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12 The Influence of Agricultural and Forest Landscapes on the Diversity of Lepidoptera

Abstract: Lepidoptera is one of the most diverse groups of insects in the neotropics. It has been thoroughly used as model in several areas of Biology, with special interest in studies of evolution and interactions with larval host plants. Although a huge body of information is available for host plant use for lepidopterans, the influence of crop plants in Brazilian agroecosystems conditions on the evolution and diversification of populations is still reduced. This chapter presents current available data on genetic diversity of moths of economic interest in Brazilian conditions, with special discussion on the role of cultivated and wild host plants surrounding crops systems affecting the genetic structure of populations. The role of host plants, including important crops in Brazil, will also be presented in the discussion on Ecological Speciation in Lepidoptera, with information about what it is been done on this subject in Brazilian agroecosystems aiming the application on Integrated Pest Management. How the information gathered with model pest insects on Ecological Speciation due to host plant use can be used to understand speciation mechanisms on wild herbivorous insects will also be discussed. The third main discussion will focus on how the surrounding vegetation formed by contact zone between pastures and secondary forests influence the structure of butterfly assemblages and determine richness and abundance of groups, and how these studies can offer broader understanding of patterns of distribution of butterflies in fragmented landscapes.

12.1 Introduction

Intensification of agriculture is one of the main drivers of biodiversity declines worldwide (Tilman et al., 2002; Benton et al., 2003; Tscharntke et al., 2007a). The main environmental impacts of agriculture come from the conversion of natural ecosystems into a fragmented landscape composed by remnants of native vegetation surrounded by a matrix of crops, forestry, pastures and/or vegetation in different stages of succession (Saunders et al., 1991). However, besides fragmentation and obvious habitat loss, connectivity among the remaining habitats becomes impaired by agricultural matrix, highly impermeable for several organisms. Moreover, the widespread use of agricultural pesticides and fertilizers has profound effects on organisms and water bodies (Pimentel & Edwards, 1982; Logan, 1993; Paoletti et al., 1995; Groenendijk et al., 2002). Conversely, agroecosystems may also provide environmental benefits and important ecosystem services, such as pollination and biological control (Tscharntke

et al., 2007b), also providing a greater diversity of conditions and resources to native organisms. As a result, they end up sheltering a larger number of species per unit area compared to more homogeneous environments (Magurran, 2004). Additionally, adoption of “conservation agriculture” measures can highly improve local biodiversity in agroecosystems (Paoletti et al., 1992; Hobbs et al., 2008).

In Brazil, vast areas of tropical forests have been converted into farmland in the last decades (Nepstad et al., 2006, Gibbs et al., 2010). As an example, from 1999 to 2011 agricultural areas grew from 530,000 to 680,000 km², especially due to large scale farming of commodity crops (such as soybean, sugarcane and corn) (Lapola et al., 2013). However, besides being one of the largest agrarian countries in the world, there is a general lack of information on the effects of agricultural landscapes on biodiversity in Brazil.

In this way, a good approach to understand the effects of agricultural landscapes on biodiversity is by better understanding the effects of habitat fragmentation on different biological groups. Studies focusing on habitat fragmentation and its effects on biodiversity have been attentive to both patch and landscape levels for several taxonomic groups, mainly insects (Duelli & Obrist, 2003; Bianchi et al., 2006; Hendrickx et al., 2007; Attwood et al., 2008). Among the insect groups, Lepidoptera (butterflies and moths) are excellent models to investigate such effects, for the following reasons: 1) they are very specific concerning their local habitat requirements, such as food resources and larval host-plants (Munguira et al., 2009), 2) many species are influenced by habitat degradation (Dover & Settele, 2009; Hanski, 1999), 3) several species may exploit resources from the surrounding matrix (Dennis & Hardy, 2007), and 4) local assemblages respond to modification on vegetation structure (Dover & Settele, 2009; Ribeiro et al., 2012).

In the present chapter we discuss two complementary approaches and levels of study with high potential to help to understand the role of agricultural and forest landscapes in shaping lepidopteran communities. First, we describe **genetic diversity** studies of polyphagous pest lepidopterans and how alternative crops and wild plants influence genetic and reproductive isolation in the field. Second, we provide examples of studies showing the effects of farmland and forested landscapes on the **community diversity** of frugivorous (fruit-feeding) butterflies.

12.2 Genetic Diversity of Lepidopteran Pests in Brazil

12.2.1 Lepidopterans-larval Host Plant Interactions and their Role in Genetic and Reproductive Incompatibility

With few exceptions, caterpillars are mainly herbivorous, that is, they feed on a broad variety of plant tissues. Most of them feed on external tissues of superior plants, a derived habit within the Order Lepidoptera, whose ancestors were endophagous that

used to feed internally as miners on plant tissues (Menken et al., 2010). Although barely present in butterflies (exceptions are some species in the family Lycaenidae and species within *Dynamine* (Nymphalidae: Biblidinae), that feed partially inside *Dalechampia* (Euphorbiaceae) sprouts (Leite et al., 2014)), the endophagous habit is broadly found in many groups of moths, mainly microlepidopterans (Powell, 1980).

Herbivorous caterpillars however do not feed indiscriminately on any species of host plant (Ehrlich & Raven, 1964), and most of them show restrictions related to host plant use, mainly due to plants secondary compounds, which distinguish many species and superior taxa (Jaenike, 1990; Futuyma et al., 1993; Bernays, 1998; Schoonhoven et al., 2008). In this way, herbivorous species can be **monophagous** and feed on a few related host plant species; otherwise, **oligophagous** or **polyphagous** species can be associated to different host plant species within the same or distinct plant families, respectively (Schoonhoven et al., 2008).

Populations of polyphagous insects associated with different host plants through their geographical range can become genetically isolated in distinct lineages (Pashley, 1986), mainly due to ecological specialization followed by reduced gene flow and speciation processes (Funk, 1998; Dres & Mallet, 2002; Nosil et al., 2008). The resulting lineages could later become differentiated host races or biotypes (Emelianov et al., 1995; Groman & Pellmyr, 2000; Martel et al., 2003; Machado et al., 2008) due to the increased reproductive isolation (Dres & Mallet, 2002).

The characterization of insect lineages associated to crops is of considerable importance to answering both basic (e.g. speciation) and applied (e.g. pest management) questions. First, the biological information obtained for one lineage may not be applied to the other, compromising the strategies of pest control. Furthermore, the quantification of intra and interpopulation divergence among pest populations is pivotal to its management as the incorrect identification of species complexes can result in an erroneous employment of control techniques (Rosen, 1986; Paterson, 1991; Mills & Kean, 2010). For example, highly divergent populations of pest insects can differently damage their hosts (Rugman-Jones et al., 2010), and can respond differentially to control methods (Bickford et al., 2007).

Molecular markers have been broadly applied to evaluate the increasing reproductive isolation among insect populations, and to investigate species boundaries (Sperling & Hickey, 1994; Porreta et al., 2007; Dumas et al., 2015). Those markers can indicate if the reproductive isolation estimated by the lack of gene flow among individuals occupying different host plants is due to: 1) genetic drift acting distinctly in each host, or 2) **divergent selection** (i.e. selection arising from environmental differences or ecological interactions that bear polymorphic characters to evolve in contrasting directions on two populations (Nosil et al., 2009)) related to host plant use (Funk, 1998; Dres & Mallet, 2002). **Ecological speciation** studies (Rundle & Nosil, 2005; Matsubayashi et al., 2010) focus on the many ways that divergent selection can cause reproductive isolation among populations (Rundle & Nosil, 2005; Funk & Nosil, 2008). For polyphagous insects, genetic divergence and reproductive isolation are

expected to be stronger between sympatric populations using different host plants than between populations using the same host because ecological divergence is indicative of divergent selection (Funk, 1998; Nosil et al., 2009).

12.2.2 Case Studies on Polyphagous Species

Population genetics studies of agricultural lepidopteran pests are indispensable to estimate genetic and reproductive isolation by the amount of gene flow among populations, in order to evaluate ecological factors shaping their present distribution (Scott et al., 2005; Endersby et al., 2006). Brazilian conditions comprise a complex scenario to evaluate the role of alternative larval host plants in the genetic structure of insect populations for several reasons. Among these we can highlight the vast human modified areas for intensive agriculture and livestock production, and more recently, forestry (Hirakurim et al., 2012); and the extraordinary natural biodiversity, coupled with high diversity of biomes and ecosystems. Abundant crop fields of the main Brazilian commodities provide food all year-round for polyphagous pest species, which allows them to maintain large persistent populations at regional levels. Simply, two possible mechanisms of genetic structure can emerge from that model: 1) populations are allowed to spread its range to all available areas containing preferred and alternative hosts, where they are permitted to evolve in isolation from other populations; 2) populations of pest species are seasonally subject to pest control practices and every season they go through a “bottleneck” that randomly sweep genetic variability. In this scenario, both divergent selection and random drift can cause genetic structuring in those populations. An additional local source of genetic variability may be composed of populations from neighbor wild host plants (Blanco et al., 2008), although those populations are hardly sampled in any study of population genetics of pest insects, and its influence is usually assumed.

12.2.2.1 *Spodoptera frugiperda*

The fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Noctuidae) is the classic lepidopteran example of insect with well characterized host strains. *S. frugiperda* is a polyphagous pest species which cause damage in corn (*Zea mays* L.), rice (*Oryza sativa* L.), cotton (*Gossypium hirsutum* L.), sorghum (*Sorghum bicolor* (L.) Moench), and other crops in Brazil and worldwide. Numerous evidences suggest the existence of host strains, or genetic groups (Groot et al., 2010), in *S. frugiperda* populations (Busato et al., 2004; Nagoshi et al., 2007; Juarez et al., 2014; Dumas et al., 2015). Caterpillars collected in corn, sorghum and cotton represent typically the **corn strain**, while individuals from rice and several other pasture grasses are usually recognized as the **rice strain** (Pashley, 1986). Corn and rice strains are morphologically indistinguishable, but they show several ecological, genetic and physiological

discriminant characters (Nagoshi & Meagher, 2008; Groot et al., 2010). Two main possible mechanisms of reproductive isolation are present: differences in female pheromones composition (Groot et al., 2008) and nocturnal timing of mating activity (Pashley et al., 1992). Hybridization between strains suggests incipient speciation (Groot et al., 2010), and although reproductive isolation is incomplete in the two lineages (Pashley, 1993), hybrids show lower fertility (Busato et al., 2008). The role of host plants to the reproductive isolation between *S. frugiperda* strains is unknown (Groot et al., 2010). Busato et al. (2004) used AFLP patterns to investigate the genetic diversity of populations from adjacent areas of corn and irrigated rice in south Brazil and found genetic variation associated to host plants on those localities. Groot et al. (2010) suggest several approaches to better understand how much host plants shape the evolution and isolation of strains in *S. frugiperda*. Certainly a broad population genetics study using *S. frugiperda* as model coupled with techniques of population genomics (Luikart et al., 2003; Ekblom & Galindo, 2011; Silva-Brandão et al., 2015b), and based on both neutral and non-neutral molecular markers (Kirk & Freeland, 2011), could provide an opportunity of finally investigate ecological aspects on the nature and amount of gene flow among Brazilian populations. That approach might contribute to the characterization of genes involved in the process of specialization due to host plant use, and could gather information on the interaction between ecological and reproductive isolation and their role in the process of speciation in herbivorous insects.

12.2.2.2 *Heliothis virescens*

The tobacco budworm *Heliothis virescens* (F.) (Noctuidae) is a polyphagous species described feeding on 14 families of host plants (Waldvogel & Gould, 1990), which could possibly lead to a high diversity related to host plant specialization. The species is an important pest of cotton in the American continent and in Brazil (Degrande, 1998), where it also has recently become an important pest of soybean (*Glycine max* (L.) Merr.) (Tomquelski & Maruyama, 2009). To investigate the possible impact on IPM strategies for controlling this pest, Albernaz et al. (2012) and Domingues et al. (2012) developed population genetics studies with *H. virescens* populations sampled from the main cotton- and soybean-producing areas in Brazil. Using mitochondrial DNA neutral markers, Albernaz et al. (2012) found unique haplotypes at specific localities (Fig. 1 A), but they found no significant genetic structure associated to host plant. The authors hypothesized however that the origin of rare haplotypes may be the migration of individuals from wild host plants found nearby crop fields every season; those rare haplotypes would be different in each sampled region due to the natural flora found in each Brazilian biome.

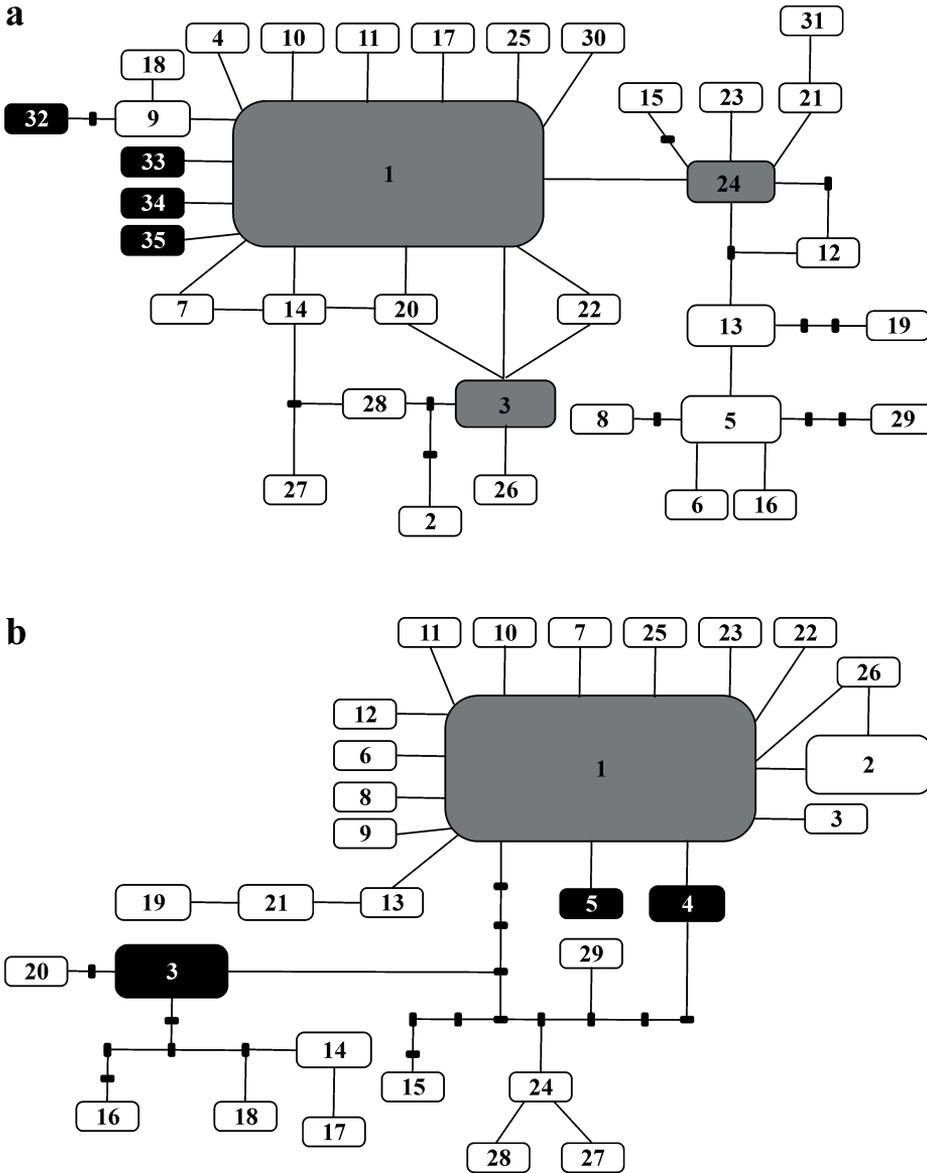


Fig. 12.1: Haplotypes networks of A) *Heliothis virescens*. White: haplotypes recorded only in populations from cotton, Black: haplotypes recorded only in populations from soybean, Grey: haplotypes recorded in cotton and soybean populations (modified from Albernaz et al., 2012); B) *Diatraea saccharalis*. White: haplotypes recorded only in populations from sugarcane, Black: haplotypes recorded only in populations from corn, Grey: haplotypes recorded in sugarcane and corn populations (modified from Silva-Brandão et al., 2015a).

12.2.2.3 *Diatraea saccharalis*

The sugarcane borer *Diatraea saccharalis* (F.) (Crambidae) feeds on several cultivated grasses, and is a pest of sugarcane (*Saccharum officinarum* L.), corn, rice, and sorghum (Dyar & Heinrich, 1928; Box, 1931; Myers, 1935; Long & Hensley, 1972; Pashley et al., 1990). The species is the main pest of sugarcane in Brazil (Pinto et al., 2006), and it is also turning into an important pest of corn following the expansion of Brazilian agriculture to the Savannah region (Cruz, 2007). A population genetic study focusing on the overall corn- and sugarcane-producing areas in Brazil suggested population structure associated to the crop plant from where individuals were sampled (Silva-Brandão et al., 2015a) (Fig. 1 B). The authors went further and raised the hypothesis of a possible influence of wild and alternative hosts as intake of individuals of the sugarcane borer to crop fields, considering that endemic species of *Saccharum* are indeed available nearby crop fields (Vianna et al., 2006). Similarly, they advocated that dispersal from cultivated rice- and sorghum-fields should certainly be estimated to better understand host plant dynamics for this important pest species in Brazil.

12.3 Diversity of Butterflies in Agricultural and Forest Ecosystems

12.3.1 Fruit-feeding Butterflies

Butterflies can be divided in two groups according to adult feeding habit: **fruit-feeding**, that acquired most of their nutritional requirements from rotten fruits, carcasses and plant sap, and **nectar-feeding**, that use flower nectar as their main nutritional source (DeVries, 1987). The fruit-feeding butterflies are represented, exclusively, by the Nymphalidae subfamilies Satyrinae (in the neotropics, three tribes are more commonly reported to be attracted to bait traps: Satyrini, Morphini and Brassolini; the Haeterini can be also captured by using horizontal bait traps), Biblidinae, Charaxinae and also some Nymphalinae (a non-monophyletic group of genera previously treated as tribe Coeini) (Wahlberg et al., 2009).

Fruit-feeding butterfly assemblages are clearly affected by land use (Barlow et al., 2007; Ribeiro et al., 2012; Ribeiro & Freitas 2012, Brito, 2013). Although these modifications rarely reflects in changes in species richness, they are evident in species composition, with some species increasing in abundance while other decreases with habitat change. These differences were documented in all studies comparing areas with contrasting levels of human disturbance, including logged versus unlogged areas (Barlow et al., 2007; Koh, 2007; Ribeiro & Freitas, 2012), continuous versus fragmented landscapes (Uehara-Prado et al., 2007), and primary versus secondary forests (Barlow et al., 2007; Uehara-Prado et al., 2009). Fruit-feeding butterfly assemblages are also affected by the surrounding landscape (Barlow et al., 2007, Ribeiro et al., 2012), as detailed in the section 12.4, and have also been successfully used as model organisms in studies of diversity in agroecosystems worldwide (Horner-Devine et al., 2003; Mas & Dietsch, 2003; Dolia et al., 2008).

The magnitude of effects on fruit-feeding butterflies is dependent on the intensity of land use modifications. In tropical forests, butterfly fauna usually shows a clear vertical stratification, with different species occurring exclusively in canopy and understory (DeVries et al., 1999; Ribeiro & Freitas, 2012). Intense forest modifications like **traditional logging** (the process of felling and extracting timber from forests without previous planning) can disrupt this pattern (DeVries, 1988; Schulze et al., 2001; Fermon et al., 2005), while **Reduced Impact Logging** (the use of several approaches to reduce damage to non-target trees and operational risks in timber extraction) apparently does not affect it (Ribeiro & Freitas, 2012). The understory fauna is usually more affected by changes in forest structure because it changes microclimatic conditions due to the increase of sunlight in the forest ground, reducing humidity and raising temperature. Another important consequence of those changes in forest structure affecting butterflies is the increase of pioneer plants and the reduction of some shadow love plants that modify the availability of host plant for butterfly larvae with consequent changes in butterfly assemblage composition.

In the opposite situation, forested habitats are mostly or completely converted in open habitats, as is the case of annual crops (e.g. corn, wheat (*Triticum* spp L.), and soybean) and even perennial cultures (e.g. coffee, *Coffea arabica* L.). In these now highly fragmented landscapes, conditions inside the small forest remnants can be usually far from ideal to harbor viable populations of forest specialists or species with poor dispersal abilities (Hanski, 1999; Steffan-Dewenter & Tscharnke, 2000). Accordingly, a recent study in a fragmented landscape in the Atlantic forest in Alfenas region, Minas Gerais State (southeastern Brazil) found a significant relationship between the degree of isolation of forest fragments, the shape of the fragment and the percentage of surrounding matrix with the functional composition of fruit-feeding butterfly assemblages. Surveys were conducted in nine sites containing forest fragments of semi-deciduous seasonal Atlantic rainforest and adjacent matrices of pastures and plantations of coffee and sugarcane. This study showed that abundance of butterflies in both habitats was equivalent; species composition however differed significantly between the forest fragments and the surrounding matrix. Species richness however was higher in forest fragments (based on rarefaction analysis).

The above results suggest that both richness and abundance of fruit-feeding butterflies can be predicted by the landscape structure of the study site (Tab. 12.1). Richness and abundance of forest species had a positive relationship with the proximity and size of surrounding forest fragments, while species that may exploit the matrix were particularly sensitive to the shape of the forest fragment and the percentage of surrounding matrix. Additionally, the species favored by more intensive agriculture in this study were typically mobile users or have grasses as host plants (Devries, 1987). It seems that generalists without habitat preference are able to compensate for a loss of their natural forest habitat by moving into the agricultural matrix. In contrast, forest specialists are less likely to move across adjacent forest fragments, therefore, the positive relationship between forest specialists and isolation may reflect their limited dispersal ability.

Tab. 12.1: Effect of the landscape structure on the richness and abundance of the ecological groups of fruit-feeding butterflies in a fragmented landscape in Southeastern Brazil. Values inside parentheses indicate the regression coefficients of the valid general linear models (Brito et al., 2014).

Ecological Groups	Factors affecting abundance		
<i>Forest specialists</i>	PROX (5.517)		
Matrix specialists	Sugarcane (1.746)	Pastures (5.167)	AWM (666.7)
Generalists	Pastures (1.667)	Coffee (0.443)	
Total forests assemblage	PROX (14.13)		
Total matrix assemblage	Pastures (7.323)	AWM (939.0)	Natural Cover (-1.915)
<i>Generalists</i>	NNA (8.206)	Pastures (0.646)	
Total forests assemblage	PROX (3.186)		
Total matrix assemblage	AWM (170.1)	Pastures (1.403)	

Natural cover = percentage of natural forest; Coffee = percentage of coffee plantations; Sugarcane = percentage of sugarcane plantations; Pastures = percentage of pastures; NNA = Nearest Neighbor Area (ha); PROX = Proximity index; AWM = forest fragment shape complexity

Microhabitat generalist insects have been shown to have more mobility among forest fragments than habitat specialists (Rosch et al., 2013), and responses to isolation could differ between matrix-tolerant species and forest specialists. Therefore, for butterflies, tolerance to the matrix may be an important criterion to predict species occurrence on fragmented landscapes. In addition, the availability of resources in the matrix is a key factor determining the presence of fragment-dependent species in fragmented landscapes (e.g. Jokimaki & Huhta, 1996)

The connectivity between fragments is an important feature of the landscape to specialist species. Therefore maintaining the connectivity among forests fragments is important for the conservation of forest specialists, and modifying the matrix in order to increase its permeability to dispersing butterflies may be an easier approach to restore connectivity than creating/restoring ecological corridors (Ricketts, 2001). For the conservation and maintenance of biodiversity management recommendations should take into account the characteristics of the ecological groups and not only focus on all of the species. To do this, it is important to understand which local and landscape factors are necessary for the conservation of habitat specialists.

12.4 Management of Agricultural Systems and Biodiversity

As previously stated, fruit feeding butterfly assemblages are affected not only by modifications in their habitats but also by what happens in the surrounding landscape (Ribeiro et al., 2012). The way butterflies use landscape is probably affected by their mobility, with more vagile butterflies exploring bigger areas than more resident species. This vagility is correlated with some species traits, like size, and long distance dispersal is very rare even in naturally fragmented landscapes (Marini-Filho & Martins, 2010). Thus, changes in the immediate vicinity vegetation (within a radius of 100-200 m) are more prone to affect local butterfly assemblages than modifications occurring in larger scales (1000-2000 m) (Ribeiro et al., 2012).

These effects are usually noted in the abundance and not in richness, and have been shown to be taxon dependent. Accordingly, for some butterfly groups whose larvae feeds mainly on monocots, the proportion of pasture lands on 100 and 200 m of radius are the most important landscape features explaining their abundances (Ribeiro et al., 2012), possibly reflecting the availability of adult and larval resources in these areas of contact between forests and pastures. Conversely, other butterfly groups showed more ambiguous responses to vegetation cover, and could probably respond to other landscape features not measured in that study.

The use of pesticides and transgenic cultures in the surrounding landscapes are also deleterious for butterflies but data about the extension of this damage are still absent. As a general pattern, we could suggest that more intensely managed landscapes have a greater potential to affect fruit-feeding butterflies assemblages than less intense ones.

12.5 Final Considerations and Future Directions

As aforementioned, though being one of the largest agrarian countries in the world, there is a general lack of information about biological diversity in agrarian systems in Brazil, and also about the effects of farmland management on its neighboring habitats. Regarding Lepidoptera, this gap is even greater, and most of the available information consists of preliminary lists of species for some few agricultural areas, published as abstracts in scientific meetings, preventing any kind of broader comparative studies.

Contrariwise, two lines of research have contributed considerably to bridge this gap: 1) Detailed studies on the genetic diversity of lepidopteran pests in agricultural habitats have increased our knowledge of how different types of agricultural management can affect many aspects of the populations of these pest species, and 2) concerning forested habitats, a growing body of information has served as the basis for an initial understanding of the main effects of different types of disturbance in the composition of local butterfly assemblages. In this chapter, we present recent

results of these two lines of research in Brazil as an initial attempt to reconcile two approaches that have been separate for many years.

Even so, studies focusing on lepidopteran biodiversity in agrarian systems are needed in Brazil, and the following research themes are considered priorities:

1. Basic inventories in different kind of agroecosystems in all Brazilian biomes, with publication of lists of species (qualitative and/or quantitative), which will serve as basis for future studies;
2. Comparative studies of lepidopteran assemblages in different agricultural habitats with different crops and/or management systems (including organic farming);
3. Studies focusing on the influence of the agricultural matrix on the taxonomic and genetic composition of lepidopteran assemblages in areas adjacent to the agricultural habitats;
4. Long-term monitoring (of both populations, assemblages and/or genetic diversity) of Lepidoptera in agricultural habitats;
5. Based on the above information, promote management strategies, which would match production and conservation of biodiversity in tropical agroecosystems, the “conservation agriculture” (see FAO CA web site: <http://www.fao.org/ag/ca/1a.html>).

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