"Services and disservices driven by ant communities in tropical agroforests"

Dissertation
zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades
"Doctor rerum naturalium"
der Georg-August-Universität Göttingen

im Promotionsprogramm Biologie
der Georg-August University School of Science (GAUSS)

vorgelegt von
Arno Christian Wielgoss

aus Bad Neustadt an der Saale
Göttingen, 2013

Betreuungsausschuss:

1. Betreuer
Prof. Dr. Teja Tscharntke, Abteilung Ararökologie,
Department für Nutzpflanzenwissenschaften DNPW

2. Betreuer
Prof. Dr. Matthias Schäfer, Abteilung Ökologie,
Johann-Friedrich-Blumenbach-Institut für Zoologie und Anthropologie

Mitglieder der Prüfungskommission
Referent:
Prof. Dr. Teja Tscharntke, Abteilung Ararökologie,
Department für Nutzpflanzenwissenschaften DNPW
Korreferent:
Prof. Dr. Matthias Schäfer, Abteilung Ökologie,
Johann-Friedrich-Blumenbach-Institut für Zoologie und Anthropologie

Weitere Mitglieder der Prüfungskommission:
PD Dr. Yann Clough, Abteilung Ararökologie,
Department für Nutzpflanzenwissenschaften DNPW

PD Dr. Klaus Hövemeyer Abteilung Ökologie,
Institut für Zoologie und Anthropologie

Prof. Dr. Kerstin Wiegand, Abteilung Ökosystemmodellierung,
Büsgen-Institut

Prof. Dr. Ulrich Brose, Institut für Zoologie und Anthropologie

Tag der mündlichen Prüfung: 15. Mai 2013

“Wir leben in einem gefährlichen Zeitalter:
Der Mensch beherrscht die Natur, bevor er gelernt hat,
sich selbst zu beherrschen.”

Albert Schweizer

Table of contents

I Summary

Agricultural productivity and human well-being are built upon ecosystem services and disservices. Ants in tropical agroecosystems drive a complex network of direct and indirect interactions between crops and their mutualists and antagonists. Until now most studies of ecosystem services of ants only focus on single interactions. But little is known about the dynamics between multiple interactions, their relative importance, how they are affected by ant community properties and how they add up to final yield quantity and quality.

We tested the hypothesis that ecosystem services of ant communities differ depending on their community structure, species richness and evenness, and on the presence and identity of dominant ants. We experimentally manipulated ant communities in 15 smallholder cacao agroecosystems with four treatments each: (i) Unmanipulated ant communities with relatively high species richness and evenness; (ii) Dominance by the native *Dolichoderus* cf. *thoracicus*, which is considered as possible biocontrol agent and maintains a similar species richness and evenness; (iii) Dominance by the invasive *Philidris* cf. *cordata*, which reduces ant species richness and evenness; (iv) Exclusion of all ants as zero-control. For 16 months we monitored the ant fauna, cacao fruit development, pests and disease incidents and yield.

Ants provided ecosystem services, including reduced leaf herbivory, reduced cacao fruit pest damage and enhanced fruit set, but also disservices, including increased density of mealybugs (their mutualistic trophobionts) and higher fruit loss due to pathogen dissemination. We discovered a negative plant trait mediated indirect effect of a minor pest, the mirid *bug Helopeltis sulawesi*, on the major pest of cacao in Southeast Asia, the pod-boring moth *Conopomorpha cramerella*, leading to yield maxima with moderate fruit damage rates by *Helopeltis.* Therefore top down control of *Helopeltis* by ants can be detrimental for cocoa production and be considered as indirect ecosystem disservice.

Marketable yields were highest with species-rich, even and unmanipulated communities. The effects of single species dominance strongly depended on the traits of the dominant species. With the invasive ant *Philidris*, ecosystem disservices outweighed the benefits leading to yield losses of 34% compared to the control, while dominance of the native *Dolichoderus* resulted in high yields as in the control. Ant exclusion decreased yield by 27%. Using the example of top down control of leaf herbivores by ants we give an example that correcting abundance data for physiological and behavioural traits like body size and food preferences can improve the accuracy of ecological models.

In conclusion, we show the need to use crop yield as a measure for final ecosystem services in order to integrate all intermediate services and disservices. Ant community structure and dominant species traits affect the balance between services and disservices in surprisingly complex ways, with high species richness and evenness ensuring the highest benefits.

II General Introduction

A planet formed by agriculture

Until now human activity has converted more than 38% of the Earth´s ice-free terrestrial surface into agroecosystems (Millennium Ecosystem Assessment 2005; FAO 2013). The super-exponential human population growth and the resulting increased demand for food, feed, fuel and fibre will result in a further expansion and intensification of agricultural area worldwide (Godfray et al. 2010). Conventional intensification of agriculture and area expansion into sensitive ecosystems are primary drivers behind many environmental threats, including climate change (West et al. 2010), biodiversity loss (Sala et al. 2000) and degradation of land and freshwater (Foley et al. 2005). The most drastic consequences are observed in tropical countries, where more than 55% of the new agricultural land comes at the expense of intact forests, and another 28% from disturbed forests (Gibbs et al. 2010). Even under the most optimistic scenarios, tropical protected areas are insufficient to preserve biological diversity and ecosystem services in the long term (Putz et al. 2001). This stresses the ecological importance of agricultural landscape in which protected areas are embedded (Tscharntke et al. 2005).

Agroforestry systems

As landscapes in the tropics are increasingly dominated by agriculture (Achard et al. 2002), often agroforests represent the only habitat with a considerable tree cover (Schroth & Harvey 2007). Complex agroforestry systems like well shaded coffee or cacao plantations are considered to serve as ecological buffer zones at the margins of conservation areas (Klein & Steffan-Dewenter 2002), which can be important refuges for biodiversity for certain groups (Bos, Steffan-Dewenter, & Tscharntke 2007; Perfecto & Vandermeer 2008). But in the course of the worldwide agricultural intensification as well tropical agroforesty ecosystems like traditional shaded coffee and cacao plantations are modified.

Farmer remove or prune the shade trees (Rice & Greenberg 2000; Siebert 2002; Perfecto et al. 2007). and invest more money in agrochemicals (Wanger, Rauf, & Schwarze 2010), even though these measure often have failed to increase yields permanently but lead to “boom-and-bust” cycles (Clough, Faust, & Tscharntke 2009). In agroecosystems there often is a change in species composition in comparison to natural habitats, because not all species may survive in farming systems (Barlow et al. 2007; Kleijn et al. 2011). But biodiversity losses and community composition changes are more drastic with increasing habitat homogenisation due intensification (Benton, Vickery, & Wilson 2003). Therefore agricultural productivity and biodiversity conservation have been traditionally viewed as incompatible. But a recent study shows that agroforests can be designed to optimize both biodiversity and crop production benefits without adding pressure to convert natural habitat to farmland (Clough et al. 2011). This is because agricultural production is highly dependent on ecosystem services such as pest control, pollination and soil fertility amongst others (Power 2010) and these ecosystem services are often associated with both “planned” and “associated” biodiversity (Tscharntke et al. 2012).

Ants in cacao plantations

In many tropical agroecosystems ants play a decisive role in ecosystem functioning. They are, beside birds, the most important predators of arthropods (Hölldobler & Wilson 1990) and may effectively limit herbivore populations, including agricultural pests (Zehnder et al. 2007; Armbrecht & Gallego 2007; Philpott, Perfecto, & Vandermeer 2008). But not all ecosystem functions of ants are beneficial for cacao farming: For example ants, as well as other arthropods, can transmit plant diseases including the cacao fruit infecting black pod disease caused by *Phytophthora palmivora* (Butler) (Evans 1973). Many ants as well form close mutualisms with homopterans with which they exchange protection for honeydew (Blüthgen, Stork, & Fiedler 2004). Predatory ants can be attracted by homopterans to specific foraging sites and deter herbivores and plant parasites (Perfecto & Vandermeer 2006). But when they attend large homopteran aggregations ants may be important “cryptic herbivores” (Hunt

2003), indirectly consuming large amounts of plant phloem.

With intensification and homogenisation of the habitats the probability increases that single ant species become numerically dominant, which often leads to species diversity losses and a disrupted evenness (Perfecto et al. 2003; Armbrecht, Perfecto, & Vandermeer 2004). There still is a lack of understanding if and how these altered ant assemblages may affect pests and diseases of cash crops (Philpott & Pardee 2012). The scope of my thesis was to fill this gap of knowledge.

In **chapter III** we introduce the reader to our ant fauna manipulation experiment in Indonesian cacao plantations, in which we experimentally established contrary ant communities which occur frequently in the study region: a) Dominace by the aggressive invasive ant species Philidris cf. cordata. b) Dominance by the presumably beneficial ant *Dolichoderus* cf. *thoracicus* c) Ant exclusion d) relatively undisturbed ant fauna as control. For 19 month monitored cacao fruit development and compared the direct and indirect effects of the different ant communities on pests and diseases. With this detailed data we depict a multi-trophic interaction network between cacao and its mutualists and antagonists, which is driven by the traits of the dominant species and the ant community properties, and we asses the final ecosystem services in terms of final yield.

In **chapter IV** we focus on a negative plant trait mediated indirect interaction between a minor and a major pest of cacao. Combining field observation data with laboratory behavioural experiments we could prove that feeding of the minor pest induces a plant trait change in cacao fruits which negatively affects the major pests. This trait mediated indirect interaction is consistent among seasons and spatial scales and leads to a yield maximum with moderate incidence rates of the minor pest. We discuss concrete implications for management and the importance of trait mediated interactions in agroecosystems.

In **chapter V** we gather evidence that correcting for behavioural and physiological traits improves prediction strength of ecological models. We use a detailed dataset of leaf herbivory rates, arboreal ants and arthropod herbivores in cacao plantations. We compare the statistical fit of models explaining leaf loss using ant abundances, ant biomasses and ant biomasses corrected for the behaviour of the single species at bait choice tests (sugar vs. protein). Explanatory power was best when we corrected abundance data for both, body size and preference of the species for protein.

III Interaction complexity matters: Disentangling services and disservices of ant communities driving yield in tropical agroecosystems

This article is under review in the Journal *Proceedings of the Royal Society B*: Biological Sciences. Date of submission: 14.02.2013
Running title: Ecosystem services and disservices of ants

Authors: Arno Wielgoss[1,2,*], Teja Tscharntke[1], Alfianus Rumede[3], Brigitte Fiala[2], Hannes Seidel[1,2], Shahabuddin[4], Yann Clough[1]

Affiliations:
[1] Agroecology, Department of Crop Sciences, University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany
[2]Animal Ecology and Tropical Biology (Zoology III), Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany
[3]Department of Agriculture, Klabat University, Airmadidi No. 1, ID-95371 Manado, Indonesia
[4]Faculty of Agriculture, University of Tadulako, ID-94118 Palu, Indonesia
*Corresponding author: Arno Wielgoss, Tel.: +49-931-3181088, E-mail address: awielgo@gwdg.de

Author contributions:
AW, YC, S and TT designed research; AW, HS and S performed research; AW, YC analyzed output data, AW wrote the first draft of the manuscript and AW, YC, BF and TT contributed substantially to revisions.

Keywords: yield, predation, indirect interactions, *Theobroma cacao*, ant fauna manipulation, ant exclusion, Indonesia, Sulawesi

Abstract

In tropical agroecosystems ants affect crops through their impact on plant mutualists and antagonists. Hitherto few studies address multiple interactions, and little is known about how these differ between ant communities, and how they integrate into crop yield.

We manipulated ant communities in cacao agroecosystems by combining ant exclusion and introduction of invasive and native dominant species and monitored cacao fruit development, pests, diseases and yield for 16 months.

Ant communities provided ecosystem services, including reduced leaf herbivory and fruit pest damage and pollination facilitation, but also disservices, such as increased mealybug density, phytopathogen dissemination and indirect enhancement of damage by a major pest in response to the reduction of a minor pest.

Yields were highest with species-rich, even, unmanipulated communities, whereas ant exclusion decreased yield by 27%. Introduction of an invasive dominant ant decreased species richness and evenness and resulted in 34% lower yields, while introduction of a non-invasive dominant species resulted in similar species richness and yields as in the unmanipulated control.

The integration of multiple effects within crop yield shows that species traits affect ant community structure and the balance between services and disservices in surprisingly complex ways, with species-rich and even communities ensuring highest crop yield.

Introduction

Ecosystem services and disservices in agriculture depend on a complex suite of direct and indirect interactions (Vandermeer et al. 2010) involving multiple herbivores (Stowe et al. 2000), pathogens (Evans 2007), predators (Schmitz 2007; Bruno & Cardinale 2008) and pollinators (Klein et al. 2007). Most studies of ecosystem services in agriculture focus on single interactions. To assess the importance of planned and associated biodiversity (Vandermeer 2011) in agroecosystems for the quantity and quality of yield, all intermediate ecosystem services and disservices need to be analyzed (Mace et al. 2012).

In tropical agroecosystems ants play a key role (Eubanks 2001; Philpott & Armbrecht 2006), with native or invasive ant species frequently achieving high abundances and becoming ecologically dominant (Hölldobler & Wilson 1990). Such dominant ant species often form particularly intensive mutualisms with hemipterans (so-called trophobionts) which provide honeydew as sugar source in exchange for protection against potential predators (Blüthgen et al. 2004), and allow ants to build large colonies with multiple (polydomous) nests (Richard et al. 2001). This can result in dominant ants reducing species richness and evenness of ant communities by aggressively excluding other species from their territory and from food sources (Gibb & Hochuli 2003). We expect this to reduce ecosystem services, because ant diversity can have significant top down effects on the arthropod fauna (Philpott et al. 2004), including agricultural pest species (James et al. 1999; Robertson & Swinton 2005). On the other hand the higher ant abundances under increasing dominance can also increase predation, so ant communities with dominance of a single ant species may be equally or more effective in suppressing pest species than more evenly structured ant communities (Gove 2007).

Ant community effects on crop yield may not only consist in ecosystem services like pest predation and changes in pollination success (Philpott et al. 2006), but also in ecosystem disservices such as pathogen spore dissemination (Evans 2007), increases in herbivory via effects on pest-pest interactions (Wielgoss et al. 2012) and mutualism with crop-damaging hemipterans (Davidson et al.

2003). However, little is known to date on the effect of dominant ants and ant community properties on the final yield outcome of such a suite of interactions and until now most studies addressing effects on ecosystem function involve only one or very few ecosystem processes (Hillebrand & Matthiessen 2009).

We hypothesise that the single effects may vary in sign and size depending on the presence of dominant ants, on their ecological traits, and on the structure of the ant community. Ant communities with high species richness and high evenness (i.e. a similar share of abundance in a community) could be beneficial by maintaining services and diluting potential disservices associated with ant dominance (Hillebrand & Bennett 2008).

And we assume that species rich, even ant communities enhance ecosystem services more than disservices, and that the service-disservice balance is negatively affected by specific traits of dominant and invasive ant species. To test these hypotheses we used a highly replicated ant fauna manipulation experiment in smallholder cacao agroforestry in Sulawesi, Indonesia comparing four distinctive ant communities which are widespread in the study region. This experimental approach reduced confounding effects of *environmental variables or land use practices on* ant community structure*.* For 16 months we monitored every two weeks ant communities, flowers, fruits, incidence of fruit damage due to pests and diseases and final yield. Here we analyze the effects of ant community structure on pests and diseases of cacao and we depict how different ant communities affect the balance between ecosystem services and disservices and drive final crop outcome. We found that traits of dominant species and ant community structure affect cacao trees via a complex crop-antagonist-mutualist interaction network. Even and species rich communities provided the best ecosystem services leading to highest yields.

Methods

Study area and study plots.

All sites were situated in Palolo valley, Central Sulawesi, Indonesia. In May 2009 we selected 15 cacao plots (50 x 50m) without insecticide use for at least one year, differing in shade intensity and with absence of *Philidris* cf*. cordata* and *Dolichoderus* cf. *thoracicus*. (hereafter called *Philidris* and *Dolichoderus* respectively). In each plot we placed 4 subplots (10 x 10m) with a minimum distance of 8m containing 9 neighbouring cacao trees each.

Ant treatments.

In cacao plantations of our study region the dolichoderine ant species *Philidris* cf. *cordata* has recently become invasive and ecologically dominant. It reduces ant species richness (Wielgoss et al. 2010) and can displace other dominant species such as the native *Dolichoderus* cf. *thoracicus* which might be beneficial as an effective predator of cacao pests (Way & Khoo 1992; Van Mele & Cuc 2001). Both ant species are associated with the mutualistic cacao mealybug *Cataenococcus hispidus* Morrison (Hemiptera: Pseudococcidae), with whom they exchange protection against honeydew. Both species can be ecologically dominant, but they differ in spatial activity patterns and tolerance towards subordinate ant species.

The ant fauna manipulation treatments were assigned randomly to four subplots: i) Undisturbed naturally occurring ant fauna as control ii) Establishment of *Philidris* or iii) *Dolichoderus* as ecologically dominant ant species on the test trees using artificial nest sites; iv) Exclusion of ants from test trees using nest destruction and insect glue on the tree stem base as barriers (Fig.III.A1). The treatments were installed in August 2009 and maintained until July 2011 (for details of methods see Appendix chapter III).

Data collecting.

Every 2 weeks from March 2010 to July 2011, on all trees in the subplots, flowers were counted, cacao fruits were classified by size and pest/disease incidence and ripe fruits were harvested and dry weight of marketable beans was recorded. All beans of fruits of one subplot were pooled and dried in the sun. Defective beans were separated to account for yield quality and were weighed separately from marketable dry beans. To avoid confounding effects of differences between the subplots we recorded tree characteristics, temperature and shade cover. The percentage of shade tree canopy cover was based on hemispheric pictures obtained above the cacao canopy. To determine the herbivory rates we collected two times twenty fully developed, mature leaves on each of three randomly selected trees per subplot using a telescopic branch-cutter. The leaves were selected in stratified random sampling to assure coverage of the different parts of the tree crown and scanned digitally. To assure that the leaves had grown during their whole lifespan in the according ant treatments the leaf herbivory surveys were conducted at the end of the study in April 2011. The area of leaf loss was calculated using the software ImageJ (Abràmoff et al. 2004). All ant-attended mealybug aggregations and their location were recorded in all test trees in May 2011. Ants were surveyed and identified to morphospecies one time before and three times after treatment installation in each subplot using standardized tuna and sugar baits on the nine cacao trees and at four ground locations per subplot (for sampling details see Appendix II).

Inoculation experiment.

The phytopathogen *Phytophthora palmivora* Butler (Peronosporales: Pythiaceae) causes the most severe cacao disease in Indonesia. Beside transmission trough wind and rain invertebrate vectors, especially tent-building ants, are the most important ways of dissemination (Evans 2007). To check for contamination with *Phytophthora* we inoculated each 50 fruits with 0.5 cm^3 of dead *Philidris* and *Dolichoderus* workers and material of the typical detritus tents of *Philidris*, which are built on cacao fruits (Fig.III.A3). As control for each group we used the same inocula, but desinfected with 5% bleach. As a baseline we used control 50 fruits without inocula. After 8 days the area of typical *Phytophthora* lesions were measured and we compared each experiment group with its according control and the baseline control using a Welch two sample t-tests. Identity of *P. palmivora* was confirmed in the laboratory (for detailed methods see Appendix II).

Data analysis.

Cacao tree characteristics: To detect possible confounding variables we fitted linear mixed effects models with canopy cover, cacao tree height, diameter at breast height and crown volume as dependent variable, treatment as explanatory variable and plot as random effect.

Ant community characteristics: To detect differences in ant community structure we aggregated the ant data per subplot and fitted linear mixed effect models by restricted maximum likelihood (REML) for mean ant abundances at the baits and ant species richness per subplot with plot and survey round as random effects. Then we conducted a Tukey's contrast test for multiple comparisons of means.

*Insect pests and diseases:*To predict ant treatment effects on the incidence of the main pest, *Conopomorpha cramerella* Snellen (Lepidoptera: Gracillaridae) and the incidence of a minor pest, *Helopeltis sulawesi* Stonedahl (Hemiptera: Miridae), we fitted binomial generalized linear mixed models by the Laplace approximation over the amount of infected harvested fruits versus the number of healthy harvested fruits per subplot, plot and harvest run. To detect differences in leaf herbivory between treatments we fitted linear mixed effect models by REML for percentage of leaf loss (mean per subplot) with plot and subplot as random factors and we fitted linear mixed models by REML to check if leaf loss was correlated with evenness. To check for differences in number trophobiont aggregations we fitted linear mixed effect models by REML for total number of mealybug aggregations (log-transformed) per subplot with plot, subplot as random factors. To compare differences in location of trophobiont aggregations we calculated the percentage of total aggregations found at leaves and shoots and we fitted linear mixed effect models by REML, with subplot and plot as random factors followed by a Tukey's contrast test for multiple comparisons of means. We fitted a binomial generalized linear mixed model by the Laplace approximation over the total amount of medium and large fruits lost due the phytopathogen *P. palmivora* during the experiment time versus the total number of harvested non infected fruits per subplot, with plot as random effect.

Fruit set: To detect differences in fruit set rates we aggregated open flower data from April 2010 to May 2011, but small fruit counts from June 2010 to July 2011 per subplot to avoid bias, because two months was the mean development time from flowers to small fruits. We then fitted binomial generalized linear mixed models (GLMM) by the Laplace approximation over the amount of small fruits versus the number of open flowers per subplot with plot and subplot as random factors.

Early fruit abortion: To detect differences in the rates of early fruit abortion we fitted binomial GLMMs by the Laplace approximation over the number of aborted fruits versus the number of survived fruits per subplot with plot and subplot as random factors. To assess possible influence of pests on early fruit abortion we repeated the analysis with leaf loss, number of mealybug aggregations and percentage of *Helopeltis* damage as explanatory variables.

Fruit development: We aggregated the flower and fruit data of all observation runs and of the nine trees per subplot and used linear mixed effect models fit by restricted maximum likelihood (REML) with plot and subplot as random effects to test for ant treatment effects on the number of flowers, total number of young cacao fruits, number of fruits which survived the early fruit abortion, number of harvested fruits.

Yield and revenue: For dry yield and total marketable dry cacao beans we used the first 12 months of data to have estimates for one complete harvesting season. Extrapolating the ant community effects on yield observed in our experiment to larger areas is legitimate, since *Philidris*, when naturally present in a cacao plantation can dominate >80% of the trees with similar high abundances as in our experimental treatments (Wielgoss et al. 2010), and as well *Dolichoderus*, can be similarly dominant over larger cacao plantations, when provided with nesting sites and trophobionts (Way & Khoo 1991; Hosang et al. 2010). The mean cacao world market price during this time was 3.14 US$ kg-1 (ICCO 2010). For each ant community treatment we calculated total harvest value per year and hectare using the first 12 months of yield data and assuming 1111 trees per ha (3m planting distance).

Results

Cacao tree characteristics.

Cacao tree height, stem diameter at breast height, crown volume and shade cover did not vary significantly between treatments in each plot (Table.III.A1).

Ant communities.

Ant abundances in subplots with the experimentally established single species dominances were higher than in the unmanipulated control treatments (Fig.III.1a, *Philidris:* t = 3.61, P < 0.01; *Dolichoderus:* t = *3.32, P* < 0.01, in Fig.III.1a,b,c we the mean of surveys and of the 9 trees per subplot). In the ant exclusion trees the mean ant abundance was reduced to < 10% of the control (t = -5.55, P <0.01). This is comparable to the reduction rates of other ant exclusion experiments (Klimes et al. 2011; Piñol et al. 2012).

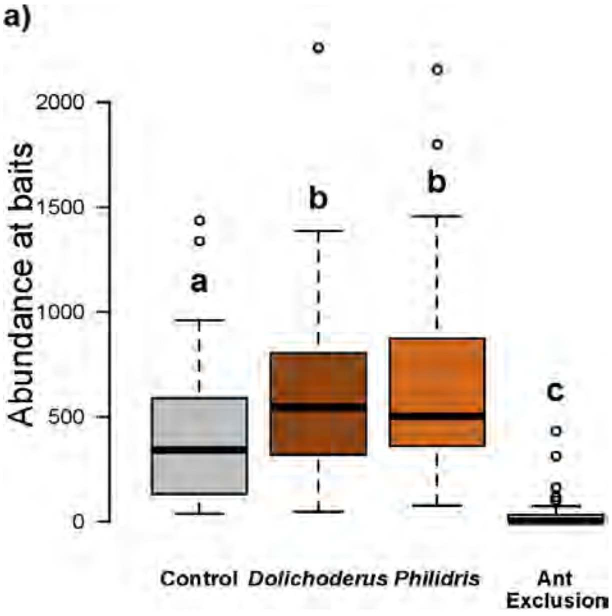

Fig.III.1a): Abundance of workers at protein and sugar baits

While species richness in *Dolichoderus* treatments was similar to the control (Fig.III.1b, *t* = -0.55, *P* = 0.59), it was ~50% lower in the other two treatments (Fig.III.1b, *Philidris : t* = -3.59, *P* < 0.01, Ant exclusion: *t* = -4.14, *P* <0.01).

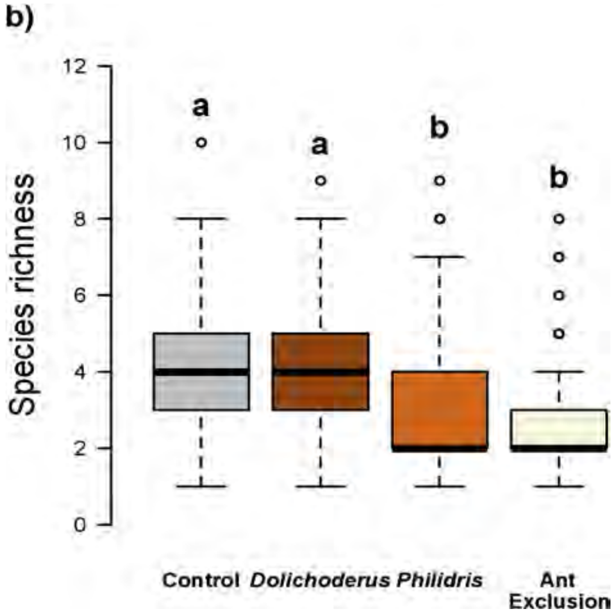

Fig.III.1b): Ant species richness at protein and sugar baits

Similarly, the evenness in *Dolichoderus* treatments was comparable to the unmanipulated communities (Fig.III.1c, *t* = -0.47, *P* = 0.64), while presence of the aggressive *Philidris* reduced evenness sharply (*t* = -3.59, *P* < 0.01). In ant exclusion treatments occurrence of ants was so rare that calculation of evenness was not meaningful.

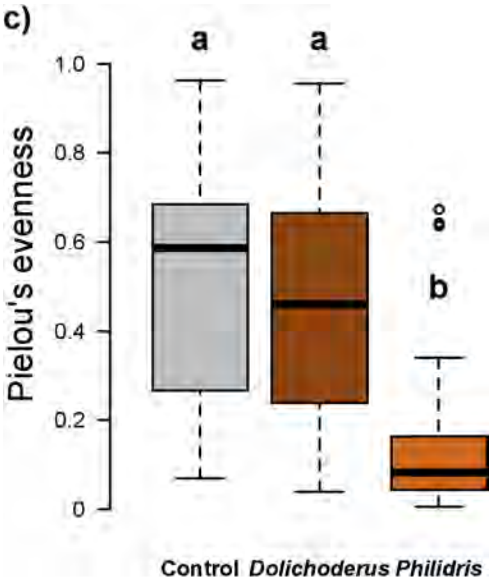

Fig.III.1c): Pielou's evenness of ants at protein and sugar baits

Composition, abundances and species richness of the ant communities in our *Philidris* or *Dolichoderus* dominance treatments were similar to natural occurrences of these species found in cacao plantations of the same region (Bos et al. 2007; Wielgoss et al. 2010). Model details are given in Table.III.A2.

Effects on fruit set and initial number of fruits.

There were no differences in number of flowers between the treatments (Table.III.A3). In ant exclusion treatments a similar proportion of flowers set fruit as in the control (Fig.III.2, Table.III.A4, $z = -26.1$, $P < 0.01$), whereas in the *Dolichoderus* ($z = 46.5$, $P < 0.01$) and *Philidris* ($z = 29.0$, $P < 0.01$) treatments the rates were higher.

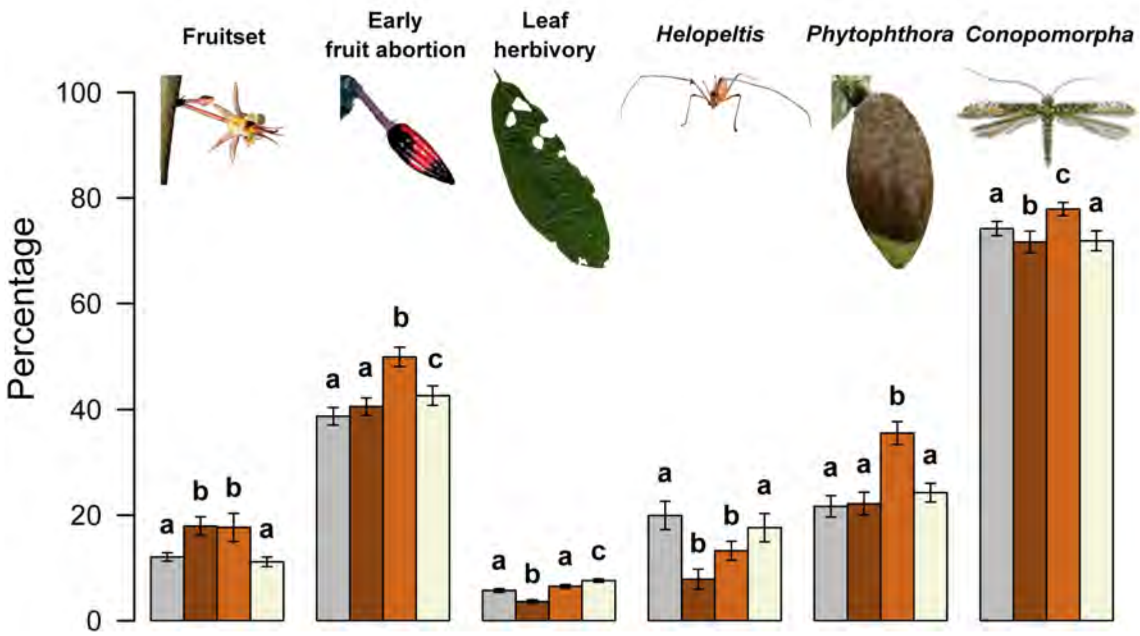

Fig.III.2: Percentages of fruits set, early fruit abortion, leaf loss due herbivory, harvested fruits with damage by *Helopeltis sulawesi* or *Conopomorpha cramerella* pests and fruits lost due *Phytophthora palmivora* disease in the different treatments of the ant manipulation experiment in cacao plantations (grey= unmanipulated control; dark brown = dominance of native *Dolichoderus* ant; light brown = dominance of invasive *Philidris* ant, beige = ant exclusion).

Fruit set correlated positively with ant abundances on the trees in the subplots (Fig.III.A2, Table.III.A4, *z* = 26.1, *P* < 0.01). The number of young fruits were similar in the control subplot and in subplots dominated by *Dolichoderus* or *Philidris*, but lower in subplots with ant exclusion (Fig.III.3, Table.III.A3, *Dolichoderus:* *t* = -0.74, *P* = 0.46; *Philidris*: *t* = 1.05, *P* = 0.30; Ant exclusion: *t* = *-2.31*, *P* = 0.026).

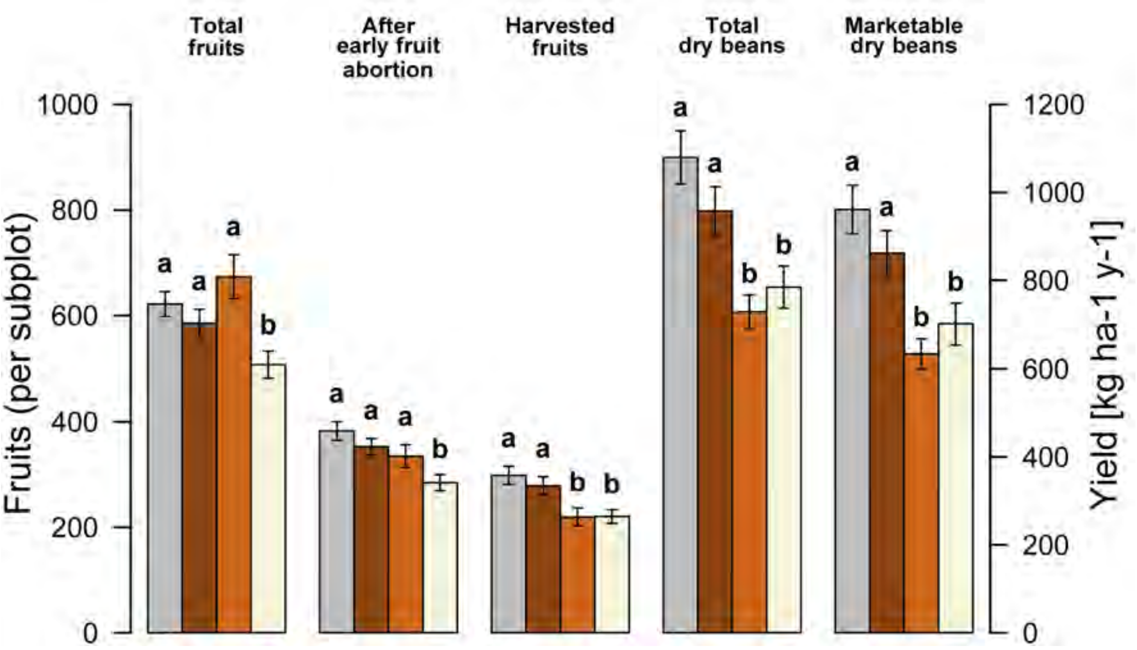

Fig.III.3: Number of total fruits, fruits after early fruit abortion and harvested fruits per subplot and total dry beans and marketable dry beans in kg per hectare and year in the different treatments of the ant manipulation experiment in cacao plantations (grey= unmanipulated control; dark brown = dominance of native *Dolichoderus* ant; light brown = dominance of invasive *Philidris* ant, beige = ant exclusion).

Effects on early fruit abortion.

Cacao trees can abort fruits in early development stages because of environmental factors, diseases and pests. The lowest abortion rates of young fruits were in non-manipulated control subplots, followed by *Dolichoderus* dominated ant communities (Fig.III.2, Table.III.A4, *z* = 2.2, *P* = 0.03) and ant exclusion ($z = 7.2$, $P < 0.01$), whereas *Philidris* dominated ant communities had highest abortion rates ($z = 2.2$, $P < 0.01$). Differences in percentage of fruit set and the subsequent fruit abortion partly counterbalanced each other and resulted in similar amounts of developing fruits in control and *Dolichoderus* dominated subplots (Fig.III.3, Table.III.A3, $t = -1.03$, $P = 0.30$). In control subplots the number of surviving fruits was lower ($t = -3.4$, $P < 0.01$) and in *Philidris* subplots it was lower on average, but not significantly so ($t = -1.03$, $P = 0.10$).

Indirect ant community effects on early fruit abortion.

The percentage of aborted fruits was positively correlated with fruit damage by the sap sucking mirid *Helopeltis sulawesi* (Table.III.A4, $t = 4.30$, $P < 0.01$), leaf loss due to herbivores ($t = 5.82$, $P < 0.01$) and amount of mealybugs ($t = -4.48$, $P < 0.01$), all of which were affected by the ant fauna. The two Dolichoderinae-dominated ant communities reduced fruit damage due to *H. sulawesi* (Fig.III.2, Table.III.A4, *Dolichoderus*: $z = -15.35$, $P < 0.01$; *Philidris:* $z = -7.71$, $P < 0.01$) compared to control subplots, while in ant exclusion subplots there was no difference ($z = -0.22$, $P = 0.83$) in fruit damage by *Helopeltis*. In comparison to control treatments herbivory rates were reduced in *Dolichoderus* dominated trees (Fig.III.2, Table.III.A1, $t = -4.14$, $P < 0.01$), but elevated in ant exclusion treatments ($t = 3.85$, $P < 0.01$) and was higher (with marginal significance) in *Philidris* treatments ($t = 2.68$, $P = 0.09$; Table.III.A1). Ant communities with dominance of single species attended more mealybug aggregations per subplot than the communities of the control (Table.III.A2, *Dolichoderus*: $t = 1.02$, $P = <0.01$; *Philidris:* $t = 5.56$, $P = <0.01$). In the ant exclusion plots, numbers of trophobiont aggregations were lower ($t = -1.37$, $P = <0.01$). A major difference between the ant communities was the distribution of the mealybug aggregations within trees, which may influence the spatial ant activity patterns (Blüthgen et al. 2004). While *Philidris* attended their mealybug partners preferably at fruits and flowers and only with a lower percentage on leaves and shoots (Table.III.A2, $t = -2.67$, $P = <0.01$) relative to control, *Dolichoderus* preferred to transfer them to young leaves and shoots ($t = 2.28$, $P = <0.01$, Table.III.A2).

Effects on fruit infesting pathogens.

The most important disease of cacao in South-East Asia is the pan-tropic black pod disease caused by *Phytophthora palmivora* (Evans 2007). In *Philidris* subplots a higher percentage of fruits were lost due to *Phytophthora* than in all other treatments (Fig.III.2, Table.III.A4, $z = 12.52$, $P < 0.01$). In the inoculation experiment we showed that *Philidris* workers and their tent material were infested with spores of *Phytophthora* (*Philidris* ants: $t = 3.63$; $P < 0.01$; *Philidris* tent material: $t = 6.18$; $P < 0.01$; Table.III.A5). *Dolichoderus* workers had also a higher infection potential than the control ($t = 5.67$, $P < 0.01$), but significantly lower than in case of *Philidris* workers ($t = -3.3$, $P < 0.01$; Table.III.A5). The fruits that were not affected by *Phytophthora* and reached ripeness.

Harvested fruits.

In the control and *Dolichoderus* treatment number of harvested fruits was similar, while in *Philidris* and ant exclusion treatments around 25% fewer fruits were harvested (Table.III.A3).

Effects on herbivores reducing bean quality and quantity.

The main cacao pest in South-East Asia is the fruit-boring moth *Conopomorpha cramerella*. The larvae mine into the fruits and reduce bean numbers and quality of remaining beans (Day 1989). In control and ant exclusion treatments the percentage of harvested fruits affected by *Conopomorpha* was similar ($z = -1.51$, $P = 0.13$). In trees dominated by *Philidris* infestation rate was higher than in control treatments ($z = 4.7$, $P < 0.01$), whereas in *Dolichoderus* dominated trees it was reduced ($z = -2.95$, $P < 0.01$; Table.III.A4, Fig.III.3). *Conopomorpha* damage rates were negatively correlated with ant community evenness ($z = 6.8$; $P < 0.01$).

Sum of all interactions: Ant community effects on marketable yield and revenue.

Compared to the control, total marketable yield was 27% lower in ant exclusion treatments, which equals a loss of 875 US$ ha-1 y-1 (*t* = -3.34, *P* <0.01) and 34% (1109 US$ ha-1 y-1) lower in *Philidris* treatments (*t* = -4.21, *P* <0.01, Fig.III.3, Table.III.A3). Yields in *Dolichoderus* and control did not differ significantly (*t* = -1.27, *P* = 0.21). Ecosystem services in terms of marketable yield correlated positively with evenness of the associated ant communities (Fig.III.4, Table.III.A3, *t* = 2.7, *P* = 0.013).

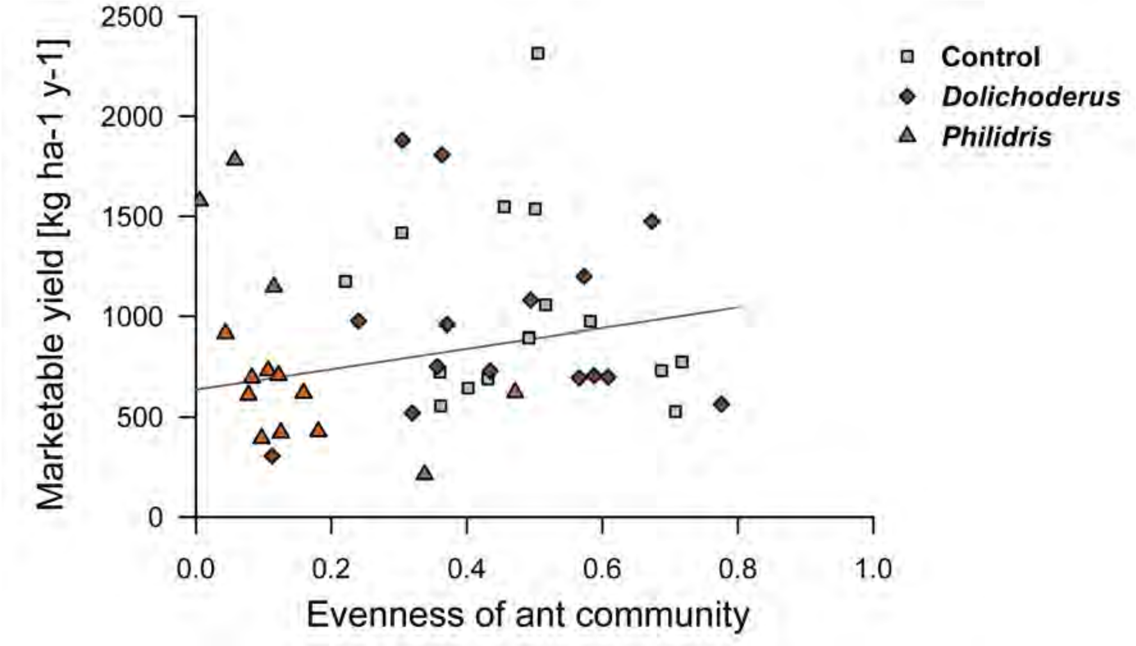

Fig.III.4: Effect of ant community evenness on marketable yield in the three treatments with ants of ant fauna manipulation experiment in 15 cacao plantations in Central Sulawesi.

Discussion

The results of this experimental study on the role of ant communities in agroecosystems show that ants drive a surprisingly complex network of direct and indirect interactions with the crop plant its pests, pollinators and pathogens. The size and in some cases even sign of the single effects changed with traits of present dominant species and with ant community properties. Prevalence of services over disservices and therefore highest marketable yield and revenue was achieved in the two most species rich and even ant treatments (Fig.III.4). The naturally occurring, non-manipulated control ant communities provided ecosystem services of 875 US$ ha-1 y-1 compared to the ant exclusion treatment, where 27% less marketable yield was harvested. In ant communities dominated by single ant species the effect strongly depended on the identity of the dominant species. We observed (relative to the unmanipulated control) yield losses of 34% (-1109 US$ ha-1 y-1) in presence of the invasive species *Philidris*, forming ant communities with very low evenness, and no significant yield losses with the native *Dolichoderus*, which allowed relatively high ant community evenness*.* As discussed in the following, these differences in marketable yield can be ascribed not only to changes in pest and disease incidence, but also to more complex effects on fruit set, fruit abortion and interference among herbivores, which were all directly or indirectly influenced by ant community structure (Fig.III.5).

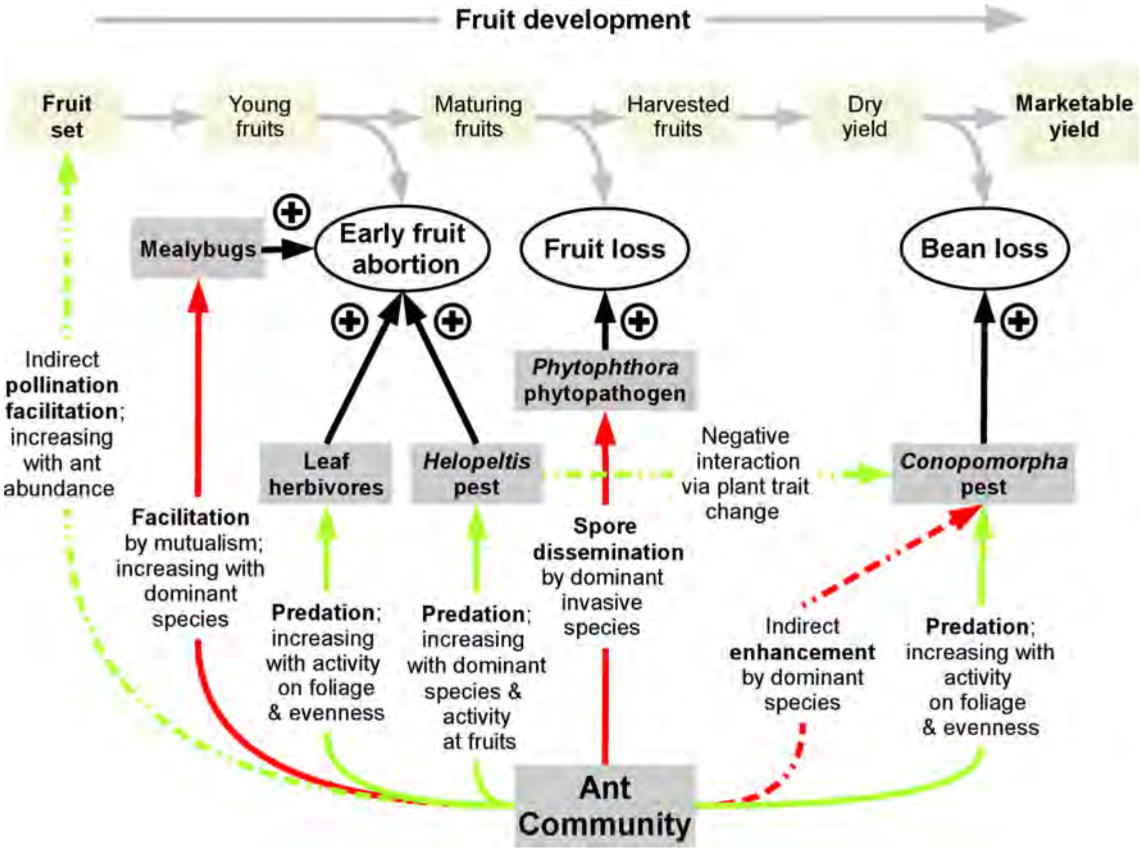

Fig.III.5: Overview of ant community effects on pests and diseases affecting cacao fruit development and final yield in ant manipulation experiment in cacao plantations. Green: Ecosystem service; Red: Ecosystem disservice; Grey: Fruit development and fruit or bean losses; (+): positive correlation.

Ant community characteristics.

The structure, composition and spatial distribution of worker activity of the ant communities is determined by presence and identity of dominant ants (Hölldobler & Wilson 1990). The non-invasive ant species *Dolichoderus*, is relatively tolerant towards other ant species (Way & Khoo 1992). Therefore presence of *Dolichoderus* resulted in ant communities with relatively high species richness and evenness, which was comparable to our unmanipulated control ant communities, but *Dolichoderus* promotes much higher total worker abundances. *Dolichoderus* placed its mealybugs, with which it forms a close mutualism, in aggregations not only at fruits but also to a high percentage (75%) at young shoots and leaves and built nests between leaves in the foliage. Since distribution of honeydew sources influences the spatial activity patterns of ants

(Blüthgen et al. 2004), *Dolichoderus* workers were active in the whole tree. In contrast the invasive dominant ant *Philidris* aggressively displaces most other ant species from the trees (Wielgoss et al. 2010). Accordingly the introduction of *Philidris* led to an uneven and species poor ant community. Because of the mealybug distribution and nesting behaviour the abundant workers were active mainly on fruits, stem and big branches, but less in the foliage and at small branches of the cacao trees.

Ant community effects on fruit set.

Fruit set of cacao flowers was positively related to the abundance of ants on the trees, being lowest in ant exclusion treatments, intermediate on the unmanipulated control trees (intermediate ant abundances) and highest in single species dominated trees (high worker abundances and activity, Table.III.A4). A plausible explanation is the pollinator-disturbance hypothesis (Greenleaf & Kremen 2006; Philpott et al. 2006): In this case nuisance by ants may cause pollinators to switch between flowers and trees more frequently and thereby enhance pollen transfer, pollen load, and number of pollen donors. In self-incompatible plants like cacao this should cause an increased pollination success and fruit set. Florivory by herbivores has been observed only very rarely in the field. Direct cacao pollination by ants has been under discussion since beginning of the 20th century (Glendinning 1972), but has not been convincingly demonstrated (Delabie 1990). Even though many ants are frequently present near the flowers, tending mealybugs at the flower buds, they would have to transfer pollen to neighbouring trees, which is unlikely, thus preventing successful cross pollination. Hence, we hypothesise that the ants indirectly influence fruit set of cacao by affecting pollinator behaviour.

Indirect ant community effects on early fruit abortion.

In our experiment percentage of young fruits being aborted by the tree increased with amount of mealybug aggregations, damage by the sap sucking pest *Helopeltis* and leaf herbivores (Table.III.A4). The ant communities with dominant species facilitated much higher numbers of trophobiont aggregations than control ant communities (Table:II.A2). Such intensive trophobiont tending by dominant ants may negatively affect crop plant fitness via cryptic herbivory (Hunt 2003). In *Dolichoderus* and *Philidris* dominated ant communities we found lower rates of fruits damaged by *Helopeltis* (Fig.III.2), which spends most of its life-cycle at the fruit surface (Stonedahl 1991). This can be explained by the high worker abundances and increased worker activity on the fruits in these ant communities. Similarly, the reduced leaf herbivory in the *Dolichoderus* and increased leaf herbivory in the *Philidris* treatment (Fig.III.2) is presumably the result of differences in spatial activity of the workers, mainly foraging in the tree foliage (*Dolichoderus*) or on fruits (*Philidris*). These ant-mediated effects of herbivory on early cacao fruit abortion resulted in lowest abortion rates of young fruits in the unmanipulated control communities, followed by *Dolichoderus* dominated ant communities, ant exclusion and *Philidris* dominated ant communities (Fig.III.2).

Ant community effects on fruit losses due to diseases.

One of the most serious threats to cacao production in South-East Asia is the pathogen *Phytophthora palmivora.* In *Philidris* dominated subplots about 65% more fruits were lost due to this plant disease relative to the mean of the other subplots (Fig.III.2). This is likely due to the species-specific tent building behaviour of *Philidris*. This ant species uses detritus material from infected rotten fruits to build nests and tent structures for protecting the trophobiont aggregations at healthy cacao fruits (Fig.III.A3). *Dolichoderus* builds its nests between leaves without the use of detritus. In inoculation tests we showed that *Philidris* ants and their nest material are highly infested with spores of *P. palmivora*. *Dolichoderus* workers had a certain infection potential, but it was much lower (Table.III.A5). This suggests that *Philidris* is an effective vector of the disease, leading to serious yield losses (Fig.III.3). Invertebrate vectors of *P. palmivora* have been observed before (Evans 2007) and even *Dolichoderus* was discussed as possible vector of *Phytophthora* (Khoo & Ho 1992). But here we show that the transmission efficiency is highly associated to specific behavioural traits and may differ widely even between related species.

Ant community effects on pests reducing bean quality and quantity.

Philidris dominated ant communities, with lower evenness and species richness, were associated with high damage by the major cacao pest (Fig.III.2), which significantly reduced bean quality and thus quantity of marketable beans (Fig.III.3). *Philidris* showed little activity in the foliage where *Conopomorpha* hides during daytime in the foliage underneath leaves and small branches, visiting fruits for oviposition only at night (Day et al. 1995). The specific traits of a *Dolichoderus* dominated ant community (higher worker abundances activity in the foliage, combined with relatively high evenness and species richness) enable it to suppress *Conopomorpha* more effectively than control ant communities (Fig.III.2). There is a plant mediated indirect effect between the two common pests (Wielgoss et al. 2012), with the major pest *Conopomorpha* showing a clear oviposition non-preference towards *Helopeltis* damaged fruits. Ant communities particularly efficient in preventing damage by *Helopeltis*, such as those dominated by *Philidris* or *Dolichoderus*, can indirectly facilitate damage due to the major pest *Conopomorpha*. Our data confirms this pattern in the case of *Philidris*, but in ant communities with presence of *Dolichoderus* this indirect effect appeared to be partly compensated by direct predation and disturbance of *Conopomorpha*.

Dominant species traits and ant community properties affect multiple crop plant-antagonist-mutualist interactions and associated ecosystem services.

Ants affect crop plant productivity via many direct and indirect pathways including both trophic and non-trophic interactions. A unique advantage of our study over previous studies of ant effects on crop plants is the integration of multiple ecosystem services and disservices and using marketable yield as measure for the final effect. We show that traits of dominant species such as high abundances and spatial activity patterns (fruit *versus* foliage oriented foraging) can cause uneven and species poor ant communities to protect crop plants better against some pests, as predicted by Gove (Gove 2007). But the enhanced pest suppression (by invasive *Philidris* ants) did not result in increased yield. On the contrary, we show how specific traits of this dominant ant species increased ecosystem disservices, such as increased fruit pathogen dissemination and reduced leaf herbivore and *Conopomorpha* suppression, which finally lead to serious yield losses. Ant communities dominated by *Dolichoderus* still showed high species richness and evenness, possibly due to its relatively low aggressiveness compared to *Philidris*. Although their high worker density reduced damage by leaf herbivores and the fruit affecting pests *Conopomorpha* and *Helopeltis*, these services were counterbalanced by disservices such as increased herbivory by mealybugs (causing higher abortion of young fruits; Fig.III.2) so that *Dolichoderus* dominance did not propagate to increased yield (compared to the control, Fig.III.3). This underlines the importance of accounting for all these potential interactions before praising a single species to be beneficial and a possible biocontrol agent (e.g. in *Dolichoderus* sp., (Way & Khoo 1992; Ho & Khoo 1997)). Crop deficits under ant exclusion can be ascribed manly to reduced fruit set and indirect enhanced young fruit abortion.

High evenness of species-rich predator communities has been assumed to be positively related to functional diversity and hence biological pest control (Philpott & Armbrecht 2006; Philpott et al. 2008a; Crowder et al. 2010). In our experiment evenness of the ant communities was correlated positively with amount of marketable yield (Fig.III.4, Table.III.A3). It is difficult to separate evenness effects from effects of dominant ant species traits in our study, because traits of single species like high aggressivity and dominance both lead to changes in community properties like low evenness and higher abundances, and were correlated with other traits impacting yield. In this particular case high evenness counterbalanced ecosystem disservices associated with single species.

Our results have implications for agricultural management. Insecticide use in the tropics, including our study region, has been increasing dramatically (Wanger et al. 2010). This has no or minimal effect on cacao herbivores (Wood et al. 1992), but appears to negatively affect evenness and diversity of ant communities and can favour dominant or invasive species (Peck 1998; Kenne et al. 2003). For example in our study area the special nest-building behaviour

(Fig.III.A3) makes the invasive ant *Philidris* less vulnerable to insecticide use than other ant species, which may have favoured the spread of this detrimental species in the recent past. We show that such changes in community composition can lead to a disruption of the ecosystem service-disservice ratio and cause substantial crop losses.

Conclusions

In our study we show that a focus on multiple interactions between ants and the agrroecosystem is needed to judge their value in delivering ecosystem services and to inform crop management. We recommend a more systematic quantification of the relevant final ecosystem services, such as marketable yield, in studies of biodiversity and ecosystem functioning, as these integrate the effect of all relevant direct and indirect interactions. Such studies should cover long time periods because ecosystem service effects associated with traits of species or community properties may accumulate in the long term (Hillebrand & Bennett 2008) and vary with the years or season.

With growing dominance of a single species its individual traits override the effects of the other species in the community. Therefore in our case species rich ant communities with a high evenness, diluted possible ecosystem disservices of single species and resulted in highest yields. This suggests that beneficial effects of natural enemy evenness on pest control in agroecosystems (Crowder et al. 2010) may extend to other intermediate ecosystem services and are finally reflected in marketable yield.

Acknowledgements

We thank Indonesian representatives in Tadulako University, field and laboratory assistants, village heads, and villagers in the study region; the Indonesian and German project coordination team. We thank Ivette Perfecto for comments on a previous version on the manuscript. This study was supported by the German Academic Exchange service DAAD.

Appendix chapter III

Study area.

All sites were situated in Palolo valley, on the northern border of the Lore Lindu National Park, Central Sulawesi, Indonesia. The elevation in this region ranges from 400 m to about 1,000 m above sealevel. Natural vegetation is lowland to submontane rainforest, although only the latter remains (Whitten *et al.* 2002). Being close to the equator, the seasonality is not very marked. Annual rainfall is around 2,500 mm (Gutzler & Koehler 2010), with a long-term pattern of 9 consecutive rainy months and 3 consecutive drier months (Whitten *et al.* 2002).Cacao is the main cash crop grown in the study area. Hybridization between out-crossing genotypes is common in smallholder cacao, and cacao trees in this study, as well as most of the other trees in the area, originate from hybrids between Forastero and Trinitario types.

Study plots.

We selected 15 cacao plantations along a gradient from full sun to heavily shaded with trees of similar age and height. Only plantations without insecticide use of at least one year before the study and with *Philidris* cf. *cordata* and *Dolichoderus* sp. being absent (obtained by a rapid ant fauna assessment) were included.

Ant fauna manipulation treatments.

In each plantation we placed a plot (50 x 50 m) containing four subplots (minimum distance 8 m) with nine cacao trees each. The plots were managed by specially hired and trained local assistants. The brunch connections of test trees with trees outside of the subplots were cut regularly. To each subplot one of the four ant manipulation treatments was assigned randomly. In one subplot per plot the ant fauna remained undisturbed as Control.

*Ant exclusion treatment:*At the base of trees at a hight of 30cm we fixed a 20cm wide cone shaped plastic collar around the stem with rubber band (see

Fig.III.A1). Cracks in the bark were stuffed with foamed rubber. The plastic collar was covered with a 0.3cm thick layer and 10cm wide layer of “Tree Tanglefoot pest barrier” (® Contech Enterprises Inc.; Tanglefoot Company, Grand Rapids, MI, USA). The trees were searched for ant nests which were removed manually and by local insecticide application. This ant exclusion treatment was inspected weekly, glue was renewed and new founded colonies were removed whenever necessary.

Dolichoderus cf. thoracicus and Philidris cf. cordata treatment: Artificial nest sites (bamboo tubes, 30cm long, 10-18cm diameter, filled with dry coconut leaves) were placed in trees of cacao plantations were the *P.* cf. *cordata* or *Dolichoderus* cf. *thoracicus* were highly abundant with large colonies. We chose source plantations with a very low incidence rate of the phytopathogen *Phytophthora palmivora* to avoid a later spread with the colony transfer. Two times per week approximately 5 cm^3 cooked fish was placed near each nest to attract ants and accelerate colonization and production of pupae. After 3-6 weeks, depending the weather conditions, most of the nests were colonized with numerous workers, brood, and various queens of the according species. In early morning hours when the majority of workers are inside the nest we sealed the nests entrances quickly using plastic bags and rubber bands and transferred them to the according subplots. Per test 3-5 nests (according to size of the tree) were fixed with metal wire in the main ramification of the test trees. The time from August 2009 to February 2010 was necessary to install the ant treatments and stabilize the populations. During this time we provided weekly for each introduced ant colony 5 cm^3 cooked fish and 20ml saturated sugar solution to avoid migration or death of the colonies. Feeding stopped when we began the cacao fruit monitoring in March 2010. In order to give the ants access to their natural symbiosis partner we transferred one cacao fruit with an aggregation of mealybugs (Hemiptera: Pseudococcidae) to each test tree. We placed the fruits with the aggregations in direct contact with cacao fruit of the test tree, so the trophobionts could migrate easily. The ant treatment trees were checked weekly. If a colony had migrated or died off or was replaced by another ant species the establishing process was repeated.

Yield data collection.

All cacao fruits on the test trees were counted fortnightly from March 2010 to July 2011. The fruits were assigned to size and health categories (small or cherelles; medium; large unripe; large ripe, i.e. harvested; damage by *H. sulawesi*; *C. cramerella*; the black pod disease caused by *Phytophthora palmivora*; rat or squirrel feeding). Fruits infected by *P. palmivora* were removed from the trees after each harvest run, like it is general farmers practice (Akrofi *et al.* 2003). Ripe fruits were harvested and the fresh weight of the beans was recorded. The beans were dried in the sun and the dry weight of marketable beans and of beans affected by the cacao pod borer *C. cramerella* were recorded separately. Mean cacao bean price from April 2010 to April 2011 was 3.17 US$ (ICCO 2010).

Ant surveys.

We used standardized plates (25 cm diameter), which were equipped with two baits of 2cm^3 of tuna in oil and two sponges saturated with 70% sugar solution, to determine the abundance of ant morphospecies. Per subplot one plate was placed in the main ramification of each experimental cacao tree (if the main ramification was too high, it was fixed at breast height on the stem with elastic rubber band; approximately 1 of 10 cases) and four were placed on the ground. The plates were observed for 1 h. Every 15 min, the abundance of all ant species occurring at the baits feeding on fish or sugar was counted separately. Of every ant species appearing on the plate 5 to 10 specimens were caught with forceps and conserved in 70% ethanol for later identification. This survey was conducted once before (July 2009) and tree times after April, October 2010, February 2011) the ant fauna manipulations in all 15 cacao plots. We identified the samples to morphospecies level.

Environmental Data.

To quantify the canopy cover per plot we used vertical digital canopy photography with a fisheye lens. Per subplot four pictures were taken above and below the cacao tree canopy (5.8m and 1.2m respectively above the ground). We calculated the mean shade cover per plot above the cacao canopy for each plot using the software “CIMES-FISHEYE” (Walter 2009). We measured tree height, stem diameter at breast height, maximal crown diameter and calculated the crown volume. Per plot two temperature dataloggers (Thermochron iButton, Maxim–Dallas Semiconductor) were placed at breast height in different cacao trees, recording the temperature every 2 h from August 2009 until May 2011. Cacao tree height, stem diameter at breast height, crown volume and shade cover above and under cacao canopy did not vary significantly between treatments in each plot (see Table.III.A1).

Phytophthora palmivora inoculation experiment.

Plant diseases like the black pod disease caused by *P. palmivora* can be disseminated by arthropods. *Philidris cf. cordata* builds detritus nests tents at the cacao pods to protect their trophobiont aggregations. To test whether the ants we used for the treatments were contaminated with spores of *P. palmivora* we conducted a inoculation experiment.

350 medium sized cacao fruits of a plantation with a minimum of *P. palmivora* incidents were harvested. The surface was desinfected using 5% bleach solution. In small punched holes in the fruit surface each 50 fruits were inoculated with:

a) ~ 0.5 cm³ dead *Philidris* ants (*Philidris)*
b) ~ 0.5 cm³ disinfected dead *Philidris* ants (*Philidris* Control)
c) ~ 0.5 cm³ tent material of a *Philidris* colony (*Philidris* tent)
d) ~ 0.5 cm³ disinfected tent material of a *Philidris* colony (*Philidris* tent Control)
e) ~ 0.5 cm³ dead *Dolichoderus* ants (*Dolichoderus)*
f) ~ 0.5 cm³ disinfected *dead Dolichoderus* ants *(Dolichoderus Control)*
g) without inoculum (Control)

After the inoculation the wounds were sealed with wax and the fruits were stored in a warm and dry place. Eight days after the inoculation the fruits were searched for the typical symptoms of a *Phytophthora* infection and the lesions areas were measured. We compared the lesion area sizes of each group with the according control and the baseline control. Of each treatment group one infected fruit was selected randomly. Pure isolate cultures on PDA medium were reared to confirm the identity of *P. palmivora* microscopically.

Appendix chapter III Tables.

Table.III.A1: Comparison of cacao tree parameters crown volume, stem diameter, tree height and canopy cover in the different experimental subplots.

Tree parameter	Treatment	Estimate	SE	*t*	*P*	Lower CI	Upper CI
Crown volume	Control	50.69	4.24			43.34	58.03
	Dolichoderus	-2.01	4.91	-0.56	0.58	-9.25	5.16
	Philidris	-0.72	4.92	-0.18	0.86	-7.87	6.54
	Ant-exclusion	-2.02	4.92	-0.54	0.59	-9.19	5.25
Stem diameter	Control	37.95	1.22			35.54	40.35
	Dolichoderus	0.91	1.1	0.83	0.41	-1.26	3.08
	Philidris	0.37	1.1	0.33	0.74	-1.8	2.54
	Ant-exclusion	0.28	1.1	0.26	0.8	-1.89	2.46
Tree height	Control	3.99	0.12			3.76	4.22
	Dolichoderus	-0.05	0.07	-0.71	0.48	-0.19	0.09
	Philidris	-0.02	0.07	-0.26	0.79	-0.16	0.12
	Ant-exclusion	0.03	0.07	0.46	0.65	-0.11	0.18
Canopy cover	Control	0.29	0.04	8.29		0.22	0.36
	Dolichoderus	0.00	0.03	-0.07	0.95	-0.06	0.06
	Philidris	-0.04	0.03	-1.32	0.19	-0.10	0.02
	Ant-exclusion	0.01	0.03	0.21	0.83	-0.06	0.07
Leaf herbivory	Control	5.83	0.33			5.17	6.48
	Dolichoderus	-1.95	0.47	-4.14	<0.01	-2.88	-1.02
	Philidris	0.79	0.47	1.68	0.09	-0.14	1.72
	Ant-exclusion	1.81	0.47	3.85	<0.01	0.88	2.74

Table.III.A2: Effects of ant community manipulations on ant abundances, species richness, evenness at baits, total number of trophobiont aggregations, number of trophobiont aggregations at leaves and fruits and leaf herbivory per subplot in cacao agroforests of Central Sulawesi.

Ant community properties	Treatment	Estimate	SE	*t*	*P*	Lower CI	Upper CI
Ant abundance	Control	403.82	57.16			290.75	516.89
	Dolichoderus	217.73	65.59	3.32	<0.01	87.98	47.48
	Philidris	236.6	65.59	3.61	<0.01	106.85	366.35
	Ant-exclusion	-363.73	65.59	-5.55	<0.01	-493.48	-233.98
Ant species richness	Control	4.29	0.28			3.74	4.84
	Dolichoderus	-0.2	0.37	-0.55	0.59	-0.91	0.51
	Philidris	-1.31	0.37	-3.59	<0.01	-2.03	-0.6
	Ant-exclusion	-1.51	0.37	-4.14	<0.01	-2.23	-0.8
Piélou's evenness	Control	0.48	0.05			0.39	0.58
	Dolichoderus	-0.03	0.07	-0.47	0.64	-0.16	0.10
	Philidris	-0.34	0.07	-5.08	<0.01	-0.48	-0.21
	Ant-exclusion	-0.01	0.07	-0.18	0.85	-0.15	0.13
log(Total mealybug aggregations)	Control	4.01	0.20			3.60	4.42
	Dolichoderus	1.56	0.27	5.80	<0.01	1.02	2.11
	Philidris	1.47	0.27	5.46	<0.01	0.93	2.01
	Ant-exclusion	-0.82	0.27	-3.03	<0.01	-1.37	-0.27
Percentage Mealybug aggregations at leaves+shoots	Control	0.51	0.06			0.05	0.81
	Dolichoderus	0.20	0.09	2.28	0.03	0.25	0.82
	Philidris	-0.23	0.09	-2.67	0.01	0.05	0.38
	Ant-exclusion	-0.10	0.09	-1.18	0.25	0.26	0.51

Table.III.A3: Effects of ant community manipulations on number of flowers, total fruits, fruits after early fruit abortion and harvested fruits and dry and marketable yield.

Class	Treatment	Estimate	SE	*t*	*P*	Lower CI	Upper CI
Flowers	Control	25310.67	5546.69			14117	36504
	Dolichoderus	-7292.00	5546.69	-1.34	0.19	-18288	3704
	Philidris	5317.67	5546.69	0.98	0.50	-7400	14691
	Ant-exclusion	3695.87	5546.69	0.68	0.33	-5678	16313
Total fruits	Control	621.80	47.32			526.30	717.30
	Dolichoderus	-36.47	49.24	-0.74	0.46	-135.84	62.90
	Philidris	51.67	49.24	1.05	0.30	-47.70	151.04
	Ant-exclusion	-113.67	49.24	-2.31	0.03	-213.04	-14.30
Fruits after early fruit abortion	Control	382.33	29.05			323.70	440.96
	Dolichoderus	-29.87	28.94	-1.03	0.31	-88.27	28.54
	Philidris	-47.93	28.94	-1.66	0.11	-106.34	10.47
	Ant-exclusion	-97.87	28.94	-3.38	0.00	-156.27	-39.46
Harvested fruits	Control	298.20	28.37			240.94	355.46
	Dolichoderus	-19.60	26.50	-0.73	0.46	-73.09	33.89
	Philidris	-78.73	26.50	-2.93	<0.01	-131.22	-24.25
	Ant-exclusion	-77.73	26.50	-2.97	<0.01	-132.22	-25.25
Dry yield	Control	8741.93	865.18			6996	101487
	Dolichoderus	-984.53	675.79	-1.02	0.31	-2348	379.27
	Philidris	-2840.13	675.79	-4.20	<0.01	-4204	-1476
	Ant-exclusion	-2388.13	675.79	-3.53	<0.01	-3752	-1024
Marketable Yield	Control	7782.33	826.62			6144	9451
	Dolichoderus	-799.33	628.00	-1.27	0.21	-2067	468.03
	Philidris	-2646.93	628.00	-4.21	<0.01	-3914	-1380
	Ant-exclusion	-2102.07	628.00	-3.35	<0.01	-3369	-834.71
Marketable yield	Estimate	5155.64	1018.46			1991	4685.58
	Evenness	4130.36	1557.03	2.65	0.01		

Table.III.A4: Effects of ant community manipulations on cacao fruit set, abortion of young fruits, proportion of fruit damage by the phytopathogen *Phytophthora palmivora* and the pests *Helopeltis sulawesi* and *Conopomorpha cramerella.*

Class	Factor	Estimate	SE	*z*	Pr(>|z|)
Fruit set	Control	-2.40	0.16		
	Dolichoderus	0.45	0.01	46.51	<0.01
	Philidris	-0.26	0.01	29.03	<0.01
	Ant-exclusion	0.27	0.01	-26.09	<0.01
Fruit set	Intercept	-3.22	0.20		
	Ant abundance	0.14	0.01	26.10	<0.01
Fruit abortion	Control	-0.48	0.08	-5.89	
	Dolichoderus	0.07	0.03	2.17	0.03
	Philidris	0.49	0.03	16.62	<0.01
	Ant-exclusion	0.23	0.03	7.20	<0.01
Fruit abortion	Intercept	-1.05	0.15		
	% *Helopeltis* damage	1.11	0.26	4.30	<0.01
	% leaf loss	0.052	0.009	5.82	<0.01
	log (mealybugs)	0.076	0.02	-4.48	<0.01
Phytophthora palmivora	Control	-1.36	0.16		
	Dolichoderus	-0.03	0.05	-0.64	0.52
	Philidris	0.71	0.05	12.52	<0.01
	Ant-exclusion	0.11	0.05	2.11	0.03
Helopeltis sulawesi	Control	-2.24	0.35		
	Dolichoderus	-1.19	0.08	-15.35	<0.01
	Philidris	-0.57	0.07	-7.71	<0.01
	Ant-exclusion	-0.02	0.07	-0.22	0.83
Conopomorpha cramerella	Control	1.34	0.2		
	Dolichoderus	0.15	0.05	-2.95	<0.01
	Philidris	0.27	0.06	4.7	<0.01
	Ant-exclusion	-0.08	0.05	-1.51	0.13

Table.III.A5: Results of inoculation experiment: Welch two sample t-test comparison of *Phytophthora palmivora* lesion area sizes of cacao fruits (N = 50 per treatment) inoculated with dead *Philidris* workers, *Philidris* tent material, *Dolichoderus* workers and the according desinfected control and not inoculated control fruits.

Group1	Group 2	t	Df	*P*	Mean lesion area group1 [cm³]	Mean lesion area group 2 [cm³]
Philidris	*Philidris* Control	3.63	56	< 0.01	182.8	39.47
Philidris	Control	4.78	49	< 0.01	182.8	0
Philidris tent	*Philidris* tent Control	6.18	71	< 0.01	100.91	11.16
Philidris tent	Control	7.72	49	< 0.01	100.91	0
Dolichoderus	*Dolichoderus* Control	5.67	52	< 0.01	54.47	15.84
Dolichoderus	Control	8.11	49	< 0.01	54.47	0
Dolichoderus	*Philidris*	-3.3	52	< 0.01	54.47	182.8

Appendix chapter III Figures.

Fig.III.A1: Ant exclusion method using a plastic collar and insect glue barrier (Foto: A. Wielgoss).

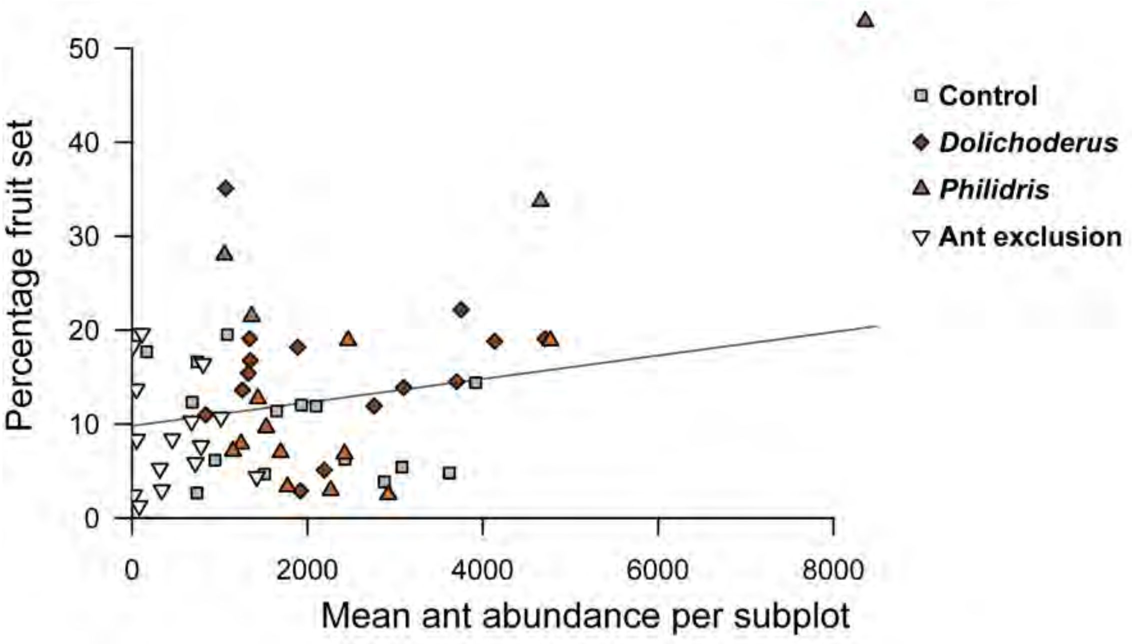

Fig.III.A2: Effect of mean ant abundance on cacao trees on early fruit abortion (cross= unmanipulated control; square = dominance of native *Dolichoderus* ant; circle = dominance of invasive *Philidris* ant, triangle = ant exclusion).

Fig.III.A3: Tent structure build by *Philidris cf. cordata* at a cacao fruit. Tent material is infected with spores of *Phytophthora palmivora* (Foto: A. Wielgoss). *Indirect interaction between cacao pests.*

IV A minor pest reduces yield losses by a major pest: plant-mediated herbivore interactions in Indonesian cacao

This article was published in the *Journal of Applied Ecology* 2012, **49**, 465–473
doi: 10.1111/j.1365-2664.2012.02122.x
Running Title: Indirect interaction between cacao pests

Authors: Arno Wielgoss[1,2,*] (awielgo@gwdg.de), Yann Clough[1] (yclough@gwdg.de), Brigitte Fiala[2] (fiala@biozentrum.uni-wuerzburg.de), Alfianus Rumede[3] (a_rumede@yahoo.com), Teja Tscharntke[1] (ttschar@gwdg.de)

Affiliations:
[1] Agroecology, Department of Crop Sciences, University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany
[2]Animal Ecology and Tropical Biology (Zoology III), Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany
[3]Department of Agriculture, Klabat University, Airmadidi No. 1, ID-95371 Manado, Indonesia
*Corresponding author: Arno Wielgoss, Tel.: +49-931-3181088, E-mail address: awielgo@gwdg.de

Author contributions: AW, YC, and TT designed research; AW and AR performed research; AW and YC analyzed output data, AW wrote the first draft of the manuscript and AW, YC, BF and TT contributed substantially to revisions.

Keywords: agroforestry, *Conopomorpha cramerella*, crop yield, *Helopeltis sulawesi*, herbivory, interference competition, oviposition choice, pest management, Sulawesi, *Theobroma cacao*

Summary

a) Herbivores inducing host plant trait changes can indirectly affect the performance, distribution, abundance and behaviour of other herbivores, even when they are temporally or spatially separated. However, it is unclear whether this occurs at scales relevant for applied purposes such as pest control in agricultural crops.

b) We studied the indirect effects of a minor pest, the mirid bug *Helopeltis sulawesi* (hereafter called *Helopeltis*), on the major pest of cacao *Theobroma cacao* in Southeast Asia, the pod-boring moth *Conopomorpha cramerella* (hereafter called *Conopomorpha*). For 2 years we surveyed herbivore damage and yield in ten focal trees in each of 43 cacao plantations and analyzed patterns of co-occurrence of the two herbivores. In a two-choice experiment we tested whether gravid females of *Conopomorpha* searching for oviposition sites discriminate against pods damaged by *Helopeltis*.

c) The proportion of pods affected by both pest species was significantly lower than expected. This pattern could not be ascribed to differential responses to environmental or management variables, but was due to avoidance of *Helopeltis* damage by ovipositing *Conopomorpha* females as shown in a two-choice experiment. The reduction in co-occurrence of damage by the two herbivores was found at tree and at plot scale, and held across 3 harvest seasons.

d) The differential yield impacts by the two herbivores and the avoidance by *Conopomorpha* of pods damaged by *Helopeltis* lead to a yield optimum at a *Helopeltis* incidence of 51%.

e) *Synthesis and application.* Plant-mediated indirect interactions between minor and major pest insects can be important drivers of yield loss at agriculturally-relevant spatial and temporal scales. In cacao, the mirid bug *Helopeltis*, a minor pest, generates conspicuous damage which often triggers pest control with insecticides. This practice may be counterproductive, because decreasing *Helopeltis* damage benefits the main pest, the cacao pod borer *Conopomorpha* resulting in a marketable yield optimum at intermediate

densities of the minor pest. Pest control recommendations should take into account the relative effect of control measures on interacting herbivores to avoid replacing one pest problem with another, potentially more serious one, during the course of a fruiting season.

Introduction

Indirect interactions between herbivores mediated by herbivore-induced plant trait changes can be more frequent and have a larger impact on biodiversity and community structure than direct competition between herbivores (Ohgushi 2005; Anderson et al. 2009). Plants respond to herbivore damage by changes in allelochemistry, cell structure and growth, physiology, morphology, phenology (Karban & Baldwin 1997; Denno & Kaplan 2007) or nutritional content (Denno et al. 2000; Sandström et al. 2000). These herbivore-induced plant responses may not only have multiple indirect effects on the performance and abundance of other herbivores (Van Zandt & Agrawal 2004; Poveda et al. 2005), but also influence their behaviour and spatial distribution (Van Dam et al. 2000). Plant-mediated indirect interactions may involve herbivores which are separated spatially (Bezemer et al. 2003), temporally (Johnson et al. 2002) and/or taxonomically (Bailey & Whitham 2006).

The applied relevance of plant-mediated interactions in terms of yield losses to invertebrate pests in agricultural crops is largely unknown. This is surprising given the large potential for such interactions, with most crops being affected by a sequence of different herbivore species with contrasting ecologies and host-plant effects. The quantitative importance of effects depends on the spatial and temporal scales at which these effects play out. While quantitative and long-term studies on plant-mediated interactions have often been called for (Bolker et al. 2003; Werner & Peacor 2003), few have gone beyond qualitative snapshot studies (Hougen-Eitzman & Karban 1995; Utsumi et al. 2010).

Here, we investigate the potential of plant-mediated indirect interactions between insect herbivore species to affect yield losses in cacao. Cacao *Theobroma cacao* L. is one of the most important cash crops worldwide, but also a species severely affected by pests and diseases. These have been estimated to be responsible for up to 30% losses in global production (Ploetz 2007), and can play a major role in cacao boom and bust cycles (Clough et al. 2009). The cocoa pod borer *Conopomorpha cramerella* Snellen (Lepidoptera: Gracillariidae) is the major cacao pest in Southeast Asia, causing crop losses up to 50% (Day 1989). The larvae mine into medium sized pods, causing quantitative and qualitative effects on the yield, and impede the separation of husk and pod contents (Fig.IV.1c). The mirid parasite *Helopeltis sulawesi* Stonedahl (Hemiptera: Miridae) feeds on pods of all ages and young shoots of cacao (Giesberger 1983). The surface of damaged pods is covered with scars and a thick sclerotic layer and this may promote the abscission of young fruits (cherelles) (Muhamad & Way 1995, Fig.IV.1b). In Southeast Asia *Helopeltis* spp*.* are considered as serious pests by farmers and agriculturalists (Muhamad & Way 1995, personal observation A Wielgoss, Y. Clough). As such, *Helopeltis* spp. are often used as a trigger for insecticide application, especially since imagos and early stages of the main pest *Conopomorpha* are difficult to detect. *Helopeltis sulawesi* and *Conopomorpha* may co-occur in the same pod at the same time but *Helopeltis* often damages the pod surface from the cherelle stage onwards, i.e. 3 months before the preferred time-window for oviposition by *Conopomorpha*.

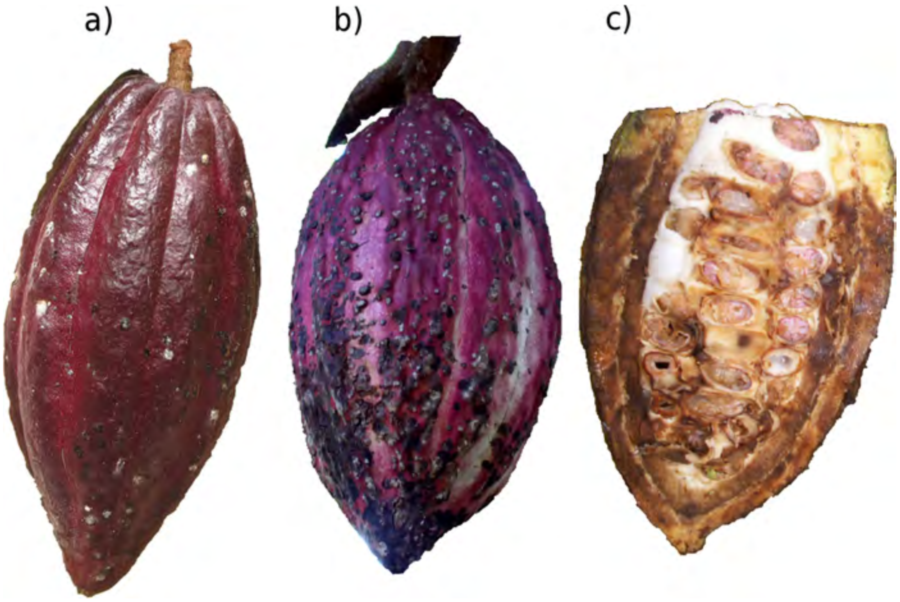

Fig.IV.1: Cacao pods: a) healthy b) epidermis with scars due to *Helopeltis* feeding c) bisected pod with feeding damage by *Conopomorpha* larvae

We hypothesized that the biology and the sequence of attack by the two herbivore species can lead to indirect interactions between them. Sap-feeding by *Helopeltis* spp. induces changes in the pod texture early in the pod development, before the stage preferred by *Conopomorpha* for oviposition, which suggests a potential for asymmetric effects of the mirid on the pod borer.

We conducted a large-scale, 2-year study in 43 smallholder cacao plots on the island of Sulawesi, the main cacao-producing region in Indonesia. We expected that the damage by the local mirid species, *Helopeltis,* will be negatively associated with subsequent damage by *Conopomorpha*. In a two-choice experiment we tested whether *Conopomorpha* females discriminate between healthy pods and pods damaged by *Helopeltis*. The results are quantified both in terms of herbivore response, potential environmental response and in terms of the impact on cacao yield.

Materials and methods

Study area and study sites.

The study was conducted in Palolo and Kulawi valleys at the margin of the Lore Lindu National Park, Central Sulawesi, Indonesia. The elevation of the plots ranged from 400 m to about 1000 m above sea level.

We chose 43 cacao plantations, 21 in Palolo, 22 in Kulawi (see Clough et al. 2011 for details), which had seen little or no insecticide applications in the previous years, based on the information given by the farmers. In each plantation we established a plot of 40 x 40 m, which was managed by local assistants from November 2006 to August 2008. Half of the plots were assigned randomly to frequent manual weeding regime (every 2 months), the other half of the plots to infrequent manual weeding (every 6 months). Each plot was separated into two 20 x 40 m subplots and one half was fertilised twice a year with urea fertiliser (46% N). Fertiliser was applied twice a year from December 2006 to June 2008 at a rate of 217 g urea (100g N) per tree with aliquots placed into ten concentric holes around each tree, which were subsequently covered with soil.

Five focal trees were selected in each of two 20 x 40 m subplots, i.e. ten trees per plot, to be used for more detailed phenological and pest and disease surveys (see below). Trees were selected randomly, with apparently non-productive or damaged trees discarded until we obtained five trees per subplot.

The temperature was recorded hourly using Dallas Thermochron ibuttons® (DS1921G, Maxim/Dallas Semiconductor, Sunnyvale, CA, USA), and the age of the trees was obtained from the farmers.

Study organisms.

Conopomorpha cramerella: Female cocoa pod borer oviposit eggs (orange, flat and oval in shape, ~0.5 mm length) on the cacao pod surface (Day 1985; Keane & Putter 1992). The preferred age of pods at time of oviposition is 3 months (Day 1989). Upon hatching the first instar larvae (~1 mm length) tunnel through the floor of the egg shell and through the epidermis until the sclerotic layer of the husk, where they seek a weak or thin point to penetrate it. The young larvae feed on the placenta until fully grown (12 mm length, 14-18 days, with 4-6 instars). Pods attacked by cocoa pod borer larvae often ripe immaturely and show uneven yellowing. An infestation often results in beans being malformed, undersized, clumped at the pod husk and significantly reduces quality and quantity of the harvest (Fig.IV.1c). The mature larvae tunnel out of the pod and descend to the ground for pupation.

Helopeltis sulawesi: The eggs of *Helopeltis* spp. are white, elongated (1.0-1.2 mm in length) and apically compressed (Ambika & Abraham 1979). Two unequal respiratory filaments arise from the anterior end of the egg, the longer being 0.4-0.5 mm long. On cacao *Helopeltis* spp. prefer to lay the eggs on the pods, but occasionally oviposit on young shoots. The incubation period of the egg varies with locality and season, but it is generally in the range of 6-11 days, although longer durations are observed occasionally. *Helopeltis sulawesi* has five larval instars which vary in size, color and development of body parts such as antennae and wings (Stonedahl 1991). Data for adult longevity and fecundity of *Helopeltis* are not available. For the closely related *H. theivora* a mean adult longevity of 30 days has been measured (Tan 1974a). On cocoa *Helopeltis* spp. feed on young shoots, flowers and developing pods (Muhamad & Way 1995). Feeding damage on pods appears as dark, circular lesions hardening as scars on the husk (Fig.IV.1b). Heavy infestations can result in pod malformation and premature drop. Tan (1974b) reported that pod abscission of young cherelles is mostly restricted to pods smaller than 5 cm and that larger pods have a reduced dry bean weight. Quantification of total yield losses due to *Helopeltis* spp. is difficult, because *Helopeltis*-induced abscission of young cherelles is masked by natural abscission and the reduction of bean weights is highly dependent on the pod age at time of attack (Muhamad & Way 1995).

Co-occurrence study.

Data collection: All cacao pods on the test trees were counted fortnightly from November 2006 to October 2008. The pods were assigned to size and health categories (small or cherelles; medium; large unripe; large ripe, i.e. harvested;

damage by *Helopeltis* or *Conopomorpha* or both; infected by *Phytophthora palmivora* (black pod disease); rodent feeding). Pods infected by *P. palmivora* and pods damaged by rat or squirrel feeding are of no value for harvest, and, as is the usual farmer's practice, were removed from the trees. Ripe pods were harvested and the fresh weight of the beans was recorded. To quantify the canopy cover per plot we used vertical digital canopy photography with a fisheye lens. For each test tree one picture was taken above the cacao tree canopy (5.8 m above the ground). We calculated the mean shade cover per plot above the cacao canopy for each plot using the software "Winscanopy" (Regent Instruments Inc.; www.http://regent.qc.ca/)

Environmental correlates of herbivore incidence: To investigate whether patterns of co-occurrence of *Conopomorpha* and *Helopeltis* are due to environmental parameters*,* we fitted a multi-level model for each of the two herbivores, using a Bayesian hierarchical framework to accommodate the aggregation of pod counts at tree, subplot and plot level, as well as the temporal structure given by the three main harvests (Gelman & Hill 2007). The model was fitted in WinBUGS (Lunn et al. 2000) using Markov-chain-Monte-Carlo sampling (3 chains, 50000 iterations, first 2500 discarded, thinning rate: 75. We tested for effects of the parameters: altitude above sea level (continues in thousand metres, centred around the mean), weeding frequency of the plot (0 = every 6 months; 1 = every 3 months), shade cover above the cacao canopy per tree (proportion 0 to 1; centred around the mean), and fertiliser treatment of the subplot (0 = unfertilised; 1 = fertilised).

Randomization tests: Co-occurrence of Helopeltis damage and Conopomorpha infection: To test for a possible effect of *Helopeltis* damage on the probability of successful *Conopomorpha* attack, we calculated the sum of all harvested pods per harvesting season per tree according to their pest incidence classification. Trees with no harvested pods in the categories "healthy", "damaged by *Helopeltis*" or "infected with *Conopomorpha* larvae" were discarded to be certain that *Conopomorpha* females were present and had a choice between pods with and without *Helopeltis* damage within each tested tree. We calculated the observed ratios of pods on which both *Conopomorpha* and *Helopeltis* damage was recorded divided by the total sum of pods with *Conopomorpha* infection. We then simulated the outcomes expected if *Conopomorpha* chooses the pods at random and repeated this 1000 times for each tree. After that we compared the randomized simulated ratios with the observed ratios for each tree and checked for significant differences. We combined the multiple *P*-values using Fisher’s method, which makes it possible to combine the results of multiple independent tests bearing upon the same overall hypothesis in a single test statistic (Borenstein et al. 2009). Because we consider it likely that oviposition site choice by *Conopomorpha* females depends on the density of conspecifics and *Conopomorpha* incidence differed between seasons (see Results), we conducted this analysis separately for each harvesting period.

To test whether the patterns within trees hold at the plot scale, which is most relevant for the farmers, we repeated this simulation at the plot scale, using the data aggregated by plot and harvesting season.

Oviposition experiment.

Cocoa pod borer rearing: To rear *Conopomorpha* we harvested medium sized cacao pods from plantations with high incidence rates. We picked pods that showed the typical symptoms of uneven, premature ripening of a *Conopomorpha* infection. Each pod was covered with a cacao leaf and the pods stacked in a shed to protect them from rain. Each morning the cacao leaves were searched for cocoons with pupating larvae. The cocoons were transferred separately in small plastic boxes closed with fine mesh, where they remained until they reached the imago state. We identified

Fig.IV.2: Oviposition experiment box with one healthy cacao pod and one with scars of *Helopeltis*-incidence.

the sex of the adults by distinguishing morphology of the tip of abdomen (Posada et al. 2011) (see Fig.IV.A1).

Oviposition choice test: In order to test whether *Conopomorpha* females show preferences between healthy and *Helopeltis*-damaged pods we conducted an oviposition choice test. We harvested medium-sized cacao pods from a plantation with low *Conopomorpha* incidence. Half of the pods showed serious incidence of *Helopeltis* damage incidence while the others were healthy. *Conopomorpha cramerella* eggs were removed carefully from the pod surface using water and a brush. In each experimental box (50 x 50 x 40 cm, mesh-covered; Fig.IV.2) we hung one healthy pod and one pod with *Helopeltis* damage. The side on which the healthy and affected pods were placed was randomized to avoid bias affecting the results. In each box we inserted one male and one female *Conopomorpha* (imago 2 days after emerging, reared in laboratory, see above). The boxes were stored in a dry, ant free place at outdoor temperatures. After 5 days and nights we opened the boxes, checked if the imagos had survived until end of the test and searched the pod's surfaces for eggs using a binocular microscope. We repeated this two-choice oviposition test 75 times in total, with different *Conopomorpha* individuals and cacao pods at each trial. To test for differences between the number of eggs on healthy and *Helopeltis*-affected pods we conducted a paired Wilcoxon signed rank test with continuity correction.

Effects on yield.

We fitted a joint multi-level model for pods affected with *Conopomorpha* only and those attacked by both *Conopomorpha* and *Helopeltis* using the total number of harvested pods and the proportion of harvested pods affected only by *Helopeltis* as explanatory variables. The model was fitted in WinBUGS (Lunn et al. 2000) using Markov-chain-Monte-Carlo sampling (3 chains, 10000 iterations, first 5000 discarded, thinning rate: 15). Based on the posterior distribution of the fixed effects we calculated (for a tree in an unfertilised, infrequently weeded subplot) the expected pod weights. In this study the dry weight of marketable beans per test tree was not measured because of the small quantities of beans per tree and harvest run. Instead we used observed dry bean data of a follow-up study in the same research area conducted by the first author (15 plots each with 26 trees, biweekly data collection with the same method from April 2010 until July 2011). The expected contribution to yield by individual pods in the different categories (undamaged, damaged by *Helopeltis*, damaged by *Conopomorpha*, damaged by both pests) was estimated using a generalized linear model with the total marketable yield as a response and the counts in each harvested pod category as explanatory variables, with the intercept removed.

Results

Harvests.

We could distinguish three main harvesting periods (Season A: February-August 2007, B: September 2007 - March 2008, C: April-October 2008; Fig.IV.3).

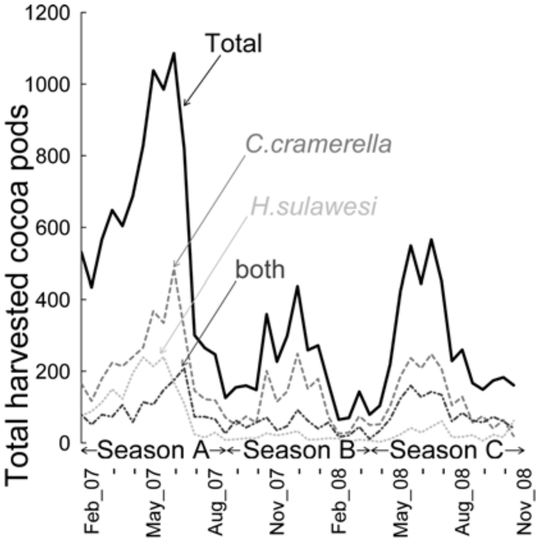

Fig.IV.3: Harvested cocoa pods (sum of 43 study plots) from February 2007 until October 2008 with the pods damaged only by *Conopomorpha cramerella* or *Helopeltis sulawesi* or affected by both pests, separated by harvesting seasons.

There were no significant seasonal differences in the percentage of pods affected by *Helopeltis* (Mean Season A: 35.50%, B: 34.75%, C: 41.98%; Fig.IV.4a). The percentage of harvested pods damaged by *Conopomorpha* differed significantly between the three harvesting periods (Mean: Season A: 54.93%, B: 73.20%, C: 72.40%; Fig.IV.4b).

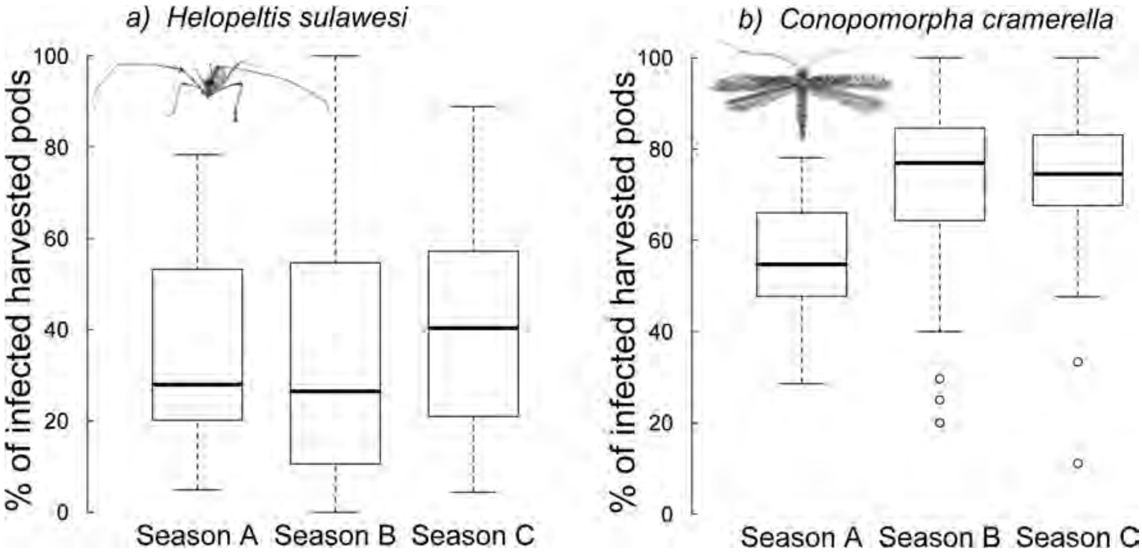

Fig.IV.4: Percentage of harvested pods in a plot (N=43) from three harvesting seasons: a) with *Helopeltis sulawesi* incidence. b) infected with *Conopomorpha cramerella*.

Co-occurence study.

Environmental correlates of herbivore damage: The multi-level model predicting *Helopeltis* damage suggests that altitude, weeding frequency of the plot and shade cover above the cacao canopy per tree did not have significant influence. The probability of *Helopeltis* incidence was significantly larger in trees with fertiliser treatment (Table.IV.1). None of the other tested environmental parameters had a significant effect on the probability of *Conopomorpha* damage (Table.IV.1).

Table.IV.1: Summaries of the 1002 samples from the posterior distribution for each of the parameters of the multi-level models fitted using WinBUGS for damage by *Helopeltis sulawesi* or *Conopomorpha cramerella* (2.5% - 97.5% = 95% credible interval; α_0 = global intercept; significant fixed effects in bold).

	***Helopeltis* damage**				**Conopomorpha damage**			
	mean	sd	2.50%	97.5%	mean	sd	2.50%	97.50%
α0	-0.02	2.6	-1.8	2.7	0.9	4.4	-3.9	7.1
$\beta_{fertilised}$	**0.3**	**0.1**	**0.1**	**0.5**	0.1	0.1	-0.2	0.4
$\beta_{altitude}$	1.6	1	-0.4	3.4	-1.1	2.3	-5.2	3.7
β_{shade}	0	0.8	-1.5	1.6	0.3	1.2	-2	2.7
$\beta_{weeding}$	0.1	0.2	-0.4	0.6	-0.2	0.5	-1.1	0.6
$\sigma^2_{subplot}$	0.1	0	0.1	0.2	0.1	0.1	0	0.3
σ^2_{plot}	0.5	0.2	0.3	0.9	0.5	0.4	0.1	1.4
$\sigma^2_{seasons}$	18.2	180.5	0.1	59.1	59.2	376.9	0.2	25.1

Co-occurrence of Helopeltis and Conopomorpha damage:

At the tree level, the observed ratio of number of pods attacked by both herbivores to the total number of pods attacked by *Conopomorpha* (median = 0.33, 1^{st} and 3^{rd} quantiles = 0, 0.67) was significantly lower than would have been expected if *Conopomorpha* females did not discriminate against damage caused by *Helopeltis* (i.e. 0.5). This was true for all seasons (Season A: $P < 0.001$, df = 710, Fishers-X^2: 3693.16; Season B: $P < 0.0001$, df = 214, Fishers-X^2: 643.21; Season C: $P < 0.0001$, df = 346, Fishers-X^2: 1254.61).

The same results were found at plot level: for all seasons the observed ratio of number of pods attacked by both

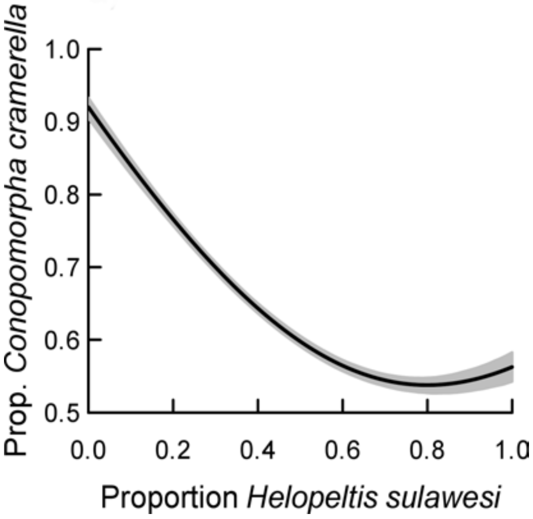

Fig.IV.5: Posterior predictive values for the percentage of cacao pods damaged by *Conopomorpha cramerella* given the percentage of pods damaged by *Helopeltis sulawesi* (black) and 95% credible interval (grey).

herbivores to the total number of pods attacked by *Conopomorpha* (median = 0.18, 1st and 3rd quantiles = 0.10, 0.48) was significantly lower than expected based on the assumption of non-discrimination by *Conopomorpha* females (Season A: $P<0.001$, Df = 88, Fishers-X^2: 438.30; Season B: $P < 0.00002$, df = 79, Fishers-X^2: 129.77; Season C: $P < 0.0003$, df = 86, Fishers-X^2: 140.17). In Fig.IV.5 we show the observed relationship between percentage of pods affected by *Helopeltis* and *Conopomorpha.*

Oviposition experiment.

In total we bred 402 imagos of *Conopomorpha*. We identified 208 males and 194 females (sex ratio did not differ from 1:1; df = 401, $P = 0.486$). Time from pupation to hatching was 8.96 ± 0.74 days (mean ± SD, N = 402). The longevity of adults in the laboratory was 4.46 ± 1.35 days. In 37 of the 75 oviposition choice tests there was no successful oviposition. In these cases the male or female pod borer did not survive until the end of the test. In the 38 successful tests *Conopomorpha* significantly preferred healthy pods instead of *Helopeltis*-affected pods for oviposition (paired Wilcoxon signed rank test with continuity correction: $P < 0.0001$; df = 27). On cacao pods damaged by *Helopeltis* we found a mean of 3.97 *Conopomorpha* eggs (SD: ± 6.2; max: 24, Total eggs on 38 pods : 151; Number of pods with no eggs: 13), on healthy cacao pods a mean of 13.66 *Conopomorpha* eggs (SD: ± 26.14; max: 152, Total: 519; Number of pods with no eggs: 0).

Effects on yield.

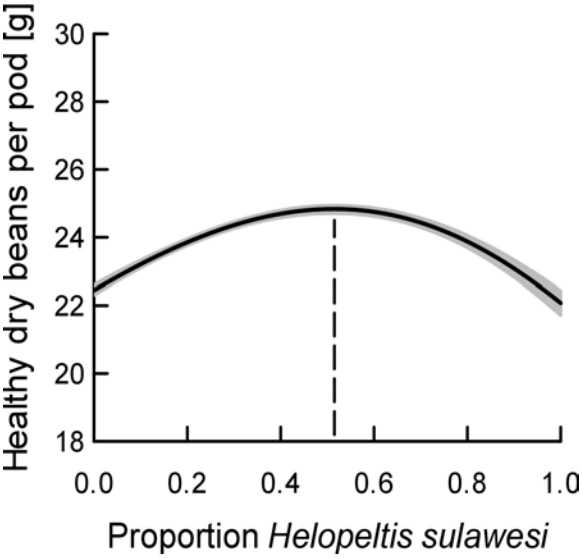

Fig.IV.6: Predicted mean weight of marketable dry beans per cocoa pod [g] as a function of percentage of *Helopeltis sulawesi*-affected pods modelled for plots with mean observed *Conopomorpha* incidence and *Helopeltis*-*Conopomorpha*-interaction (black) and 95% credible interval (grey).

According to our generalized linear model predicting yield weights per pod, pods damaged by *Helopeltis* contained a similar mass of marketable beans (32.3 g ± 10.4 g; mean ± SE) as healthy pods (mean: 32.5 g ± 6.9 g). The weight of marketable beans in pods infected by *Conopomorpha* was 33.8% lower (mean: 21.5 g ± 3.7 g) than in healthy pods and the outcome per pod was reduced by 56% (mean: 14.0 g ± 5.8 g) if a pod was infected by both pests.

In Fig.IV.6 we show the predicted weight of healthy dry beans per cacao pod as a function of percentage of pods with *Helopeltis* damage in presence and absence of *Conopomorpha.* In the absence of *Conopomorpha* the mean weight of marketable beans per pod maintains the same level, i.e. around a mean of 32 g per fruit. When *Conopomorpha* is present, our model predicts a maximum mean weight of dry marketable beans per pod when 51% of cacao pods are affected by *Helopeltis* (24.8 g; 9.6% more than at 0% Helopeltis incidence; with 0% *Helopeltis*-affected pods: 22.4 g; 33%: 24.5 g; 66%: 24.6 g ; 100%: 22.1 g).

Discussion

Top-down and/or bottom-up control are commonly used to explain herbivore population dynamics, while indirect herbivore-herbivore interactions, which may lead to complex ecological consequences for arthropod community compositions, still only get minor attention. We reveal a plant-mediated indirect negative interaction between two important, taxonomically separated cacao pests in South-East Asia*,* the mirid bug *Helopeltis sulawesi* and the cocoa pod borer *Conopomorpha cramerella.*

Plant mediated interactions between the two herbivores.

In our field observations the percentage of cacao pods damaged by both pests was lower than expected based on the expectation of non-discrimination by *Conopomorpha* females between pods affected by the mirid *Helopeltis* and healthy pods. These results were mirrored in two-choice oviposition tests, in which *Conopomorpha* showed a clear discrimination against cacao pods affected by *Helopeltis*. Determining the physiological mechanisms behind the avoidance behaviour was beyond the scope of this study. However, due to the feeding scars which are inflicted from the early stage of pod development, *Helopeltis* affected cacao pods have a harder and thicker sclerotic layer than healthy pods (Stonedahl 1991; Muhamad & Way 1995, Fig.IV.1c). It has been reported previously that Lepidoptera are able to detect physical surface traits of host plants and choose the preferred morphological phenotype for oviposition (Thompson & Pellmyr 1991) and that plant surface texture appears to be more critical for moths than for butterflies in the evaluation of potential oviposition sites (Renwick & Chew 1994). It has been shown that the physical properties of the sclerotic layer of the pods are associated with larval mortality and performance of *Conopomorpha* (Azhar & Long 1996), so the oviposition discrimination of pods with traits associated with *Helopeltis* damage appears to be adaptive. There are few other examples of indirect plant-mediated interactions via altered oviposition choice behaviour (Kruess 2002; Wise & Weinberg 2002; Poelman et al. 2008). We cannot eliminate the possibility of a reversed indirect effect of a *Conopomorpha* infection on feeding or oviposition preferences of *Helopeltis.* We expect the size of such an effect on oviposition behaviour to be rather small, because the dispersing abilities of *Helopeltis* are weak (the first larval instars are wingless and the adults are poor flyers) and alternatively lays eggs on shoots of cocoa, if no suitable pod is found (Stonedahl 1991). Since *Helopeltis* feeding only has a direct effect on bean quantity or quality when it affects very young pods (cherelles, Muhamad & Way 1995), it is likely that a possible indirect interaction of a *Conopomorpha* infection on feeding preference would not be economically relevant.

Consistency across spatial scales and seasons.

Local patterns need not translate to larger scales, i.e. local host-plant level avoidance by a pest species could be assumed to cause increased incidences on neighbouring host plants. However, our results not only confirm plant-mediated indirect interactions between *Helopeltis* and *Conopomorpha* on single fruits or trees, but also show that *Helopeltis* negatively affects the incidence of *Conopomorpha* at the scale of a plot (40 x 40 m). The size of the plot was chosen to mirror the smallholder management unit as commonly found in Central Sulawesi, suggesting our results are relevant to the scale at which management decisions are made by the farmer. The mechanisms behind the larger-scale patterns were not studied directly, but it is known that when encountering low densities of host plants appropriate for oviposition, gravid Lepidoptera females can alter their search patterns (Thompson & Pellmyr 1991), e.g. by flying longer distances between landings and doing fewer sharp turns (Odendaal et al. 1989), which causes an individual female to move faster between patches until it reaches a more rewarding area with more suitable oviposition sites. A similar change in searching behaviour combined with a reduced larval performance due to thicker sclerotic layers of *Helopeltis*-affected cacao pods may be responsible for the reduced densities of *Conopomorpha*-damaged pods in plots with higher *Helopeltis* incidence rates. It may not be uncommon that plant-mediated indirect interactions are important for larger-scale insect herbivore distributions and dynamics. While relatively few studies addressed larger scale patterns driven by plant-mediated indirect interactions, of the 90 studies on herbivore-induced plant trait-mediated interactions (71 studies reviewed by Ohgushi (2005) and 19 studies published since 2005; see Table.IV.A1), nine could show a propagation of plant level-effects to larger spatial scale. For instance, (Karban 1986) reported the case of a folivorous spittlebug that had lower persistence when feeding on leaves affected by a leaf-herbivorous moth, resulting in lower spittlebug densities in areas with higher moth abundances.

In addition to being valid across scales, our findings suggest that the ecological importance of plant-mediated indirect competition in our study holds across seasons. Field experiments have shown that due to variation in climate and/or herbivore development times, the outcome can differ dramatically among replicates or years (Van Zandt & Agrawal 2004). In our field study, even though *Conopomorpha* incidence changed between seasons, we observed the same plant-mediated indirect interaction patterns in three consecutive harvesting seasons.

Plant-mediated indirect interactions affect yield losses.

To our knowledge, there are no studies addressing economic relevance of plant-mediated indirect interactions in any crop species. Yield losses, or increases (Poveda et al. 2010), due to herbivory are usually studied for single pest species. Muhamad & Way (1995) hypothesized that abscission of pods due to early damage of *Helopeltis theivora* on cacao yield is unlikely to contribute importantly to ultimate crop losses because it is overlapped by natural cherelle wilt and later compensated by increased cherelle production. In their data, yield losses were closely related to time of damage: *Helopeltis*-affected medium sized pods had ~15% lower yield, but yield was unaffected when full-sized but not yet ripe pods were heavily damaged. In the simulation of our observation data, where no differentiation of pod age at attack could be made, there were only marginal direct crop losses on pods that were affected by *Helopeltis* (<1%). In the study of Day (1989) the crop losses due to *Conopomorpha* reached about 40% with 90% of pods attacked. In our study, the first to integrate the effects of both pest organisms, the estimated yield losses directly linked to *Conopomorpha* at an infection rate of 90% and in absence of *Helopeltis* was comparable (37.1%).

Our results show that in areas where *Conopomorpha* is absent *Helopeltis* does not lead to significant yield losses. But it is notable that pods affected by both pests contained significantly fewer marketable beans than a pod affected by *Conopomorpha* alone. Nevertheless in regions where *Conopomorpha* is common, as in our study area (mean infection rate ~ 67%), there is a yield optimum at an incidence rate of 51% *Helopeltis*-damaged pods (Fig. 5b). At this level the crop losses due to *Conopomorpha* are minimized via the indirect negative interaction between the two pests, which overcompensates the direct crop losses due to *Helopeltis* resulting in 9.6% more marketable cacao beans than if *Helopeltis* is absent. We deliver an example of how indirect plant mediated interactions between two agricultural pests result in minimized overall yield losses in co-occurrence of the two pest species.

Management implications.

The cocoa pod borer *Conopomorpha* is the most destructive pest of cacao plantations in Southeast Asia, but the fact that the *Helopeltis* spp. mirids are conspicuous and *Conopomorpha* is rather cryptic can lead to a disproportionate role of the mirids in affecting management decisions such as whether to spray insecticides or not. The authors have observed that insecticide use is often triggered by early season *Helopeltis* feeding scars. In this case the insecticide is sprayed directly on the pods. The sap-feeding *Helopeltis* nymphs are day-active, flightless and remain at the pods most of the time and therefore are much more affected by this management practice than *Conopomorpha,* which hides for most of the day underneath branches and visits the pods only for short time periods for oviposition at night (Day et al. 1995). In areas where *Conopomorpha* is common the described negative indirect interaction between the two pest organisms would make application of broad-spectrum insecticides on the cocoa fruits against *Helopeltis* pointless or even counterproductive, because the reduction of losses due to *Helopeltis* is likely to be exceeded by the increasing yield losses due to *Conopomorpha*. The same might be true for integrated pest management practices against *Helopeltis* spp. by ants, as proposed by Graham (1991) and Way & Khoo (1989). Ant species which are effective predators of *Helopeltis* might indirectly increase the probability of a *Conopomorpha* infection, given that the two pests have contrasting spatial and temporal activity patterns, and are therefore unlikely to be equally exposed to any particular predator species. The relatively immobile *Helopeltis* is possibly a much easier prey for ants such as *Dolichoderus* spp. (Way & Khoo 1989, 1992; Stonedahl 1991) than the rather cryptic *Conopomorpha*. In consideration of these facts it might be preferable to use more specific *Conopomorpha* control strategies such as complete regular harvesting to break the development cycle, pheromone traps or selection of resistant genotypes.

More generally, our results demonstrate that plant-mediated indirect interactions can be quantitatively relevant at spatial and temporal scales relevant for agricultural management. Given the large potential for such interactions in most other crops, we suggest that pest management strategies could benefit significantly from being adapted to account for these effects. In particular, this study underlines that efficiency of any pest control measure should not only be measured in impact on the target species alone, but should also consider effects on species which might directly alter host-plant traits and indirectly other species, which includes not only natural enemies and pollinators but also other herbivores.

Acknowledgements

This study was part of the DFG Project STORMA (‘‘Stability of Rainforest Margins of Indonesia’’; SFB 552). The German Academic Exchange Service (DAAD) covered the personal funding of A.W.. We thank S. Erasmi and D. Seidel for sharing the canopy cover data, the coordination of STORMA, A. Anshari for support and M. Iqbal for assistance in the field.

Appendix chapter IV

Appendix chapter IV Tables.

Table.IV.A1: Studies about plant trait mediated indirect effects between herbivores since the review of Ohgushi (2005)

Ando, Y., Utsumi, S. & Ohgushi, T. (2011) Community-wide impact of an exotic aphid on introduced tall goldenrod. *Ecological Entomology*, **36**, 643-653.

Bailey, J.K. & Whitham, T.G. (2006) Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology*, **31**, 294-297.

Colgan, L.J. & Erbilgin, N. (2011) Tree-mediated interactions between the jack pine budworm and a mountain pine beetle fungal associate. *Ecological Entomology*, **36**, 425-434.

Erb, M., Robert, C.A.M., Hibbard, B.E. & Turlings, T.C.J. (2011) Sequence of arrival determines plant-mediated interactions between herbivores. *Journal of Ecology*, **99**, 7-15.

Gonzalez Megias, A. & Mueller, C. (2010) Root herbivores and detritivores shape above-ground multitrophic assemblage through plant-mediated effects. *Journal of Animal Ecology*, **79**, 923-931.

Griffin, C.A.M. & Thaler, J.S. (2006) Insect predators affect plant resistance via density- and trait-mediated indirect interactions. *Ecological Letters*, **9**, 335-343.

Huffman, D.W., Laughlin, D.C., Pearson, K.M. & Pandey, S. (2009) Effects of vertebrate herbivores and shrub characteristics on arthropod assemblages in a northern Arizona forest ecosystem. *Forest Ecology and Management*, **258**, 616-625.

Ilse, L.A. & Hellgren, E.C. (2007) Indirect interactions among dendrophages: Porcupines predispose pinyon pines to bark beetle attack. *Forest Ecology and Management*, **242**, 217-226.

Jaber, L.R. & Vidal, S. (2009) Interactions between an endophytic fungus, aphids and extrafloral nectaries: do endophytes induce extrafloral-mediated defences in Vicia faba? *Functional Ecology*, **23**, 707-714.

Johnson, S.N., Hawes, C. & Karley, A.J. (2009) Reappraising the role of plant nutrients as mediators of interactions between root- and foliar-feeding insects. *Functional Ecology*, **23**, 699-706.

Kaplan, I., Sardanelli, S. & Denno, R.F. (2009) Field evidence for indirect interactions between foliar-feeding insect and root-feeding nematode communities on Nicotiana tabacum. *Ecological Entomology*, **34**, 262-270.

Mouttet, R., Bearez, P., Thomas, C. & Desneux, N. (2011) Phytophagous Arthropods and a Pathogen Sharing a Host Plant: Evidence for Indirect Plant-Mediated Interactions. *PLoS ONE*, **6**.

Poelman, E.H., Gols, R., Snoeren, T.A.L., Muru, D., Smid, H.M. & Dicke, M. (2011) Indirect plant-mediated interactions among parasitoid larvae. *Ecology Letters*, **14**, 670-676.

Poelman, E.H., Loon, J.J.A. Van, Dam, N.M. Van, Vet, L.E.M. & Dicke, M. (2010) Herbivore-induced plant responses in Brassica oleracea prevail over effects of constitutive resistance and result in enhanced herbivore attack. *Ecological Entomology*, **35**, 240-247.

Rayapuram, C. & Baldwin, I.T. (2008) Host-plant-mediated effects of Nadefensin on herbivore and pathogen resistance in Nicotiana attenuata. *BMC Plant Biology*, **8**.

Roode, J.C. de, Rarick, R.M., Mongue, A.J., Gerardo, N.M. & Hunter, M.D. (2011) Aphids indirectly increase virulence and transmission potential of a monarch butterfly parasite by reducing defensive chemistry of a shared food plant. *Ecology Letters*, **14**, 453-461.

Swope, S.M. & Parker, I.M. (2010) Trait-mediated interactions and lifetime fitness of the invasive plant Centaurea solstitialis. *Ecology*, **91**, 2284-2293.

Veen, F.J.F. van, Brandon, C.E. & Godfray, H.C.J. (2009) A positive trait-mediated indirect effect involving the natural enemies of competing herbivores. *Oecologia*, **160**, 195-205.

Yang, J.W., Yi, H.-S., Kim, H., Lee, B., Lee, S., Ghim, S.-Y. & Ryu, C.-M. (2011) Whitefly infestation of pepper plants elicits defence responses against bacterial pathogens in leaves and roots and changes the below-ground microflora. *Journal of Ecology*, **99**, 46-56.

V Considering traits improves prediction of pest predation by tropical ant communities

Running Title: Ant traits in ecological modelling

Arno Wielgoss[a,b,1], Teja Tscharntke[a], Alfianus Rumede[c], Brigitte Fiala[b] , Hannes Seidel[a,b], Yann Clough[a]

[a]Agroecology, Department of Crop Sciences, University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany

[b]Animal Ecology and Tropical Biology (Zoology III), Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany

[c]Department of Agriculture, Klabat University, Airmadidi No. 1, ID-95371 Manado, Indonesia

[1]Corresponding author: Arno Wielgoss, Tel.: +49-931-3181088, E-mail address: awielgo@gwdg.de

Keywords: predation, leaf herbivory, bait choice, food preference, biomass, *Theobroma cacao*, *Sulawesi*

Abstract

Most theoretical and empirical studies on predation use population densities to predict predation strength without regarding species traits.

Ants are a major predator group, but differ widely in body size and food preference. It is widely unknown how these ecological traits affect predation by the ant community, and whether integrating traits into ecological models makes predictions more accurate.

We surveyed leaf herbivores, measured leaf herbivory and collected data of ant abundances, their body sizes and food preferences at baits in a 16 month ant fauna manipulation experiment, which has been established in Indonesian cacao plantations.

Higher leaf herbivore abundances increased leaf losses, while higher ant abundances reduced leaf damage due to herbivores. By correcting the ant abundance data for body mass and relative preference for protein we greatly improved the fit of the model explaining leaf loss. Similarly, leaf herbivores predicted leaf loss better when herbivores’ biomass was taken into account. Our study shows that integrating ecological traits into ecological models can improve their fit and prediction strength.

Introduction

In community ecology, most current models of trophic interactions are based on the assumption that species within the same guild have identical effects on lower levels in the food web (Schmitz & Suttle 2001). This simplification, however, tends to disregard important mechanistic details about the relative interaction strength of individual species in food webs (Paine 1992; Werner & Peacor 2003). The emergence of differing effect size of single predator species on lower trophic levels of has been variously attributed to differing morphological traits (Rudolf 2006), microhabitat use (Schmitz et al. 2004), and foraging behaviour (Finke & Denno 2004; Ives et al. 2004; Duffy et al. 2007), but also to interactions between predators (Martin et al. 2013). These factors can enhance or weaken effects of predator species on ecosystem structure and functioning (Schmitz 2007). As important traits, predator–prey body mass ratios may be key to enabling persistence of populations in complex food webs and stabilizing the diversity of natural ecosystems (Brose et al. 2006).

Ants are most efficient predators of arthropods in the tropics and can limit herbivore populations, including potential insect pests in agroecosystems, which is an ecosystem service of enormous financial value (Philpott & Armbrecht 2006; Armbrecht & Gallego 2007; Van Mele 2007; Rosumek et al. 2009). Ants cover a wide spectrum of body sizes (~1-30 mm) (Weiser & Kaspari 2006), vary widely in their behaviour such as temporal-spatial activity, hunting strategy and food preference (Hölldobler & Wilson 1990). Many ants are omnivorous and opportunistic feeders, while some subfamilies and genera comprise highly specialized predators, and others may largely live on vegetarian diets (including seeds, honeydew, plant nectar, food bodies and fungi) (Blüthgen et al. 2003). These traits may influence the relative impact of ant species on ecosystem processes via differing prey demand per worker and prey spectrum in matters of size and identity. There is evidence that in species rich ant communities with high evenness (i.e. each single species having a similar share of the overall abundance) overall predatory pressure on herbivores is enhanced due to additive or even synergistic effects of complementary traits (Philpott & Armbrecht 2006; Philpott et al. 2008a).

Habitat conversion and simplification (Gibb & Hochuli 2003; Bihn et al. 2010), agricultural intensification (Philpott & Foster 2005; Philpott et al. 2008b; Ottonetti et al. 2010) and the invasion of dominant ants ((Holway et al. 2002; Sanders et al. 2003; Bos et al. 2008; Wielgoss et al. 2010) can lower ant species richness and disrupt ant community evenness. Dominant ants achieve superiority due to their aggressiveness, numerical dominance,superior interference behaviour and exploitative competition ability (Parr & Gibb 2010) and are frequently found in disturbed habitats like agroecosystems (Hölldobler & Wilson 1990). Species with high abundances often determine the whole species community by overruling the traits of the other ant species (Hooper et al. 2005). Nevertheless until now most studies disregard ant species traits and use only worker abundance as variable to predict predation effects.

The objective of this study was to test if and how ecological traits of ants affect ecosystem processes such as leaf damage by folivory. We established a 16 month ant manipulation experiment in Indonesian cacao plantations. We use leaf herbivory and leaf-insect monitoring data to fit models explaining the observed leaf herbivory patterns with ant community traits. We hypothesize that correcting ant abundance for traits such as body size and diet improves accuracy of predictions in ecological modelling.

Methods

Study area / Study plots.

All sites were situated in the Palolo valley, on the northern border of the Lore Lindu National Park, Central Sulawesi, Indonesia. The elevation in this region ranges from 400 m to about 1,000 m above sea level. Natural vegetation is lowland to submontane rainforest, although only the latter remained (Whitten et al. 2002). Being close to the equator, the seasonality is not very marked. Annual rainfall is around 2,500 mm (Gutzler & Koehler 2010) with a long-term pattern of 9 consecutive rainy months and 3 consecutive drier months (Whitten et al. 2002). Cacao is the main cash crop grown in the study area. Hybridization between out-crossing genotypes is common in smallholder cacao, and cacao trees in this study, as well as most of the other trees in the area, originate from hybrids between Forastero and Trinitario types. 15 cacao plantations without insecticide use for at least one year, differing in shade and with absence of *Philidris cf. cordata* and *Dolichoderus* cf. *thoracicus* (obtained by a rapid ant fauna assessment), were selected in May 2009.

Ant fauna manipulation treatments.

In each plantation we placed a plot (50 x 50 m) containing four subplots (minimum distance 8 m) with nine neighbouring cacao trees each. The branch connections of test trees with trees outside of the subplots were cut regularly. In each subplot one of the four ant manipulation treatments was assigned randomly. In one subplot per plot the ant fauna remained undisturbed as Control and in another ants were excluded from the trees using insect glue barriers and colony removal. In the third subplots we established the native ant species *Dolichoderus* cf. *thoracicus* as dominant species in the cacao trees by transferring colonies using artificial nest sites. Because of their high abundances *Dolichoderus* spp. were proposed as biocontrol agent for cacao (See & Khoo 1996; Van Mele & Cuc 2001). In the last subplots the invasive ant *Philidris* cf. *cordata* transferred to the cacao trees. This ant species is known to aggressively defend food sources from other ant species and to lower ant species richness (Wielgoss et al. 2010). Both ant species belong to the "dominant dolichoderines", which are able to form large colonies that numerically dominate habitats (Hölldobler & Wilson 1990). For detailed ant fauna manipulation methods see Appendix chapter III.

Ant surveys.

We used standardized plates (25 cm diameter), which were equipped with two baits of 2cm^3 of tuna in oil and two sponges saturated with 70% sugar solution, to determine the abundance of ant species (Fig.V.1). Each observation plate was a choice test where the ant workers can choose between carbohydrate and protein rich food. We offered two baits of each kind to reduce possible competition.

Fig.V.1: Ant observation bait with each two tuna and sugar solution baits

Per subplot one plate was placed in the main ramification of each experimental cacao tree (if the main ramification was too high, it was fixed at breast height on the stem with elastic rubber band; this occurred in approximately 1 of 10 cases) and four were placed on the ground. The plates were observed for 1 h. Every 15 min, the abundance of all ant species occurring at the baits feeding on fish or sugar was counted separately. For each species we checked the observation time at which the maximum of individuals were present at each plate. Then we summed up the numbers of individuals at protein and sugar baits respectively to get the ratio how the workers of each species were distributed between sugar and protein baits. Of every ant species appearing on the plate 5 to 10 specimens were caught with forceps and conserved in 70% ethanol for later identification. For each species we measured head length of eight individuals, and calculated the closely correlated biomass (Kaspari & Weiser 1999). This survey was conducted once before and tree times after the ant fauna manipulations in all 15 cacao plots (July 2009, April, Oktober 2010, February 2011). We identified the samples to morphospecies level.

Arthropod surveys.

The abundance of herbivores and spiders was evaluated by inspecting three randomly chosen trees per subplot visually between 7.45 am and 2.00 pm. Surveys were conducted twice per tree in intervals of three to four weeks. All tree of one plot were sampled at the same day. Each tree was searched for insects and spiders for 25 min using a standardized time-interval-based sampling scheme (5 min sampling at the tree stem; 4 times 5 min sampling leaves and brunches of tree crown using a ladder. Detected arthropods were identified to family level using field guides (Borror & White 1970; Zborowski & Storey 2010) and photos were taken when no in-field identification was possible. Additionally we recorded their position in the tree and approximate body length. We calculated biomasses of the different arthropod orders using published body length to biomass correlations (Hódar 1996).

Herbivory data.

For herbivory data collection we used the same 3 trees per subplot as in the arthropod survey. We twice sampled twenty leaves per tree from different strata and different distances of the main trunk using stratified random sampling. The leaves were scanned and herbivory rates were measured digitally using the program ImageJ (3 trees per subplot, 20 leaves per tree, 2 replicates). In tropical trees leaf area loss due to herbivory occurs mainly in young emerging leaves and often shows a temporal or spatial pattern within trees (Lowman 1992; Coley & Barone 1996). The mean longevity of cacao leaves ranges from 160 to 370 days depending on their position (Miyaji et al. 1997). We sampled fully developed, mature cacao leaves at the end of the study to assure that the leaves had grown during their whole lifespan in the according ant treatments. Leaf area losses occurring at leaves before reaching maturity results in an expanded leaf area missing in mature leaves, which is proportional to leaf growth. Thus relative loss in leaf area would be similar in young and mature leaves but absolute leaf loss may differ considerably. Therefore chose to use relative leaf losses in percent and not leaf area for our analysis.

Data analysis.

Leaf herbivory, herbivores and ants: To detect differences in leaf herbivory, herbivore and ant abundance and biomass between treatments we fitted linear mixed effect models by REML with plot and subplot as random factors.

Importance of herbivore families for leaf herbivory: To detect the relative importance of leaf herbivore families for contributing to leaf loss, we fitted a linear mixed-effects model fit by maximum likelihood over the leaf herbivory data (in percent, logit transformed, see (Warton & Hui 2011)) versus the biomass of each herbivore family per plot as explanatory variable. The models of all possible permutations of the variables used in the full model were calculated (with a maximum of 4 explanatory variables to avoid overfitting) using multi model inference (R package “MuMIn”, (Barton 2012) and were ranked by their explanatory power using AIC (Akaike’s Information Criterion,(Akaike 1983)). We identified the best models where the value of difference to the model with the best AIC was ≤ 7 units (Δ-AICc ≤ 7). For each model of this top set of models we calculated the log-likelihood (LL) and the AIC-weights, also termed "model probabilities" sensu (Burnham & Anderson 2002) and (Anderson 2008). These measures indicate the level of support (i.e., weight of evidence) in favour of any given model being the most parsimonious among the candidate model set. For each herbivore family we then calculated the average of the estimates and standard errors and the confidence intervals. After that we calculated the weighted biomasses of the herbivore families by multiplying the biomasses with the according importance (i.e. sum of the AIC-weight of the models in which the according factor appeared). Families with a sum of the AIC-weight were considered as “important families”. We additionally calculated the weighted biomasses of these herbivore families separately.

Which leaf herbivore community traits explain leaf loss best? To detect which herbivore related variable explains the measured leaf losses best we fitted five linear mixed-effects model fit by maximum likelihood over the leaf herbivory data (in percent, logit transformed) per plot using a) abundance of all herbivores, b) biomass of all herbivores, c) biomass of all herbivores weighted by the relative importance of the according family, d) biomass of the important families (importance > 0.3) and e) biomass of the important families weighted by the relative importance of the according family as explanatory variable respectively (all standardized by subtracting the mean divided by the standard error). Then we compared AIC values to determine the best model.

Which ant community traits explain leaf loss best? For this analysis we did not use data from the ant exclusion subplots, because this is the most unnatural ant treatment with very low ant abundances and we wanted to model ant community trait – herbivory relationships in more natural environments. To detect which ant community related variable explains best the measured leaf losses we fitted nine linear mixed-effects model fit by maximum likelihood over the leaf herbivory data (in percent, logit transformed) per plot using:

a) abundance of all ants at the baits

b) biomass of all ants

c) abundance of ants only at protein baits

$$\sum_{i=1}^{R}[total\ abundance_i * (\frac{abundance\ at\ protein_i}{abundance\ at\ sugar_i})]$$

d)abundance of ants only at sugar baits

$$\sum_{i=1}^{R}[total\ abundance_i * (\frac{abundance\ at\ sugar_i}{abundance\ at\ protein_i})]$$

e) biomass of ants only at protein baits

f) biomass of ants only at sugar baits

(all log transformed and standardized by subtracting the mean divided by the standard error). Then we compared AIC values to determine the best model.

Results

Leaf herbivory, herbivores and ants.

In comparison to control treatments herbivory rates were reduced in *Dolichoderus* dominated trees (*t* = -4.14, *P* < 0.01), but elevated in ant exclusion treatments (*t* = 3.85, *P* < 0.01) and also higher (with marginal significance) in *Philidris* treatments (*t* = 2.68, *P* = 0.09, Fig.V.2, Table.V.A1).

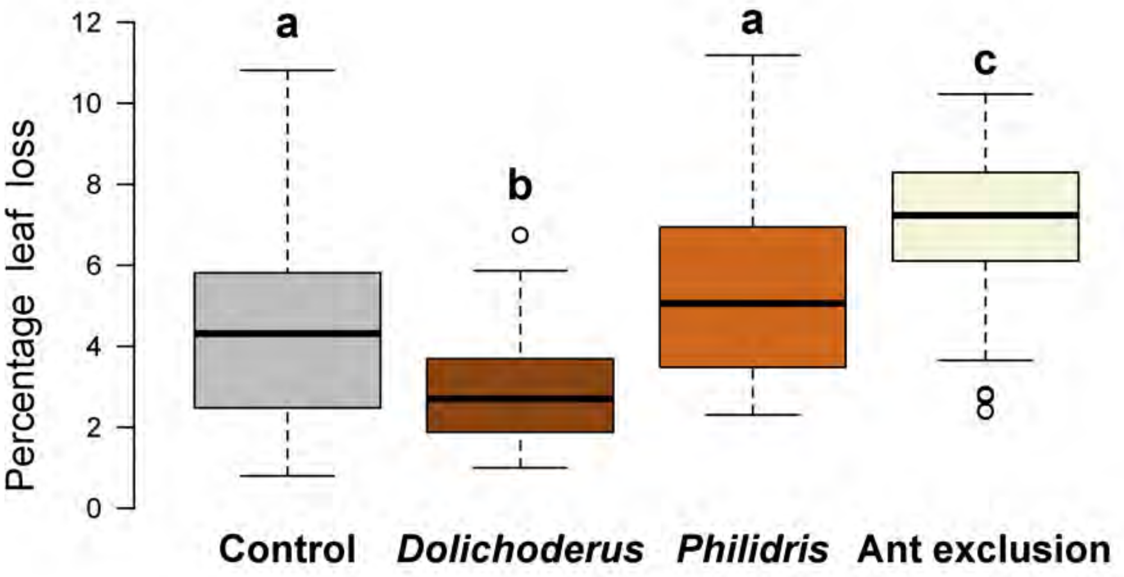

Fig.V.2: Leaf loss due to herbivores in the different treatments of the ant manipulation experiment in cacao plantations. Control = undisturbed ant communities; *Dolichoderus* = with experimentally established dominance of *Dolichoderus* cf. *thoracicus*; *Philidris* = with experimentally established dominance of *Philidris* cf. *cordata*

Total abundances of leaf herbivores were similar in Control, *Dolichoderus* and *Philidris* treatments and decreased with ant exclusion (*t* = -1.96, *P* < 0.05, Fig.V.3a, Table.V.A1), but biomass of leaf feeding herbivores did not differ between the four subplots (Fig.V.3b, Table.V.A1). Ant abundances in subplots with the experimentally established single species dominances were higher than in the unmanipulated control treatments (Fig.V.3c, *Philidris*: t = 3.61, *P* < 0.01; *Dolichoderus*: t = 3.32, *P* < 0.01). In the ant exclusion trees the mean ant abundance was reduced too < 10% of the control (t = -5.55, *P* <0.01), and as well biomass of ant was reduced (t = -4.06, *P* <0.01 Fig.V.3d), while ant biomasses in Control, *Dolichoderus* and *Philidris* did not differ.

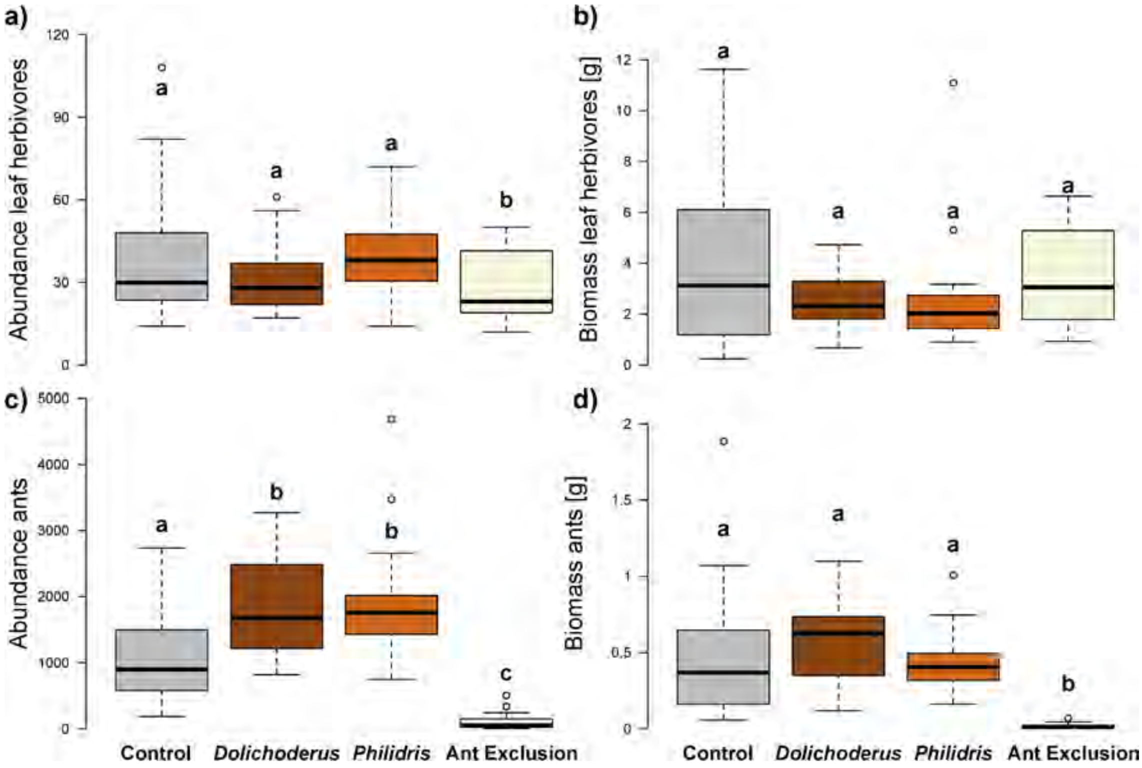

Fig.V.3: a) Leaf herbivore abundance *b)* biomass of leaf herbivores *c)* abundance of ant at baits in trees *d)* biomass of ant workers at baits in trees in the different treatments of the ant manipulation experiment in cacao plantations (all per subplot, sum of all sampling runs). For treatments, see legend of Fig.V.2

Size of ants sampled at the baits varied between a head length of 2.9 mm and a worker biomass of 13.3 mg (*Diacamma rugosom)* and 0.3 mm and 0.01 mg respectively (*Monomorium* sp.1). Food preference of the workers at the baits differed widely between the ants: While in some species the majority of the workers preferred protein over sugar baits (e.g. *Tetramorium pasificum*: 0.95), in other species the ratio (abundances at protein baits) : (abundances at sugar baits) was much lower (e.g. *Tetramorium smithii:* 0.26). The focus species of our experiment *Dolichoderus* cf. *thoracicus* and *Philidris* cf. *cordata* had a similar preference ratio (0.69 and 0.67 respectively). Food preference at the baits, head length and worker biomass are displayed in Table.V.A2.

Importance of herbivore families for leaf herbivory.

Model details of the top set of models are displayed in Table.V.A3. The importance of each herbivore family regarding explanation potential for the observed leaf loss is displayed in Fig.V.4.

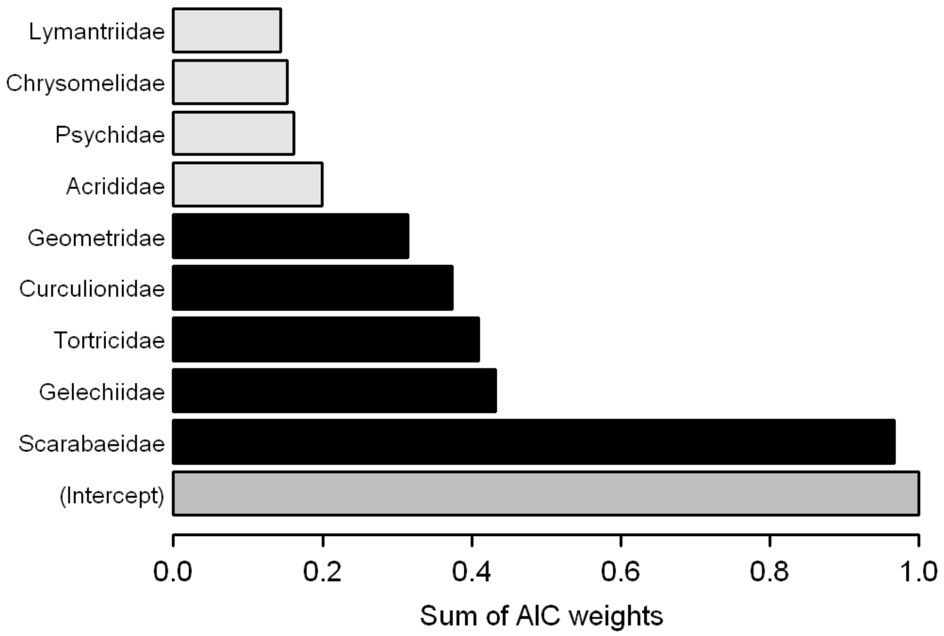

Fig.V.4: Sum of AIC weights (=importance) of herbivore families calculated by multi model comparison explaining leaf herbivory. Families with Σ AIC weights > 0.3 (black) are considered as important families.

In Table.V.1 we give details of model averaging of the top set of models with a delta-AIC < 7. The herbivore family contributing most to the observes leaf herbivory patterns was the Scarabeidae with a sum of AIC-weights (i.e. importance) of 0.97, followed by Gelechiidae with an importance of 0.43. In addition Tortricidae (Σ of AIC-weights 0.41), Curculionidae (0.37) and Geometridae (0.31) were considered as "important families" (Σ of AIC-weights > 0.3) for later calculations.

Table.V.1: Results of multi model averaging of biomass of herbivore families explaining leaf loss (logit)

Family	Estimate	Standard Error	Adjusted SE	z value	*P* value	Importance (Σ AIC weights)
(Intercept)	-3.1930	0.1097	0.1122	28.46		
Acrididae	-0.0018	0.0022	0.0022	0.80	0.42	0.20
Chrysomelidae	0.0012	0.0046	0.0047	0.25	0.80	0.15
Curculionidae	-0.0035	0.0020	0.0021	1.70	0.09	0.37
Gelechiidae	0.0036	0.0022	0.0022	1.58	0.11	0.43
Geometridae	0.0002	0.0001	0.0001	1.29	0.20	0.31
Lymantriidae	0.0000	0.0001	0.0001	0.21	0.83	0.14
Psychidae	0.0000	0.0000	0.0000	0.51	0.61	0.16
Scarabaeidae	0.0009	0.0003	0.0004	2.57	0.01	0.97
Tortricidae	0.0002	0.0002	0.0002	1.54	0.12	0.41

Which leaf herbivore community traits explain leaf loss best?

The variable which explained leaf loss patterns best was biomass of the defined important herbivore families weighted by their sum of AIC-weights, followed by biomass of all herbivores weighted by the importance of the according family (Δ-AIC: 3.03), non weighted biomass of important families (Δ-AIC: 4.27), counts of all herbivores (Δ-AIC: 4.54) and biomass of all herbivores (Δ-AIC: 6.68). Details of the AIC comparison are listed in Table.V.2 and model details of are given in Table.V.A4.

Table.V.2: Results AIC-comparison of models explaining leaf loss with herbivore community traits

Model with	AIC	Δ-AIC	AIC-weights	log likelihood
Biomass of important families (weighted)	92.99	0.00	0.68	-42.50
Biomass all herbivores (weighted)	96.02	3.03	0.15	-44.01
Biomass important families	97.27	4.27	0.08	-44.63
Counts all herbivores	97.53	4.54	0.07	-44.77
Biomass all herbivores	99.68	6.68	0.02	-45.84

Which ant community traits explain leaf loss best?

The best ant community variable to explain leaf loss patterns was ant biomass corrected for ant species preference for protein baits (Table.V.3, Fig.V.5), followed by biomass of all ants (at both protein and sugar baits, Δ-AIC: 3.18), biomass ants only at sugar baits (Δ-AIC: 7.72). All other variables including abundance of ants not corrected for body mass had a lower statistical importance in matter of explanatory power for leaf herbivory (Table.V.3). Model details are given in Table.V.A3.

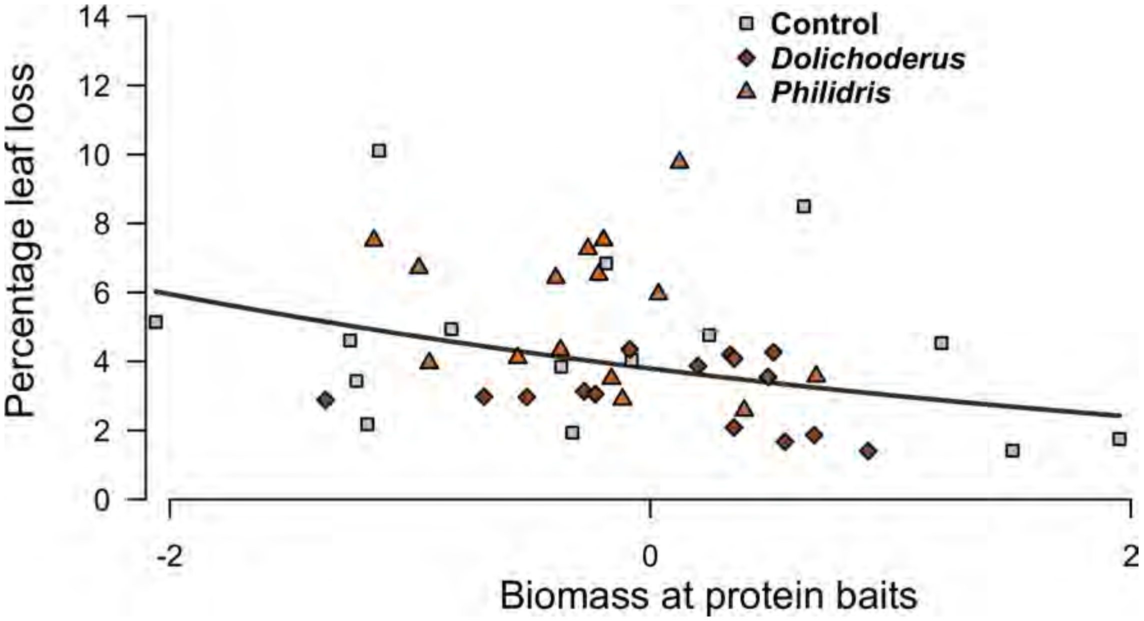

Fig.V.5: Effect of biomass at baits corrected for protein preference of the according species on leaf herbivory in cacao agroforests in Indonesia. For treatments, see legend of Fig.V.2

Table.V.3: Results AIC-comparison of models explaining leaf loss with ant community traits

Model with	AIC	Δ-AIC	AIC-weights	log likelihood
Biomass ants at protein	68.26	0	0.62	-30.13
Biomass all ants	70.14	1.88	0.24	-31.07
Biomass ants at sugar	72.60	4.34	0.07	-32.30
Abundance ants at protein	74.35	6.09	0.03	-33.18
Abundance all ants	74.87	6.61	0.02	-33.43
Abundance ants at sugar	75.11	6.85	0.02	-33.55

Discussion

Our study shows that integrating traits such as body size and diet into ecological models can improve fit and therefore prediction of ecological models. The model fit with leaf herbivore abundances explaining leaf loss improved when estimated biomasses were taken into account (Table.V.2). Similarly we could enhance the fit of the model including ant abundance as explanatory variable by integrating food preference for protein and biomass of the according ant species (Table.V.3).

Herbivore community traits.

Until now the majority of studies on leaf herbivory use count data of individual insects without regarding their body size. But such traits may be of high importance regarding folivory, since arthropod herbivores of larger body size consume more leaf tissue than smaller individuals. Indeed, considering herbivore biomass resulted in a much better prediction of leaf area losses in cacao than using count data only. Integrating biomass into models predicting ecological impact is usually easy, as it can be measured without killing of individuals. Biomass may affect consumption rates directly via increased resource demand and indirectly by influencing the diet, because smaller herbivore species tend to be more specialized than larger-bodied ones (Davis et al. 2013). Differences in diet width, temporal activity and behavioural traits like forming of aggregations may affect ecological impact of herbivore species (Schmitz & Price 2011). In our models, biomass alone cannot explain all variation, but improved prediction strength in comparison to abundance data.

Ant community traits.

Ant abundances at baits were higher in the two single species dominated subplots than in control subplots. But when correcting for ant biomass, there was no significant difference between these three treatments. This appeared to be due to the small worker size of the dominant species *Dolichoderus* and *Philidris* and due to the fact that they, like other “dominant dolichoderines”, displace larger species from the baits, while being more tolerant towards smaller, subdominant species (Hölldobler & Wilson 1990).

In our study correcting ant abundance for biomass improved the predictions of leaf herbivory. Measuring body size provides a relatively simple means of encapsulating and condensing a large amount of the biological information embedded within an ecological network (Woodward et al. 2005). Biomass of ants at the baits gave us a better measure of the ecological functions of ants concerning top down control of herbivores in the tree than using only abundance data. This can be explained by the great variation in biomass and body size between the sampled ants (head length varied from 0.3 to 2.9 mm). In addition, body size of ants can strongly influence preferred prey sizes, discovery times and monopolisation rates of resources (Gibb & Parr 2010). Similarly, ant body size can affect other ecosystem functions of ants such as the dispersal distance of ant-adapted seeds (Ness et al. 2004). Using baits and rather short observation times might underestimate the occurrence of large ants (Longino et al. 2002). In large ants the correlation between abundance and predation as ecosystem function might be stronger than in small ants, because one single worker of a large species already may prey on leaf herbivores, while a worker of a small ant species first needs to recruit nest-mates to overwhelm the prey.

Food demand of social insects is not directly linked to body size of the individuals. In ants colony size, number of queens, brood and production of sexual offspring affect the protein demand of a colony (Cook et al. 2010) and vice versa ants are able to control colony growth to a certain extent according to the protein availability (Kay et al. 2006). Arboreal ant communities are more nitrogen limited than carbohydrate limited (Yanoviak & Kaspari 2000), because they have good access to carbohydrate sources as extrafloral nectaries and honeydew (Blüthgen et al. 2004). Protein demand may result in a seasonal behaviour shift from carbohydrate to protein preference of the workers (from honeydew or nectar feeding towards predation) with possible effects on predation pressure (Cook et al. 2010). We used four ant surveys in different years and seasons in this study to cope with this seasonal variation, but a higher temporal resolution of the surveys and estimation of colony sizes might be useful to further improve predictions.

Our models explained most of the variation of leaf herbivory when we weight the biomass of each ant species with the share of its workers that preferred protein baits over carbohydrate baits. According to optimal foraging theory for ant feeding preference (Kay 2002, 2004; Blüthgen et al. 2003), consumers should show stronger preferences towards food which is relatively less available for this species (Blüthgen & Feldhaar 2010). In our study, preference at the baits reflected the natural food preference. Comparing ant species food preference in baits choice tests with their trophic level using stable isotope analysis could give a deeper insight in this matter.

Conclusion.

There are many ecological traits of predators that might affect ecosystem functioning. Not all traits can be incorporated into statistical models for practical reasons. According to our results, considering at least body size and food preference when explaining ecosystem functions of ant communities can increase the quality of the according model substantially.

Acknowledgements

We thank the representatives in Tadulako University, field assistants, village heads, and villagers in the study region; the Indonesian and German project coordination team. This study was supported by the German Academic Exchange service DAAD and the German Science Foundation (DFG).

Appendix chapter V

Appendix chapter V Tables.

Table.V.A1: Effects of ant community manipulation treatments on leaf herbivory, abundances and biomass of herbivores and abundance and biomass of ants at baits in cacao agroforests of Central Sulawesi.

	Treatment	**Estimate**	**SE**	***t***	***P***	**Lower CI**	**Upper CI**
Leaf herbivory	Control	5.83	0.33			5.17	6.48
	Dolichoderus	-1.95	0.47	-4.14	<0.01	-2.88	-1.02
	Philidris	0.79	0.47	1.68	0.09	-0.14	1.72
	Ant-exclusion	1.81	0.47	3.85	<0.01	0.88	2.74
Abundances herbivores	Control	2.86	0.11			2.64	3.09
	Dolichoderus	-0.13	0.16	-0.82	0.42	-0.45	0.19
	Philidris	0.04	0.16	0.28	0.78	-0.27	0.36
	Ant-exclusion	-0.31	0.16	-1.96	0.05	-0.64	0.01
Biomass herbivores	Control	3826.55	605.34			2605	5048
	Dolichoderus	-1289.77	681.27	-1.89	0.07	-2665	85.09
	Philidris	-326.54	681.27	-0.48	0.63	-1701	1048
	Ant-exclusion	-1050.95	681.27	-1.54	0.13	-2426	323.91
Abundances ants	Control	403.82	57.16			290.75	516.89
	Dolichoderus	217.73	65.59	3.32	<0.01	87.98	47.48
	Philidris	236.6	65.59	3.61	<0.01	106.85	366.35
	Ant-exclusion	-363.73	65.59	-5.55	<0.01	-493.5	-234
Biomass ants	Control	0.80	0.14			0.53	1.08
	Dolichoderus	-0.24	0.19	-1.23	0.22	-0.63	0.15
	Philidris	-0.37	0.19	-1.91	0.06	-0.76	0.02
	Ant-exclusion	-0.78	0.19	-4.06	<0.01	-1.17	-0.39

Table.V.A2: Food preference at the baits, headlength and worker biomass of ants sampled with protein and sugar baits in Indonesian cacao agroforests (only species present on more than 5 observation plates).

Species	Share of workers feeding at protein baits	Head length [mm]	Biomass per worker [mg]
Tetramorium sp. 6	0.95	0.97	0.43
Tetramorium pasificum	0.93	0.91	0.35
Pheidole sp. 3	0.87	0.65	0.12
Plagiolepis sp. 1	0.76	0.30	0.01
Paratrechina sp. 1	0.69	0.64	0.11
Pseudolasius sp. 2	0.69	1.10	0.63
Dolichoderus cf. *thoracicus*	0.69	0.93	0.38
Philidris cf. *cordata*	0.68	1.02	0.50
Paratrechina sp. 4	0.68	0.60	0.10
Polyrhachis abdominalis	0.67	2.26	6.32
Monomorium sp. 3	0.67	0.43	0.03
Crematogaster sp. 1	0.64	0.67	0.13
Monomorium floricola	0.63	0.40	0.03
Pheidole sp. 1	0.63	0.44	0.04
Pheidole sp. 4	0.62	0.45	0.04
Oecophylla smaragdina	0.61	1.73	2.70
Philidris sp. 1	0.60	0.78	0.21
Monomorium sp. 1	0.58	0.29	0.01
Tapinoma sp. 1	0.57	0.49	0.05
Polyrhachis sp. 7	0.56	1.81	3.12
Crematogaster sp. 3	0.54	1.20	0.84
Camponotus sp. 1	0.50	1.88	3.54
Technomyrmex albipes	0.48	0.85	0.28
Tapinoma melanocephalum	0.46	0.45	0.04
Polyrhachis dives	0.45	1.91	3.73
Anoplolepis gracilipes	0.43	0.70	0.15
Camponotus recticulatus	0.36	1.57	1.98
Diacamma rugosum	0.33	2.86	13.30
Echinopla lineata	0.33	1.90	3.61
Polyrhachis sp. 1	0.33	2.05	4.63
Tetramorium sp. 2	0.33	0.63	0.11
Tetramorium smithi	0.26	0.41	0.03

*Table.V.A3:*Top set of models of multi model comparison explaining leaf herbivory using biomass of herbivore families

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geometridae	Lymantriidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.22			-0.0038	0.0034				0.0011	0.0003	7	-39.64	95.44	0.00	0.041
-3.21			-0.0038					0.0011	0.0003	6	-40.99	95.57	0.13	0.039
-3.17				0.0037				0.0008		5	-42.24	95.59	0.15	0.038
-3.24				0.0035				0.0009	0.0002	6	-41.10	95.78	0.34	0.035
-3.27			-0.0042		0.0002			0.0012	0.0003	7	-39.89	95.94	0.50	0.032
-3.22								0.0008	0.0002	5	-42.46	96.02	0.59	0.031
-3.15								0.0008		4	-43.68	96.09	0.65	0.030
-3.23				0.0037	0.0001			0.0009		6	-41.28	96.15	0.71	0.029
-3.14			-0.0031	0.0036				0.0010		6	-41.29	96.17	0.73	0.029
-3.22			-0.0035		0.0002			0.0011		7	-40.07	96.30	0.86	0.027
-3.12			-0.0031					0.0010		5	-42.74	96.58	1.14	0.023
-3.20			-0.0036		0.0002			0.0011		6	-41.51	96.60	1.17	0.023
-3.21					0.0001			0.0008		5	-42.78	96.67	1.24	0.022
-3.29				0.0035	0.0001			0.0009	0.0002	7	-40.26	96.68	1.24	0.022
-3.27					0.0001			0.0009	0.0002	6	-41.69	96.96	1.52	0.019
-3.15	-0.0016			0.0036				0.0008		6	-41.86	97.30	1.86	0.016
-3.13	-0.0017							0.0007		5	-43.24	97.60	2.16	0.014
-3.19				0.0037			0.0000	0.0008		6	-42.03	97.65	2.21	0.014

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geome-tridae	Lyman-triidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.27				0.0036			0.0000	0.0008	0.0002	7	-40.76	97.67	2.24	0.013
-3.22	-0.0013			0.0034				0.0008	0.0002	7	-40.81	97.76	2.33	0.013
-3.23			-0.0036				0.0000	0.0011	0.0003	7	-40.82	97.79	2.35	0.013
-3.17			-0.0041			0.0000		0.0011	0.0003	7	-40.83	97.81	2.37	0.013
-3.20	-0.0014							0.0008	0.0002	6	-42.12	97.83	2.39	0.013
-3.19	-0.0010		-0.0036					0.0011	0.0003	7	-40.84	97.84	2.40	0.012
-3.21	-0.0015			0.0036	0.0001			0.0008		7	-40.90	97.95	2.51	0.012
-3.25							0.0000	0.0008	0.0002	6	-42.20	97.99	2.55	0.012
-3.17		-0.0004		0.0037				0.0008		6	-42.23	98.05	2.61	0.011
-3.17				0.0037		0.0000		0.0008		6	-42.24	98.06	2.62	0.011
-3.21		0.0008	-0.0039					0.0011	0.0003	7	-40.97	98.09	2.65	0.011
-3.17							0.0000	0.0008		5	-43.54	98.19	2.75	0.010
-3.19	-0.0016				0.0001			0.0008		6	-42.35	98.29	2.85	0.010
-3.24				0.0035		0.0000		0.0009	0.0002	7	-41.10	98.35	2.91	0.010
-3.24		0.0000		0.0035				0.0009	0.0002	7	-41.10	98.35	2.91	0.010
-3.13	-0.0011		-0.0029	0.0035				0.0010		7	-41.11	98.37	2.93	0.010
-3.14						0.0000		0.0008		5	-43.66	98.44	3.00	0.009
-3.21						0.0000		0.0008	0.0002	6	-42.44	98.46	3.02	0.009
-3.14		-0.0004						0.0008		5	-43.67	98.46	3.02	0.009
-3.22		0.0000						0.0008	0.0002	6	-42.46	98.50	3.06	0.009

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geometridae	Lymantriidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.25				0.0037	0.0001		0.0000	0.0009		7	-41.18	98.51	3.07	0.009
-3.16			-0.0029	0.0036			0.0000	0.0010		7	-41.18	98.52	3.09	0.009
-3.11	-0.0013		-0.0028					0.0009		6	-42.51	98.60	3.16	0.009
-3.12			-0.0033	0.0035		0.0000		0.0010		7	-41.23	98.62	3.18	0.008
-3.24				0.0037	0.0001	0.0000		0.0009		7	-41.28	98.71	3.28	0.008
-3.23		-0.0001		0.0037	0.0001			0.0009		7	-41.28	98.72	3.28	0.008
-3.14		0.0003	-0.0032	0.0036				0.0010		7	-41.29	98.73	3.29	0.008
-3.18	-0.0011		-0.0033		0.0002			0.0011		7	-41.32	98.80	3.36	0.008
-3.09			-0.0034			0.0000		0.0010		6	-42.62	98.82	3.38	0.008
-3.25	-0.0013				0.0001			0.0009	0.0002	7	-41.38	98.91	3.47	0.007
-3.13			-0.0030				0.0000	0.0010		6	-42.66	98.91	3.47	0.007
-3.17			-0.0039		0.0002	0.0000		0.0011		7	-41.38	98.92	3.48	0.007
-3.22					0.0001		0.0000	0.0008		6	-42.72	99.02	3.58	0.007
-3.12		0.0003	-0.0032					0.0010		6	-42.73	99.05	3.61	0.007
-3.16	-0.0035	0.0048		0.0035				0.0008		7	-41.47	99.08	3.65	0.007
-3.21		0.0009	-0.0037		0.0002			0.0011		7	-41.48	99.11	3.67	0.007
-3.21			-0.0035		0.0002		0.0000	0.0011		7	-41.48	99.12	3.68	0.007
-3.20					0.0001	0.0000		0.0008		6	-42.77	99.13	3.70	0.007
-3.14	-0.0039	0.0054						0.0008		6	-42.78	99.15	3.71	0.006
-3.21		0.0000			0.0001			0.0008		6	-42.78	99.15	3.71	0.006

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geometridae	Lymantriidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.29					0.0001		0.0000	0.0009	0.0002	7	-41.55	99.26	3.82	0.006
-3.22	-0.0037	0.0057						0.0008	0.0002	7	-41.58	99.32	3.88	0.006
-3.27					0.0001	0.0000		0.0009	0.0002	7	-41.68	99.51	4.07	0.005
-3.28		0.0003			0.0001			0.0009	0.0002	7	-41.68	99.51	4.08	0.005
-3.17	-0.0015			0.0037			0.0000	0.0008		7	-41.69	99.53	4.09	0.005
-3.21	-0.0041	0.0063			0.0002			0.0008		7	-41.71	99.57	4.13	0.005
-3.06										3	-46.68	99.79	4.35	0.005
-3.14	-0.0016						0.0000	0.0007		6	-43.14	99.86	4.42	0.005
-3.15	-0.0016			0.0036		0.0000		0.0008		7	-41.86	99.87	4.43	0.005
-3.23	-0.0013						0.0000	0.0008	0.0002	7	-41.91	99.98	4.54	0.004
-3.11	-0.0017					0.0000		0.0007		6	-43.22	100.03	4.60	0.004
-3.07				0.0032						4	-45.67	100.07	4.63	0.004
-3.12	-0.0036	0.0056	-0.0029					0.0010		7	-42.00	100.15	4.72	0.004
-3.19		-0.0003		0.0037			0.0000	0.0008		7	-42.03	100.21	4.77	0.004
-3.19				0.0037		0.0000	0.0000	0.0008		7	-42.03	100.21	4.77	0.004
-3.19	-0.0014					0.0000		0.0008	0.0002	7	-42.09	100.34	4.90	0.004
-3.24						0.0000	0.0000	0.0008	0.0002	7	-42.17	100.49	5.06	0.003
-3.25		0.0002					0.0000	0.0008	0.0002	7	-42.20	100.56	5.12	0.003
-3.15						0.0000	0.0000	0.0008		6	-43.51	100.61	5.17	0.003
-3.16		-0.0005		0.0037		0.0000		0.0008		7	-42.23	100.61	5.18	0.003

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geometridae	Lymantriidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.16		-0.0003					0.0000	0.0008		6	-43.53	100.65	5.22	0.003
-3.20	-0.0016				0.0001		0.0000	0.0008		7	-42.32	100.79	5.35	0.003
-3.11									0.0002	4	-46.05	100.84	5.40	0.003
-3.18	-0.0016				0.0001	0.0000		0.0008		7	-42.34	100.84	5.40	0.003
-3.13		-0.0005				0.0000		0.0008		6	-43.66	100.90	5.46	0.003
-3.08	-0.0012		-0.0031			0.0000		0.0010		7	-42.41	100.97	5.53	0.003
-3.12	-0.0013		-0.0027				0.0000	0.0009		7	-42.43	101.02	5.59	0.003
-3.21		0.0000				0.0000		0.0008	0.0002	7	-42.44	101.03	5.59	0.003
-3.03	-0.0019									4	-46.21	101.14	5.70	0.002
-3.10			-0.0032			0.0000	0.0000	0.0010		7	-42.54	101.24	5.80	0.002
-3.12				0.0031					0.0002	5	-45.12	101.36	5.92	0.002
-3.09					0.0001					4	-46.32	101.38	5.94	0.002
-3.09		0.0004	-0.0034			0.0000		0.0010		7	-42.61	101.38	5.94	0.002
-3.14		0.0003	-0.0030				0.0000	0.0010		7	-42.66	101.47	6.03	0.002
-3.16	-0.0038	0.0055					0.0000	0.0008		7	-42.66	101.47	6.03	0.002
-3.21					0.0001	0.0000	0.0000	0.0008		7	-42.70	101.56	6.13	0.002
-3.22		0.0001			0.0001		0.0000	0.0008		7	-42.72	101.59	6.15	0.002
-3.05	-0.0018			0.0031						5	-45.24	101.60	6.16	0.002
-3.08							0.0000			4	-46.47	101.66	6.23	0.002
-3.13	-0.0038	0.0054				0.0000		0.0008		7	-42.77	101.69	6.26	0.002

Estimate	Acrididae	Chrysomelidae	Curculionidae	Gelechiidae	Geometridae	Lymantriidae	Psychidae	Scarabaeidae	Tortricidae	df	logLik	AIC	Δ-AiC	AIC-weight
-3.20		0.0000			0.0001	0.0000		0.0008		7	-42.77	101.70	6.26	0.002
-3.11				0.0032	0.0001					5	-45.32	101.76	6.32	0.002
-3.10				0.0033			0.0000			5	-45.40	101.90	6.46	0.002
-3.05			-0.0006							4	-46.65	102.02	6.58	0.002
-3.05		-0.0009								4	-46.65	102.02	6.59	0.002
-3.04						0.0000				4	-46.65	102.03	6.59	0.002
-3.09	-0.0018								0.0002	5	-45.61	102.33	6.89	0.001
-3.13	-0.0016					0.0000	0.0000	0.0007		7	-43.11	102.38	6.94	0.001
-3.06		-0.0010		0.0032						5	-45.63	102.38	6.94	0.001
-3.06			-0.0004	0.0032						5	-45.66	102.42	6.98	0.001

Table.V.A4: Details of single models explaining leaf herbivory with herbivore community traits

Model	Estimate	SE	*t*	*P*	Lower CI	Upper CI
(Intercept)	-3.057	0.065			-3.194	-2.919
Biomass of important families (weighted)	0.197	0.065	3.025	0.004	0.006	0.278
(Intercept)	-3.057	0.069			-3.193	-2.920
Biomass all herbivores (weighted)	0.160	0.068	2.359	0.023	0.026	0.294
(Intercept)	-3.057	0.069			-3.194	-2.919
Biomass important families	0.142	0.069	2.069	0.044	0.006	0.278
(Intercept)	-3.057	0.071			-3.198	-2.915
Counts all herbivores	0.135	0.068	1.971	0.055	-0.001	0.270
(Intercept)	-3.057	0.074			-3.203	-2.910
Biomass all herbivores	0.091	0.070	1.292	0.203	-0.049	0.230

Table.V.A5: Details of single models explaining leaf herbivory with ant community traits

Model	Estimate	SE	*t*	*P*	Lower CI	Upper CI
(Intercept)	-3.01	0.4			-3.82	-2.2
Abundance at all baits	-0.06	0.12	-0.49	0.63	-0.29	-0.18
(Intercept)	-2.89	0.38			-3.65	-2.13
Abundance at protein baits	-0.1	0.12	-0.85	0.4	-0.33	-0.13
(Intercept)	-3.22	0.36			-3.93	-2.51
Abundance at sugar baits	-0.01	0.12	-0.06	0.95	-0.22	0.24
(Intercept)	-3.18	0.09			-3.35	-3.01
Biomass at all baits	-0.21	0.09	-2.24	0.03	-0.39	-0.02
(Intercept)	-3.23	0.08			-3.4	-3.06
Biomass at protein baits	-0.24	0.09	-2.66	0.01	-0.42	-0.06
(Intercept)	-3.25	0.09			-3.44	-3.07
Biomass at sugar baits	-0.15	0.09	-1.58	0.13	-0.34	0.04

VI General conclusions

Ant as basis of ecosystem functioning in agroforestry

In our experimental study we reveal that ants occupy a central position in a complex interaction network which drives yields in Indonesian cacao agroecosystems (Fig.III.5). Ants provided ecosystem services like top down effects on cacao pests and leaf herbivores, but as well disservices like phytopathogen dissemination, enhancement of sap sucking homopterans (their mutualist partners) and indirect enhancement of a major cacao pest by predation on the antagonistic minor pest. A similarly complex multitrophic interaction network has been described in organic coffee agroforestry in Chiapas, Mexico (Vandermeer et al. 2010). Here one ant species (*Azteca sp.*) was the driving keystone species in the centre of the network. This system involves at least 13 components (insects and fungi) and six ecological processes (competition, predation, parasitism, hyper-parasitism, disease and mutualism). Vandermeer and colleagues conclude that the complexity of such ecological networks effectively generates the ecosystem service of buffering production systems against extreme outbreaks of pests and diseases. One of the main findings of this dissertation was, that in order to judge about the ecosystem services of a predator community, it is not enough highlight the effects on single pests or diseases, but to integrate all direct and indirect interactions with the crop plant it is necessary to analyse effects on the marketable yield, which is the final ecosystem service. We show that interactions between agricultural pests, like in our example between *Helopeltis sulawesi* and *Conopomorpha cramerella*, can blur positive effects of pest control by ants or insecticides. More generally, our results demonstrate that plant-mediated indirect interactions can be quantitatively relevant at spatial and temporal scales relevant for agricultural management.

Trait diversity sustains ecosystem services

The balancing ecosystem service in our system seems to be provided best by ant communities with high evenness, as in the unmanipulated relatively species rich control subplots and the dolichoderus dominated ant communities, where yields where highest. With ant exclusion and *Philidris* dominance ecosystem disservices predominated the beneficial effects the services and we could measure a yield reduction of about 27% and 34% respectively. The strength of the multiple direct and indirect interactions leading to these final yield differences changed with ant community properties like ant species richness and evenness but also with the individual traits of the dominant ant species. There are many behavioural and physiological traits of predators can affect ecosystem functioning (Duffy et al. 2007). For practical reasons it is not possible to include all of these traits in models predicting ecosystem functions of predator communities. The results of our study show that correcting abundance data of ants for biomass and food preference can already improve predicting strength of ecological model significantly. With a single ant species dominance the traits of the dominant species defines the effects of the ant community. Agricultural intensification can lead to uneven species poor species communities and a loss of functional diversity, which has been defined as ‘‘the value and range of those species and organismal traits that influence ecosystem functioning’’ (Tilman 2001). In the long term, the link between ecological functions and species diversity might have very important effects on the complex interactions affecting human well-being (Bihn et al. 2010), since the functional diversity of in agroecosystems may buffer possible ecosystem disservices and react to changing environment like climate change, pest outbreak or species invasion (Philpott & Armbrecht 2006). A single species dominated community might even have stronger effects on some ecosystem functions than a diverse communities (Gove 2007), because worker densities ant ant activity of such communities are generally higher (Hölldobler & Wilson 1990). But if and in what extend simply structured ant communities still can provide all ecosystem services of a diverse species community strongly depends on the traits of the few species remaining in the system. Therefore trait diversity facilitated by high species richness is the key to maintain ecosystem services especially when the environment is changing, for example emergence of new pest species or in the context of climate change.

Implications for management

The coffee plantations of the study in Mexico have been under careful organic management since almost 100 years (Philpott et al. 2009; Vandermeer et al. 2009) suggesting that ant communities have reached a certain equilibrium, while cacao plantations in our study region are far from being organic and ant communities are in a ongoing flux. We reported a far reaching change of ant communities in cacao plantations in our study region, in Central Sulawesi, Indonesia, where the dolichoderine invasive ant species *Philidris* cf. *cordata* recently became ecologically dominant, reducing ant species richness by displacing other dominant species such as the native *Dolichoderus* cf. *thoracicus* (Wielgoss et al. 2010). which might be beneficial as effective predators of cacao pests (Way & Khoo 1992; Van Mele & Cuc 2001). We gathered evidence that this dominance shift may be a consequence of mismanagement and agricultural intensification: In the past cacao farmers, captured by the hope to reduce fungal and viral diseases and increase yield (Rice & Greenberg 2000), removed shade trees from their agroforestry systems (Siebert 2002; Perfecto et al. 2007), which may promote *Philidris* establishment, since prefers higher temperatures of low shaded plantations (Wielgoss *et al.* 2010). Furthermore this species builds its nests in dead wood, which is abundant in cacao trees when farmers prune brunches improperly. The increased and partially careless use of insecticides in this region (Wanger et al. 2010) may have given *Philidris* an decisive advantage over other ant species. *Philidris* covers its food trails and trophobiont aggregations with detritus tents structures (Fig.III.A3) and builds its nests in brunch stumps where it is relatively well protected from direct insecticide application. All these actions might have favoured the spread *Philidris*. Experiences with the Red Imported Fire Ant, *Solenopsis invicta,* in the USA or the Argentine Ant *Linepithema humile* in southern Europe has shown that the fight against detrimental invasive ant species affiliated with great expenses and often desperate (Holway et al. 2002). We state that measures to counteract ant invasions in agroforestry before they happen, like increasing habitat heterogeneity by using multi-crop cultures, cover-crops, hedges and a variety of intercropped shade trees and avoidance of unspecific insecticides, are much more cost-efficient and have higher chances of success.

VII References

Abràmoff, M.D., Magalhães, P.J. & Ram, S.J. (2004). Image processing with ImageJ. *Biophotonics international*, 11, 36–42.

Akaike, H. (1983). Information measure and model selection. *Bulletin of the International Statistical Institute*, 50, 277–291.

Ambika, B. & Abraham, C.C. (1979). Bioecology of *Helopeltis antoni* (Miridae, Hemiptera, Heteroptera) infesting cashew trees. *Entomon*, 4, 335–342.

Anderson, D.R. (2008). *Model based inference in the life sciences: A primer on evidence*. Springer New York, New York.

Anderson, K.E., Inouye, B.D. & Underwood, N. (2009). Modelling herbivore competition mediated by inducible changes in plant quality. *Oikos*, 118, 1633–1646.

Armbrecht, I. & Gallego, M.C. (2007). Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata*, 124, 261–267.

Azhar, I. & Long, G. (1996). Effect of cocoa pod age on egg distribution and egg parasitism of the cocoa pod borer in Malaysia. *Entomologia Experimentalis et Applicata*, 81, 81–89.

Bailey, J.K. & Whitham, T.G. (2006). Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology*, 31, 294–297.

Barton, K. (2012). MuMIn: Multi-model inference. R package version 1.7.11. http://CRAN.R-project.org/package=MuMIn.

Bezemer, T.M., Wagenaar, R., Van Dam, N.M. & Wackers, F.L. (2003). Interactions between above- and belowground insect herbivores as mediated by the plant defense system. *Oikos*, 101, 555–562.

Bihn, J.H., Gebauer, G. & Brandl, R. (2010). Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*, 91, 782–92.

Blüthgen, N. & Feldhaar, H. (2010). Food and shelter: how resources influence ant ecology. In: *Ant ecology* (eds. Lach, L., Parr, C.L. & Abbott, K.). Oxford University Press, Oxford, pp. 115–136.

Blüthgen, N., Gebauer, G. & Fiedler, K. (2003). Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia*, 137, 426–35.

Blüthgen, N., Stork, N.E. & Fiedler, K. (2004). Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos*, 106, 344–358.

Bolker, B.M., Holyoak, M., Křivan, V., Rowe, L. & Schmitz, O.J. (2003). Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, 84, 1101–1114.

Borenstein, M., Hedges, L., Higgins, J. & Rothstein, H. (2009). *Introduction to Meta Analysis (Statistics in Practice)*. Wiley, Chichester.

Borror, D.J. & White, R.E. (1970). *A field guide to the insects of America north of Mexico*. Boston, Houghton Mifflin.

Bos, M.M., Steffan-Dewenter, I. & Tscharntke, T. (2007). Shade tree management affects fruit abortion, insect pests and pathogens of cacao. *Agriculture, Ecosystems & Environment*, 120, 201–205.

Bos, M.M., Tylianakis, J.M., Steffan-Dewenter, I. & Tscharntke, T. (2008). The invasive Yellow Crazy Ant and the decline of forest ant diversity in Indonesian cacao agroforests. *Biological Invasions*, 10, 1399–1409.

Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–36.

Bruno, J.F. & Cardinale, B.J. (2008). Cascading effects of predator richness. *Frontiers in Ecology and the Environment*, 6, 539–546.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. Springer New York, New York.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T.C., Anshary, A., et al. (2011). Combining high biodiversity with high yields in tropical agroforests, *Proceedings of the National Academy of Sciences of the United States of America*, 108, 8311.

Clough, Y., Faust, H. & Tscharntke, T. (2009). Cacao boom and bust: sustainability of agroforests and opportunities for biodiversity conservation. *Conservation Letters*, 2, 197–205.

Coley, P.D. & Barone, J.A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 27, 305–335.

Cook, S.C., Eubanks, M.D., Gold, R.E. & Behmer, S.T. (2010). Colony-level macronutrient regulation in ants: mechanisms, hoarding and associated costs. *Animal Behaviour*, 79, 429–437.

Crowder, D.W., Northfield, T.D., Strand, M.R. & Snyder, W.E. (2010). Organic agriculture promotes evenness and natural pest control. *Nature*, 466, 109–112.

Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua, T.H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, 300, 969–72.

Davis, R.B., Ounap, E., Javoiš, J., Gerhold, P. & Tammaru, T. (2013). Degree of specialization is related to body size in herbivorous insects: a phylogenetic confirmation. *Evolution*, 67, 583–9.

Day, R.K. (1985). Control of the Cocoa Pod Borer (*Conopomorpha cramerella*).

Day, R.K. (1989). Effect of cocoa pod borer, *Conopomorpha cramerella*, on cocoa yield and quality in Sabah, Malaysia. *Crop Protection*, 8, 332–339.

Day, R.K., Mumford, J.D. & Hing, H.S. (1995). Adult resting sites as a target for chemical control of the cocoa pod borer, *Conopomorpha cramerella* (Lepidoptera: Gracillariidae), in Malaysia. *Bulletin of Entomological Research*, 85, 45-52.

Delabie, J.H.C. (1990). The ant problems of cocoa farms in Brazil. In: *Applied myrmecology: a world perspective.* (eds. Vander Meer, R.K., Jaffe, K. & Cedeno, A.). Westview Press in Insect Biology, Boulder, Colorado, pp. 555–

569.

Denno, R.F. & Kaplan, I. (2007). Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past. In: *Ecological Communities: Plant Mediation in Indirect Interaction Webs* (eds. Ohgushi, T., Craig, T.P. & Price, P.W.). Cambridge University Press, London, pp. 19–50.

Denno, R.F., Peterson, M.A., Gratton, C., Cheng, J., Langellotto, G.A., Huberty, A.F., et al. (2000). Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology*, 81, 1814-1827.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, 10, 522–538.

Eubanks, M. (2001). Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biological Control*, 21, 35–43.

Evans, H.C. (2007). Cacao diseases-the trilogy revisited. *Phytopathology*, 97, 1640–1643.

Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 22–24.

Gelman, A. & Hill, J. (2007). Data analysis using regression and multilevel/hierarchical models. *Journal of Educational Measurement*. Cambridge University Press, New York.

Gibb, H. & Hochuli, D.F. (2003). Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. *Oikos*, 103, 469–478.

Gibb, H. & Parr, C.L. (2010). How does habitat complexity affect ant foraging success? A test using functional measures on three continents. *Oecologia*, 164, 1061–73.

Giesberger, G. (1983). Biological control of the Helopeltis pest of cocoa in Java. In: *Cocoa research in Indonesia 1900-1950, Volume Two* (eds. Toxopeus,

H. & Wessel, P.C.). International office of cocoa and chocolate, Wageningen, pp. 91–180.

Glendinning, D. (1972). Natural pollination of cocoa. *New Phytologist*, 71, 719–729.

Gove, A.D. (2007). Ant biodiversity and the predatory function (A response to Philpott and Armbrecht, 2006). *Ecological Entomology*, 32, 435–436.

Graham, M.K. (1991). Biological control of (*Helopeltis* spp. in mature cocoa by the black ant (*Dolichoderus bituberculatus*) and the cocoa mealybug (*Planococcus lilacinus*). *Planter*, 67, 516–520.

Greenleaf, S.S. & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 13890–13895.

Gutzler, C. & Koehler, S. (2010). A comparison of throughfall rate and nutrient fluxes in rainforest and cacao plantation in Central Sulawesi, Indonesia. In: *Tropical rainforests and agroforests under global change* (eds. Tscharntke, T., Leuschner, C., Veldkamp, E., Faust, H., Guhardja, E. & Bidin, A.). Springer, Berlin Heidelberg, pp. 309–326.

Hillebrand, H. & Bennett, D. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510–1520.

Hillebrand, H. & Matthiessen, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters*, 12, 1405–1419.

Ho, C. & Khoo, K. (1997). Partners in biological control of cocoa pests: mutualism between *Dolichoderus thoracicus* (Hymenoptera: Formicidae) and *Cataenococcus hispidus* (Hemiptera: Pseudococcidae). *Bulletin of Entomological Research*, 87, 461–470.

Hódar, J. (1996). The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica*, 17, 421–433.

Hölldobler, B. & Wilson, E.O. (1990). *The ants*. Harvard University Press.

Holway, D.A., Lach, L., Suarez, A. V., Tsutsui, N.D. & Case, T.J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, 33, 181–233.

Hooper, D.U., Chapin Iii, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, John, Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecologocal Monographs*, 75, 3–35.

Hosang, M.L.A., Schulze, C.H., Tscharntke, T. & Buchori, D. (2010). The potential of artificial nesting sites for increasing the population density of the black cacao ants. *Indonesian Journal of Agriculture*, 3, 45–40.

Hougen-Eitzman, D. & Karban, R. (1995). Mechanisms of interspecific competition that result in successful control of Pacific mites following inoculations of Willamette mites on grapevines. *Oecologia*, 103, 157–161.

Hunt, J.H. (2003). Cryptic herbivores of the rainforest canopy. *Science*, 300, 916–917.

ICCO. (2010). Quarterly bulletin of cocoa statistics, 36.

Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2004). A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters*, 8, 102–116.

James, D.G., Stevens, M.M., O’Malley, K.J. & Faulder, R.J. (1999). Ant foraging reduces the abundance of beneficial and incidental arthropods in citrus canopies. *Biological control*, 14, 121–126.

Johnson, S.N., Mayhew, P.J., Douglas, A.E. & Hartley, S.E. (2002). Insects as leaf engineers: can leaf-miners alter leaf structure for birch aphids? *Functional Ecology*, 16, 575–584.

Karban, R. (1986). Interspecific competition between folivorous insects on *Erigeron glaucus*. *Ecology*, 67, 1063–1072.

Karban, R. & Baldwin, I.T. (1997). *Induced responses to herbivory*. University of Chicago Press, Chicago.

Kaspari, M. & Weiser, M.D. (1999). The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology*, 13, 530–538.

Kay, A. (2002). Applying optimal foraging theory to assess nutrient availability ratios for ants. *Ecology*, 83, 1935–1944.

Kay, A. (2004). The relative availabilities of complementary resources affect the feeding preferences of ant colonies. *Behavioral Ecology*, 15, 63–70.

Kay, A., Rostampour, S. & Sterner, R.W. (2006). Ant stoichiometry: elemental homeostasis in stage-structured colonies. *Functional Ecology*, 20, 1037–1044.

Keane, P.J. & Putter, C.A.J. (1992). Cocoa pest and disease management in Southeast Asia and Australasia. *FAO Plant Production and Protection Paper*.

Kenne, M., Djiéto-Lordon, C., Orivel, J., Mony, R., Fabre, A. & Dejean, A. (2003). Influence of insecticide treatments on ant-hemiptera associations in tropical plantations. *Journal of Economical Entomology*, 96, 251-258.

Khoo, K. & Ho, C. (1992). The influence of *Dolichoderus thoracicus* (Hymenoptera: Formicidae) on losses due to *Helopeltis theivora* (Heteroptera: Miridae), black pod disease, and mammalian pests in cocoa in Malaysia. *Bulletin of Entomological Research*, 82, 485–491.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., et al. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313.

Klimes, P., Janda, M., Ibalim, S., Kua, J. & Novotny, V. (2011). Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities. *Ecological Entomology*, 36, 94–103.

Kruess, A. (2002). Indirect interaction between a fungal plant pathogen and a herbivorous beetle of the weed *Cirsium arvense*. *Oecologia*, 130, 563–569.

Longino, J., Coddington, J. & Colwell, R. (2002). The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, 83, 689–

702.

Lowman, M.D. (1992). Leaf growth dynamics and herbivory in five species of Australian rain forest canopy trees. *Journal of Ecology*, 80, 433–447.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000). WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing*, 10, 325–337.

Mace, G.M., Norris, K. & Fitter, A.H. (2012). Biodiversity and ecosystem services: a multilayered relationship. *Trends in ecology & evolution*, 27, 19–26.

Martin, E.A., Reineking, B., Seo, B. & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* (early edition online).

Miyaji, K.-I., Da Silva, W.S. & Alvim, P.D.T. (1997). Longevity of leaves of a tropical tree, *Theobroma cacao*, grown under shading, in relation to position within the canopy and time of emergence. *New Phytologist*, 135, 445–454.

Muhamad, R. & Way, M.J. (1995). Damage and crop loss relationships of *Helopeltis theivora*, Hemiptera, Miridae and cocoa in Malaysia. *Crop Protection*, 14, 117–121.

Ness, J.H., Bronstein, J.L., Andersen, A.N. & Holland, J.N. (2004). Ant body size predicts distance of ant-adapted seeds: Implications of small-ant invasions. *Ecology*, 85, 1244–1250.

Odendaal, F.J., Turchin, P. & Stermitz, F.R. (1989). Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia*, 78, 283–288.

Ohgushi, T. (2005). Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics*, 36, 81–105.

Ottonetti, L., Tucci, L., Frizzi, F., Chelazzi, G. & Santini, G. (2010). Changes in ground-foraging ant assemblages along a disturbance gradient in a tropical agricultural landscape. *Ethology Ecology Evolution*, 22, 73–86.

Paine, R.T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73–75.

Parr, C.L. & Gibb, H. (2010). Competition and the role of dominant ants. In: *Ant ecology* (eds. Lach, L., Parr, C.L. & Abbott, K.). Oxford University Press, New York, pp. 77–83.

Peck, S. (1998). Using ant species (Hymenoptera: Formicidae) as a biological indicator of agroecosystem condition. *Environmental Entomology*, 27, 1102–1110.

Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L. & Dietsch, T.V. (2007). Shaded coffee and the stability of rainforest margins in northern Latin America. In: *Stability of Tropical Rainforest Margins* (eds. Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E. & Bidin, A.). Springer, Berlin Heidelberg, pp. 225–261.

Philpott, S.M. & Armbrecht, I. (2006). Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, 31, 369–377.

Philpott, S.M. & Foster, P.F. (2005). Nest-site limitation in coffee agroecosystems: Artificial nests maintain diversity of arboreal ants. *Ecological Applications*, 15, 1478–1485.

Philpott, S.M., Greenberg, R., Bichier, P. & Perfecto, I. (2004). Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa. *Oecologia*, 140, 140–149.

Philpott, S.M., Perfecto, I. & Vandermeer, J. (2008a). Behavioral diversity of predatory arboreal ants in coffee agroecosystems. *Environmental Entomology*, 37, 181–191.

Philpott, S.M., Perfecto, I. & Vandermeer, J. (2008b). Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. *Journal of Animal Ecology*, 77, 505–511.

Philpott, S.M., Perfecto, I., Vandermeer, J. & Uno, S. (2009). Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid. *Environmental Entomology*, 38, 790–796.

Philpott, S.M., Uno, S. & Maldonado, J. (2006). The Importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodiversity and Conservation*, 15, 487–501.

Piñol, J., Espadaler, X. & Cañellas, N. (2012). Eight years of ant-exclusion from citrus canopies: effects on the arthropod assemblage and on fruit yield. *Agricultural and Forest Entomology*, 14, 49–57.

Ploetz, R.C. (2007). Cacao diseases: Important threats to chocolate production worldwide. *Phytopathology*, 97, 1634–1639.

Poelman, E.H., Broekgaarden, C., Van Loon, J.J.A. & Dicke, M. (2008). Early season herbivore differentially affects plant defence responses to subsequently colonizing herbivores and their abundance in the field. *Molecular Ecology*, 17, 3352–3365.

Posada, F.J., Virdiana, I., Navies, M., Pava-Ripoll, M. & Hebbar, P. (2011). Sexual dimorphism of pupae and adults of the cocoa pod borer, *Conopomorpha cramerella*. *Journal of Insect Science*, 11, 1–8.

Poveda, K., Jímenez, M.I.G. & Kessler, A. (2010). The enemy as ally: herbivore-induced increase in crop yield. *Ecological Applications*, 20, 1787–1793.

Poveda, K., Steffan-Dewenter, I., Scheu, S. & Tscharntke, T. (2005). Effects of decomposers and herbivores on plant performance and aboveground plant-insect interactions. *Oikos*, 108, 503–510.

Renwick, J.A.A. & Chew, F.S. (1994). Oviposition behavior in Lepidoptera. *Annual Review of Entomology*, 39, 377–400.

Rice, R.A. & Greenberg, R. (2000). Cacao cultivation and the conservation of biological diversity. *Ambio*, 29, 167–173.

Richard, F.J., Fabre, A. & Dejean, A. (2001). Predatory behavior in dominant arboreal ant species: the case of *Crematogaster sp.* (Hymenoptera:

Formicidae). *Journal of Insect Behavior*, 14, 271–282.

Robertson, G.P. & Swinton, S.M. (2005). Reconciling agricultural productivity and environmental integrity: A grand challenge for agriculture. *Frontiers in Ecology and the Environment*, 3, 38-46.

Rosumek, F.B., Silveira, F. a O., De S Neves, F., De U Barbosa, N.P., Diniz, L., Oki, Y., et al. (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, 160, 537–549.

Rudolf, V.H.W. (2006). The influence of size-specific indirect interactions in predator-prey systems. *Ecology*, 87, 362–371.

Sanders, N.J., Gotelli, N.J., Heller, N.E. & Gordon, D.M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 2474–2477.

Sandström, J., Telang, A. & Moran, N.A. (2000). Nutritional enhancement of host plants by aphids - a comparison of three aphid species on grasses. *Journal of Insect Physiology*, 46, 33–40.

Schmitz, O.J. (2007). Predator diversity and trophic interactions. *Ecology*, 88, 2415–2426.

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7, 153–163.

Schmitz, O.J. & Price, J.R. (2011). Convergence of trophic interaction strengths in grassland food webs through metabolic scaling of herbivore biomass. *Journal of Animal Ecology*, 80, 1330–1336.

Schmitz, O.J. & Suttle, K.B. (2001). Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, 82, 2072–2081.

See, Y.A. & Khoo, K.C. (1996). The influence of *Dolichoderus thoracicus* (Hymenoptera: Formicidae) on cocoa pod damage by *Conopomorpha cramerella* (Lepidoptera: Garcillariidae) in Malaysia. *Bulletin of Entomological Research*, 86, 467–474.

Siebert, S.F. (2002). From shade-to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility.

Biodiversity and Conservation, 11, 1889–1902.

Stonedahl, G.M. (1991). The oriental species of *Helopeltis* (Heteroptera: Miridae): a review of economic literature and guide to identification. *Bulletin of Entomological Research*, 81, 465.

Stowe, K.A., Marquis, R.J., Hochwender, C.G. & Simms, E.L. (2000). The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics*, 31, 565–595.

Tan, G.S. (1974a). *Helopeltis theivora theobromae* on cocoa in Malaysia. I. Biology and population fluctuations. *Malayan Agricultural Research*, 3, 127–132.

Tan, G.S. (1974b). *Helopeltis theivora theobromae* on cocoa in Malaysia II. Damage and Control. *Malayan Agricultural Research*, 3, 204–212.

Thompson, J.N. & Pellmyr, O. (1991). Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology*, 36, 65–89.

Tilman, D. (2001). Functional diversity. In: *Encyclopedia of biodiversity* (ed. Levin, S.A.). Academic Press Ltd, San Diego, pp. 109–120.

Utsumi, S., Ando, Y. & Miki, T. (2010). Linkages among trait-mediated indirect effects: a new framework for the indirect interaction web. *Population Ecology*, 52, 485–497.

Van Dam, N.M., Hadwich, K. & Baldwin, I.T. (2000). Induced responses in *Nicotiana attenuata* affect behavior and growth of the specialist herbivore *Manduca sexta*. *Oecologia*, 122, 371–379.

Vandermeer, J. (2011). *The ecology of agroecosystems*. Jones and Bartlett Publishers, Sudbury.

Vandermeer, J., Perfecto, I. & Liere, H. (2009). Evidence for hyperparasitism of coffee rust (*Hemileia vastatrix*) by the entomogenous fungus, *Lecanicillium lecanii*, through a complex ecological web. *Plant Pathology*, 58, 636–641.

Vandermeer, J., Perfecto, I. & Philpott, S.M. (2010). Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *BioScience*, 60, 527–537.

Van Mele, P. (2007). A historical review of research on the weaver ant *Oecophylla* in biological control. *Agricultural and Forest Entomology*, 10, 13–22.

Van Mele, P. & Cuc, N.T.T. (2001). Farmers' perceptions and practices in use of *Dolichoderus thoracicus* (Smith)(Hymenoptera: Formicidae) for biological control of pests of sapodilla. *Biological Control*, 20, 23–29.

Van Zandt, P.A. & Agrawal, A.A. (2004). Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology*, 85, 2616–2629.

Wanger, T.C., Rauf, A. & Schwarze, S. (2010). Pesticides and tropical biodiversity. *Frontiers in Ecology and the Environment*, 8, 178–179.

Warton, D. & Hui, F. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92, 3–10.

Way, M.J. & Khoo, K.C. (1989). Relationships between *Helopeltis theobromae* damage and ants with special reference to Malaysian cocoa smallholdings. *Journal of Plant Protection in the Tropics*, 6, 1–11.

Way, M.J. & Khoo, K.C. (1991). Colony dispersion and nesting habits of the ants, *Dolichoderus thoracicus* and *Oecophylla smaragdina* (Hymenoptera: Formicidae) in relation to their success as biological control agents on cocoa. *Bulletin of Entomological Research*, 81, 341–350.

Way, M.J. & Khoo, K.C. (1992). Role of ants in pest management. *Annual Review of Entomology*, 37, 479–503.

Weiser, M.D. & Kaspari, M. (2006). Ecological morphospace of new world ants. *Ecological Entomology*, 131–142.

Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.

Whitten, A.J., Mustafa, M. & Henderson, G.S. (2002). *The Ecology of Sulawesi*. Gajah Mada University Press, Yogyakarta, Indonesia.

Wielgoss, A.C., Clough, Y., Fiala, B., Rumede, A. & Tscharntke, T. (2012). A minor pest reduces yield losses by a major pest: plant-mediated herbivore interactions in Indonesian cacao. *Journal of Applied Ecology*, 49, 465–473.

Wielgoss, A.C., Tscharntke, T., Buchori, D., Fiala, B. & Clough, Y. (2010). Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian cacao plantations. *Agriculture, Ecosystems & Environment*, 135, 253–259.

Wise, M.J. & Weinberg, A.M. (2002). Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology*, 27, 115–122.

Wood, B.J., Fee, C.G., Cheong, S.S. & Foh, C.C. (1992). Trials on control of the cocoa pod borer *Conopomorpha cramerella* (Snellen) in Sabah by regular complete harvesting. *Tropical Pest Management*, 38, 271–278.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., et al. (2005). Body size in ecological networks. *Trends in ecology & evolution*, 20, 402–409.

Yanoviak, S.P. & Kaspari, M. (2000). Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos*, 89, 259–266.

Zborowski, P. & Storey, R. (2010). *A field guide to insects of Australia*. 3rd edn. Reed, New Holland.

VIII Promovierendenerklärung der Georg-August-Universität Göttingen

Name: Wielgoss, Arno Christian
Anschrift: Elstergasse 4a, 97082 Würzburg

Ich beabsichtige, eine Dissertation zum Thema "Services and disservices driven by ant communities in tropical agroforests" an der Georg-August-Universität Göttingen anzufertigen. Dabei werde ich von Herrn Prof. Dr. Teja Tscharntke betreut.

Ich gebe folgende Erklärung ab:

1. Die Gelegenheit zum vorliegenden Promotionsvorhaben ist mir nicht kommerziell vermittelt worden. Insbesondere habe ich keine Organisation eingeschaltet, die gegen Entgelt Betreuerinnen und Betreuer für die Anfertigung von Dissertationen sucht oder die mir obliegenden Pflichten hinsichtlich der Prüfungsleistungen für mich ganz oder teilweise erledigt.
2. Hilfe Dritter wurde bis jetzt und wird auch künftig nur in wissenschaftlich vertretbarem und prüfungsrechtlich zulässigem Ausmaß in Anspruch genommen. Insbesondere werden alle Teile der Dissertation selbst angefertigt; unzulässige fremde Hilfe habe ich dazu weder unentgeltlich noch entgeltlich entgegengenommen und werde dies auch zukünftig so halten.
3. Die Richtlinien zur Sicherung der guten wissenschaftlichen Praxis an der Universität Göttingen werden von mir beachtet.
4. Eine entsprechende Promotion wurde an keiner anderen Hochschule im In- oder Ausland beantragt; die eingereichte Dissertation oder Teile von ihr wurden nicht für ein anderes Promotionsvorhaben verwendet.

Mir ist bekannt, dass unrichtige Angaben die Zulassung zur Promotion ausschließen bzw. später zum Verfahrensabbruch oder zur Rücknahme des erlangten Grades führen.

Göttingen, den 10.03.2013

Arno Christian Wielgoss

IX Curriculum vitae

Name: **Arno Wielgoss**
Address: Elstergasse 4a; 97082 Würzburg
Phone.: +49-931-32096934
Mobile phone: +49-178-6680854
E-Mail: arno.wielgoss@uni-wuerzburg.de
Date of Birth: 17. April 1982 in Bad Neustadt/Germany

Education

1992 - 2001 Jack-Steinberger Gymnasium Bad Kissingen

University

10/2002 - 06/2008 *Diploma Studies* Julius-Maximilian University Würzburg
Major subject: -Tropical biology and Animal ecology
Subsidiary *subjects:*-Molecular plant physiology and Biophysics
-Ecophysiology of plants and Vegetation ecology
07/2005-09/2005 Lab-training: HPLC-Analysis of secondary plant products
08/2006-10/2006: Two month field research in Indonesia; DAAD-scholarship
09/2007-06/2008 *Diploma thesis*
“***The Impacts of Ants on Pests and Diseases of Cocoa in Indonesian Agroforestry Systems”***
with four month of field research in Sulawesi, Indonesia
DAAD-Master student scholarship
06/2008 Exam: Diploma in Biology (1.35)
since 10/2009: *PhD -Studies:* Georg-August Universtity Göttingen, Agroecology, Department of crop sciences

"Effects of Invasive Ants in Indonesian Agroforestry Systems on Ant Diversity and Associated Ecosystem Processes such as Biocontrol of Cacao Pests and Pathogens"

Georg-August Universtity Göttingen, Agroecology, Department of crop sciences
(Total 19 Month of field studies in Central-Sulawesi/Indonesia)

Scholarships:

2011	Travel-grant fro particularly gifted young scientists for attending an International conference as speaker (Unibund University Göttingen)
2009-2011	19 month PhD-scholarship (German Academic Exchange Service)
2007	4 month Master-scholarship (DAAD)
2006	3 month Travel grant for attending an international internship (DAAD)

Conference participations:

2013	Speaker at: **GTÖ 2013, Vienna** (German Society of Tropical Ecology)
2012	Speaker at: **GTÖ 2012, Erlangen** (German Society of Tropical Ecology)
2012	Speaker at: **GFÖ 2012, Lüneburg** (German Society of Ecology)
2011	Speaker at: **ATBC&SCB 2011, Arusha/Tansania** (Association for Tropical Biology and Conservation & Africa Section of the Society for Conservation Biology)
2011	Speaker at: **GTÖ 2011, Frankfurt am Main** (Society of Tropical Ecology)
2010	Speaker at: **ATBC 2010, Bali/Indonesia**
2009	Speaker at: **DGaaE 2009, Göttingen** (Deutsche Gesellschaft für allgemeine und angewandte Entomologie)
2007	Poster presentation at: **GTÖ 2007, Bonn**

Language skills English, Spanish, Bahasa Indonesia

Further activities/interests

09/2001 - 09/2002	Volunteer in development work in Peru (Projects to support organic waste processing in the slums of Lima, reforestation and ecological agriculture)
since 2002	Founding member of the non-profit NGO „Frederic – Hilfe für Peru“ (www.frederic-hfp.de) Organisation supervisor and executive function of all projects to support

X Publication list

Clough, Y., Abrahamczyk, S., Adams, M., Ariyanti, N., Betz, L., Buchori, D., Darras, K., Putra, D.D., Fiala, B., Robbert, S., Kessler, M., Klein, A.-M., Pitopang, R., Sahari, B., Scherber, C., Schulze, C.H., Shababuddin, S., Sporn, S.G., Stenchly, K., Tjitrosoedirdjo, S.S., Wanger, T.C., Weist, M., **Wielgoss, A.C.** & Tscharntke, T. (2010) Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulawesi (Indonesia): plants, arthropods and vertebrates. *Tropical rainforests and agroforests under global change* (eds T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja & A. Bidin), pp. 15–71. Springer Berlin Heidelberg, Berlin, Heidelberg.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T.C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D.D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C.H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., **Wielgoss, A.C.** & Tscharntke, T. (2011) Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 8311–8316.

Wanger, T.C., **Wielgoss, A.C.**, Motzke, I., Clough, Y., Brook, B.W., Sodhi, N.S. & Tscharntke, T. (2011) Endemic predators, invasive prey and native diversity. *Proceedings. Biological sciences / The Royal Society*, **278**, 690–4.

Wielgoss, A.C., Clough, Y., Fiala, B., Rumede, A. & Tscharntke, T. (2012) A minor pest reduces yield losses by a major pest: plant-mediated herbivore interactions in Indonesian cacao. *Journal of Applied Ecology*, **49**, 465–473.

Wielgoss, A.C., Tscharntke, T., Buchori, D., Fiala, B. & Clough, Y. (2010) Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian cacao plantations. *Agriculture, Ecosystems & Environment*, 135, 253–259.

XI Acknowledgements

I thank Teja Tscharntke for the opportunity to work on a fascinating topic on the wonderful island Sulawesi, for the given supervision, motivation and scientific input and for giving me the freedom to develop own ideas and to collaborate with the zoology department of the University of Würzburg. I thank Yann Clough for being my mentor and friend. You supported me since my early study years. I thank you for your support in the field your motivating words and the invaluable statistical help. This thesis would not have been the same without you! Prof. Dr. Schaefer: thank you for your efforts in reviewing my doctoral thesis. Brigitte Fiala, I thank you for reading and commenting all my manuscript versions in late office hours and on the weekends! Together with Eduard Linsenmair you introduced me into tropical ecology and guided me through my studies. Ingolf Steffan-Dewenter, I am deeply grateful that you not only gave me the opportunity to join you dynamic working group, but also that you helped me through difficult times! I thank Shahabuddin for his help as local supervisor. I thank the representatives in Tadulako University, village heads, and villagers in the study region; the Indonesian and German project coordination team. I thank the wonderful people in the agroecology group in which loved the warm and constructive atmosphere, even I was not around very often! Especially I want to thank all the precious people of Würzburg where I spend most of my Germany-time: Bernhard for fruitful discussions and even more fruitful Dominion-sessions, (Sou-)Verena for much more than only the morning tea, Annette for the climbing and everything else, which is just so much better when you are around! Bea for being such a warm and nice franconian fellow! Emily as the best part-time “Mitbüroner” ever! And all the others (Gudrun, Juliane, Alice, SAMUEL): You made my time in Würzburg just wonderful! Iris, Pierre and Rizal: it was great to have you as a colleague in the field! Nining you are the best chief-assistant one can imagine! “Team chokelat” only because of your endless hours of surveys and data collecting this huge dataset could be gathered. I thank the DAAD with all it´s organisers in Bonn and Jakarta for the support. Finally a hug to my parents and Christine for your constant support, you patience and love!