable microclimate for the development of herbivore parasitoid populations (Fernandes and Price 1991); as well as provides a more diversified habitat (e.g. flowering plants in the understorey) with the necessary resources for the parasitoids to complete their life cycle.

Effect of season on populations in forested fields

We did not find a statistically significant impact of season on leafhopper egg abundance. Young (1982) found that, in seasonal tropical regions, xylem feeders, including leafhoppers, should show less seasonality than other insect groups due to their generalist feeding habits and high capacity for dispersion. Different results have been reported by Prado *et al.* (2008) on *D. marginata* fields in Costa Rica, who found a higher number of leafhopper eggs during the rainy season, while comparing two evaluations carried out on each, dry and rainy seasons. They also found that leafhopper egg abundance differed among farms, and these variations were attributed to differences on the agricultural practices carried out by individual growers. Hidalgo (2012), evaluating seasonality on pest abundance in *D. marginata* through a twelve-month period with monthly sampling, also indicated that leafhopper egg abundance fluctuates over time but differences depend on other factors such as the plant variety. Even though Prado *et al.* (2008) and Hidalgo (2012) were not evaluating forest effect on *D. marginata* fields, their results suggest that other factors, besides seasonality may influence leafhopper egg abundance in Dracaena.

The higher population of *Empoasca* nymphs during rainy season is consistent with the results of Hidalgo (2012). Due to the high vagility of the nymphal instars (Tipping and Mizell 2004), nymphs are able to disperse to new plant tissues to acquire the highest quality nutrients for development and reproduction (Mizell *et al.* 2008), which are more likely to be found in the rainy season.

The proportion of *Caldwelliola* sp. and total parasitized leafhopper eggs were lower during the rainy season and parasitism proportion also tended to decrease as the distance from forest edge increases. Studies in temperate zones have demonstrated seasonal fluctuations for leafhopper parasitoids of the Mymaridae family; including *Gonatocerus* spp. Mizell *et al.* 2008 reported, in northern Florida, a low rate of parasitism of *Homalodisca vitripennis* (Hemiptera: Cicadellidae) eggs during the rainy spring. In the Society Marquesas and Austral archipelagos of French Polynesia, Grandgirard *et al.* (2009) found lower parasitism rates by the parasitoid *Gonatocerus ashmeadi* during the cooler dry season. Williams and Martinson (2000) also determined that the leafhopper parasitoid *Anagrus* sp. *(Hymenoptera:Mymaridae)* are aggregated at the vineyard edge early in the season (May and June), and by midseason or later (August and September), the parasitoids are more widely dispersed in the vineyards. They also found that parasitoid abundance in the early season were higher at vines adjacent to a wooded edge than at intermediate and interior vines.

In tropical zones, such as Costa Rica, where actual rainfall and not months mark seasonality, precipitation may be influential in the parasitism abundance and distribution. Hidalgo (2012) found, in *D. marginata* fields in Costa Rica, that the proportion of leafhopper eggs parasitized by *Gonatocerus* spp. over a one year period was lowest after a period of high precipition. Thus, variation in parasitism proportion between seasons may be the result of the physical effect of an increse in rainfall during the rainy season. Some studies have demostrated that heavy rainfall can have a negative effect on the efficacy and reproductive behavior of parasitoids (Weisser *et al.* 1997). Aditionally, it could be possible that leafhopper parasitoids during the rainy season move from *D. marginata* fields into the forests, so that they use can natural areas as temporal habitats which provide them

alternative prey, refuge, plant food resources, and a more stable microclimate (Landis *et al.* 2000) while increasing their protection against rainy conditions.

Katydid eggs and parasitism level

Effect of forest and distance

Similar to leafhoppers, katydids also have high dispersal capacities, which allow them to easily migrate to new areas looking for preferred hosts. However, unlike leafhoppers, katydids are less selective in terms of nutritional needs. Thus, the putative nutritional differences, which explained the lower leafhopper abundance on forested plots, may not be a key factor for katydid egg abundance. Instead, other factors such as host plant abundance, diversity, taxonomic composition and physical structure of the vegetation reported for other Orthopterans could be more important for habitat selection and distribution (Vestal 1913, Otte and Joern 1977, Joern 1979, Kemp *et al.* 1990, Fielding and Brusven 1992, Cuningham and Sampson 2000, Squitier and Capinera 2002).

The field border seems to provide a more suitable microhabitat for katydid survival. We found higher katydid egg abundance at the edge of Dracaena plots. Other studies have demonstrated that the abundance of invertebrates can increase at field margins when bordered by strips of land planted with different vegetation composition (e.g. Chiverton and Sotherton 1991, Hassal *et al.* 1992, Lagerlöf and Wallin 1993, Frank 1997, Denys and Tscharntke 2002, Pollard and Holland 2006, Le Viol *et al.* 2008). In general, our results for katydid egg abundance concurred with these studies that show insect populations decreasing with increasing distance from the field edge (Fournier and Loreau 1999, Murchie *et al.* 1999, Denys and Tscharntke 2002). Preference for egg oviposition could be explained by the weed community composition which occurs at the field border of Dracaena fields. Villalobos (2007) found that the most predominant species in field borders of Costa Rican Dacaena fields belonged to families such as Poaceae (including the grasses *Axonopus* sp, *Eleusine indica* and *Digitaria ciliaris*) and Scrophulariaceae (*Mecardonia procumbens*). Different studies have demonstrated preference of orthopterans for grassess (Vestal 1913, Hewitt and Blickens 1974, Fielding and Brusven 1993, Thompson *et al.* 1996, Porter and Redak 1997, Torrusio *et al.* 2002); while others have reported orthopterans feeding on plants of the Scrophulariaceae family (Joern 1979). Thus, the

presence of these hosts at the field borders may provide a plausible explanation for increased katydid abundance.

Despite the reported capacity of natural habitats to increase the abundance of natural enemies on adjacent farmlands (Chacoff and Aizen 2006, Tscharntke *et al.* 2005, Thomson and Hoffmann 2009, 2010, Thomson *et al.* 2010), we found the lower katydid and leafhopper egg parasitism at 0 meters from field edge compared to 10 and 20 meters, independently to the forest adjacency. It seems that field border represents a unstable microhabitat for the parasitoids to survive, even though the highest katydid egg abundance is found it at this distance. Villalobos (2007) found that the highest richness and abundance of vegetation associated with *D. marginata* was found within fields rather than between fields or at field borders. The capacity of these weeds to favor the development of natural enemies could explain both the higher abundance of katydid eggs and rates of parasitism within the fields.

Effect of season on forested fields

As observed for leafhopper eggs, katydid egg abundance was higher during the dry season. Presence of parasitoids seemed to be playing an important role regulating katydid populations between seasons. We found that the interaction between season and distance from the forest have an influence on parasitism proportion of katydid eggs. Parasitism proportion was high during rainy season, coinciding with low katydid egg abundance at all distances from forest edge. Conversely, during dry season a lower parasitism proportion was found with higher katydid egg population. This effect was strongest at the forest edge where we found the highest parasitism proportion during the rainy season and the lowest proportion during the dry season.

Other factors have also reported to influence katydid egg abundance. Prado *et al.* (2008), found differences in katydid egg abundance depending on the interaction between season and zone. They found more katydid eggs during the rainy season in the Atlantic zone of Costa Rica, where only minor differences in precipitation were found; while no differences were found in the North zone, in spite of the large differences in rainfall. They explained that other factors such as variety, fertilization and use of insecticides and

herbicides have strong influences on katydid population creating dissimilarities among *D. marginata* farms.

Armored scales and their relation with predatory insect populations

Effect of forest and distance

In contrast to leafhoppers and katydids, which are highly mobile, armored scales are sessile for most of their life cycle. Even though they are able to survive on a broad range of plant hosts (Culik *et al.* 2008, Hanks and Denno 1994, Magsig-Castillo *et al.* 2010) their dispersion is limited and has been attributed mainly to the wind, although other phoretic means such as insects, birds, animals, other insects and man have been reported (e.g. Beardsley and Gonzalez 1975, Magsig-Castillo *et al.* 2010). This limited dispersion does not allow them to easily select their preferred host plant or migrate to other areas looking for new suitable hosts. As such, other factors have been reported to play a determinant role on their patchy distribution pattern on crops (Hanks 1991, Hanks and Denno 1993), including the presence and distribution of natural enemies, host plant-water relations (Hanks and Denno 1993) and management practices (Prado 2006, Prado *et al.* 2008).

For our study, presence and distribution of natural enemies seemed to play a key factor for armored scale abundance. Scales had the lowest insect abundance at the field edge, which coincided with the highest predatory insect population. Different studies have demonstrated that natural enemies are capable of effectively controlling different species of armored scales where the environmental conditions of the habitats are favorable (Reeve and Murdoch 1985, Smith and Maelzer 1986, Hanks and Denno 1993, Rebek *et al.* 2006). Even though in natural habitats, including forested habitats, higher densities of scale predators have been found (Hanks and Denno 1993, Tooker and Hanks 2000), we did not find an effect of forest on predatory insect abundance. However, it has been also demonstrated that different scale predators may be present depending on the habitat. For example, Hanks (1991) identified, for the white peach scale (*Pseudaulacaspis pentagona*), that in forested habitats it was possible to find generalist predators such as earwigs, lacewings and spiders, while in urban landscapes scales are commonly attacked by coccinellids. Similar findings have been reported by Tooker and Hanks. (2000). In our study we could identify some of

these predatory insects in Dracaena fields. Thus, it is posible that habitat conditions in both forest and non-forest field edges provide optimal conditions for the development of different species of predators that provide control of armored scale population.

On the other hand, agricultural practices carried out within the Dracaena fields can also explain the higher scale abundance found at 10 and 20 m distance from field edge. Due to the high plant density within the field, workers can easily disperse scales while different tasks are being realized. Prado *et al.* 2008 have also found that other agricultural practices such as fertilization, weed management and application of insecticides have a strong influence on armored scales populations. Other studies have also reported that the application of insecticides can trigger pest outbreaks by eliminating natural enemies (Debach and Bartlett 1951, Trumper and Holt 1998, Rehman *et al.* 2000). These practices as well as the fact that *D. marginata* has demonstrated its suitability for supporting armored scale populations, as has been reported as host of a number of armored scale genera (Prado 2006); increase their possibility of resurgence within the field.

Effect of season on forested fields

We found an effect of season on armored scale abundance in forested plots. Higher population was found on *D. marginata* fields during the dry period. Similar findings have been reported in other studies. Hidalgo (2012) reported the highest peaks of pest population in the months of high precipitation preceded by long periods of low rain, suggesting that during the dry season armored scales are more likely to survive. On the other hand, Prado *et al.* (2008) found a higher number of scales during the dry season, but differences also responded to other factors including the production zone, which mainly differed in terms of topography and agricultural practices.

Predatory insect population follows a similar pattern of that observed for katydid parasitism in forested fields, confirming that shade structure and overstory may have a strong influence on natural enemy and herbivore trophic levels (Dyer and Stireman 2003, Sperber *et al.* 2004). As such, during the rainy season, predatory insects seemed to be aggregated at the forest edge, decreasing as distance increases. It is known that the physical effect of high precipitations may wipe out populations of arthropods, including parasitoids

(Weisser *et al.* 1997). Thus, this aggregation at the field edge may be a result of the physical protection offered by the forest during the raining periods. On the contrary, during the dry season, a lower predatory insect population was found at the forest edge and insects appeared to be dispersed along the field.

The highest abundances of predatory insects were found at the forest edge during the rainy season, which coincided with low populations of armored scales. This suggests that the interaction between the forest effect and optimal weather conditions may increase the predation levels which may result in a lower density of scales (Reeve and Murdoch 1985, Smith and Maelzer 1986, Hanks and Denno 1993, Rebek *et al.* 2006). Conversely, during the dry season where predatory insect population remains low, leaves infested with armored scales tended to increase as the distance from forest edge increased, maybe taking advantage of the enemy-free spaces (Jeffries and Lawton 1984).

Movement of leafhoppers and natural enemies in fields adjacent to forest

The number of leafhopper adults trapped at the field edge was very low and no movement was identified from forest sites to fields and *vice versa*. Ramos (2008) found that other species of leafhoppers appeared to move from forest areas to coffee fields, but not in the other direction. In other areas of Costa Rica, Irwin *et al.* (2000) also found movement of leafhoppers from forest to pastures. Nevertheless, in our study it seems that even though leafhoppers adults are highly polyphagous and forest provides a wide variety of resources, they remain on the *D. marginata* fields to complete their life cycle. This could be explained because movement into the forest may be accompanied by a higher risk from predation, exposure to pathogens and the risk of not finding a host plant of the same or higher quality (Mizell *et al.* 2008). This risk is augmented if we take into consideration that our results reported a higher number of natural enemies at the edges of field near forest.

Analyzing natural enemy abundances, we found a higher number of natural enemies moving from *D. marginata* fields to forest sites than vice versa. Perhaps natural enemies move into the forest to find non-prey foods to complete their biological requirements. It has been found that non-prey foods can improve the survival and longevity of natural enemies, providing the metabolic requirements for maintaining reproductive potential and dispersal,

which are critical to the establishment of natural enemies (Landis *et al.* 2000, Lundgren 2009). Non-prey food may also influence the movement of natural enemies in and out of agricultural fields. Some studies have demonstrated that natural enemies tend to disperse and aggregate to sources of natural resources, in search of non-prey foods (Corbett and Rosenheim 1996, Grafton-Cardwell *et al.* 1999, Pontin *et al.* 2006, Lundgren 2009).

Forests may act as a refuge for natural enemies, as they represent complex habitats. Not only support higher biodiversity, providing alternative non-prey foods, shelter and alternative prey, but also offer a greater diversity of microclimates for natural enemies (Landis *et al.* 2000, Bianchi *et al.* 2006). These non-crop habitats are also more stable in time and space than crop fields, which are ephemeral habitats subject to frequent and more intensive disturbances (Landis and Marino 1999). *D. marginata* is a highly managed crop so that natural enemies may be moving into the forest to find refuge and other resources during the crop practices, preventing population extinction.

3.5 Conclusion

Abundance of leafhoppers, katydids and armored scales showed different responses to presence of forest patches and distance of the sampling point from the edge of the field. These differences were mainly attributed to a combined influence of the biology and life history of each group and the presence of natural enemies that may suppress pest populations. Leafhopper egg and nymph populations were lower in plots near forest patches, suggesting that adult leafhoppers may migrate away from the Dracaena plants near the forest edge looking for plants with better nutritional quality, since the microclimate near the forest may reduce the sap flow content of crops under shaded conditions.

On the other hand, katydids, which also have high dispersal capacities, seem to have been less selective in terms of nutritional needs and mainly responded to the composition and structure of vegetation. Weed composition at field edges on both forest and non-forest plots seemed to include plant species, which provide katydids with optimal conditions for their development. Levels of parasitism also played an important role regulating leafhopper and katydid populations when conditions were appropriate.

In contrast to leafhoppers and katydids, armored scales are sessile for most of their life cycle and other factors, including the presence and distribution of natural enemies, host plant-water relation and management practices are more likely to explain their distribution. In our study, the presence and distribution of natural enemies was determined as a key factor, which seems to suppress armored scale populations at the field edges. Seasonality variations showed by the different pests in our study were consistent with other reports supporting the validity of our sampling methods.

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CHAPTER 4. EFFECT OF WEED COVER COMPOSITION ON INSECT PEST AND NATURAL ENEMY ABUNDANCE IN A FIELD OF DRACAENA MARGINATA IN COSTA RICA

4.1 Introduction

Non-crop vegetation can play a significant role on the ecology of crop pests and their natural enemies. Many of these habitats can provide a diversified system with a wide variety of resources, including alternative prey, plant food sources, optimal microclimate and refuge for natural enemies (Landis *et al.* 2000, 2005). Management of these habitats may not only improve the conservation of biodiversity but also increase the abundance of beneficial arthropods, which have the potential to reduce pest outbreaks (Thies and Tscharntke 1999, Schmidt *et al.* 2005, Bianchi *et al.* 2006, Issacs *et al.* 2009, Lundgren 2009, Thomson and Hoffmann 2009, 2010). Lundgren (2009) has listed a series of agricultural practices, related to weed management, which can encourage plant diversity within farm fields, improving the effectiveness of natural enemies on pest populations.

Depending on the composition, non-crop habitats provide a suitable environment that may favor increased pest abundance (Bianchi *et al.* 2006). For instance, some studies have found a link between orthopterans and vegetation community, diversity and structure (Vestal 1913, Kemp *et al.* 1990, Cuningham and Sampson 2000, Squitier and Capinera 2002), showing a preference of orthopterans for grassess (Vestal 1913, Hewitt and Blickens 1974, Fielding and Brusven 1993, Thompson *et al.* 1996, Porter and Redak 1997, Torrusio *et al.* 2002). Leafhoppers have also been associated with a wide range of hosts including certain weed species from families such as Poaceae and Rubiaceae (Nault and Rodriguez 1985, Lamp *et al.* 1994, Pérez 2007). Finke and Denno (2002) also reported how structurally complex vegetation habitats may improve the joint action of predators against leafhoppers whereas habitats with low complexity resulted on intra-guild predation decreasing the control preasure over the pest insect.

In Costa Rica, *Dracaena marginata* Lam. (Rusaceae) is an important ornamental crop plant, which provides an opportunity to study population dynamics of herbivorous

arthropods in three families Cicadellidae (leafhoppers), Tettigoniidae (katydids) and Diaspididae (armored scales). These arthropods differ greatly in their biology and vegetation preference. Leafhoppers are obligate sucking herbivores with a wide range of hosts in crops and non-crop habitats (Nault and Rodriguez 1985, Denno and Perfect 1994, Mizell *et al.* 2008). Katydids are a diverse group of chewing insects that are largely herbivorous but include many facultative predators. They are mostly present in grasslands and weedy areas, and typically feed on either grasses or forbs, although some species feed on both (Joern 1979, Squitier and Capinera 2002). Armored scales are sap-feeding insects with a wide range of host plants (Culik *et al.* 2008, Magsig-Castillo *et al.* 2010). While leafhoppers and katydids have high dispersal capacities, armored scales are sessile for most of their life cycle.

In Costa Rica, *D. marginata* production fields are characterized by their high diversity of vegetation. Villalobos (2007) found a total of 118 species of plants, distributed among 44 families growing in fields representative of the different production zones in the country. Most representative families included: Asteraceae, Poaceae, Euphorbiaceae, Cyperaceae, Fabaceae, Rubiaceae, Malvaceae, Schrophulariaceae, Solanaceae, Amaranthaceae, Piperaceae and Urticaceae. These plants were classified into five functional groups that correspond to their capacity to attract leafhoppers and or their natural enemies by using characteristics such as succulence, leaf shape, pubescence, presence of aromatic compounds, nitrogen fixation and presence of extra floral and floral nectaries determined which In a multiple choice host trial, comparing leafhopper behavior on weeds commonly found in *D. marginata* fields in Costa Rica, Perez (2007) observed that *Oncometopia clarior* used some species for feeding and resting whereas others were not visited. Prado *et al.* (2008) found that weed management practices in *D. marginata* fields produced significant changes in populations of leafhoppers and katydid eggs.

The objective of this study was to evaluate the response of pest populations and their natural enemies to the presence of weeds from selective functional groups in the ground cover of *D. marginata* production fields. In particular we asked the following questions: (1) Do the levels of insect pest abundance differ among specific weed cover? (2) Do leafhoppers, katydids and armored scales show the same responses to different weed

functional groups? (3) Does weed cover have an effect on the proportion of parasitism and number of predatory insects?

4.2 Material and methods

The experiment was carried out in a commercial ornamental farm growing *D. marginata* variety *green* in the Atlantic zone of Costa Rica in 2009. At the time of this experiment, this farm had not applied chemical insecticides for more than one year. The field was 10,000 m^2 (200 m × 50 m) in size and had homogenous conditions of topography and management.

Baseline survey

Before establishing the experiment, a baseline survey was carried out in February 2009 to characterize and map the weed community within the field. Additionally, abundance of pests and natural enemies was recorded during the process. The production plot was sampled systematically by sectioning it into in a 5 m by 5 m grid, using the line intersections to define the sampling points. Total area covered by weeds was characterized by placing a 0.5 m × 0.5 m frame at each point, and visually estimating the total percentage of ground covered by weed vegetation. To characterize the contribution of each weed species to the total weed cover, the cover percentage of each species at each point was recorded separately. Once the cover was estimated, all individuals of the species, which were rooted within the sample frames, were physical removed and counted. This process was repeated until all weed species and relative coverage were recorded.

To estimate the abundance of pests and natural enemies on *D. marginata*, nine commercial plant tips were selected from a plant adjacent to each of the sampling point describe above. Each tip was also visually inspected for numbers of leafhopper nymphs. After field inspection, each tip was removed, placed into a plastic bag and transported to the laboratory to count leafhopper and katydid eggs under a dissecting microscope. The number of parasitized eggs determined parasitism level. The abundance of armored scale insects (*Chrysomphalus* sp.) per tip was measured by counting the number of infested

leaves. In previous work, Prado *et al.* (2008) found that the number of leaves with scales was a reliable estimator for their abundance.

The spatial distribution of the most important weed species and of the key pest abundance was plotted using Surfer 9.9 (Golden software, Golden, CO, USA). The x and y coordinates represented the sampling points and z represented the total number of pests or weed density per 0.25 m^2 found at each point. Z values were interpolated by using the interpolation algorithm linear Kriging, producing a grid of values. Kriging, which interpolates values between observations through weighted linear combinations of nearby samples that minimizes the variance of errors (Horowitz and Ishaaya 2004), has been widely applied in ecology and entomology (Liebhold *et al.* 1991, Hohn *et al.* 1993, Gilbert and Grégoire 2003). The interpolation grid obtained was used to produce contour maps, which showed the spatial distribution of the pests and weeds in the field. Weed distribution was used to determine the position of the experimental units of the different treatments in the field.

Selection of weed cover treatments

Weed treatments ranged from weed free to completely covered with unmanipulated weed cover. The remaining treatments included species belonging to four of the five functional groups defined by Villalobos (2007) in terms of traits that describe the potential of weeds to serve hosts for leafhoppers and/or natural enemies (**Table 4.1**). One functional group (FG 2) described by Villalobos was omitted from this study because the baseline sampling showed that less than 5% of the weed species endemic to the field belonged to this group.

Table 4.1. Summary of functional traits of four of the functional groups (FG) of weeds identified in *Dracaena* agroecosystems in Costa Rica. Modified from Villabolos (2007).

Functional trait	FG1	FG2	FG3	FG4	FG5
Phenology	Perennial and annual	Perennial	Mainly annual plants (68%)	Mostly perennial (78%)	Mostly annuals (75%)
Stem	Erect	Erect	Mostly sub-erect (42%) and erect (37%)	Mostly erect (83%)	Erect
Succulence*	74%	81%	79%	76%	83%
Leaf shape	Elliptic-ovate-obovate	Peltate-orbicular (50%), deltoid (25%), elliptic-ovate (25%)	Variable leaf shape, mainly lanceolate-oblanceolate (42%)	Mostly acicular (72%)	Lanceolate-oblanceolate
Pubescence	Present in most of the sp. (93%)	Only present in some sp. (25%)	Absent (52%); Present (47%)	Present in most of the sp. (78%)	Present in most of the sp. (75%)
Aromatic compounds	No	Most of the sp. (75%)	Present in 42% of the sp.	No	Present in few sp. (17%)
Nitrogen fixation	No	No	Only few sp. (10%)	No	No
Extra-floral nectarines	Only some sp. (30%)	No	Only some sp. (26%)	No	Only few sp. (8%)
Floral nectarines	Yes (100%)	Yes (100%)	Most of the sp. (95%)	No	Yes
Entomophilous pollination	Most of the sp. (75%)	Most of the sp. (75%)	Yes (100%)	Only few sp. (5%)	Most of the sp. (83%)

*Succulence is shown as the average percentage of water content in the tissue.
** Percentage for other functional traits (%) represents the proportion of species (sp.) within the functional group that show the trait.

4.3 Field experiment

Seven treatments were arranged in a completely randomized design with ten replicates. The treatments were established as defined in **Table 4.2**. Each experimental unit was 10×10 m in size. In order to establish the target weed cover composition for each treatment plot, a combination of manual and chemical controls was carried out periodically for a period of 7 months. Treatments were considered as implemented when the percentage of weed cover was at least 70% of the representative species of the treatments. Weed cover was estimated from random samples from a 0.25 m^2 sampling frame, and counting the plant species within the sampling area.

In October 2009 the abundance of pests and natural enemies was characterized following the mapping procedure similar to what was used in the baseline study. Nine commercial plant tips were selected at a sampling point at the center of each 10 m × 10 m experimental plots. Each tip was visually inspected for numbers of leafhopper nymphs, spiders and other predacious insects. Then the tips were taken to the laboratory where they were dissected to count leafhopper and katydid eggs and parasitism rate under a dissecting microscope. The number of leaves infested with armored scale insects (*Chrysomphalus* sp.) per tip was measured by counting. Additionally, in order to determine leafhopper adult abundance, one yellow sticky trap (20 cm × 15 cm) was placed at the center of each plot at a height of 0.5 m, for a total of ten traps per treatment. Traps were collected after 48 hours in the field. All samples were taken to the Entomology Laboratory at CATIE, where leafhoppers were identified to morphotypes using a reference collection and counted.

4.4   Statistical analysis

Total number of leafhopper eggs and parasitism proportion were analyzed with analysis of variance (ANOVA) under the general and mixed model framework in order to take into account lack of homogeneity of variances and correlations among experimental units. We used the Akaike's Information Criterion (AIC) and the Bayesian information criterion (BIC) to select the best-fitted model (smaller is better for both criteria). In each case where the model values for these criteria were close, we used likelihood ratio test (LRT) to test hypothesis to decide which model provided the best fit. When the variances were heterogeneous, we used appropriate functions and based on AIC and BIC we decided the best one. Other variables (number of leafhopper nymphs, katydid eggs, armored scales and predatory insects), which did not fit normality assumption, were analyzed using Poisson regression using a log-linear link canonical function (Agresti 1990). To compare groups of means we used orthogonal contrasts and to compare all the means we used a Fisher protected least significant difference (LSD) (alpha = 0.05). Data were analyzed with the software InfoStat professional version 2010 (Di Rienzo *et al.* 2010). As we evaluated pests with different biology and vegetation preference, orthogonal contrasts differed between evaluated variables.

Table 4.2. Treatments for selective weed community composition in *D. marginata* experimental plots.

Code	Treatment	Rational for treatment selection	Management strategy	Final cover composition and functional groups* (FG)
T1	Weedy	Unmanaged populations of endemic weeds to allow a natural assortment of species	Free growth of weeds allowed	*Spermacoce latifolia*(55%) (FG1); *Lindernia diffusa*(12%) (FG3); *Youngia japónica*(5%)(FG5); *Phyllanthus urinaria* (4%)(FG3); *Peperomia pellucida*(4%)(FG3); **Other species<5%(20%)
T2	Weed free	Absence of weed cover to eliminate any possible influence on pest behavior.	Weeds eliminated using herbicides: Glyphosate (Ranger 24 SL) and Difenil-eter-oxifluorfen (Goal 24 EC) and additionally using manual control when necessary.	
T3	*Drymaria cordata* cover	*Drymaria cordata* (Caryophyllaceae) was found to repel leafhoppers (Perez 2007) and growers have used it as cover crop. Reported as Katydid host (Rivera 1988, Vinokurov and Rubov 1930)	Other weeds were controlled using Glyphosate (Ranger 24 SL) and Fluazifop-p-butil (Fusilade 12.5 EC) with additional manual control when necessary.	*Drymaria cordata*(51%)(FG3); *Cardamine bonariensis*(14%)(FG3); *Peperomia pellucida* (8%)(FG3); Other species<5%(27%)
T4	Poaceae Cover	Reported as Leafhopper host (Maes y Godoy 1993, Perez 2007). Reported as Katydid host (Joern 1980, Kemp *et al.* 1990, Cuningham and Sampson 2000, Squitier and Capinera 2002)	Broad leaved weeds were eliminated with herbicides: Picloram-Fluroxypyr (Plenum 16 EW), Metsufluron methyl (Met-Weed 60 WG.), and manual control when necessary.	*Eleusine indica*(72%)(FG4); *Digitaria* (15%)(FG4) Other species<5%(13%)
T5	Cyperaceae Cover	Classified by Villalobos (2007) in the same functional group with T4 but described as repellent to leafhoppers by Perez (2007)	Other weeds were controlled with herbicides: Terbutrina (Igram 50 SC), Picloram-Fluroxypyr (Plenum 16 EW), Fluazifop-p-butil (Fusilade 12.5 EC), and manual control when necessary.	*Cyperus* sp. (40%)(FG4); *Cyperus tenuis*(37%)(FG4); *Kyllinga brevifolia* (21%)(FG4) Other species(2%)
T6	Rubiaceae Cover	Described by Perez (2007) as attractant to leafhoppers	Predominantly weeds from the Rubiaceae family (*Spermacoce latifolia*). Other groups were controlled with Fluazifop-p-butil (Fusilade 12.5 EC) and manual control when necessary.	*Spermacoce latifolia* (88%)(FG1); *Phyllanthus urinaria*(10%)(FG3) Other species<5%(2%)
T7	Flowering Broad leaf	Mixture of endemic broad leaf weeds with flowers and nectaries that can attract natural enemies of the pests. Mainly from the Scrophulariaceae and Asteraceae family. Reported as Katydid host (Joern 1980)	Herbicide Fluazifop-p-butil (Fusilade 12.5 EC) and manual control were used to maintain the weed selection.	*Lindernia diffusa*(52%)(FG3); *Youngia japónica*(24%)(FG5); *Lindernia crustaceae*(11%)(FG3) Other species<5%(13%)

*Plants characterized and classified by Villalobos (2007) in five functional groups based on succulence, leaf shape, pubescence, volatile production, nitrogen fixation, presence of extra floral and floral nectaries (see text for detail composition of the functional groups). Percentages refer to the relative abundance of the individual species respect to other weed species on the treatment.
**Other species with population below 5% were grouped in this category.

4.5 Results

Baseline survey

We found 59 weed species associated with *D. marginata* in the field from 21 families. The twelve most common species in descending order were: *Spermacoce latifolia* (Rubiaceae)*, Lindernia diffusa* (Scrophulariaceae)*, Phyllanthus urinaria* (Euphorbiaceae)*, Youngia japonica* (Asteraceae)*, Peperomia pellucida* (Piperaceae)*, Lindernia crustaceae* (Scrophulariaceae)*, Eleusine indica* (Poaceae)*, Cyperus* sp. (Cyperaceae)*, Ludwigia octovalvis* (Onagraceae)*, Cyperus tenuis* (Cyperaceae)*, Kyllinga brevifolia* (Cyperaceae) *and Drymaria cordata* (Caryophyllaceae). These species accounted for 83.4% of the abundance registered in the field (**Annex 4.1**). The five most abundant families in descendent order were: Poaceae, Asteraceae, Euphorbiaceae, Cyperaceae and Scrophulariaceae; other families were represented with less than three species (**Annex 4.2**). Most of the species collected in the field belonged to functional groups four (31%), one (25%) and three (24%). The remaining weed species belonged to functional groups five (15%) and two (5%).

We used weed density to determine the spatial distribution of the weeds and position of the experimental units of the treatments. Contour maps allow us to identify the "hot spots", *i.e.* sites with high densities, shown by different weed families at the field (**Figure 4.1**). We could identify that some weed families were aggregated in different locations of the field. For example, the Cyperaceae family showed the highest densities in areas located in the northern half of the field (above Y = 100 m), while the Rubiaceae family was distributed along the field with some "hot spots" in the middle and at the southern edge of the field.

With respect to the abundance and distribution of pests, we identified different responses depending on the pest. We found a low average number of leafhopper eggs (0.13±0.002; n=415) and katydid eggs (0.002±0.001; n=415) per tip. The highest number of leafhopper eggs was concentrated in small "hot spots" at the center (Y = 100 m) and northern (Y = 140-160 m) areas of the field; while katydid eggs were aggregated at the

center of the field. The proportion of leafhopper parasitism was low with an average of 0.02±0.01 (n=415). On average, there were 0.56±0.021 (n=415) leaves with armored scales and showed the hot spots of larger sizes in different areas of the field. The most abundant pest recorded was leafhopper nymphs with an average of 1.65±0.032 (n=415) per tip, showing a more uniform distribution along the field with hot spots of large sizes (**Figure 4.2**). The most abundant leafhopper nymphs belonged to the genus *Empoasca* (68.3%), but we also found *Caldwelliola* (23.7%) and others including the genus *Oncometopia*, *Diestostemma*, and *Gypona* (8%).
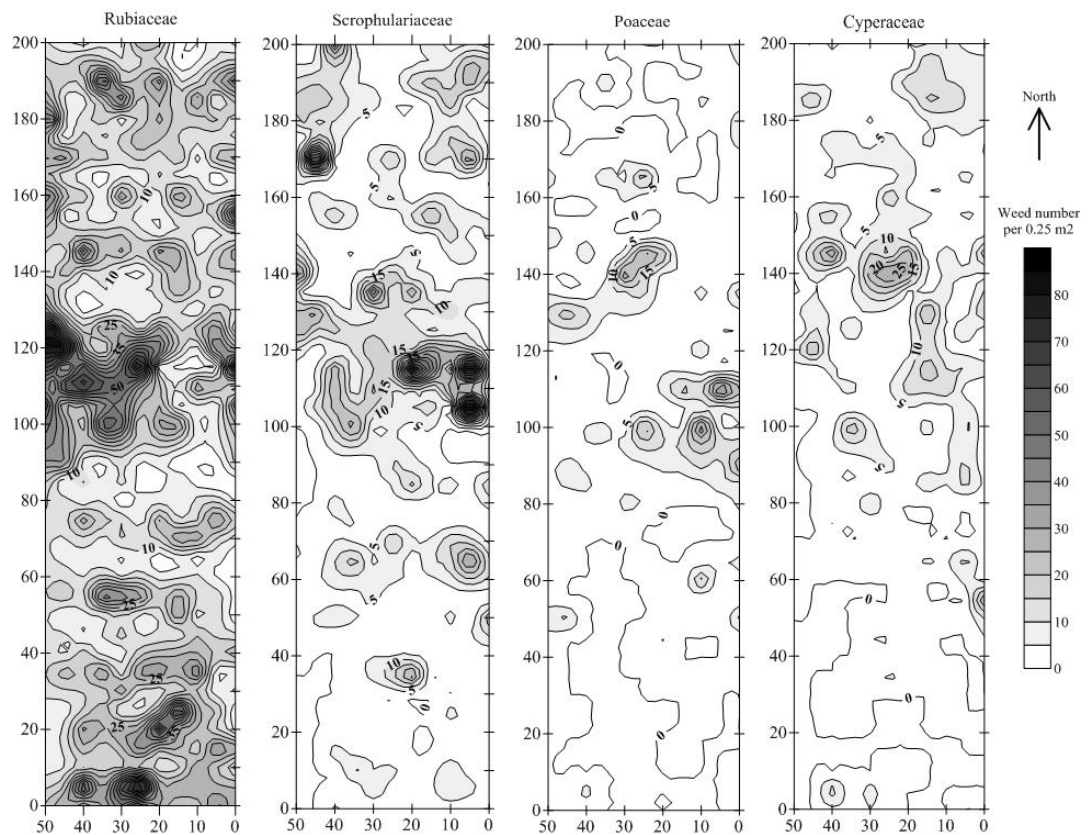
Figure 4.1.   Examples of spatial patterns of weed density for Rubiaceae, Scrophulariaceae, Poaceae and Cyperaceae family found in a *D. marginata* field in Costa Rica. Weed density, *i.e.* the number of individuals per 0.25 m^2, of each family is indicated on the contour lines. Axes indicate coordinates in meters.
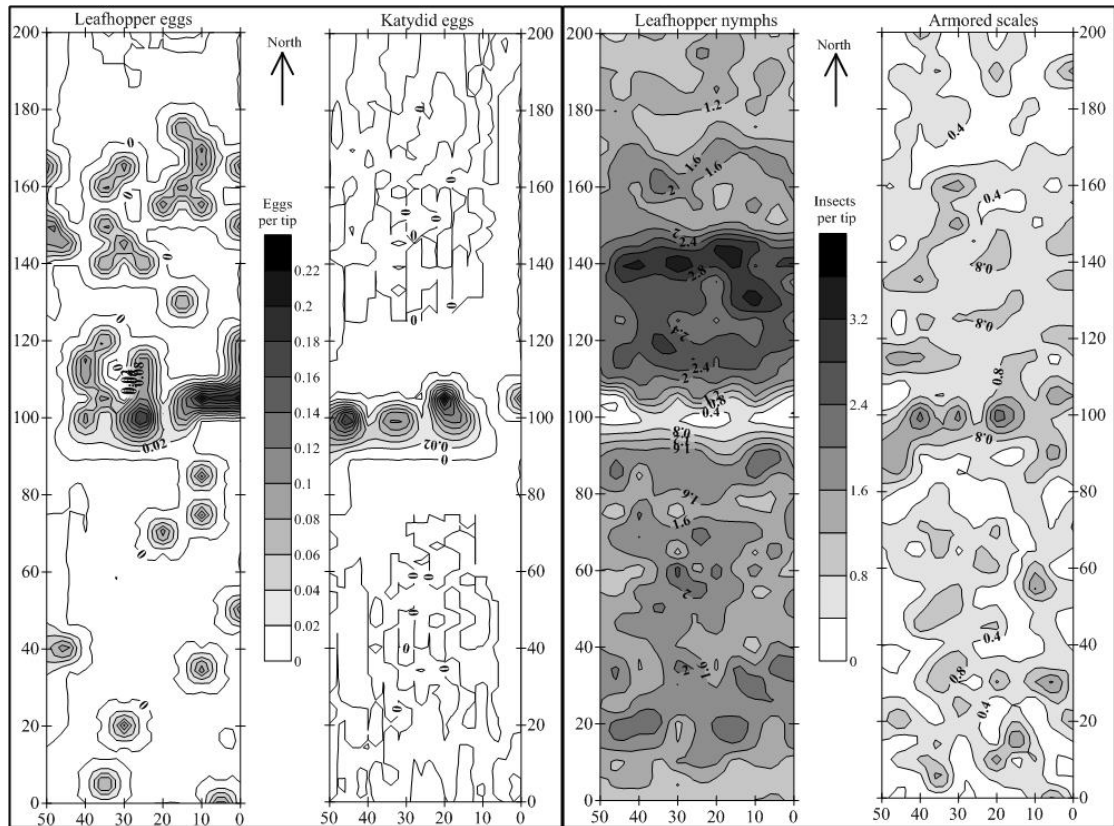
Figure 4.2.   Spatial distribution of pests associated with *D. marginata* in a field in the Atlantic zone of Costa Rica. Egg number (left) and number of insects (right) per tip are indicated on the contour lines. Axes indicate coordinates in meters.

We found significant Spearman correlations when we related the number of insect pests per tip and weed density per sampling point. For instance, the Rubiaceae family, the most abundant weed species in the field, was negatively related with leafhopper nymphs, but positively correlated with katydid eggs and armored scales. Poaceae weeds were positively associated with leafhopper eggs and nymphs as well as to armored scale populations. Other families also showed positive significant correlations depending on the insect pests (**Table 4.3**).

Table 4.3. Spearman correlations (*r*) between insect pests and some of the most abundant weed families found at each sampling point in a *D. marginata* field in Guapiles, Costa Rica, in 2009. Numbers in bold indicated significant correlations (*p<0.05*).

Weed family	Leafhopper eggs		Leafhopper nymphs		Katydid eggs		Armored scales	
	R	p	R	p	R	p	R	p
Asteraceae	-0.01	0.8764	0.13	**0.0103**	-0.07	0.1427	0.12	**0.0116**
Cyperaceae	0.10	**0.0347**	0.07	0.1689	0.11	**0.0215**	0.27	**<0.0001**
Euphorbiaceae	0.02	0.6484	0.04	0.4454	-0.01	0.7835	0.08	0.1067
Poaceae	0.14	**0.0045**	0.16	**0.0013**	0.09	0.0645	0.13	**0.0089**
Rubiaceae	0.02	0.6278	-0.10	**0.0479**	0.17	**0.0004**	0.16	**0.0011**
Scrophulariaceae	0.12	**0.0129**	0.03	0.5802	0.08	0.0910	0.20	**0.0001**

*Baseline with n=415 sampling points in a 5 m × 5 m grid.

Effect of weed cover composition on insect pests and natural enemies

Identification of leafhopper eggs revealed that there were five egg morphotypes classified in the following genus *Caldwelliola*, *Oncometopia*, *Diestostemma*, *Gypona* and a non-identified genus (CSP 2008, **Figure 4.3**). The two most abundant leafhoppers, comprising 99% of total of eggs found in the field, were in the genus *Caldwelliola* sp. (Subfamily: Cicadellinae; Tribe: Cicadellini) (93.7%) and *Oncometopia* sp. (Subfamily: Cicadellinae; Tribe: Proconiini) (5.3%). The number of leafhopper eggs reached an average of 2.49±0.38 (n=7) eggs per tip and was substantially higher than the numbers found during the baseline study (0.02±0.001). The number of parasitized eggs per tip was consistently high (> 75 %) across the treatments (**Table 4.4**). The proportion of parasitism shown during the sampling was also higher than observed during the baseline sampling, with an average 0.90±0.19 per tip. We identified a significant positive correlation between the total number of eggs and parasitism proportion ($r_p(70)=0.29$, *p<0.01*). Micro-hymenopteran wasps from the genus *Gonatocerus* (Hymenoptera: Mymaridae) were found parasitizing the leafhopper eggs identified in the field.
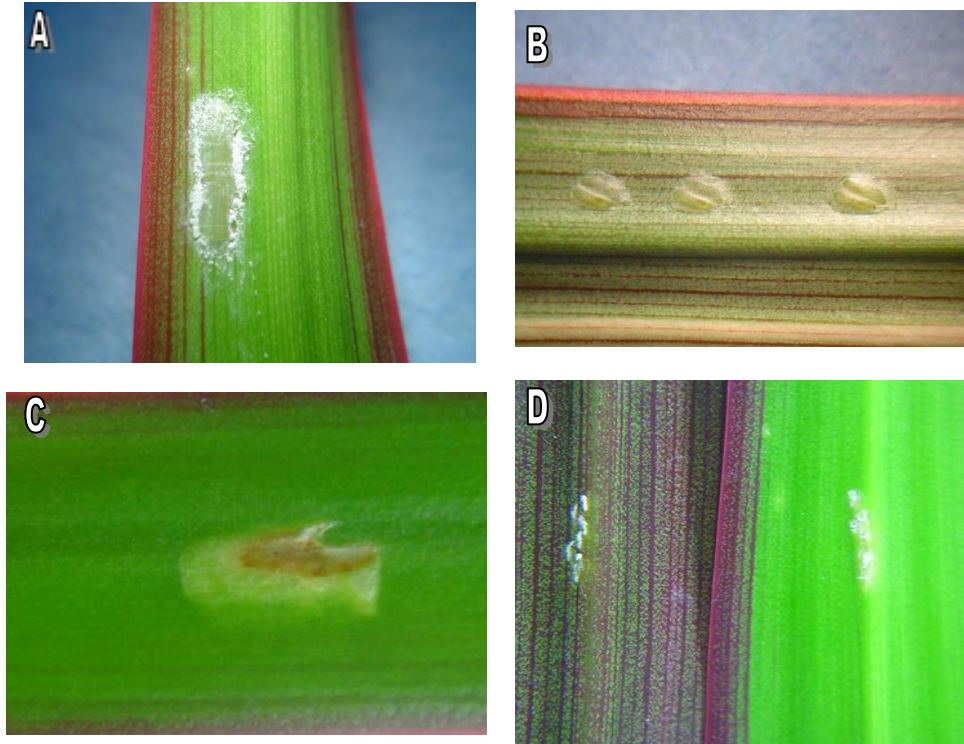
Figure 4.3. Morphotypes of four of the eggs of leafhoppers found in a *D. marginata* field in the Atlantic zone of Costa Rica. (A) *Oncometopia* sp. (B) *Caldwelliola* sp. (C) *Diestostemma* sp.and (D) *Gypona* sp. (Photos. E. Hidalgo)

The ANOVA of the data indicated that weed cover composition had an effect on the abundance of the total number of leafhopper eggs (F=7.03; df=6,63; p<0.0001). The highest number of leafhopper eggs per tip were found in the Cyperaceae treatment and significantly differed from all the other treatments except for Poaceae treatment (**Table 4.4**).

Table 4.4. Mean and SE of insect pests and natural enemies per plant tips found on *D. marginata* grown under seven different combinations of ground cover in Guapiles, Costa Rica, in 2009.

Treatment	n	Leafhopper eggs	Leafhopper parasitism proportion	Leafhopper nymphs	Leafhopper adults	Katydid eggs	Armored scales	Predatory insects
Weedy	10	2.12±0.42	0.98±0.01*	4.30±0.97	2.20±0.74	1.50±0.48	2.20±0.51	1.00±0.33
Weed free	10	2.36±0.33	0.94±0.01	4.00±0.82	3.50±1.04	0.60±0.27	3.10±0.62	0.50±0.31
Drymaria cover	10	1.46±0.21	0.88±0.08	3.20±0.65	3.00±0.37	1.70±0.68	3.50±0.75	1.60±0.50
Poaceae	10	3.51±0.84	0.95±0.01	3.80±0.77	1.60±0.45	1.50±0.48	2.90±0.64	0.90±0.28
Cyperaceae	10	4.20±0.42	0.96±0.01	3.20±0.96	2.30±0.76	1.90±0.53	3.60±0.88	1.10±0.23
Rubiaceae cover	10	1.68±0.25	0.75±0.08	2.70±0.63	2.90±0.92	2.10±0.85	3.00±0.58	0.30±0.15
Flowering BL	10	2.10±0.38	0.86±0.08	3.90±0.85	2.30±0.45	1.40±0.43	4.00±0.88	1.00±0.30

*For parasitism proportion n=9 in the weedy treatment because we did not find leafhopper eggs in one repetition.

Orthogonal contrasts of the treatments (**Table 4.5**) also showed an effect of ground cover composition on the total number of leafhopper eggs. The combination of narrow leaf treatments (Poaceae and Cyperaceae) showed statistical differences on the total number of eggs (F=18.02; df=1.63; $p<0.0001$) and parasitized eggs compared (F= 6.88; df=1.63; $p<0.0010$) to the combined broad leaf treatments (*Drymaria*, Rubiaceae and flowering broad leaf). A higher number of total eggs and parasitism per tip were found on the narrow leaf group than in the broad leaf treatments. Comparing the narrow leaf treatments, we found a higher number of leafhopper eggs (F=31.70; df=1.63; $p<0.0001$) in the plots with Cyperaceae (4.20 eggs per tip) than in the Poaceae treatment (3.51 eggs per tip).

In terms of rates of parasitism, we also found an effect for ground cover composition. ANOVA analysis showed that the higher rate of parasitism per tip was found on the weedy plots (0.98±0.01) differing statistically from the Rubiaceae treatment where we found the lowest parasitism levels (0.75±0.08) (**Table 4.4**). Additionally, orthogonal analysis showed us that narrow leaf treatments (Poaceae and Cyperaceae) also showed statistical differences compared to the combined broad leaf treatments (*Drymaria*, Rubiaceae and flowering broad leaf) (F=6.88; df=1.63; $p<0.0110$). A higher average parasitism proportion was found on the narrow leaf group (0.96 per tip) than in the broad leaf treatments (0.83 per tip) (**Table 4.5**).

Poisson regression analysis of the incidence of leafhopper nymphs indicated that the tips from the natural weed cover treatment (Weedy) differed significantly from all the other treatments except weed free, (χ^2 =4.72; df=1.63; p=0.0298). We found a higher number of leafhopper nymphs in the weedy treatment (4.30 nymphs per tip) than in the other combined treatments (3.36 nymphs per tip). The 98.8% of the nymphs found belonged on the genus *Empoasca,* while the rest of nymphs were identified as *Caldwelliola* sp.

Using sticky traps we identified 14 different species of leafhopper adults present in the experimental field (**Annex 4.3**). The more common species, accounting for 69% of abundance recorded in the field, were *Caldwelliola reservata* (48%) and *Empoasca* sp. (21%). The number of leafhoppers was higher for the weed free treatment, with an average of 3.50 individuals per plot, and statistically differed (χ^2 =9.09; df=1.63; p=0.0026) from the others combined treatments with an average of 2.38 insects per plot. The number of leafhopper adults on the treatment with Rubiaceae cover was also significantly higher than the number observed on the combined treatments with *Drymaria* and flowering broad leaf cover (χ^2 =6.80; df=1.63; p=0.0091) with 2.90 and 2.65 individuals per plot respectively (**Table 4.5**).

Most of the predators observed were spiders (order Aranae) accounting for 90.6% of the total abundance of a group that included lacewings (Chrysopidae), mantids (Mantidae) and ladybird beetles (Coccinellidae). Orthogonal contrasts (**Table 4.6**) showed that *D. marginata* tips from the weed free treatment had a significantly lower (χ^2 =4.99; df=1,63; p=0.0256) average number of predatory insects (0.50 insects per tip) than the other treatments (0.98 insects per tip). Additionally, a higher average number of predatory insects was found on the combination of the treatments with *Drymaria* and flowering broad leaf cover (1.30 insects per tip) than on plots with the Rubiaceae family (0.30 insects per tip), differing significantly (χ^2 =5.54; df=1,63; p=0.0186).

Katydid eggs collected in the field were identified to two genera *Microcentrum* and *Conocephalus*. Poisson regression indicated significant differences when comparing all the means of the treatments. The lowest number of eggs was found on the weed free treatment (0.60±0.27 eggs per tip) and statistically differed (χ^2 =7.32; df=1,63; p=0.0068) from levels found in the Rubiaceae cover, where the highest number of eggs was found (2.10±0.85).

Other treatments did not differ significantly from the weed free and Rubiaceae treatment. We did not find differences between orthogonal contrasts of the treatments for katydid eggs (**Table 4.7**).

In general we found a high number of leaves infested with armored scales (primarily Florida red scale, *Chrysomphalum aonidum* (L.)) in all the cover treatments with an average of 3.19 ± 0.22 (n=7; min=2.20; max=4.00) (**Table 4.4**). We did not find statistical differences between the means of all the treatments nor orthogonal contrasts (**Table 4.7**).

Table 4.5. Orthogonal contrasts for the average number of leafhopper eggs, parasitism proportion, and leafhopper nymphs per plant tip on *D. marginata* cover in Guapiles, Costa Rica, in 2009. Treatments of ground cover: Weed free (WFree), Weedy, Poaceae (Poa), Cyperaceae (Cyp), *Drymaria* , Rubiaceae (Rub), Flowering broad leaf (FB), Broad leaf (*Drymaria*, Rub and FB), Narrow leaf (Poa and Cyp).

Contrast	Total eggs				Parasitism proportion				Leafhopper nymphs			
	*Mean1	*Mean2	F**	p-value	Mean1	Mean2	F	p-value	Mean1	Mean2	χ^{2}**	p-value
WFree *vs* Others	2.36±0.33	2.51±0.22	0.16	0.6942	0.94±0.01	0.90±0.03	2.23	0.1402	4.00±0.82	3.52±0.33	2.78	0.0956
Weedy *vs* Others	2.12±0.42	2.59±0.26	1.31	0.2568	0.98±0.01	0.88±0.03	10.02	0.0024	4.30±0.97	3.36±0.34	4.72	0.0298
Broad *vs* Narrow leaf	1.74±0.17	3.86±0.47	18.02	<0.0001	0.83±0.05	0.96±0.01	6.88	0.0110	3.27±0.41	3.50±0.60	0.24	0.6268
Cyp *vs* Poa	4.20±0.42	3.51±0.84	31.70	<0.0001	0.96±0.01	0.95±0.01	0.31	0.5801	3.20±0.96	3.80±0.77	0.51	0.4738
Drymaria and FB *vs* Rub	1.78±0.22	1.68±0.25	0.06	0.8135	0.87±0.05	0.75±0.08	1.49	0.2269	3.55±0.53	2.70±0.63	1.41	0.2351
Drymaria vs FB	1.46±0.21	2.10±0.38	1.75	0.1909	0.88±0.08	0.86±0.08	0.05	0.8219	3.20±0.65	3.90±0.85	0.69	0.4069

*Means 1 and 2 correspond to the means of the first and second parameter compared on the contrast.

** df(Num) =1 and df(Denom) = 63 for each treatment. F value is indicated for ANOVA analysis and χ^{2} value for Poisson analysis.

Table 4.6. Orthogonal contrasts for average number of and leafhopper adults per plot and predaceous insects per plant tip on *D. marginata* cover in Guapiles, Costa Rica, in 2009. Treatments of ground cover: Weed free (WFree), Weedy, Poaceae (Poa), Cyperaceae (Cyp), Drymaria, Rubiaceae (Rub), Flowering broad leaf (FB), Broad leaf (Drymaria, Rub and FB), Narrow leaf (Poa and Cyp).

Contrast	Leafhopper adults				Predaceous insects			
	Mean1	Mean2	χ^{2}	p-value	Mean1	Mean2	χ^{2}	p-value
WFree *vs* Others	3.50±1.04	2.38±0.26	9.09	0.0026	0.50±0.31	0.98±0.13	4.99	0.0256
Weedy *vs* Others	2.20±0.74	2.42±0.28	0.41	0.5205	1.00±0.33	0.98±0.15	0.39	0.5308
Broad *vs* Narrow leaf	2.73±0.36	1.95±0.44	0.02	0.8929	0.97±0.22	1.00±0.18	0.54	0.4609
Cyp *vs* Poa	2.30±0.76	1.60±0.45	1.24	0.2649	1.10±0.23	0.90±0.28	0.20	0.6553
Drymaria and FB *vs* Rub	2.65±0.29	2.90±0.92	6.80	0.0091	1.30±0.29	0.30±0.15	5.54	0.0186
Drymaria vs FB	3.00±0.37	2.30±0.45	0.92	0.3377	1.60±0.50	1.00±0.30	1.36	0.2436

*Means 1 and 2 correspond to the means of the first and second parameter compared on the contrast.

** df(Num) =1 and df(Denom) = 63 for each treatment. χ^{2} value is indicated for Poisson analysis.

Table 4.7. Orthogonal contrasts for average number of katydid eggs per tip and leaves with armored scales on *D. marginata* cover in Guapiles, Costa Rica, in 2009. Treatments of ground cover: Weed free (WFree), Weedy, Poaceae (Poa), Cyperaceae (Cyp), Broad leaf (Drymaria, Rub and FB), Narrow leaf (Poa and Cyp), Drymaria, Rubiaceae (Rub), Flowering broad leaf (FB).

	Katydid eggs				Leaves with armored scales			
Contrast	***Mean1***	***Mean2***	χ^{2**}	**p-value**	**Mean1**	**Mean2**	χ^2	**p-value**
WFree *vs* Others	0.60±0.27	1.68±0.24	3.35	0.0670	3.10±0.62	3.20±0.29	0.71	0.4001
Weedy *vs* Others	1.50±0.48	1.72±0.28	0.32	0.5692	2.20±0.51	3.40±0.33	0.78	0.3758
Broad *vs* Narrow leaf	1.73±0.97	1.70±0.40	3.41	0.0648	3.27±0.41	3.50±0.60	2.37	0.1241
Cyp *vs* Poa	1.90±0.53	1.50±0.48	0.47	0.4937	--	--	--	--

*Means 1 and 2 correspond to the means of the first and second parameter compared on the contrast.

** df(Num) =1 and df(Denom) = 63 for each treatment. χ^2 value is indicated for Poisson analysis.

4.6 Discussion

In general we found a higher level of insect pest abundance and parasitism during the experimental sampling than during the baseline sampling. This could be explained by the differences in the rainfall regimens presented between each census. Hidalgo (2012), studying the seasonal dynamic of quarantine pests on *Dracaena marginata* fields in Costa Rica, found that insect pests and parasitism levels fluctuate over time showing peaks in different times of the year. He found that the distribution of leafhopper eggs and nymphs were higher during the wet season, and that parasitism level and armored scales drop after periods of high precipitation. In our study, the lowest number of insect pests and parasitism levels was in the month of February, which is typically a dry month. However for 2009, this month was completely atypical reporting rainfalls of 832 mm, which is a 400% increase over the historical precipitation of this month (IMN 2010). The physical effect of the high precipitation rate could have wiped out the population of parasitoids and armored scales; as well as having a negative influence on adults, reducing leafhopper and katydid egg abundance. The physical effect of heavy rain on arthopods has been also reported for other studies (Weisser *et al.* 1997).

Effect of weed cover composition on insect pests and natural enemies

Insect pests and natural enemies showed different responses to specific arrangements of weed cover composition. Thomas *et al.* (2002) determined that distribution

patterns of arthropods within habitats of the same type may differ between species for different reasons, but mainly occur in response to specific environment requirements associated with life history traits such as reproductive strategies and dispersal.

Leafhoppers were more sensitive to changes in weed cover composition in comparison to the other insect groups. We found leafhopper eggs across all the treatments but a higher abundance was identified on the narrow leaf treatments in comparison with plots with the broad leaf treatments; and within the narrow leaf treatments the highest egg abundance was found on the Cyperaceae treatment. Our baseline results also showed that, even in natural habitats there was a significant positive correlation between leafhopper egg abundance and the Cyperaceae and Poaceae families. Even though leafhoppers have been identified as obligate sucking herbivores with a wide range of hosts in crops and non-crop habitats (Nault and Rodriguez 1985, Denno and Perfect 1994, Lamp *et al.* 1994), responses to these weed families have been reported to differ among species. Some studies (Turner and Pollard 1959 and Tipping *et al.* 2004) have reported that females of *Homalodisca coagulata* and *Oncometopia nigricans* will oviposit on host plants in the Poaceae even when these weeds are not suitable for successful nymphal development. Perez (2007) in a choice test experiment found that *O. clarior* use weeds from the Poaceae family for feeding and refuge but not for oviposition; while weeds from Cyperaceae family were not attractive to this leafhopper. Similar results were reported by Lamp *et al.* 1994 and 1984 for the polyphagous leafhopper *Empoasca fabae*. Even though this insect may use host plant species in the class Liliopsida (including grasses (Poaceae) and sedges (Cyperaceae) for refuge when hosts are unavailable, these weeds are considered as non-hosts due to the inability of this insect to produce offspring on any of these plants. During a concurrent evaluation of our field plots for where the cryptic *Empoasca* sp. eggs are visible only after staining, Hidalgo (2012), also found a low average number of eggs per tip on narrow leaf treatments.

The results of the present study show that most of the leafhopper eggs visible on the leaf surface with the naked eye belonged to *Caldwelliola* sp. for which there have been no reported scientific studies on host preference. However, considering the behavior showed by other leafhopper species, we could expect that the lack of preference for grasses (Poaceae) and sedges (Cyperaceae) should have an influence on their oviposition behavior.

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Females may prefer to concentrate their oviposition on Dracaena plants, which represent a suitable host to produce offspring, increasing the density of eggs on these treatments. The opposite behavior could explain the lower density of eggs per tip found on the broad leaf treatments. The presence of alternate weed hosts turns these Dracaena plots into a more diffuse resource allowing females to distribute their eggs over the tips of *Dracaena* and other plant hosts. The resource diffusion hypothesis has also been used to explain this oviposition behavior for other highly mobile pests (Yamamura 1999).

Although most of the nymphs found during this study belonged on the genus *Empoasca*, it was not possible to evaluate egg abundance due to their small size (0.5mm) and cryptic location inside the Dracaena leaves that make them impossible to detect in the field. Based on the high population of adult *Empoasca* and the high egg abundance reported by Hidalgo (2012) the leafhopper egg counts reported in this study underestimate the total egg population but gives a good estimation for those eggs large enough to be counted using simple inspection methods. As such, the results of this study should be complemented with the results of Hidalgo (2012).

Although *Oncometopia* sp. is a common leafhopper in *D. marginata* fields in Costa Rica, their eggs were relatively rare in this study (Perez 2007, Hidalgo 2012). This could be explained due to the proximity of our field to a riparian forest (approximately 100 m). In a separate study (see Chapter 3), we found that *Oncometopia* egg abundance was almost null in Dracaena fields adjacent to forests in comparison to fields not surrounding by forest.

Overall, we found high proportions of parasitism across the treatments, with rates higher than 0.75. However, the highest rates of parasitism were found in the weedy, weed free and narrow leaf treatments in comparison to the broad leaf treatments. The natural assortment of weed species in the weedy treatments may provide a more diversified habitat for parasitoid survival. Natural diversified systems are known to provide a wide variety of resources, including alternative prey, plant food sources, optimal microclimate and refuge for natural enemies (Marino and Landis 1996, Landis *et al.* 2000, 2005, Olson and Andow 2008, Rusch *et al.* 2010, Thomson and Hoffmann 2009). Some other studies have also noted the importance of vegetation diversity for enhancing the biological control of the

pests by the parasitoids (Patt *et al.* 1997, Bezemer *et al.* 2004, de Queiroz and Garcia 2009).

On the other hand, we did not expect to find high levels of leafhopper parasitism in treatments such as the weed free (less diversified habitat for parasitoid survival) or even in the narrow leaf treatments, as they have not been characterized as attractive for natural enemies (Villalobos 2007) because they do not show functional traits such as presence of extra floral and floral nectaries, which are important for parasitoid survival. The presence of extrafloral nectaries in *D. marginata* (Bentley 1977, Keeler 1985) may explain how parasitoids were able to survive in plots with narrow leaves or even without weeds. If parasitoid wasps are able to obtain food resources and refuge from the Dracaena plants, host density may become a key factor influencing parasitoid distribution. We found a positive correlation between parasitism rate and egg density. So the high rates of parasitism found in the narrow leaf treatments and weed free treatments could be explained by the spatial density dependence between parasitoids and leafhopper eggs (Walde and Murdoch 1988).

Conversely, functional traits of the weeds found in the broad leaf treatments increase the possibility that natural enemies are moving from the crop to the ground cover of these treatments to find refuge and complement their resources. This and the lower number of leafhopper eggs found in these plots, which are distributed over the tips of *Dracaena* and other plant hosts; then diluting the spatial distribution of parasitoids as they represent a more diffuse habitat in terms of resources (Yamamura 1999), may be also explaining the lower rate of parasitism of these treatments.

Most of leafhopper nymphs found in this experiment belonged on the genus *Empoasca* sp. Due to the small size and cryptic oviposition pattern of this leafhopper it was impossible for us to quantify egg abundance during field evaluations. However, the high presence of nymphs of this species on *D. marginata* plants is a good indicator that this is one of the more abundant species. Although the adult of *Empoasca* sp. is considered highly polyphagous, reproducing on a wide range of plant species and families, and with ability to vary feeding behaviors in response to its host plant (Poos and Wheeler 1943, Lamp *et al.* 1994); fewer plants serve as hosts for female oviposition and survival of small nymphs

(Lamp *et al.*, 1984). As a consequence, nymph's development is limited to fewer species in comparison to plant species suitable for adult survivorship.

In general, we identified a high abundance of nymphs in all the treatments; but a higher number of nymphs were found in the weedy treatment than in the average of the other combined treatments (excluding weed free treatment). Hidalgo (2012) also found, through staining procedures on Dracaena tips, a high number of *Empoasca* sp. eggs in the weedy treatment in comparison to the other treatments. He explained these differences due to a low preference of *Empoasca* for laying eggs on this weed cover composition. The same behavior could explain the higher number of nymphs on the weedy plots. Most of the weed species found on the weedy treatment (81%) belonged to the families Rubiaceae, Scrophulariaceae, Cyperaceae and Poaceae. All these families have been considered as unsuitable hosts for this leafhopper (Lamp *et al.* 1994). For instance, reduction on *Empoasca* sp. leafhoppers populations have been reported in cropping systems in the presence of grasses and sedges (Aguyoh *et al.* 2004, Lamp *et al.* 1984, 1994, Roda *et al.* 1997a, 1997b, Roltsch and Gage 1990). The inability of nymphs to access the relatively smaller vascular bundles on these monocotyledonous plants (Lamp *et al.*, 1984b); as well as the presence of physical barriers may explain why females look for other hosts that can best support nymphal development (Roda *et al.* 1997b, Roltsch and Gage 1990). The Scrophulariaceae family has also been reported by Lamp *et al.* (1994) as non-hosts for *Empoasca fabae* due to the production of prominent chemical defenses. Then, the high proportion of non-host weeds in the weedy treatment could repel *Empoasca* nymphs, which may emigrate from the ground to the Dracaena plants. The presence of most of the families described above in the individual treatments could also explain the high presence of *Empoasca* nymphs on Dracaena tips of those treatments, although the repellence showed by these weeds in individual treatments seemed not to be as stronger as in the weedy treatment. For the specific case of the weed free treatment, even though when we did not find significant differences, we identified the second highest nymph abundance in plots without weeds. This also coincided with the results of Hidalgo (2012), who found the highest *Empoasca* egg abundance in the weed free treatment.

We found that the pattern of distribution of leafhopper adults in the sticky traps differed from the pattern of abundance of eggs. For instance, the lowest number of adults

on the Poaceae treatment coincided with a high number of eggs in the Dracaena plants of these plots. This supports our expectations that there is lack of preference of leafhopper adults for grasses (Poaceae) (Lamp *et al.* 1994, 1984, Perez 2007) as we found a lower number of adults at the ground level (sticky traps were placed at a height of 0.5 m). However this lack of preference may have an influence on the oviposition behavior as females avoid the ground and prefer to move to Dracaena plants, which represent a suitable host to produce offspring, increasing the density of eggs on these treatments.

On the other hand, Rubiaceae, one of the broad leaf treatments with low number of leafhopper eggs, also had one of the highest number of leafhopper adults at the ground level. The main weed component of the Rubiaceae treatment (*Spermacoce latifolia*) have been identified to be used for refuge and feeding by the leafhopper *Oncometopia clarior* (Perez 2007). Even though we did not find *Oncometopia* sp. but *Caldwelliolla* sp. and *Empoasca* sp. in our experimental, results from Perez (2007) could suggest that it is an attractive host for this group of insects. This attraction may reduce the pressure of this pest to oviposit on Dracaena plants as weed hosts turns these Dracaena plots into a more diffuse resource allowing female to distribute their eggs over the tips of *Dracaena* and other plant hosts.

Analyzing the predatory insect abundance, we found significant differences between the same contrasts described for leafhopper adults, but in the opposite direction. We detect a lower predator population on the weed free treatment in comparison to the combination of the other treatments, where a higher abundance of natural enemies was found. Equally, the lowest number of predatory insects was found on the Rubiaceae treatment, where we found a higher adult population, in comparison to the combined treatments of *Drymaria* and flowering broad leaf. *Drymaria cordata* and weeds from the flowering broad treatment (mainly Scrophulariaceae family) have been classified by Villalobos (2007) as attractive to natural enemies as they show functional traits, such as presence of floral and extrafloral nectaries and presence of aromatic compounds, which increase their abundance.

The high number of predatory insects coincided with a low number of leafhopper adults and viceversa. One important mortality factor identified for other leafhoppers (*H. vitripennis*) is predation by spiders. Different families of spiders including Salticidae,

Agelenidae, Oxyopidae, and Lycosidae have been observed feeding on the nymph and adult stages of this insect (Lopes *et al.* 2003, Tipping *et al.* 2004). Spiders were the most common predatory insect in our experimental field, so dispersal within treatments with high population of natural enemies has a potential risk associated as leafhopper adults are vulnerable to predation (Mizell 2008). In this way, leafhoppers may prefer to remain on the plots with the lower predator population as they increase their probability to survive.

The higher number of spiders in other treatments different than the weed free treatment could be explained by the structurally complex habitat present in most of the treatments in comparison to plots without weeds. Architecturally complex vegetation can provide spiders the structure necessary to build silken snares increasing their predation efficiency. Additionally, according to Finke and Denno (2002) structurally complex vegetation has the potential to mediate multiple-predator effects on herbivores. Vegetation structure can diminish antagonistic interactions among predators, and thus increase overall enemy impact on shared herbivore prey. For instance, intraguild predation between spiders and leafhopper parasitoids is reduced in complex habitats, by providing a refuge for parasitoid wasps which can improve parasitism levels in the field, and thus predatory insects can enhance the suppression of leafhopper adults.

Katydid distribution and abundance seemed to be more affected by the presence and structure of specific vegetation. We found a lower number of katydid eggs per tip in the weed free treatment. This could be explained as katydids are not able to find alternative hosts different from the Dracaena plants on plots without weeds, so they prefer to migrate to other areas of the field in order to find other weed hosts which provide them with plant food sources, optimal microclimate and refuge to complete their life cycle. Anderson (1964) also found that orthopterans were never found in areas that were lacking their preferred hosts, concluding that vegetation was a key factor upon grasshopper distribution. Crypsis has also been reported as an important factor in habitat selection because coloration and texture of the background influence on the ability of orthopterans to evade predators (Joern 1980). Weed free plots have a more homogeneous matrix in comparison to other treatments, where the combination of different weeds increase the possibility for katydids to camouflage and escape from predators.

Different factors such as plant species, plant abundance, taxonomic composition and physical structure of the vegetation have been found to play an important role in the habitat selection and distribution of orthopterans (Otte and Joern 1977, Joern 1979, Kemp *et al.* 1990, Fielding and Brusven 1992).   For instance, some studies have demostrated a preference of orthopterans for grassess (Vestal 1913, Hewitt and Blickens 1974, Fielding and Brusven 1993, Thompson *et al.* 1996, Porter and Redak 1997, Torrusio *et al.* 2002). Other studies, have reported orthopterans feeding on plants of the Scrophulariaceae and Asteracea family, which are the most abundant species of the flowering broad leaf treatment, as well as in the Brassicaceae family, which is the second most abundant family in the Drymaria treatment (Joern 1979). Also, orthopterans of the Romaleidae and Acrididae have been reported resting on weeds of the Caryophyllaceae family, same family of *Drymaria* sp. (Vinokurov and Rubov 1930, Rivera 1988,). The wide range of hosts of katydids could explain why we did not find significant differences in the oviposition behavior between other treatments different than the weed free plots. Even though most studies have been focused on feeding behavior and habitat preference we could expect that katydids may be also using these weeds as alternative hosts for oviposition. This suggests that female katydids have a wide range of hosts available on these plots becoming these microhabitats in a more diffuse resource (Yamamura 1990), which combined with their high ability of dispersion, allows female to distribute their eggs over the tips of *Dracaena* and other plant hosts.

The number of leaves infested with armored scales was consistently high across all the treatments (3.19 leaves per tip in average), showing no differences among weed cover compositions. Although the distribution pattern of armored scales is commonly found to be patchy (Hanks 1991, Hanks and Denno 1993b) and affected by management practices (Prado *et al.* 2008), these insects are able to survive on a broad range of plant hosts (Hanks and Denno 1994, Culik *et al.* 2008, Magsig-Castillo *et al.* 2010), preferring long-lived host plants (Miller and Kosztarab 1979) such as *D. marginata*. However, the biological dispersal of this insect is limited, since they are sessile for most of their life cycle. Crawlers (first nymph instar) are capable of dispersing and colonizing new areas within a range of less than 1 m (Magsig-Castillo *et al.* 2010), and winged males just move to mate with nearby females (Hanks and Denno 1993a). The most important means of dispersion has been

attributed to the wind, although other phoretic means such as insects, birds, animals, other insects and man have been reported (e.g. Beardsley and Gonzalez 1975, Magsig-Castillo *et al.* 2010). This limited dispersion does not allow them to easily select their preferred host plant or migrate to other areas looking for new suitable hosts.

4.7   Conclusion

Crop pests (leafhoppers, katydids and armored scales) and natural enemies showed different responses to specific arrangement of weed cover compositions. These differences were attributed to a combination of factors including insect host preference, insect biology, specific environment requirements, presence of natural enemies and agricultural practices. Life history traits, such as dispersal ability, were identified as key factors that have the potential to influence insect distribution. While leafhoppers and katydids are able to migrate to different areas in the presence of unsuitable hosts or environmental conditions, armored scales are sessile most of their lives so other factors, such as spreading agents and management practices, are more important for their distribution.

Leafhoppers were more sensitive to changes in weed cover composition. The resource diffusion hypothesis was used to explain the egg distribution, as females seemed to prefer to concentrate their oviposition on Dracaena plants, which are a suitable host to produce offspring, increasing eggs density on grassy treatments. On the other hand, the presence of alternate host plants represented a more diffuse habitat, which combined with a high ability of dispersion, allowed female to distribute their eggs over the tips of *Dracaena* and other plant hosts reducing the final pest pressure on the crop. The presence of predacious insects was identified as an important mortality factor for leafhopper adults.

Vegetation was a key factor upon katydid distribution as they were never found in areas lacking their preferred hosts. Crypsis was used as a possible mechanism to explain katydid habitat selection as the structure of the background vegetation may help them to evade predators.

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4.9 Annexes

Annex 4.1 Table of absolute frequency (af) and relative frequencies (rf) of weed species associated with Dracaena marginata in Costa Rica, 2009 (n = 415).

Species	af	rf	Species	af	Rf
Spermacoce latifolia	403	0.157	Richardia scabra	7	0.021
Lindernia diffusa	303	0.118	Chamaesyce hirta	6	0.021
Phyllanthus urinaria	254	0.099	Cyperus laxus	6	0.021
Youngia japonica	251	0.098	Pilea microphylla	6	0.021
Peperomia pellucida	199	0.078	NI 1	5	0.021
Lindernia crustaceae	157	0.061	Ageratum conyzoides	4	0.021
Eleusine indica	139	0.054	Alternanthera sessilis	4	0.021
Cyperus sp.	116	0.045	Panicum trichoides	3	0.021
Ludwigia octovalvis	105	0.041	Rottboellia cochinchinensis	3	0.021
Cyperus tenuis	91	0.036	Sonchus oleraceus	3	0.021
Kyllinga brevifolia	67	0.026	Dracaena marginata	2	0.021
Drymaria cordata	54	0.021	Euphorbia graminea	2	0.021
Oxalis barrelieri	50	0.021	NI 2	2	0.021
Digitaria sp.	41	0.021	Acalypha arvensis	1	0.021
Cardamine bonariensis	35	0.021	Chloris radiata	1	0.021
Vernonia cinerea	32	0.021	Cyperus odoratus	1	0.021
Paspalum conjugatum	31	0.021	Echinochloa colona	1	0.021
Mecardonia procumbens	20	0.021	Vitaceae NI	1	0.021
Pityrogramma calomelanos	20	0.021	Cucurbitaceae NI	1	0.021
Scoparia dulcis	19	0.021	NI 3	1	0.021
Cyathula prostrata	18	0.021	NI 4	1	0.021
Miconia argentea	15	0.021	Galinsoga quadriradiata	1	0.021
Chamaesyce hipericifolia	13	0.021	Garrobo	1	0.021
Stemodia verticillata	12	0.021	Panicum conjugatum	1	0.021
Synedrella nodiflora	10	0.021	Paspalum sp.	1	0.021
Commelina diffusa	9	0.021	Poaceae NI2	1	0.021
Poacea NI1	9	0.021	Piper umbellatum	1	0.021
Emilia fosbergi	8	0.021	Sida acuta	1	0.021
Dichondra sp.	7	0.021	Sonchus sp.	1	0.021
Eclipta prostrata	7	0.021			

*NI = Non identified species

Annex 4.2. Table of absolute frequency (af) and relative frequencies (rf) of weed families associated with *Dracaena marginata* in Costa Rica, 2009.

Species	Af	Rf
Poaceae	11	0.190
Asteraceae	10	0.170
Euphorbiaceae	6	0.100
Cyperaceae	5	0.090
Scrophulariaceae	5	0.090
Piperaceae	3	0.050
Amaranthaceae	2	0.030
Rubiaceae	2	0.030
Urticaceae	2	0.030
Brassicaceae	1	0.020
Caryophyllaceae	1	0.020
Commelinaceae	1	0.020
Convolvulaceae	1	0.020
Cucurbitaceae	1	0.020
Dracaenaceae	1	0.020
Malvaceae	1	0.020
Melastomataceae	1	0.020
Onagraceae	1	0.020
Oxalidaceae	1	0.020
Pteridaceae	1	0.020
Vitaceae	1	0.020

Annex 4.3. Total number of leafhopper individuals collected for each species with yellow sticky traps in *Dracaena marginata* in Costa Rica, 2009. Absolute frequency (af) and relative frequencies (rf) are indicated (n=70).

Species	Af	rf
Caldwelliola reservata (Fowler)	85	0.48
Empoasca sp.	37	0.21
Scaphytopius sp.	17	0.1
Agallia sp. 1	8	0.04
Agallia sp. 2	7	0.04
Sibovia occatoria (Say)	5	0.03
*Xestocephalus tesellatu*s (Van Duzee)	5	0.03
Gyponana sp.	4	0.02
Alebrini sp.	3	0.02
Graphocephala crusa	2	0.01
Osbornellus affinis (Osborn)	2	0.01
Hortensia similis (Walker)	1	0.01
Oncometopia clarior (Walker)	1	0.01
Tantulidia rufifruns (Walker)	1	0.01

CHAPTER 5.   CONCLUDING CHAPTER

5.1   Introduction

Ornamental production is one of the most important economical sources of income for Costa Rica and a significant part of its agricultural landscape. Among the ornamental plants, *Dracaena marginata* Lam. (Rusaceae) provides an opportunity to study the population dynamics of three families of herbivorous arthropods: Cicadellidae (leafhoppers), Tettigoniidae (katydids) and Diaspidiidae (armored scales), which have been on the target of national and international authorities as they are quarantine pests in the USA entry ports (Colpetzer 2005).   Different studies have been carried out in order to minimize the phytosanitary risk associated with *Dracaena* exportation. These studies include the generation of information on the population dynamics of these quarantine pests on the crop, as well as the evaluation of the effect of different factors such as weed presence, fertilization and other production practices on the pest population dynamics (Prado 2006, Pérez 2007, Villalobos 2007, Prado *et al.* 2008, Hidalgo 2012).

Other factors such as landscape context have also been demonstrated to have an influence on insect ecological and spatial processes such as dispersion, distribution, movement, population size and richness (e.g. Kareiva 1990, Turner 1989, Fahrig and Merriam 1985, Harrison and Tomas 1991, Dunning *et al.* 1992, Coll and Bottrell 1994, Hanski 1994, Jonsen and Fahrig 1997, With *et al.* 1999, 2002, Chust *et al.* 2004).   As such, this dissertation sought to discern how the landscape context, in which the *D. marginata* is embedded, has an effect on the abundance and distribution of insect pest groups with different biology traits and their natural enemies.

Our first leading question was: Does the different insect pest groups respond to the landscape context at the macro level? With this approach we sought to characterize landscape in which the *D. marginata* was embedded and detect relationships among specific land uses types and insect pest groups. Furthermore, as insect dispersal capacity is species-specific we attempted to detect the spatial scale, at which each of the insect groups responded to the landscape context. This information provided was meant to provide a

baseline for further experimental studies with specific land uses and spatial scales under controlled conditions.

The second part of our research was related to the presence of forest patches in the nearby of *D. marginata* fields. Forests have been highlighted for their capacity to provide ecosystem services on farms such as biodiversity, biological control and pollination (e.g. Janzen 1987, Marino and Landis 1996, Klein *et al.* 2003a,b, De Marco and Coelho 2004, Kremen *et al.* 2004, Ricketts 2004, Chacoff *et al.* 2006, Bianchi *et al.* 2006, Banks *et al.* 2007, Benevides *et al.* 2009, Brosi 2009, Thomson *et al.* 2010). Hence, motivated by this evidence our second leading question was: Can forest patches near *D. marginata* fields provide ecosystem services by reducing pest population through the enhancement of natural enemies and predator population? This is especially important since in Costa Rica over 48% of the land is covered by forest lands (Calvo-Alvarado 2009). As such, patches of secondary forests are likely to be near *D. marginata* production fields in the Atlantic and Northern zone of Costa Rica.

The high diversity found at the within-field level in the microlandscape of the *D. marginata* production fields was the motivation for our third leading question: Do insect pest groups and their natural enemies respond differently to weed cover in *D. marginata* production fields from selected functional groups? This is important since in Costa Rica, *D. marginata* production fields are characterized by their high diversity of vegetation (Villalobos 2007), and some of these weeds have proven some level of attraction or repellenct to leafhoppers (Perez 2007). Furthermore Prado *et. al* (2008) also found that weed management practices in *D. marginata* fields produced significant changes in populations of leafhoppers and katydid eggs. Information of the effect of weed covers on insect pests may be used as another strategy to manage the Dracaena landscape at the smallest scale and reduce pest population in the fields.

5.2   Principal findings and remarks

1.   Effects of macro landscape context on the Dracaena pest complex.

Responses to landscape structure, including landscape metrics and landscape composition have been reported to be species specific (e.g. Taylor *et al.* 1993, Jonsen and Fahrig 1997, Wiens *et al.* 1997, Kruess 2003, Thies *et al.* 2003, Chust *et al.* 2004). We found that katydids, leafhoppers and armored scale insects responded to the landscape context in a different manner. These differences were mainly attributed to the idiosyncrasies of the insect group, such as differences in dispersal and colonization abilities, feeding and habitat requirements (Fahrig 2001, Tscharntke and Brandl 2004).

Katydids mainly responded to the landscape diversity, as these insects responded mainly to factors such as host plant abundance, diversity, taxonomic composition and physical structure of the vegetation for their habitat selection and distribution (Vestal 1913, Otte and Joern 1977, Joern 1979, 1982, Kemp *et al.* 1990, Fielding and Brusven 1992, Cuningham and Sampson 2000, Squitier and Capinera 2002). Leafhoppers, on the other hand, responded to other metrics such as abundance and connectivity of specific land uses (including pastures and ornamental lands). This was explained by the tendency of leafhoppers to respond principally to other factors such as host plant availability and nutritional quality of the agricultural crops (Park *et al.* 2006, Mizell *et al.* 2008, Northfield *et al.* 2009). They need to feed frequently on plants in a specific physiological state make it more likely for them to find suitable hosts when abundance and connectivity of their preferred habitats is higher. Finally, armored scale insects did not respond to the landscape context at any of the spatial scales set in our study. This is probably due to the fact that this insect group respond to other factors such as the presence and distribution of natural enemies, host plant-water relation (Hanks and Denno 1993) and management practices (Prado *et al.* 2008) that have been reported to occur at smaller scales (Jonsen and Farigh 1997).

Connectivity between forest patches played an important role on leafhopper egg abundance as their abundance decreased when connectivity between forest patches increased. This was explained as forests may be providing ecosystemic services via 'top-

down' effects through the enhancement of natural enemy populations which lead to leafhopper suppression in the *D. marginata* fields.

2. Response of insect pest groups to the spatial scale within the macro landscape context.

Responses of insect groups to the spatial scale have been demonstrated to be species-specific and related to the dispersal abilities of the organisms (e.g. Wiens and Milne 1989, Wiens 1992, Jonsen and Farigh 1997, Dauber *et al.* 2003, Thies *et al.* 2003, Chust *et al.* 2003, 2004, Tews *et al.* 2004, Aviron *et al.* 2005). This was also true for our study as we found that the responses of katydids, leafhopper and armored scale insects to the macro landscape characteristics, was scale-dependent and differed among insect groups depending on their dispersal abilities. While katydids and leafhoppers, which have high dispersal capacities, showed responses at the different spatial scales set in our study, armored scale population, sedentary for most of their life cycle, did not respond to our spatial scales. Differences between katydids and leafhoppers were also found. Katydid, oviposition responded to the landscape context at the most coarse scales (from Ø 2.0 to Ø 3.0 km), whereas leafhopper egg abundance was the most sensitive group responding to all our spatial scales (from Ø 0.5 to Ø 3 km), depending on the land use and metric.

3. Effect of the presence of forest near *D. marginata* fields on pest abundance, natural enemies abundance and parasitism levels.

We found that leafhoppers, katydids and armored scales showed different responses to presence of forest patches at varying distances from the edge of the field. These differences were again attributed to a combined influence of the biology and life history of each group and the presence of natural enemies that may affect suppress pest populations.

Leafhopper eggs and nymph populations were lower in plots near forest patches. This was explained as forests are effectively providing ecosystem services for the *D. marginata* fields through bottom up and top down effects. First, leafhoppers were affected via "bottom up", as the forest shade is altering the plant physiology by its impact on microclimate and then providing unsuitable conditions for the development of leafhopper populations, which are very selective in terms of nutritional needs (Park *et al.* 2006, Mizell *et al.* 2008, Northfield *et al.* 2009). Second, via 'top-down' effects, by providing optimal

conditions for the enhancement of natural enemy populations (Fernandes and Price 1991, Dyer and Stireman 2003, Sperber *et al.* 2004) that can reduce pest populations.

On the other hand, katydids were not affected by the presence of forest but showed a response to the field edge. Katydid responses to the composition and structure of vegetation (Vestal 1913, Otte and Joern 1977, Joern 1979, Kemp *et al.* 1990, Fielding and Brusven 1993, Cuningham and Sampson 2000, Squitier and Capinera 2002) were used to explain this behavior. Weed composition at field edges on both forest and non-forest plots seemed to include plant species which provide katydids with optimal conditions for their development.

In the case of armored scales, other factors including the presence and distribution of natural enemies, host plant-water relation and management practices (Hanks 1991, Hanks and Denno 1993, Prado *et. al* 2008) have been used to explain their patch distribution in the fields. We determined that the key factor in our study was the presence and distribution of natural enemies in the field as it seems to suppress armored scale populations at the field edges.

4. Response of pest populations and their natural enemies to the presence of weeds.

Leafhoppers, katydids and armored scales and their natural enemies showed different responses to weed ground cover in the field. Thomas *et al.* 2002 determined that distribution patterns of arthropods within habitats of the same type may differ between species for different reasons, but mainly occur in response to specific environment requirements associated with life history traits such as reproductive strategies and dispersal. Dispersal ability was identified as a key factor that influenced insect distribution. While leafhoppers and katydids are able to migrate to different areas in the presence of unsuitable hosts or environmental conditions, armored scales are sessile most of their lives so other factors, such as spreading agents and management practices, are more important for their distribution.

The resource diffusion hypothesis (Yamamura 1990) was used to explain the low number of katydid and leafhopper eggs under specific weed cover as the presence of alternate host plants represented a more diffuse habitat, which combined with a high ability

of dispersion, allowed female to distribute their eggs over the tips of Dracaena and other plant hosts reducing the final pest pressure on the crop.

Taking into account that leafhoppers, katydids and armored scales and their natural enemies showed different responses to the landscape characteristics from broad to local scales, it is not possible to recommend an overall management of the landscape to control their populations in the *D. marginata* fields. However, based in our results, the better approach could be to transfer the knowledge about the biology and life history of each group to the farmers. Thus, they will be able to identify their main pest problem in the field and understand what is the best agricultural practice or landscape management that should be applied focused on the target pest and the specific results found in our study for each insect group. Also it would be highly recommended to highlight the importance of the presence of natural enemies that may affect suppress pest populations in *D. marginata* fields.

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