“INSECT DIVERSITY AND TROPHIC INTERACTIONS IN SHADED CACAO AGROFORESTRY AND NATURAL FORESTS IN INDONESIA”

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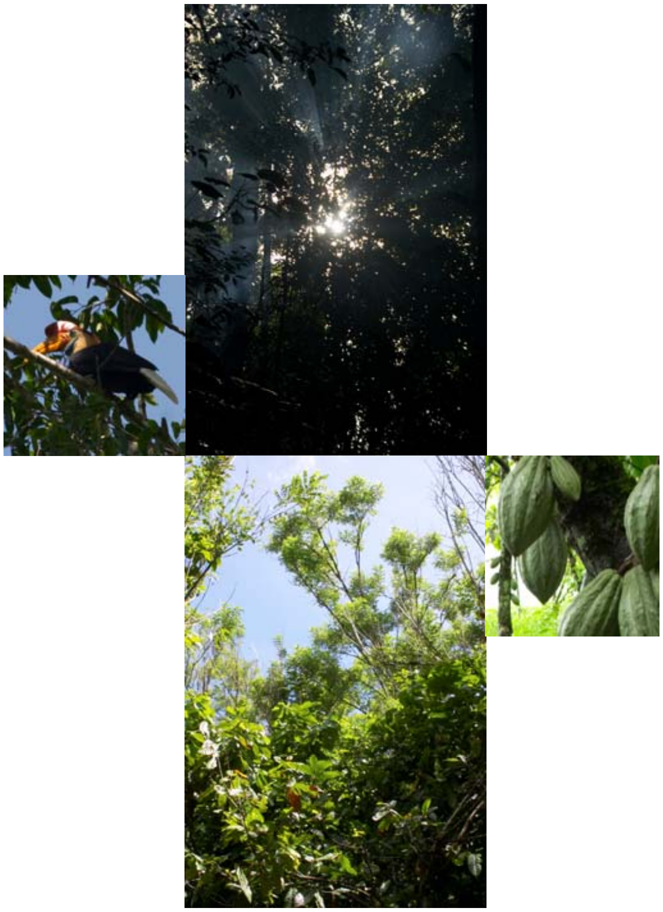
CHAPTER 1

GENERAL INTRODUCTION



Tropical forests in the 21st century

The world's tropical rainforests lost an estimated 32% of its cover in the past 50 years, and a further loss of 10-15% has been projected by 2050 (Millenium Ecosystem Assessment 2005). Annually, millions of hectares of pristine tropical forests are lost to agricultural expansions, most of which takes place in Brazil and Southeast Asia where each year a total of 5 million hectare of forest is lost or degraded (Achard *et al.* 2004). Tropical rainforests are one of the most species-rich and functionally important terrestrial ecosystems (Myers *et al.* 2000) and global-scale conversions are a major cause of worldwide biodiversity declines, which threatens ecosystem functioning, sustainable land use and economies (Hoekstra *et al.* 2005). With the continuing loss of tropical forests, cultivated areas are gaining interest for their potential benefits to the conservation of tropical biodiversity and ecosystem services (Rice and Greenberg 2000; Putz *et al.* 2001; Bawa *et al.* 2004; McNeely 2004; Schroth *et al.* 2004).

After the conversion of tropical rainforests, land-use is dominated by plantations of woody crops. This 'agroforestry' is used for cultivating some of the world's most important cash crops, including oil palm (*Elaeis* spp), rubber (*Ficus elastica*), cacao (*Theobroma cacao*) and coffee (*Coffea* spp.) (Schroth *et al.* 2004). Additionally, these agroforests are often used to grow various kinds of timber trees, local fruit trees and annual crops, thereby providing building material, firewood and food to local economies (e.g., Rice and Greenberg 2000; Siebert 2002).

Thus, in deforested landscapes agroforests provide the dominant habitat type with a substantial tree cover. The biodiversity supported in such systems can be very high, but remained mainly studied in the context of pest management (Room 1971; Entwistle 1972; Campbell 1984). Acknowledging the intrinsic and economic values of biodiversity (e.g., Meffe 1998; Altieri 1999; Sodhi 2004; Foley *et al.* 2005), studies during the last decade increasingly focused on the role agroforestry can play in the conservation of tropical biodiversity outside natural forests.

Well-shaded agroforests with multiple canopy layers (e.g., the crop complemented by shade trees) do resemble natural forests in structure as well as in the wide variety of flora and fauna that characterize tropical biodiversity (Lawton *et al.* 1998; Chung *et al.* 2004; Schulze *et al.* 2004; Waltert *et al.* 2004; Shahabuddin *et al.* 2005). In Chapter 2 of this dissertation we investigate the lower canopy ant and beetle fauna in forest and agroforests and provide an answer to the question whether cacao dominated agroforests resemble natural forests in terms of ant and beetle assemblages.

Management intensification and biodiversity in agroforests

Management of agroforests differs greatly in time and space. First, agroforestry is a broad term for land management that ranges from heterogeneous, shaded coffee and cacao agroforests (Perfecto et al. 1996; Johns 1999; Siebert 2001; Klein et al. 2003; Chapter 1 in this dissertation), to the vast monocultures of oil palm plantations in Malaysia and Indonesia (Chung et al. 2001). Second, subsequent to conversion of pristine forests to agroforests, management intensifies throughout the tropics. In South America, extensively managed, densely shaded small-scale coffee plantations are changing to large-scale, non-shaded and monotonous plantations (e.g., Perfecto *et al.* 1997; Perfecto *et al.* 2005; Philpott 2005). In cacao agroforests, the intensification is also represented by thinning and removal of shade trees; whereas young trees need shade for healthy growth (Entwistle 1972), productivity of fruiting trees is predicted to increase without shade (Zuidema et al. 2005). Hence, Southeast Asian cacao agroforests change from well shaded systems to zero-shade monocultures that consist of the main crop only (Siebert 2002).

The diversity of insects in agroforests is strongly affected by the type of agroforest and by subsequent changes in management. For example, species richness of canopy beetles remained in extensive timber plantations similar to that of nearby forest sites, but species richness declined sharply in intensive, homogeneous oil palm plantations (Chung *et al.* 2000). Furthermore, compared to extensive, shaded coffee agroforests, beetle species richness decreased by 26% in large-scale, intensive coffee agroforests with less or no shade (Perfecto *et al.* 1997).

Whether an animal species is present or absent in an agroforest depends on favorable habitat characteristics. Because fruit-feeding bird and butterfly species in agroforests have been related to food resources provided by shade trees (Perfecto *et al.* 2003; Schulze et al. 2004; Waltert *et al.* 2004), their occurrence in agroforests is threatened by shade tree removal. Ant communities are affected by shade tree removal by structural changes that are represented by losses of nesting availability (Armbrecht et al. 2004; Philpott 2005). Moreover, the destruction of natural habitats threatens the important presence of social bee species as pollinators in nearby coffee agroforests (Klein *et al.* 2003) and grapefruit plantations (Chacoff et al. 2006) because most social bee species depend on (near) natural habitats for nesting.

In Chapter 2 and 3 we investigate the effect of two important management aspects on supported biodiversity in cacao dominated agroforests, being homogenization of shade tree stands and thinning of the shading canopy. We answer the question whether modification of the shade canopy of agroforests affects the diversity of forest and non-forest species within these two insect groups.

Mutualistic and antagonistic trophic interactions

Trophic interactions occur between species that belong to different trophic levels, such that fluctuations in one trophic level may lead to cascading effects in others (Polis et al. 1999). For example, decreasing parasitoid populations may lead to increases in prey populations (Snyder et al. 2006) and long-term pollinator declines may explain declines in flowering plants (Biesmeyer et al. 2006). Biodiversity research is accompanied by an ongoing debate on the relationship between species richness, species interactions and ecosystem functions and stability (McCann 2000). Stability of natural systems may profit from high levels of species richness, but anthropogenic habitat disturbance can alter this relationship greatly. For example, pollination by bees profits from high species richness in that behavioral diversity increases pollination success and temporal stability (Fontaine et al. 2006), but agricultural intensifications and habitat loss threaten pollinator populations and thus crop pollination (Klein et al. 2003; Kremen et al. 2003; Ricketts et al. 2004).

In natural systems, the intrinsic value of species interactions is increasingly recognized as an important aspect worth to protect (Lewis et al. 2002). In cultivated systems under low to moderate agricultural intensity, unmanaged pollinator communities (Ricketts et al. 2004) and naturally occurring pest predators (Snyder et al. 2006) can enhance crop productivity and sustainability through better pollination and biological control.

Invasive species and biodiversity

Species invasions occur when non-native species establish populations in indigenous ecosystems (Elton 1958). Invasion biologists have identified the effects of invasive species on indigenous community diversity as a major cause of global biodiversity declines (e.g., Vitousek *et al.* 1996; Rosenzweig 2001; Holway *et al.* 2002a).

The relationship between species invasions and indigenous diversity declines has been particularly well studied in the context of competitive interactions between ant species. Ant invasions are suggested to be driven by abiotic changes in the environment (Perfecto and Vandermeer 1996; Holway 1998; Holway *et al.* 2002b; Gibbs & Hochuli 2003), which has been shown experimentally with the increased competitive dominance of the Argentine Ant, *Linepithema humile*, on irrigated land (Menke and Holway 2006).

Dominant ant species drive dominance hierarchies that result in 'mosaics' of ant interactions (e.g., Room 1971; Majer *et al.* 1994). Thus, invasions by ecologically dominant species can in particular seriously disrupt indigenous ant assemblies, which can even lead to overall biodiversity losses (Holway *et al.* 2002a; Hill *et al.* 2003; O'Dowd *et al.* 2003; Sanders *et al.* 2003).

Species invasions in general may be largely context dependent, such that anthropogenic disruption of ecosystems facilitates species invasions (Elton 1958; Didham *et al.* 2005). In the context of agroforestry, management that includes thinning of shade canopy leads to those microclimatic changes that alter ant species activities asymmetrically (Room 1971) such that altered interactions can lead to disrupted ant communities (Perfecto and Vandermeer 1996; Chapter 2 in this dissertation). In Chapter 3 the hypothesis is tested whether modifications of the agroforest habitat can explain dominance by a common invasive ant species, the Yellow Crazy Ant *Anoplolepis gracilipes*, and discuss the potential effects on native ant assemblages that are still supported in non-invaded, shaded agroforests.

Herbivory, pollination and the productivity of cacao

The cacao tree (*Theobroma cacao* L. 1759) originates from the understory of Central American lowland rainforests. Since its discovery by Spanish colonialists in the 15th century, cacao has become one of the world's leading cash crops grown throughout the tropics (ICCO 2005). The annual world production reached 3.5 million tons of dry cacao beans in 2004, which equaled 3.7 billion US$ of income to farmers. Throughout the tropics, wide ranges of local insect species have taken over important functions as pollinators or as pests (Entwistle 1972). Nevertheless, surprisingly little is known about trophic interactions between pollinators, pests and cacao's productivity.

Cacao's small, cauliflorous flowers are hermaphroditic, with each of five anthers separated from the central stigma by a folded sepal, indicating the importance of vectors in its pollination. Parthenogamy does not occur and most cultivars are self-incompatible (Entwistle 1974). Because its pollen is sticky, dispersal is more likely to occur by insects than by wind and insects such as aphids, ants, thrips, but mostly midges of the family Ceratopognidae have been observed transferring pollen (review by Entwistle 1972). Nevertheless, cacao's reproductive biology is characterized by very high flower:fruit ratios and fruit-set after natural pollination can be increased up to 10 fold by manual pollen supplementation (Valle et al. 1990; Falque et al. 1995; Chapter 5 in this dissertation).

The main pollinators - ceratopogonid midges - are active at dawn and dusk and depend on moist habitats rich of rotting plant material, where they breed, feed and remain during the day (Entwistle 1972). Such substrates are rare in cacao mocultures that are frequently cleaned, in comparison to shaded agroforestry systems and lowland rainforests. This could explain pollinator deficits on cacao plantations. Management that controls the availability of nesting habitats for ceratopoginid midges can play an important role in local increases of pollinator abundances (Young 1982).

However, high flower:fruit ratios are common in hermaphroditic flowering plants (Stephenson 1980) and do not only reflect pollinator deficits, but may be an adaptation to increase the plant's male fitness (pollen production) or may serve as insurance against fluctuations in pollinator abundances and pest and nutrient pressures (Ehrlen 1996). The persistence of such flowering strategies in agricultural crops is likely, but remains poorly considered in agroecological studies (but see Brown and McNeill 2006).

Productivity of cacao can be seriously impeded by soil conditions or by pathogens and insects that feed on (parts of) the cacao trees. Unfavorable soil conditions lead to increased rates of fruit abortion by the trees (Nichols and Walmsley 1965; Valle et al. 1990) and outbreaks of pest organisms can even lead to regional abandonment of cacao farming (Purdy and Schmidt 1996; Krauss and Soberanis 2001). The importance of pollination relative to fruit attacking pests and nutrient availability and the role of shade management remain poorly understood, but are studied in closer detail in Chapter 4 and 5 of this dissertation.

Study area

The here presented study focuses on cacao agroforests in Central Sulawesi, Indonesia (Figure 1.1a). The island underwent a "cacao boom" throughout the 1990s (Potter 2001; Belsky and Siebert 2003) in which coffee-dominated agroforestry was largely replaced by cacao-dominated agroforestry systems, turning Indonesia into the world's third most important contributor to the international cacao production. Indonesia harbours some of the world's most important hot spots in terms of biodiversity (Myers et al. 1994), but also in terms of tropical rainforest conversion (Achard *et al.* 2002), resulting in unprecedented losses of biodiversity (Sohdi *et al.* 2004). In the light of the disappearing primary rainforest habitats, agroforestry gains increasing interest for its potential role in the conservation of tropical biodiversity, especially in intensively cultivated regions of Sulawesi, where 80% of Indonesia's cacao is grown (Vingerhoets 2002).

The study took place in and around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (Figure 1.1b, 1°30'24" S, 120°2'11" E, 800 – 900 masl). Toro is located at the western border of the unfragmented, 231,000 hectare Lore Lindu National Park, about 100 kilometers south of Palu, the capital city of Central Sulawesi. The region has an annual average (± SE) temperature of 24.0 (± 0.16) °C and a mean monthly rainfall of 143.7 (± 22.74) mm. There are no clear seasonal fluctuations. The natural vegetation of the National Park around the village is submontante rainforest.

The agricultural landscape in the region is highly heterogeneous, consisting of a patchy mosaic of pasture, hedges and cacao dominated agroforests, which is typical for the region. Cacao agroforests in the Toro village are owned and managed by small-scale farmers. Shade tree management in the region was dynamic and farmers generally planned to remove shade trees in the opinion that this would increase cacao production.

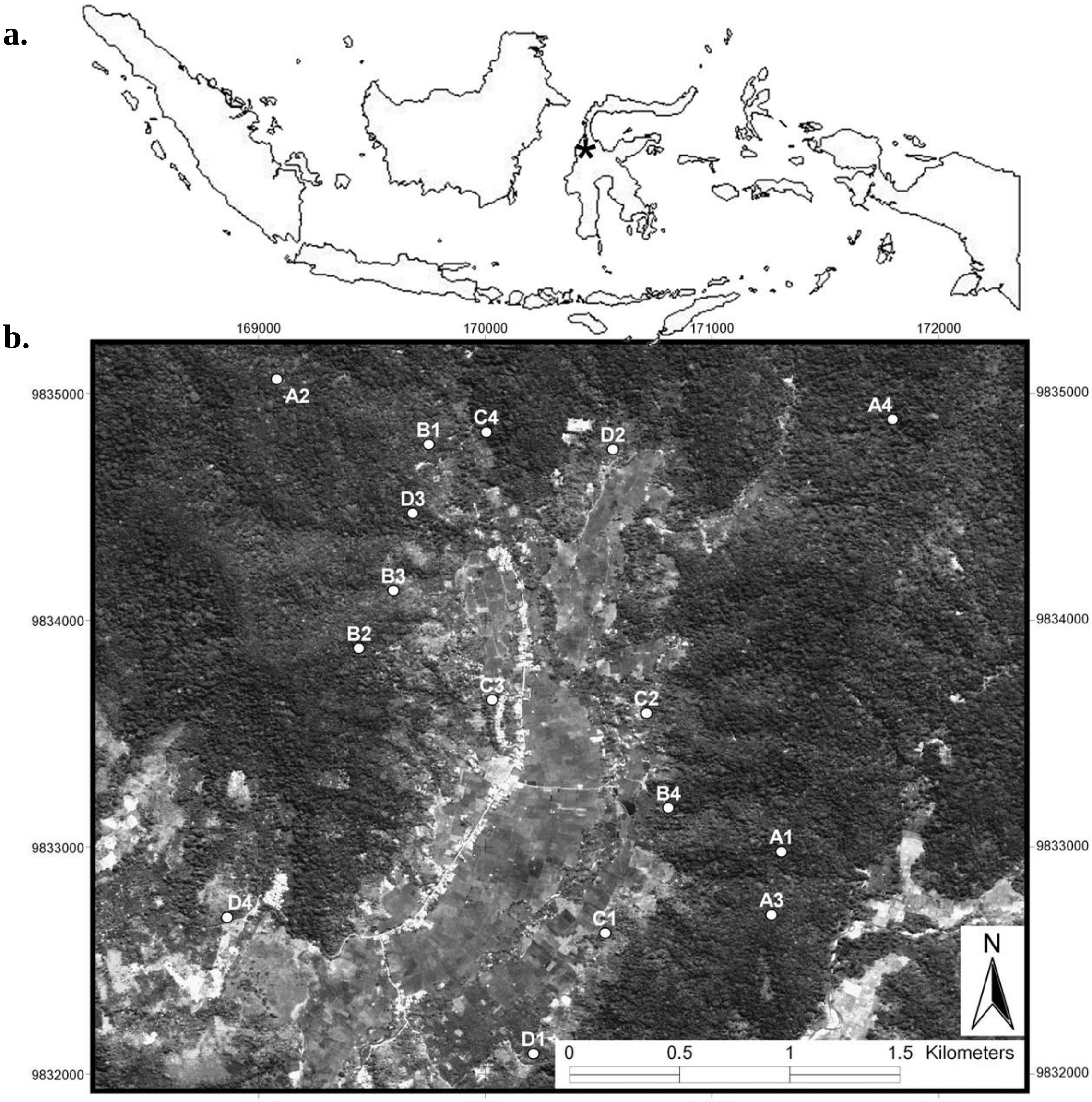


Figure 1.1a: A map of Indonesia with * indicating the study area. b: Satellite image of the Toro village in the margin of the Lore Lindu National Park with the selected study sites: A1-4 = Forest sites within the National Park. B1-4 = Agroforests dominated by cacao in the undergrowth, with shade trees that remain from the previous forest cover. C1-4 = Agroforests dominated by cacao in the undergrowth, with a diverse stand of planted shade trees. D1-4 = Agroforests dominated by cacao in the undergrowth, with a stand of planted shade trees dominated by one or two species of non-native legiminous trees (Satellite image: QUICKBIRD UTM51S-WGS84. Processed and provided by André Twele, Göttingen University, Germany).

Study systems

We defined *a priori* three types of agroforests, which represented a gradient of shade tree diversity but were comparable in terms of basal area and stem density (Table 1.1 and Gradstein et al., in press):

I. Cacao agroforests with diverse, natural shade trees that had been retained from previously undisturbed forest when it was thinned and underplanted with cacao trees (DNS). Cacao agroforestry was the first form of cultivation in these sites (since 8-15 years) that still had high numbers of native shade trees, and even some endemic species (Table 1.1, Figure 1.2b).

II. Cacao agroforests with shade tree stands dominated by various species of planted shade trees (DPS). These sites had a longer history of cultivation (longer than 20 years e.g., as coffee agroforests) and trees from the previous forest cover were all replaced by various planted fruit and timber trees that provided the owners with non-market products. Among these trees were some native (including a few endemic) species (Figure 1.2c).

III. Cacao agroforests with a low diversity of planted shade trees (SPS). These sites also had a longer history of cultivation (longer than 20 years e.g., as coffee plantations). Management of these agroforests was aimed at maximum cacao productivity. Shade was provided predominantly by the non-indigenous leguminous trees *Gliricidia sepium* and *Erythrina subumbrans* that are nitrogen fixing. Some native timber or fruit tree species were also grown, none of which were endemic (Figure 1.2d).

Sites were selected based on the age of the cacao trees, which was on all sites between 7 and 10 years. At the time of this study, agroforestry was non-intensive in each site, with little use of fertilizers and pesticides. Farmers regularly pruned trees and weeded the plantations (2-3 times per year).

Four forest sites (NF) were selected close to the village (Figure 1.2a), but well within the national park and representative for the submontane forest in the area. These forest sites were part of the continuous Lore Lindu National Park and at least 300 m away from forest sites where selective logging occurred. Selective logging was allowed in the national park's margins, only by local people and only for local timber use. In the selected sites minor rattan extraction occurred.

Figure 1.2a: Forest (site A1 in figure 1.1b). b: Cacao agroforest with shade trees that remain from previous forest cover (site B4 in figure 1.1b). c: Cacao agroforest with a diverse stand of planted shade trees (site C2 in figure 1.1b). d: Cacao agroforest with one or two species of planted shade trees (site D4 in figure 1.1b).

Table 1.1. Characteristics of the tree flora of natural forest and three types of cacao agroforests at the study sites in Central Sulawesi, Indonesia, averaged per habitat type (means ± SE). All data except shade canopy cover are adapted from Gradstein et al. in press.

Site characteristic	NF (n=4)	DNS (n=4)	DPS (n=4)	SPS (n=4)
Tree species[1]	55.8 ± 2.75^{a}	20.8 ± 3.90^{b}	19.0 ± 3.75^{b}	9.0 ± 2.25^{b}
Tree families[1]	27.0 ± 1.70^{a}	14.3 ± 1.80^{b}	13.5 ± 2.25^{b}	6.8 ± 1.65^{b}
Native tree species[1]	55.8 ± 2.75^{a}	18.5 ± 3.95^{b}	10.3 ± 4.40^{bc}	5.5 ± 1.85^{c}
Endemic tree species[1]	8.0 ± 0.40^{a}	2.3 ± 1.30^{b}	0.8 ± 0.75^{b}	0^{b}
Planted tree species[1]	0^{a}	2.3 ± 0.50^{b}	8.8 ± 0.65^{c}	3.5 ± 0.50^{b}
Stems ≥ 10 cm dbh[1]	140.5 ± 8.65^{a}	77.5 ± 10.55^{b}	70.0 ± 11.05^{b}	81.0 ± 27.75^{b}
Basal area (m^2 ha^{-1})	56.7 ± 9.10^{a}	20.5 ± 4.20^{c}	14.9 ± 4.85^{c}	11.9 ± 3.15^{c}
Canopy cover (%)	95.8 ± 0.42^{a}	72.5 ± 2.22^{b}	61.4 ± 3.96^{c}	58.1 ± 4.55^{c}

[1] Values are per 0.25 ha

NF = Natural forest, DNS = cacao plantation with diverse natural shade, DPS = cacao plantation with diverse planted shade, SPS = cacao plantation with simple planted shade, dbh = diameter at breast height.

The minimum distance between study sites was 300 meters and the maximum distance was about 5 kilometers. All sites were between 850 and 1,100 meters above sea level. The agroforests did not have sharp borders with other habitat types, but gradually changed into other forms of land-use. The agroforests formed a continuous band along the forest margin. Boundaries between agroforests were arbitrary based on ownership. Therefore, we marked core areas of 30 x 50 m in the middle of each site. Land-use and types of shade tree stands did not change within these areas. Sites of different habitat types were geographically interspersed so that none of the habitat types were spatially clustered.

The percent canopy cover above the cacao layer was estimated using a Spherical Densiometer. Canopy cover was estimated at two spots around each studied tree and the mean of these two estimates per tree was used in the analyses.

Diversity of lower canopy ants and beetles in the study area

In the selected study sites, we quantified lower canopy ant and beetle diversity from canopy knockdown samplings (see ‘Methods’ sections of chapter 2 and 3 for more details). Ants and beetles are the two major contributors to tropical biodiversity and to date the extremely high species richness remains largely undescribed by taxonomists (Basset 2001). Therefore, biodiversity assessments of insect groups often use morphospecies approaches to avoid time consuming taxonomic identifications (Oliver and Beattie 1996). In our assessments of ant and beetle diversity in tropical agroforests and forests, taxonomic identifications were impossible based on literature only and ants and beetles were sorted to species by respectively Akhmad Rizali (Bogor, Indonesia) and Boris Büche and Christoph Bayer (Berlin, Germany). Taxonomic levels were identified to the family, subfamily and genus level when possible based on literature (e.g., Bolton 1994; Lawrence *et al.* 2001). Where necessary, beetle species were sorted based on genitalia preparations.

In total, we collected 107 ant species. These species belonged to 7 subfamilies and 27 genera. The genus *Polyrhachis* (*Formicinae*) was with 41 represented species the most species rich genus. The genus is currently being revised by R. Kohout (Queensland, Australia) who identified the 41 species, and recognized 11 as yet undescribed species. This finding illustrates the extent to which tropical fauna remains understudied, even in cultivated systems.

The collected beetles were sorted to 783 species that represented 68 families. For the beetles a detailed approach to the genus or higher level depends strongly on expert knowledge and is impossible with the use of literature only. Because such expert knowledge is scattered throughout the world, a comprehensive photographic collection of all recognized species was made and posted on the internet (http://www.beetle-diversity.com).

The website proved highly successful in contacting and involving specialists internationally (see acknowledgements). By now, about 30 specialists have provided taxonomic identifications based on the beetle photography. From the 783 collected beetle species 64% was identified to 66 subfamilies, 34% to 138 genera and 4% to 28 species. Figure 1.3 shows the 30 most common lower canopy beetles from cacao trees and Figure 1.4 those from lower canopy forest trees.

Chapter outline

Chapter 2 investigates the role of cacao dominated agroforests in the conservation of beetle and ant diversity. Beetles and ants were collected by canopy knockdown foggings, a technique commonly used to collect insect communities from tree crowns as complete as possible. The 100s of beetle and ant species were categorized as “forest” and “non-forest” species, a new method that revealed a contrasting response: Whereas overall species richness of ants and beetles remained similar on cacao trees compared to forest trees, “forest” beetles hardly occurred in cacao agroforests, and the occurrence of “forest ants” decreased along with increasing openness of the shading canopy.

Chapter 3 focuses more closely on the arboreal ant communities in cacao trees and lower canopy trees in nearby natural forests. In this chapter the effect of the microclimate is investigated, which is closely related to canopy openness, but from itself did not explain the declining trend in “forest” ants. Much stronger was the effect of the microclimate on the occurrence of the Yellow Crazy Ant, *Anoplolepis gracilipes*, an aggressive invasive ant species that was common inside houses, homegardens and some cacao plantations, but hardly occurred in the natural forest. Dominance by this ant species was related to a sharp decrease in “forest” ants. Thus, the openness of the shade canopy and associated changes in the microclimate may have a mediating effect on native ant assemblages by promoting the dominance of invasive ants.

Because Chapter 2 and 3 argue for the protection of shaded cacao agroforests, Chapter 4 discusses whether the productivity of cacao is indeed limited by shade tree stands, as commonly predicted. It is investigated whether the different types of shade tree stands affect causes of cacao’s fruit mortality. The high rates of fruit-loss are put into a spatio-temporal context in order to discuss the applicability of general ecological theories that predict pest occurrences and whether there are feasible management potentials to increase cacao productivity in shaded agroforests, without the necessity of removing shade tree stands.

In Chapter 5 we study the pollination biology of three important tropical crops in agroecosystems: Coffee in Ecuador, Passion fruit in Brasil and cacao Indonesia. By recording fruit set immediately after pollination and at the time of harvest, the importance of pollinators for the productivity of the three crops is discussed. By linking agronomic, ecological and evolutionary literature, we emphasize an important yet poorly considered aspect of studies on ecosystem services: The service provided by a chain of ecosystem processes is impeded by its weakest link. Economic translations of ecosystem services should include the complete set of processes that deliver the service in order not to overestimate benefits from single processes.

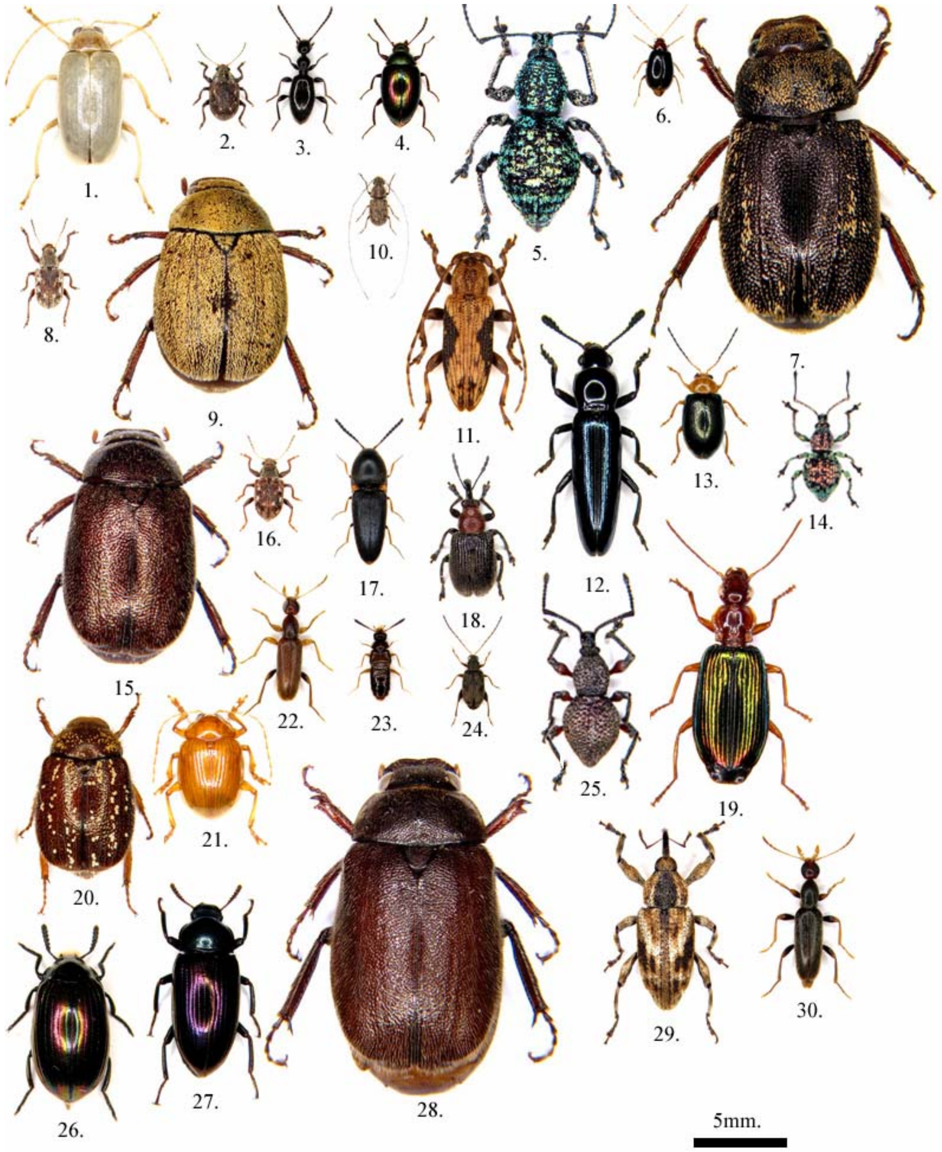


Figure 1.3. The 30 most common lower canopy beetle species from agroforests in the study area (from most to least abundant): 1. *Monolepta* sp. 40 (Chrysomelidae); 2. *Demotina* sp. 6b (Chrysomelidae); 3. *Anthelephila* sp. 1 (Anthicidae); 4. *Amarygmus* sp. 5a (Tenebrionidae); 5. Entiminae sp. 1a (Curculionidae); 6. *Monolepta* sp. 15a (Chrysomelidae); 7. *Apogonia* sp. 1 (Scarabaeidae); 8. Eumolpinae sp. 6a (Chrysomelidae); 9. *Apogonia* sp. 7 (Chrysomelidae); 10. *Exillis* sp. 3 (Anthribidae); 11. *Sybra* sp. 5 (Cerambycidae); 12. Languriidae sp. 1; 13. *Cassena* sp. 16 (Chrysomelidae); 14. Entiminae sp. 3 (Curculionidae); 15. *Apogonia* sp. 6b (Scarabaeidae); 16. Eumolpinae sp. 6c (Chrysomelidae); 17. Elateridae sp. 3a; 18. Rhynchitidae sp. 4; 19. *Callida* sp. 3a (Carabidae); 20. *Apogonia farinosa* (Scarabaeidae); 21. *Rhyparida* sp. 13 (Chrysomelidae); 22. *Macratria* sp. nov. (Anthicidae); 23. Aleocharinae sp. 43 (Staphylinidae); 24. *Hespera lomasa* (Chrysomelidae); 25. Entiminae sp. 2 (Curculionidae); 26. *Hemicera helleri* (Tenebrionidae); 27. *Tetragonomenes* sp. 17a (Tenebrionidae); 28. *Apogonia* sp. 6a (Scarabaeidae); 29. Cryptorhynchinae sp. 23 (Curculionidae); 30. *Macratria pallidicornis* (Anthicidae). Source: www.beetle-diversity.com.

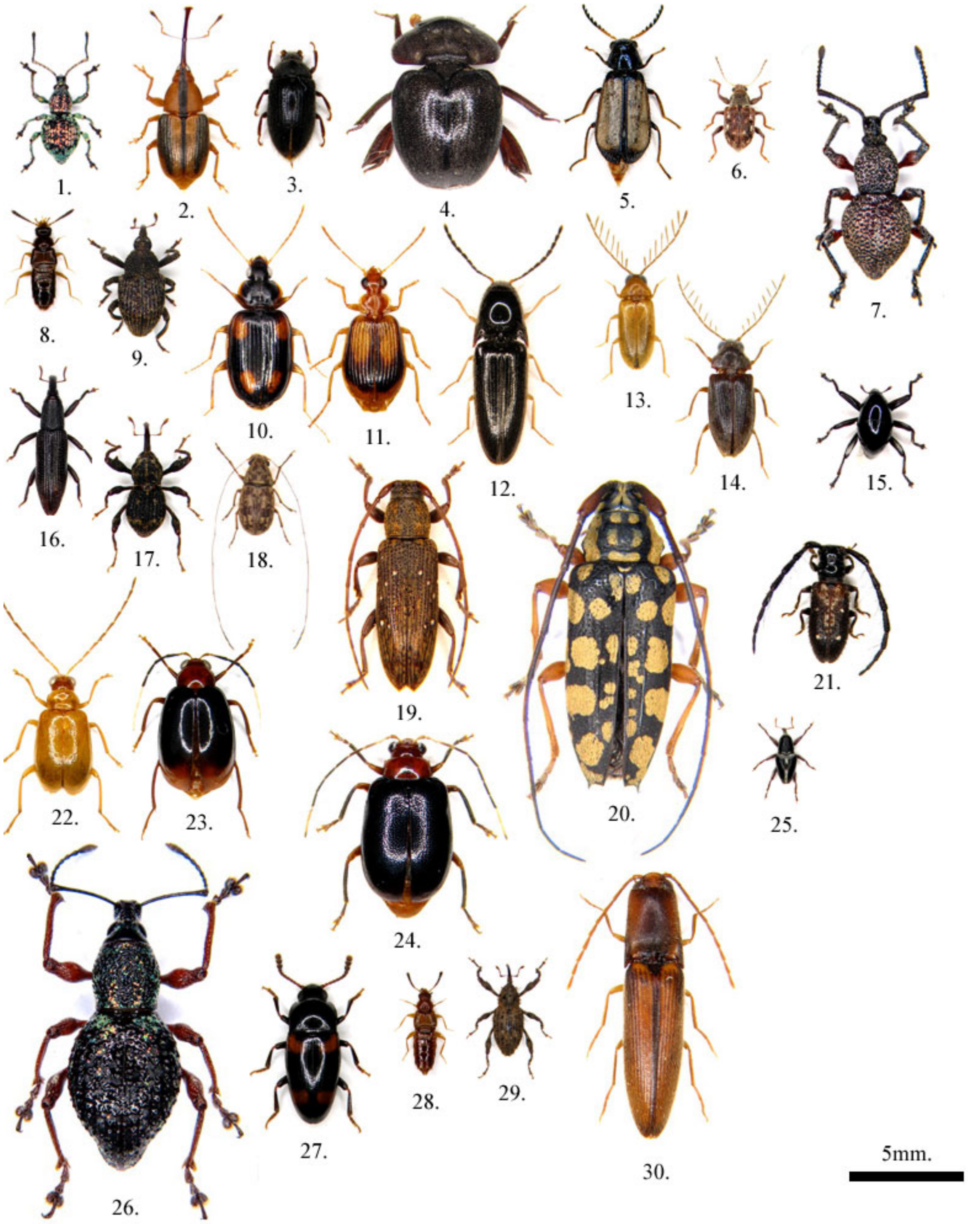


Figure 1.4. The 30 most common lower canopy beetle species from forest sites in the study area (from most to least abundant): 1. Entiminae sp. 3 (Curculionidae); 2. Curculioninae sp. 6 (Curculionidae); 3. *Sostea* sp. 1 (Dryopidae); 4. *Paulianostes meryni* (Ceratocanthidae); 5. Melyridae sp. 1; 6. Eumolpinae sp. 6c (Chrysomelidae); 7. Entiminae sp. 2 (Curculionidae); 8. Aleocharinae sp. 43 (Staphylinidae); 9. Cryptorhynchinae sp. 69 (Curculionidae); 10. *Dolichoctis tetracolon* (Carabidae); 11. *Lebia* sp. 7a (Carabidae); 12. Elateridae sp. 2; 13. Ptilodactylidae sp. 5; 14. Ptilodactylidae sp. 6; 15. Brachyceridae sp. 1; 16. Cossoninae sp. 16b (Curculionidae); 17. Molytinae sp. 5c (Curculionidae); 18. *Exillis* sp. 2 (Anthribidae); 19. *Sybra* sp. 7a (Cerambycidae); 20. *Tmesisternus wallacei* (Cerambycidae); 21. Lamiinae sp. 19 (Cerambycidae); 22. *Aulacophora* sp. 2f (Chrysomelidae); 23. *Monolepta* sp. 38 (Chrysomelidae); 24. *Monolepta* sp. 9b (Chrysomelidae); 25. Conoderinae sp. 61 (Curculionidae); 26. Entiminae sp. 1c (Curculionidae); 27. Erotylidae sp. 2; 28. Aleocharinae sp. 4 (Staphylinidae); 29. Molytinae sp. 43 (Curculionidae); 30. Elateridae sp. 5. Source: www.beetle-diversity.com.

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CHAPTER 2

THE CONTRIBUTION OF CACAO AGROFORESTS TO THE CONSERVATION OF LOWER CANOPY ANT AND BEETLE DIVERSITY IN INDONESIA

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Abstract

The ongoing destruction of tropical rainforests has increased the interest in the potential value of tropical agroforests for the conservation of biodiversity. Traditional, shaded agroforests may support high levels of biodiversity, for some groups even approaching that of undisturbed tropical forests. However, it is unclear to what extent forest fauna is represented in this diversity and how management affects forest fauna in agroforests. We studied lower canopy ant and beetle fauna in cacao agroforests and forests in Central Sulawesi, Indonesia, a region dominated by cacao agroforestry. We compared ant and beetle species richness and composition in forests and cacao agroforests and studied the impact of two aspects of management intensification (the decrease in shade tree diversity and in shade canopy cover) on ant and beetle diversity. The agroforests had three types of shade that represented a decrease in tree diversity (high, intermediate and low diversity). Species richness of ants and beetles in the canopies of the cacao trees was similar to that found in lower canopy forest trees. However, the composition of ant and beetle communities differed greatly between the agroforest and forest sites. Forest beetles suffered profoundly from the conversion to agroforests: only 12.5% of the beetle species recorded in the forest sites were also found in the agroforests and those species made up only 5% of all beetles collected from cacao. In contrast, forest ants were well represented in agroforests, with 75% of all species encountered in the forest sites also occurring on cacao. The reduction of shade tree diversity had no negative effect on ants and beetles on cacao trees. Beetle abundances and non-forest ant species richness even increased with decreasing shade tree diversity. Thinning of the shade canopy was related to a decrease in richness of forest ant species on cacao trees but not of beetles. The contrasting responses of ants and beetles to shade tree management emphasize that conservation plans that focus on one taxonomic group may not work for others. Overall ant and beetle diversity can remain high in shaded agroforests but the conservation of forest ants and beetles in particular depends primarily on the protection of natural forests, which for forest ants can be complemented by the conservation of adjacent shaded cacao agroforests.

Keywords: arthropods, biodiversity, cultivated land, deforestation, habitat preference, knockdown fogging, lower canopy

Introduction

Landscapes throughout the tropics are increasingly dominated by agriculture (Achard et al. 2002). In such landscapes, agroforests often represent the only habitat with considerable tree cover (Schroth et al. 2004) and may be important refuges for tropical biodiversity (Rice and Greenberg 2000; Donald 2004; Schroth et al. 2004). Assessments of tropical biodiversity that have included agroforests have often found high levels of species richness within these systems, even resembling that of undisturbed tropical forests for certain groups (e.g., Perfecto et al. 1997; Lawton et al. 1998; Schulze et al. 2004; Pineda et al. 2005; Shahabuddin et al. 2005).

However, species-rich tropical agroforests are increasingly subject to modifications that involve reductions in shade tree diversity and thinning or even the complete removal of shade canopies. Such losses of agricultural heterogeneity are expected to increase the yields of the main crops (Johns 1999; Belsky and Siebert 2003; Zuidema et al. 2005), but decrease the diversity of most animal groups within the agroforests, including ants (Perfecto et al. 2003; Armbrecht et al. 2004; Philpott and Foster 2005), bees (Klein et al 2002), beetles (Perfecto et al. 1997), butterflies (Perfecto et al. 2003) and birds (Perfecto et al. 2003).

There are two main reasons why the modifications of the shade canopy can result in biodiversity losses. First, reductions of shade tree diversity represent a form of habitat simplification that promotes a few ‘winner’ plant and animal species at the cost of many pristine ‘loser’ species (McKinney and Lockwood 1999). This increasing habitat homogeneity can drive biodiversity loss as the availability of nesting sites declines (Klein et al. 2002 for bees; Armbrecht et al. 2004 and Philpott and Foster 2005 for ants) and important food plants disappear (Perfecto et al. 2003 for fruit-feeding butterflies; Waltert et al. 2004 for birds). Second, the reduction or complete removal of the shade canopy is usually accompanied by changes in temperature and humidity that may indirectly lead to decreases in particularly ant diversity (Perfecto and Vandermeer 1996; Armbrecht et al. 2005) by favoring ecologically dominant ant species (Room 1971; Gibb and Hochuli 2003), which can even lead to cascades of further biodiversity losses (O’Dowd et al. 2003).

Studies on biodiversity conservation in agroforests that also included beta diversity, have found considerable changes in faunal composition between pristine forests and coffee or cacao dominated agroforests. These studies mostly focused on insects (e.g., Armbrecht et al. 2005; Pineda et al. 2005; Shahabuddin et al. 2005) but such a large turnover from natural to cultivated forests has also been found for birds (Waltert et al. 2004). Despite the wealth of studies on the role of agroforestry in biodiversity conservation, it remains largely unknown to what extent agroforests can support forest fauna, and how this faunal component responds to changing shade canopy management (but see Perfecto et al. 2003; Armbrecht et al. 2005).

In the tropics, ants and beetles are the major contributors to the richness of canopy dwelling insect fauna (e.g., Erwin 1982; Lawton et al. 1998). Moreover, ants are dominant elements of tropical ecosystems because of frequent interactions with other insect groups and include abundant predators, decomposers and herbivores (Room 1971; Majer 1972, 1976; Majer et al. 1994; O'Dowd et al. 2003). Nevertheless, the diversity of ants and beetles in cacao dominated agroforests still remains poorly studied, particularly in the context of biodiversity conservation (but see Room 1971; Majer 1972, 1976; Majer et al. 1994; Delabie et al. this issue for cacao ants).

We examined ants and beetles in the lower part of the canopy of natural forests and cacao dominated agroforests in order to investigate the following two questions concerning the role of shaded agroforests in the conservation of biodiversity: (i) Do agroforests resemble natural forests in terms of the ant and beetle assemblages in the lower canopy? and (ii) Does modification of the shade canopy of agroforests affect the diversity of forest and non-forest species within these two groups? The systems selected for our study were in the margin area of a large natural rainforest in Central Sulawesi, Indonesia, a major cacao producing region (Potter 2001) and a major biodiversity hotspot (Myers et al. 2000). By distinguishing between 'forest' and 'non-forest' species of two important insect groups in tropical canopies, we provide a quantification of the proportion of species richness that is possibly native to forest habitats that can also be supported by agroforests. Whereas biodiversity may overall remain high, forest species may be particularly sensitive to changing management practices.

Methods

Study sites

This study took place in and around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (1°30'24" S, 120°2'11" E, 800 – 900 masl). Toro is located at the western border of the unfragmented, 231,000 hectare Lore Lindu National Park, about 100 kilometres south of Palu, the capital city of Central Sulawesi. The region has an annual average (± SE) temperature of 24.0 (± 0.16) °C and a mean monthly rainfall of 143.7 (± 22.74) mm. There are no clear seasonal fluctuations. The natural vegetation of the National Park around the village is submontante rainforest.

The agricultural landscape in the region is highly heterogeneous, consisting of a patchy mosaic of pasture, hedges and cacao dominated agroforests, which is typical for the region. Cacao production in the region increased strongly in the 1990s when large areas of coffee agroforests were converted to cacao agroforests (Potter 2001). Cacao agroforests in the Toro village are owned and managed by small-scale farmers. Shade tree management in the region was dynamic and farmers generally planned to remove shade trees in the opinion that this would increase cacao production.

We defined a priori three types of agroforests, which represented a gradient of shade tree diversity but were comparable in terms of basal area and stem density:

I. Cacao agroforests with diverse, natural shade trees that had been retained from previously undisturbed forest when it was thinned and underplanted with cacao trees (DNS). Cacao agroforestry was the first form of cultivation in these sites (since 8-15 years). These agroforests still had high numbers of native shade trees, and even some endemic species.

II. Cacao agroforests with shade tree stands dominated by various species of planted shade trees (DPS). These sites had a longer history of cultivation (longer than 20 years e.g., as coffee agroforests) and trees from the previous forest cover were all replaced by various planted fruit and timber trees that provided the owners with non-market products. Among these trees were some native (including a few endemic) species.

III. Cacao agroforests with a low diversity of planted shade trees (SPS). These sites also had a longer history of cultivation (longer than 20 years e.g., as coffee plantations). Management of these agroforests was aimed at maximum cacao productivity. Shade was provided predominantly by the non-indigenous leguminous trees *Gliricidia sepium* and *Erythrina subumbrans* that are nitrogen fixing. Some native timber or fruit tree species were also grown, none of which were endemic.

We selected four replicates of each of the three types of cacao agroforests. Sites were selected based on the age of the cacao trees, which was on all sites between 7 and 10 years. At the time of this study agroforestry was non-intensive in each site, with little use of fertilizers and pesticides. Farmers regularly pruned trees and weeded the plantations (2-3 times per year).

Additionally, four forest sites (NF) were selected close to the village, but well within the national park and representative for the submontane forest in the area. These forest sites were part of the continuous Lore Lindu National Park and at least 300 m away from forest sites where selective logging occurred. Selective logging was allowed in the national park's margins, only by local people and only for local timber use. In the selected sites minor rattan extraction occurred. The sites had more than 50 tree species per 0.25 ha and a basal area (m^2/hectare) that was high compared to other primary forests in Southeast Asia. The forest sites had significantly higher basal areas and stem densities than the agroforests.

The minimum distance between study sites was 300 meters and the maximum distance was about 5 kilometers. All sites were between 850 and 1,100 meters above sea level. The agroforests did not have sharp borders with other habitat types, but gradually changed into other forms of land-use. The agroforests formed a continuous band along the forest margin. Boundaries between agroforests were arbitrary based on ownership. Therefore, we marked core areas of 30 x 50 m in the middle of each site. Land-use and types of shade tree stands did not change within these areas. Sites of different habitat types were geographically interspersed so that none of the habitat types were spatially clustered.

The percent canopy cover above the cacao layer was estimated using a Spherical Densiometer. Canopy cover was estimated at two spots around each studied tree and the mean of these two estimates per tree was used in the analyses.

Collecting ants and beetles from small, lower canopy trees

Within the marked core areas, four trees were selected, which were of similar age and size. These were cacao trees in the agroforests (n=48, height: 3.4 ± 0.56 m standard error) and small, shade-dwelling lower canopy trees (n=15, height: 6.3 ± 1.90 m) in the natural forest sites with canopy sizes similar to those of the selected cacao trees. At one forest site, ants and beetles from only three trees could be sampled due to a technical problem.

In order to characterize the forest insect fauna as completely as possible, we sampled insects on a diverse set of trees in the forest understory. The 15 trees in the forest sites were identified by R. Pitopang (Herbarium Celebense, Palu, Indonesia) and belonged to 14 species of 10 families. Only on one occasion, two subject trees in one forest site were of the same family. None of the forest trees were recorded flowering or fruiting at the time the sampling took place. At the time of the survey, cacao in the region was between a main flowering and a harvesting period, although minor flowering and fruiting occurred throughout the year.

Lower canopy dwelling ant and beetle fauna was sampled using canopy knockdown fogging, which is an effective and widely used technique for collecting arthropods from tree crowns (Perfecto et al. 1997; Lawton 1998). With a SwingFog TF35, a fog of 1% pyrethroid insecticide (Permethrin) was blown horizontally into the target canopy to avoid collecting insects from higher canopy layers. Killed arthropods were collected from a 4 square meter sheet of white canvas placed directly under each tree. We randomly selected one site per day and sampled all four trees between 8:00 and 9:00 at the time of day of lowest wind speed and rainfall probability from December 17 2003 to January 1 2004.

Identifications

To date, the extremely high species richness of tropical regions remains largely undescribed by taxonomists and the insect fauna in Indonesia is no exception (Basset 2001). Therefore, we chose to sort the collected insects into units based on external morphology (morphospecies). Ant sorting was carried out by Indonesian ant specialist Akhmad Rizali (IPB Bogor, Indonesia), based on literature (Bolton 1994) and reliable digital resources (e.g., http://www.antweb.org and http://www.antbase.de). Identifications of beetles were carried out by Boris Büche and Christoph Bayer (Berlin, Germany). Where necessary, beetle morphospecies were sorted based on genitalia preparations. All morphospecies were photographed and posted on the internet (http://www.ant-diversity.com and http://www.beetle-diversity.com) through which specialists were contacted internationally for identifications based on the photographs (see acknowledgements) and for further taxonomic work.

In our quantifications of faunal turnover between the natural forest sites and the agroforests, we categorized species as ‘forest species’ when they occurred on any of the selected trees (n=15) in the forest sites and as ‘non-forest species’ if they were only found on cacao trees. We acknowledge that the resulting summed amount of ‘non-forest species’ could be an overestimate that can reduce when more forest sites are included. Therefore, we only compare amounts of ‘non-forest species’ on the tree or site level.

Data analysis

From the observed species richness per site we calculated first order Jackknife estimators for species richness. Observed species richness in field studies is typically an underestimate of the actually occurring number of species (Colwell and Coddington 1994), which calls for the use of species richness estimators (see also Schulze et al. 2004). We calculated the Bray-Curtis similarity index for each pair-wise site comparison as a measure for between-site similarity of ant and beetle assemblages. This similarity index ranges between 0 (no shared species) and 1 (fully similar community composition) and takes abundances of species into account. Using the Bray-Curtis similarity indices we conducted a multidimensional scaling (MDS) to obtain a two-dimensional representation of the similarities between species composition at the study sites (Shahabuddin et al. 2005). MDS is a powerful method for ordinating similarity matrices as it is independent of the type of data distribution. The accompanied stress value of an ordination indicates the goodness of fit of the scaling to the similarity matrix. Stress values of 0.20 and lower indicate a good fit (StatSoft Inc. 1984-2004). The first order Jackknife estimator for total species richness and the Bray-Curtis index for faunal similarity served well in comparable studies (Schulze et al. 2004 and Armbrecht et al. 2005).

The effects of habitat types (forest and three types of cacao agroforests) on observed and estimated species richness per site were tested in one-way ANOVA's. To test for effects of forest conversion to cacao agroforests on species richness and abundance per tree, we used general linear models (GLMs) with habitat type as a fixed factor and trees nested within sites. The effect of shade cover was only tested within the agroforests (12 sites and 48 trees, pooled across the three types of agroforests) in a GLM with habitat type as a fixed factor, trees nested within sites and canopy cover included as a covariate. Trees and sites were in all models entered as random factors. Post-hoc tests were conducted using Tukey's HSD (honestly significantly different) tests.

Data were square root transformed where necessary to achieve normal distribution of model residuals. Arithmetic means are given ± one standard error. The species richness estimator and similarity indices were calculated using EstimateS 7.0 (Colwell 2004). All other analyses were carried out using Statistica 7.0 (StatSoft Inc. 1984-2004).

Results

Upper canopy cover in the agroforests ranged from 82.3 ± 1.65% to 42.5 ± 7.46%. This was significantly less than in any of the natural forest sites ($F_{(3,\ 56)}=32.0$, $p<0.001$, Table 2.1). Further, canopy cover in agroforests with planted shade was significantly less than in the agroforests with natural shade.

Effects of cacao agroforestry and shade management on ant and beetle communities

In total 3,247 ants were collected (55% of all arthropods) belonging to 6 subfamilies, 18 genera and 44 species (Appendix 2.1). The five most common species (Table 2.2) made up 34% of all ants collected and were encountered in both the forest sites and agroforests. The observed species richness per site did not differ between forest and agroforests ($F_{(3,\ 12)}=1.64$, $p=0.23$, Figure 2.1a), and the same was true for the estimated species richness ($F_{(3,\ 12)}=2.68$, $p=0.09$, Figure 2.1a).

In total, 15 ant species (75% of all ant species recorded in the forest sites) were recorded in both the forest sites and in agroforests. However, the multidimensional scaling (MDS) of the Bray-Curtis similarity indices (Figure 2.2a) showed that the ant fauna of cacao in agroforests was distinct from that of forest lower canopy trees. Moreover, agroforests with natural shade had a distinct ant community from that of agroforests with shade tree stands dominated by one or two species of planted leguminous trees.

Ant species richness and abundance per tree did not differ between forest and cacao trees (overall averaged species richness: 3.8 ± 0.26, $F_{(3,\ 55.3)}=1.57$, $p=0.21$; overall averaged abundance: 51.4 ± 7.46, $F_{(3,\ 55)}=0.27$, $p=0.85$, Figure 2.3a). Overall ant species richness on cacao trees was, however, negatively affected by decreasing shade cover ($R^2=0.09$, $p=0.02$).

Table 2.2. Total abundance of the five most common ant species (34% of all collected ant individuals) in natural forest and three types of cacao agroforests in central Sulawesi.

	NF	DNS	DPS	SPS	Total
Dolichoderus sp. 1 (Dolichoderinae)	3	364	48	54	469
Paratrechina sp. 1 (Formicinae)	1	24	346	66	437
Polyrhachis (Myrmhopla) sp. nov. (Formicinae)	180	70	34	19	303
Crematogaster sp. 2 (Myrmicinae)	276	1	1	24	302
Anoplolepis gracilipes (Formicinae)	1	0	1	287	289

NF = Natural forest, DNS = Diverse natural shade, DPS = Diverse planted shade, SPS = Simple planted shade

A total of 633 beetles were collected (10% of all arthropods) belonging to 37 families and 209 species (Appendix 2.2). The five most abundant beetle species (Table 2.3) made up 30% of all beetles and none of them was among the species collected from the lower canopy trees in the forests. Neither the observed species richness per site ($F_{(3,\ 12)}$= 2.03, p=0.16, Figure 2.1b) nor the estimated species richness ($F_{(3,\ 12)}$ =1.92, p=0.18, Figure 2.1b) differed between forest and agroforest sites.

Only five forest beetle species (12.5% of all species recorded in the forest sites) were recorded on cacao. The MDS of the Bray-Curtis similarity indices (Figure 2.2b) showed a sharp distinction between the beetle fauna of cacao trees in agroforests and that of lower canopy trees in the forest sites. Moreover, agroforests with natural shade trees had a distinct faunal assemblage from that of the agroforests with shade tree stands dominated by one or two species of planted leguminous trees.

On a per tree basis, beetle species richness did not differ between forest and cacao trees (overall average: 6.2 ± 0.63, $F_{(3,\ 55)}$=2.30, p=0.09, Figure 2.3b). Conversely, beetle abundance on cacao trees under simple planted shade (15.9 ± 3.26) was significantly higher than on lower canopy forest trees (4.7 ± 0.91; $F_{(3,\ 55)}$=3.37, p=0.02, Figure 2.3b). Changes in canopy cover affected neither species richness nor abundance of beetles on cacao trees (species richness: R^2=0.09, p=0.21; abundance: R^2=0.04, p=0.12).

Table 2.3. Total abundance of the five most common beetle species (30% of all collected beetle individuals) in natural forest and three types of cacao agroforests in central Sulawesi.

	NF	DNS	DPS	SPS	Total
Monolepta sp. 40 (Chrysomelidae)	0	7	22	38	67
Anthelephila sp. 1 (Anthicidae)	0	0	15	25	40
Demotina sp. 6b (Chrysomelidae)	0	10	7	15	32
Apogonia sp. 1 (Scarabaeidae)	0	2	14	11	27
Amarygmus sp. 5a (Tenebrionidae)	0	11	5	10	26

NF = Natural forest, DNS = Diverse natural shade, DPS = Diverse planted shade, SPS = Simple planted shade.

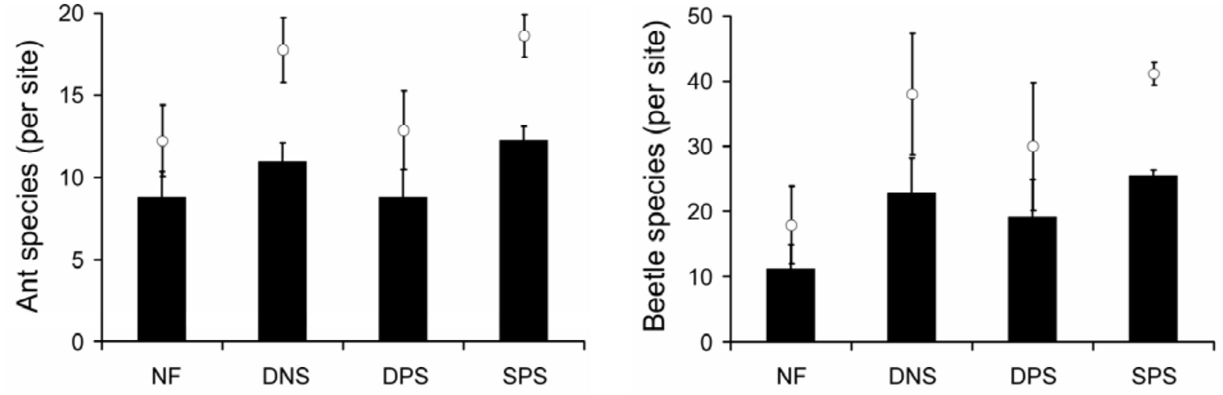

Figure 2.1. Means and standard errors of species richness of ants (a) and beetles (b) in the lower canopy of four habitat types in Central Sulawesi, Indonesia: natural forest (NF), cacao agroforests with diverse natural shade trees (DNS), cacao agroforests with diverse planted shade trees (DPS) and cacao agroforests with simple shade tree stands dominated by one or two species (SPS). Bars are observed values and circles are first order Jackknife estimators.

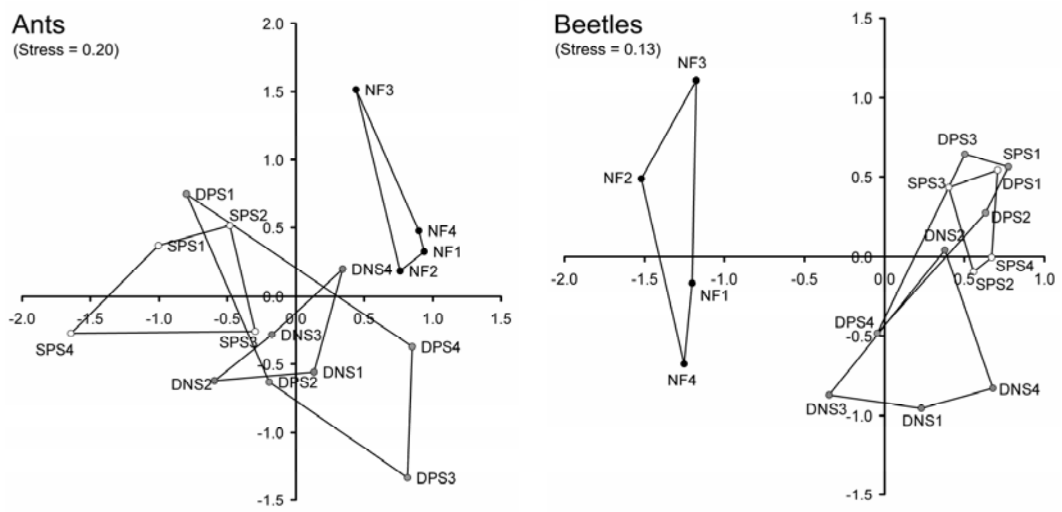

Figure 2.2. Multidimensional scaling plots based on Bray-Curtis similarity indices for ant (a) and beetle (b) species assemblages observed in the lower canopy of four habitat types in Central Sulawesi, Indonesia (four sites each): natural forest (NF), cacao agroforests with diverse natural shade trees (DNS), cacao agroforests with diverse planted shade trees (DPS), and cacao agroforests with simple shade tree stands dominated by one or two species (SPS). The stress values are 0.20 or lower, indicating a good fit of the scaling with the similarity index.

Responses of forest versus non-forest ant and beetle species to shade canopy composition and openness

The richness of non-forest ant species increased on cacao under shade tree stands that were dominated by planted leguminous trees ($F_{(2,\ 41)}$=3.66, p=0.03, Figure 2.3a), whereas the species richness of forest ants on cacao trees was unaffected by shade tree composition ($F_{(2,\ 41)}$=1.07, p=0.35, Figure 2.3a). However, the number of forest ant species on cacao trees declined significantly with increasing openness of the shade canopy (R^2=0.22, p<0.001, Figure 2.4), whereas the effects of shade thinning on the richness of non-forest species were not significant (R^2<0.001, p=0.96).

Because the five beetle species that were shared between forest and agroforestry sites represented only 5% of all beetle individuals collected from cacao (Figure 2.3b), we did not distinguish between forest and non-forest species in further analyses.

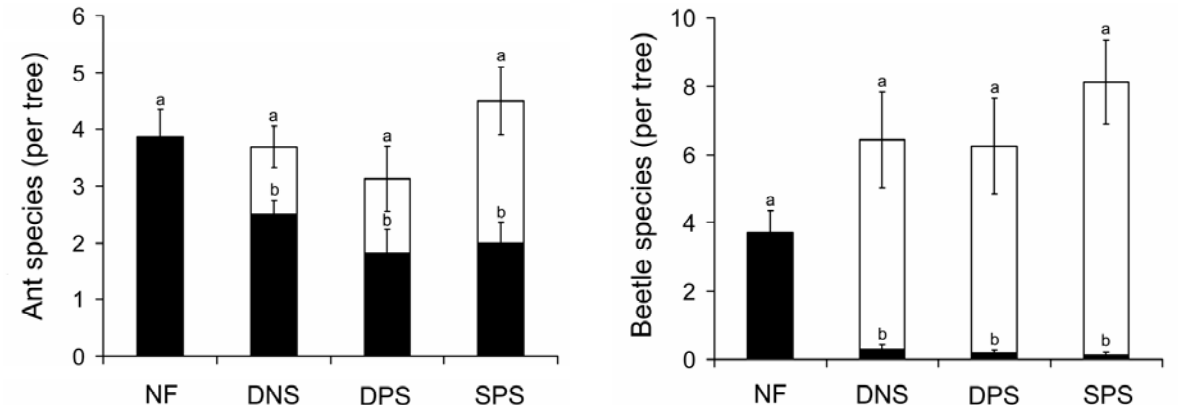

Figure 2.3. Effect of forest conversion on the species richness of ants (a) and beetles (b) per tree in natural forest sites (NF) and cacao agroforests with diverse forest shade (DNS), diverse planted shade (DPS) and simple planted shade (SPS) in Central Sulawesi, Indonesia (means and standard errors). Black bars indicate forest species, white bars indicate other species. Different letters indicate significant differences at $p<0.05$.

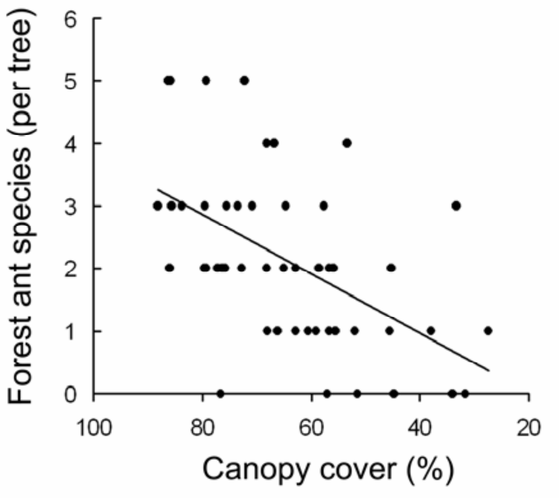

Figure 2.4. Relationship between canopy cover (%) and the number of forest ant species observed per cacao tree in three types of cacao agroforests in Central Sulawesi, Indonesia. The relationship was not significantly different between the three types of agroforests.

Discussion

The species richness of ants and beetles was similar on cacao trees in shaded, cacao dominated agroforests and on lower canopy trees in forest sites, thus underlining the potential of such agroforests for maintaining tropical insect species richness. However, there was a sharp distinction in the composition of ant and beetle communities across forest and agroforestry sites. Hence, without information on the identity of species, species richness comparisons may lead to erroneous conclusions concerning the actual conservation potential of agroforests.

Ant species that occurred in the four forest sites were well represented in the 12 agroforests, with 75% percent of the species observed in the lower canopy of the forest being also observed on cacao trees. These results may be explained by the fact that ant species can profit from the nesting availabilities that are still offered by shaded agroforests (Armbrecht et al. 2004; Philpott and Foster 2005). In contrast, forest beetle communities changed drastically from forest lower canopy to cacao trees in agroforests. Only 12.5% of the beetle species recorded on the forest trees was also found on cacao trees, and these shared species made up only 5% of all collected beetle individuals. Thus, the replacement of forest by agroforests has pronounced effects on the ant and beetle communities. Conservation on the species level strongly depended on the taxon examined. Whereas forest beetles were almost completely replaced by non-forest species, forest ant species were comparably well preserved in the cacao agroforests.

The effect of agroforestry management on forest and non-forest beetles and ants depends on whether management changes the diversity of shade trees or the cover of shade canopy. Firstly, reduced habitat heterogeneity may drive species losses in that complex, heterogeneous habitats harbour higher species richness than simple, homogeneous habitats (McKinney and Lockwood 1999; Armbrecht et al. 2004). In our study, the reduction of shade tree diversity increased habitat homogeneity. Ant and beetle communities on cacao under homogeneous, planted shade were distinct from those on cacao shaded by trees from the original forest. The reduced shade tree diversity, however, did not affect total ant and beetle species richness per site and per tree, which suggests that none of the shaded agroforests were under such intense management that species richness per se was threatened. Such threats are known to occur in conversions to zero-shade cacao plantations or annual crops (Perfecto et al. 1997; Schulze et al. 2004; Armbrecht et al. 2005; Shahabuddin et al. 2005). Moreover, the richness of non-forest ant species even increased on cacao trees in agroforests shaded by just leguminous trees, compared to the other two types of agroforests. Similarly, the reduction of shade tree diversity led to an increase in beetle abundance (almost only non-forest species), but not species richness, which suggests that a few beetle species also profited from increasing shade tree homogeneity.

The species that profit from cultivation and management practices are least interesting from a conservation point of view and are unlikely to be threatened by conversions of forests to agroforests. For example, the invasive Crazy Ant *Anoplolepis gracilipes* (Smith 1857) (O'Dowd et al. 2003) was rarely found at forest sites, but was abundant under planted shade tree stands (Table 2.2). Additionally, the most wide-spread and abundant beetle species (10% of all beetles collected) on cacao in our study was a leaf beetle of the genus *Monolepta* (Chrysomelidae: Galerucinae) that was only found on cacao trees (Table 2.3), although it did not feed on its leaves but was the most important herbivore on the planted shade tree species *Erythrina subumbrans* (Leguminosae) (M.M. Bos and B. Büche *unpublished data*).

Secondly, agroforest modification can be accompanied by the thinning of shade tree stands (e.g., Perfecto et al. 1997; Klein et al. 2002). In our study, planted trees created less shade than natural trees. Ant and beetle abundance and beetle species richness per tree were not affected by increasing canopy openness, whereas ant species richness declined when the canopy became more open, particularly because of the strong response of forest ant species. Responses of ants to microclimatic changes that are associated with shade thinning – higher temperatures and lower humidity – are known, and a reduction in shade levels may increase dominance by a few ant species (Room 1971; Perfecto and Vandermeer 1996; Gibb and Hochuli 2003).

Conclusions

Shaded agroforests that are dominated by cacao in the lower canopy appear to contribute to the conservation of ant and beetle species richness. However, biodiversity assessments should include direct comparisons with adjacent natural forests to avoid overestimates of actual conservation potential of agroforests for forest fauna. Our results support previous studies (e.g., Waltert et al. 2004; Armbrecht et al. 2005; Shahabuddin et al. 2005) that showed that forest species are often sensitive to the changes in habitat characteristics that accompany the conversion of natural forests into agroforests. Highly diverse taxonomic groups such as beetles may show drastic species turnover after conversion to agroforests. In contrast, shaded agroforests may be a suitable surrogate habitat for native ant communities, but management also matters in that forest ants suffer from reduced canopy cover, possibly because of altered interactions with ecologically dominant species that are promoted by the accompanied changes in the microclimate.

Ant and beetle assemblages in the cacao agroforests were dominated by species of low conservation priority that are unlikely to be threatened by the ongoing destruction of tropical rainforests. The different responses to the same agroforest modifications of the ecologically important ants and beetles emphasize the need to use multiple taxa as indicator organisms for habitat destruction and effects of conservation strategies. Shaded agroforests can support a high diversity of ants and beetles, but few forest species in the case of beetles, so conservation plans should primarily build upon the protection of natural forests, complemented by well-shaded agroforests.

Acknowledgments

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Appendix

Appendix 2.1. Number of ant individuals (Ind.) and species (Spp.) per subfamily and genus collected in natural forest and three types of cacao agroforests in Central Sulawesi, Indonesia.

		NF		DNS		DPS		SPS		Total	
Subfamily	Genus	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.
Dolichoderinae	*Dolichoderus*	3	1	364	1	48	1	78	2	493	2
	Tapinoma	0	0	48	1	0	0	22	1	70	1
	Technomyrmex	0	0	3	1	0	0	0	0	3	1
Ectatomminae	*Gnamptogenys*	102	1	23	1	1	1	0	0	126	1
Formicinae	*Anoplolepis*	1	1	0	0	1	1	287	1	289	1
	Camponotus	2	2	38	3	75	2	9	2	124	3
	Echinopla	13	2	2	1	1	1	7	1	23	2
	Oecophylla	8	1	18	1	8	1	0	0	34	1
	Paratrechina	1	1	28	2	484	3	78	3	591	4
	Polyrhachis	289	8	164	8	97	6	297	11	856	15
Myrmicinae	*Cataulacus*	0	0	0	0	0	0	4	1	4	1
	Crematogaster	276	1	48	3	190	3	61	3	575	3
	Paratopula	0	0	6	2	4	1	1	1	11	2
	Pheidole	2	1	1	1	0	0	0	0	3	1
	Secostruma	1	1	0	0	0	0	0	0	1	1
	Tetramorium	0	0	0	0	10	1	15	2	25	3
Ponerinae	*Pachycondyla*	0	0	1	1	0	0	0	0	1	1
Pseudomyrmecinae	*Tetraponera*	0	0	4	1	7	1	7	1	18	1
Total		707	20	748	27	926	22	866	29	3247	44

NF = Natural forest, DNS = cacao under diverse natural shade, DPS = cacao under diverse planted shade, SPS = cacao under simple planted shade.

Appendix 2.2. Number of beetle individuals (Ind.) and species (Spp.) per superfamily and family collected in natural forest and three types of cacao agroforests in Central Sulawesi, Indonesia.

		NF		DNS		DPS		SPS		Total	
Superfamily	Family	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	S
Buprestoidea	Buprestidae	1	1	1	1	0	0	1	1	3	3
Byrrhoidea	Dryopidae	2	1	0	0	0	0	0	0	2	1
	Limnichidae	0	0	3	3	0	0	3	1	6	3
	Ptilodactylidae	2	2	1	1	1	1	1	1	5	5
Cantharoidea	Cantharidae	1	1	2	2	0	0	1	1	4	4
	Lycidae	2	2	7	5	2	2	0	0	11	7
Caraboidea	Carabidae	3	3	3	3	4	4	8	6	18	11
	Cicindelidae	1	1	0	0	0	0	0	0	1	1
Chrysomeloidea	Cerambycidae	2	2	4	3	2	1	13	5	21	10
	Chrysomelidae	7	4	42	17	43	9	96	13	188	33
Cleroidea	Cleridae	1	1	2	2	2	2	0	0	5	5
Cucujoidea	Coccinellidae	0	0	1	1	3	2	1	1	5	4
	Endomychidae	0	0	2	2	0	0	0	0	2	2
	Languriidae	1	1	0	0	10	1	4	1	15	2
	Phalacridae	1	1	0	0	0	0	0	0	1	1
	Rhizophagidae	0	0	1	1	0	0	0	0	1	1
Curculionoidea	Anthribidae	1	1	2	2	7	2	6	4	16	7
	Apionidae	0	0	0	0	0	0	1	1	1	1
	Attelabidae	1	1	0	0	0	0	0	0	1	1
	Brentidae	0	0	0	0	2	2	2	2	4	4
	Curculionidae	38	14	26	11	14	8	24	14	102	36
	Dryophtoridae	0	0	1	1	0	0	0	0	1	1
	Rhynchitidae	0	0	0	0	1	1	1	1	2	2
Elateroidea	Elateridae	3	1	8	6	6	3	3	2	20	11
	Eucnemidae	0	0	0	0	1	1	1	1	2	2
Histeroidea	Histeridae	0	0	1	1	0	0	1	1	2	1
Scarabaeoidea	Ceratocanthidae	2	1	0	0	0	0	0	0	2	1
	Scarabaeidae	0	0	4	3	25	5	28	5	57	8
Staphylinoidea	Staphylinidae	0	0	1	1	0	0	0	0	1	1
Tenebrionoidea	Aderidae	1	1	0	0	1	1	0	0	2	2
	Anthicidae	1	1	1	1	19	2	28	2	49	4
	Colydiidae	0	0	1	1	0	0	1	1	2	1
	Melandryidae	0	0	0	0	1	1	0	0	1	1

	Mordellidae	0	0	6	5	0	0	1	1	7	6
	Othniidae	0	0	0	0	1	1	0	0	1	1
	Salpingidae	0	0	1	1	0	0	0	0	1	1
	Tenebrionidae	0	0	17	6	25	10	29	16	71	24
Total		71	30	138	57	170	51	254	65	633	209

NF = Natural forest, DNS = cacao under diverse natural shade, DPS = cacao under diverse planted shade, SPS = cacao under simple planted shade.

CHAPTER 3

MICROCLIMATIC CHANGES MEDIATE LOSSES OF FOREST ANTS BY PROMOTING SPECIES INVASIONS INTO INDONESIAN AGROFORESTS

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In review with *Diversity and Distributions*

Abstract

Throughout the tropics, agroforests are often the only remaining habitat with a considerable tree cover. Such systems can support high numbers of species and are therefore frequently heralded as the future for tropical biodiversity conservation. However, even slight anthropogenic habitat modification can affect species interactions, thereby facilitating species invasions and suppressing native fauna. We compared the ant fauna of lower canopy trees at natural rainforest sites with that collected from cacao trees in agroforests in Central Sulawesi, Indonesia. The shade tree stands in the agroforests were of three management categories that represented a gradient in canopy cover and shade tree species richness. Ant species assemblages from the lower canopy of primary forest ('forest species') were in agroforests largely replaced by an equally diverse assemblage of species that did not occur at forest sites ('non-forest species'). Within the agroforests, changes in microclimate promoted dominance by one non-forest species in particular: the invasive Crazy Ant *Anoplolepis gracilipes*. Less shaded, warmer and drier agroforests were most likely to be invaded by this species. The richness of 'forest' ant species on cacao trees was not related to the decrease in shade tree diversity or to the microclimate, but decreased significantly in response to the increased dominance by *A. gracilipes*, while numbers of 'non-forest' species remained unaffected. Microclimatic changes in ecologically valuable, shaded agroforests were paralleled by an increase in one of the world's most invasive ant species, which in turn was accompanied by a clear loss in forest ant species. The facilitation of invasive species dominance in forest margins comprises an indirect consequence of anthropogenic habitat modifications that can accelerate native species loss but remains overlooked by simple biodiversity comparisons.

Keywords: Biological invasion, Indonesia, Formicidae, Managed land, Biodiversity, Interspecific interactions, Sulawesi

Introduction

Global-scale conversion of natural ecosystems to agriculture is recognized as the major cause of biodiversity loss, and threatens ecosystem functioning, sustainability and economic security (Hoekstra *et al.* 2005). Tropical rainforests are one of the most species rich and functionally important terrestrial ecosystems on earth (Myers *et al.* 2000). However, in the past 50 years an estimated 32% has been converted to human-dominated systems and a further loss of 10-15% has been projected by 2050 (Millenium Ecosystem Assessment 2005). The hot spot of tropical rainforest conversion is Southeast Asia, with average annual deforestation rates of 2.5 million hectares (0.91%) (Achard *et al.* 2002). With the continuing loss of tropical forests, cultivated areas are gaining interest for their potential value for conserving tropical biodiversity in the frontier between human cultivation and pristine ecosystems (Rice & Greenberg 2000; Bawa *et al.* 2004; Tscharntke *et al.* 2005).

Conservation research has begun to examine the contribution of cultivated forests (agroforests) to local and regional biodiversity, partly due to their low management intensity, and the superficial resemblance of these systems to natural forest (Rice & Greenberg 2000; Bawa *et al.* 2004; McNeely 2004; Schroth *et al.* 2004). Agroforests can indeed support high levels of species richness, even resembling that of undisturbed tropical forests (Room 1971; Majer *et al.* 1994; Perfecto *et al.* 1997; Schulze *et al.* 2004; Tylianakis *et al.* 2006). However, the species richness supported depends on the complexity of the agroforest habitat (Armbrecht *et al.* 2004), and recent intensification of existing tropical agroforests has caused rapid declines in associated biodiversity (Perfecto *et al.* 1997; Siebert 2002; Schulze *et al.* 2004). Despite this wealth of recent studies, little is known about the mechanisms driving detected trends in biodiversity, and the extent to which indigenous forest fauna is represented in the diversity of agroforests.

An independent line of research has examined the effects of invasive species on indigenous community diversity (e.g., Vitousek *et al.* 1996; Rosenzweig 2001; Holway *et al.* 2002a). Because dominant ant species drive dominance hierarchies that result in ‘mosaics’ of ant interactions (e.g., Room 1971; Majer *et al.* 1994), invasions by such species can seriously disrupt indigenous ant assemblies and even threaten native species (Holway *et al.* 2002a; Hill *et al.* 2003; O’Dowd *et al.* 2003; Sanders *et al.* 2003). Species invasions in general may be largely context dependent, such that anthropogenic disruption of ecosystems facilitates species invasions (Elton 1958; Didham *et al.* 2005). For example, competitive interactions between ant species may change as a result of abiotic changes in the environment, which has been suggested to drive ant invasions (Perfecto and Vandermeer 1996; Holway 1998; Holway *et al.* 2002b; Gibbs & Hochuli 2003), and has been shown experimentally with the increased competitive dominance of the Argentine Ant, *Linepithema humile* (Mayr 1868), on irrigated land (Menke and Holway 2006). In the context of biodiversity changes along the frontier of tropical forest conversion, disturbance-mediated species invasions remain unstudied.

Here we examine the direct effects on ant biodiversity of forest conversion to agroforest, and the mediating effect of agroforest management on the dominance of an invasive species in a tropical biodiversity hotspot. We use the Long-legged Crazy Ant, *Anoplolepis gracilipes* (Smith 1857) (Hymenoptera: Formicidae), in Sulawesi, Indonesia to demonstrate that an invasive species can become dominant with increasing anthropogenic habitat modification. Further, we show that richness of forest species, which are most important from a conservation perspective, decreases disproportionately with the invasive species dominance. Invasions of species into disturbed habitats may thus comprise an important, yet unstudied indirect effect of habitat modification on the conservation of native species in cultivated land.

Methods

Study site selection and characterisation

The study took place in and around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (Figure 3.1). The village is at the western border of the 231,000 hectare Lore Lindu National Park, about 100 kilometres south of Palu, the capital city of Central Sulawesi. The region has an annual average (± SE) temperature of 24.0 (± 0.16) °C and a mean monthly rainfall of 143.7 (± 22.74) mm. There is no clear seasonality. The natural vegetation of the National Park around the village is submontante rainforest.

We defined *a priori* three types of agroforests, characterized by different shade tree stands that represented a gradient in tree diversity, but were comparable in terms of basal area and stem density.

i) Cacao agroforests with diverse, natural shade trees that were retained from previously undisturbed forest when it was thinned and underplanted with cacao. Cacao agroforestry was the first form of cultivation in these sites. These agroforests still have high numbers of native shade tree species, and even some endemic species.

ii) Cacao agroforests with shade tree stands dominated by various planted species. These sites have a longer history of cultivation (e.g., as coffee agroforests) and trees from the previous forest cover were all replaced by various planted fruit and timber trees, that provide the owners with non-market products. Among these trees were some native (occasionally endemic) species.

iii) Cacao agroforests with a low diversity of planted shade trees. These sites also have a longer history of cultivation (e.g., as coffee plantations). Management of these agroforests was aimed at maximum cacao productivity, and shade is therefore provided predominantly by the non-indigenous leguminous trees *Gliricidia sepium* and *Erythrina subumbrans,* which are planted because of their nitrogen fixing capabilities that increase resource availability for the cacao trees. Some native timber or fruit tree species are grown, none of which are endemic.

We selected four replicate plots of each of these habitat types (information on tree diversity in the studied sites is given in Gradstein *et al.*, in press):

Cacao production in the region increased strongly in the 1990s (Potter 2001). Cacao agroforests in the Toro village are owned and managed by small-scale farmers. At the time of this study, agroforestry is generally non-intensive, with little use of fertilizers and pesticides on the selected sites. Farmers regularly prune trees and remove herb and litter layers (2-3 times per year). The selected cacao agroforests form part of a continuous band of agroforests along the forest margin. Boundaries between agroforests were arbitrarily based on ownership. Therefore, we marked core areas of 30 x 50m in the middle of each site. Land-use and types of shade tree stands did not change within these areas.

Four forest sites were selected close to the village, but well within the national park, and were representative for the submontane forest in the area. In these forest sites minor rattan extraction occurred. The sites had over 50 tree species per 0.25 ha and a basal area (m^2/hectare) that was high compared to other primary forests in Southeast Asia (Gradstein *et al.* in press).

The different habitat types were geographically interspersed and sites were at least 300 meters away from one another (figure 3.1). The maximum distance between two study sites was about 5 kilometers. All sites were between 850 and 1,100 meters above sea level.

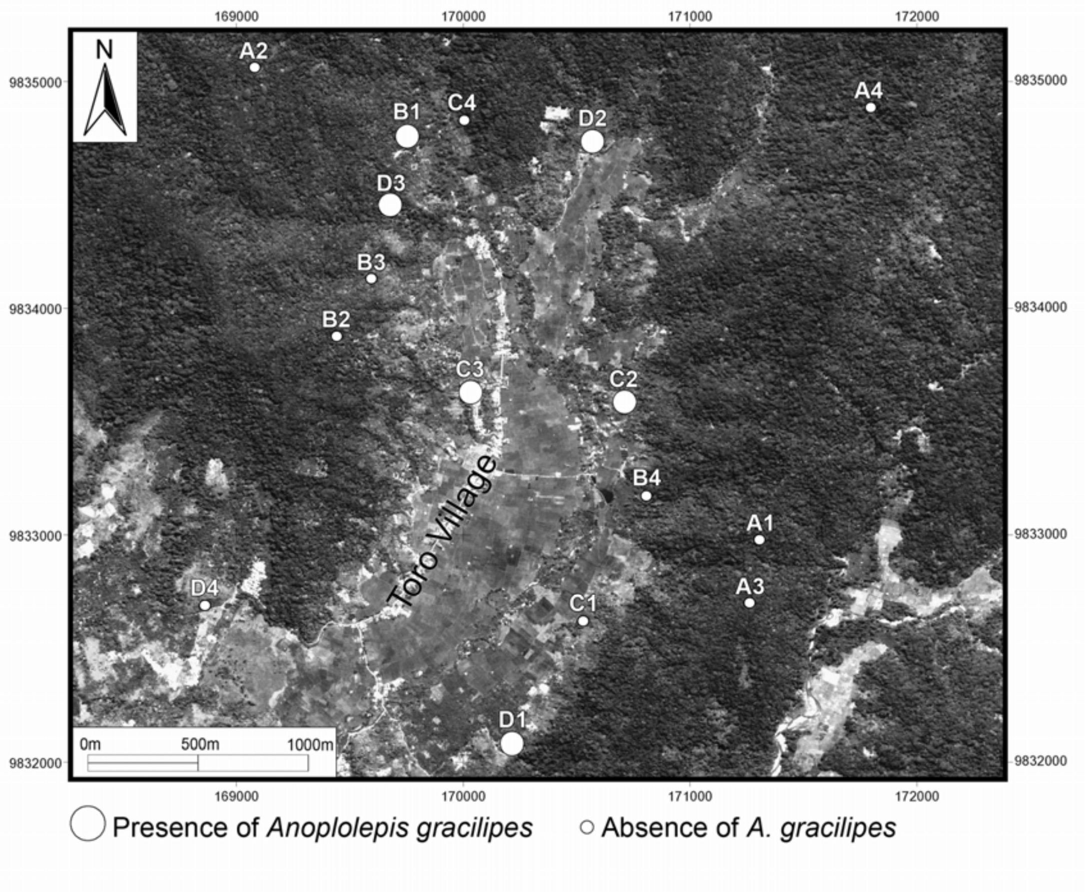

Figure 3.1: A satellite image of the study area showing the distribution of study sites around the village Toro, Central Sulawesi, Indonesia. A1-4 are natural forest sites within the Lore Lindu National Park, B1-4 are agroforests shaded by forest remnants, C1-4 are agroforests shaded by diverse stands of planted trees and D1-4 agroforests shaded by one or two species of planted shade trees. Study sites are indicated with small circles where *Anoplolepis gracilipes* was absent and with large circles where the invasive ant was present. (Image source: QUICKBIRD UTM51S-WGS84. Processed and provided by André Twele, Göttingen University, Germany).

The temperature (ºC) and relative humidity (% RH) at all sites were measured using HOBO$^{©}$ Pro Series data loggers. The loggers recorded the variables digitally every 15 minutes from 7.00-10.00, on three consecutive mornings from a central and shaded spot, at two meters height.

Approximate values for cover (%) by the upper, shading canopy layer were obtained using a Spherical Densiometer©; a concave mirror divided into squares (produced by R.E. Lemmon Forest Densiometers, USA). Canopy cover was measured at eight locations per site, and means were calculated per site.

Collecting ants from small lower canopy trees

The ant fauna was captured from six trees per site, all subject trees were cacao in the agroforests (within the marked core areas) and a highly heterospecific set of similar sized lower canopy trees at the forest sites (96 trees in total). The 24 trees at the forest sites were identified by R. Pitopang of the Herbarium Celebense, Palu, Indonesia and belonged to 21 species of 15 families. On one occasion only were two trees on one site of the same family. By sampling a variety of tree species, we ensured the broadest possible characterization of ant fauna that can be found in lower forest canopy.

Lower canopy-dwelling ant fauna was sampled using canopy knockdown fogging which is an effective and widely used technique for collecting arthropods from tree crowns (e.g., Erwin 1982; Perfecto *et al.* 1997). With a SwingFog TF35 a fog of 1% pyrethroid insecticide (Permethrin©) was blown horizontally into the subject canopy to avoid affecting higher, shading canopy layers. All sampling was carried out on one randomly selected site per day between 8.00 and 9.00am from April to May 2005. Killed ants were collected from a 4 square meter sheet of white canvas placed directly under each tree. With this standardized collection method care was taken to reduce bias due to contamination of our samples with specimens from outside the subject canopy.

Identifications

The study of biodiversity in the tropics is a challenge due to extremely high species richness and the fact that the majority of that richness to date remains undescribed by taxonomy (Basset 2001). With the help of Indonesian ant specialist Akhmad Rizali (Bogor, Indonesia), literature (Bolton 1994) and reliable digital resources (e.g., http://www.antweb.org and http://www.antbase.de) the ants were identified to genus and further sorted to morphospecies (hereafter: species). Additionally, all species were photographed and presented on the internet (http://www.storma.de/ants) through which specialists were contacted internationally and specimens were offered to assure further taxonomic work.

Ant species were categorized as 'forest species' when they occurred at forest sites and the remaining species found only in agroforests were termed 'agroforest species'. The Long-legged Crazy Ant *Anoplolepis gracilipes* was observed locally to be extremely abundant in houses, homegardens and to a lesser extent in agroforests. Although abundance of social insects can be difficult to interpret, we broadly categorised the occurrence of *A. gracilipes* as either ‘dominant’ (more than 50 individuals), ‘present’ (less than 30 individuals) and ‘absent’ to represent the large, naturally occurring differences in abundance.

Statistical analyses

The environmental variables: canopy cover, relative humidity and temperature were significantly correlated with each other (Spearman rank correlation, $p<0.05$). Therefore, we combined the three variables into a single ‘microclimate’ factor using factor analysis. The resulting microclimate factor represented 82% of overall variation of the combined variables and 66% of the variation between agroforests. The factor differed significantly between habitats (ANOVA: $F_{(3, 68)}=64.9$, $p<0.0001$); the forest sites were significantly more shaded, cooler and more moist than any of the agroforests whereas the three different agroforestry types did not differ significantly. The increase in the microclimate factor represented an increase in temperature and decreases in relative humidity and percent canopy cover.

The variation in ant species richness per tree was compared in forests and agroforests using a nested ANOVA with habitat type as a fixed factor and trees nested within sites. As the focus of our investigation was on the effects of agroforest simplification and because the diversity of tree species in the forest made comparison with agroforestry difficult, all further analyses were conducted solely on agroforestry sites ($n_{sites}=12$ and $n_{trees}=72$).

Impacts of shade simplification (habitat type) and the microclimate factor on cacao dwelling ant species richness were tested simultaneously in general linear models (GLMs) with habitat type as a fixed variable and trees nested within sites. Responses of cacao-dwelling ant species richness to the occurrence of *Anoplolepis gracilipes* were evaluated using similar models with the dominance by the invasive species also included as categorical predictor variable. To ensure that effects of *A. gracilipes* on species richness were not simply due to covariation of this ant with microclimate changes, we used Type 1 sums of squares (decomposition of variance) and included the microclimate factor ahead of dominance by *A. gracilipes* in the GLM. Data were square root transformed where necessary to achieve normal distribution of model residuals.

All analyses were done using Statistica 7.0 (StatSoft inc. 1984-2004). Arithmetic means are given ± 1 standard error.

Results

A total of 13,835 ants were collected from 24 small lower canopy trees in four forest sites and from 72 cacao trees in 12 agroforests (shaded by three types of tree stands: diverse natural shade, diverse planted shade and simple planted shade). The ants were identified to 7 subfamilies and 16 genera and sorted to 84 species (Appendix 3.1). Species richness did not correlate with abundance (Spearman rank r=0.03, p>0.7).

Forty species were assigned as forest species (i.e., found in the forest sites), and 44 as non-forest species (i.e., found in the agroforests only). Twenty-two forest species (55%) were also collected from cacao trees in agroforests. In total 2,287 individuals of the Crazy Ant *Anoplolepis gracilipes* were collected from 14 trees, which made this species the most abundant non-forest species (Appendix 3.1). Occurrence was categorized as present but not dominant on eight trees (average number of individuals 11.7 ± 3.97) and dominant on six (average 366.2 ± 141.68). This species was found only once on cacao under complex, natural shade and not at all on the lower canopy trees in the nearby forest sites.

Habitat type did not have a significant effect on total species richness per tree (ANOVA $F_{(3, 88)}$=0.92, p=0.43, Figure 3.2). Average species richness on the lower canopy forest trees was 4.16 ± 0.38 and on cacao trees 3.77 ± 0.20. The number of forest species dropped significantly in the agroforests, but did not differ between agroforestry types (ANOVA $F_{(3, 88)}$=14.25, p<0.0001 and Tukey's HSD post hoc test, Figure 3.2), indicating a large turnover in species from forest to agroforest. Cacao trees supported on average 1.58 ± 0.13 forest species.

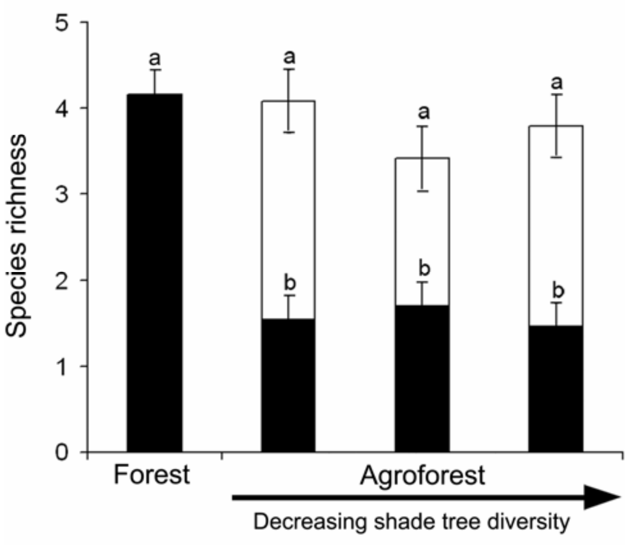

Figure 3.2: The effect of forest conversion on the overall and forest ant species richness per tree (± SE) given per habitat type. Habitat types from left to right: natural forest, cacao under diverse natural shade, cacao under planted diverse shade and cacao under simple, planted shade. Forest species are in black. Letters show significant differences according to Tukey's HSD post hoc test after the General Linear Model.

Anoplolepis gracilipes response to habitat and microclimate modification

Dominance by *Anoplolepis gracilipes* within the agroforests was not affected by habitat type (Shade simplification, GLM: $F_{(2,\ 4.2)}$=1.87, p=0.26). However, dominance was correlated with the microclimate factor, which explained 8% of the variance in *A. gracilipes* dominance (GLM: $F_{(1,\ 44)}$=8.69 p<0.01, Figure 3.3), such that drier, warmer sites with less shade had higher densities of this invasive ant.

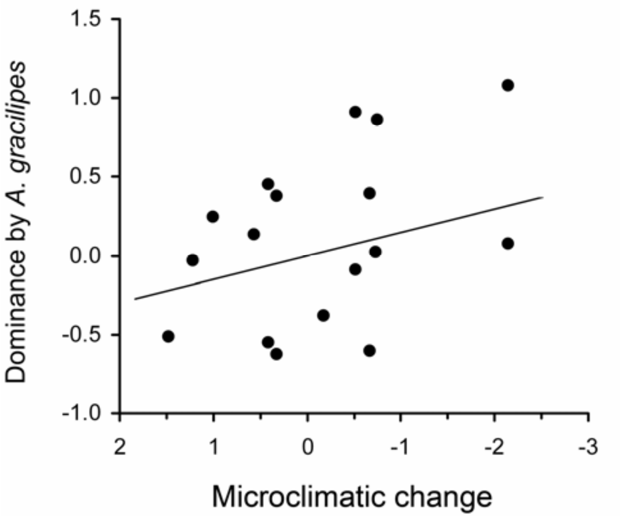

Figure 3.3: The significant effect of microclimate modification on the dominance of the invasive Crazy Ant *Anoplolepis gracilipes* on cacao trees (residuals after removal of variation due to sites and habitat type). The 'microclimate' factor calculated from the covarying environmental variables canopy cover (%), relative humidity (%RH) and temperature (^{o}C) is charted on the x-axis. The smaller the values of the factor the drier, warmer and less shaded the environment.

Species richness response to habitat, microclimate, and dominance by *Anoplolepis gracilipes* in agroforest sites

Richness of 'forest' and 'non-forest' ant species on cacao trees were not affected by either shade simplification (GLM forest spp.: $F_{(2, 42)}$=0.76, p=0.47, non-forest spp.: $F_{(2, 42)}$=2.75, p=0.07) or changes in the microclimate (GLM: $F_{(1, 42)}$=0.56, p=0.46 and $F_{(1, 42)}$=0.58, p=0.45 respectively).

However, within the agroforests, 'forest' ant richness was significantly and negatively related to dominance by *Anoplolepis gracilipes* ($F_{(2, 42)}$=6.86, p<0.005, Figure 3.4). This contrasted with agroforest species richness, which remained unaffected by *A. gracilipes* dominance ($F_{(2, 42)}$=1.44, p=0.25, Figure 3.4).

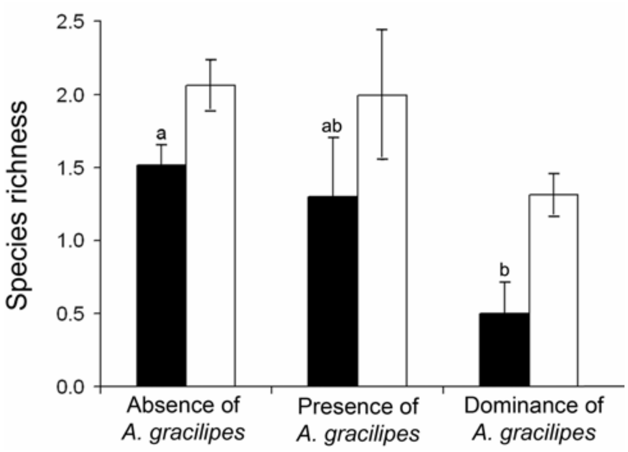

Figure 3.4: The significant, negative effect of dominance by *Anoplolepis gracilipes* on forest ant species (black) and the insignificant effect on non-forest species (white) on cacao trees. We did not separate habitats or sites because these had no significant effects. Absence was defined as no individuals were encountered on a tree. Presence was defined as 30 or fewer individuals collected from one tree (average 11.7 ± 3.97). Dominance was defined as more than 50 individuals of *A. gracilipes* on one tree (average 366.2 ± 141.68). Letters show significant differences according to Tukey's HSD post hoc test after the General Linear Model.

Discussion

Total ant species richness on lower canopy trees was unaffected by the conversion of forest to agroforests. However, the identity of the species changed considerably. Almost half of the 'forest' species were not found in agroforests and vice versa, and this is still an overestimate because we studied more trees in the agroforests than in the forests. Such a high turnover between natural and cultivated forest systems would not be detected by simple species richness comparisons, as overall species richness per tree did not differ significantly. Within the agroforests themselves, total richness and richness of 'forest' ant species on cacao trees did not change across the three categories of shade tree diversity (habitat type) or with independent changes in the microclimate.

The most abundant 'non-forest' species was the Long-legged Crazy Ant *Anoplolepis gracilipes* (18% of all ants collected from cacao trees), which was not found in forest sites, even though these were sometimes less than a kilometer away from sites where *A. gracilipes* was observed (Figure 3.1). The minimum distances between study sites were within the foraging range of *A. gracilipes* (Abbott 2006), which means absence in a site was more likely to result from habitat characteristics than from dispersal limitation. Microclimatic changes associated with thinning of the shade canopy were concomitant to the increased dominance by this invasive species. *A. gracilipes* was mostly dominant on cacao trees in more open, warmer and drier systems. The dominance on cacao trees was concomitant with a significant decline in 'forest' species. 'Non-forest' species richness did not respond to either microclimatic change or increasing Crazy Ant dominance. This asymmetric response of 'forest' species versus 'non-forest' species emphasizes the threats of invasive species to rare or endemic fauna (see also Hill *et al.* 2003; O'Dowd *et al.* 2003; Sanders *et al.* 2003).

The Crazy Ant *Anoplolepis gracilipes* is among the most aggressive invasive ant species in the world. It most likely originates from tropical Asian moist lowland forests from where it spread and established in higher regions and numerous islands throughout the Indo-Pacific region (Holway *et al.* 2002). On the American continent it has to date only been able to settle in an arid Mexican region, probably facilitated by irrigation (Wetterer 2005). The Crazy Ant has been implicated in ecological meltdowns (Hill *et al.* 2003; O'Dowd *et al.* 2003; Sanders *et al.* 2003; Lester &Tavite 2004) where it had profound direct effects on local land crab populations and insect communities, as well as indirect effects on undergrowth, tree health and endemic bird populations. Such invasions are therefore posed as a basic mechanism behind worldwide declines in biodiversity (Vitousek *et al.* 1996).

However, anthropogenic disruption of ecosystems has been suggested to be a prerequisite to biological invasions (Elton 1958), and invasive species may be one of many proximate mechanisms through which habitat modification causes declines in species richness (Didham *et al.* 2005). As only a minority of the studies on species invasions take anthropogenic disturbance of the environment into account, its importance as a mediator of the effect of invasive species on endemic fauna has, until now, been unclear. Furthermore, the current focus on direct effects of habitat modification on biodiversity has overlooked the possibility of indirect effects on species interactions (Henneman & Memmott 2001) and these effects may undermine the apparent conservation value of managed systems.

The importance of habitat modification for ant dominance patterns has been shown empirically with increased dominance by ant species in altered habitats (Gibb & Hoculi 2003; Menke & Holway 2006). On the Seychelles, dominance by *A. gracilipes* threatens endemic island bird populations (Hill *et al.* 2003), and these islands have undergone intensive open phosphate mining prior to the current land cover by non-indigenous trees. Invasive dominance by the Crazy Ant *Anoplolepis gracilipes* on Christmas Island, Australia caused an "ecological meltdown" (O'Dowd *et al.* 2003), and although it was not proposed as a mechanism in that study, the development of nearby tourist resorts, or the long-term open phosphate mining that still continues on the island (source: Christmas Island Tourist Association; http://www.christmas.net.au), was likely to be an important factor. Similarly, the results from our study demonstrate that a management-induced gradient of microclimatic change can facilitate invasive species dominance, and that this has a disproportionately negative effect on native forest species.

Conclusions

Our results underscore the important effects of potentially invasive, alien species on the forest fauna that may remain in cultivated systems. More than half of the ant species we found on cacao trees were not found in adjacent forest sites and one of those species had well-known invasive qualities. The intimate link between ecologically dominant, invasive species and anthropogenic habitat modification is important to acknowledge in future studies that assess the effects of habitat destruction on native and invasive species. Combating species losses after forest conversions may require a broader approach that incorporates habitat management in addition to the control of invasive species.

Conservation biologists have identified tropical agroforests as one of the most species rich cultivated systems (e.g., Schulze *et al.* 2004; Tylianakis *et al.* 2005) and the ant richness of cacao agroforests in our study remained comparable to that of lower canopy trees in nearby natural forest. However, the difference in species composition between forest and agroforests showed that species richness alone is not the best indicator of the conservation value of these systems. Increased ecological dominance by invasive species may drive further losses of characteristic forest fauna as an indirect consequence of habitat modification.

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Appendix

Appendix 3.1. Number of ant individuals (Ind.) and species (Spp.) per subfamily and genus collected in natural forest and cacao agroforests in Central Sulawesi, Indonesia.

Subfamily	Genus	Forests		Agroforests		All species	
		Ind.	Spp.	Ind.	Spp.	Ind.	Spp.
Aenictinae	*Aenictus*	2	1	0	0	2	1
Dolichoderinae	*Dolichoderus*	5	2	302	5	307	6
	Philidris	1	1	0	0	1	1
	Technomyrmex	8	1	1268	2	1276	2
Ectatomminae	*Gnamptogenys*	93	1	59	1	152	1
Formicinae	*Anoplolepis*	0	0	2287	1	2287	1
	Camponotus	43	5	569	8	612	9
	Echinopla	9	4	19	3	28	4
	Oecophylla	4	1	69	1	73	1
	Paratrechina	559	2	3772	5	4331	5
	Polyrhachis	413	15	928	23	1341	33
Myrmicinae	*Cataulacus*	2	1	0	0	2	1
	Crematogaster	27	2	2381	4	2408	4
	Pheidole	105	1	0	0	105	1
	Pheidologeton	0	0	4	1	4	1
	Tetramorium	0	0	867	7	867	7
Ponerinae	*Diacamma*	21	2	2	1	23	2
	Myopias	0	0	1	1	1	1
	Odontomachus	0	0	1	1	1	1
	Platythyrea	0	0	2	1	2	1
Pseudomyrmecinae	*Tetraponera*	2	1	10	1	12	1
Total		1294	40	12541	66	13835	84

CHAPTER 4

SHADE TREE MANAGEMENT AFFECTS FRUIT ABORTION, INSECT PESTS AND PATHOGENS OF CACAO

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Abstract

The mortality of cacao fruits caused by early fruit abortion or insect and pathogen attacks was investigated in differently managed agroforestry systems in Central Sulawesi, Indonesia. Nine agroforestry systems shaded by three different types of tree stands were selected, which represented a decrease in structural heterogeneity: forest remnants, diverse planted trees and one or two species of planted leguminose trees. After standardized manual cross pollination, the development of 600 fruits on 54 trees (six trees per agroforest) was followed during 18 weeks of fruit development. In total, 432 of all fruits were lost before maturity, which seriously undermined yields. The proportion of harvested fruits per tree (overall average: 27 ± 4%) was not affected by canopy type. Although shade cover did not have a significant effect, losses due to fruit abortion were most likely under forest shade, where nitrogen-fixing leguminose shade trees were absent. Fruit losses due to pathogenic infections and insect attacks increased with the homogenization of the agroforests, supporting the hypothesis that agricultural homogenization increases risks of pest outbreaks. These results suggest that the reduced pathogen load under natural shade may be combined with reduced fruit abortion in that natural-shade agroforestry is enriched with planted leguminose trees. In conclusion, shade management may be improved to increase yields from cacao using highly diversified natural-shade agroforestry systems.

Keywords: flower-fruit ratio; *Helopeltis*; herbivory; Indonesia; pollination; *Phytophthora*; Theobroma cacao yield

Introduction

A common phenomenon in plants is that numbers of flowers exceed final numbers of mature fruits (Stephenson, 1981), and fruit mortality due to internal (e.g., Nichols and Walmsley, 1965; Marquis, 1992; Pías and Guitián, 2006) and external (e.g., Louda, 1982; Windus and Snow, 1993; Arnold et al., 2003; Knight, 2004) factors can be a major bottleneck in plant reproductive success. Cacao (*Theobroma cacao* L. 1759) is among the most common crops grown in tropical agroforestry systems. Its reproductive system is characterized by high numbers of flowers, of which generally no more than 5% develop into mature fruits (Entwistle, 1972; Young, 1994). The highest ever annual global production of 3.5 million t dry cacao beans was reached in 2004, which equaled a total of 3.7 billion US$ of income to farmers (International Cacao Organization, 2005). Despite the increasing economic importance of cacao, surprisingly little is known about the mechanisms that determine its yields.

Because productivity of cacao is predicted to decrease under dense shade regimes (Zuidema et al., 2005), recent agricultural intensifications led to large scale landscape homogenization, turning heterogeneous, shaded agroforestry systems into poorly shaded monocultures at local and regional scales (Siebert, 2002). Such intensifications and consequent landscape homogenizations can threaten tropical biodiversity and profitable ecosystem services (e.g., Perfecto et al., 1997; Klein et al., 2002) and increase risks of pest outbreaks (Schroth et al., 2000; Wilby and Thomas, 2002; Tscharntke et al., 2005).

Cash crops grown in tropical agroforestry systems depend strongly on ecosystem services provided by naturally occurring species (Schroth et al., 2000; Tylianakis et al., 2005). In cacao, pollination is carried out by small insects such as midges (Entwistle, 1972; Young, 1994) and some ants are suggested to play important roles in the regulation of insect pests (Entwistle, 1972; See and Khoo, 1996). However, a wide range of herbivorous insects (e.g. Figure 4.1a) and pathogens attack (e.g. Figure 4.1b) cacao, and many of them are able to develop high densities, causing severe harvest losses and even regional abandonment of cacao farming (Fowler et al., 1956; Entwistle, 1972; Purdy and Schmidt, 1996; See and Khoo, 1996; Krauss and Soberanis, 2001).

In addition to pest attacks, a major cause of fruit mortality on cacao trees is active abortion, or “cherelle wilt” (Figure 4.1c; Nichols and Walmsley, 1965; Valle et al., 1990; Young, 1994; Falque et al., 1995; Hasenstein and Zavada, 2001). Such losses are regulated by the plant, primarily as a response to pollen incompatibility (Hasenstein and Zavada, 2001) and nutrient limitations that result from low photosynthetic rates or poor soils (Nichols and Walmsley, 1965; Valle et al., 1990).

Here cacao fruit losses in shaded agroforestry systems are investigated, evaluating internal causes (fruit abortion) and external causes (insect attacks and pathogens) of fruit-mortality. The question is whether shade density and composition of shade trees in agroforestry systems affect mechanisms of fruit loss. Management recommendations are derived for increasing cacao yields from shaded agroforests.

Figure 4.1a: *Helopeltis sulawes* Stonedahl, 1991 (Hemiptera: Miridae) attacking a cacao fruit. The arrow indicates where the damage is caused by its piercing mouthparts penetrating the fruit's skin. *H. sulawesi* was the most common insect pest in the study region. 1b: Cacao fruit heavily attacked by *H. sulawesi*, but the fruit remained harvestable. Each attack kills a piece of the fruit's skin, which becomes visible as a black dot. 1c: Cacao fruits attacked by *Phytophthora* sp., the most common pathogen causing harvest loss in the research area. 1d: A wilted cherelle. Cherelle wilt (abortion of fruits in a young stage) is caused by within tree competition for nutrients and was the most common cause of fruit loss in this study. (Photography: MMB)

Methods

Study sites

The study was conducted in nine cacao dominated agroforestry systems in the Toro village, about 100 km southwest of Palu, the capital city of Central Sulawesi, Indonesia. The systems were characterized by three different types of shade tree stands: trees remaining from previous rainforest cover, diverse planted trees (secondarily grown forest trees, fruit and timber trees and leguminose trees) and stands dominated by one or two species of planted trees (dominated by the leguminose *Glyricidia sepium* and *Erythrina subumbrans*). For each of these types of agroforestry, three sites were selected with cacao trees between 8 and 10 years old. The minimum distance between sites was 300 m and agroforestry types were geographically interspersed and not spatially clustered.

In the study area, cacao trees were mainly hybrids ("Trinitario" type) between the "Criollo" and "Forastero" varieties. In contrast to cacao growing regions in West Africa and Central America, the usage of genetic varieties of cacao is not controlled in Central Sulawesi, and grown genotypes are not defined.

The percent canopy cover of the shade tree stands was estimated using a Spherical Densiometer$^{©}$; a concave mirror divided into squares (produced by R.E. Lemmon Forest Densiometers, USA). Canopy cover was measured at four locations per site, and means were calculated per site. The cover by the shade tree stands (72.1 - 90.5%) in the study sites is considered dense agroforestry shade (Zuidema et al., 2005) and did not differ significantly between the three different shade tree types (ANOVA: $F_{(2, 6)}=1.07$, $p=0.40$).

Experimental set-up

In each study site six flowering cacao trees of the "Trinitario" type were selected (54 trees in total). Although different genotypes may differ in flowering frequency and rates of fruit abortion (Hasenstein and Zavada, 2001), the experimental set-up with randomized cacao tree selection avoided systematic genetic differences between cacao trees from different sites.

The experiment began in October 2004 and the major harvesting season in the study area lasted from April to June. All fruits from the main stems were removed and each opened flower was manually cross pollinated until between eight and 16 flowers were pollinated per tree. All manual pollination took place between the 17th and 20th of November, 2004.

Each manually pollinated flower was marked with a number that was attached to the tree's bark with a needle.

Standardized manual cross pollination was carried out by rubbing three anthers from flowers of three different trees (from the same plantation) against the selected flower's stigma. This method maximizes the likelihood of optimal pollination (Falque et al., 1995) and ensures a standardized number of fruits of similar age on each of the experimental trees.

Fruit mortality, fruit abortion (also known as 'cherelle wilt', in which fruits stop growing and dry out), insect attacks and pathogens were quantified. The most common pathogen in the study area was Black Pod Disease, which is caused by an oomycete of the genus *Phytophthora* sp., but further pathogens may have also occurred.

Fruits were monitored once every three weeks until fruits died or were harvested. The experiment ended in the first half of April 2005 when the remaining fruits were harvested. All fruits were monitored six times at three week intervals during the 18 weeks (4.5 month) of fruit development.

Statistical analyses

To investigate the three-weekly fruit mortality, repeated measures ANOVAs were used on the fruit loss per site as a proportion of the surviving fruits (i.e., fruits of similar age). Mortality differences between habitat types were analyzed per tree using General Linear Models (GLMs). Using type I hierarchical variance decomposition, habitat type was entered first as a fixed variable, followed by site as a random effect. Because there was one value of canopy cover per site, its effects were tested on a per site level in a GLM with habitat type as fixed factor, canopy cover as a covariate and Type I sums of squares. All post-hoc tests were carried out using Tukey's HSD tests.

All analyses were done using Statistica 6.1 ($^{©}$Statsoft Corp.). The response variable for each model was the mortality as a proportion of successfully pollinated flowers, and was therefore arcsine squareroot transformed before analyses. Moreover, data were transformed where necessary to reach normal distribution of model residuals. Arithmetic means are given ± one standard error.

Results

In total, 600 fruits on 54 trees (average per tree: 11.3 ± 0.58) were monitored. Of the monitored fruits, 432 (72%) were lost before harvest. Half (n = 300) of all fruits were lost due to abortion by the plants themselves. A further 111 fruits (19%) did not reach maturity due to pathogens and 21 fruits (4%) were lost due to insect attacks, which in all cases was due to attacks by *Helopeltis sulawesi* Stonedahl, 1991 (Hemiptera: Miridae). In total, *H. sulawesi* fed upon 55 fruits, of which 62% still reached the mature stage. Conversely, only 18% of the fruits that were infected with pathogens could eventually be harvested. Ten percent of the fruits lost due to pathogens were also fed upon by insects, although only 3% of the infections were preceded by insect feeding. Fruits that were completely covered by the pathogen were not subsequently fed upon by insects. Two percent of the cases of fruit abortion were preceded by insect feeding.

All fruit abortion took place during the first nine weeks of fruit development and 60% took place during the first three weeks. Rates of abortion were highest during the first three weeks (repeated measures ANOVA for week three to 9: $F_{(3, 18)}=16.3$, $p<0.0001$, figure 4.2), and this did not differ between the three habitat types (interaction effect between time and habitat type: $F_{(6, 18)}=1.33$, $p=0.38$). Fruits were lost due to pathogens throughout the 18 weeks of fruit development. The proportional loss due to pathogens was highest between week nine and 13 (repeated measures ANOVA: $F_{(5, 30)}=2.62$, $p=0.04$, figure 4.2), and this did not differ between the three types of agroforestry (interaction effect between time and habitat type: $F_{(10, 30)}=1.25$, $p=0.30$). Fruit loss due to insect attacks began after the first three weeks of fruit development and was constant through time (repeated measures ANOVA: $F_{(4,24)}=0.62$, $p=0.65$, figure 4.2).

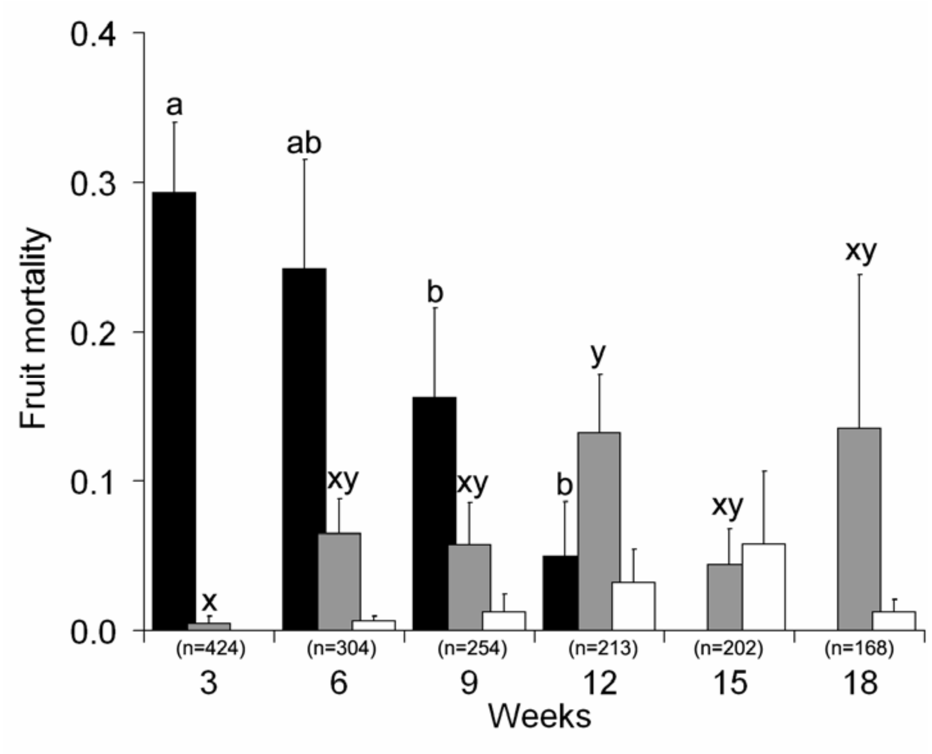

Figure 4.2: Overall averaged cacao fruit-mortality during six periods of three weeks, until harvest of mature fruits. Fruit mortality is given as the proportion of fruits that survived after previous monitoring (total n is given under the x-axis). Mortality was due to abortion (black), pathogens (grey) and attacks by insects (white). Bars indicate one standard error. Values indicated with respectively a and b and x and y are significantly different based on Tukey's HSD post-hoc test.

The total proportion of fruits lost due to abortion was lowest on trees under diverse planted shade and highest on trees under natural shade (GLM: $F_{(2, 48)}$=6.6, p=0.003, figure 4.3). The proportions of fruits lost per tree due to pathogens were highest on cacao trees under planted shade and lowest under natural shade (GLM: $F_{(2, 48)}$=6.3, p=0.004, figure 4.3). There was a trend towards higher fruit loss due to insect attacks under homogeneous shade, however this trend showed only marginal statistical significance (GLM: $F_{(2, 48)}$=2,45, p=0.10, figure 4.3). Hence, the proportion of fruits eventually harvested did not differ between habitat types (overall average per tree: 27 ± 4%; GLM: $F_{(2, 48)}$=2.5, p=0.10).

After removal of variation due to the type of shade trees, neither fruit abortion (GLM: $F_{(1, 6)}$=1.7, p=0.25), pest attacks (GLM pathogens: $F_{(1, 6)}$=0.6, 0.48 and insect attacks: $F_{(1, 6)}$=0.5, p=0.52), nor harvest ($F_{(1, 6)}$=4.45, p=0.13) were affected by canopy cover.

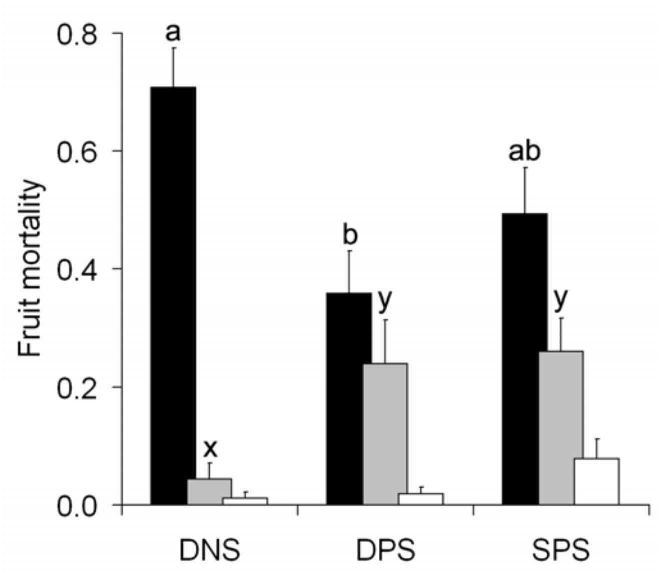

Figure 4.3: Cacao fruit mortality per tree due to abortion (black), pathogens (grey) and attacks by insects (white) in agroforestry systems with different types of shade tree stands: diverse natural shade (DNS), diverse planted shade (DPS) and simple planted shade (SPS). Bars indicate one standard error. Values indicated with respectively a and b and x and y are significantly different based on Tukey's HSD post-hoc test.

Discussion

The results of this study show the enormous influence that fruit mortality had on potential yields of cacao: 72% of the pollinated flowers did not develop into mature fruits. The majority of fruit mortality was driven by within-tree factors (i.e., abortion), over half of which took place during the first three weeks of fruit development. The recorded fruit mortality is within the range of reported estimates in poorly shaded, intensive cacao plantations in Brazil (79%: Hasenstein and Zavada, 2001), Costa Rica (62%: Young, 1982), and Ivory Coast (29%: Falque et al., 1995).

In this study we also showed for the first time that the composition of shade tree stands had a strong effect on the mechanisms that drive fruit losses on cacao trees. Losses due to early fruit abortion were highest under natural shade, whereas losses due to pathogens generally increased under planted shade, so that the overall proportion of fruits reaching the mature stage did not differ. In contrast to expectations, yields of cacao trees were not affected by canopy cover (in the range of 72.1 - 90.5%), implying that light intensity was not limiting fruit production.

The agroforestry systems shaded by forest remnants had a shorter history of agroforestry use and harbored no planted leguminose trees. Planting leguminose shade trees is a common measure to relieve agroforestry crops from nutrient deficiencies (Beer et al., 1998), which most likely explains the increased fruit abortion on cacao under shade tree stands that remained from the previous rainforest cover. In the study region, leguminose trees have been reported to enrich agroforestry with 70 kg/ha nitrogen (Dechert et al., 2005). However, under the simple shade of planted leguminose trees, fruit abortion was intermediate, which indicates that nitrogen was not the only limiting factor, but may have been complemented by external factors that were not visible in the field, such as early pathogen infections. Sites with diverse, planted shade tree stands performed best in relieving cacao trees from pressures that drive trees to fruit abortion.

In contrast to fruit abortion, the proportion of fruits lost due to external causes increased under simple planted shade, which supports the hypothesis that homogenized agricultural systems increase the risk of pest outbreaks (Schroth et al., 2000; Wilby and Thomas, 2002; Tscharntke et al., 2005). In this study, pathogens (mainly *Phytophthora* sp.) were, after fruit abortion, the most common cause of fruit-mortality. This was in part because the farmers in the study area did not know of management practices that reduce risks of pathogenic infections. Successful disease management includes frequent removal of diseased fruits and sustainable shade management (e.g., Krauss and Soberanis, 2001). The highly diversified fungal cacao endophytes, which may be particularly important in high-diversity natural-shade agroforestry, are known to be important antagonists of *Phytophthora* sp. (Arnold et al., 2003).

Mortality due to insect attacks (4% of all fruits) was of less importance than pathogen attacks (19% of all fruits). Nearly all fruits attacked by insects were attacked by the mirid bug *H. sulawesi*. However, the majority of those fruits (62%) still reached maturity. In this study only a minority of fruit loss due to pathogens was preceded by insect attacks, although fruit damage by mirids in particular may increase subsequent vulnerability to pathogens (Muhamad and Way, 1995).

Fruit losses due to internal and external causes were largely separated in time. After the initial ‘mass fruit-wilt’ during the first six weeks of fruit development, the risk of fruit-loss due to insect and pathogenic infections peaked between the ninth and 13th week of fruit development. Therefore, differences in the number of fruits lost due to pest attacks are likely because of the initial differences in rates of fruit wilt. Hence, achieving a decrease in fruit wilt only may not lead to increased yields.

Conclusions

Fruit mortality is an important bottleneck in the reproductive success of flowering plants. The results of this study show that mechanisms of cacao's fruit mortality within well-shaded agroforestry systems may differ greatly among shade management types. The distinction between fruit abortion and insect and pathogen attacks as causes of fruit mortality revealed an as yet unexploited management potential for realizing higher yields from cacao in shaded agroforestry systems. Natural shade was associated with reduced Black Pod Disease, possibly because of more endophytic antagonists (see Arnold et al. 2003), but higher fruit abortion than planted shade, which may be due to nitrogen limitation. Hence, an enrichment of natural shade agroforestry with planted leguminose trees appears to be a promising management option to improve cacao yields and keep complex agroforestry systems with their high functional biodiversity (see Rice & Greenberg 2000). Management practices aimed at decreasing pest pressures were largely unknown among farmers in the study area, which underlines the importance of educational programmes in the conservation of shaded agroforestry systems.

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CHAPTER 5

CAVEATS TO QUANTIFYING ECOSYSTEM SERVICES: FRUIT ABORTION BLURS THE BENEFITS OF CROP POLLINATION

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Abstract

The recent trend to place monetary values on ecosystem services has led to studies on the economic importance of pollinators for agricultural crops. Recent studies indicate regional, long-term pollinator declines and economic consequences have been derived from declining pollination efficiencies. However, before benefits from pollinator services can be used as economic incentives for conservation, environmental factors such as drought, pests and diseases can also limit yields. Moreover, “flower excess” is a well-known reproductive strategy of plants as insurance against unpredictable, external factors that limit reproduction. With three case studies on the importance of pollination levels for amounts of harvested fruits of three tropical crops (passion fruit in Brazil, coffee in Ecuador, and cacao in Indonesia) we illustrate how reproductive strategies and environmental stress can obscure initial benefits from improved pollination. By interpreting these results with literature from evolutionary sciences, agronomy and studies on wild plant populations, we argue that studies on economic benefits from pollinators should include the total of ecosystem processes that 1) lead to successful pollination and 2) mobilize nutrients and improve plant quality to the extent that crop yields indeed benefit from enhanced pollinator services. Conservation incentives that use quantifications of nature’s services to human welfare will benefit from approaches at the ecosystem level that take into account the broad spectrum of biological processes that deliver the service.

Keywords: bet-hedging; carrying capacity; ecosystem services; flower surplus; fruit-maturation; ovule fertilization; pollen production.

Introduction

Human-induced modifications of the environment continue to reduce biodiversity on a global scale (Vitousek *et al.* 1997), prompting concern over the potential loss of important ecosystem services, on which human health and welfare depend (Foley *et al.* 2005; Kremen & Ostfeld 2005). This concern has led to the estimation of monetary values for ecosystem services (Costanza *et al.* 1997; Schroter *et al.* 2005), which provide an economic justification for species conservation (Kearns *et al.* 1998; Kremen *et al.* 2002; Balmford *et al.* 2002; Steffan-Dewenter *et al.* 2005).

Pollination by insects comprises an important ecosystem service, as reproduction and yields of many flowering wild (Larson & Barrett 2000) and crop plants (Klein et al. *in press*) benefit from faunal pollinating vectors. This service to human agriculture has been shown to be negatively related to anthropogenic habitat changes, such as land-use intensification and habitat isolation (Steffan-Dewenter & Tscharntke 1999, Klein *et al.* 2003b; Quesada *et al.* 2003; Kremen *et al.* 2004; Ricketts 2004; Chacoff & Aizen 2006; Greenleaf & Kremen 2006), and the possible economic consequences of these losses have been derived (Ricketts *et al.* 2004, Olschewski *et al.* 2006, Morandin & Winston 2006; Priess *et al. in press*). Long-term declines in pollinator populations and related threats to plant reproduction have led to concerns of a wide-spread loss of pollination services in which pollen limited plants will suffer reduced yields from declining pollen supply (Figure 5.1a; Kremen *et al.* 2002; Steffan-Dewenter *et al.* 2005, Biesmeijer *et al.* 2006).

Evolutionary approaches to the common phenomenon of high flower-to-fruit ratios in hermaphroditic plants, revealed adaptive flowering strategies aimed at optimizing the female (fruit production) versus male (pollen production) contribution to the plant's fitness (Ehrlen 1991). Moreover, apparent flower surpluses may serve as insurance for hermaphroditic plants against fluctuations in pollinator and nutrient availability ('bet-hedging', Bond 1995; Brown & McNeil 2006). Agronomic approaches to crop yields and studies on wild plant populations compared benefits from pollinator services with the effects of environmental factors. Environmental factors that limit fruit maturation are from the plant's perspective unpredictable and include stress such as drought (Windus & Snow 1993), nutrient deficiencies (Pías & Guitián 2006), herbivory (Windus & Snow 1993; Knight 2004) or within-plant competition for assimilates (Valle *et al.* 1990; Brown &

McNeil 2006). Thus, whether or not effects of pollination declines are reflected in agricultural crop productivity may depend on species-specific flowering strategies (Figure 5.1b) and on context dependent carrying capacities of plants (Figure 5.1c, d). True limitation of fruit production by pollen supply is most likely for self incompatible, animal pollinated fruit crops that are pollinator specific and grown with optimal nutrient availability and absence of fruit/seed attacking pests (e.g., fertilization and pesticide use in agricultural systems, Figure 5.1a; Ghazoul 2005).

Recent studies that use premature measures of yield, such as pollen deposition (Kremen *et al.* 2003; Ricketts 2004; Quesada *et al.* 2003; Larsen *et al.* 2005) or fruit set before harvest (Klein *et al.* 2003a-c; Morandin & Winston 2005), in assessing the importance of pollinator declines for agricultural productivity, do not acknowledge possible persistence of adaptive flowering strategies that may also explain flower excess in cultivated crops, and the effects that the environment may have on fruit-maturation. If premature loss of pollinated flowers (fruit abortion) would not occur or comprise a constant proportion of set fruits, analysis of premature measures would be adequate for comparing pollination efficiency and inferring pollen limitation (Figure 5.1a). Conversely, if plants are limited by other factors that are not related to declines in pollination, premature measurements might lead to overestimation of the actual importance of pollination limitation (Figure 5.1b-d). Increasing pollination can in such instances be superfluous as it may result in fruit set that exceeds the energetic budget of the mother plant, disrupting its metabolism and causing decreasing seed quality (Stanton *et al.* 1987) or even elevated rates of fruit abortion (Stephenson 1981; Sutherland 1987; Ehrlen 1991; Brown & McNeil 2006).

With case studies on the pollination of passion fruit in Brazil, coffee in Ecuador and cacao in Indonesia, we investigate the importance of pollinator services to fruit set at two points in time: as soon as successful pollination was visible ("initial fruit-set", a premature measure) and at the time of harvest ("final fruit set"). We show that fruit losses between "initial" and "final fruit set" can obscure the apparent benefit of increased pollination to fruit set, which is important for quantifying the economic role of pollinators.

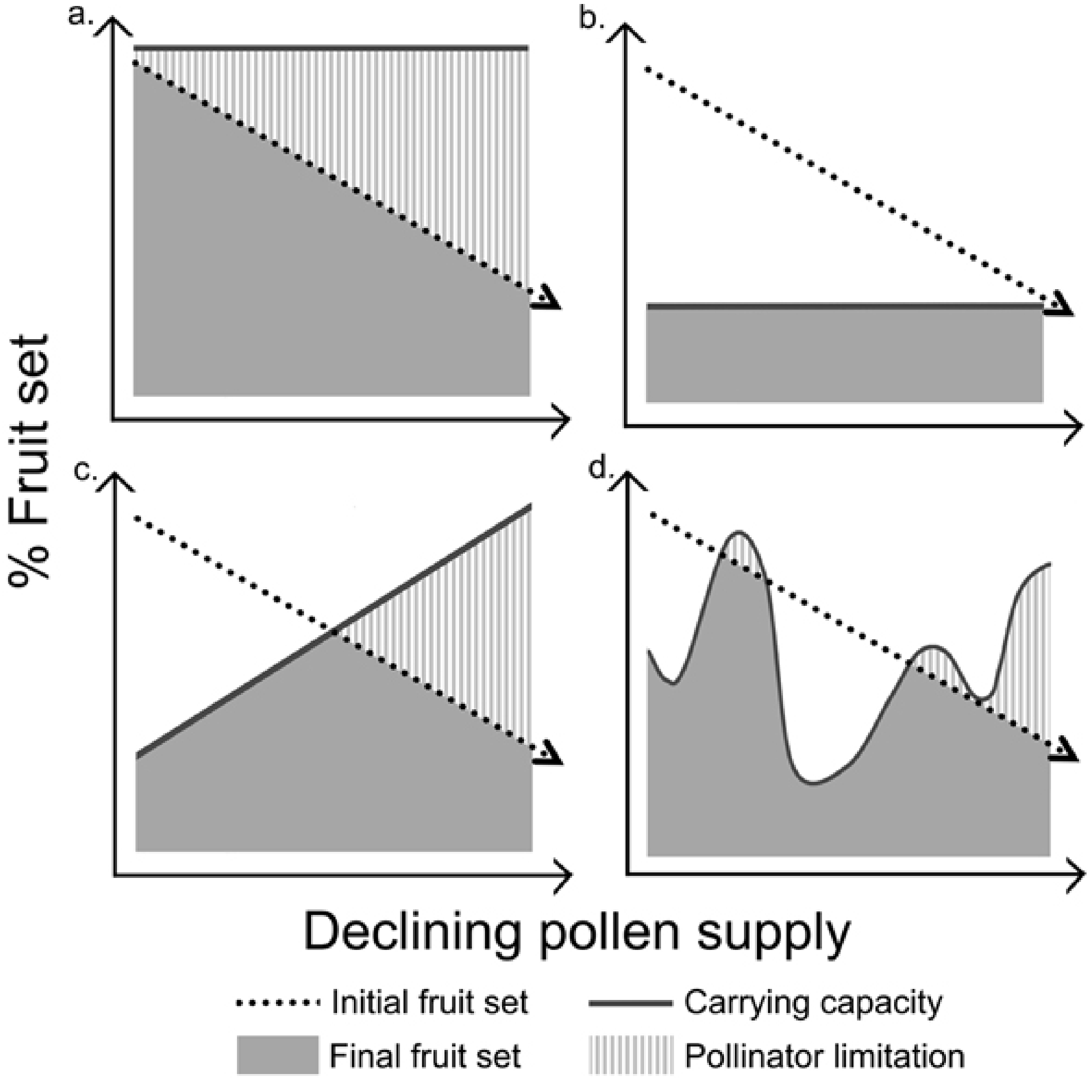

Figure 5.1: Four scenarios for possible effects of declining pollen supply (for example as a result from habitat destruction or agricultural intensification) on initial and final fruit set with a carrying capacity of the crop that is a) always higher than initial fruit set (i.e., pollinator limitation increases with decreasing pollination), b) always lower than initial fruit set (e.g., as a result from species-specific adaptive flowering strategies), c) increases along the intensification gradient (e.g., because of intensifying fertilization regimes) and d) not related to the intensification gradient (e.g., plant-specific in highly heterogeneous, low intensity tropical landscapes).

Case studies

Materials and Methods

We defined initial fruit set as the proportion of flowers that was successfully pollinated (quantified as soon as successful pollination was visible) and final fruit set as the proportion of flowers that eventually resulted in mature, harvested fruits. Fruit abortion was quantified as the proportion of fruits that was lost between initial and final fruit set.

In the following, we outline the locations and methods for each crop studied, and give the initials of the authors responsible for the field work in each region. The studied crops are hermaphroditic (both male and female parts per flower) and, except for highland coffee, self-incompatible.

Pollination and fruit set of passion fruit (A.K.B.)

We carried out the study on passion fruit (Yellow Passion fruit, *Passiflora edulis* Sims. forma *flavicarpa* O. Deg., Passifloraceae) in Juazeiro, Bahia State, Northeast Brazil (9°24´38” S, 40°30´26” W, 286 m above sea level). This region is characterized by a deficit of nesting habitats for solitary bees from the genus *Xylocopa* - the natural pollinators attending the large and conspicuous flowers (A.K. Bogdanski *unpublished data*). Cultivated honey bees (*Apis mellifera*) were also observed attending flowers, but were not observed depositing pollen on flower stigmas (A.K. Bogdanski *unpublished data*). Therefore, farmers in this region pollinate the large flowers by hand. All studied passion fruit fields were fertilized by the farmers.

In each of 16 sites we used 30 flowers for each of three different pollination treatments: natural pollination, manual cross pollination (with pollen from different plants to avoid effects of self-incompatibility) and exclusion of pollination by animals, making a total of 16 x 30 x 3 = 1440 flowers. With the latter two treatments, flowers were enclosed in mesh gauze bags to avoid additional pollination by insects before and after the treatments. For the manual cross pollination treatment, pollen was transferred by hand, similar to the method used by the plantation workers. The experiments began in March 2005 and ended 8 weeks later with the harvest of the fruits.

Pollination and fruit set of coffee (D.V.)

We carried out pollination experiments on the self-compatible highland coffee (*Coffea arabica* L., Rubiaceae) from October 2003 to August 2004 in the cantons Jipijapa (1°19’60”S, 80 34’60”W, 259 m above sea level), Pajan (1°34’00” S, 80°25’00” W, 142 m above sea level), and Noboa (1°24’00” S, 80°23’00” W, 260 m above sea level), Manabi province, coastal Ecuador. Coffee is the second most traded commodity (after oil) in the world and its production affects the livelihood and income of millions of farmers throughout the tropics (Perfecto and Armbrecht 2003; source: website of the International Coffee Organization, http://www.ico.org). In the study area highland coffee (“Caturra” variety) was cultivated in traditional agroforestry systems, under a canopy of various shade trees. No fertilizers or other chemical inputs were used. In the region, coffee flowered during 1 or 2 days, once per year in the dry season. After flowering, fertilized ovules remained dormant until the rainy season (generally 1-3 months later) when fruit development began synchronously.

In each of 22 agroforestry systems, we selected 3 inflorescences on 4 trees, making a total of 22 x 3 x 4 = 264 inflorescences (3311 flowers), and investigated the importance of three pollination types (methodology described in Klein *et al.* 2003a): self pollination by enclosing flowers in bags of fine nylon mesh gauze (10 µm) to exclude pollination by insects and wind, wind pollination by enclosing flowers in bags of cotton mesh (0.8 - 1.0 mm), which allowed self pollination and pollen transfer by wind (not by insects), and natural pollination of flowers by leaving inflorescences open for free access by pollinators (self and wind pollination included). Bags were placed around inflorescences before flowering. The short, synchronous flowering periods (see above) made it logistically unfeasible to include manual pollination treatments. We applied sticky glue to the branches to prevent ants from disturbing the experiment. Mesh bags were removed when flowers withered and began to fall off. Inflorescences subjected to the experiment were marked and numbered with tape. Numbers of flowers were counted before the buds opened. Initial fruit set was recorded in March 2004 (about 5 weeks after initiation of fruit development, as in Klein et al. 2003a) and final harvest when the fruits were harvested in August 2004.

Pollination and fruit set of cacao (M.M.B.)

We carried out pollination experiments on cacao trees (*Theobroma cacao* L., Sterculiaceae) within agroforestry systems around the village of Toro, on the western border of the Lore Lindu National Park, Central Sulawesi, Indonesia (1°30'24" S, 120°2'11" E, 800 – 900 m above sea level). The Island of Sulawesi is among the world's most productive cacao growing regions (ICCO 2005) and particularly Central Sulawesi recently underwent a drastic increase in cacao production (Potter 2001). Despite its economic importance, little is known about the pollination biology of cacao. The generalist pollination system mainly involves pollination of the small, cauliflorous flowers by small midges of the family Ceratopogonidae (Entwistle 1972), which depend on dense shade and high humidity (Young 1982). In the agroforestry systems selected for the experiment, no chemical inputs such as fertilizers or herbicides were used, which was typical for the region.

In three agroforests we selected 4 trees (total of 12 trees) and divided the main stems into three zones: one where all flowers were left for natural pollination, one where each emerging flower was manually cross-pollinated and around one zone we constructed a net of mesh gauze to exclude insects from pollinating each emerging flower. The positions of the three zones on the main stems were randomized per tree. Manual cross-pollination was carried out by rubbing anthers from flowers of three different, non-neighbor trees against the flower stigma using a pair of tweezers. Treatments were carried out on the 1758 flowers that emerged during the 50 days starting from the 17th of October, 2004, and the number of flowers did not differ significantly between treatments. The resulting fruits were harvested between 18 and 22 weeks after pollination.

Statistical analyses

The effects of the different pollination treatments were tested in general linear models with treatment as a fixed factor. Using type I sequential sums of squares, site (random factor) entered the model first, followed by trees (random factor) nested within sites (coffee and cacao only), then by pollination treatment. Thus, trees or shrubs within sites were not treated as independent from one another. All models were carried out in Statistica 7.0 (Statsoft Inc. Tulsa, Oklahoma, USA). The response variables, initial fruit set and final harvest, were calculated as proportion of flowers, and abortion was calculated as the proportion of fruits that were lost. Therefore, the response variables were arcsine square root transformed before analyses to meet the assumptions of normality and homogeneity of variances. Arithmetic means are always given ± 1 standard error.

Results

Passion fruit (*Passiflora edulis*)

The proportion of flowers that set fruit on Passion fruit was significantly higher after manual cross pollination than after natural pollination (Table 5.1). Exclusion of insects from flowers completely prevented fruit set which indicates that pollination of this cultivar required a vector for pollen transfer. Because exclusion did not lead to fruit set, this treatment was excluded from the GLMs that were used to analyse fruit abortion. On average 17 ± 2% of all fruits were aborted, which did not differ significantly between the pollination treatments (Table 5.2), although there was a tendency towards higher fruit abortion in manually cross pollinated flowers. Nevertheless, the proportion of flowers that eventually resulted in mature fruits was still significantly higher after manual cross pollination (Table 5.1). Interaction effects between sites and treatments on the response variables were not tested because the 30 flowers per site were selected randomly.

Coffee (*Coffea arabica*)

The proportion of coffee flowers that was successfully pollinated (fruit set) was highest after natural pollination and lowest among flowers that were self pollinated (Table 5.1). The proportion of aborted fruits was high (60 ± 3%) and significantly affected by the pollination treatment, with highest proportions aborted after natural pollination (Table 5.2). The proportion of flowers that resulted in mature fruits was highest after wind pollination and lowest after natural pollination (Table 5.1).

Cacao (*Theobroma cacao*)

The proportion of cacao flowers that was successfully pollinated was also highest after manual cross pollination (Table 5.1) and exclusion of flying insects did not result in any pollinated flower. Overall, abortion was high (58 ± 9%). However, manual cross pollination resulted in significantly higher proportions of aborted fruits (Table 5.2), which offset the increase in fruit set, such that the proportion of flowers that eventually resulted in mature fruits did not differ significantly between open and manually pollinated flowers (Table 5.1). Additionally, there was a significant interaction effect between pollination treatment and site on the initial fruit set and harvest, but not on the percentage of fruits that were aborted.

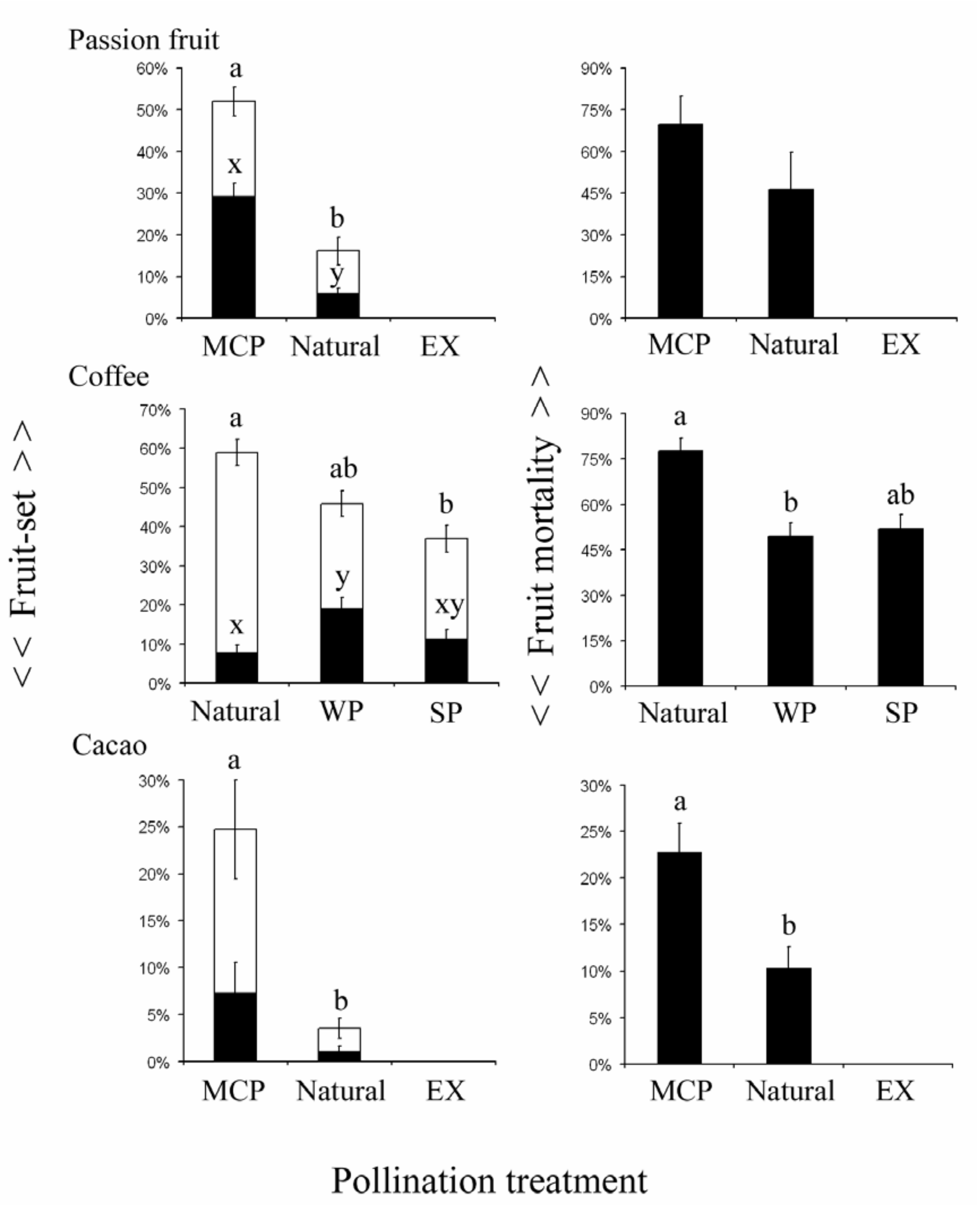

Figure 5.2: Fruit-set (% flowers developing fruits, left graphs) and fruit mortality (% fruits, right graphs) of passion fruit in Brazil, coffee in Ecuador and cacao in Indonesia. The left graphs give the % of flowers developing fruits just after the pollination treatments (white) and at the time of harvest (black). Natural = natural pollination; MCP = manual cross pollination; EX = pollinator exclusion; WP = wind pollination; SP = self pollination. Averages are given ± 1 SE. Values indicated with an a and b and with an x and y differ significantly based on Tukey’s HSD post-hoc tests.

Table 5.1: General Linear Model results for fruit set and harvest (as percent of flowers) in response to site and treatment. Models were of type 1 variance decomposition and variables are given in the order of model entry. Before analyses, data were arcsine squareroot transformed. SS = Sums of squares, D.f. = Degree(s) of freedom, MS = Means of squares.

	Effect (F/R)	**SS**	**D.f.**	**MS**	**F**	**p**
Passion fruit						
INITIAL FRUIT SET						
Site	Random	0.30	15	0.02	1.49	0.17
Treatment	Fixed	4.34	2	2.17	162.84	0.00
Error		0.40	3	0.01		
FINAL FRUIT SET						
Site	Random	0.19	15	0.01	1.15	0.36
Treatment	Fixed	2.32	2	1.16	105.47	0.00
Error		0.33	30	0.01		
Coffee						
INITIAL FRUIT SET						
Site	Random	10.78	21	0.51	3.15	0.00
Tree(Site)	Random	9.69	66	0.145	1.93	0.00
Treatment	Fixed	3.18	2	1.59	17.30	0.00
Site*Treatment	Random	3.86	42	0.09	1.21	0.21
Error		10.01	132	0.08		
FINAL FRUIT SET						
Site	Random	4.21	21	0.20	1.83	0.07
Tree(Site)	Random	5.81	66	0.09	1.06	0.36
Treatment	Fixed	1.54	2	0.77	7.43	0.00
Site*Treatment	Random	4.34	42	0.10	1.26	0.16
Error		10.81	132	0.08		
Cacao						
INITIAL FRUIT SET						
Site	Random	0.13	2	0.07	5.29	0.03
Tree(Site)	Random	0.11	9	0.01	0.57	0.81
Treatment	Fixed	1.30	2	0.65	29.79	0.00
Site*Treatment	Random	0.27	4	0.07	5.58	0.00
Error		0.21	18	0.01		
FINAL FRUIT SET						
Site	Random	0.15	2	0.08	12.59	0.00
Tree(Site)	Random	0.06	9	0.01	0.34	0.95
Treatment	Fixed	0.19	2	0.09	5.22	0.01
Site*Treatment	Random	0.24	4	0.06	6.60	0.00
Error		0.16	18	0.01		

Table 5.2: General Linear Model results for fruit abortion (as percent of fruits) in response to site and treatment. Models were of type 1 variance decomposition and variables are given in the order of model entry. Before analyses, data were arcsine squareroot transformed. SS = Sums of squares, D.f. = Degree(s) of freedom, MS = Means of squares.

	Effect (F/R)	SS	D.f.	MS	F	p
Passion fruit						
Site	Random	1.85	15	0.12	1.08	0.44
Treatment	Fixed	0.01	1	0.01	0.13	0.72
Error		1.72	15	0.11		
Coffee						
Site	Random	17.36	21	0.83	2.97	0.00
Tree(Site)	Random	17.60	66	0.27	1.29	0.11
Treatment	Fixed	6.95	2	3.48	15.86	0.00
Site*Treatment	Random	9.21	42	0.22	1.06	0.39
Error		27.22	132	0.21		
Cacao						
Site	Random	0.54	2	0.27	1.13	0.39
Tree(Site)	Random	2.44	9	0.27	2.33	0.06
Treatment	Fixed	5.10	2	2.55	29.21	0.00
Site*Treatment	Random	0.35	4	0.09	0.75	0.57
Error		2.10	18	0.12		

Discussion

In each of the three tropical cash crops the premature measure of "initial fruit set" would have lead to overestimates of pollination benefits to yields (measured as "final fruit set" in our studies). In each crop, abortion of set fruits was highest after the highest levels of pollination (although this was only statistically significant for coffee and cacao). In passion fruit, abortion rates were overall high (17 ± 2%), but did not differ between pollination treatments such that fruit set at the time of harvest still reflected the benefits from enhanced pollination. In coffee, fruit abortion reversed the benefit of the treatments to initial fruit set, such that final fruit set was highest after wind pollination, perhaps due to less dry and harsh microclimatic conditions in the bagged treatments. For cacao the high abortion rates overshadowed the initial benefit of intensive pollination to fruit set, such that final fruit set was not significantly higher after manual cross pollination compared with natural pollination.

Of the three studied crops, highland coffee was the only self-compatible crop, although initial fruit set increased when insects had access to the flowers. Traditionally, productivity of this crop was thought to be independent of faunal pollinating vectors (Reddy *et al.* 1988;

Free 1993), and Philpott *et al.* (2006) found no effect of flying pollinators on fruit set or fruit weight of coffee in Mexico, except in the presence of positive interactions with ants, which were excluded in our study. Other recent studies from Indonesia and Central America showed the value of insect pollination for coffee pollination, fruit set and harvest (Manrique & Thimann 2002; Klein *et al.* 2003a-c, De Marco & Coelho 2004 Ricketts 2004, Ricketts *et al.* 2004). Roubik (2002) observed up to 50% harvest increases from highland coffee concomitant with an increase in abundance of naturalized honey bees on plantations in Panama, and suggested a link between global pollinator declines and global declines in coffee harvests. The contrasts with our results on final fruit set suggest strong regional differences in the benefits of pollinators to coffee production, possibly due to local nutrient availability, climatic differences or differences between cultivars. These results underline the importance for future research on the exact processes that affect the relationship between pollination intensity, ovule fertilization and coffee berry maturation.

Most cultivars of cacao are self-incompatible (Entwistle 1972; Falque *et al.* 1995; Klein *et al. in press*) and the cacao trees used in this study required pollinating vectors, made clear by the differences between pollination treatments. Cacao flowers have been observed to be attended by various small insects (reviewed by Entwistle 1972) and natural initial fruit set generally ranges from less than 5% to 40% (this study; Young 1982; S.G. Sporn *unpublished data*). The observed increase in initial cacao fruit set after intensive manual cross pollination compared with open pollination is in accordance with previous studies (Valle *et al.* 1990, Falque *et al.* 1995), and such apparent excesses of flowers are often used to infer pollinator limitation (reviewed by Knight *et al.* 2005). However, at final harvest the significant benefit of increased pollination was site-dependent, and overall not significant. These results are supported by theory that explains high flower-to-fruit ratios in plants as a bet-hedging strategy in times of poor pollination or low resource availability (Sutherland 1987; Brown & McNeil 2006). Additionally, because cacao fruits contain up to 400 times more energy than flowers (Valle *et al.* 1990), flower surpluses are predicted to be a strategy of plants for maintaining high male fitness in terms of pollen production (Ehrlen 1991).

In our study, passion fruit was the only crop that showed true pollen limitation of productivity. Both initial and final fruit set increased after manual cross pollination compared to natural pollination, and pollination required insect pollinators. Although rates of fruit abortion did not differ significantly between treatments, abortion was high and reduced the overall effect of pollination on yields. Passion fruit also meets all the criteria proposed by Ghazoul (2005) for sensitivity to pollinator declines: it is a fruit crop, self incompatible, animal pollinated, pollinator rather than resource limited (due to fertilizer inputs) and it is pollinator specific (carpenter bees of the genus *Xylocopa*). In contrast, coffee can also be wind pollinated and cacao is less pollinator specific. Moreover, the studied coffee and cacao agroforests lacked external inputs such as fertilizers which might reduced the carrying capacity in the systems and increased the chance that factors other than pollination were limiting for final fruit set (see Figure 5.1b). Our results call for further comparative studies to assess how representative our case studies are, which indicate that quantifications of pollinator's services to human agriculture based on premature measures (pollen deposition, initial fruit set) might be unrealistic (Figure 5.1b and d). Similarly, analyses of pollination limitation along a gradient of agricultural intensification may be confounded by reduced nutrient limitation and herbivory (due to application of fertilizers and pesticides), thereby increasing the significance of pollination as a limiting factor for yields in intensively managed land (Figure 5.1c).

Implications and perspectives

Pollination is a crucial stage in the reproduction of most flowering plants and pollen vectors are essential for maintaining genetic transfer (Kearns *et al.* 1998). However, plant reproductive strategies may have evolved to cope with fluctuating pollination levels by producing more flowers than the plant could possibly generate mature fruits. Thus, declines in pollination services may not have immediate effects on fruit production (Figure 5.1b). The rates of fruit abortion we observed following increased pollination suggests the persistence of such a strategy in our study crops with low management intensity in tropical agroecosystems. Not in all cases the dependence of ovule fertilization on pollinators is sufficient to infer that pollination services limit agricultural yields.

Measurements of initial fruit set only would provide a proportional estimate of pollinator benefits for passion fruit, but could result in overestimation of pollinator benefits for coffee and cacao. Therefore, we urge caution in the use of economic justifications for biodiversity conservation derived from incomplete (premature) measures of ecosystem services, and recommend more careful use of terminology relating to pollen limitation. Future studies addressing the effects of habitat destruction and agricultural intensification on agricultural productivity should aim to include other important services that mediate nutritional and herbivore pressures (e.g., Bardgett *et al.* 1998; Arnold *et al.* 2003; Poveda *et al.* 2003; Bos *et al. in press*), and even future economic benefits through insurance effects (Yachi &

Loreau 1999; Kremen *et al.* 2002). The chain of ecosystem services that facilitates fruit maturation is as strong as its weakest link.

Quantifications of ecosystem services to agricultural yields will benefit from a holistic approach, considering the wide variety of ecosystem services, and their synergies. In order to strengthen our case in the conservation of biodiversity we need to understand the services that mobilize nutrients and improve plant quality to the extent that crop yields can optimally benefit from pollinator services.

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SUMMARY

In the tropics, human modification of pristine habitats is currently causing unprecedented biodiversity losses. During the last decade conservation biologists have investigated the utility of managed land for slowing this tide of diversity decline. In tropical landscapes, traditional shade agroforestry increasingly makes up the only remaining habitat with a considerable tree cover and supports high levels of biodiversity. Throughout the tropics, heterogeneous, shaded agroforests are increasingly converted to homogeneous, unshaded systems. Such large-scale habitat homogenizations are predicted to increase crop yields, but threaten biodiversity, and important ecological processes that influence crop pollination, pest pressures and land-use sustainability.

In this study we investigated the extent to which cacao dominated agroforests can contribute to the conservation of insect diversity. We used differences between agroforests to assess proximate and ultimate drivers of lower canopy beetle and ant diversity. Concomitantly, we investigated the cacao-pest and cacao-pollinator interactions in relation to the differences between shade management.

The study took place in and around the Toro village in the border of the large Lore Lindu National Park, Central Sulawesi, Indonesia. The region is one of the world's major biodiversity hotspots and the world's third most important cacao growing region. Forest conversions to agricultural land pose a continuing threat to local and regional biodiversity. We selected cacao dominated agroforests that were shaded by three different stands of shade trees: Trees that remained from the previous forest cover, a diverse stand of planted shade trees and a stand of shade trees dominated by two non-native species of planted leguminous trees. From each type of agroforest we selected four replicate sites. Additionally, four forest sites were selected for biodiversity comparisons.

For the first time, we show that cacao trees in shaded agroforests can harbor levels of beetle and ant diversity that resemble that of lower canopy trees in undisturbed forests (Chapter 2). However, species turnover was high between forests and agroforests, particularly of beetles. Although total ant species richness on cacao trees was not related to canopy cover, the proportion of species that also occurred in one of the forest sites, decreased clearly with canopy reduction. Moreover, associated changes in microclimate appeared to promote the increase in dominance by the aggressive invasive Crazy Ant *Anoplolepis gracilipes* (Chapter 3). The proportion of ant species that also occurred in the forest sites was not

affected by the changing microclimate, but decreased significantly with increasing abundance by *A. gracilipes*, which illustrates an important, indirect effect of changing management practices in shaded agroforests.

Our study on the causes of fruit mortality (Chapter 4) was the first that underlined the fact that shade removal may not represent the only management measure that needs to be taken in order to increase cacao yields. A heterogeneous stand of (natural) shade trees released the trees from pest pressures. The intercropping of leguminose trees released the trees from pressures that drive early fruit abortion, possibly due to nitrogen fixing qualities of those trees. The study on cacao pollination illustrated that those environmental factors that drive fruit mortality could even blur initial benefits from artificially increased pollen deposition (Chapter 5). By comparing these results with those from pollination and yield studies on coffee and passion fruit, we exposed an important aspect that is overlooked in numerous recent ecological studies on pollinator services: that the chain of ecosystem processes that make up the final service (e.g., crop yields) is as strong as its weakest link. This means that, for example, enhanced crop pollination will not be expressed in crop yields as long as factors that drive fruit abortion and herbivore pressures are not optimized.

In conclusion, shaded cacao agroforests are important habitats for species rich beetle and ant communities, two major aspects of tropical biodiversity. However, species from natural forests are rare among beetles on cacao and forest ants on cacao may indirectly depend on shade management in that microclimatic changes mediate dominance by invasive ants, which can drive losses of native assemblages. Cacao is productive in wide ranges of habitats, but factors that drive fruit mortality can be of major importance for yields. Although shade removal is predicted to increase cacao yields, we experimentally approached cacao fruit mortality and showed that sustainable shade management has a potential to increase yields. Shaded cacao agroforests are important aspects of tropical landscapes that undergo continuing deforestation, and should be protected in order to serve as a powerful tool in the conservation of tropical biodiversity.

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