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**Pavla Halamová**

Changes of biodiversity and composition of insect communities during  
restoration of tropical environments

Změny biodiverzity a složení společenstev hmyzu při obnově tropických  
ekosystémů

Bachelor Thesis

Supervisor: RNDr. Robert Tropek, Ph.D

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## **Prohlášení**

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, 25.07.2017

Pavla Halamová

## **Abstract in English**

Tropical rainforests are the richest habitats, but most endangered habitats on the world as well. Given the current global trend of deforestation, successful restoration of secondary forests is necessary for maintaining the rich fauna and flora of tropical rainforests. Insects are the most diverse group of animals in the tropics and they have crucial roles in an ecosystem functioning. Restoration interventions in degraded forests are nowadays more common and case studies are involving insect communities, however no review of them has been conducted. The aim of this thesis was to summarize the results of hitherto published studies dealing with the insect responses to the restoration of the tropical rainforests. With the emphasis on logged forests and lands converted for agriculture, the insect species richness, abundance, diversity, and the changes of composition were studied. If ecological conditions are suitable, insect species richness, abundance, diversity, and similarity of composition tend to increase towards primary forests for majority of insect groups. However, we observe some differences across groups of insects, based on the type and severity of disturbance, and on specific conditions on the site.

**Keywords:** insect recovery, tropical rainforest, disturbance, species diversity, assemblage

**Abstrakt v češtině:**

Tropické deštné lesy jsou nejbohatším, ale zároveň nejohroženějším biotopem světa. Současná míra odlesňování činí úspěšnou obnovu degradovaných lesů nezbytnou k zachování bohaté fauny a flóry, která je pro tropy vlastní. Hmyz je nejrozmanitější skupinou tropů a je nepostradatelný v mnoha ekologických procesech. Čím dál častěji bývá hmyz cílem studií zaměřující se na změnu jejich společenstev při obnově tropického lesa, avšak doposud nebyla vytvořena žádná review zabývající se touto tematikou. Cílem této bakalářské práce je shrnout výsledky z dosavadních studií s důrazem na území degradována těžbou dřeva či zemědělskou činností. Druhá bohatost, početnost, diverzita hmyzu stoupala za vhodných podmínek směrem k hodnotám pozorovaným v primárním nenarušeném lese. Složení hmyzích společenstev se s časem proměňovalo a čím dál více se podobalo původním společenstvím. Bylo pozorováno ale i několik odchylek závisící na cílové skupině hmyzu, podmínkách dané lokality a síle a typu disturbance.

**Klíčová slova:** obnova hmyzu, tropický deštný les, disturbance, druhová diverzita, druhové složení

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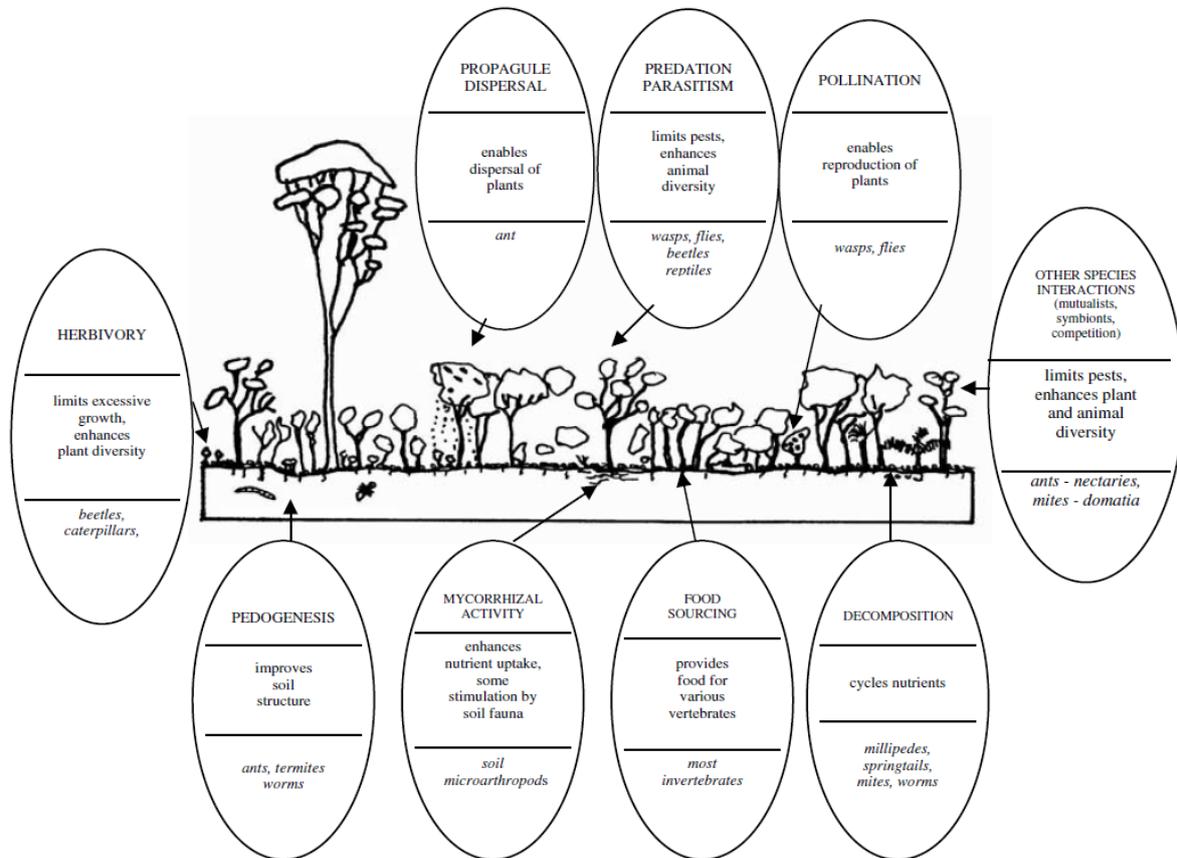
# 1 Introduction

Tropical environments, especially tropical rainforests, harbour an incredible variety of organisms. Many hotspots of biodiversity lay within the tropics, showing how plants and vertebrates are diverse in those habitats (Myers et al., 2000). In addition, the co-evolution of insect and plants is strongly developed. It has been estimated that every plant species has a least one species of insect that feeds on it (Grimaldi and Engel, 2005), so the biodiversity of insects most likely follows the trend of plant biodiversity.

However, tropical forests are facing strong pressure from human driven disturbances. FAO (2010) reported an annual loss of 5.2 million hectares of forest between 2000 and 2010. Fragmentation and clearing of forests caused by logging, change of the land for agricultural purposes - plantations, farmlands and pastures are among the main dangers (Geist and Lambin, 2002). After some time, these disturbed plots are abandoned and usually left for spontaneous development (natural regeneration). Although active approaches to the restoration of tropical forests are still rather rare, applications of such approaches are growing and the area of the secondary forest is increasing (Chazdon, 2008; Lamb et al., 2005). Efficient restoration of tropical forest should support the entire complexity of the environment. To ensure this, the area's surroundings and past usage must be considered (Holl, 2007). The direction of restoration will depend greatly on the availability of the sources on the site and on colonization from outside (Holl, 2013). Nevertheless, effects of restoration are typically documented for vascular plants while vertebrates and other groups of organisms are presumably neglected.

Insects create one of the most important components of many tropical forests (Fittkau and Klinge, 1973). Today estimates of insect diversity suggest between 4 to 6 million species of insects worldwide (Chapman, 2009) and there are more insect species in the tropics than anywhere else as shown with swallowtail butterflies (Condamine et al., 2012) as well as ants (Dunn et al., 2009). Consequently, insects often play crucial roles in many ecological relationships and processes and some groups are even considered ecosystem engineers (Speight et al., 2009). Insects are major pollinators (Grimaldi and Engel, 2005), especially in humid tropics where wind pollination is ineffective (Price et al., 2011). They are also crucial predators, herbivores and dispersal vectors of seeds of many plant species (Miller, 1993) and important as a food resource for many taxa (DeFoliart, 1989; Noyce et al., 1997). Furthermore, they are crucial decomposers, dung buriers and pest controllers (Speight et al., 2009). To accomplish

successful restoration, ecosystem processes must be re-established and very often that could not be possible without the insects.



**Fig. 1:** Ecosystem processes that are needed to re-establish on degraded land and indications of typical organisms involved (Majer et al., 2002).

The aim of the thesis is to summarize available knowledge from hitherto published studies about restoration of insect communities in degraded tropical forests worldwide. This knowledge is fundamental for optimisation of any restoration and conservation efforts. Two main human driven threats to tropical forest – logging and agricultural activities – were chosen as other disturbances have not been sufficiently studied yet. To get better perspective of insect behaviour during the succession and restoration I will cover how insect communities change in the respond to the habitat degradation too. Main questions are: 1) How insect changes its species richness, abundances, diversity, and assemblages in response to disturbance and then following restoration? 2) What factors have an impact on insect restoration? 3) How long does it take to achieve at least similar levels of insect species richness, abundances, diversity, and assemblages after a disturbance?

## 2 Threats to tropical forests

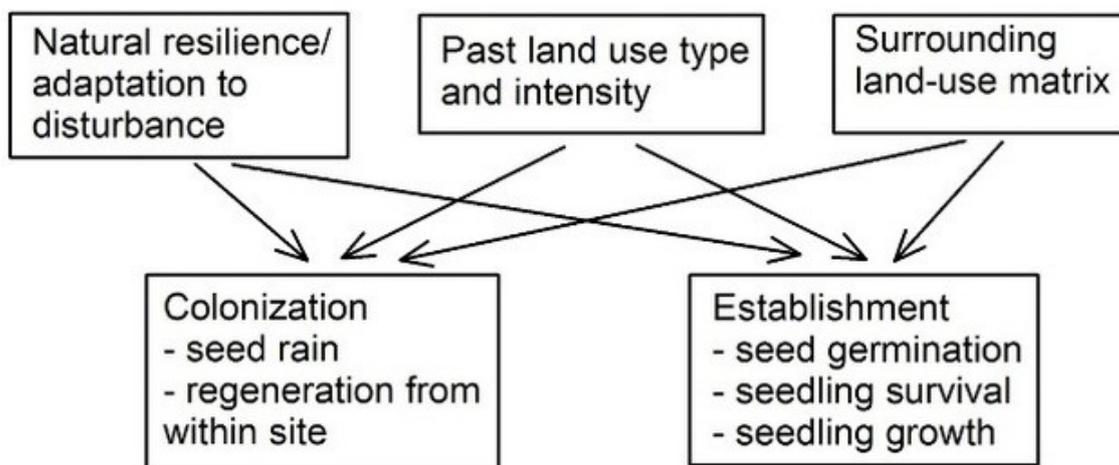
Tropical rainforests are forests that lay within the tropics of Cancer and Capricorn. They have high stable temperatures, where the coldest month has a mean temperature around 18 °C (except mountainous areas), and high precipitation all 12 months (mean of at least 60 mm) (Whitmore, 1990). Vegetation of rainforests is composed of several layers, where high trees create a connected tree canopy, hence limit sunlight for the vegetation layer beneath the canopy (Parker, 1995). Tall trees in tropical rainforests have shallow roots and are very vulnerable to strong tropical winds. Winds blow down the trees, often connected to the others by many woody vines creating gaps in the canopy, which causes removal of dominant species and establishes a new habitat for pioneer species (Primack and Corlett, 2005). Tropics have higher carrying capacity, higher speciation rates together with the lower extinction rates and they are older than many other environments. Consequently, tropics harbour high diversity of floral and faunal species (Mittelbach et al., 2007).

Human activities has been damaging to the tropical forest and the trend repurposing the land is nothing new – agriculture in tropical areas could be considered extensive even before European colonization (Hecht et al., 2006). As long as people inhabit tropical areas, they will exploit the forest for wood, space for agriculture and for creation of settlements too. Human driven threats (e.g. logging, clearance for agriculture, mining) have developed rapidly in recent decades together with the growing population (Primack and Corlett, 2005).

Every forest region has slightly distinct disturbances. West African forests are the ones most fragmented (Minnemeyer, 2002) due to the high density of people and high poverty, causing herding and driving the use of land for agriculture (Primack and Corlett, 2005). Asian forests are under immense pressure from commercial logging (Laurance, 2000), and they have the highest rate of deforestation of all tropic areas (Laurance, 2007). For example, in some parts of Borneo up to 39.5% forests have been deforested through 2010 (Gaveau et al., 2014). Deforestation is not only caused by commercial logging, but also by planting of cash crops and timber (Bawa and Dayanandan, 1997). The most common cash crops are rubber, cocoa and oil palm. Because of these pressures, the number of forest butterflies has decreased by 83% compared to the primary forest (Koh and Wilcove, 2008). The Amazonian region has the lowest population density of humans (Times Books, 1994) and besides logging, there is tremendous pressure to convert land for agriculture, with the most common use being cattle pastures (Laurance et al., 2001). Kinds of crops are planted according to their current value on the global

market on unsuitable soils, unsuitable management practices, such as using more cattle than the productive capacity of the land can carry, are used (Hobbs and Cramer, 2007). This results in lower soil fertility, increased risk of erosion, higher probability of outbreaks of inedible plants for cattle, and usually a decline in the limiting nutrient phosphorus. Therefore, to sustain agriculture on such lands, expensive fertilization or other heavy practices are needed. In the tropics especially, farmers cannot afford this, and so the land is simply abandoned.

All these threats create different barriers to recovery. Physical environment is another major thing which differs in disturbed areas. Hydrological processes are damaged, the probability of erosion is higher and the micro-environment is changed (humidity, sunlight, temperature, wind) (Whisenant, 2002). A second group of barriers includes biotic factors e.g. colonization by invasive plants (such as pasture grasses on abandoned farmland), increased level of predation on seeds or seedlings and damaged or destroyed sources of seeds (seed bank, seed rain or resprouting of remaining vegetation or dispersal ability of seeds) (Holl, 2002).



**Fig. 2:** Factors affecting recovery of tropical forest in formerly disturbed lands (Holl, 2013).

The scale and impact of these factors can vary greatly from site to site and are mostly dependent on past land use, intensity of disturbance, and the nature of the vegetation (Holl, 2007). Therefore, this review is organised according to the past land use to the chapters about the restoration of forest and its insect communities following logging and agriculture activities, the two main threats to tropical forests.

### 3 Succession of tropical rainforests and its communities

Forest succession is a colonization and gradual change of floral and faunal species in an ecosystem. Primary succession occurs when new substrates such as lava are introduced (Whittaker et al., 1989). Secondary succession begins after a disturbance reduces an already existing ecosystem (Horn, 1974). The dynamics of secondary succession in tropical rainforests is explained by the formation of gaps. Gaps in the canopy usually account for 1% of forest area, representing approximately 100 years of turnover of trees (Kellner et al., 2009). They provide suitable conditions for plant growth (e.g. no or lower competition of existing plants and higher level of light) (Schnitzer and Carson, 2001). Plants in tropical rainforests have to trade-off between survival in the shade or growth in the gaps. This indicates there must be certain species oriented towards disturbances and others avoiding them (Wright, 2002). Two categories of trees are defined: pioneer species, which take advantage of newly formed gaps and primary species – shade tolerant species of late – climax stages (Swaine and Whitmore, 1988). Pioneer species grow fast and create a budding secondary forest. They also form a patchy canopy, causing an unpleasant environment for slower growing plants and for shade-intolerant species (Chazdon et al., 2005). With time, pioneer species are starting to be replaced by long-living primary forest species. Species of primary forests form vertical zonation in the tree canopy which is hardly light permeable. This favours shade-tolerant species (LaFrankie et al., 2006). The climax, the last stage of the succession, is currently seen as a dynamic stage with continuous small-scale processes of disturbances and regeneration, rather than a stable and non-changeable community (Berry et al., 2010; Kellner et al., 2009). In tropical rainforests, this succession is to be faster compared to temperate forests, mainly because of the higher humidity and decomposition (Ewel, 1980).

Not only does composition of plants change during the succession. With the turnover of tree species, the chemical composition and structure of their leaves and litterfall change, and, therefore, the composition of all organisms will be affected (Burghouts et al., 1992; McKey et al., 1978).

After a disturbance, animal species try to recolonize the biotope which, if successful at all, can take several decades, in some cases even hundreds of years, if it is successful at all (Sáfián et al., 2011). The severity and kind of disturbance strongly influences which pathway succession takes and which faunal species will establish in the forest (Majer et al., 2002; Mesquita et al., 2001). During recolonization, turnover of the insect species is common and many taxa occur

only at certain stages of succession (Dunn, 2004; King et al., 1998). It is important to realize that even if the species richness stagnates along a succession gradient, the species composition will be distinct if the succession is ongoing (Itioka et al., 2015). Achieving a comparable insect species composition to the primary forest, takes substantially longer than a simple recovery of the number of species (which may take around 20 to 40 years) (Dunn, 2004). Hence species richness alone is not a good parameter of a successful recovery of the forest as in the early stages, insects species of mature forests will not be present due to the lack of suitable biotypes.

The response of insects to succession is intrinsically linked to the vegetation. General studies of insects-plants relationships during succession reveal that with the time and changes in plant forms, habitat permanence, habitat complexity and resource diversity/availability increase and insects show particular responses (Brown, 1985). Taking a group of Hymenoptera, for example it was explored how generation time was modified. With ongoing succession, a significant decrease in the number of species with more than 1 generation per year was observed. An identical response was observed for exopterygote herbivores (Brown and Southwood, 1983). Hymenoptera also developed more fully winged species in the early stages of succession, which indicates good migration ability (Brown, 1985). Furthermore, the niche specialization has been studied in weevils and Hymenopterans. The number of generalist phytophagous species declined, while the specialists to a single genus increased during succession (Brown, 1982a; Hyman, 1983). Diversity of Hymenoptera in body shape and size also increased with time since disturbance (Brown, 1982b).

Interactions between insects and plants are very complex (Brown, 1985). When colonization by insects starts, it tends to cause a rapid increase in species richness for few years after a disturbance following the greater growth of plants (Brown, 1985; Itioka et al., 2015). It is, however, substantially slowed down during the subsequent decades as was shown with the example of butterflies in Borneo (Itioka et al., 2015). This could be linked to the increasing protection of plants against herbivores and the decreasing level of nitrogen in plant tissues with the increasing age of the plant (Coley and Barone, 1996). This results in lower resource availability. Grazing insects affect plants in many ways: a comparative study of the early stages of succession showed that insect-free plots had greater vegetation cover compared to those under impact of herbivores (Stinson, 1983). In the tropics, even the top predators greatly influence the species richness and composition of plants greatly. The vegetation structure is modified from the peak of the trophic levels from the top predators through the ants and herbivores (Letourneau et al., 2004).

Succession is used as a restoration tool for the manipulation of the biotope (Walker et al., 2007). The goal of a successful restoration is to recreate the structure and the function of the ecosystem, while frequently hastening the natural succession (Luken, 1990). Ecological restoration can be accomplished by an unassisted succession, but if harsh disturbances preceded, the more intensive approaches of restoration are needed (Prach et al., 2007).

#### 4 Restoration of tropical rainforests and its insect communities

Restoration is ‘the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed’ (SER 2004). Restoration differs from conservation; as conservation tries to preserve degradation, restoration tries to reverse it (Macdonald et al., 2002). In general, the main goal of restoration is to establish independent and self-sustaining populations (Griffith et al., 1989) of not just plants, but faunal species too (Horwitz et al., 1999). However, it begins with vegetation because plants significantly modify the micro-environment (Whisenant, 2002), and animal species need the correct habitat to create viable populations (Gilpin and Soulé, 1986).

Insects have many crucial roles in ecosystems, and any restoration should try to restore both the role and diversity of insect populations to ensure good ecosystem functioning (Majer et al., 2002). Even during restoration, insects alter the soil structure by building cavities, burying organic material and enriching the soil with nutrients (Abbott, 1989). Insect herbivores can suppress dominant species of plants and therefore increase the diversity of vegetation (Letourneau et al., 2004). Due important relationships that have to be restored are plant-pollinator interactions. These relationships are very vulnerable to disturbances (Kearns and Inouye, 1997), and have to be renewed to achieve a self-sustaining ecosystem (Majer et al., 2002).

With the increasing degradation of the rainforests, the interest in restoration started to develop two decades ago (Holl and Kappelle, 1999; Parrotta et al., 1997). As the tropical rainforests are seen as important to maintain high levels of biodiversity (Gibson et al., 2011) and as the major carbon stocks worldwide (Gibbs et al., 2007), many scientists together with the public accepted restoration of tropical rainforest as a step towards saving their future (Chazdon, 2013). There are no accurate estimates so far, but approximately 2 billion hectares of forest worldwide have been marked as a possible target of restoration efforts (Laestadius et al., 2011). An increasing interest in rainforest restoration has been confirmed in Bonn Challenge (2016), where twenty-

four countries that laying within the tropics and having some rainforests committed to restore approximately 78 million of hectares of tropical rainforest.

All restoration efforts must overcome barriers of succession. The key step is removing the existing stress (e.g. logging, grazing, ...), followed by allowing a natural regeneration (Holl, 2002). If the disturbances have not been intense, degraded lands can achieve similar levels of biomass of plant species as an intact forest within 15 to 60 years (Aide et al., 2000; Finegan and Delgado, 2000). However, the speed of forest recovery decreases with the higher intensity of stress (Aide et al., 1995; Uhl et al., 1988) and human interventions to overcome barriers that slow down the succession are necessary on more damaged lands (Holl, 2002).

Possibly the biggest challenges of restoration of disturbed environments are the very likely destroyed seed bank and limited seed dispersal (Holl and Kappelle, 1999). Seed banks of indigenous species can be easily destroyed by agricultural activities or by heavy machinery while timber harvesting, and many climax species of tropical forests often do not have dormancy. Hence they cannot create a seed bank (Vieira and Scariot, 2006). Animal seed dispersals also tend to avoid more open areas – clear-cuts, pastures, and very disrupted tree canopies. Since majority of seeds in the tropics are dispersed by animals (Howe and Smallwood, 1982), the absence of dispersals creates another barrier (Janzen and Vázquez-Yanes, 1991). Moreover, if the goal of restoration is original species composition of both vegetation and insects, natural regeneration without any intervention is unable to establish it (Parrotta, 1995).

One of the other conditions of natural restoration is availability of nutrients in the soil. Seeds need a suitable environment to germinate and to establish seedling. Soil erosion and compaction results in lower fertility of the soil, and together with higher temperature and lower humidity due to the of tree cover, the conditions move further away from the optimal for tree species (Zimmerman et al., 2007). The establishment of tree seedling can also be prevented by a competition from existing vegetation – often grasses and weeds such as *Imperata* (Lamb et al., 2005; Otsamo, 2000).

Insects can be a major barrier to restoration as well. Their predation on seeds and seedlings, such as leaf cutting ants, can cause the restoration to fail (Nepstad et al., 1991). The size of this effect depends on the density and abundance of herbivores, where higher rates can cause a total failure in the restoration of the forest (Vasconcelos and Cherrett, 1997). However, the predation can be reduced by the growth of pioneer species (Ganade, 2007).

If any of this take place or if the recovery speed is too slow, the natural regeneration can be enhanced by assisted natural regeneration (Dugan et al., 2003; Shono et al., 2007). Among the key approaches of assisted natural regeneration are: enrichment planting and seeding of indigenous tree species, controlled fires, suppression of growth of grass species (Holl, 2002; Otsamo, 2000). Assisted natural regeneration is a good approach, especially when the goal of restoration is restored biodiversity and species composition (Lamb et al., 2005). When the quality of habitat is being improved with restoration (directed towards the primary type of biotope), it allows indigenous insect species to colonize the habitat once again.

While plants can be easily introduced to the degraded land, invertebrates have highly specific ecological niches – the introduction of invertebrates may not be enough on its own (Majer et al., 2002). When the quality of habitat is being improved with the restoration of vegetation (directed towards the primary type of biotope), it allows indigenous insect species to colonize the habitat once again. It was found that the species richness, abundance, and diversity of insects can increase significantly, resembling the primary forest by using tools of assisted natural regeneration such as planting. These results have been found in the tropical communities of butterflies (Nyafwono et al., 2014), but also on arthropods in subtropical Australia (Nakamura et al., 2003). Nevertheless, there were no significant changes in those three factors on plots where the land has been led to natural non-assisted regeneration (Neves et al., 2010a). As mentioned above, natural regeneration tends to be slower and it is very likely that the increase of insect species richness, abundance and diversity have not occurred yet.

## 5 Logging and its impact on the tropical rainforest

There is no doubt that timber harvesting within tropical rainforests stands as a one of the major causes of deforestation in the tropical environment. Wood and its export account for 30% of international trade in developing countries (Myers, 1996) and in the 1990s, six million of hectares of tropical forests were every year (Laurance and Bierregaard, 1997). Moreover, there are two to forty trees logged on every hectare, but up to 40% of the surrounding forest is damaged or destroyed during harvesting operations (Verissimo et al., 1992). Even though, no exact estimations of the rate of logging have been made, there is a visible upward trend (Montagnini and Jordan, 2005).

The desire for a highly valuable forest with many commercial trees per logging cycle created silviculture, a manipulation of biological principles towards higher value to humans (Whitmore, 1990). Silviculture creates different timber harvesting approaches and the direct effect of

logging on the forest communities is affected by it. The two basic categories are clearing systems and natural regeneration systems (Montagnini and Jordan, 2005). Clearing systems are approaches in which all the trees are cut down, not just the ones with commercial value (Johns, 1997). The low rate of regrowth of desired trees and long-rotation times mean that nowadays those systems are being abandoned in favour of systems that use natural regeneration (Montagnini and Jordan, 2005). The second category contains two major approaches: monocyclic and polycyclic methods (Whitmore, 1990). During monocyclic logging all potentially profitable trees of suitable size are logged in a single operation (Sabogal and Nasi, 2005), followed by practices like cutting the vines or lianas regularly until the forest is logged again in 70 years, after the trees have matured (Montagnini and Jordan, 2005; Sabogal and Nasi, 2005). The monocyclic method was designed for forests which are rich in valuable trees and have fertile soils – e.g. dipterocarp forests in southeast Asia (Montagnini and Jordan, 2005). Thanks to the high density of logged trees, the forest canopy is very disconnected and unintentional damage of a monocyclic system can reach up to 40 or 60% (Sabogal and Nasi, 2005). Because of the long cycle of logging, the selective polycyclic method was created (Montagnini and Jordan, 2005).

Polycyclic logging systems try to reduce any human restoration interventions to the minimum in order to be as cost-effective as possible. Profitable trees are harvested in more cycles where only certain amounts of trees can be logged per hectare (Johns, 1997; Whitmore, 1990). Felling cycles are relatively short compared to the monocyclic, around twenty to thirty years. Thanks to the limits of trees per hectare, it is a less drastic approach than a one-time harvest, but the polycyclic system results in high amounts of extracted wood (Montagnini and Jordan, 2005) with small but widely spread gaps in the canopy (Whitmore, 1990).

With the higher awareness of logging as a threat to the tropical rainforest, an alternative approach has been designed – reduce-impact logging (RIL). RIL is an attempt to reduce the environmental impacts of timber harvesting using pre-harvest planning, mapping of suitable trees, controlling felling trees, mitigating the damage to the surrounding vegetation during logging along with post-harvesting evaluations of the log intervention (Putz et al., 2008).

Systems which use natural regeneration, however, often do not consider the crucial role of fauna and biodiversity (Bennett, 2000). Nevertheless, the loss of invertebrate communities and their roles in ecosystem could be the key to success (Ghazoul and Hill, 2001); hence, it is important to conduct studies on them.

## 5.1 Responses of insect to the logging

Insects in the tropical rainforests follow vegetation as they form clear vertical stratification of various communities, creating two basic strata – the canopy and the understory (Barlow et al., 2007a; Dumbrell and Hill, 2005; Ribeiro and Freitas, 2012). Assemblage of insects in those layers is very distinctive depending on the optimum level of light for certain species (Dumbrell and Hill, 2005; Fermon et al., 2003). During selective logging, this stratification is damaged and this can result in the loss of primary canopy species as it was shown with the composition of butterflies (Dumbrell and Hill, 2005; Ribeiro and Freitas, 2012; Shahabuddin et al., 2005a; Spitzer et al., 1997). Butterfly communities in the canopy have higher species richness and lower abundance than the communities of the understory (Ribeiro and Freitas, 2012) and the closed canopy is inhabited by species with narrower geographical distribution (Hamer et al., 2003; Spitzer et al., 1997). With the openness of the canopy caused by selective logging, species with the shade preference differ most in their composition compared to the unlogged forest (Hamer et al., 2003). Canopy species should be more tolerable to light and higher levels of temperatures of the newly formed gaps (Ribeiro and Freitas, 2012), which means they can inhabit lower strata in the gap, whereas understory species cannot survive there (Spitzer et al., 1997). That increases the similarity of the understory and canopy layers in a logged forest (Wood and Gillman, 1998). Not only is light the crucial factor, also vegetation as a food resource – increased growth of pioneer plant species and some shade tolerant plants subsequently changes the assemblages of insects which are dependent on it (Ribeiro and Freitas, 2012).

In the terms of overall forest parameters, logged and unlogged forests will most likely vary in their insect species richness (Ghazoul, 2002). Many studies show a higher species richness of butterflies in disturbed logged forest than in a primary one (Bobo et al., 2006; Ghazoul, 2002; Gunawardene et al., 2010; Hill et al., 1995). This effect is possibly caused by an invasion of a large number of generalists and species with wide geographical distributions (Ghazoul, 2002; Hamer et al., 2003). Growing species richness has been observed on ground-living ants too (Gunawardene et al., 2010; Kalif et al., 2001). Richness of ant species increases with higher structural heterogeneity of the habitat (Ribas and Schoereder, 2007) caused by logging created gaps in the canopy (Johns, 1997).

Even though some studies noted lower diversity of butterflies in a logged forest (Dumbrell and Hill, 2005), it does not have to be that way. However, the majority of butterfly species who are

abundant in logged forest are generalists (Hamer et al., 1997) which results in a lowered number of specialists – the opposite what typical for tropical rainforests (Ghazoul, 2002). These changes in compositions are the major distinction between an unlogged and a logged forest. The number of specialist species of butterflies declines with logging (Hill et al., 1995), because they cannot live in more heterogeneous habitat since they are able to tolerate a small range of environments (Spitzer et al., 1997). A similar situation can be found on the ground. What changes mainly among ground-living ants is abundance of different species. The majority of ant species found in the primary forest have been observed in logged forests too (Vasconcelos et al., 2000). However, there have been more dominant species, while in unlogged forests dominant species were absent (King et al., 1998). However, there is some species turnover, in which native ants are replaced by more tolerable species (Gunawardene et al., 2010; Kalif et al., 2001). Dung beetles are also variable, but not as much as butterflies. Seventy percent of primary dung beetle species have were in the logged forest (Scheffler, 2005).

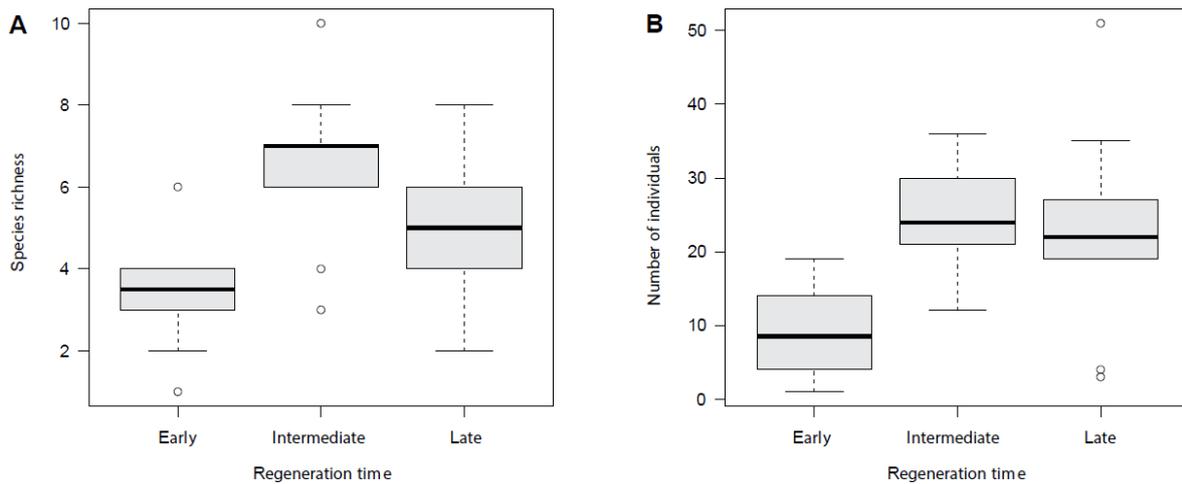
Insects, and all the changes in their communities mentioned above, directly or indirectly influence other animals in tropical rainforests. Insectivorous birds react to forest logging with the loss of abundance from 98% to 37% (Thiollay, 1997). This huge transformation causes an exclusion of insectivores which may result in increased plant damage by insect herbivores as birds are one of the predators who control the abundance of insects (Şekercioğlu et al., 2004). On the other hand, the loss of bird abundance can be a result of the lack of a suitable food, insects (Thiollay, 1997). Since many tropic insectivorous birds have shown food specialization (Canaday, 1996), any apparently small change in the insect composition can have a devastating effect on animals of higher trophic level. Insects are influenced by top-down effects too. The open structure of a logged forest results in easier hunting, which can lead to severe decline of many mammals. Decline of mammals has an impact on dependent species, such as dung beetles who use mammal dung as their main food resource and as protection for laid eggs (Nichols et al., 2009). This will surely have an impact on restoration of the whole habitat, as dung beetles contribute to the ecosystem functioning with their activity, e.g. nutrient cycling and secondary seed dispersal (Nichols et al., 2008). Up to two thirds of dung beetle species richness was lost with the decline in mammals (Andresen and Laurance, 2007). Lower food resource availability results in higher competition, followed by changes in species composition of beetles – generalists will become more dominant (Culot et al., 2013).

Even logged tropical forests can serve as refuge for certain forest species, hence they form an important source of species for biodiversity restoration and should be considered important for conservation and protection efforts (Berry et al., 2010).

## 5.2 Changes of insect communities during the logged forest restoration

With the ongoing succession after disturbances caused by logging, species richness of dung beetles appeared to recover from early successional habitats to the intermediate old habitats. Both species richness and abundance were lower than average on sites of early restoration (Fig 3). The growing abundance of insects can be explained by the tight relationship of abundance of species and increasing biomass of their host plants (Yamamoto et al., 2007). On the contrary, no significant connection of butterfly species richness on biomass of trees has been found (Valtonen et al., 2017). The different abundance between habitats of different recovery ages is most likely caused by the occurrence of rare (not numerous) species of insects. Most abundant species remain similar during the restoration (Bitencourt and da Silva, 2016).

The process of community recovery is independent from the changes to species richness and diversity (Valtonen et al., 2017). When studying leaf-litter and its arthropod communities, it has been observed that the abundance of species recovers faster than community composition in logged forests (Cole et al., 2016). For the recovery of community composition, habitat quality is the crucial factor (Barlow et al., 2007a). Surroundings appear less important, but its effect cannot be neglected. Good flyers, such as butterflies from genus *Charaxes* can migrate and disperse into surrounding suitable habitats, hence their presence or absence can influence the butterfly community (Shahabuddin and Terborgh, 1999). While restoring a logged forest, the community composition of insects is strongly related to the environmental factors and to the plant composition (Barlow et al., 2007a; Valtonen et al., 2017). The age of the forest, the connected canopy and how common gaps were accounted for 31,8% of the differences between communities of fruit feeding butterflies (Valtonen et al., 2017). In general, the community structure of arthropods and its variations in tropical rainforest are explained by plant compositions from 2 to 18% (Schaffers et al., 2008). The strong relationship between herbivorous insect communities and trees in a recovering logged forest can be explained

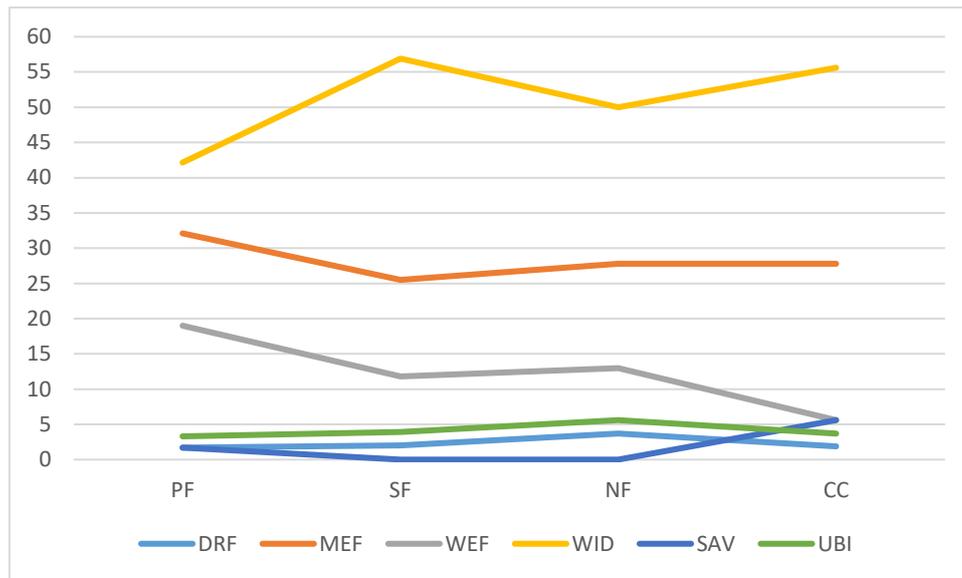


**Fig. 3:** Species richness and abundance of dung beetles along recovery gradient (Bitencourt and da Silva, 2016)

by the specialization of larval stages or even adults towards their host plants (Barlow et al., 2007a; Bonebrake et al., 2010; Valtonen et al., 2017) e.g. butterflies of genus *Euphaedra* had been found most nearby their host plants (larval host tree or adult feeding trees) (Valtonen et al., 2017). In Figure 4, the change of species and their ecological groups is visible on the restoration gradient of the disturbed logged forest.

In early stages of regeneration, soon after the disturbance, the species richness and abundance of insect species will be low compared to the primary forest (Bitencourt and da Silva, 2016; Sáfián et al., 2011). The composition of these stages will be most likely very different from the original insect assemblage. The difference depends the amount of harvested wood, since a sufficiently sized gap in the canopy can lead to the establishment of a new ecological group of insects (Sáfián et al., 2011). Soon after logging operations, a logged forest will still have high levels of leaf-litter and soil organic matter which can lead to distorted results, such as comparable species richness in early stages and primary forest (Gormley et al., 2007).

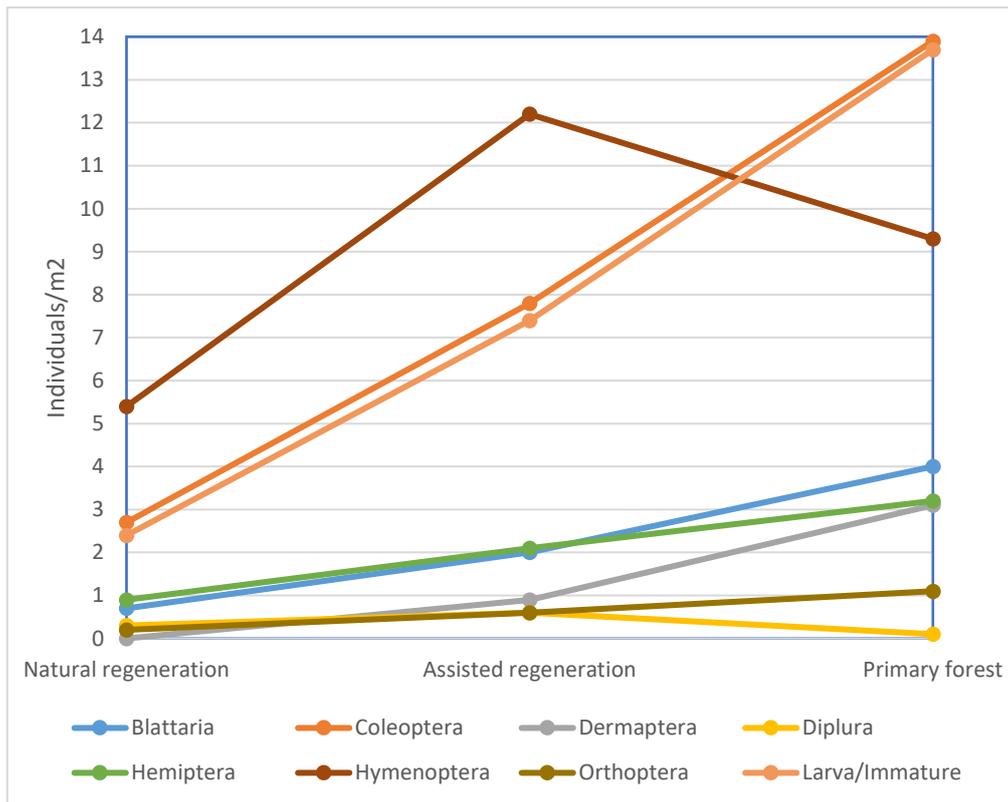
When the restoration proceeds to the intermediate stage, the insect species richness does not show any significant increase or decrease (Bitencourt and da Silva, 2016). Intermediate stages can harbour species of both habitats – disturbed logged forest and primary untouched forest (Bitencourt and da Silva, 2016; Neves et al., 2010b), and higher diversity is expected on intermediate recovery age as a result (Sant’Anna et al., 2014). Moreover, the evenness can reach its lowest in this stage [studied on dung beetles (Bitencourt and da Silva, 2016)], or very close to the lowest one in primary forest [studied on butterflies (Sáfián et al., 2011)].



**Fig. 4:** Proportion of butterfly species of different ecological categories in the habitats, simulating restoration of tropical rainforest after logging [axis x – PF primary forest, SF secondary forest (formerly logged, middle secondary growth), NF newly planted forest (logged, 9 years ago planted with indigenous trees), CC clear-cut area (1 year prior the sampling); DRF – dry forest species, MEF mesophilous forest species, WEF wet forest species, WID forest species with wide ecological tolerance, SAV savannah species, UBI ubiquitous species] (adapted from Sáfián et al. 2011)

Decreasing evenness is caused by the occurrence of more rare (low in abundance) species than in the early restoration plots (Sánchez-de-Jesús et al., 2016). To recognize whether the recovery is ongoing, species replacement must take place over time (Sant’Anna et al., 2014). Butterflies of genus *Charaxes* or genus *Bicyclus* should have decreasing abundance and species richness, as they are typical for low canopy habitats and thus their habitat is disturbed (Sáfián et al., 2011; Valtonen et al., 2017).

Later stages of recovery and their insect species are connected to the parameters of the primary forest – typically greater basal tree area, taller trees, a closed canopy and a higher amount of leaf-litter (Campos and Hernández, 2015). Lepidopteran genera *Euphaedra* and *Euriphene* appeared to be indicators of a successful restoration of a tropical rainforest after logging (Sáfián et al., 2011; Valtonen et al., 2017). Later stages have higher carrying capacity, they can harbour larger populations of insects and thus the abundance of species that belong to the primary forest is higher (Bitencourt and da Silva, 2016). While comparing assisted natural regeneration with regeneration without approaches or interventions, the human controlled one appeared to recover arthropod communities faster (Fig. 5).



**Fig. 5:** Abundance within *Insecta* orders for litter samples across habitats with a different restoration approach compared to the primary forest (Based on Cole et al. 2016)

When planting the trees, increased patchiness supported an arthropod community which resembled the primary forest (Holl et al., 2013). Some insect communities can regenerate in fifty to sixty years (Sáfián et al., 2011) but assisted natural regeneration may be crucial for the return of a logged forests and its communities to the primary forest levels as the differences have been visible even after 30 to 60 years from logging operations (Cole et al., 2016).

## 6 Agriculture in the tropics

Cultivating crops and raising cattle can be challenging in the tropics, mostly due to the soil. In the tropics, mostly oxisols and utisols occur. These are red, acidic soils low in nutrients (National Research Council, 1993). With the increasing intensity of agricultural practises, agriculture in tropics is becoming unsustainable, so farmlands are being abandoned and more of the forest area is being cut and damaged (Holl, 2007).

Shifting cultivation is the most common approach – up to 30% of world’s farmable land is under this practise (Andriessse and Schelhaas, 1987). However, it also causes most issues, as shifting practises account for 70% of the forest canopy clearing in Africa (Brown and Thomas, 1990). This method has been protecting efficient nutrient cycling, has been preventing soil

erosion and has regulated weed invasion (National Research Council, 1993). It starts by clearing a forest patch, followed by burning the remaining vegetation, planting and harvesting for a few years and then allowing the land to fallow. After that, the fallow vegetation is burned again (Christanty, 1986). However, those cycles are often broken with the intensification where fallow periods are shortened, which leads to the loss of fertility, overcoming of the plot by weeds and to the degradation of forest land (National Research Council, 1993). In such degraded areas the grasslands are established and used as pastures for cattle (Hobbs and Walker, 2007). However, thanks to the low fertility, grasses which can be used as a food resource for animals do not thrive, and the weed, which is inedible for cattle, can invade a pasture. This invasion is inevitably followed by the abandonment of the pasture thanks to the low productivity (National Research Council, 1993). To create a sustainable agriculture, agroforestry systems have been developed. Trees, herbs, valuable crops and animals are all on one plot improving the productivity while not completely destroying the forest (Nair, 1993).

## 6.1 Responses of insects to the agricultural activities

Animal taxa show small or large changes in response to the land conversion for agricultural purposes. However, in most of the cases, the change results in a decline in species richness (Lawton et al., 1998). On the gradient of forest degradation from intact forest to agroforestry-managed plots, from plantations to pastures, primary forests appeared to always be the richest in insect species, even though the agroforestry system can carry up to 75% of the original species richness (Shahabuddin et al., 2005b). This declining trend of species richness with the intermediate values in agroforestry managed habitats has been observed in dung beetles (Davis and Philips, 2005; Harvey et al., 2006; Shahabuddin et al., 2005b; Ueda et al., 2015), an Longhorn beetles (Meng et al., 2013). It is observed in ground living insects, but also in flying Hymenopterans (Ruiz-Guerra et al., 2013). Pasture seems to be the most changed and poorest habitat in most of the studies. It is possibly the result of increased mean temperature on the ground, which most of the forest insect species cannot handle (King et al., 1998).

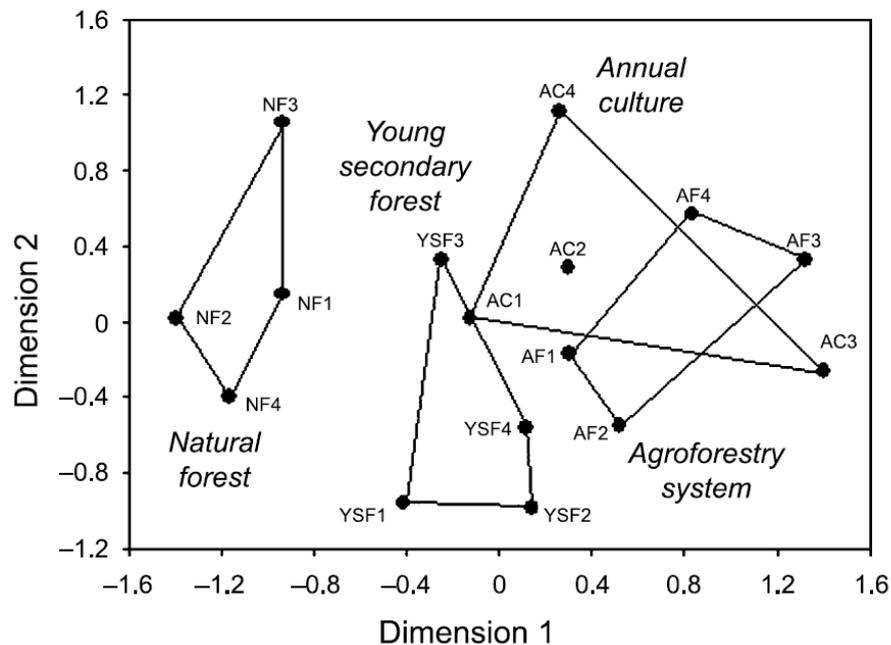
Species abundance does not have such a clear trend. In the agriculture habitats, abundance of dung beetle communities is usually higher than in a continuous primary forest. Certain species have been significantly more abundant in pastures or plantations (Davis and Philips, 2005; Harvey et al., 2006; Nichols et al., 2007), especially small dung beetles (Scheffler, 2005). A higher abundance of smaller dung beetle species can be caused by the presence of large mammals on a pasture where small species occurred to be mainly generalist and thus can reach

higher abundances (Hanski and Cambefort, 1991). High abundance of a few small bodied species of dung beetles leads to a lowered evenness of the community (Nichols et al., 2007). On the other hand, families *Ichneumonidae* or *Silphidae* have been observed to be most abundant in the primary forest (Ruiz-Guerra et al., 2013; Vulinec, 2002). Solitary bees were more abundant on converted land, while social bees declined in abundance and species richness. The higher abundance of solitary bees can be explained either by more available nesting plots on open land, or by exclusion of social bees and thus lower interspecific competition that allows for growth of solitary bee populations (Klein et al., 2002). Herbivorous butterflies and their abundance in plantations have also increased - homogenous plantations offer a food resource in a high density (Dall'Oglio et al., 2013).

Arthropod diversity showed a significant decrease after conversion (Perfecto et al., 1997). Hymenopterans displayed great diversity in an undisturbed forest (Ruiz-Guerra et al., 2013). Additionally dung beetles were diverse in the forest, but their diversity has been decreasing with the increasing intensity of agriculture practises (Davis and Philips, 2005; Harvey et al., 2006; Scheffler, 2005; Ueda et al., 2015). How huge the impact of the land conversion is on diversity differs due to the geographical and latitudinal location of habitats – dung beetles of low montane forest in Indonesia were shown to be quite resistant, with the forest habitats having higher 25% more compared to the arable lands, and most of the dung beetle species were able to endure in a wide range of habitats (Shahabuddin et al., 2005b). Another example of less than devastating impacts is the slightly lowered diversity of carrion beetles (Vulinec, 2002). Some groups of insects can even thrive on converted land. Most of the hawkmoth species in tropical regions are well adapted for surviving in a disturbed habitat and thus will remain diverse (Schulze and Fiedler, 2003). It appears that plantations can carry a high diversity of primary forest species, and thus it is not that big intervention to the diversity of insects. However, that is possible only for new plantations and with the time, monocultures cannot harbour most of the forest species in the long time scale (Meng et al., 2013).

While plantations can carry similar diversity for a while, the composition of insect communities will be eventually become distinct. Different assemblages of dung beetles have been studied again and a significant difference was shown (Barlow et al., 2007b; Davis and Philips, 2005; Gardner et al., 2008; Ueda et al., 2015). These results are also consistent with a study on communities of other ground dwelling beetles (Gormley et al., 2007). Ants on pastures showed differences too. There was up to a 55% increase in dominant or opportunistic species on

pastures in compared to the intact forest, while specialists were almost absent from disturbed the habitat (King et al., 1998).



**Fig. 6:** Similarity of dung beetle fauna on a two-dimensional scale in different habitats, the species of one habitat are connected by lines (Shahabuddin et al., 2005b).

The composition of butterflies differed by 64% in crop farmlands and primary forests (Bobo et al., 2006) and Ichneumonidae showed low similarity along habitats, too (Ruiz-Guerra et al., 2013). One interesting pattern is that species typical for mature forests have not been found or only rarely occurred in converted habitats, while indicator species of grasslands were commonly collected in agricultural land (Ueda et al., 2015). This suggests a higher similarity of converted land to grasslands than to intact forest.

Nevertheless, the arboreal ant community of the cocoa tree plantation was very similar to that of natural forest (da Conceição et al., 2015; Delabie et al., 2007) and agroforestry systems have been proven to establish suitable conditions for insect colonization by primary forest species, increasing the similarity of the composition to that at the intact forest (Harvey et al., 2006; Shahabuddin et al., 2005a; Ueda et al., 2015).

## 6.2 Changes of insect communities during the abandoned farm land restoration

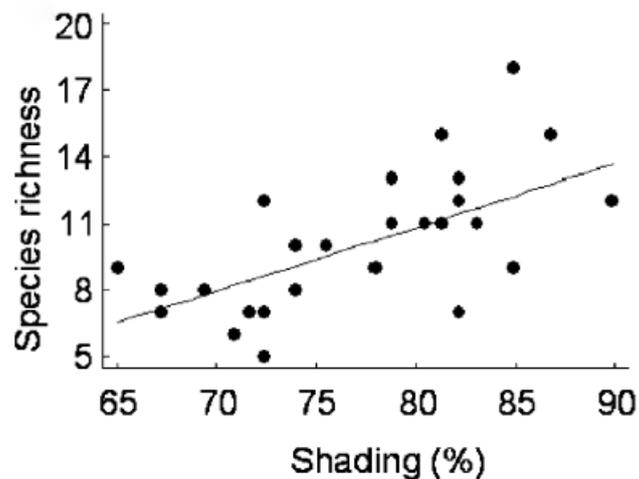
Abandoned fields and pastures typically consist of a smaller area than logged forests and those are abandoned on a different time, creating fragmented habitats and a matrix of distinct stages of succession (Guevara et al., 2004). This fragmented character of the landscape can potentially

harbour higher species richness of insects that are unique for each habitat (Gormley et al., 2007). Nevertheless, preserving and maintaining natural primary forest, in addition to enhancing the restoration of some degraded areas is necessary, as it was demonstrated to have irreplaceable value for biodiversity (Takano et al., 2014).

The succession of past agriculture lands towards the forest can lag for roughly 10 years due to the herbs, ferns and other non-woody species who inhibit the establishment and growth of woody species (Aide et al., 1995). The length of the lag and the probability of a successful restoration is dependent on the intensity of the pasture (Uhl et al., 1988), e.g. lightly used areas can be inhabited by pioneer trees in just 6 years (Mesquita et al., 2001).

The main reason indigenous tree species cannot grow on this land is the low availability of seeds in the seed bank and its limited dispersal. The seed bank can be easily destroyed by agricultural activities and many seeds of climax species in the tropical forest often do not have dormancy and cannot create a seed bank (Vieira and Scariot, 2006). Nearby forest remnants can provide seeds, but the dispersal is very limited, because larger seeds of climax species are not able to disperse more than 5 meters from the forest edge (Ganade, 2007). Animal seed dispersals tend to avoid clear-cut areas of pastures and fields, and since the majority of seeds from Neotropics are dispersed by animals (Howe and Smallwood, 1982), the absence of dispersals creates another barrier (Janzen and Vázquez-Yanes, 1991).

Butterfly species richness increases along the restoration gradient (Mihindikulasooriya et al., 2014; Nyafwono et al., 2014; Veddeler et al., 2005). The rate of increase in species richness began rapidly, but slowed after a few years, and continued to slow during the following decades (Itioka et al., 2015). Butterfly species richness increases with increasing tree density, but shows a negative correlation with a more dense understory (Bobo et al., 2006). Additionally, increased shading from trees leads to an increase in number of butterfly species (Fig 7). The number of ant species and their response to the restoration is not consistent as ants have many ecological groups – army and myrmecophilous ants increase with the age of the restoring forest (Takano et al., 2014), while on arboreal ants no effect of succession has been observed on species richness (Neves et al., 2010a; Schmidt et al., 2013). However, Neves et al. (2010a) suggest that the absence of clear a gradient could be caused by higher species richness in the early stages of ground-nesting ants foraging on trees, whereas no behaviour like that has been observed in ground nesting ants in late stages.

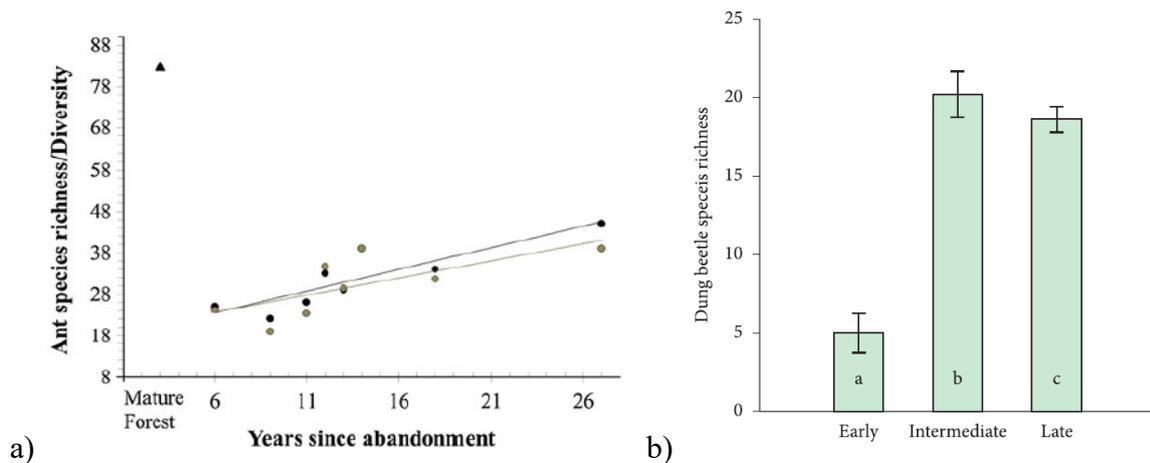


**Fig 7.:** Species richness of butterflies in relation to shade under ground vegetation of recovering forest fragments (Veddeler et al., 2005).

It was reported that *Coleoptera* are more sensitive to disturbances (Gibson et al., 2011). On past agricultural and restoring lands species richness of dung beetles was highest in intermediate stages (Figure 8b) and for herbivorous Scarabaeids it has been very similar or slightly lower than in the primary forest (Kishimoto-Yamada et al., 2011; Takano et al., 2014).

The abundance of insect species was reported as increasing in most of the studies. It was reported for ants, butterflies, Orthopterans, and dung beetles (Barnes et al., 2014; Hugel, 2012; Matsumoto et al., 2009; Nyafwono et al., 2014; Takano et al., 2014). The population size of Orthopterans increased four to seven times (Hugel, 2012) and populations of dung beetles increased by 53% in 3 years after abandonment (Barnes et al., 2014).

The majority of the restoring lands are not capable of maintaining biodiversity of insect species on the same level of primary or old secondary forests (Silva et al., 2007), but with time, the alpha diversity of insects is slowly increasing (Bihn et al., 2008; Dunn, 2004; Kishimoto-Yamada et al., 2011; Nyafwono et al., 2014). Diversity of ants is increasing as well (Rocha-Ortega and Favila, 2013) and is a result of increasing tree diversity (Riedel et al., 2014). Increased tree diversity offers a wide range of food resources, which enables more species of ants or other insects to coexist (Armbrecht et al., 2004; Delabie et al., 2007). Species of dung beetles and their diversity seemed to be more resistant to the changes of habitats – diversity was similar to the levels of mature forest even in intermediate stages (Kishimoto-Yamada et al., 2011; Neves et al., 2010b).



**Fig 8.:** a) Linear regression of the richness and Shannon entropy of ant species in an old field over time (Rocha-Ortega and Favila, 2013). b) Richness of dung beetles in three successional stages (Neves et al., 2010b).

Species richness, abundance and even diversity can reach levels similar to the primary forest. Restoration of insect assemblages on abandoned farmland, on the other hand, does not necessarily have to approach to the assemblage of the mature forest. After 7 years of natural regeneration, the composition of insects shared only 31.6% of the species of late stages (Neves et al., 2010b). Nevertheless, the dissimilarity between past agricultural land and forest is increases with the age of the plot and insect species assemblages changes along the recovery gradient (Audino et al., 2014; Floren et al., 2001; Neves et al., 2010a; Schmidt et al., 2013). One thing which possibly enhances the speed of insect composition recovery is the presence of a mature forest nearby – while restoring abandoned fields and pastures it is an important source of not just seeds, but faunal species of the mature forest (Rocha-Ortega and Favila, 2013). Degraded habitats were typical for higher rates of generalist, so with ongoing succession, more specialists have been appearing in the different stages of recovery. These results were observed in assemblages of dung beetles, and an increasing percentage of specialized *Scarabaeidae* can be considered proof of a successfully recovering habitat (Audino et al., 2014). Butterflies also displayed great turnover along the time gradient, and species who prefer shade were absent in regenerating areas (Bobo et al., 2006; Mihindikulasooriya et al., 2014). Coleopterans using woody debris preferred habitats similar to a primary forest and hence are absent from early successional stages (Takano et al., 2014). Another good indicator of ongoing succession is arboreal ants. They nest on trees and the ant communities of one tree species can be very distinct depending on the age of the tree. The same tree species at 15 years old and 40 years old

previously cleared forest hosted different ant communities, while 5 years old and 15 years old forest showed increased similarity (Floren et al., 2001).

One special case of restoration is planting fast-growing trees such as *Acacia mangium*. This approach is used mainly when the grasslands resulting from agricultural activities have to be overcome to enhance the native tree establishment and to start up the recovery of the forest and its species (Otsamo, 2000). For some of the insect groups an increase in the species richness and a higher similarity of composition with the forest have been reported for some of the insect groups. Braconid wasps showed not just a higher number of species in plantations, but also a different turnover of species where an increase in species of old secondary forest was visible (Maeto et al., 2009). Similar results have been observed for dung beetle communities (Ueda et al., 2015). Butterflies showed increased species richness in plantations as well (Matsumoto et al., 2015). Even though plantations cannot harbour such diverse communities as primary forests or old secondary forests they can help to achieve ongoing recovery towards the forest on very disturbed lands (Ueda et al., 2015).

Ants and butterflies are good indicators – ants are stationary animals with large populations and their composition reflects changes in habitat (Dunn, 2004; Rocha-Ortega and Favila, 2013). Butterflies from Nymphalidae family are sensitive and vulnerable to disturbance, hence their presence and higher abundances can be a sign of successful restoration (Bobo et al., 2006).

Different estimations of time needed to restore the insect communities after agriculture driven disturbances have been reported. For ants, 25 years seemed to be enough to recover up to two-thirds of their mature forest diversity (Neves et al., 2010a; Takano et al., 2014), while butterflies needed at least 40 years to achieve mean 75% similarity with the composition of primary forest (Nyafwono et al., 2014). For dung beetles 18 years was not enough for establishing steady a composition (Audino et al., 2014).

## 7 Conclusion

For insects, as the most diverse class of organisms, thereby any generalisation of the group is problematic. Therefore the choice of a proper target group of insects for our studies is crucial. Considering impacts of disturbances and the recovery of habitats, some insects are more resistant (dung beetles and carrion beetles) (Shahabuddin et al., 2005b; Vulinec, 2002), whereas others are more vulnerable (Nymphalidae butterflies) (Bobo et al., 2006). For instance, arboreal ants show similar compositions in agricultural plantations as in primary forests (da Conceição et al., 2015; Delabie et al., 2007), wrongly suggesting that the plantations can replace rainforests in preserving biodiversity and conservation of rainforest insect species. Based on my review, insect assemblage or the combination of multiple other factors seem suitable for the evaluation of restoration processes.

Both logging and agriculture show their largest impact on insect species composition; up to 64% of insect species were altered, and insect assemblages were the slowest to recover (Bobo et al., 2006; Dunn, 2004). The number of specialists in these assemblages is one metric which decreases with disturbance and increases to similar levels as in the primary forest after undergoing recovery. Initially, specialists are replaced by species with wider ecological tolerance during degradation (increase of up to 55% of dominant species), but eventually the specialists return (King et al., 1998). Timber harvesting alters the vegetation stratification and suppress shade-preferring insect species of deep forest (Dumbrell and Hill, 2005; Ribeiro and Freitas, 2012; Shahabuddin et al., 2005b; Spitzer et al., 1997). On the other hand, agricultural activities cause habitat fragmentation, and thus result in very poor or different communities (such as those found on pastures) (Guevara et al., 2004; King et al., 1998).

Species richness increases during restoration, more often than not, in most relevant literature (so does abundance). For richness and abundance of insect species, a prevalent influence is the percentage of tree cover and shading provided. Total biomass of plants is another valuable correlate (Yamamoto et al., 2007). The highest diversity of insect species is typically observed in intermediate stages of forest restoration, perhaps due to the mid-domain effect (Bitencourt and da Silva, 2016; Neves et al., 2010b; Sant'Anna et al., 2014). The number of insect species does not always decline following a disturbance; logging results in higher structural heterogeneity and a range of generalised species can colonise the disturbed habitats (Brown, 1982a; Culot et al., 2013; Ghazoul, 2002; Hamer et al., 2003; Hyman, 1983). Similarly, degraded open areas are often colonised by various non-forest insect species increasing the

community diversity and abundances (Sáfián et al., 2011; Valtonen et al., 2017; Vasconcelos et al., 2000). Surrounding habitats are more crucial for the restoration of former agricultural land than of logged forests. This is because agriculture typically represents a heavier disturbance. For the restoration of a logged forest, environmental factors like canopy openness were of a higher importance, explaining 32% of the difference in insect communities. Additionally, plant composition explained up to 18% of the differences (Schaffers et al., 2008; Valtonen et al., 2017).

It is difficult to set the time necessary for the forest restoration. It is known, however, that different levels of disturbances have visibly unequal effects. Insect communities of logged forests reach the levels of primary forests in roughly 55 years; this is reduced to the mean value of 45 years if assisted restoration approaches are applied. Insect communities on former agricultural land reach 75% similarity with those in a primary forest in about 40 years (Nyafwono et al., 2014), where more than 18 years are necessary for the establishment of a steady composition (Audino et al., 2014). On former farmland, the efficient forest recovery needs more time. This is chiefly due to the creation of barriers associated with agricultural conversion, which hinders successful colonisation by primary forest species.

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\* secondary citation