Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest

Kumulative Dissertationsschrift

zur Erlangung des akademischen Grades

Doktor der Naturwissenschaften

-Dr. rer. nat.-

Angefertigt am Institut für Ökologie

der Fakultät Nachhaltigkeit

der Leuphana Universität Lüneburg

Vorgelegt von

Michael Staab

geb. am 01.06.1985 in Alzenau i. Ufr.

Eingereicht am:	25.04.2014
Betreuerin und Gutachterin:	Prof. Dr. Alexandra-Maria Klein
Gutachter:	___________________________
Gutachter:	___________________________
Tag der Disputation:	______________

Copyright notice

Contents

Summary **1**

Zusammenfassung **3**

Chapter I **6**

Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest

Chapter II **38**

Ant community structure during forest succession in a subtropical forest in South-East China

Chapter III **66**

Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest

Chapter IV **90**

Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment

Chapter V **112**

A new species of the Aenictus wroughtonii *group (Hymenoptera, Formicidae) from South-East China*

Chapter VI **122**

The first observation of honeydew foraging in army ants since 1933: Aenictus hodgsoni *Forel, 1901 tending* Eutrichosiphum heterotrichum *(Raychaudhuri, 1956) in Southeast China*

Chapter VII **126**

A unique nest-protection strategy in a new species of spider wasp

Danksagung **144**

Lebenslauf **145**

Eigenständigkeitserklärung **149**

Summary

On a large geographical scale, the latitudinal diversity gradient accounts for much of the variations in regional species numbers, making tropical and subtropical forests the most diverse terrestrial ecosystems. A high plant diversity facilitates diversity in other trophic levels, and these forests support a substantial proportion of the biodiversity on Earth. Unfortunately, in the last decades (sub)tropical forests were subject to large-scale exploitation, and future human land-use pressure is predicted to remain high. As a consequence, a large part of the forests which remain are either plantations or secondary forests of varying successional age and of varying tree diversity. On a smaller geographical, scale most evidence for the effect of plant diversity on other taxa comes from biodiversity experiments conducted in grasslands. These studies have shown that plant diversity generally has a positive effect on the diversity of most other trophic levels, and that plant diversity stabilizes food webs. However, as they are much more structurally complex and longer-lived ecosystems, forests are fundamentally different from grasslands. In addition, species diversity across trophic levels is higher in forests, and thus forest species communities may react differently to varying plant diversity than grassland communities. The overall aim of this dissertation is to understand the relationships between tree diversity and arthropod communities in a highly diverse subtropical mixed evergreen broad-leaved forest in South-East China.

The first part of my dissertation consists of two studies focusing on ground-dwelling ants in the Gutianshan National Nature Reserve (GNNR). I used a well-replicated dataset consisting of 13,441 ant individuals belonging to 71 species that were collected with pitfall traps in 27 study plots. In the first study I investigated if and how ant diversity and community composition are influenced by biotic (*e.g.* tree diversity, successional age) and abiotic (*e.g.* elevation, soil pH) environmental plot variables. Ant diversity was only related to elevation and there was a substantial species community turnover between plots which is best explained by elevation and by successional age.

Since I found no effect of tree diversity on the total ant community in the first study, I divided in the second study the ants into two main trophic groups, predators and omnivores. I tested each trophic group separately for their relationship to the environmental variables, including tree diversity. I could show that only the diversity of predator ants increased with increasing tree diversity, while omnivores were most strongly and positively related to soil pH.

After I gained insight into how tree diversity and other environmental variables influence a single group of organisms in a semi-natural, but very heterogeneous forest, in the third study I tested if tree diversity also affects multi-trophic interactions. I chose trophobioses, the tri-trophic interactions between plants, sap-sucking Hemiptera, and honeydew-collecting ants on the controlled experimental tree diversity gradient of the BEF-China Experiment as a model system. I found that

that increasing tree diversity positively correlated to the generality, and thus the stability, of mutualistic aphid-ant network but not of the antagonistic plant-aphid network.

In conclusion, my research shows that even young secondary forests can maintain high ant diversity although the recovery of old-growth forest ant communities takes more time. I prove that more diverse forests support a higher diversity of potentially beneficial predator ants, and that tree diversity can stabilize mutualistic aphid-ant networks. However, each of the positive effects of tree diversity was only revealed when analyzing the different trophic and functional groups separately. I suggest considering that various trophic and functional groups may respond differently when analyzing biodiversity relationships between and across trophic levels.

During my extensive field work in subtropical China I made several intriguing discoveries that I consider worthy of interest to the scientific community. Unsurprisingly, I found that some of the ant species in the first two studies were undescribed. The fourth study describes one of these species, *Aenictus gutianshanensis*, as new to science. There are, however, still several ant species in South-East China awaiting discovery and scientific description.

In the fifth study I describe an unexpected observation of trophobiotic behavior in an army ant species that until now was thought to be a specialized predator. This finding shows that even highly specialized predators may occasionally supplement their diet with plant-based resources such as honeydew.

Lastly, I discovered in the GNNR a new cavity-nesting spider wasp species which shows a novel and fascinating nesting behavior that I report on in the sixth study. This new species, *Deuteragenia ossarium*, closes its nests with a vestibular cell filled with dead ants, which is a behavior unique not only in spider wasps but also in the entire animal kingdom. I showed that nests of *D. ossarium* were attacked less frequently by parasitoids than nests of other sympatric cavity-nesting wasp species, suggesting an effective nest-protecting strategy that most likely utilizes chemical cues exhaling from the dead ants.

By including these three additional studies into my dissertation, I highlight that ecological studies have the often unused potential to make important natural-history observations, or even to discover and describe species unknown to science. With the three descriptions of new species and life-history traits I aim to encourage fellow ecologists to report on the many fascinating phenomena yet unknown to science and society.

Zusammenfassung

Tropische und subtropische Wälder sind die artenreichsten terrestrischen Ökosysteme. Jedoch sind diese Wälder durch menschliche Aktivitäten in den letzten Jahrzehnten massiv degradiert worden, eine Entwicklung, die auch für die Zukunft vorhergesagt wird. Große Teile der verbliebenen Wälder sind inzwischen Plantagen oder Sekundärwald verschiedenen Alters und mit verschiedener Baumartenvielfalt. Im großen Maßstab hängt die Biodiversität von Pflanzen und Tieren eng zusammen: Gebiete mit hoher Pflanzendiversität haben üblicherweise eine höhere Diversität von Organismen anderer trophischer Ebenen. Im kleinen Maßstab wurden die meisten Hinweise für den Effekt von Pflanzendiversität auf andere Organismen, wie zum Beispiel Insekten, durch Biodiversitätsexperimente auf Wiesen gesammelt. Diese Experimente schlussfolgern, dass Pflanzendiversität generell einen positiven Effekt auf die Diversität anderer trophischer Ebenen hat und Nahrungsnetze stabilisieren kann. Wälder unterscheiden sich jedoch deutlich von Wiesen durch ihre Langlebigkeit, ihre deutlich komplexere Vegetationsstruktur und ihre höhere Artenvielfalt pro Flächeneinheit. Somit ist es möglich, dass Artengemeinschaften in Wäldern auf eine andere Art und Weise von Pflanzendiversität beeinflusst werden als dies bei Wiesen der Fall ist. Das Ziel dieser Arbeit war somit, den Zusammenhang zwischen Baumartenvielfalt und Insektengemeinschaften in einem subtropischen Wald in Süd-Ost China zu erforschen.

Der erste Teil meiner Arbeit besteht aus zwei Studien über am Boden lebende Ameisen im Naturreservat „Gutianshan National Nature Reserve“ (GNNR). Ich analysierte einen Datensatz mit 13.441 Individuen von 71 Ameisenarten, die mit Bodenfallen in 27 Untersuchungsflächen gesammelt wurden. In der ersten Studie untersuchte ich, ob Diversität und Lebensgemeinschaftszusammensetzung von Ameisen durch biotische (z.B. Baumartenvielfalt, Waldalter) und abiotische (z.B. Höhe über NN, Boden pH-Wert) Umweltvariablen beeinflusst werden. Ameisendiversität hing nur mit der Höhe über NN zusammen, welche einen negativen Effekt ausübte. Es gab einen deutlichen Artenwechsel zwischen den Untersuchungsflächen, der am besten durch Höhe über NN und Waldalter erklärt werden konnte.

Während ich in der ersten Studie keinen Effekt von Baumartenvielfalt auf die gesamte Ameisenlebensgemeinschaft fand, testete ich in der zweiten Studie Räuber und Omnivore - die beiden wichtigsten funktionellen Ameisengruppen - separat auf ihre Beziehung zu den Umweltvariablen. Ich konnte zeigen, dass nur die Vielfalt der Räuber aber nicht die der Omnivoren positiv von Baumartenvielfalt beeinflusst wurden. Im Gegensatz dazu waren die Omnivoren positiv von einem höheren pH-Wert des Bodens beeinflusst.

Nachdem ich einen Einblick erhalten hatte, wie Baumartenvielfalt und andere Umweltvariablen eine einzige Organismengruppe in einem naturnahen, aber sehr heterogenen Wald beeinflussen, wollte ich in der dritten Studie testen, ob Baumartenvielfalt sich ebenso auf multi-

trophische Interaktionen auswirkt. Dazu wählte ich Trophobiosen - die tri-trophischen Interaktionen zwischen Pflanzen, Blattläusen und honigtausammelnden Ameisen - als Modellsystem und arbeitete auf dem kontrollierten Baumdiversitätsgradienten des BEF-China Experiments. Ich fand heraus, dass sich die Generalität und damit die Stabilität der mutualistischen Blattlaus-Ameisen-Interaktionen aber nicht die der antagonistischen Pflanzen-Blattlaus-Interaktionen mit steigender Baumartenvielfalt erhöht.

Zusammenfassend zeigte meine Arbeit, dass auch junge Sekundärwälder eine hohe Ameisendiversität beherbergen können, aber dass jedoch die Erholung von für alte Wälder typischen Ameisenlebensgemeinschaften deutlich längere Zeiträume benötigt. Ich fand Beweise dafür, dass diverse Wälder eine höhere Artenzahl von potentiell nützlichen räuberischen Ameisen beherbergen, und dafür dass eine höhere Baumartenvielfalt mutualistische Blattlaus-Ameisen-Netzwerke stabilisiert. Die positiven Effekte von Baumartenvielfalt konnten nur dadurch aufgedeckt werden, dass verschiedene trophische und funktionelle Gruppen getrennt voneinander analysiert wurden. Ich schlage vor, dass die möglicherweise verschiedenen Reaktionen von trophischen und funktionellen Gruppen berücksichtigt werden sollten, wenn Biodiversitätseffekte zwischen und über verschiedene trophische Ebenen analysiert werden.

Während meiner umfangreichen Feldarbeit in den Chinesischen Subtropen machte ich einige interessante Entdeckungen, die für Biodiversitätsforschung von großem Wert sind. Wenig überraschend stellte sich heraus, dass mehrere der Ameisenarten aus den ersten beiden Studien noch nicht wissenschaftlich beschrieben waren. Deshalb beschrieb ich in der vierten Studie eine dieser neuen Arten, *Aenictus gutianshanensis*. Es gibt jedoch weiterhin viele Ameisenarten aus Süd-Ost China die auf ihre Entdeckung und Erstbeschreibung warten.

In der fünften Studie informiere ich über die unerwartete Beobachtung von trophobiotischem Verhalten einer Armeeameise, von der man bisher ausging, dass sie ein spezialisierter Räuber ist. Dies zeigt, dass selbst hoch spezialisierte Räuber gelegentlich ihre Ernährung mit pflanzlichen Ressourcen wie Honigtau ergänzen können.

Schließlich entdeckte ich im GNNR eine neue hohlraumnistende Wegwespenart mit einem neuartigen und faszinierenden Brutverhalten, über das ich in der sechsten Studie berichte. Diese neue Art, *Deuteragenia ossarium*, schließt einzigartig für Wegwespen und das gesamte Tierreich ihre Nester durch eine mit toten Ameisen gefüllte Kammer ab. Ich konnte zeigen, dass Nester von *D. ossarium* weniger häufig als Nester anderer hohlraumnistender Wespen von Parasitoiden befallen werden. Dies weißt auf eine wirksame Nestverteidigungsstrategie hin, die sehr wahrscheinlich die chemischen Signale der toten Ameisen ausnutzt.

Durch die Aufnahme dieser drei Studien als Kapitel in meine Arbeit möchte ich zeigen, dass ökologische Studien häufig das Potential haben wichtige Beobachtungen zu machen oder sogar neue

Arten zu entdecken und zu beschreiben. Ich möchte Ökologen ermutigen über die vielen noch unbekannten Phänomene zu berichten, die sie während ihrer Arbeit entdecken, und diese sowohl der Wissenschaft als auch der Gesellschaft zugänglich zu machen.

Chapter I

Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest

The Gutianshan Nature Reserve during flowering in May 2011.

General introduction

Forests in the tropics and subtropics are famous for their enormous species diversity. Globally the highest numbers of terrestrial species can be found in these low latitude forests (e.g. Primack and Corlett 2005, Corlett 2009). The strong latitudinal diversity gradient is one of the most consistent patterns in ecology and was already noticed by early naturalists (Darwin 1859, Wallace 1878). This is true across geographical regions, spatial scales, habitat types, and taxonomic groups (Hillebrand 2004), as it is illustrated for four well-known examples (Figure 1): plants (Barthlott et al. 2005), mammals (Buckley et al. 2010), birds (Jetz et al. 2012b), and ants (Guénard et al. 2012). Many hypotheses seek to explain the latitudinal diversity gradient. Conclusively, a favorable warm and humid present-day climate in the tropics, combined with historically stable climates, faster diversification rates, and reduced extinction risk facilitate the enormous diversity (Willig et al. 2003, Mittelbach et al. 2007, Rolland et al. 2014).

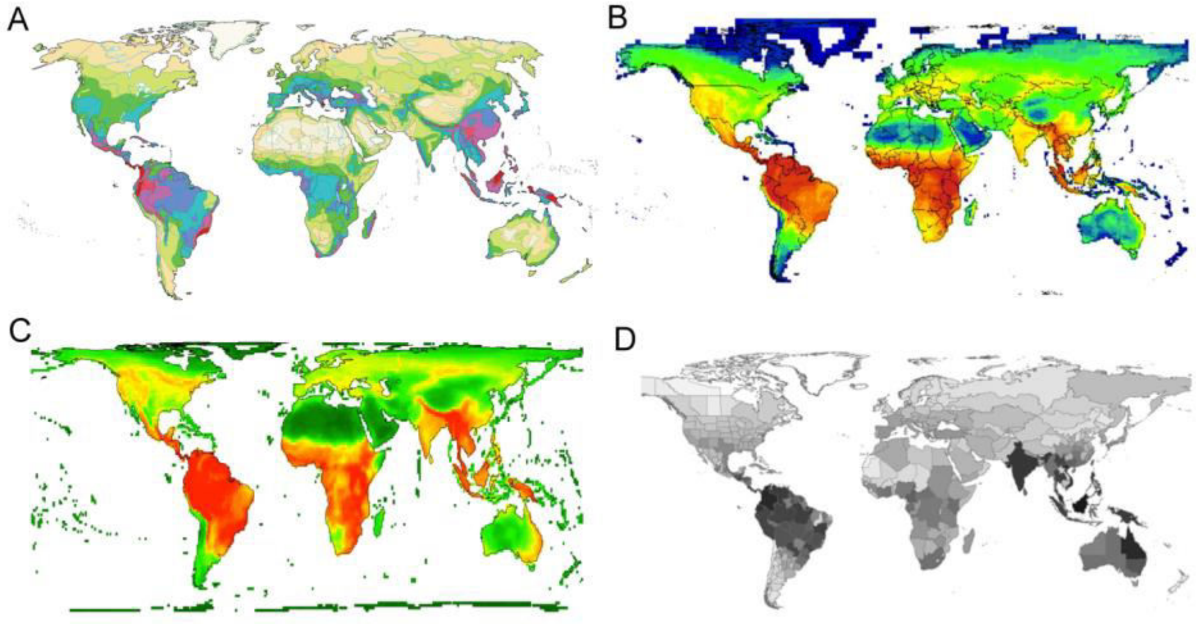


Figure 1. Large-scale global species richness gradients for **A)** plants (modified after Barthlott et al. 2005), **B)** mammals (after Buckley et al. 2010), **C)** birds (modified after Jetz et al. 2012), and **D)** ants (after Guénard et al. 2012). In A) red colors mark the areas of highest species richness and fawn colors the areas of lowest species richness. In B) and C) warmer colors refer to areas with higher species richness. In D) darker shading marks political regions with high species richness.

Over the last decades, an exponentially increasing human population, together with growing international commerce in timber and agricultural products from the (sub)tropics has led to large-scale forest disturbance and conversion into agricultural land (e.g. Gibbs et al. 2010, Hansen et al. 2013). Today, most of the (sub)tropical forests are in a non-primary state (Asner et al. 2009). Frighteningly, global deforestation rates are still increasing and will likely remain high, especially in the most diverse regions (Hansen et al. 2013). Forest disturbance, for example by logging, changes the structure and the appearance of a forest, alters the species composition, and usually leads to a reduced diversity of forest organisms (Barlow et al. 2007, Gibson et al. 2011). Most forest species are now bound to non-natural, secondary forests that at local scales may in some cases support a surprising number of old-growth forest species, as long as minimal habitat requirements are retained (e.g. Dunn 2004, Edwards et al. 2011).

Diversity inside one trophic level facilitates diversity of other trophic levels. For example, the diversity of plants and vertebrates is highly correlated at regional scales (Zhao et al. 2006, Quian 2007). At more local scales, plant diversity has been show to directly increase arthropod diversity (e.g. Siemann et al. 1998, Haddad et al. 2009). Thus, even when a high level of species richness can be found in the secondary habitat, long term changes in species communities and trophic interactions are likely (e.g. Hector et al. 2011). As ecosystem functioning is directly linked to its biodiversity (e.g. Balvarena et al. 2006, Cardinale et al. 2011), and as biodiversity stabilizes trophic cascades (Scherber et al. 2010), it is inevitable that the biodiversity loss is directly related to, and even more importantly is a major driver of ecosystem change (Cardinale et al. 2012, Hooper et al. 2012).

Most of the evidence for the biodiversity-ecosystem functioning (BEF) relationship comes from large-scale BEF-experiments that manipulate plant diversity in order to investigate if and how plant diversity relates to ecosystem functioning. Well-known examples for BEF-experiments are the Cedar-Creek Experiment in the United States (e.g. Tilman et al. 1996, Siemann et al. 1998, Tilman et al. 2001, Haddad et al. 2009) and the Jena Experiment in Germany (e.g. Roscher et al. 2004, Scherber et al. 2010). Like almost all other BEF-experiments, these two experiments have been conducted in temperate grassland ecosystems, and BEF-experiments in forests, particularly in the more diverse regions, are largely underrepresented (see Bruelheide et al. 2014). This is surprising because forests cover over 30% of the Earth's land area and are estimated to support 80% of the terrestrial biodiversity (FAO 2010). Moreover, forests are as ecosystems much more important globally than grasslands, for example in maintaining global physical processes (Bonan 2008) such as carbon sequestration (e.g. Pan et al. 2011). Being complex multi-layered ecosystems characterized by long-living plant individuals, a very high standing biomass, and, at least in the sub(tropics), much more species rich animal communities than grasslands, plant diversity might affect BEF relationships differently in forests. Finally, BEF-experiments in grasslands as well as in forests have with few exceptions (e.g. Petermann et al. 2010, Ebeling et al. 2011) neglected to study the effect of plant diversity on trophic interactions and food-web structure (Balvanera et al. 2006, Hillebrand and Matthiessen 2009).

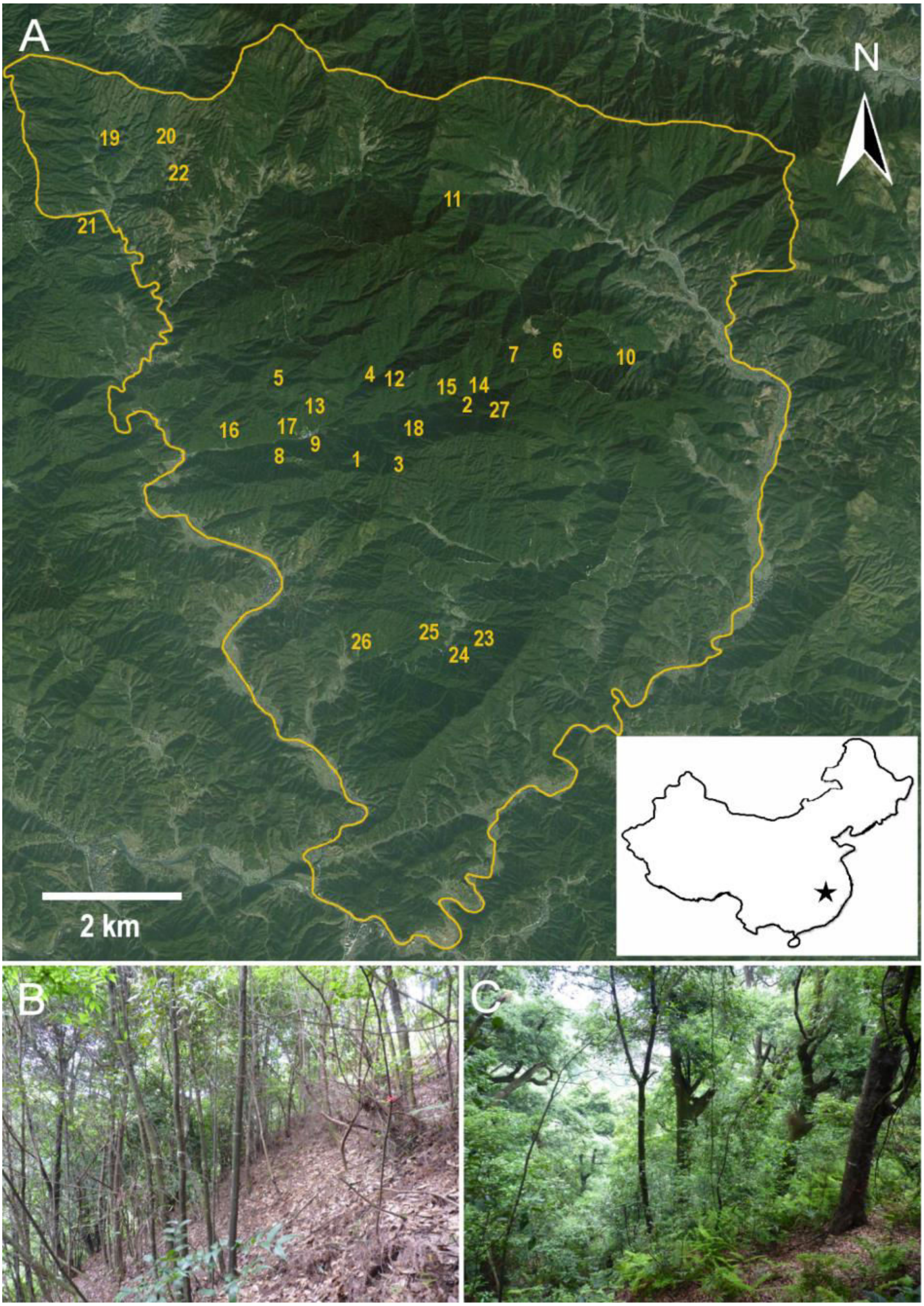


Figure 2. The Gutianshan National Nature Reserve (GNNR) in subtropical South-East China. **A)** Overview map (based on Google^{TM} Earth) of the GNNR showing the boundary of the reserve, the location of each study plot (numbers), and the location in China (embedded picture). **B)** Example of young (plot 24) and **C)** old-growth (plot 21) secondary forest. Photographs: Michael Staab, taken in May 2012.

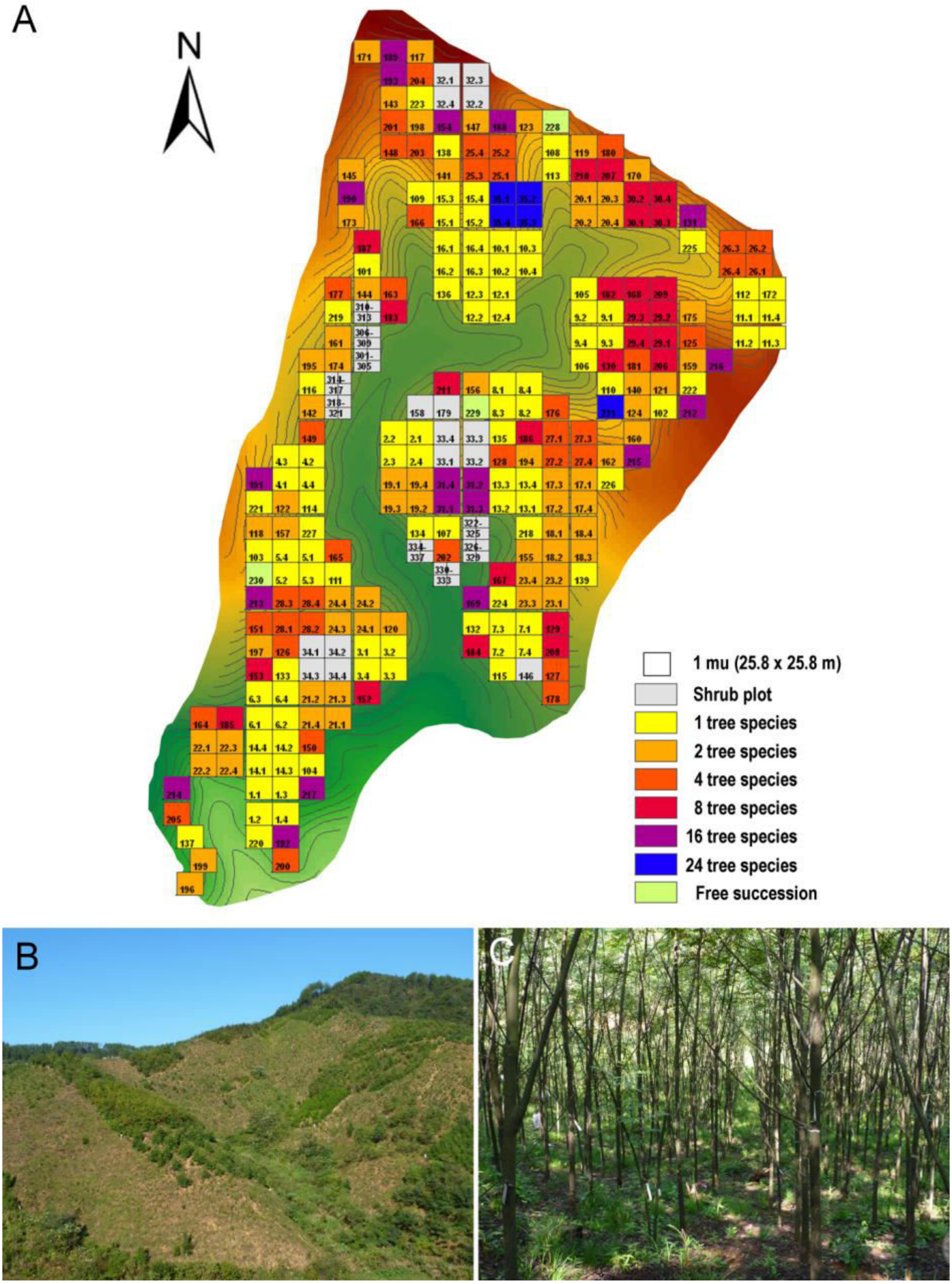


Figure 3. Site A of the BEF-China Experiment. **A)** Map showing the spatial location of plots; different colors refer to different tree diversity levels (modified after Yang et al. 2013). **B)** Overview of the site (October 2012); plot boundaries are clearly visible by different tree growth and tree habitus. **C)** Monoculture (plot 7.1 in A)) of *Choerospondias axillaris* (Roxb.) Burtt. et Hill, a fast-growing deciduous tree planted in site A (May 2013). Photographs: Michael Staab.

Therefore, one aim of my dissertation was to investigate the relationship between tree diversity and the diversity of ants, a functionally important arthropod taxon that is directly involved in many important BEF relationships. I also wanted to test if tree diversity influences the structure of a tri-trophic food web consisting of plants ants and aphids. All studies of this dissertation were done in the subtropical forests of South-East China.

Why subtropical South-East China: The BEF-China Project?

Before the rise of human civilization and the accompanying forest clearance, East Asia was continuously and extensively covered in forests that persisted in similar conditions for several million years (Corlett 2009). Subtropical broadleaved forests covered large areas of Southern and Eastern China and served as an essential part of the East-Asian forest continuum by connecting the tropical evergreen forests of South-East Asia with the temperate and boreal forests of Northern China and the Russian Far East. Subtropical forests in China are highly diverse (e.g. Legendre et al. 2009, Bruelheide et al. 2011) (Figure 1A) and contain many endemic plant species (Huang et al. 2012). These ecosystems are very interesting for research as they are similarly diverse to some tropical forests (Corlett 2009) and as they are characterized by typical species of both, tropical and temperate biomes (Hoffmann 2001, Fellowes 2006). Unfortunately, large parts of South-East China were deforested during the Great Leap Forward of the late 1950s, and the region's forests still face a high land-use pressure today. Virtually all low-land forests have been cleared, no primary forests are left, and forests are now restricted to slopes and to commercial monoculture plantations (López-Pujol et al. 2006, Wang et al. 2007).

The BEF-China Project established the worldwide largest tree diversity experiment that is also the only tree diversity experiment in the species-rich subtropics in the bordering region of Zhejiang and Jiangxi provinces, approximately 400 km west of Shanghai (Bruelheide et al. 2011, 2014). They potential natural vegetation is a diverse mixed evergreen broad-leaved forest with approximately similar numbers of deciduous and evergreen tree species, although evergreen species dominate in terms of individual numbers. BEF-China consists of two integral parts, the comparative study plots in the secondary forest of the Gutianshan National Nature Reserve (GNNR) (Figure 2) and the experimental tree plantations (Figure 3). In 2008, 27 plots of 30 m x 30 m were selected in the GNNR along independent gradients of tree species richness and successional age. For every plot a comprehensive set of biotic (e.g. tree species richness, herb layer cover) and abiotic (e.g. elevation, soil properties) environmental variables were recorded. The purpose of the comparative study plots was to provide baseline and reference data for the Experiment which was planted in 2009 and 2010. The Experiment, located near the village of Xingangshan, Jiangxi province, consists of 566 plots of 25.8 m x 25.8 m with 400 tree individuals each. Plots were assigned to the diversity levels 1, 2, 4, 8, 16, and 24 using a total of 42 naturally occurring tree species (Yang et al. 2013, Bruelheide et al. 2014). Since their planting, plots are maintained twice yearly by manual removal of weed species and by replanting of dead tree individuals.

Why ants as a model system?

In (sub)tropical forests ants (Hymenoptera: Formicidae) are an important group of arthropods. Their biomass and abundance is rivaled only by other social insects such as termites (Fittkau and Klinge 1973, Hölldobler and Wilson 1990). Due to their prevalence and functional importance in ecosystems, their relatively moderate diversity, and reasonably resolved taxonomy in comparison to almost all other arthropod taxa, ants are well established, suitable, and frequently used model organisms in biodiversity studies (reviewed in Alonso 2000, Majer et al. 2007, Gerlach et al. 2013). Ants are central contributors to important ecosystem functions such as seed dispersal, soil bioturbation, and soil nutrient enrichment (reviewed in Hölldobler and Wilson 1990, Folgarait 1998, Del-Toro et al. 2012). Moreover, they are found in essentially every trophic level above primary production (Blüthgen et al. 2003, Pfeiffer et al. 2014).

Ants from all trophic levels can have a significant effect on their surroundings. While most ant species are essentially omnivores that opportunistically feed on a broad range of food objects, several ant species are successful predators. The high predation pressure exerted by ants can control the populations of co-occurring arthropods, affect the behavior of the entire arthropod community, and has been hypothesized to be one of the mechanisms that facilitates high diversity in (sub)tropical forests (e.g. Floren et al. 2002, Cerda and Dejean 2011). Other ant species, are cryptic herbivores which dwell in tree canopies can consume substantial parts of the primary production by foraging on liquid food gathered from mutualistic plants or sap-sucking Hemiptera (Blüthgen et al. 2003, Davidson et al. 2003). Especially trophobioses, the tri-trophic interactions between plants, Hemiptera, and ants are regarded as key-stone interactions as they significantly contribute to the fluxes of matter and energy in forest canopies

While numerous case studies have focused on the response of ant communities to environmental conditions and to land use in tropical forests, subtropical forests are less studied. These studies found, in accordance with general predictions, that primary forests were usually more diverse than disturbed forests (e.g. Vasconcelos 1999, Floren and Linsenmair 2005), and found that strong abiotic variables such as elevation also affect ant diversity and community composition (e.g Brühl et al. 1999). However, only few studies have explicitly tested for the effect of tree diversity (e.g. Gunawardene et al. 2012). It has been simply assumed that disturbed or younger forests have fewer tree species, which is not necessarily the case (e.g. Hector et al. 2011). None of these studies have distinguished between the main feeding guilds of ants, exclusive predators and opportunists, despite that following the enemies hypothesis (Root 1973), they may react differently to varying environmental conditions, particularly tree species richness.

Summary of included studies

This dissertation can be divided in three different parts. In the first part (**Chapters II** and **III**), I analyze if and how biotic (e.g. tree species richness, successional age) and abiotic (e.g. elevation, soil properties) environmental variables influence ground-dwelling ant communities in the diverse and heterogeneous subtropical forest of the GNNR. To get a deeper understanding of the relationship between the ant community and the environment, I also assessed if the main trophic groups of ants, exclusive predators and omnivores, are influenced differently. In the second part (**Chapter IV**), I tested if tree diversity influences the structure of trophobiotic networks in the controlled environment of the BEF-China Experiment.

Thus this dissertation addresses the following main questions:

(1) Do ant communities react to tree species richness or to other environmental variables?

(2) Do the main trophic groups of ants, predators and omnivores, react differently?

(3) Does tree diversity influence the structure of a trophobiotic network?

Chapter II addresses question **(1)**. The goal of this study was to investigate how ant communities, as proxies for entire arthropod communities, react to a broad set of environmental gradients and to changing habitat conditions during forest succession after human land use. Therefore, I used a large and well-replicated dataset of ground-dwelling ants that were collected with pitfall traps in all 27 study plots established in the GNNR. The dataset contained 13,441 ant individuals that I identified to 71 species. Ant abundance was not influenced by any environmental variable. As expected, ant species richness decreased with elevation, but was unexpectedly not related to tree species richness or to successional age. An ordination analysis revealed that the composition of ant communities differed considerably between plots, a result that could be best explained by elevation, by successional age, or by variables dependent on succession such as shrub layer cover. Shannon diversity was also negatively related to shrub cover.

While elevation was the only environmental variable significantly related to ant species richness, my results show that even younger secondary forests about 20-40 years old can, independently of tree species richness, recover a species richness of ants that is similar to old-growth forests. Nevertheless, my results also showed ant communities in old-growth forests were markedly different when compared to younger forests, indicating that the recovery of the original arthropod fauna will take considerably longer. My results thus support and confirm the conservation value of secondary subtropical forests, which is especially important in regions like South-East China where no primary forest is left, and human land-use pressure on the remaining secondary forest is predicted to stay high. I could also identify several ant species whose presence is indicative of old-growth forest. Maybe these species can help local conservation authorities to detect and preserve old-growth forest sites that have so far been overlooked.

Chapter III builds up on the results of Chapter II by analyzing the same dataset on a finer scale. In order to address question **(2)**, I grouped the total ant community into the two main trophic groups, exclusive predators and omnivores, based on literature records, studies of stable isotopes, and my own natural-history observations. While omnivores feed on a broad range of food objects such as seeds, extrafloral nectar, honeydew, carrion, as well as hunting for arthropod prey, predators are completely carnivorous. Ecological theory predicts that predators should benefit from increasing habitat heterogeneity that is directly connected to increasing tree species richness and increasing successional age. To test this prediction, I analyzed predator and omnivore ants separately for their response to the same environmental variables as in Chapter II and also included additional environmental variables which describe the tree community on a finer scale, such as tree evenness. Of the total 71 ant species I classified 26 species as exclusive predators and 46 species as omnivores. I showed that the occurrence and species richness of omnivores were positively influenced by increasing soil pH and that omnivore ant evenness is only influenced by variables related to successional age. Predator species richness and evenness were positively related to increasing tree species richness, while leaf functional diversity and shrub layer cover had a negative influence on predator richness.

The direct and positive relationship between tree species richness and predator richness and evenness, indicates the value of diverse forest ecosystems for diverse predator ant communities. While omnivore ants seemed to be more dependent on favorable nesting habitats in less acidic soils, my data suggest that predators might directly benefit from the higher structural heterogeneity in forests with more tree species. Although the exact mechanism behind the tree species richness - predator ant relationship is unknown, more rich forests may support a more even and a more diverse set of prey arthropods and nesting sites. My results also highlight the importance of analyzing different trophic or functional groups inside a given taxon separately when studying BEF-relationships. Only by disentangling the two main trophic ant groups the importance of diverse forests for diverse predator communities and thus for the vulnerable ecosystem processes associated with predation became apparent.

After studying how a species rich ant community is influenced by its environment (**Chapters II** and **III**), I was interested in the question if tree diversity also has, beyond pure correlations with e.g. ant species richness, an effect on trophic interactions involving ants. In forest ecosystems, trees constitute the lowest trophic level and there is experimental evidence from grassland BEF experiments showing that higher plant diversity has a stabilizing effect on trophic interactions. So far, this has not been studied in forest BEF experiments. Forests are fundamentally different from grasslands, and therefore conclusions from grassland experiments should only be transferred to forests with great caution. I address this knowledge gap in **Chapter IV**, where I studied trophobiotic interactions between plants, sap-sucking Hemiptera (mostly aphids), and ants to answer question **(3)**. Trophobioses are an ideal model system for this question as they consist of two essentially different types of interactions. While the interaction between plants and aphids is a form of herbivory and thus antagonistic, the interaction between aphids and ants is mutualistic. In exchange for nutritious honeydew, the ants provide protection to the aphids. In total, I inspected almost 7000 trees in 146 plots that had 1, 2, 4, 8, or 16 tree species each. I found 194 trophobiosis on 15 tree species involving 33 Hemiptera and 18 ant species. My results show that tree diversity increases the density of trophic interactions expressed as the proportion of trees having trophobiosis. Furthermore, I discovered that the generality, and thus the stability, of the mutualistic aphid-ant networks, but not of the antagonistic plant-aphid networks increased with higher levels of tree diversity.

My results are thus in accordance with the prediction that antagonistic interactions and mutualistic networks should react differently to changing environments. In conclusion, I demonstrate that high tree diversity can stabilize mutualistic networks in higher trophic levels, and hence buffer them against habitat change. However, I also showed that the herbivorous plant-aphid network was always complementary which makes the host-specific aphids prone to the negative effects of tree species loss. On the basis of the results of this study, I discuss further research directions which will deepen our understanding of trophobioses and trophic networks in general.

During my extensive field work in subtropical South-East China and during the later in depth study of the local ant fauna, I discovered several formerly unknown species and intriguing phenomena that I partly describe in the third part of this dissertation (**Chapters V**-**VII**). The ground-dwelling ant dataset analyzed in Chapter II and III contained several species that I could not identify to a known species. In order to broaden the knowledge of the understudied Chinese ant fauna, I described one of these species, the dorylomorph army ant *Aenictus gutianshanensis* Staab, 2014. **(Chapter V)**. The description of this new species may also help to resolve the taxonomic confusion regarding a very similar species, *A. camposi* Wheeler & Chapman, 1925. This species is clearly restricted to Sundaland, the Philippines, and the southernmost part of continental South-East Asia, but has frequently been recorded from China. I propose that the Chinese *A. camposi* as they are likely *A. gutianshanensis*.

In **Chapter VI** I report a surprising behavior of an additional *Aenictus* army ant species. Army ants are known to be specialized predators, mostly of other ant species and to reject other food objects. However, I observed an *A. hodgsoni* (Forel, 1901) colony collecting honeydew from aphids. The ants defended their mutualistic partner aggressively and displayed all behavioral elements characteristic for trophobiotic ants. This was only the third ever made observation of trophobiotic army ants, and it shows that even highly specialized predators are capable of establishing mutualistic relationships with trophobionts, and to occasionally feed on plant based resources.

The final chapter of my dissertation, **Chapter VII**, describes a new species of cavity-nesting spider wasp (Pompilidae) with a fascinating nesting behavior. This species closes its nest with a vestibular cell filled with dead ants, a behavior unknown not only in spider wasps but in the entire animal kingdom. When I saw such a nest for the first time, it reminded me of the ossuaries in historical graveyards and thus the ‘Bone-House Wasp’ *Deuteragenia ossarium* Ohl, 2014 was named in allusion to its biology. It is likely that the ant chamber serves a protective function for the wasps’ offspring. Nests of *D. ossarium* are significantly less attacked by parasitoids than nests of co-occurring cavity nesting wasps. I thus hypothesize that chemical cues emanating from the dead ants might either camouflage the nests or repel potential natural enemies.

I included Chapters V-VII in my dissertation for two reasons. First, I would like to demonstrate that even in areas that have been disturbed by humans as severely as the South-East Chinese subtropical forests, many new species with their fascinating life-history await discovery. Second, I want to show that ecological studies can also lead to the discovery of new species and of intriguing natural history observations. My dissertation shows that ecology, natural history and taxonomy are not excluding each other but are interdisciplinary and vividly connected. I would like to encourage ecological graduate students to report on the many phenomena they will discover during their research.

General discussion

To the best of my knowledge, my dissertation is one of the few studies investigating ants in the diverse but threatened subtropical forests of South-East China. In particular, I provide new information on how tree diversity in species-rich forests influences diversity, community composition, and trophic interactions of ants. I was able to show that the total ground-dwelling ant community was not influenced by tree diversity whilst, as revealed at a finer analytical scale, predator ants reacted positively to greater tree diversity. In contrast, the total and the omnivore ant communities reacted most strongly to the abiotic environmental variables elevation and soil pH. Along the multiple biotic and abiotic environmental gradients of my heterogeneous study site in the GNNR there was a clear turnover of ant species that was mostly related to elevation and successional age. While several of my results support and confirm previous studies on ants in forests, other results were less expected and will be discussed in a broader context and greater detail. Furthermore, I was able to show that tree diversity is influences multi-trophic interaction networks of plants, aphids, and ants.

Effects of abiotic processes on South-East Chinese ant communities

What latitude is on a continental scale is (with few exceptions) elevation at local scales: the most important environmental variable for predicting species diversity (Rahbek 1995). Elevation has several effects on a variety of abiotic environmental variables. Most importantly temperature and land area, and thus the availability of energy and habitat area, decrease continuously with increasing elevation (Körner 2007). The diversity of most taxa declines at higher elevation (e.g. McCain 2009, 2010). Previous studies on ants found the same effect which was also confirmed by my data (e.g. Brühl et al. 1999, Sanders et al. 2007). My data also support the hypothesis that declining species richness is accompanied by a profound change in species community composition. Due to the narrow optimal temperature niches of (sub)tropical ant species (e.g. Mezger and Pfeiffer 2010), most ant species are only distributed in a small elevation zone.

In the light of ongoing global change, associated with constantly rising temperatures, up-slope shifts of species communities have been predicted. This has already been proven for European plants (Lenoir et al. 2008) and South-East Asian moths (Chen et al. 2009). The immigration of lowland species to higher elevations will, together with the strongly reduced available habitat area, inevitably lead to species loss: species adapted to present-day high elevation conditions will literally be driven off the mountain. This species loss will have far reaching but, as of yet, unpredictable changes in BEF relationships (see Sundqvist et al. 2013, Rasmann et al. 2014) which will be especially critical in areas like South-East China where mountain ranges are low and where the remaining forests are largely restricted to higher elevations.

Besides elevation, soil pH was the abiotic environmental variable most strongly influencing ground-dwelling ant diversity and community composition. In my study site, the GNNR, soils are highly weathered and eroded (Geißler *et al.* 2012); the pH of the topsoil is commonly lower 4.0, and the high acidity of the soil is also reflected in the diversity and abundance of plant genera such as *Camellia*, *Eurya* and *Symplocos* that are all known to tolerate high concentrations of free Al^{3+} ions which are toxic at low pH (Jansen et al. 2002). Under such harsh conditions soil pH can likely relate to the diversity of ants. However, studies on the effect of acidic soils on ground-dwelling ants are rare. Under less harsh conditions, soil pH only weakly affects ground-dwelling ants (Boulton et al. 2005, Jacquemin et al. 2012); under harsh conditions, in turn, a low pH can affect the physiology of arthropods and reduce their diversity (Lavelle et al. 1995).

At first, I was puzzled by the differing reaction of omnivore and predator ants towards low pH. The species of both groups share the same habitat. While all species classified as predators are restricted to the ground, I observed several of the larger omnivore species foraging in the vegetation. Hence, an explanation for the differing effect of pH is probably not connected to foraging. However, the nesting behavior of both groups differs. In the GNNR, omnivores showed a broad variety of nesting types including dead-wood, arboreal nests, and leaf litter, with several species excavating soil nests. This brings them and in particular their immature stages in direct contact with the acidic soil. In contrast, the majority of the collected predator ant genera nest in the leaf litter (Brown 2000), and leaf litter might buffer the ants' nests against unfavorable soil conditions (compare Noble et al. 1996). I conclude that a consistent and closed litter layer is particularly important for predator ants in South-East China. It is likely that the most common forest habitats outside protected areas, monocultures that are harvested approximately in regular intervals by complete clear-cutting (Wang et al. 2007), affects predators more severely than omnivores. After each cutting cycle, almost no litter remains. This probably favors soil-nesting omnivores that can withstand the unfavorable soil conditions while the predator ant community gets impoverished.

Effects of biotic processes on South-East Chinese ant communities

The diversity of herbivores in forests is directly related to the diversity of potential host plants (e.g. Novotny et al. 2006). As a consequence, (sub)tropical forests intuitively support a tremendous diversity of herbivorous insects (e.g. Erwin 1982, Basset et al. 2012). Following the 'enemies hypothesis' of Root (1973) a high plant diversity, mediated through a high herbivore diversity, directly supports a high diversity of predators. In my dissertation, I found in congruence with Root's hypothesis that the predator part of a diverse ant community is positively related to tree diversity. Most previous evidence for the positive effect of plant diversity on predatory arthropods had been collected in grassland experiments (e.g. Haddad et al. 2009) or low diversity forest ecosystems

(Vehviläinen et al. 2008), and my study helps to extend the enemies hypothesis to diverse natural forests.

In forests, trees account for the majority of the primary production and biomass. Being ecosystem engineers (Jones et al. 1994, 1997), trees influence basically all environmental processes in a forest and tree diversity can have far reaching consequences on all co-occurring organisms including ground-dwelling ants. Ants, as many other insects are, except in the most extreme habitats, mainly dependent on two resources: food and nesting space (Blüthgen and Feldhaar 2010). The richness, heterogeneity and temporal stability of both resources should be positively related to tree diversity, and thus more diverse forests should support a higher diversity of ants.

In an extensive survey of the ecological literature on ants I found that tree diversity was rarely assessed as independent environmental variable (but see Gunawardene et al. 2012, Kone et al. 2012). Usually, studies investigated gradients of disturbance or land-use intensity, and assumed that less disturbed or less intensively used forests have higher tree diversity, a relationship that is not necessarily causal (Hector et al. 2011). The obtained results were contrasting. A lower ant diversity in disturbed habitats (e.g. Vasconcelos 1999, Ribas et al. 2003, Floren and Linsenmair 2005, Bihn et al. 2008, Klimes et al. 2012) was reported in the majority of studies, whilst other studies found no effect of land use (e.g. Belshaw and Bolton 1993, Woodcock et al. 2011). Most studies that report negative land-use intensity - ant diversity relationships investigated arboreal ants (e.g. Ribas et al. 2003, Floren and Linsenmair 2005, Klimes et al. 2012). For ground-dwelling ants, I suspect that even intensively used habitats such as cocoa plantations (Belshaw and Bolton 1993) or twice-logged rainforest (Woodcock et al. 2011) can maintain a high ant diversity, presumably as long as minimum habitat requirements are kept and the forest is not heavily fragmented (see Brühl et al. 2003). It is likely that the different response of arboreal and ground-dwelling ants is related to the natural history of (sub)tropical arboreal ants. Several of these ant species live in close relationship to specific plants (Meyer et al. 2014) making them much more dependent on higher tree diversity than ground-dwelling ants.

The connection between tree diversity and ground-dwelling ant diversity is less intuitive than for arboreal ants and probably mediated via the physical and chemical properties of the leaf-litter layer (e.g. Burghouts et al. 1992, 1998). Higher tree diversity increases the nutrient quality and heterogeneity of the leaf litter (Hättenschwiler 2005), which has a positive feedback on ground-dwelling ants. As already described for the effect of low soil pH, all predator ant species and parts of the omnivore ant species in the GNNR nest and forage in the leaf litter. Higher leaf litter quantity (dos Santos Bastos and Harada 2011), leaf litter heterogeneity (Silva et al. 2011, Queiroz et al. 2013), and leaf litter nutrient concentration (McGlynn et al. 2009) have been shown to increase nest density and species diversity of ground-dwelling ants, in particular of genera that I classified as predators. I expect that the effect of tree diversity is especially pronounced for rare and cryptic predator ant species which, despite being mostly rare, can play important roles in the arthropod community of an ecosystem, and by having distinct and unique trait characteristics (Bihn et al. 2010) maintain predation pressure on specific taxa (e.g. Ito 1998).

Effects of tree diversity on trophic interactions

Predator ants are generally regarded as beneficial insects as they can control populations of pest insects (Philpott and Armbrecht 2006, Cerda and Dejean 2011). By doing so, predator ants and other predatory arthropods, can affect other trophic levels and structure entire food webs (Bruno and Cardinale 2008, Letourneau et al. 2009). My data suggest that the potentially beneficial effect of predator ants on ecosystem functioning is larger in forest stands of higher tree diversity which might indicate a better control of pest-insect outbreaks in more diverse forests. I highlight that the correlation between tree diversity and predator ants was only revealed by dividing the total ant community into trophic groups. Analyzing different functional or trophic groups separately could be a promising approach for future BEF studies and probably help to further understand how species communities and the connected ecosystem functions are influenced by diversity.

The importance to analyze functional groups separately was confirmed by my study on trophobiosis conducted in the BEF-China Experiment. I showed that the generality and thus the stability of the mutualistic aphid-ant but not of the antagonistic plant-aphid networks was positively related to higher tree diversity. My results proved that, following the diversity-stability hypothesis (reviewed in McCann 2000), the effective number of mutualistic aphid partners for ants was larger in plots with higher tree diversity, while the aphids were always host specific and restricted to a low number of host plant species. Thus, my results are in accordance with the prediction of Thebault and Fontaine (2010) who identified that mutualistic and antagonistic networks are generally structured differently. The authors conclude that both types of networks will likely react in distinct ways to changing environmental conditions, which has received support from two comprehensive meta-analyses. For antagonistic networks, Morris et al. (2014) showed that network specialization is independently of the study system and geographical location always high, and that networks are always structured and complementary, pointing at a generally low number of possible hosts for each antagonist species (e.g. herbivores, parasitoids). These findings can be explained by evolutionary processes. In antagonistic interactions, for example between plants and herbivores, there is a steadily ongoing coevolution between host and herbivore species (Ehrlich and Raven 1964). As soon as novel plant resistance traits evolve, the herbivores will evolve counter strategies, which lead to narrow host spectra that might explain the general complementarity of antagonistic networks. For mutualistic networks, in turn, Schleuning et al. (2012) detected a latitudinal trend in network structure. Networks specialization decreased along a gradient from temperate to tropical ecosystems, while network generality increased. Both trends were significantly related to local plant diversity, and my data from a biodiversity experiment support the globally obtained results.

The low generality of the plant-aphid networks points at an important problem of complementary trophic interactions. If a plant species gets extinct, secondary extinctions of herbivores, in my study aphids, are expected. This can have cascading effects on species in higher trophic levels and may ultimately alter the structure of the entire food web (see Dunne and Williams 2009, Cardinale et al. 2012). As mutualistic food webs in habitats with high plant diversity are more generalized they will likely be more buffered against changing environmental conditions and global change (Blüthgen 2010, Barnosky et al. 2012).

Moreover, it seems that tree diversity can, at least in the forests of my study sites, increase the density of trophic interactions. I found that the number of trophobioses was larger in plots of higher tree diversity, a pattern that is consistent with the results of Moreira et al. (2012). In the GNNR, Schuldt et al. (2010) found a similar an increase of leaf-chewing herbivory with tree diversity. This so far limited evidence may point at a more general positive effect of tree diversity on the density of trophic interactions and the stability of food webs (sensu Haddad et al. 2011).

Implications for forest conservation and species discovery in South-East China

Subtropical forests in South-East China are an endangered ecosystem (López-Pujol et al. 2006). The formerly wide-spread mixed evergreen broad-leaved forests and their resident species (Figure 4) are now restricted to secondary forests of varying successional age in protected areas, of which the GNNR is one of the larger fragments. To my surprise, the effect of forest succession on species communities has rarely been studied in the region. The available data for plants (Both et al. 2011, Bruelheide et al. 2011) and spiders (Schuldt et al. 2011, 2012) suggest that successional age has no or only a minor effect on species diversity. However, for all studied taxa, there was a large turnover of species associated with successional age, and old-growth forests had distinctly different species communities. My research on ant communities found the same patterns: diversity of ants and of ant trophic groups was not different between young, approximately 20 years old forests on abandoned agricultural fields, and old-growth forests that were not logged for over 100 years. In summary, my results as well as those from other studies in Gutianshan confirm the conservation value of secondary (sub)tropical forests (Dunn 2004, Edwards et al. 2011, Woodcock et al. 2011). Such forests can be very effective in conserving ants and a large diversity of other forests organisms as long as the remaining forest fragments are not too small (see Brühl et al. 2003).

Nevertheless, my data also support the finding that old-growth forests have a distinct species community that probably resembles that of the original primary forest, and have thus a high conservation value. I was able to identify a set of wide-spread and common ant species which are characteristic for old-growth forest. These species can together with other old-growth forest taxa (see Both et al. 2011, Bruelheide et al. 2011, Schuldt et al. 2012) be used as valuable biological indicators and help local conservation authorities to identify and protect old-growth forest that has so far remained undetected.

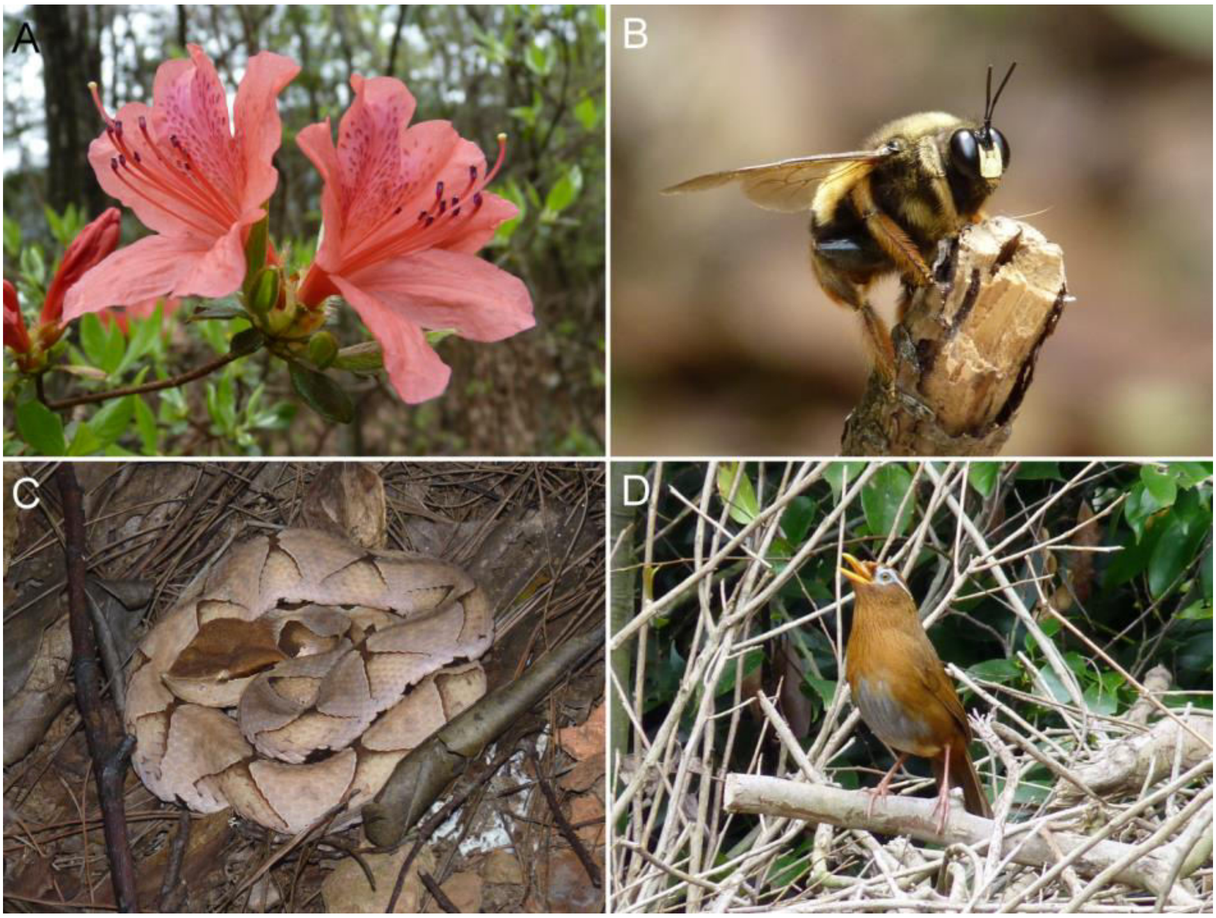


Figure 4 Examples of the manifold species diversity in South-East China. **A)** *Rhododendron simsii* Planch. a common understory shrub in evergreen subtropical forests, **B)** *Xylocopa chinensis* Friese, 1911 a conspicuous carpenter bee that is one of the main pollinators of *Rhododendron* species, **C)** *Deinagkistrodon acutus* (Günther, 1888), a deadly pitviper called '100 step snake' by local people, and **D)** *Garrulax canorus* (Linnaeus, 1758), a popular laughing thrush often seen at forest edges. Photographs: Michael Staab.

By providing accurate species lists of the ant species collected in the GNNR and the BEF-China Experiment my dissertation adds valuable knowledge to the ecology and distribution of Chinese ants. For the over 900 ant species recorded from China, ecological information and recent distribution records are only available for a minority (see Guénard and Dunn 2012 for a checklist of Chinese ants by province). I provide several new ant species and genera records for the provinces of Zhejiang and Jiangxi. Nevertheless, there are still many species of ants and other arthropods awaiting discovery in subtropical South-East China (Guénard et al. 2012). The two species descriptions and my descriptions of natural history phenomena included into my dissertation are just a starting point and highlight the conservation priority of the remaining forests in the region. These forests are still under a high land-use pressure (Miettinen et al. 2011, Hansen et al. 2013), but globally new species discoveries are most likely in the most endangered ecosystems (Joppa et al. 2011, Guénard et al. 2012). As there is evidence that a sixth mass extinction on Earth is already under way (Barnosky et al. 2011), it is very likely that several species in China and elsewhere have gone and will go extinct together with their unique life-history traits before they are known to science. An alarming example for this are several land snail species from a pacific island that were only known to science years after their extinction (Richling and Bouchet 2013).

Fortunately, we are living in the age of biodiversity discovery and never before in the history of science have new species been described at higher rates (Costello et al. 2013). Despite the general opinion and the, in some parts of the scientific community, low valuation of taxonomy and taxonomists, there have been approximately 20,000 new species descriptions per year since 2009, raising the number of formally described species to approximately 1,950,000 (ISSE 2011). Accurate data on species numbers, species communities, and their responses to a changing environment are vitally important for developing effective conservation schemes and for the preservation of critical ecosystem functions that depend to a high degree on biodiversity. Ecologists have the potential to gather the data needed and I hope that my dissertation can contribute somewhat to the understanding of species dynamics and ecosystem functions by providing examples of the effect of tree diversity on plant-insect interactions in a South-East Chinese forest.

References

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, pp 80-88.

Asner GP, Rudel TK, Aide TM, Defries R, Emerson R (2009) A contemporary assessment of change in humid tropical forests. Conservation Biology 23:1386-1395.

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146-1156.

Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, Motta CdS, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104:18555-18560.

Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, Fortelius M, Getz WM, Harte J, Hastings A, Marquet PA, Martinez ND, Mooers A, Roopnarine P, Vermeij G, Williams JW, Gillespie R, Kitzes J, Marshall C, Matzke N, Mindell DP, Revilla E, Smith AB (2012) Approaching a state shift in Earth's biosphere. Nature 486:52-58.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? Nature 471:51-57.

Barthlott W, Mutke J, Rafiqpoor D, Kier G, Kreft H (2005) Global centers of vascular plant diversity. Nova Acta Leopoldina 92:61-83.

Basset Y, Cizek L, Cuenoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Odegaard F, Roslin T, Schmidl J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H-P, Bail J, Barrios H, Bridle JR, Castano-Meneses G, Corbara B, Curletti G, da Rocha WD, de Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, de Oliveira EG, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sorensen L, Leponce M (2012) Arthropod diversity in a tropical forest. Science 338:1481-1484.

Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. Biodiversity and Conservation 2:656-666.

Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91:782-792.

Bihn JH, Verhaagh M, Brändle M, Brandl R (2008) Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biological Conservation 141:733-743.

Blüthgen N (2010) Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. Basic and Applied Ecology 11:185-195.

Blüthgen N, Feldhaar H (2010) Food and shelter: How resources influence ant ecology. In: Lach L, Parr CL, Abbott KL (eds) Ant Ecology. 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 137:426-435.

Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320:1444-1449.

Both S, Fang T, Böhnke M, Bruelheide H, Geissler C, Kühn P, Scholten T, Trogisch S, Erfmeier A (2011) Lack of tree layer control on herb layer characteristics in a subtropical forest, China. Journal of Vegetation Science 22:1120-1131.

Boulton AM, Davies KF, Ward PS (2005) Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: Role of plants, soil, and grazing. Environmental Entomology 34:96-104.

Brown WL (2000) Diversity of ants. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithonian Institution Press, Washington, pp 45–79.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81:25-41.

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, Buscot F, Chen X-Y, Ding B, Durka W, Erfmeier A, Gutknecht JLM, Guo D, Guo L-D, Härdtle W, He J-S, Klein A-M, Kühn P, Liang Y, Liu X, Michalski S, Niklaus PA, Pei K, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang X, Yu M, Zhang S, Zhou H, Fischer M, Ma K, Schmid B (2014) Designing forest biodiversity experiments: General considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5:74-89.

Brühl CA, Eltz T, Linsenmair KE (2003) Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation 12:1371-1389.

Brühl CA, Mohamed V, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15:265-277.

Bruno JF, Cardinale BJ (2008) Cascading effects of predator richness. Frontiers in Ecology and the Environment 6:539-546.

Buckley LB, Davies TJ, Ackerly DD, Kraft NJB, Harrison SP, Anacker BL, Cornell HV, Damschen EI, Grytnes J-A, Hawkins BA, McCain CM, Stephens PR, Wiens JJ (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proceedings of the Royal Society Series B 277:2131-2138.

Burghouts T, Ernsting G, Korthals G, Devries T (1992) Litterfall, leaf litter decomposition abd litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. Philosophical Transactions of the Royal Society Series B 335:407-416.

Burghouts TBA, Van Straalen NM, Bruijnzeel LA (1998) Spatial heterogeneity of element and litter turnover in a Bornean rain forest. Journal of Tropical Ecology 14:477-505.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59-67.

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. American Journal of Botany 98:572-592.

Cerda X, Dejean A (2011) Predation by ants on arthropods and other animals. In: Polidori C (ed) Predation in the Hymenoptera: An evolutionary perspective. TransWorld Research Network, Kerala, pp 39-78.

Chen IC, Shiu HJ, Benedick S, Holloway JD, Cheye VK, Barlow HS, Hill JK, Thomas CD (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America 106:1479-1483.

Corlett R (2009) The ecology of tropical East Asia. Oxford University Press, Oxford.

Costello MJ, May RM, Stork NE (2013) Can we name Earth's species before they go extinct? Science 339:413-416.

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300:969-972.

Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News 17:133-146.

dos Santos Bastos AH, Harada AY (2011) Leaf-litter amount as a factor in the structure of a ponerine ants community (Hymenoptera, Formicidae, Ponerinae) in an eastern Amazonian rainforest, Brazil. Revista Brasileira De Entomologia 55:589-596.

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conservation Biology 18:302-309.

Dunne JA, Williams RJ (2009) Cascading extinctions and community collapse in model food webs. Philosophical Transactions of the Royal Society Series B 364:1711-1723.

Ebeling A, Klein A-M, Tscharntke T (2011) Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic and Applied Ecology 12:300-309.

Edwards DP, Larsen TH, Docherty TDS, Ansell FA, Hsu WW, Derhe MA, Hamer KC, Wilcove DS (2011) Degraded lands worth protecting: The biological importance of Southeast Asia's repeatedly logged forests. Proceedings of the Royal Society Series B 278 (1702):82-90.

Ehrlich PR, Raven PH (1964) Butterflies and plants - A study in coevolution. Evolution 18:586-608.

Erwin TL (1982) Tropical forests - their richness in Coleoptera and other arthropod species. Coleopterists Bulletin 36:74-75.

FAO (2010) Global forest resources assessment 2010. FAO Forestry Paper 163:1-340.

Fellowes JR (2006) Ant (Hymenoptera: Formicidae) genera in southern China: Observations on the Oriental-Palaearctic boundary Myrmecological News 8:239-249.

Fittkau EJ, Klinge H (1973) On biomass and throphic structure of the Central Amazonian rain forest ecosystem. Biotropica 5:2-14.

Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia 131:137-144.

Floren A, Linsenmair KE (2005) The importance of primary tropical rain forest for species diversity: An investigation using arboreal ants as an example. Ecosystems 8:559-567.

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221-1244.

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. Journal of Insect Conservation 17:831-850.

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 107:16732-16737.

Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378-381.

Guénard B, Dunn RR (2012) A checklist of the ants of China. Zootaxa 3558:1-77.

Guénard B, Weiser MD, Dunn RR (2012) Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. Proceedings of the National Academy of Sciences of the United States of America 109:7368-7373.

Gunawardene NR, Majer JD, Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. Myrmecological News 17:81-90.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029-1039.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D (2011) Plant diversity and the stability of foodwebs. Ecology Letters 14:42-46.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850-853.

Hättenschwiler S (2005) Effect of tree species diversity on litter quality and decomposition. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function: Temperate and boreal systems. Springer, Heidelberg, pp 149-164.

Hector A, Philipson C, Saner P, Chamagne J, Dzulkifli D, O'Brien M, Snaddon JL, Ulok P, Weilenmann M, Reynolds G, Godfray HCJ (2011) The Sabah Biodiversity Experiment: A long-term test of the role of tree diversity in restoring tropical forest structure and functioning. Philosophical Transactions of the Royal Society Series B 366:3303-3315.

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. American Naturalist 163:192-211.

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

Hoffmann RS (2001) The Southern boundary of the Palearctic realm in China and adjacent countries. Acta Zoologica Sinica 47:121-131.

Hölldobler B, Wilson EO (1990) The Ants. Belknap Press of Harvard University Press, Cambridge.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105-108.

Huang J, Chen B, Liu C, Lai J, Zhang J, Ma K (2012) Identifying hotspots of endemic woody seed plant diversity in China. Diversity and Distributions 18:673-688.

IISE (2011) State of observed species. International Institute for Species Exploration, Tempe.

Ito F (1998) Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). Insectes Sociaux 45:79-83.

Jacquemin J, Drouet T, Delsinne T, Roisin Y, Leponce M (2012) Soil properties only weakly affect subterranean ant distribution at small spatial scales. Applied Soil Ecology 62:163-169.

Jansen S, Broadley MR, Robbrecht E, Smets E (2002) Aluminum hyperaccumulation in angiosperms: A review of its phylogenetic significance. Botanical Review 68:235-269.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491:444-448.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373-386.

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Joppa LN, Roberts DL, Myers N, Pimm SL (2011) Biodiversity hotspots house most undiscovered plant species. Proceedings of the National Academy of Sciences of the United States of America 108:13171-13176.

Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103-1112.

Kone M, Konate S, Yeo K, Kouassi PK, Linsenmair KE (2012) Changes in ant communities along an age gradient of cocoa cultivation in the Oume region, central Cote d'Ivoire. Entomological Science 15:324-339.

Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22:569-574.

Lavelle P, Chauvel A, Fragoso C (1995) Faunal activity in acid soils. In: Date RA, Grundon NJ, Payment GE, Probert ME (eds) Plant soil interactions at low pH: Principles and management. Kluwer Academic Publishers, Dordrecht, pp 201-211.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF, He F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768-1771.

Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 40:573-592.

López-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: richly varied, endangered, and in need of conservation. Biodiversity and Conservation 15:3983-4026.

Majer JD, Orabi G, Bisevac L (2007) Ant (Hymenoptera: Formicidae) pass the bioindicator scorecard. Myrmecological News 10:69-76.

Mayer VE, Frederickson ME, McKey D, Blatrix R (2014) Current issues in the evolutionary ecology of ant–plant symbioses. New Phytologist 202:749-764.

McCain CM (2009) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346-360.

McCain CM (2010) Global analysis of reptile elevational diversity. Global Ecology and Biogeography 19:541-553.

McCann KS (2000) The diversity-stability debate. Nature 405:228-233.

McGlynn TP, Fawcett RM, Clark DA (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. Biotropica 41:234-240.

Mezger D, Pfeiffer M (2010) Is nest temperature an important factor for niche partitioning by leaf-litter ants (Hymenoptera: Formicidae) in Bornean rain forests? Journal of Tropical Ecology 26:445-455.

Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17:2261-2270.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315-331.

Moreira X, Mooney KA, Zas R, Sampedro L (2012) Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. Proceedings of the Royal Society Series B 279:4464-4472.

Morris RJ, Gripenberg S, Lewis OT, Roslin T (2014) Antagonistic interaction networks are structured independently of latitude and host guild. Ecology Letters 17:340-349.

Noble AD, Zenneck I, Randall PJ (1996) Leaf litter ash alkalinity and neutralisation of soil acidity. Plant and Soil 179:293-302.

Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? Science 313 (5790):1115-1118.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the World's forests. Science 333:988-993.

Petermann JS, Müller CB, Weigelt A, Weisser WW, Schmid B (2010) Effect of plant species loss on aphid–parasitoid communities. Journal of Animal Ecology 79:709-720.

Pfeiffer M, Mezger D, Dyckmans J (2014) Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) – A stable isotope study in four types of Bornean rain forest. Myrmecological News 19:31-41.

Philpott SM, Armbrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecological Entomology 31:369-377.

Primack RB, Corlett R (2005) Tropical Rain Forests: An ecological and biogeographical comparison. Blackwell Publishing, Oxford.

Qian H (2007) Relationships between plant and animal species richness at a regional scale in China. Conservation Biology 21:937-944.

Queiroz ACM, Ribas CR, França FM (2013) Microhabitat characteristics that regulate ant richness patterns: The Importance of leaf litter for epigaeic ants. Sociobiology 60:367-373.

Rahbek C (1995) The elevational gradient of species richness - A uniform pattern. Ecography 18:200-205.

Rasmann S, Pellissier L, Defossez E, Jactel H, Kunstler G (2014) Climate-driven change in plant–insect interactions along elevation gradients. Functional Ecology 28:46-54.

Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecology 28:305-314.

Richling I, Bouchet P (2013) Extinct even before scientific recognition: A remarkable radiation of helicinid snails (Helicinidae) on the Gambier Islands, French Polynesia. Biodiversity and Conservation 22:2433-2468.

Rolland J, Condamine FL, Jiguet F, Morlon H (2014) Faster speciation and reduced extinction in the tropics contribute to the Mammalian latitudinal diversity gradient. PLoS Biology 12:e1001775.

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-120.

Roscher C, Schumacher J, Baade J, Wilcke W, Gleixner G, Weisser WW, Schmid B, Schulze ED (2004) The role of biodiversity for element cycling and trophic interactions: An experimental approach in a grassland community. Basic and Applied Ecology 5:107-121.

Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640-649.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein A-M, Koller R, Koenig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Mueller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schleuning M, Fründ J, Klein A-M, Abrahamczyk S, Alarcon R, Albrecht M, Andersson GKS, Bazarian S, Boehning-Gaese K, Bommarco R, Dalsgaard B, Dehling DM, Gotlieb A, Hagen M, Hickler T, Holzschuh A, Kaiser-Bunbury CN, Kreft H, Morris RJ, Sandel B, Sutherland WJ, Svenning J-C, Tscharntke T, Watts S, Weiner CN, Werner M, Williams NM, Winqvist C, Dormann CF, Blüthgen N (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology 22:1925-1931.

Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou HZ, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology 98:917-926.

Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS ONE 6:e22905.

Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. Biotropica 44:793-800.

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. American Naturalist 152:738-750.

Silva PSD, Bieber AGD, Correa MM, Leal IR (2011) Do leaf-litter attributes affect the richness of leaf-litter ants? Neotropical Entomology 40:542-547.

Sundqvist MK, Sanders NJ, Wardle DA (2013) Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. Annual Review of Ecology, Evolution, and Systematics 44:261-280.

Thebault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853-856.

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843-845.

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720.

Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity and Conservation 8:409-420.

Vehviläinen H, Koricheva J, Ruohomaki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117:935-943.

Wallace AR (1878) Tropical nature, and othe essays. Macmillan and Co., London.

Wang X-H, Kent M, Fang X-F (2007) Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration. Forest Ecology and Management 245:76-87.

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273-309.

Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. Philosophical Transactions of the Royal Society Series B 366:3256-3264.

Yang XF, Bauhus J, Both S, Fang T, Härdle W, Kröber W, Ma KP, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Scholten T, Seidler G, Schmid B, Von Oheimb G, Bruelheide H (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). European Journal of Forest Research 132:593-606.

Zhao SQ, Fang JY, Peng CH, Tang ZY (2006) Relationships between species richness of vascular plants and terrestrial vertebrates in China: Analyses based on data of nature reserves. Diversity and Distributions 12:189-194.

Article overview

(in accordance with the guideline for cumulative dissertations in Sustainability Science [January 2012], in the following termed "the guideline")

Overview of articles included in this cumulative Ph.D. thesis

Title of Ph.D. thesis: "Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest"

Papers included

[1] **Staab M**, Schuldt A, Assmann T, Bruelheide H, Klein AM (under review) Ant community structure during forest succession in a subtropical forest in South-East China. Acta Oecologica.

[2] **Staab M**, Schuldt A, Assmann T, Klein AM (under review) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. Ecological Entomology.

[3] **Staab M**, Blüthgen N, Klein AM (submitted) Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. Oikos.

[4] **Staab M** (2014) A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China. ZooKeys 391: 65-73. doi:10.3897/zookeys.391.7213.

[5] **Staab M** (in press) The first observation of honeydew foraging in army ants since 1933: *Aenictus hodgsoni* Forel, 1901 tending *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) in Southeast China. Asian Myrmecology.

[6] **Staab M**, Ohl M, Zhu CD, Klein AM (under review) A unique nest-protection strategy in a new species of spider wasp. PLoS ONE.

Table 1. Authors’ contributions to the articles and articles publication status (according to §16 of the guideline).

Article #	Short title	Specific contributions of all authors	Author status	Weighting factor	Publication status	Conference contributions
[1]	Ant community structure in a subtropical Chinese forest	**MS**: literature review AS, **MS**: data collection **MS**: data analysis AS, AMK, **MS**: question of the paper AS, AMK, HB, **MS**, TA: research design, writing of the paper	Co-author with predominant contribution	1.0	Under review in *Acta Oecologica* (IF=1.62; submitted on 25.03.2014)	
[2]	Tree diversity promotes predator ants	**MS**: literature review AS, **MS**: data collection **MS**: data analysis AS, AMK, **MS**: question of the paper AS, AMK, **MS**, TA: research design, writing of the paper	Co-author with predominant contribution	1.0	Under review in *Ecological Entomology* (IF=1.95; submitted on 14.11.2013, decided for major revision on 06.03.2014, revision submitted on 17.03.2014)	
[3]	Tree diversity alters the structure of a tri-trophic network	**MS**: literature review **MS**: data collection **MS**: data analysis AMK, **MS**, NB: question of the paper, research design, writing of the paper	Co-author with predominant contribution	1.0	Submitted to *Oikos* (IF=3.32; submitted on 23.04.2014)	GfÖ 2012
[4]	A new species of the *Aenictus wroughtonii* group		**Single authorship**	1.0	Published in *ZooKeys* (IF=0.86)	
[5]	Honeydew collection in army ants		**Single authorship**	1.0	In press in *Asian Myrmecology* (IF=0.25)	
[6]	Unique nest-protection in a new spider wasp	MO, **MS**: literature review, data collection **MS**: data analysis AMK, **MS**: question of the paper, research design AMK, CDZ, MO, **MS**: writing of the paper	Co-author with equal contribution	1.0	Under review in *PLoS ONE* (IF=3.73; submitted on 31.03.2014)	
			Sum:	6.0		

Explanations

Specific contributions of all authors

AMK = Alexandra-Maria Klein, AS = Andreas Schuldt, CDZ = Chao-Dong Zhu, HB = Helge Bruelheide, MO = Michael Ohl, **MS = Michael Staab**, NB = Nico Blüthgen, TA = Thorsten Assmann

Author status

according to §12b of the guideline:

Single author [Allein-Autorenschaft] = Own contribution amounts to 100%.

Co-author with predominant contribution [Überwiegender Anteil] = Own contribution is greater than the individual share of all other co-authors and is at least 35%.

Co-author with equal contribution [Gleicher Anteil] = (1) own contribution is as high as the share of other co-authors, (2) no other co-author has a contribution higher than the own contribution, and (3) the own contribution is at least 25%.

Co-author with important contribution [Wichtiger Anteil] = own contribution is at least 25%, but is insufficient to qualify as single authorship, predominant or equal contribution.

Co-author with small contribution [Geringer Anteil] = own contribution is less than 20%.

Weighting factor

according to §14 of the guideline:

Single author [Allein-Autorenschaft]	1.0
Co-author with predominant contribution [Überwiegender Anteil]	1.0
Co-author with equal contribution [Gleicher Anteil]	1.0
Co-author with important contribution [Wichtiger Anteil]	0.5
Co-author with small contribution [Geringer Anteil]	0

Publication status

IF = ISI Web of Science - Impact factor 2012

Conference contributions *(acronym, society, date, venue, website)*

GfÖ 2012, Annual Meeting of the Ecological Society of Germany, Switzerland and Austria, 10. - 14.09.2012, Lüneburg (Germany), www.gfoe-2012.de. Talk.

Chapter II

Ant community structure during forest succession in a subtropical forest in South-East China

Michael Staab, Andreas Schuldt, Thorsten Assmann, Helge Bruelheide and Alexandra-Maria Klein

Acta Oecologica, under review, submitted on 25.03.2014

A worker of Polyrhachis illaudata *(Walker, 1859) foraging on a* Rhaphiolepis indica *(L.) Lindl. ex Ker shrub in Gutianshan.*

Abstract

Understanding how communities respond to environmental gradients is critical to predict responses of species to changing habitat conditions such as in regenerating secondary habitats after human land use. Ground-dwelling ants collected with pitfall traps in 27 plots in a heterogeneous and diverse subtropical forest were sampled to test if and how a broad set of environmental variables including altitude, successional age and tree species richness influence ant diversity and community composition. In total, 13,441 ant individuals belonging to 71 species were found. Ant abundance was unrelated to all environmental variables. Ant species richness was negatively related to altitude and Shannon diversity decreased with shrub cover. There was a considerable ant species turnover between plots associated to altitude, successional age and variables related to succession such as shrub cover. It is shown that even younger secondary forests can support a high diversity of ants and probably other organisms in subtropical forests. These results confirm the conservation value of secondary subtropical forests, which is critical because subtropical forests have been heavily exploited by human activities globally. Furthermore, a set of ant species identified by our study may serve as indicators of forest regeneration in South-East China and support local conservation planning.

Introduction

Tropical and subtropical forests are across taxa and trophic levels the most diverse terrestrial ecosystems (e.g. Gaston 2000, Primack and Corlett 2005, Basset et al. 2012). However, a steadily increasing human population has together with new agricultural practices caused large-scale exploitation and habitat conversion of these forests (e.g. Gibbs et al. 2010, Hansen et al. 2013). Human disturbance results in a change of species composition, and in general, in a diversity decline of forest organisms (Barlow et al. 2007, Gibson et al. 2011).

As land-use pressure on primary forest is predicted to remain high (e.g. Miettinen et al. 2011, Hansen et al. 2013), regenerating secondary forests will become even more important as habitats for forest organisms. Thus it is critical to assess if such secondary forests can conserve native forest organisms (Dunn 2004), and which environmental conditions explain the diversity and community composition of organisms in secondary forests, particularly in areas like subtropical South-East China where virtually none of the original species-rich primary forests remained after the 1950s Great Leap Forward (López-Pujol et al. 2006).

Ants (Hymenoptera: Formicidae) are ideal target organisms for these questions. As a taxonomic group they have a long history as biological indicators (Alonso 2000, Andersen and Majer 2004), because they are reliably and easily assessable with ecologically interpretable responses to disturbance (Hoffmann and Andersen 2003, Gerlach et al. 2013). By being key-stone organisms as e.g. predators, seed dispersers and partners in countless mutualisms they directly relate to ecosystem processes (reviewed in Folgarait 1998, Del-Toro et al. 2012), especially in tropical and subtropical forests where they are dominant arthropods contributing greatly to total animal abundance and biomass.

Many studies have investigated the responses of ant communities to land use in tropical forests but there are less studies in subtropical forests. As a general trend, ongoing forest recovery and succession tended to increase ant diversity. With increasing recovery time, ant communities resembled more closely old-growth forest communities (e.g. Vasconcelos 1999, Floren and Linsenmair 2005, Bihn et al. 2008).

Ground ant communities in forests are also known to be responsive to a wide range of environmental variables such as altitude (e.g. Brühl et al. 1999), soil moisture (e.g. Kaspari and Weiser 2000), litter cover (e.g. McGlynn et al. 2009) or understory vegetation cover (e.g. Gunawardene et al. 2012). It is therefore crucial to include a wide range of potentially confounding biotic and abiotic variables when studying ground ant communities in diverse and heterogeneous forest ecosystems, particularly when habitats change along environmental gradients such as forest succession. Understanding how individual species and entire communities respond to such gradients will help to better predict responses to future conditions, e.g. along altitudinal gradients in the light of likely altitudinal shifts of species with ongoing global warming (Lenoir et al. 2008).

A further so-far unresolved question is whether producer diversity has an impact on ant diversity, as there is usually a direct relationship between plant and arthropod species (sensu Haddad et al. 2009, Scherber et al. 2010). However, studies correlating tree diversity with ground-dwelling ant diversity are scarce. The few studies conducted so far found no influence of tree diversity on ground-dwelling ants (Donoso et al. 2010, Gunawardene et al. 2012), but are not representative to reject cross group diversity relationships.

We tested if and how the abundance, species richness, diversity (Shannon index) and community composition of ground-dwelling ants are influenced by forest succession and a comprehensive set of environmental variables, including tree diversity and altitude, in a species-rich subtropical forest in South-East China. In particular, we hypothesized (1) that the diversity of the overall ground-dwelling ant community is, as indicated for example by Gunawardene et al. (2012), not or only marginally influenced by tree species richness but instead driven by forest succession or environmental variables; (2) that there is pronounced species turnover along environmental gradients and during forest succession. Finally, we aimed at identifying those ant species that may be characteristic for a certain successional age and could be used as biological indicators for forest succession.

Material and methods

Study site

Our study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°08’-29°17’ N, 118°27’-118°11’ E), Zhejiang Province, in South-East China. Along an altitudinal gradient of 250-1260 m asl, the GNNR protects 8000 ha of a highly-diverse mixed evergreen broad-leaved forest. About half of the naturally occurring tree species are deciduous, but evergreen species numerically dominate in old-growth forest. Common canopy tree species are *Castanopsis eyrei* (Fagaceae), *Cyclobalanopsis glauca* (Fagaceae) and *Schima superba* (Thecaceae) (Legendre et al. 2009, Bruelheide et al. 2011).

As almost everywhere in South-East China (López-Pujol et al. 2006), most of the area in and around the GNNR has been heavily logged or converted to agricultural land. However, slopes steeper than 30° were left relatively undisturbed because they were inappropriate for agriculture. The GNNR is now one of the most prominent semi-natural forest remnants in South-East China. The reserve consists of a mosaic of secondary forests in different successional stages, ranging from <20 years to >80 years recovery time since the last logging activities or the abandonment of former agriculture. Outside the protected areas, forests are dominated by two commercial coniferous plantation species, *Cunninghamia lanceolata* (Cupressaceae) and *Pinus massoniana* (Pinaceae). Apart from anthropogenic disturbance, occasional heavy ice storms are the main drivers of succession (Du et al. 2012). The area is located in a typical subtropical summer monsoon climate. Mean annual precipitation is 1964 mm, with the strongest rainfalls from May to July and a short dry period from October to December (Geissler et al. 2012).

In 2008, 27 plots, 30 m x 30 m, were established in the GNNR as part of the newly founded ‘Biodiversity-Ecosystem Functioning (BEF) China’ Project (Bruelheide et al. 2011, 2014). Plots were selected along gradients of tree species richness and successional age, and were randomly distributed over the entire reserve excluding areas that were inaccessible due to steep slopes >55°. In total, 147 species of trees were recorded, ranging from 25-69 species per plot (Table 1). The classification of successional stages was based on local knowledge on former agriculture and forestry. Five successional stages were distinguished: < 20 yrs (5 plots), < 40 yrs (4), < 60 yrs (5), < 80 yrs (6) and > 80 yrs (7) post disturbance. To accurately measure the age of the secondary forest on a plot and to verify the successional stage, diameter at breast height (dbh) was measured on all trees with dbh > 10 cm and year rings were counted on stem core drillings from a subset. As single large trees are commonly kept in local agricultural and forestry systems to provide shade to crops, and these trees are still present in our plots, successional age was defined as the age of the tree with the fifth largest dbh. This measure corresponded well with successional stages (Bruelheide et al. 2011), except that plots of the youngest successional stage (< 20 yrs), usually had more than five large trees, resulting in an estimated successional age of above 20 years. For more details on the study site, including a map, tree species lists per successional stage and more detailed botanical information see Bruelheide et al. (2011).

Ant sampling

Ground-dwelling ants were collected with pitfall traps. In each plot, we placed four plastic pitfall traps (diameter 8.5 cm, height 15 cm) filled with about 150 ml preserving solution (40 % ethanol, 30 % water, 20 % glycerol, 10 % acetic acid and few drops of dishwashing detergent) at the corners of the central 10 m x 10 m square. We sampled consecutively from 30 March to 2 September 2009 to cover the main growing season. The traps were replaced every second week resulting in ten samples per trap, 40 samples per plot and 1080 samples in total. Ant specimens were identified to genera using Bolton (1994) and, whenever possible, identified to species level with the resources listed in Appendix A. Voucher specimens were deposited at the Institute of Earth and Environmental Sciences, University of Freiburg, Germany.

Environmental variables

During plot setup in 2008 we recorded a comprehensive set of environmental variables (Table 1). This allowed us to test which biotic (e.g. tree species richness) and abiotic (e.g. altitude) environmental variables influence ground-dwelling ant communities. Detailed technical descriptions of data collection methodologies are described in Bruelheide et al. (2011) and Schuldt et al. (2011). Tree species richness per 30 x 30 m plot was defined as the number of species of all woody plants > 1 m height (from here on termed “trees” for simplicity). Tree abundance was the number of those individuals per 30 m x 30 m. Canopy cover was measured as the percentage of the plot area covered by the upper tree layer. Shrub cover was measured as the percentage area covered by the low woody vegetation > 1 m high. Within the central 10 m x 10 m of each plot we measured basal area (m^2), based on all trees > 3 cm diameter, herb species richness, which included all herbs and woody recruit species < 1 m high and herb cover, being the percentage area covered by all plants < 1 m high. Soil moisture was measured gravimetrically as the mean percentage of water in three samples of the top-soil (0-50 cm) from each plot. Soil pH was averaged from nine independent top-soil samples measured in 1 M KCl solution. Temperature per plot was measured continuously every 30 minutes with HOBO data loggers over a year from July 2011 to June 2012 and the mean temperature was calculated.

Table 1. Environmental variables of the 27 study plots in the GNNR. For details on measurements see methods section and Bruelheide et al. (2011).

Variable	Range	Median	Mean ± SD
Altitude (m)	251-903	569	547 ± 168
Basal area[a,b] (m²)	0.2-4.9	2.1	2.2 ± 1.3
Canopy cover[a] (%)	5-50	20	21 ± 12
Successional age (yrs)	21-116	72	67 ± 26
Herb cover[b] (%)	1-80	5	18 ± 22
Herb species richness[b]	25-71	42	43 ± 10
Litter cover[c] (%)	21-92	70	66 ± 15
Litter depth[c] (cm)	0.6 – 3.0	1.6	1.6 ± 0.5
Mean temperature[a] (°C)	15.1-18.0	17.3	17.0 ± 0.8
Shrub cover (%)	5-80	10	22 ± 19
Soil pH	3.4-4.5	3.8	3.9 ± 0.3
Soil moisture[a] (%)	21-55	32	33 ± 7
Tree abundance[a]	207-1233	513	597 ± 290
Tree species richness	25-69	39	42 ± 10
Vegetation cover[c] (%)	2-55	15	17 ± 12
Vegetation height[a,c] (cm)	4-55	24	25 ± 13

[a] variables showing collinearity with other variables that were excluded from statistical analyses.

[b] measured in the central 10 x 10 m area of every plot.

[c] measured on a 1m² square around each pitfall-trap.

To account for trap-specific microhabitat conditions, we recorded litter depth, percent litter cover, percent vegetation cover of the herb layer (hereafter termed ‘vegetation cover’) and vegetation height of the herb layer (hereafter termed ‘vegetation height’) in a 1 m² quadrat centered on each trap during the 2009 sampling time.

Statistical analyses

All analyses were conducted with R 2.15.1 (http://www.r-project.org). Prior to analyses, the ten samples per trap and the four traps per plot were pooled, resulting in a single value per plot for ant abundance and species richness. Likewise, the four values of trap-specific microhabitat conditions were averaged per plot.

Sampling completeness was tested using a plot based species accumulation curve based on 999 permutations and the first-order jackknife (jackknife1) estimator using the R-package 'vegan' (http://www.cran.r-project.org/package=vegan). We also calculated the Shannon index to the power of e to obtain a measure of effective species diversity (Jost 2006). The relationships between the response variables ant abundance, ant species richness, Shannon index and the explanatory environmental variables were tested with linear models. Prior to analyses ant abundance was log-transformed to meet assumptions of normality and variance homogeneity of the data.

We tested for collinearity between all environmental variables (see Table 1). When two variables were correlated with Spearman's $\rho > 0.7$ (Dormann et al. 2013), only one of the variables was retained. The use of Spearman's ρ was appropriate as not all variables (e.g. canopy cover, tree abundance) were normally distributed. Plot altitude was strongly correlated with mean temperature (ρ=-0.85, P<0.01) and soil moisture (ρ=0.74, P<0.01). Thus only altitude was included in the analyses as it is a more comprehensive measure of the interacting environmental conditions. The successional age of forest plots was strongly correlated with tree abundance (ρ=-0.74, P<0.01), basal area (ρ=0.91, P<0.01) and canopy cover (ρ=0.77, P<0.01), so the latter three variables describe patterns caused by successional age and were excluded from analyses. Successional age, however, was not correlated with tree species richness (ρ=0.25, P=0.21) and altitude (ρ=0.22, P=0.28). Vegetation cover surrounding a trap was strongly correlated with vegetation height (ρ=0.86, P<0.01), so vegetation height was omitted from the dataset. Hence, the initial full linear models contained tree species richness, successional age, altitude, soil pH, herb cover, herb species richness, vegetation cover, litter cover and litter depth as explanatory variables. The interaction term between tree species richness and successional age was also included to account for the possible interdependence between tree species richness and successional age. Because the environmental variables were recorded in different units, all environmental variables were standardized prior to modelling to allow comparison of model parameters.

Based on the Akaike Information Criterion corrected for small sample sizes (AICc), full models were simplified in order to receive the most likely parsimonious models (Burnham et al. 2011). If two models were calculated to be equally likely (ΔAICc ≤ 2) the model with the smaller number of variables was chosen. Model residuals were always checked for normality and homoscedasticity.

We used non-metric multidimensional scaling (NMDS) in 'vegan' to analyze ant community composition per plot and species turnover between plots. The NMDS was calculated on the Morisita-Horn index of square root transformed, Wisconsin double standardized abundance data. We selected this similarity index as it is robust against potentially undersampled communities (Wolda 1981). Stable ordination solutions were centered and NMDS axes were rotated until maximum variance in the ordination was explained on the first NMDS axis (Quinn and Keough 2002). To test which environmental variables are most associated with species turnover, we fitted the same set of non-collinear variables that were tested in the linear models post-hoc to the ordination plot. The environmental fit was based on a regression analysis of all variables with the NMDS axes scores (Quinn and Keough 2002). P-values of the regressions were obtained from 999 permutations.

We calculated group-equalized phi coefficients based on ant occurrences to test if particular ant species were associated with particular successional stages (De Cáceres and Legendre 2009). A permutation test (N=999) was used to test for the significance of the correlations between phi coefficients and the successional stages.

Results

Ant diversity and general community patterns

In total, we collected 13,441 ants belonging to nine subfamilies, 31 genera and 71 species (Appendix A). The most species rich subfamilies were Myrmicinae (24 species, 27% individuals; 12 genera), Formicinae (21 species, 28% individuals; 6 genera) and Ponerinae (12 species, 33% individuals; 5 genera). The five most species-rich genera were *Polyrhachis* (Formicinae, 7 species, 433 individuals), *Camponotus* (Formicinae, 6 species, 2979 individuals), *Pachycondyla* (Ponerinae, 6 species, 2966 individuals), *Tetramorium* (Myrmicinae, 5 species, 694 individuals) and *Aenictus* (Aenictinae, 5 species, 1147 individuals).

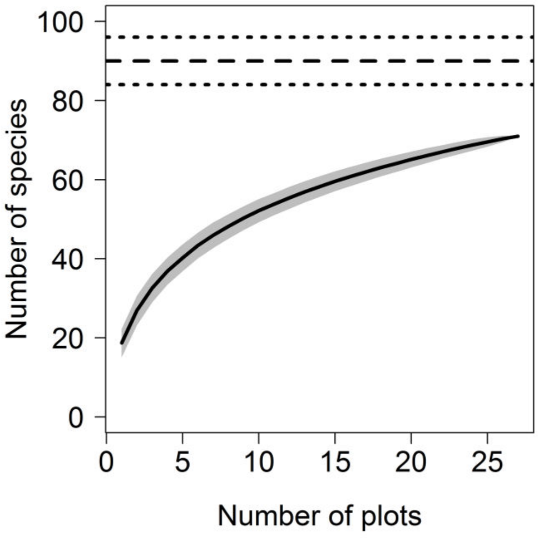


Figure 1. Sample-based species accumulation curve of ant species collected on 27 study plots in subtropical South-East China. Grey shaded area marks 95% CI of the species accumulation curve; dashed line marks the expected number of 90 species based on jackknife1 estimator; dotted lines the SE of the jackknife1 estimation. The ant community was sampled sufficiently well, with 79% (71 species) of the expected total species number having been collected.

The seven most common species accounted for 69% of total ant abundance: *Pachycondyla astuta* (12%), *Camponotus friedae* (11%), *Pheidole noda* (10%), *C. pseudoirritans* (10%), *Leptogenys kitteli* (9%), *Aphaenogaster sp.* CN01 (9%) and *P. luteipes* (9%). Twelve species (17%) were singletons and six species (8%) doubletons. Twenty species (28 %) were only collected in one plot.

The species accumulation curve and the jackknife1 species richness estimator revealed that sampling was not quite complete, with 90 ± 6 (SE) ground-dwelling ant species being expected to occur, of which the 71 collected species represent 79% (Figure 1).

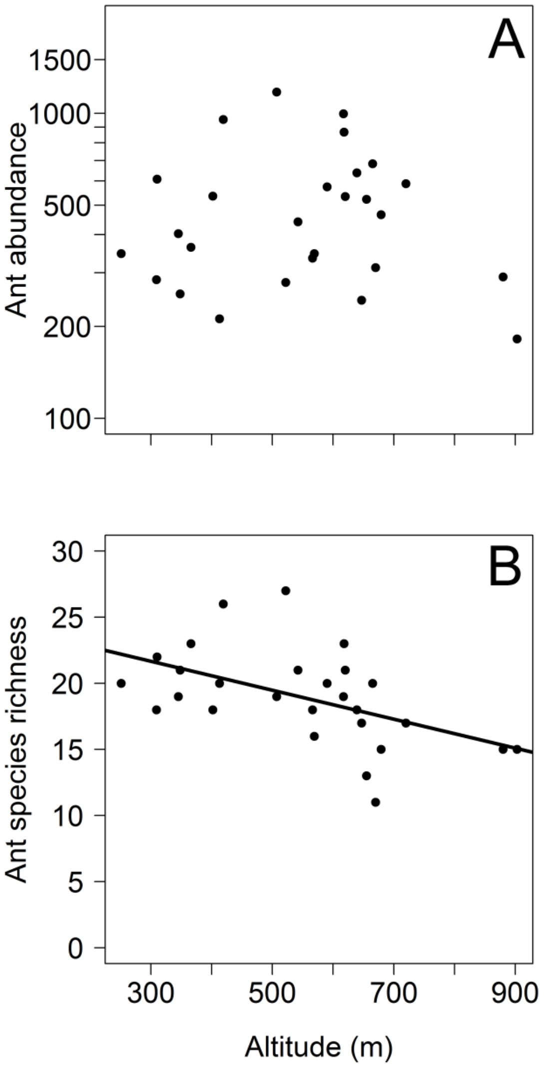


Figure 2. Relationship between plot altitude and the abundance (log-transformed; A) and species richness (B) of the ant community. The regression line shows a significant relationship at P<0.05 (see Table 2).

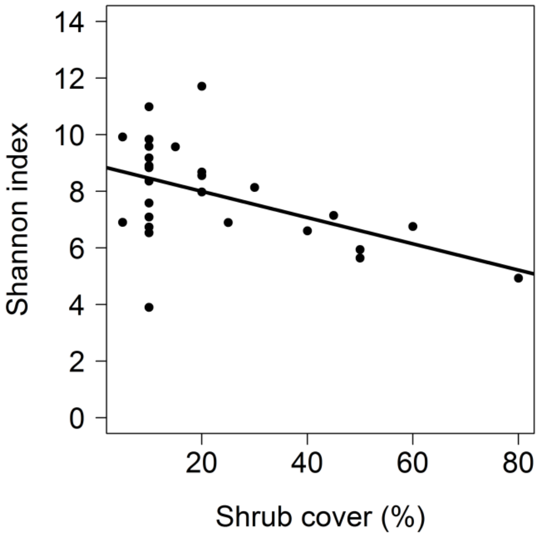


Figure 3. Relationship between the Shannon index of the ant community on a plot and shrub cover. The regression line shows a significant relationship at P<0.05 (see Table 2).

Ant abundance per plot (498 ± 257 SD, range: 182-1175) could not be explained by any of the environmental variables, including plot altitude (Figure 2A). Ant species richness (19 ± 4 SD, range: 11-27) was explained best by a minimal linear model only retaining a negative influence of altitude (estimate=-1.8 ± 0.6, t=-3.0, R^2=0.26, P<0.01; Table 2; Figure 2B) after AICc based model selection. The Shannon index (7.9 ± 1.8 SD, range: 3.9-11.7) decreased with increasing shrub cover (estimate=-0.9 ± 0.3, t=-2.8, R^2=0.24, P<0.01; Table 2; Figure 3) and was unrelated to all other environmental variables. Tree species richness, successional age, soil pH, herb layer cover, herb layer species richness, litter cover, litter depth and vegetation cover were not influencing ant abundance, ant species richness and Shannon index. Non-simplified full linear models for all response variables are shown in Appendix B.

Ant community composition and species turnover

Multivariate analysis displayed a considerable spatial turnover of ant species among the study plots, with clustering according to successional stage (Figure 4). With the exception of two plots from the second oldest successional stage (<80 yrs), ant communities on younger plots were clearly separated from the communities on older plots.

Table 2. Results of the linear models for ant species richness and Shannon index. Shown are standardized model estimate ± SE, t-value, correlation coefficient R² and probability P of the t-statistic. Significant P-values are in bold.

Variable[a,b]	Estimate ± SE	t	R²	P
Ant species richness				
Altitude	-1.8 ± 0.6	-3.0	0.26	**<0.01**
AICc full[c] / minimal[d]: 177.3 / 143.9				
Shannon index				
Shrub cover	-0.9 ± 0.3	-2.8	0.24	**<0.01**
AICc full[c] / minimal[d]: 139.1 / 107.3				

[a] Successional age, herb cover, herb species richness, litter cover, litter depth, shrub cover, soil pH, tree species richness, vegetation cover and the interaction tree species richness:successional age were dropped during model simplification and are not shown.

[b] every variable accounted for one df of the numerator; full models always had 26 df in the denominator.

[c] initial linear model containing the entire set of variables.

[d] reduced minimal most parsimonious linear model.

Table 3. Pearson correlation coefficients, explained variance (R²) and probabilities P (based on a permutation test with N=999) for the relationship between the environmental variables (ordered by decreasing R²) and the axes scores of the first two NMDS axes (NMDS 1, NMDS 2). Significant P-values are indicated in bold.

Variable	NMDS 1	NMDS 2	R²	P
Altitude	-0.87	-0.50	0.84	**<0.01**
Shrub cover	0.15	-0.99	0.47	**<0.01**
Successional age	-0.44	0.90	0.40	**<0.01**
Soil pH	0.75	0.66	0.28	**0.02**
Litter cover	0.62	0.79	0.20	0.07
Herb cover	0.87	0.50	0.20	0.07
Vegetation cover	0.58	-0.82	0.17	0.10
Litter depth	0.79	0.61	0.17	0.11
Tree species richness	-0.16	0.99	0.11	0.23
Herb species richness	0.88	-0.47	0.09	0.33

The post-hoc correlation of the environmental variables with the NMDS axes scores of plots was strongest for altitude ($R^2=0.84$, $P<0.01$; Table 3; Figure 4). Successional age ($R^2=0.40$, $P<0.01$) and shrub cover ($R^2=0.47$, $P<0.01$) were also significantly correlated with the NMDS axes, but with opposing influences. Soil pH ($R^2=0.28$, $P=0.02$), was the only other variable with a significant correlation, being opposite to altitude. Tree species richness and the remaining environmental variables were not related to the spatial turnover.

Only six species had phi values indicating significant association with one or more successional stages. The species *Prenolepis naoroji*, *Tetramorium aptum* and *Tetraponera convexa* were associated with the two youngest stages, *Pachycondyla annamita* with the second youngest stage, and *Camponotus compressus* as well as *C. friedae* were associated with the three oldest successional stages (Table 4; Figure 4).

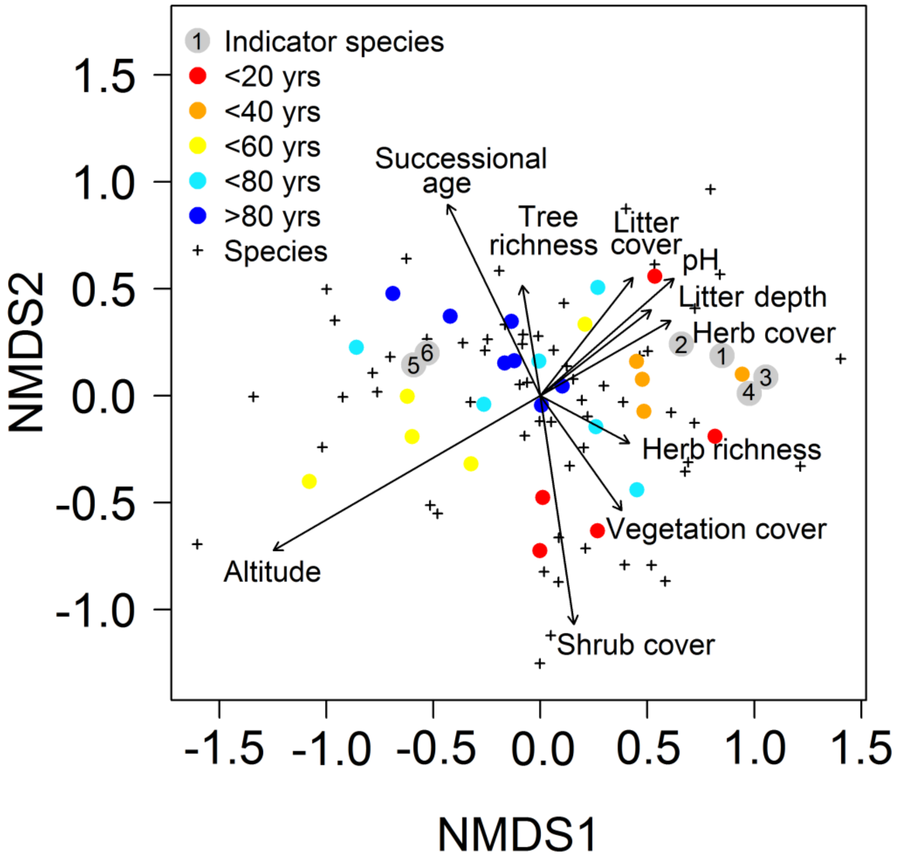


Figure 4. NMDS ordination plot (stress=0.17) based on the Morisita-Horn index of square-root transformed, Wisconsin-double standardized abundance data of all ground-dwelling ant species (N=71, crosses) collected in the 27 study plots. Successional stage of plots is indicated by colored circles. Grey circles indicate location of indicator species (based on Phi coefficents, see Table 4 for further details); 1 = *Prenolepis naoroji*, 2 = *Tetramorium aptum*, 3 = *Tetraponera convexa*, 4 = *Pachycondyla annamita*, 5 = *Camponotus compressus*, 6 = *C. friedae*). Arrows show the environmental variables fitted in a post-hoc procedure with the axes scores. Lengths of arrows indicate the strength of correlations (see Table 3).

Table 4. Ant species that were significantly associated with at least one of the five successional stages (1-5: < 20, < 40, < 60, < 80 and > 80 years old), based on the correlation r^g_Φ of the group-equalized phi coefficient. P-values are based on a permutation test (N=999).

Species	Subfamily	Successional stage	r^g_Φ	P
Prenolepis naoroji	Formicinae	1+2	0.57	**0.02**
Tetramorium aptum	Myrmicinae	1+2	0.57	**0.03**
Tetraponera convexa	Pseudomyrmicinae	1+2	0.59	**0.02**
Pachycondyla annamita	Ponerinae	2	0.74	**<0.01**
Camponotus compressus	Formicinae	3+4+5	0.63	**<0.01**
Camponotus friedae	Formicinae	3+4+5	0.79	**<0.01**

Discussion

Altitude as main driver of ant species richness

Altitude is known to have a direct influence on many abiotic variables, most prominently on mean annual temperature (Körner 2007) that across biomes decreases with about 0.5°C per 100 m increase in altitude. Being ectothermic organisms, ants are sensitive to altitudinal gradients (Hodkinson 2005) and mean annual temperature is globally the best predictor for ant species richness (Jenkins et al. 2011). Regionally, ant species richness generally declines with increasing altitude (e.g. Brühl et al. 1999, Sanders et al. 2007) and the decline is accompanied by a profound change in species composition as most ant species have narrow temperature niches (e.g. Mezger and Pfeiffer 2010, McGlynn et al. 2013).

In the GNNR, altitude provided the best explanation for ant species turnover, even though the altitudinal gradient was rather small (~650 m) and associated with a difference in mean temperature of only 2.9°C. At lower altitudes, species of widespread ant genera such as Camponotus or tropical genera such as Polyrhachis were prevalent. The species richness of these genera was reduced at higher altitudes, where species of typical temperate genera such as Formica and Lasius started to occur, as it is characteristic for the boundary between the Oriental and Palearctic zoogeographic regions in South-East China (Fellowes 2006).

However, mountain ranges in South-East China are not tall by global standards; the highest peak in the GNNR is just above 1250 m. High elevation areas act as islands of temperate climate in a subtropical matrix and have distinct species communities of ants and other organisms (e.g. Bruelheide et al. 2011). Global warming will not only directly cause up-slope migration of animal species (e.g. Lenoir et al. 2008, Chen et al. 2009) but also change forest structure by increasing the mortality of trees adapted to high altitudes and by facilitating the immigration of lowland tree species (Feeley et al. 2011, 2013). Unfortunately, land area strongly decreases at higher elevations, so that up-slope range movements will increase the extinction risk of a species (Körner 2007) and lead to local extinction of species adapted to cooler climates such as temperate ants in subtropical forests.

Responses of ant communities to forest succession

By directly influencing various ecosystem properties including microclimate (Aussenac 2000), trees are ecosystem engineers in forests (Jones et al. 1994), and thus directly influencing ground-dwelling arthropods. Ecological theory predicts an increase of arthropod species richness with increasing plant species richness and habitat complexity, i.e. in forests with increasing tree species richness (Root 1973) and increasing successional age (Guariguata and Ostertag 2001). A more complex or tree species-rich forest will provide more heterogeneous and temporarily more stable resources, and will maintain more diverse consumers across trophic levels.

It is assumed that disturbed or younger secondary forests have reduced tree species richness, which must not be the case (Hector et al. 2011). In our study, young plots were already characterized by high tree species richness, so effects of successional age cannot be explained by differences in tree species richness. While some studies showed that primary forests contained a more species-rich and more distinct ant community than disturbed forests (e.g. Vasconcelos 1999, Floren and Linsenmair 2005, Klimes et al. 2012), a direct positive relationship between ant species richness and tree species richness is shown mostly for canopy ants (e.g. Ribas et al. 2003, Floren and Linsenmair 2005, Klimes et al. 2012). Canopy ant communities are markedly different from ground-dwelling ant communities, both in terms of taxonomic composition and habitat requirements (Floren et al. 2014) and ecological consequences of forest disturbance persist longer in the canopy than on the ground. While, for example, the litter layer on the ground closes after decades, the regrowth of the original canopy structure takes centuries (Primack and Corlett 2005). Thus we assume that canopy ant communities will be influenced more severely and longer lasting by anthropogenic activities such as logging.

Most ground-dwelling ant species nest and forage in or on the leaf litter (Wilson and Hölldobler 2005, Blüthgen and Feldhaar 2010). It appears that, as long as a litter layer is present, a habitat can maintain diversity and abundance of ants and other organisms (Burghouts et al. 1992), independent of anthropogenic disturbance, successional age and tree species richness (Belshaw and Bolton 1993, Woodcock et al. 2011). Our results support the findings by Donoso et al. (2010) and Gunawardene et al. (2012) who concluded that variables other than tree species richness influence ground ant communities. A possible explanation could be that the large morphological heterogeneity of living leafs in the canopy might be less pronounced in the matrix of decaying leaf litter on the forest floor. However, tree identity on a plot might be a proxy for the ant community. In the GNNR the NMDS ordination of the tree community (Bruelheide et al. 2011) was highly similar to the NMDS ordination of the ant community (Procrustes rotation, 999 permutations, Procrustes sum of squares=0.42, R^2=0.58, P<0.01). This correlation probably reflects a structuring role of the identity of the vegetation in higher strata on the ground-dwelling ant communities. While we found no influence of either tree species richness or successional age on ant abundance and measures of diversity, successional age had a profound influence on ant species turnover. Community composition in young successional forests was clearly different from older forests.

During forest succession the vertical and horizontal structure of the forest changes (Guariguata and Ostertag 2001). With increasing succession, for example, tree abundance declines, while canopy cover increases, resulting in a higher light interception which has negative effects on lower vegetation strata through changed microhabitat conditions (Lebrija-Trejos et al. 2011). In the NMDS ordination, shrub cover and successional age had opposing effects on ant species composition. We conclude that environmental conditions such as light availability (McGlynn et al. 2013) or moisture (Kaspari and Weiser 2000) may be mediated by lower vegetation strata and can have strong influences on ant communities. This is probably stronger in younger plots that are more dominated by low vegetation. We are, however, aware that different trophic groups inside the overall ant community may be influenced differently by changes in forest succession and other environmental variables.

Implications for subtropical forest conservation in South-East China

Before anthropogenic disturbance, there was a forest continuum from the equatorial tropical rainforests of Sundaland to the boreal coniferous forests of the Russian Far East where subtropical forests connected tropical and temperate biomes (Corlett 2009). In order to conserve the remaining forest patches subtropical South-East China it is important to understand how biodiversity dynamics follow disturbance. However, only a few studies have in China examined how forest succession influences forest species communities. Both et al. (2011) for herbaceous plants, Bruelheide et al. (2011) for trees and Schuldt et al. (2012) for spiders found that species communities in older successional forests are different from younger forests. Ecological studies on ants are rare in non-tropical Asia (Guénard et al. 2010) and for the over 900 ant species known from China only little ecological information is available (Guénard and Dunn 2012). As shown in our study, regenerating secondary forests can be effective to conserve ants, and this could also apply to other ground-dwelling arthropods, as long as forest fragments are large enough (e.g. Brühl et al. 2003, Bickel et al. 2006).

In the GNNR we found several ant species to be strongly associated with either young or old successional stages. These species are likely restricted in their habitat requirements to the specific conditions provided by young or old growth forests. As all these ant species are widely distributed in the region (Guénard and Dunn 2012) we propose that they might serve as valuable indicators to identify successional age of subtropical forests in South-East China. Thereby, ants could be used together with other taxa such as plants (Both et al. 2011, Bruelheide et al. 2011) or spiders (Schuldt et al. 2012) that have also been shown to comprise several species suitable as indicators of successional age.

Conclusions

Our study showed that altitude explains overall ground-dwelling ant species richness in a heterogeneous secondary subtropical forests, but that succession influences the ant community through changing microhabitat conditions. We demonstrated that secondary forests already 20-40 years after land abandonment attain the ant diversity of old-growth forests and likely support diverse other organisms (see Dunn 2004). Thus, secondary forests are valuable for conservation, especially when primary habitats are almost eradicated as in South-East China. However, at higher altitude even old-growth secondary forest may not be able to protect species from extinction due to up-slope movements. Ant species indicative for old successional stages were identified in our study and could help to preserve forest sites of high conservation concern that have remained unnoticed by researchers and conservation authorities.

Acknowledgments

We thank administration of the Gutianshan National Nature Reserve for generously granting research permissions. Bernhard Schmid, Sabine Both, Keping Ma, Xiaojuan Liu and the entire team of BEF-China are gratefully acknowledged for their support. Jiang Zaigen helped with trap maintenance, Marianne Peters with sorting trap samples, Rabea König and Merle Noack with ant mounting. Data on tree species were provided by Martin Böhnke, data on herb species by Sabine Both and data on microclimate by Katherina Pietsch. Tamar Marcus helped to improve the English. Michael Staab thanks especially Brian Fisher (California Academy of Sciences) and the Ant Course Team for encouraging his interest in ant ecology. Funding by the German Research Foundation (DFG FOR 891, 891/2, KL 1849/6-1) and by the Sino-German Centre for Research Promotion in Beijing (GZ 698, 699 and 785) is gratefully acknowledged.

References

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, pp 80-88.

Andersen AN, Majer JD (2004) Ants show the way Down Under: Invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2:291-298.

Aussenac G (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Annals of Forest Science 57:287-301.

Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, Motta CdS, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104:18555-18560.

Basset Y, Cizek L, Cuenoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Odegaard F, Roslin T, Schmidl J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H-P, Bail J, Barrios H, Bridle JR, Castano-Meneses G, Corbara B, Curletti G, da Rocha WD, de Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, de Oliveira EG, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sorensen L, Leponce M (2012) Arthropod diversity in a tropical forest. Science 338:1481-1484.

Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. Biodiversity and Conservation 2:656-666.

Bickel TO, Brühl CA, Gadau JR, Hölldobler B, Linsenmair K (2006) Influence of habitat fragmentation on the genetic variability in leaf litter ant populations in tropical rainforests of Sabah, Borneo. Biodiversity and Conservation 15:157-175.

Bihn JH, Verhaagh M, Brändle M, Brandl R (2008) Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biological Conservation 141:733-743.

Blüthgen N, Feldhaar H (2010) Food and shelter: How resources influence ant ecology. In: Lach L, Parr CL, Abbott KL (eds) Ant Ecology. Oxford University Press, Oxford, pp 115-136.

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge.

Both S, Fang T, Böhnke M, Bruelheide H, Geissler C, Kühn P, Scholten T, Trogisch S, Erfmeier A (2011) Lack of tree layer control on herb layer characteristics in a subtropical forest, China. Journal of Vegetation Science 22:1120-1131.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81:25-41.

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, Buscot F, Chen X-Y, Ding B, Durka W, Erfmeier A, Gutknecht JLM, Guo D, Guo L-D, Härdtle W, He J-S, Klein A-M, Kühn P, Liang Y, Liu X, Michalski S, Niklaus PA, Pei K, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang X, Yu M, Zhang S, Zhou H, Fischer M, Ma K, Schmid B (2014) Designing forest biodiversity experiments: General considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5:74-89.

Brühl CA, Eltz T, Linsenmair KE (2003) Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation 12:1371-1389.

Brühl CA, Mohamed V, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15:265-277.

Burghouts T, Ernsting G, Korthals G, Devries T (1992) Litterfall, leaf litter decomposition abd litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. Philosophical Transactions of the Royal Society Series B 335:407-416.

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behavioral Ecology Sociobiology 65:23-35.

Chen IC, Shiu HJ, Benedick S, Holloway JD, Cheye VK, Barlow HS, Hill JK, Thomas CD (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America 106:1479-1483.

Corlett R (2009) The ecology of tropical East Asia. Oxford University Press, Oxford.

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. Ecology 90:3566-3574.

Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News 17:133-146.

Donoso DA, Johnston MK, Kaspari M (2010) Trees as templates for tropical litter arthropod diversity. Oecologia 164:201-211.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Marquez JRG, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46.

Du Y, Mi X, Liu X, Ma K (2012) The effects of ice storm on seed rain and seed limitation in an evergreen broad-leaved forest in east China. Acta Oecologica 39:87-93.

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conservation Biology 18:302-309.

Feeley KJ, Hurtado J, Saatchi S, Silman MR, Clark DB (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. Global Change Biology 19:3472-3480.

Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, Malhi Y, Meir P, Salinas Revilla N, Quisiyupanqui MNR, Saatchi S (2011) Upslope migration of Andean trees. Journal of Biogeography 38:783-791.

Fellowes JR (2006) Ant (Hymenoptera: Formicidae) genera in southern China: Observations on the Oriental-Palaearctic boundary. Myrmecological News. 8:239-249.

Floren A, Linsenmair KE (2005) The importance of primary tropical rain forest for species diversity: An investigation using arboreal ants as an example. Ecosystems 8:559-567.

Floren A, Wetzel W, Staab M (2014) The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. Myrmecological News 19:65-74.

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: A review. Biodiversity and Conservation 7:1221-1244.

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220-227.

Geissler C, Kühn P, Böhnke M, Bruelheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. Catena 91:85-93.

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: An overview of available taxonomic groups. Journal of Insect Conservation 17:831-850.

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 107:16732-16737.

Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378-381.

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: Changes in structural and functional characteristics. Forest Ecology and Management 148:185-206.

Guénard B, Dunn RR (2012) A checklist of the ants of China. Zootaxa 3558:1-77.

Guénard B, Weiser MD, Dunn RR (2010) Global generic richness and distribution: New maps of the world of ants with examples of their use in the context of Asia. Asian Myrmecology 3:21-28.

Gunawardene NR, Majer JD, Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. Myrmecological News 17:81-90.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029-1039.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850-853.

Hector A, Philipson C, Saner P, Chamagne J, Dzulkifli D, O'Brien M, Snaddon JL, Ulok P, Weilenmann M, Reynolds G, Godfray HCJ (2011) The Sabah Biodiversity Experiment: A long-term test of the role of tree diversity in restoring tropical forest structure and functioning. Philosophical Transactions of the Royal Society Series B 366:3303-3315.

Hodkinson ID (2005) Terrestrial insects along elevation gradients: Species and community responses to altitude. Biological Reviews 80:489-513.

Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology 28:444-464.

Jenkins CN, Sanders NJ, Andersen AN, Arnan X, Brühl CA, Cerda X, Ellison AM, Fisher BL, Fitzpatrick MC, Gotelli NJ, Gove AD, Guénard B, Lattke JE, Lessard J-P, McGlynn TP, Menke SB, Parr CL, Philpott SM, Vasconcelos HL, Weiser MD, Dunn RR (2011) Global diversity in light of climate change: The case of ants. Diversity and Distributions 17:652-662.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373-386.

Jost L (2006) Entropy and diversity. Oikos 113:363-375.

Kaspari M, Weiser MD (2000) Ant activity along moisture gradients in a neotropical forest. Biotropica 32:703-711.

Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103-1112.

Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22:569-574.

Lebrija-Trejos E, Perez-Garcia EA, Meave JA, Poorter L, Bongers F (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. Journal of Tropical Ecology 27:477-489.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF, He F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768-1771.

López-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: Richly varied, endangered, and in need of conservation. Biodiversity and Conservation 15:3983-4026.

McGlynn TP, Alonso-Rodriguez AM, Weaver M (2013) A test of species-energy theory: Patch occupancy and colony size in tropical rainforest litter-nesting ants. Oikos 122:1357-1361.

McGlynn TP, Fawcett RM, Clark DA (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. Biotropica 41:234-240.

Mezger D, Pfeiffer M (2010) Is nest temperature an important factor for niche partitioning by leaf-litter ants (Hymenoptera: Formicidae) in Bornean rain forests? Journal of Tropical Ecology 26:445-455.

Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17:2261-2270.

Primack RB, Corlett R (2005) Tropical rain forests: An ecological and biogeographical comparison. Blackwell Publishing, Oxford.

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecolology 28:305-314.

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-120.

Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640-649.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein A-M, Koller R, Koenig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Mueller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS ONE 6:e22905.

Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. Biotropica 44:793-800.

Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity and Conservation 8:409-420.

Wilson EO, Hölldobler B (2005) The rise of the ants: A phylogenetic and ecological explanation. Proceedings of the National Academy of Sciences of the United States of America 102:7411-7414.

Wolda H (1981) Similarity indeces, sample size and diversity. Oecologia 50:296-302.

Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia's highly degraded forests: Evidence from leaf-litter ants. Philosophical Transactions of the Royal Society Series B 366:3256-3264.

Appendix

Appendix A. Ant species collected by pitfall traps in the 27 study plots in the GNNR. Shown is the number of individuals per species, the number of plots on which a species was collected, and the abundance rank of the species in the ant community. High resolution photographs of most species can be found on www.antweb.org and www.antbase.net.

Species	Individuals	Plots	Rank	Identification source
Aenictinae				
Aenictus bobaiensis Zhou & Chen, 1999	514	4	9	Jaitrong & Wiwatwitaya 2013
Aenictus fuchuanensis Zhou, 2001	132	6	17	Jaitrong & Yamane 2013
Aenictus henanensis Li & Wang, 2005	4	1	52	Li & Wang 2005
Aenictus hodgsoni Forel, 1901	518	12	8	Jaitrong & Yamane 2011
Aenictus gutianshanensis Staab, 2014	6	1	47	Staab 2014
Cerapachyinae				
Cerapachys sulcinodis Emery, 1898	1	1	71	Brown 1975
Dolichoderinae				
Dolichoderus incisus Xu, 1995	2	2	59	Xu 2001
Liometopum sinense Wheeler, 1921	5	2	50	Del Toro et al. 2009
Technomyrmex antennus Zhou, 2001	11	6	37	Bolton 2007
Technomyrmex obscurior Wheeler, 1928	311	23	12	Bolton 2007
Ectatomminae				
Gnamptogenys panda (Brown, 1948)	42	12	27	Lattke 2004
Formicinae				
Camponotus compressus (Fabricius, 1787)	31	12	30	antweb.org
Camponotus friedae Forel, 1912	1540	15	2	Wang & Wu 1994
Camponotus itoi Forel, 1912	1	1	71	Wang & Wu 1994
Camponotus pseudoirritans Wang, Xiao & Wu, 1989	1277	27	4	Wang & Wu 1994
Camponotus rubidus Wang, Xiao & Wu, 1989	129	5	18	Wang & Wu 1994
Camponotus sp. CN08	1	1	71	
Formica japonica Motschoulsky, 1866	167	5	15	antweb.org
Lasius alienus (Foerster, 1850)	18	1	34	Seifert 1992

Nylanderia sp. CN02	5	4	50	
Nylanderia sp. CN03	7	4	43	
Nylanderia sp. CN05	11	4	37	
Nylanderia sp. CN06	18	10	34	
Polyrhachis cyphonota Xu, 1998	7	2	43	Xu 2002
Polyrhachis dives Smith, 1857	14	2	35	W. Dorow pers. comm.
Polyrhachis illaudata Walker, 1859	335	26	11	W. Dorow pers. comm.
Polyrhachis lamellidens Smith, 1874	44	1	25	Hung 1970
Polyrhachis shixingensis Wu & Wang, 1995	31	1	30	Kohout 2013
Polyrhachis striata Mayr, 1862	1	1	71	antweb.org
Polyrhachis (Myrmhopla) sp. CN04	1	1	71	
Prenolepis naoroji Forel, 1902	23	8	32	Wang & Wu 2007
Prenolepis umbra Zhou & Zheng, 1998	72	10	23	Wang & Wu 2007
Myrmicinae				
Aphaenogaster sp. CN01	1176	23	6	
Aphaenogaster sp. CN02	114	14	19	
Aphaenogaster sp. CN03	77	10	21	
Carebara sp. CN01	1	1	71	
Carebara sp. CN02	2	2	59	
Crematogaster cf. biroi Mayr, 1897	1	1	71	antweb.org
Crematogaster cf rogenhoferi Mayr, 1879	73	11	22	antweb.org
Crematogaster cf. subnuda Mayr, 1879	6	5	47	antweb.org
Crematogaster sp. CN05	6	3	47	
Dilobocondyla fouqueti Santschi, 1910	2	2	59	Bharti & Kumar 2013
Kartidris galos Bolton, 1991	113	2	20	Xu 1999
Myrmecina sauteri Forel, 1912	3	3	53	Zhou et al. 2008
Myrmecina taiwana Terayama, 1985	1	1	71	Zhou et al. 2008
Pheidole noda Smith, 1874	1308	16	3	Zhou & Zheng, 1999
Pheidole sp. CN04	55	2	24	
Pheidologeton melasolenus Zhou & Zheng, 1997	39	14	28	Zhou et al. 2006
Pristomyrmex punctatus Smith, 1860	6	1	47	Wang 2003
Rhoptromyrmex wroughtonii Forel, 1902	151	1	16	Bolton 1986
Rotastruma stenoceps Bolton, 1991	2	2	59	Bolton 1991

Temnothorax sp. CN01	2	1	59	
Tetramorium aptum Bolton, 1977	30	8	31	Bolton 1977
Tetramorium bicarinatum (Nylander, 1846)	1	1	71	Bolton 1977
Tetramorium shensiense Bolton, 1977	505	17	10	Bolton 1977
Tetramorium sp. CN08	7	2	43	
Ponerinae				
Anochetus risii Forel, 1900	9	5	39	Brown 1978
Cryptopone sauteri (Wheeler, 1906)	1	1	71	Zhou 2001
Leptogenys kitteli (Mayr, 1870)	1240	23	5	Xu 2000
Leptogenys laozi Xu, 2000	42	9	27	Xu 2000
Odontomachus monticola Emery, 1892	207	25	14	Brown 1976
Odontomachus sp. CN02	2	2	59	
Pachycondyla annamita (Andre, 1892)	8	5	40	antweb.org
Pachycondyla astuta Smith, 1858	1579	27	1	antweb.org
Pachycondyla chinensis (Emery, 1895)	222	23	13	Xu 1994
Pachycondyla javana (Mayr, 1867)	5	4	50	antweb.org
Pachycondyla luteipes (Mayr, 1862)	1151	25	7	Xu 1994
Pachycondyla (*Brachyponera*) *sp.* CN03	1	1	71	
Proceratiinae				
Discothyrea sauteri Forel, 1912	4	3	52	antweb.org
Pseudomyrmicinae				
Tetraponera allaborans (Walker, 1859)	1	1	71	Xu & Chai 2004
Tetraponera convexa Xu & Chai, 2004	9	4	39	Xu & Chai 2004

References cites in Appendix A

Antbase (2013) Mongolian National University, Ulan Bator, Available at www.antbase.net. Accessed 22. November 2013.

Antweb (2013) California Academy of Science, San Francisco, Available at www.antweb.org. Accessed 16. November 2013.

Bharti H, Kumar R (2013) Five new species of *Dilobocondyla* (Hymenoptera: Formicidae) with a revised key to the known species. Asian Myrmecology 5:29-44.

Bolton B (1977) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Oriental and Indo-Australian regions, and in Australia. Bulletin of the British Museum (Natural History) Entomology 36:67-151.

Bolton B (1986) A taxonomic and biological review of the tetramoriine ant genus *Rhoptromyrmex* (Hymenoptera: Formicidae). Systematic Entomology 11:1-17.

Bolton B (1991) New myrmecine ant genera from the Oriental region (Hymenoptera, Formicidae). Systematic Entomology 16:1-13.

Bolton B (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. Contributions of the American Entomological Institute 35:1-150.

Brown WL (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. Search Agriculture 5:1-115.

Brown WL (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. Studia Entomologia 19:67-171.

Brown WL (1978) Contributions toward a reclassification of the Formicidae.Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section B. Genus *Anochetus* and bibliography. Studia Entomologia 20:549-638.

Del Toro I, Pacheco JA, Mackay WP (2009) Revision of the ant genus *Liometopum* (Hymenoptera: Formicidae). Sociobiology 53:299-369.

Hung ACF (1970) A revision of ants of the subgenus *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae). Oriental Insects 4:1-36.

Jaitrong W, Wiwatwitaya D (2013) Two new species fo the *Aenictus pachycerus* species group (Hymenoptera: Formicidae: Aenictinae) from Southeast Asia. Raffles Bulletin of Zoology 61:97-102.

Jaitrong W, Yamane S (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). Zootaxa 3128:1-46.

Jaitrong W, Yamane S (2013) The *Aenictus ceylonicus* species group (Hymenoptera, Formicidae, Aenictinae) from Southeast Asia. Journal of Hymenoptera Research 31:165-233.

Kohout RJ (2013) A review of the *Polyrhachis xiphias* species-group of the subgenus *Campomyrma* Wheeler (Hymenoptera: Formicidae: Formicinae) Asian Myrmecology 5:21-27.

Lattke JE (2004) A taxonomic revision and phylogenetic analysis of the ant genus *Gnamptogenys* Roger in Southeast Asia and Australasia (Hymenoptera: Formicidae: Ponerinae). University of California Publications in Entomology 122:1-266.

Li SP, Wang YL (2005) A new species of the ant genus *Aenictus* Shuckard (Hymenoptera: Formicidae) from Henan, China. Entomotaxonomia 27:157-160.

Seifert B (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s.str. (Hymenoptera: Formicidae). Abhandlungen und Berichte des Naturkundemuseums Görlitz 66:1-67.

Staab M (2014) A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China. ZooKeys 391:65-73.

Wang CL, Wu J (1994) Second revisionary studies on genus *Camponotus* Mayr of China (Hymenoptera: Formicidae). Journal of Beijing Forestry University (English Edition) 3:23-34.

Wang MS (2003) A monographic revision of the ant genus *Pristomyrmex* (Hymenoptera: Formicidae). Bulletin of the Museum of Comparative Zoology 157:383-542.

Wang W, Wu WL (2007) Two new species of Formicidae (Hymenoptera) from Hubei province, China. Acta Zootaxonomica Sinica 22:721-723.

Xu ZH (1994) A taxonomic study of the ant genus *Brachyponera* Emery in southwestern China (Hymenoptera, Formicidae, Ponerinae). Journal of Southwest Forestry College 14:181-185.

Xu ZH (1999) Systematic studies on the ant genera of *Carebara*, *Rhopalomastix* and *Kartidris* in China (Hymenoptera: Formicidae: Myrmicinae). Acta Biologica Plateau Sinica 14:129-136.

Xu ZH (2000) Five new species and one new record of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) from Yunnan Province, China. Entomologia Sinica 7:117-126.

Xu ZH (2001) Two new species of the ant genus *Dolichoderus* Lund from Yunnan, China. Acta Zootaxonomica Sinica 26:355-360.

Xu ZH (2002) A systematic study of the ant subgenus *Cyrtomyrma* Forel of the genus *Polyrhachis* Smith of China (Hymenoptera: Formicidae). Acta Entomologica Sinica 45:522-530.

Xu ZH, Chai ZQ (2004) Systematic study on the ant genus *Tetraponera* F. Smith (Hymenoptera: Formicidae) of China. Acta Zootaxonomica Sinica 29:63-76.

Zhou SY (2001) Ants of Guangxi. Guangxi Normal University Press, Guilin.

Zhou SY, Huang JJ, Ma LB (2008) Two new species of the ant genus *Myrmecina* (Hymenoptera: Formicidae), with a key to Chinese species. Sociobiology 52:283-291.

Zhou SY, Zhao S, Jia FL (2006) A taxonomic study on the ant genus *Pheidologeton* Mayr (Hymenoptera, Formicidae, Myrmicinae) from China. Acta Zootaxonomica Sinica 31:870-873.

Zhou SY, Zheng ZM (1999) Taxonomic study of the ant genus *Pheidole* Westwood from Guangxi, with descriptions of three new species. Acta Zootaxonomica Sinica 24:83-88.

Appendix B. Results of the full initial linear models for log-transformed ant abundance, ant species richness and Shannon index. Shown are standardized model estimate ± SE, t-value, correlation coefficient R^2 and probability P of the t-statistic. The results are only shown to provide general trends. As environmental variables in a heterogeneous landscape might be non-independent, parameters and P-values of non-reduced full models should be interpreted with great caution. Significant P-values are indicated in bold.

Variable[a]	Estimate ± SE	t	R^2	P
Ant abundance[b]				
Altitude	-0.2 ± 0.2	-0.9	<0.01	0.37
Herb cover	-0.3 ± 0.2	-1.8	0.11	0.09
Herb species richness	-0.3 ± 0.2	-1.4	0.08	0.18
Litter cover	0.05 ± 0.1	0.4	<0.01	0.69
Litter depth	-0.07 ± 0.1	-0.5	0.01	0.62
Shrub cover	0.1 ± 0.2	0.7	<0.01	0.51
Soil pH	0.09 ± 0.2	0.6	0.02	0.58
Successional age	-0.03 ± 0.1	-0.2	0.01	0.82
Tree species richness	-0.09 ± 0.1	-0.3	0.05	0.75
Vegetation cover	0.08 ± 0.1	0.6	0.02	0.58
Successional age: tree species richness	0.05 ± 0.2	0.2	<0.01	0.84
AICc	80.7			
Ant species richness				
Altitude	-2.1 ± 1.1	-1.9	0.26	0.08
Herb cover	-0.6 ± 1.1	-0.6	0.06	0.59
Herb species richness	-0.7 ± 1.1	-0.6	0.02	0.55
Litter cover	-1.1 ± 0.7	-1.6	0.07	0.13
Litter depth	-0.2 ± 0.8	-0.2	<0.01	0.86
Shrub cover	-0.9 ± 1.0	-0.9	0.07	0.39
Soil pH	0.6 ± 0.9	0.6	0.02	0.56
Successional age	-0.9 ± 0.9	<0.1	0.01	0.97
Tree species richness	0.8 ± 0.7	0.3	0.02	0.75
Vegetation cover trap	-0.6 ± 0.9	-0.7	0.02	0.53
Successional age: tree species richness	-0.2 ± 1.4	-0.1	<0.01	0.91

AICc	177.3			
Shannon index				
Altitude	-0.3 ± 0.6	-0.6	0.15	0.57
Herb cover	0.2 ± 0.5	0.3	<0.01	0.78
Herb species richness	0.3 ± 0.5	-0.2	0.03	0.87
Litter cover	-0.4 ± 0.3	-1.2	0.04	0.23
Litter depth	0.04 ± 0.4	0.1	<0.01	0.92
Shrub cover	-1.4 ± 0.5	-2.8	0.21	**0.02**
Soil pH	0.02 ± 0.5	<0.1	<0.01	0.97
Successional age	-0.7 ± 0.4	-0.7	0.01	0.48
Tree species richness	0.6 ± 0.4	-0.2	0.11	0.87
Vegetation cover	-0.2 ± 0.4	0.4	<0.01	0.70
Successional age: tree species richness	0.3 ± 0.7	0.5	<0.01	0.62
AICc	139.1			

[a] every variable accounted for one df of the numerator; full models always had 26 df in the denominator.

[b] log-transformed.

Chapter III

Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest

Michael Staab, Andreas Schuldt, Thorsten Assmann and Alexandra-Maria Klein

Ecological Entomology, revision submitted on 17.03.2014

Workes of the group-hunting predator Leptogenys kitteli *(Mayr, 1870) have captured a large moth caterpillar.*

Abstract

1. Ground-dwelling ants are functionally important arthropods in tropical and subtropical forests, particularly by acting as predators. High predation pressure has been hypothesized to be a mechanism facilitating high diversity across trophic levels.
2. In this study standardized pitfall traps were used in a highly diverse subtropical forest to test if and how ant species richness is related to tree species richness and a comprehensive set of other environmental variables such as successional age, soil properties or elevation.
3. 13,441 ant individuals belonging to 3839 species occurrences and 71 species were collected, of which 26 species were exclusive predators and 45 species were omnivores.
4. Occurrence and species richness of total and omnivore ants were positively related to soil pH. Predator ant occurrence was unrelated to all environmental variables tested.
5. The species richness of predator ants increased with tree species richness but decreased with leaf functional diversity and shrub cover. Elevation negatively influenced only total ant species richness.
6. The evenness of predators increased with tree species richness, whilst the evenness of all ants and omnivore ants was influenced by variables related to successional age.
7. The results highlight the value of diverse forests in maintaining species richness and community evenness of a functionally important predator group. Moreover, the results stress the importance of analyzing trophic groups separately when investigating biodiversity effects.

Introduction

Tropical and subtropical forests are the most diverse terrestrial habitats (e.g. Kier et al. 2005, Basset et al. 2012). In a warm and wet climate mediated by low latitude diverse plant communities have evolved (Kier et al. 2005) that facilitate high diversity of other trophic levels (Hillebrand 2004). In the last decades, these species-rich forests have been exploited worldwide by a growing human population (Gibbs et al. 2010, Miettinen et al. 2011). Forest use, such as logging or agroforestry, reduce the diversity of trees and other forest organisms (Barlow et al. 2007, Gibson et al. 2011). However, it has widely been recognized that biodiversity loss is strongly related to ecosystem change (Cardinale et al. 2011, Hooper et al. 2012) and that high biodiversity enhances ecosystem functioning and services (Duffy 2009, Gamfeldt et al. 2013) e.g. by stabilizing trophic cascades (Scherber et al. 2010).

Ants (Hymenoptera: Formicidae) are the dominant arthropods in terms of biomass and abundance in tropical and subtropical forest ecosystems (Hölldobler and Wilson 1990). They are important keystone organisms contributing to mutualisms, seed dispersal, and soil fertilization (Hölldobler and Wilson 1990, Folgarait 1998, Del-Toro et al. 2012). Moreover, ants are successful and effective predators that influence the populations and community composition of almost all other co-occurring arthropods (e.g. Floren et al. 2002, Berghoff et al. 2003, Philpott and Armbrecht 2006, Cerda and Dejean 2011). Being ubiquitous but moderately diverse and sensitive to changing habitat conditions, ants are well established as indicator organisms for biodiversity studies (Alonso 2000, Majer et al. 2007).

By exerting a high predation pressure, ants can have cascading effects across trophic levels and structure the diversity, abundance, and community composition of other arthropods in the lower levels of a food web (Bruno and Cardinale 2008, Letourneau et al. 2009, Finke and Snyder 2010). Several studies have reported a positive relationship between plant diversity and arthropod diversity across trophic guilds including predators (e.g. Haddad et al. 2009, Scherber et al. 2010, Dinnage et al. 2012). These patterns are mainly attributed to higher habitat heterogeneity in more diverse ecosystems leading to a higher availability of more heterogeneous prey objects caused by more heterogeneous plant resources. In forests, higher tree diversity can also influence the properties and conditions of vegetation structure and leaf litter, thus increasing habitat heterogeneity and the number of available niches such as for nesting sites (e.g. Burghouts et al. 1992, Kaspari 1996, dos Santos Bastos and Harada 2011).

However, to date only a few studies have examined the relationship between the plant diversity and the diversity of ground-dwelling ants in natural and diverse forests. With the exception of Basset et al. (2012) and Gunawardene et al. (2012), which both address plant-ant-diversity correlates in tropical forests, existing studies have either been conducted in agricultural landscapes comparing different land-use types with natural forests (e.g. Belshaw and Bolton 1993, Kone et al. 2012) or addressed arboreal ants (e.g. Floren and Linsenmair 2005, Klimes et al. 2012). None of these studies explicitly focused on the functionally important predator part of the ant community.

This study tests if tree species richness or other biotic and abiotic variables such as elevation, soil and leaf litter properties or vegetation structure influence occurrence, species richness, and evenness of ground-dwelling ants in a highly diverse subtropical forest in South-East China (Bruelheide et al. 2011). To gain deeper insight into the extent to which ant trophic groups are influenced differently by the environmental variables tested, the total ant community was divided into omnivores and exclusive predators and both groups tested separately. Specifically, this study tests the hypothesis that ground-dwelling predator ants are positively influenced by tree species richness as there are probably more heterogeneous prey objects available in forests with higher tree species richness (sensu Haddad et al. 2009, Dinnage et al. 2012). It is also hypothesized that ground-dwelling omnivore ants are less influenced by tree species richness as they do not exclusively depend on prey organisms and feed on a broad variety of food resources that are readily available in the forest studied.

Material and methods

Study site

The study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°14’ N/ 118°07’ E), Zhejiang Province, in South-East China. The GNNR covers 8000 ha of highly-diverse mixed evergreen broad-leaved forest along an elevation gradient from 250-1260 m a.s.l.. Most of the area has been used for agriculture or forestry in the past. Today the reserve consists of a mosaic of secondary forests, ranging from about 20 years to >100 years recovery time since abandonment. About half of the naturally occurring tree species are deciduous, but evergreen species dominate tree individual numbers. Common canopy tree species are the evergreen *Castanopsis eyrei* (Champion ex Benth.) Hutch. (Fagaceae), *Cyclobalanopsis glauca* (Thunberg) Oers. (Fagaceae) and *Schima superba* Gardn. et Champion (Thecaceae) (Bruelheide et al. 2011). The area is located in a typical seasonal subtropical monsoon climate. Mean annual temperature is 15.3 °C and mean annual precipitation 1964 mm (Geißler et al. 2012). Leaf fall phenology has a peak in October and November when deciduous and semi-deciduous tree species shed leaves. For the rest of the year, leaf shed of evergreen species is continuous.

In 2008, the ‘Biodiversity-Ecosystem Functioning China’ Project selected 27 plots with a size of 30 m x 30 m in the GNNR (Bruelheide et al. 2011). Plots were selected based on tree species richness (ranging from 25-69 species per plot) and successional age (ranging from < 20yrs - > 100yrs) and were distributed over the entire reserve with the exception of areas that were inaccessible due to very steep slopes. In total, 147 species of woody plants with a height > 1 m (from here on termed “trees” for simplicity) were identified in the secondary forest within the study plots. Patterns of tree species richness are not driven by rare species and are independent of abiotic variables such as elevation or soil properties (Bruelheide et al. 2011). For more details on site characteristics, a list of tree species, and a map of the study area are given in Bruelheide et al. (2011).

Environmental variables

In order to test for the influences of abiotic (e.g. elevation, soil pH) and biotic (e.g. tree species richness, successional age) habitat characteristics on ground-dwelling ant species richness, a comprehensive set of environmental variables was recorded during plot establishment in 2008. Tree species richness per plot was defined as the species richness of all tree and shrub individuals > 1 m height. The age of the secondary forest growing within a plot was determined by counting growth rings from stem core drillings of the tree with the fifth largest diameter at breast height within the respective plot. This approach was chosen as single large trees were commonly kept in local cropping systems to provide shading and multiple regression analysis revealed that the diameter of the fifth largest tree corresponds with local knowledge on former land use (Bruelheide et al. 2011).

In addition to tree species richness and successional age, canopy cover (%), shrub cover (%), tree abundance, tree basal area, herb layer cover (%), herb layer species richness, and elevation were also measured. To include the effect of soil on ground-dwelling ants, total organic C, total organic N, C/N ratio, soil moisture and pH of the mineral soil were meassured per plot. The proportion of deciduous tree species and the Shannon-based evenness of the tree community were calculated. As further measures of functional aspects of the tree community tree phylogenetic diversity based on genera and family occurrences was calculated using Rao's Q in the R-package ade4 (http://CRAN.R-project.org/package=ade4) and mean leaf functional diversity was obtained from Kröber et al. (2012), who measured morphological and chemical leaf traits.

To account for trap-specific microhabitat conditions, mean litter depth, litter cover (%), vegetation cover of the herb layer (%), and vegetation height of the herb layer in a square of 1 m² centered on each trap was recorded in summer 2009. Mean annual temperature on the plot level was measured continuously with data loggers (HOBO U23 Pro v2, Onset Computer Corporation, Cape Cod, Massachusetts, U.S.A.) from June 2011 to June 2012. Detailed descriptions of the environmental variables used in this study can be found in Bruelheide et al. (2011) and Schuldt et al. (2011). A list of all 23 environmental variables measured is given in Appendix A.

Ant sampling

Ground-dwelling ants were sampled with standardized plastic pitfall traps. Four pitfall traps (diameter 8.5 cm, height 15 cm) were placed at the corners of a central 10 m x 10 m square in each of the 27 plots (summing up to 108 traps in total). Traps were filled with approximately 150 ml preserving solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, few drops of dishwashing detergent). Sampling was conducted from 30-Mar-2009 to 02-Sep-2009 and covered the main vegetation period. Traps were emptied and the preserving solution was replaced every second week, giving ten samples per trap and 1080 samples in total.

Ants were sorted to genera following Bolton (1994) and identified to the species or morphospecies level. Voucher specimens have been deposited at the Institute of Earth and Environmental Sciences, University of Freiburg.

The functional role of ants is closely linked to their trophic niche (Blüthgen et al. 2003, Gibb and Cunningham 2011, Pfeiffer et al. 2014) and it has been shown that the trophic position of ant genera is relatively stable across habitats (Gibb and Cunningham 2011). Based on published literature about their feeding ecology (reviewed in Hölldobler and Wilson 1990, Brown 2000), a recent study on the trophic position of oriental ant genera (Pfeiffer et al. 2014), and personal field observations (M. Staab unpublished data), all ant genera were classified as either “predators” or “omnivores”. While predators such as *Aenictus* or *Odontomachus* rely exclusively on active hunting for arthropod prey, omnivores such as *Camponotus* or *Pheidole* can hunt as well but do not solely depend on prey arthropods as they also commonly scavenge and feed on a wide range of plant-based food objects such as honeydew, extra-floral nectar or seeds (Hölldobler and Wilson 1990, Brown 2000, Blüthgen and Feldhaar 2010, Cerda and Dejean 2011).

All genera of the subfamilies Aenictinae, Cerapachyinae, Ponerinae, and Proceratiinae were classified as predators. Ectatomminae were also classified as predators because in China none of the extra-floral nectary visiting genera of this subfamily occur (Guénard and Dunn 2012). All Myrmicinae genera listed to be predacious or cryptic litter species in Brown (2000) were also treated as predators. The remaining Myrmicinae, all Formicinae, Dolichoderinae, and Pseudomyrmicinae were classified as omnivores.

It should be noted that this genus-based separation approach cannot rule out that single species with wide trophic ranges such as *Pheidole* or *Aphaenogaster* may change their trophic position depending on forest type (Pfeiffer et al. 2014) or soil biogeochemistry (McGlynn et al. 2009a). In some cases, large-scale habitat disturbance might even lead to changes in the trophic position of the entire ant community shortly after the disturbance (Woodcock et al. 2013). Despite this, there are few studies available to date (Gibb and Cunningham 2011, Woodcock et al. 2013, Pfeiffer et al. 2014) that compare ground-dwelling ant communities across habitats using isotope signatures and conclusive results have yet to be obtained. Moreover, the study was only carried out in regenerating secondary forests of a single forest type. Even the youngest plots had not been affected by human activities for around 20 years. Hence a major bias of habitat disturbance and forest type on the trophic position of ant species is not expected.

Statistical analyses

All analyses were conducted with R 2.15.1 (http://www.r-project.org). Prior to analyses, the ten samples per trap were pooled, resulting in four samples per plot. For every sample the total number of species and the number of species occurrences was recorded, i.e. the sum of all species occurrences for the ten original samples taken together. The effectiveness of the sampling was tested with species accumulation curves based on 1000 permutations of individual samples without replacement. First-order jackknife (jack1) estimators were calculated for total ants, predators, and omnivores. Pooled traps were taken as sample units and calculations were performed with the R-package “vegan” (http://CRAN.R-project.org/package=vegan). Evenness was calculated based on the Shannon-index of occurrences for each group.

Table 1. Ant genera collected in pitfall traps within the 27 study plots in the GNNR. Shown are the number of occurrences and the number of species per genus. The overall ant community is split into exclusive predators (P) and omnivores with broad dietary niches (O) based on the reviews of Hölldobler and Wilson (1990), Brown (2000) and own observations.

Subfamily	Genus	Occurrence	Species	Group
Aenictinae	*Aenictus*	51	5	P
Cerapachyinae	*Cerapachys*	1	1	P
Dolichoderinae	*Dolichoderus*	2	1	O
	Liometopum	2	1	O
	Technomyrmex	191	2	O
Ectatomminae	*Gnamptogenys*	26	1	P
Formicinae	*Camponotus*	880	6	O
	Formica	41	1	O
	Lasius	7	1	O
	Nylanderia	34	4	O
	Polyrhachis	272	7	O
	Prenolepis	48	2	O
Myrmicinae	*Aphaenogaster*	485	3	O
	Carebara	3	2	P
	Crematogaster	50	4	O
	Dilobocondyla	2	1	O
	Kartidris	7	1	P
	Myrmecina	4	2	P
	Pheidole	175	2	O
	Pheidologeton	17	1	P
	Pristomyrmex	1	1	O
	Rotastruma	2	1	O
	Rhoptromyrmex	8	1	O
	Temnothorax	2	1	O
	Tetramorium	153	4	O
Ponerinae	*Anochetus*	8	1	P
	Cryptopone	1	1	P
	Leptogenys	238	2	P
	Odontomachus	138	2	P
	Pachycondyla	979	6	P
Proceratiinae	*Discothyrea*	4	1	P
Pseudomyrmicinae	*Tetraponera*	7	2	O

To analyze the relationship between a) ant occurrence, b) ant species richness and c) ant evenness as response variables and environmental variables as explanatory variables linear mixed-effects models were computed using the R-package "nlme" (http://CRAN.R-project.org/package=nlme). Mixed-effect models account for a possible non-independence of the data and for hierarchical data structures by inclusion of random effects (Zuur et al. 2009). In this study, the four pitfall traps were nested inside the respective plot; thus plot identity was treated as random effect to account for plot-specific biotic and abiotic effects.

Before fitting the initial full models, all environmental variables were analyzed for collinearity. If two variables were correlated with $\rho > 0.7$ (Dormann et al. 2013), only one of the correlated variables was used. In total, nine of the 23 variables were excluded. Spearman's ρ was taken as a measure of correlation as not all variables (e.g. canopy cover, vegetation cover around traps) were normally distributed. Correlation coefficients for all pairwise Spearman correlations between environmental variables are shown in Appendix A.

Accordingly, the initial full models were fitted with elevation, herb layer cover, herb layer species richness, leaf functional diversity, shrub cover, soil C/N ratio, soil pH, successional age, proportion of deciduous tree species, tree evenness and tree species richness as variables describing plot characteristics. To account for the microhabitat around a trap inside a plot, litter cover, litter depth and vegetation cover were used. Finally, the interaction between tree species richness and successional age was included to test for possible interdependence of tree species richness and successional age.

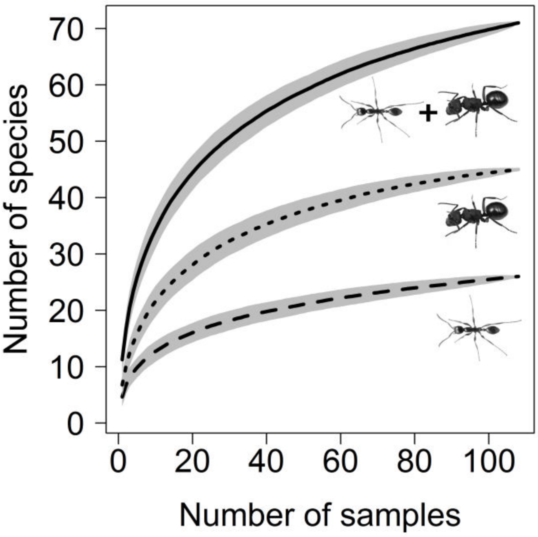


Figure 1. Sample-based species accumulation curves based on 1000 permutations for total ants (solid line), omnivore ants (dotted line), and predator ants (dashed line). Grey shaded areas mark 95% CI. In total, 71 species were collected that belong to 45 omnivore and to 26 predator species. All three groups have been sampled equally, as indicated by the similar shape of each species accumulation curve. Embedded pictures from www.alexanderwild.com, ©Alex Wild, used with permission.

The initial full models were simplified to obtain the most parsimonious explanatory models containing a minimum number of variables. Model simplification was based on Akaike Information Criterion, corrected for small sample sizes (AICc). Using a modified version of the stepAIC function in R (Scherber et al. 2010) all variables whose exclusion improved the model fit by reducing AICc were removed until a minimal best fitting model with the lowest AICc was obtained.

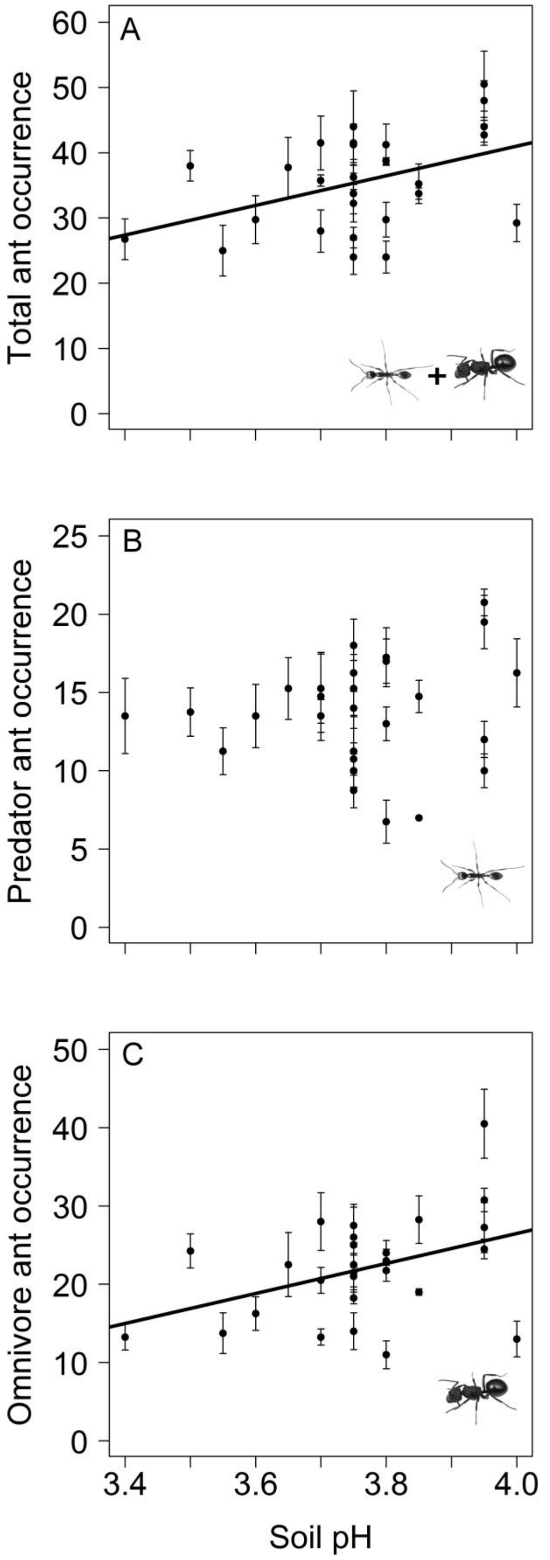


Figure 2. Relationship between soil pH and occurrence of **A)** total ants, **B)** predator ants, and **C)** omnivore ants in the 27 study plots in the GNNR. Shown are means per trap ± 1 SE. Regression lines show significant relationships at P<0.05 (see Table 2). Embedded pictures from www.alexanderwild.com, ©Alex Wild, used with permission.

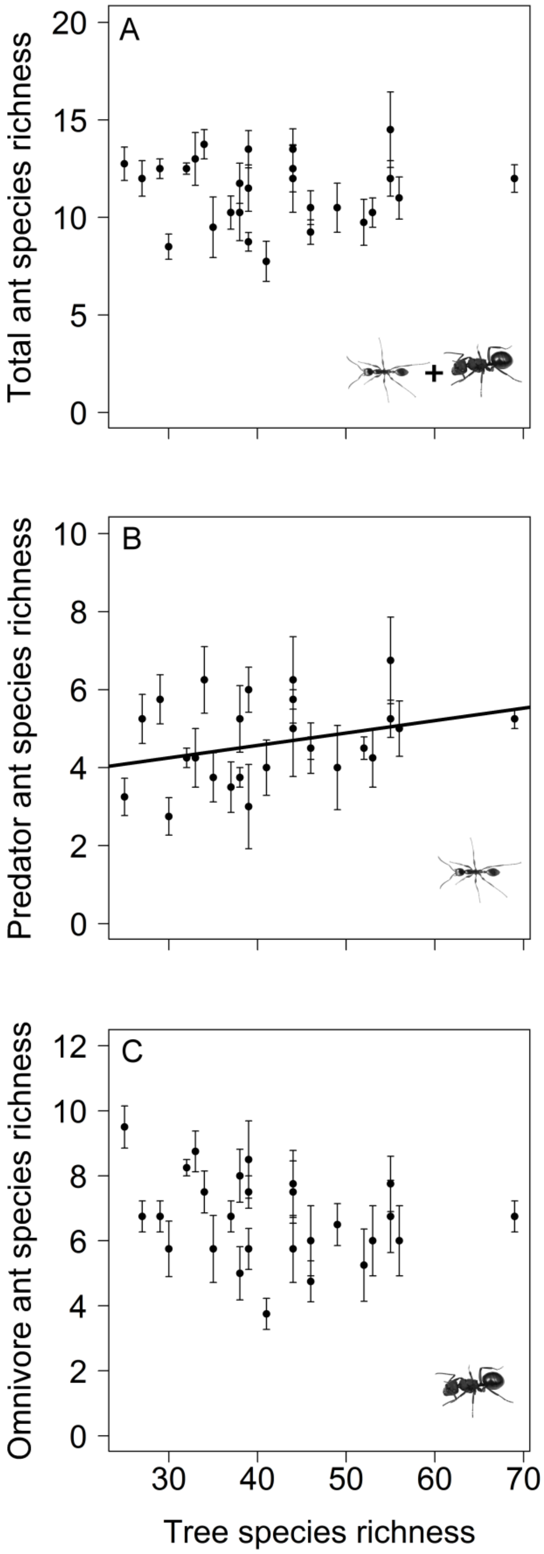


Figure 3. Relationship between tree species richness and species richness of **A)** total ants, **B)** predatory ants, and **C)** omnivore ants along a tree diversity gradient of 27 study plots in the GNNR. Shown are means per trap ± 1 SE. Regression line shows significant relationship at P<0.05 (see Table 2). Embedded pictures from www.alexanderwild.com, ©Alex Wild, used with permission.

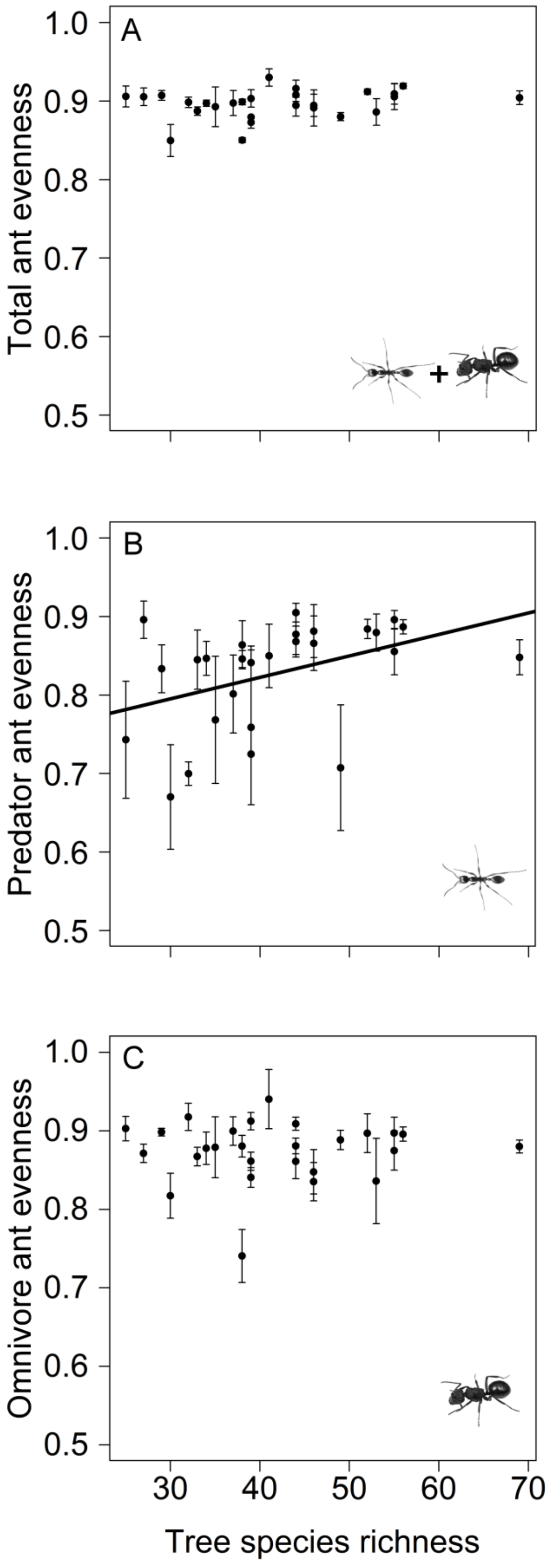


Figure 4. Relationship between tree species richness and evenness based on the Shannon-index of occurrences for **A)** total ants, **B)** predator ants, and **C)** omnivore ants along a tree diversity gradient of 27 study plots in the GNNR. Shown are means per trap ± 1 SE. Regression line shows significant relationship at P<0.05 (see Table 2). Embedded pictures from www.alexanderwild.com, ©Alex Wild, used with permission.

If two models were almost equally likely (ΔAICc ≤ 2) the model with the smaller number of variables was chosen as it was more parsimonious. Residuals of all models were analyzed for normality and homoscedasticity.

Results

A total of 13,441 ant individuals and 3839 ant occurrences belonging to nine subfamilies, 31 genera, and 71 species were sampled. In total, five species were collected with 300 or more occurrences (out of 1080 possible total occurrences) accounting for 53% of all occurrences. Twelve species (17%) occurred as singletons and six species (8%) as doubletons. All species found are native to China (Guénard and Dunn 2012), no invasive ant species occurred. The species accumulation curve indicates that the total ground-dwelling ant community was adequately sampled (Figure 1). Jack1 indicates that 86 (± 4 SE) species are expected to occur, of which 83% were collected.

Twenty-six species (37%) were considered to be exclusive predators and 45 species to be omnivores (see Table 1 for a list of genera and their trophic group). Predator species accounted for 5847 individuals (44%) and 1447 occurrences (38%). Community structure of both groups resembled the structure of the total community: two (three) species of predators (omnivores) accounted for 56% (52%) of occurrences, five (seven) species as singletons and two (four) species as doubletons. Sampling efficiency for predators and omnivores was high. Species accumulation curves were shaped similarly and started to converge to an asymptote (Figure 1). Based on jack1, 79% of the expected predator ant species (expected richness ± SE: 33 ± 3) and 85% of the expected omnivore ant species (53 ± 3) were collected.

Soil pH was the most important environmental variable explaining patterns of total and omnivore ants. The minimal model for the occurrences of these two groups contained only soil pH as a significant and positive explanatory variable (see Table 2 for statistical information; Figure 2A,C). Increasing soil pH also increased the species richness of both groups. In addition, the minimal model for total ant species richness indicated a negative influence of increasing elevation (Table 2). Predator occurrence was not related to soil pH (Figure 2B) or any other environmental variable.

In contrast, patterns of predator ants were best explained by tree species richness and environmental variables related to vegetation structure. Predator species richness and evenness increased significantly with increasing tree species richness (Table 2; Figure 3B; Figure 4B). The model for predator species richness also contained negative effects of leaf functional diversity and shrub cover (Table 2). Likewise, the model for predator evenness indicated a positive influence of herb layer species richness (Table 2) that was, however, not significant. Tree species richness neither influenced occurrence nor species richness nor evenness of total (Figure 3A; Figure 4A) and omnivore ants (Figure 3C; Figure 4C). Total ant evenness was explained by a minimal mixed-effects model containing only a negative influence of shrub cover, while omnivore ant evenness increased with increasing tree evenness but decreased with increasing successional age (Table 2).

Discussion

This study provides novel insights into the influence of tree species richness and other abiotic and biotic environmental variables on an ground-dwelling ant community. This is the first ant study conducted in the highly diverse subtropical forests of South-East China and, in particular, it was shown that species richness and evenness of predator, but not of omnivore ants, increased with tree species richness. So far, most studies showing an increase of predator species richness with increasing plant species richness have been conducted in experimental or low diversity systems and largely neglected species-rich natural habitats (Duffy et al. 2007, Hillebrand and Matthiessen 2009).

The influence of abiotic environmental variables

Elevation strongly influences the abiotic characteristic of a habitat, most prominently due to the decrease in mean annual temperature with increasing elevation. Ant species richness usually declines with increasing elevation (e.g. Brühl et al. 1999, Sanders et al. 2007), a pattern that is supported by a weak but significant decline of total ant species richness found in this study.

Table 2. Results of minimal most parsimonious mixed-effects models for ant occurrence, ant species richness, and ant evenness separated for total ants, predator ants, and omnivore ants. Shown are standardized model estimates ± SE which enables a direct comparison of explanatory variables, t-value, and probabilities *P* of the t-statistics. Variables dropped during model simplification are marked by a dash. Significant P-values are in bold.

	Total ants			Predator ants			Omnivore ants		
Variable[a]	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P
Occurrence									
Soil pH	3.15 ± 1.29	2.45	**0.022**	-	-	-	2.66 ± 1.16	2.30	**0.03**
AICc full[b]/minimal[c]	778.1 / 748.6			623.9 / 607.8			732.8 / 708.7		
Richness									
Elevation	-0.64 ± 0.29	-2.23	**0.035**	-	-	-	-	-	-
Leaf functional diversity	-	-	-	-0.45 ± 0.16	-2.88	**0.009**	-	-	-
Shrub cover	-	-	-	-0.47 ± 0.15	-3.14	**0.005**	-	-	-
Soil pH	0.60 ± 0.29	2.10	**0.047**	-	-	-	0.59 ± 0.23	2.60	**0.015**
Tree species richness	-	-	-	0.41 ± 0.15	2.69	**0.013**	-	-	-
AICc full[b]/minimal[c]	517.8 / 495.6			415.5 / 392.7			461.9 / 440.8		
Evenness									
Herb layer cover	-	-	-	0.021 ± 0.011	1.91	0.069	-	-	-
Shrub cover	-0.008 ± 0.003	-2.49	**0.02**	-	-	-	-	-	-
Successional age	-	-	-	-	-	-	-0.018 ± 0.008	-2.23	**0.035**
Tree evenness	-	-	-	-	-	-	0.022 ± 0.008	2.70	**0.012**
Tree species richness	-	-	-	0.029 ± 0.011	2.64	**0.014**	-	-	-
AICc full[b]/minimal[c]	-450.6 / -471.8			-184.3 / -201.7			-308.8 / -329.3		

[a] herb layer species richness, litter cover, litter depth, soil C/N ratio, proportion of deciduous trees, vegetation cover, and the interaction tree species richness:successional age were dropped during model simplification in all cases and are not shown.

[b] initial mixed-effects model containing the entire set of variables.

[c] reduced minimal most parsimonious mixed-effects model.

Soil properties directly shape plant communities by having far reaching consequences on nutrient availability and cycling (Ashman and Puri 2008). Ground-dwelling ants, in particular ground-nesting species, are in direct contact with the soil and are thus strongly influenced by soil properties. While the ant community was not influenced by soil nutrients, it was strongly influenced by soil pH. Under normal properties (at pH values between 4 and 9), soil acidity has only a marginal influence on ground-dwelling ants (Boulton et al. 2005, Jacquemin et al. 2012). This general pattern might change under extreme properties that can seriously interfere with the physiology of the ants or even be toxic. Soils in the GNNR are derived from granite bedrock which is covered by a weathered and highly eroded saprolite (Geißler et al. 2012). The pH of the top-soil is highly acidic, ranging from pH 3.4 to 4.0. The local plant community mostly consists of genera that are well adapted to low pH e.g. by having a high tolerance to free Aluminum ions (reviewed in Jansen et al. 2002) that reach high concentrations in acidic soils. Under such harsh properties, pH can have a strong negative influence on arthropods (Lavelle et al. 1995, van Straalen and Verhoef 1997), as reflected by the significantly lower occurrence and species richness of total and omnivore ants. It is suspected that these results may partly be explained by the nesting habits of ground-dwelling ants. In the study site, most predator ant genera nest in the leaf litter (Brown 2000, M. Staab unpublished data) where they are less prone to the negative effects of soil acidity as are several litter-nesting omnivores, such as *Pheidole*. While other omnivore genera dwell in dead-wood or build arboreal nests, several genera excavate soil nests, making them susceptible to harsh soil properties such as low pH.

The influence of tree species richness and biotic variables

While the sign of the effect of abiotic environmental variables on ground-dwelling ants matches with general expectations and with patterns reported from other ecosystems, the influences of biotic variables are often interwoven and less clear. On a large scale there is a close association between plant and arthropod species richness in tropical forests across taxonomic groups and trophic levels (Basset et al. 2012). However, there is little information available on how ant species richness, and in particular the richness of predator ants, changes across gradients of tree species richness at more local scales. Usually, primary forests have a more species-rich ant community than disturbed forests (e.g. Olson 1991, Floren and Linsenmair 2005, Klimes et al. 2012), but most of these studies have focused on arboreal ants and did not specifically analyze tree species richness gradients. Arboreal ants are profoundly different from ground-dwelling ants (e.g. Floren et al. 2014), compromising mostly omnivore canopy specialists that are more likely to benefit from higher structural heterogeneity caused by higher tree species richness (Ribas et al. 2003, Klimes et al. 2012). For ground-dwelling ants, in contrast, even degraded forests can maintain high ant species richness (e.g. Belshaw and Bolto 1993, Woodcock et al. 2011). This supports the findings by Gunawardene et al. (2012) who conclude from a study in a primary forest that variables other than tree species richness influence ground-dwelling ant richness.

For ground-dwelling predator ants the 'enemies hypothesis' (Root 1973) suggests an increase of predator species richness with increasing plant species richness. It is predicted that higher plant richness will provide more heterogeneous resources for herbivores and decomposers, both in space and time, and thus support a more diverse community of prey arthropods that would promote a more diverse and more even set of predators. Most evidence for this hypothesis so far comes either from low diversity forest ecosystems (e.g. Vehviläinen et al. 2008) or from grassland experiments (e.g. Haddad et al. 2009, 2011, Dinnage et al. 2012). Root's hypothesis also implies an increase of omnivore ant species richness, and thus also of total ant species richness with increasing tree species richness, which was not found. Omnivore ants have broad trophic niches and do not depend exclusively on prey organisms (Blüthgen and Feldhaar 2010).

Trees have a direct influence on the leaf-litter matrix (Burghouts et al. 1992). Higher leaf-litter cover (e.g. McGlynn et al. 2009b), leaf-litter quantity (e.g. dos Santos Bastos and Harada 2011), moisture (e.g. Levings and Windsor 1984), and litter leaf morphology (Silva et al. 2011) are known to positively influence ants by increasing nesting resources. The availability of diverse nest sites is a prime factor explaining ant species richness (Benson and Harada 1988, Kaspari 1996, Blüthgen and Feldhaar 2010). As discussed above, predator ants are mainly nesting in leaf litter and are therefore more likely than omnivore ants to benefit from increased leaf-litter heterogeneity and quantity (dos Santos Bastos and Harada 2011). Whilst measures of litter attributes such as cover and depth had no influence on predator ants, tree species richness increased the species richness and evenness of this group, suggesting a direct positive effect of trees on predators only. This effect was invariant of the community evenness of trees that had a positive influence only on omnivore species that are more dependent on plant-based resources (Blüthgen and Feldhaar 2010). In contrast to the findings of Silva et al. (2011), functional attributes of leaves had a negative influence on predator ant richness. In the present study, tree species richness and leaf functional diversity were positively correlated (see Appendix A). Living leaves are more variable than dead and decaying leaves in the homogenous litter matrix. Unfortunately, information on the functional diversity of the leaf litter was not available and it seems unlikely that this statistical correlation has a biological meaning.

The positive influence of tree species richness on predator ants was independent of successional age, and thus not driven by forest succession. Usually, successional age and tree species richness are directly positively correlated which was not the case in this study. Nevertheless, successional age strongly influences habitat properties in regenerating forests (Guariguata and Ostertag 2001), and has cascading effects on arthropod communities, such as shifting the foraging preferences of the ant community (Bihn et al. 2008). Successional age only had a negative influence on omnivore ant evenness. However, the successional age of a plot had direct consequences for a variety of environmental variables that relate to the structure of the vegetation such as tree abundance or the cover of different vegetation layers.

Shrub cover was the variable with the strongest negative influence on predator species richness, and the evenness of the total ant community also decreased with shrub cover. Shading levels of the forest floor relate closely to the cover of the shrub and canopy layers. A dense shrub layer might be particularly effective in shading as it is, unlike the canopy, not steadily moved by wind. The cover of lower vegetation strata is known to influence ground-dwelling ant species richness (e.g. Gunawardene et al. 2012) probably by mediating changes in microclimatic conditions on the forest floor. Increased shading has been shown to have an impact on ant colonies, both positively in a tropical forest (Armbrecht et al. 2005) and negatively in a temperate forest (Higgins and Lindgren 2012). While shade decreases the amount of sunlight reaching the ground and thus the energy availability, shading also lowers desiccation risk due to higher moisture availability. Ants are sensitive to both effects (e.g. Levings and Windsor 1984, McGlynn et al. 2013). In the GNNR the hottest time of the year coincides with the period of highest precipitation (Geißler et al. 2012) making desiccation risk less likely to have negative effects on ants. Consequently, following the species-energy hypothesis (Wright 1983), a dense shrub layer might reduce energy availability with effects especially visible on organisms in higher trophic levels such as predator ants.

Consequences for trophic interactions

The prime ecosystem function of predator ants, exhibiting a high predation pressure on other arthropods (e.g. Floren et al. 2002, Berghoff et al. 2003, Cerda and Dejean 2011) may be enhanced in more tree species-rich forests. But, interestingly, within the same plots Schuldt et al. (2011) found that the species richness and abundance of ground-dwelling spiders was negatively related to trees species richness. Spiders are prevalent generalist predators that frequently exhibit intraguild competition with ants (Sanders and Platner 2007, Sanders et al. 2011). Both taxa also predate on each other. There is likely an effect of predator ants on spiders causing these divergent correlations with tree species richness. In diverse natural forests it is largely unknown how interactions between different predator taxa relate to overall predation and the control of herbivorous insects. Such biotic interactions are probably crucial for maintaining a high diversity. For example, in the GNNR, herbivore damage on tree saplings increased with tree species richness (Schuldt et al. 2010), which does not correspond well to the pattern found for predator ants while supporting the pattern found for spiders. In a different study, ants and spiders had a positive interactive effect on herbivore control (Nahas et al. 2012) and were thus complementing the ecosystem service predation. These results highlight the complexity of trophic interactions in species-rich forests and show that more research is needed to further disentangle the influence of tree species richness and other environmental variables on different predator taxa. Ideally, future approaches should also address the complex biotic interactions between predator groups.

Limitations and conclusions

Pitfall traps were used to collect ground-dwelling ants with a high number of replicates over the main growing season in a subtropical forest. The collection method has been claimed to bias arthropod sampling towards mobile and large species, and to systematically underrepresent smaller, less mobile species (e.g. Olson 1991, Ivanov and Keiper 2009). Various studies have shown that Winkler extraction is more effective to collect leaf-litter ants than pitfall traps and is especially effective to collect rarely found species (e.g. Bestelmeyer et al. 2000, Parr and Chown 2001). For future studies on predator ants the use of a broad set of collection methods, including pitfall traps and Winkler extraction is recommended, to rule out the particular biases of single collection methods. In the present study, pitfall traps have probably resulted in an underrepresentation of small cryptic litter-dwelling ants such as *Hypoponera* which are mostly predators. Due to their small body size these species might react sensitively to changes in environmental conditions and could be positively influenced by tree species richness, strengthening the main result of the study.

Ground-dwelling predatory arthropods influence the entire ground-dwelling arthropod community and can even influence food webs in other strata (Pringle and Fox-Dobbs 2008). The present study revealed effects of tree species richness on predator but not on omnivore ant species. The results therefore highlight the importance of considering functional and trophic groups separately when analyzing biodiversity. Only by disentangling the influence of tree diversity on the two main functional groups of the ground-dwelling ant community it was shown that diverse forests maintain species-rich predator ant communities and thus the ecosystem functions dependent on predation (see Bruno and Cardinale 2008, Finke and Snyder 2010).

Acknowledgements

We thank administration of the Gutianshan National Nature Reserve for research permissions. Helge Bruelheide, Bernhard Schmid, Sabine Both, Keping Ma, Xiaojuan Liu and the entire coordination team of the BEF China consortium are gratefully acknowledged for their support. Jiang Zaigen helped with trap maintenance and Marianne Peters with sorting trap samples. Data on tree species were provided by Martin Böhnke, data on herb layer species by Sabine Both, data on tree evenness and tree phylogenetic diversity by Karin Nadrowski, data on leaf functional diversity by Wenzel Kröber, data on plot-specific microclimate by Katherina Pietsch and soil data by Christian Geißler, Thomas Scholten and Peter Kühn. Rabea König and Merle Noack assisted with ant sorting and mounting. David Walmsley helped to improve the English. Michael Staab thanks especially Brian Fisher (California Academy of Sciences) and the Ant Course Team for encouraging his interest in ant ecology. Funding by the German Research Foundation (DFG FOR 891, 891/2) is gratefully acknowledged.

References

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, pp 80-88.

Armbrecht I, Rivera L, Perfecto I (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. Conservation Biology 19:897-907.

Ashman M, Puri G (2008) Essential soil science: A clear and concise introduction to soil science. Wiley-Blackwell, New York.

Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, Motta CdS, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104:18555-18560.

Basset Y, Cizek L, Cuenoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Odegaard F, Roslin T, Schmidl J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H-P, Bail J, Barrios H, Bridle JR, Castano-Meneses G, Corbara B, Curletti G, da Rocha WD, de Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, de Oliveira EG, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sorensen L, Leponce M (2012) Arthropod diversity in a tropical forest. Science 338:1481-1484.

Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. Biodiversity and Conservation 2:656-666.

Berghoff SM, Maschwitz U, Linsenmair KE (2003) Influence of the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities. Oecologia 135:149-157.

Bestelmeyer BT, Agosti D, Alonso LE, Brandao CRF, Brown WL, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants: An overview, description, and evaluation. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithonian Institution Press, Washington DC, pp 122-144.

Bihn JH, Verhaagh M, Brand R (2008) Ecological stoichiometry along a gradient of forest succession: Bait preferences of litter ants. Biotropica 40:597-599.

Blüthgen N, Feldhaar H (2010) Food and shelter: How resources influence ant ecology. In: Lach L, Parr CL, Abbott KL (eds) Ant Ecology. 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 137:426-435.

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge.

Boulton AM, Davies KF, Ward PS (2005) Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: Role of plants, soil, and grazing. Environmental Entomology 34:96-104.

Brown WL (2000) Diversity of ants. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithonian Institution Press, Washington, pp 45–79.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81:25-41.

Brühl CA, Mohamed V, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15:265-277.

Bruno JF, Cardinale BJ (2008) Cascading effects of predator richness. Frontiers in Ecology and the Environment 6:539-546.

Burghouts T, Ernsting G, Korthals G, Devries T (1992) Litterfall, leaf litter decomposition abd litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. Philosophical Transactions of the Royal Society Series B 335:407-416.

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. American Journal of Botany 98:572-592.

Cerda X, Dejean A (2011) Predation by ants on arthropods and other animals. In: Polidori C (ed) Predation in the Hymenoptera: An evolutionary perspective. TransWorld Research Network, Kerala, pp 39-78.

Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News 17:133-146.

Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. Ecology Letters 15:1308-1317.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Marquez JRG, Gruber B, Lafourcade B, Leitao PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46.

dos Santos Bastos AH, Harada AY (2011) Leaf-litter amount as a factor in the structure of a ponerine ants community (Hymenoptera, Formicidae, Ponerinae) in an eastern Amazonian rainforest, Brazil. Revista Brasileira De Entomologia 55:589-596.

Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. Frontiers in Ecology and the Environment 7:437-444.

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: Incorporating trophic complexity. Ecology Letters 10:522-538.

Finke DL, Snyder WE (2010) Conserving the benefits of predator biodiversity. Biological Conservation 143:2260-2269.

Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia 131:137-144.

Floren A, Linsenmair KE (2005) The importance of primary tropical rain forest for species diversity: An investigation using arboreal ants as an example. Ecosystems 8:559-567.

Floren A, Wetzel W, Staab M (2014) The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. Myrmecological News 19:65-74.

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: A review. Biodiversity and Conservation 7:1221-1244.

Gamfeldt L, Snall T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Froberg M, Stendahl J, Philipson CD, Mikusinski G, Andersson E, Westerlund B, Andren H, Moberg F, Moen J, Bengtsson J (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340.

Geissler C, Kühn P, Böhnke M, Bruelheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. Catena 91:85-93.

Gibb H, Cunningham SA (2011) Habitat contrasts reveal a shift in the trophic position of ant assemblages. Journal of Animal Ecology 80:119-127.

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 107:16732-16737.

Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378-381.

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: Changes in structural and functional characteristics. Forest Ecology and Management 148:185-206.

Guénard B, Dunn RR (2012) A checklist of the ants of China. Zootaxa 3558:1-77.

Gunawardene NR, Majer JD, Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. Myrmecological News 17:81-90.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029-1039.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D (2011) Plant diversity and the stability of foodwebs. Ecology Letters 14:42-46.

Higgins RJ, Lindgren BS (2012) The effect of manipulated shading on the colony abundance of two species of ants, *Formica aserva* and *Leptothorax muscorum*, in dead wood. Entomologia Experimentalis et Applicata 143:292-300.

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. American Naturalist 163:192-211.

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

Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University Press, Cambridge.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105-108.

Ivanov K, Keiper J (2009) Effectiveness and biases of winkler litter extraction and pitfall trapping for collecting ground-dwelling ants in northern temperate forests. Environmental Entomology 38:1724-1736.

Jacquemin J, Drouet T, Delsinne T, Roisin Y, Leponce M (2012) Soil properties only weakly affect subterranean ant distribution at small spatial scales. Applied Soil Ecology 62:163-169.

Jansen S, Broadley MR, Robbrecht E, Smets E (2002) Aluminum hyperaccumulation in angiosperms: A review of its phylogenetic significance. Botanical Review 68:235-269.

Kaspari M (1996) Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76:443-454.

Kier G, Mutke J, Dinerstein E, Ricketts TH, Küper W, Kreft H, Barthlott W (2005) Global patterns of plant diversity and floristic knowledge. Journal of Biogeography 32:1107-1116.

Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103-1112.

Kone M, Konate S, Yeo K, Kouassi PK, Linsenmair KE (2012) Changes in ant communities along an age gradient of cocoa cultivation in the Oume region, central Cote d'Ivoire. Entomological Science 15:324-339.

Kröber W, Böhnke M, Welk E, Wirth C, Bruelheide H (2012) Leaf trait-environment relationships in a subtropical broadleaved forest in South-East China. PLoS ONE 7:e35742.

Lavelle P, Chauvel A, Fragoso C (1995) Faunal activity in acid soils. In: Date RA, Grundon NJ, Payment GE, Probert ME (eds) Plant soil interactions at low pH: Principles and management. Kluwer Academic Publishers, Dordrecht, pp 201-211.

Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 40: 573-592.

Levings SC, Windsor DM (1984) Litter moisture-content as a determinant of litter arthropod distribution and abundance during the dry season on Barro-Colorado Island, Panama. Biotropica 16:125-131.

Majer JD, Orabi G, Bisevac L (2007) Ants (Hymenoptera: Formicidae) pass the bioindicator scorecard. Myrmecological News 10:69-76.

McGlynn TP, Alonso-Rodriguez AM, Weaver M (2013) A test of species-energy theory: Patch occupancy and colony size in tropical rainforest litter-nesting ants. Oikos 122:1357-1361.

McGlynn TP, Choi HK, Mattingly ST, Upshaw A, Poirson EK, Betzelberger J (2009a) Spurious and functional correlates of the isotopic composition of a generalist across a tropical rainforest landscape. BMC Ecology 9:23.

McGlynn TP, Fawcett RM, Clark DA (2009b) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. Biotropica 41:234-240.

Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17:2261-2270.

Nahas L, Gonzaga MO, Del-Claro K (2012) Emergent Impacts of ant and spider interactions: Herbivory reduction in a tropical savanna tree. Biotropica 44:498-505.

Olson DM (1991) A comparison of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. Biotropica 23:166-172.

Parr CL, Chown SL (2001) Inventory and bioindicator sampling: Testing pitfall and Winkler methods with ants in a South African savanna. Journal of Insect Conservation 5:27-36.

Pfeiffer M, Mezger D, Dyckmans J (2014) Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) - A stable isotope study in four types of Bornean rain forest. Myrmecological News 19:31-41.

Philpott SM, Armbrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecological Entomology 31:369-377.

Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. Ecology Letters 11:1328-1337.

Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecology 28:305-314.

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-120.

Sanders D, Platner C (2007) Intraguild interactions between spiders and ants and top-down control in a grassland food web. Oecologia 150:611-624.

Sanders D, Schaefer M, Platner C, Griffi GJK (2011) Intraguild interactions among generalist predator functional groups drive impact on herbivore and decomposer prey. Oikos 120:418-426.

Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640-649.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein A-M, Koller R, Koenig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Mueller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou HZ, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology 98:917-926.

Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS ONE 6:e22905.

Silva PSD, Bieber AGD, Correa MM, Leal IR (2011) Do leaf-litter attributes affect the richness of leaf-litter ants? Neotropical Entomology 40:542-547.

Van Straalen NM, Verhoef HA (1997) The development of a bioindicator system for soil acidity based on arthropod pH preferences. Journal of Applied Ecology 34:217-232.

Vehviläinen H, Koricheva J, Ruohomaki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117:935-943.

Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia's highly degraded forests: Evidence from leaf-litter ants. Philosophical Transactions of the Royal Society Series B 366:3256-3264.

Woodcock P, Edwards DP, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2013) Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. PLoS ONE 8:e60756.

Wright DH (1983) Species-energy theory - An extension of species-area theory. Oikos 41:496-506.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health. Springer, Berlin.

Appendix

Appendix A. Spearman correlation coefficients (ρ) for all pairwise comparisons of all environmental variables measured. Bold numbers indicated when two variables were correlated with ρ > 0.70 and hence one of the variables was excluded from all following analyses. Units of all variable measurements are shown in brackets.

	Vegetation height^{*,b} (cm)	Vegetation cover^{b} (%)	Tree species richness	Tree phylogenetic diversity*	Tree evenness	Trees deciduous (%)	Tree basal area^{*,a} (m^2)	Tree abundance*	Successional age (yrs)	Soil moisture* (%)	Soil pH	Soil N* (%)	Soil C/N	Soil C* (%)	Shrub cover (%)	Mean temperature* (°C)	Litter depth^{b} (cm)	Litter cover^{b} (%)	Leaf functional diversity	Herb species richness^{a}	Herb cover^{b} (%)	Elevation (m)	Canopy cover* (%)
Canopy cover* (%)	-0.17	-0.13	0.15	0.30	0.43	-0.40	**0.81**	-0.61	**0.76**	0.21	-0.03	0.33	0.14	0.35	-0.39	-0.07	-0.10	-0.16	0.09	-0.25	-0.19	0.25	1
Elevation (m)	-0.18	-0.17	0.05	-0.13	-0.23	0.36	0.22	0.13	0.22	**0.74**	-0.38	0.46	-0.03	0.48	0.25	**-0.85**	-0.33	-0.22	0.45	-0.22	-0.37	1	
Herb cover^{b} (%)	0.44	0.47	0.14	0.21	0.11	-0.06	-0.13	0	-0.08	-0.17	-0.18	0.03	0.33	0.09	0.06	0.33	-0.01	-0.02	-0.05	0.09	1		
Herb species richness^{a}	0.06	0.09	0.28	-0.07	-0.05	0.17	-0.30	0.28	-0.22	-0.04	0.28	-0.06	-0.4	-0.16	0.26	-0.06	-0.02	0.11	-0.09	1			
Leaf functional diversity	0.16	0.14	0.41	0.38	0.22	0.10	0.04	0.04	0.12	0.36	-0.43	0.17	0	0.18	0.45	-0.38	0.06	-0.15	1				
Litter cover^{b} (%)	-0.09	-0.14	0.07	-0.16	-0.15	0.05	-0.19	0.26	-0.17	-0.17	0.18	-0.28	-0.13	-0.32	-0.04	0.05	0.19	1					
Litter depth^{b} (cm)	0.04	-0.03	0.05	0.19	0.16	-0.27	-0.01	-0.06	-0.06	-0.21	0.06	-0.13	0.01	-0.12	-0.01	0.29	1						
Mean temperature* (°C)	0.15	0.10	-0.22	0.24	0.36	-0.49	0.03	-0.39	-0.04	**-0.76**	0.46	-0.46	0.3	-0.42	-0.41	1							
Shrub cover (%)	0.23	0.23	0.03	-0.21	-0.47	0.54	-0.54	0.60	-0.33	0.10	-0.14	-0.13	-0.39	-0.16	1								
Soil C* (%)	-0.15	-0.12	0.36	0.22	0.26	0.01	0.47	-0.26	0.51	**0.80**	-0.58	**0.98**	0.03	1									
Soil C/N	0.09	0.10	-0.17	0.24	0.31	-0.31	0.38	-0.41	0.31	-0.27	0.03	-0.11	1										
Soil N* (%)	-0.17	-0.13	0.41	0.20	0.24	0.04	0.41	-0.20	0.46	**0.82**	-0.60	1											
Soil pH	-0.09	-0.12	-0.33	-0.04	0.06	-0.16	-0.04	-0.09	-0.11	-0.60	1												
Soil moisture* (%)	-0.16	-0.13	0.25	-0.05	-0.06	0.31	0.19	0.02	0.24	1													
Successional age (yrs)	-0.20	-0.18	0.25	0.48	0.55	-0.36	**0.91**	-0.66	1														
Tree abundance*	0.11	0.11	0.05	-0.49	-0.64	0.60	**-0.74**	1															
Tree basal area^{*,a} (m^2)	-0.21	-0.21	0.16	0.42	0.52	-0.49	1																
Trees deciduous (%)	0.07	0.07	-0.05	-0.53	-0.60	1																	
Tree evenness	0.05	0.05	0.42	**0.86**	1																		
Tree phylogenetic diversity*	0.13	0.09	0.56	1																			
Tree species richness	0.01	0	1																				
Vegetation cover^{b} (%)	**0.86**	1																					
Vegetation height^{*,b} (cm)	1																						

* variables showing collinearity with other variables that were excluded from statistical analyses.

[a] variables measured in the central 10 x 10 m area of every plot.

[b] variables measured on a 1m^2 square around each pitfall-trap.

Chapter IV

Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment

Michael Staab, Nico Blüthgen and Alexandra-Maria Klein

Oikos, submitted on 23.04.2014

A Polyrhachis dives *(Smith, 1857) worker while collecting honeydew from two different Centrotinae treehoppers.*

Abstract

Species and processes in ecosystems are part of multi-trophic interaction networks. Plants represent the lowest trophic level in terrestrial ecosystems, and experiments showed a stabilizing effect of plant diversity on higher trophic levels. Such evidence has been mainly collected in experimental grasslands. Forests are structurally more complex than grasslands and support the majority of the global biodiversity, but studies on multi-trophic interaction networks are missing in experimental tree diversity gradients. We examined in a forest diversity experiment in South-East China, how tree diversity affects the structure of trophobiotic networks. Trophobioses are tri-trophic interactions between plants, sap-sucking aphids and honeydew-collecting ants that can be subdivided into a largely mutualistic aphid-ant and an antagonistic plant-aphid network. We inspected almost 7000 trees in 146 plots ranging from monocultures to 16 tree species mixtures and found 194 trophobioses consisting of 15 tree, 33 aphid and 18 ant species. We found that tree diversity increased the density of trophobioses. Consistent with the prediction that mutualistic and antagonistic networks respond differently to changing environments, we found that the generality of the mutualistic aphid-ant but not the antagonistic plant-aphid network increased with tree diversity. High generality, maintained by high tree diversity corresponds to higher functional stability. Hence, our results suggest that tree diversity increases via bottom-up processes the robustness of ant-aphid associations against changing environmental conditions. In turn, the plant-aphid network was highly complementary, making host-specific aphid species vulnerable to co-extinction if their host plants disappear. Based on our results, we give possible future research directions to further disentangle the bottom-up effect of tree diversity on the structure of trophobiotic networks.

Introduction

Species assemblages in ecosystems form food webs consisting of multiple trophic levels, with producers such as plants representing the lowest level and various primary and secondary consumers representing the higher trophic levels. Plant diversity and productivity influence the complexity of multi-trophic interactions, which can feed back on plant community structure and performance (e.g. Scherber et al. 2010).

This complex associations between species can be described in species interaction networks, and since the benchmark paper by Jordano (1987), the analysis of such networks has become a lively field in ecology (e.g. Bersier et al. 2002, Blüthgen et al. 2007, Dormann et al. 2009, Pocock et al. 2012). In parallel, the first large-scale biodiversity-ecosystem functioning (BEF) experiments started to investigate how the diversity of plants relates to ecosystem processes such as productivity (e.g. Tilman et al. 2001) or overall community stability (Hector et al. 2010). Network analyses have, however, rarely been considered in the context of BEF experiments, albeit knowledge on multi-trophic interactions is important to understand the relationship between plant diversity and BEF processes (Balvanera et al. 2006, Hillebrand and Matthiessen 2009). The available studies in grassland experiments suggest that plant diversity has a stabilizing effect on food webs by, for example, providing more consistent and more heterogeneous resources to higher trophic levels (e.g. Petermann et al. 2010, Ebeling et al. 2011, Haddad et al. 2011). In contrast to grasslands, forests are structurally much more complex habitats that are characterized by long-living plant individuals. As a biome, forests cover almost a third of the global land area, support approximately 80% of the terrestrial biodiversity and are critical for maintaining global physical processes (Bonan 2008, FAO 2010). The majority of network studies conducted in forests addressed either plant-frugivore (e.g. Albrecht et al. 2013) or extrafloral nectar plant-ant interactions (e.g. Rico-Gray et al. 2012, Dáttilo et al. 2013). While some of these studies focused on land use such as logging which might reduce tree diversity and found a reduced network complexity in modified landscapes (e.g. Albrecht et al. 2013), the pure effect of tree diversity alone has not yet been explored.

Here we study in a recently established forest BEF experiment (Bruelheide et al. 2014) if tree diversity affects tri-trophic interactions between plants, various groups of sap-sucking Hemiptera including aphids (termed 'aphids' from here on for simplicity) and ants (Figure 1). These so-called trophobioses consist of two essentially different trophic interactions: the exploitation of plants by aphids (antagonism), and the largely mutualistic aphid-ant relationship. In exchange for the carbohydrate-rich honeydew excreted by the aphids, ants usually provide protection against natural enemies (Way 1963). Trophobioses are common in forests, especially after habitat disturbance (Crist 2009), and contribute significantly to fluxes of matter and energy to dominant canopy ants (Davidson et al. 2003). Due to their simplicity and commonness trophobioses have been studied in many ecosystems (e.g. Blüthgen et al. 2004, 2006, Moreira et al. 2012). Interestingly, it became apparent from a network perspective that the antagonistic plant-aphid networks are usually more specialized and more complementary than the mutualistic aphid-ant networks, as e.g. shown by Blüthgen et al. (2006) in a Bornean rainforest.

Comparing plant-pollinator and plant-herbivore networks based on unweighted metrics, Thebault and Fontaine (2010) argued that antagonistic and mutualistic networks are structured differently. Based on weighted network metrics, most antagonistic networks are much more complementary than mutualistic networks (e.g. compare Blüthgen et al. 2007 and Schleuning et al. 2012 with Morris et al. 2014). Changes in plant diversity may thus affect trophic interaction networks in complex ways with different effects on antagonistic and mutualistic networks. For our study system we hypothesize that aphid-ant associations are relatively generalized, and increasing tree diversity further increases the generality of the partners which, from the ant's perspective, may stabilize their resource availability. In turn, we predict that plant-aphid networks are more complementary and constrained, and the generality of host plants for each aphid species may not benefit from an increase in tree diversity.

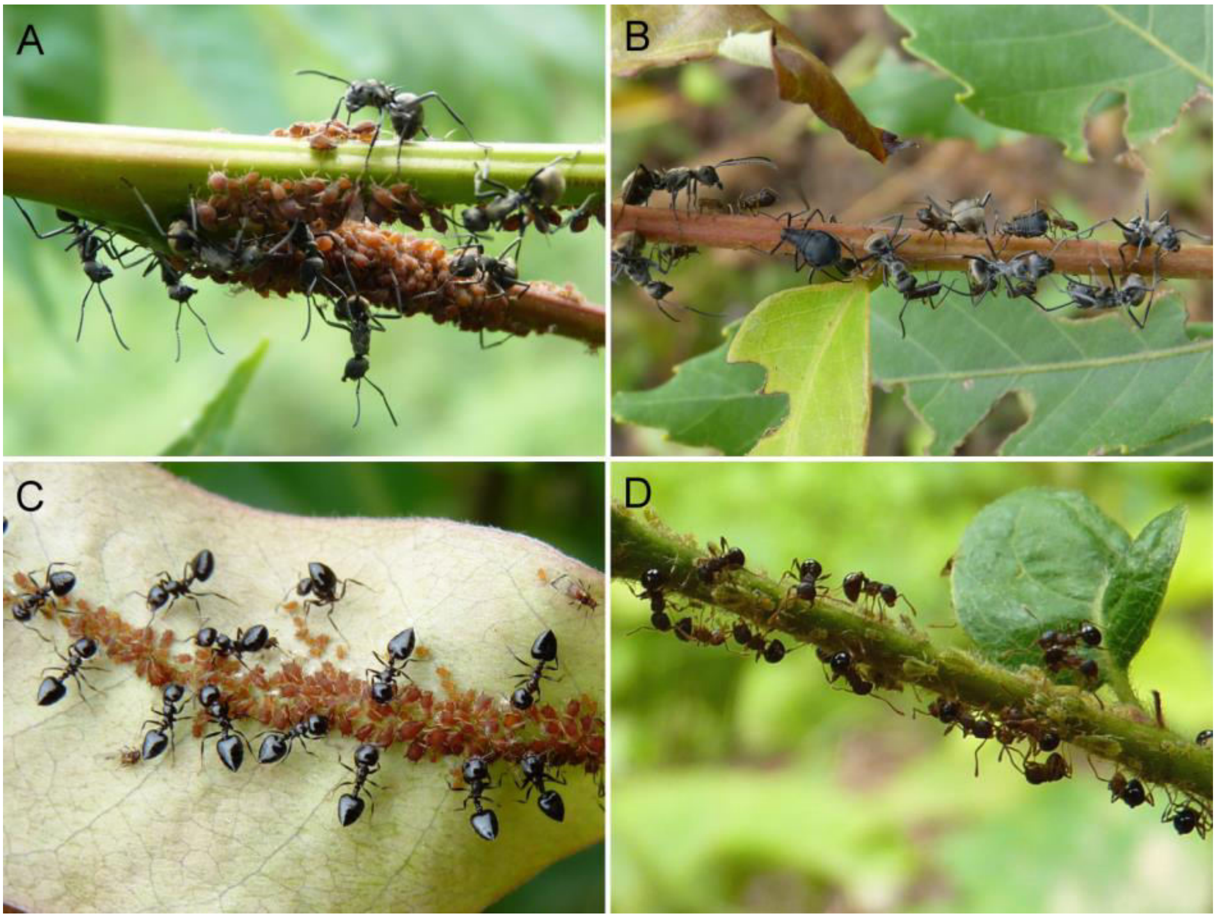


Figure 1. Exemplary trophobioses found in this study illustrating the diversity of participating ants, aphids, and plants. (A) *Polyrhachis dives* (ant 12) tending *Toxoptera sp.* CN01 (aphid 30) on *Choerospondias axillaris* (plant 3), (B) *P. dives* tending *Lachnus tropicalis* (aphid 16) on *Quercus serrata* (plant 12), (C) *Crematogaster cf. nawai* (ant 4) tending *Aphis odinae* (aphid 1) on *Schima superba* (plant 15), and (D) *Pristomyrmex punctatus* (ant 15) tending *Cervaphis quercus* (aphid 8) on *Q. fabri* (plant 11). Numerical codes refer to Appendix A and are identical to Figure 3 and Appendix B.

Material and methods

Study site

The study site was located in South-East China, a region that is characterized by a typical seasonal subtropical monsoon climate with hot and humid summers contrasted by cool and relatively dry winters. Mean annual temperature is 16.7 °C and mean annual precipitation 1821 mm (Yang et al. 2013). Topographically the study area is characterized by distinct slopes on 100-300 m elevation above sea level. The potential natural vegetation is a diverse mixed evergreen broad-leaved forest that is numerically dominated by evergreen tree species but deciduous species contribute to about half of the total tree species richness (Bruelheide et al. 2011). In old growth forests *Castanopsis eyrei*

(Fagaceae; species authorities not mentioned in the main text are listed in Appendix A), *Cyclobalanopsis glauca* (Fagaceae), and *Schima superba* (Thecaceae) are the most abundant canopy tree species. In the shrub layer *Loropetalum chinensis* (R. Br.) Oliv. (Hamamelidaceae), *Quercus serrata* (Fagaceae), *Rhododendron sp.* (Ericaceae) and *Camellia sp.* (Thecaceae) are most abundant (Bruelheide et al. 2011). Nowadays, forests are restricted to steeper slopes and most natural forests have been converted to commercial monocultures of the conifers *Pinus massoniana* Lamb. (Pinaceae) and *Cunninghamia lanceolata* (Lamb.) Hook (Cupressaceae) or to agricultural land.

Near Xingangshan, Dexing County, Jiangxi Province (117°54'E, 29°07'N) the BEF-China project (www.bef-china.de) established the currently largest tree diversity experiment in the world (Bruelheide et al. 2014). Using a total of 42 naturally occurring tree species including all locally common canopy species, 566 experimental plots were established on two different sites that were planted in 2009 and 2010 respectively. Every plot has a size of 25.8 x 25.8 m in horizontal projection which corresponds to the traditional Chinese area unit of 1 mu. On each plot 400 tree individuals were planted in 20 x 20 regularly arranged columns and rows. As the main objective of the BEF-China Experiment is to investigate the influence of tree diversity on ecosystem processes and functions, the plots span a tree diversity gradient from 1, 2, 4, 8, 16, to 24 tree species. The spatial location of plots in a site was randomized as was the position of individuals of each tree species in a plot. For a comprehensive description of the BEF-China Experiment, including maps, elevation profiles, and a full list of planted tree species we refer to Yang et al. (2013) and Bruelheide et al. (2014).

Table 1. Details of sampling per tree diversity level. The number of plots samples, the number of trees sampled per plot, the total number of sampled trees, the number of trees with aphids, and the number of trees with trophobioses are shown. Values in parentheses refer to the proportion of living trees per level.

Tree diversity	Number of plots	Trees per plot sampled	Total live trees	Trees with aphids	Trees with trophobioses
1	41	36	1146	119 (10.4%)	23 (2.0%)
2	42	36	1094	102 (9.3%)	11 (1.0%)
4	27	81	1368	136 (9.9%)	41 (3.0%)
8	20	144	1931	190 (9.8%)	56 (2.9%)
16	16	144	1445	153 (10.6%)	52 (3.6%)
total	146		6984	700 (10.0%)	183 (2.6%)

Data collection

We sampled trophobioses from May 21st to August 20th 2011 on the site that was planted in 2009, 25 month before the start of the sampling. Most of the 24 planted tree species were established well (Yang et al. 2013) and had a height of 100 cm or more. We selected 41 plots with tree diversity level 1, 42 plots with diversity 2, 27 plots with diversity 4, 20 plots with diversity 8, and 16 plots with diversity 16, summing up to 146 plots in total (Table 1). Because there are only two plots with tree diversity 24, we did not study the highest available tree diversity level. As the abundance of a tree species in a plot decreases with increasing tree diversity, we increased the number of sampled trees per plot accordingly. In 1 and 2 species plots, we sampled the central 6 x 6 trees (i.e. 36 trees per plot), in 4 species plots the central 9 x 9 trees (i.e. 81 trees per plot), and in 8 and 16 species plots the central 12 x 12 trees (i.e. 144 trees per plot; Table 1), summing up to 10.359 trees. By only sampling the central area in each plot there was always a distance of over 10 m between the closest sampled trees in two adjacent plots, reducing possible effects of the tree community of neighboring plots on the sampling.

On each tree, 20 randomly selected young leaves and the attached branch sections were visually inspected for the occurrence of sap-sucking aphids and honeydew-collecting ants. Voucher specimens of each trophobiosis were collected with soft insect forceps and stored in 70% ethanol. Aphids were grouped into morphospecies and sent to taxonomic experts (see Acknowledgements) for further identification. Non-ant-tended aphids were also recorded but not further identified. Ants were first assorted to genera with Bolton (1994) and then identified to species level whenever possible with primary taxonomic literature and the Antweb Database (www.antweb.org). In a few cases ants could only be identified to morphospecies. For simplicity we use the term species for both, species that could be assigned to a scientific name and to species that could only be grouped to an operational morphospecies name (see also Appendix A).

Data analyses

Data were analyzed with the software package R 3.0.2 (www.r-project.org). In all analyses we used the occurrence of trophobioses as the smallest data unit, i.e. every interaction between an aphid and an ant species observed on an individual tree was only counted once, regardless of the number of individuals involved (Blüthgen et al. 2006, 2007). This conservative approach rules out potential biases of abundances, as most aphid species are capable of very rapid population growth by reproducing asexually in parts of their life cycles (Blackman and Eastop 1994). However, if one aphid species was tended on the same tree by two different ant species, or if one ant species tended two different aphid species, we counted them as two separate trophobioses.

We pooled all trophobioses for each of the five tree diversity levels to obtain one network each. Pooling was necessary as network analyses require a minimal network size to work reliably (Dormann et al. 2009). Consequently, we had only one data point per diversity level which was too low for formal statistical testing, a common problem in ecological network analyses (see Blüthgen 2010). Properties of trophobiotic networks per tree diversity level were analyzed and visualized with the R-package ‘bipartite’ (www.cran.r-project.org/package=bipartite). Out of the variety of available network indices (reviewed in Dormann et al. 2009) we choose the weighted ‘generality’ index to describe interactions between trophic levels. This index is a robust measure for the connectivity and thus the stability of networks. Hence it is suitable to address our main question, if and how tree diversity affects trophobiotic interactions. In a bipartite network, weighted generality is defined as the weighted mean effective number of species in the lower trophic level per species in the higher trophic level, with each species weighted by the number of trophobioses in which it was found (marginal row sums) (see Bersier et al. 2002, Dormann et al. 2009).

$$\mathrm{G_{qw}} = \sum_{\mathrm{j=1}}^{\mathrm{J}} \cdot \frac{\mathrm{A_j}}{\mathrm{m}} \mathrm{e}^{\mathrm{H_j}} \qquad \text{(Eq. 1)}$$

G_{qw} (Eq. 1) is calculated with J being the number of species in the higher trophic level, A_j the total number of interaction of species j from the higher trophic level, m the total number of interactions for all species, and H the Shannon diversity of interactions for the higher trophic level (Dormann et al. 2009). The index G_{qw} is 1 if each aphid species has only a single host plant species or each ant species has only a single aphid partner. Higher G_{qw}, suggests higher redundancy, which is thought to contribute to higher stability. G_{qw} may increase with the species' abundances and overall diversity (Blüthgen 2010, Albrecht et al. 2013). We checked whether these two parameters may explain the change in weighted generality. Lastly, to test if the observed values for G_{qw} are different from random interactions of the species, we calculated for each network null models based on the Patefield algorithm with 10,000 random model runs (Blüthgen et al. 2006, Dormann et al. 2009).

We also pooled the total number of aphid occurrences, i.e. the number of trophobioses and the number of untended aphid occurrences to one value each per tree diversity level. We then calculated for every tree diversity level the proportion of trees that were infested by aphids and the proportion of trees that had trophobioses (from here on termed ‘density’). Analyses are based on the number of living trees only; dead trees were excluded. We tested for the completeness of our sampling with the jackknife 1 (jack1) species richness estimator. Plots were taken as sample units and calculations were done in the R-package ‘vegan’ (www.cran.r-project.org/package=vegan). While species richness estimation for aphids and ants is a measure for the number of species we may expect with very high sampling effort, for the plant level the total species richness in all diversity levels was 24. Thus we interpret species richness estimation for the plant level as a measure for the possibility that additional plant species had trophobioses which were not detected by us.

Table 2. Properties of trophobiotic networks per tree diversity level. The number of trophobioses as well as the number of tree, aphid and ant species that were observed and expected (based on the jack1 estimator ± SE; in parentheses) in trophobioses are shown. The generality index G_{qw} is shown for the plant-aphid (p-a) and for the aphid-ant (a-a) level. G_{qw} values in brackets are derived from Patefield null models with 10,000 randomizations. P-values indicate if G_{qw} of observed and randomized networks differ. Significant P-values are in bold.

Tree diversity	Trophobioses	Tree richness	Aphid richness	Ant richness	G_{qw} p-a	p_{p-a}	G_{qw} a-a	p_{a-a}
1	25	7 (12±2)	12 (22±4)	9 (14±2)	1.14 (2.34)	**<0.001**	3.20 (4.05)	**0.05**
2	11	5 (8±2)	7 (12±2)	4 (7±1)	1.00 (1.77)	**0.002**	2.27 (3.06)	**0.007**
4	43	9 (14±2)	14 (23±4)	9 (15±2)	1.20 (3.24)	**<0.001**	5.03 (7.07)	<**0.001**
8	61	9 (11±1)	15 (25±4)	10 (14±2)	1.70 (3.67)	<**0.001**	5.13 (6.87)	<**0.001**
16	54	11 (14±2)	18 (29±6)	9 (13±2)	1.44 (3.87)	<**0.001**	4.67 (6.46)	<**0.001**
total	194	15 (19±2)	33 (49±5)	18 (26±3)	1.79 (5.81)	<**0.001**	9.16 (11.45)	<**0.001**

Results

In total, 700 of 6984 trees were infested by aphids, including 183 trees (Table 1) with 194 trophobioses (Figure 1). The proportion of trees with aphids was similar for all tree diversity levels. However, the proportion of trees with trophobioses was higher in the higher tree diversity levels compared to the lower levels (Table 1; Figure 2).

At least one aphid occurrence was found on 23 out of the 24 possible tree species, with 15 tree species holding trophobiosis (Appendix A). These trophobioses consisted of 33 aphid species that were tended by 18 ant species. Trophobioses were most common on tree species of the family Fagaceae. 68.0% (132 interactions) of all trophobioses were found on Fagaceae that contributed only 48.5% (3390 trees) to all inspected tree individuals (Appendix A). The three *Quercus* species - *Q. acutissima*, *Q. fabri* and *Q. serrata* - had 51.6% (100 interactions) of all trophobioses while only accounting for 14.3% (999 trees) tree individuals. Among the Hemiptera, true aphids (Aphididae) represented 82.0% (159) of all trophobioses, and the 15 aphid species 45.5% of the 33 total Hemiptera species. *Cervaphis quercus* and *Diphyllaphis quercus* were the most common trophobiotic aphid species (each 15.5%). Treehoppers (family Membracidae) were most common (15 interactions) after Aphididae. The ant community consisted of species of the subfamilies Dolichoderinae, Formicinae and Myrmicinae. A single species, *Polyrhachis dives* (Formicinae) participated in most trophobioses (106 or 54.6%), followed by two species of *Crematogaster* (38 or 19.6%) (Appendix A).

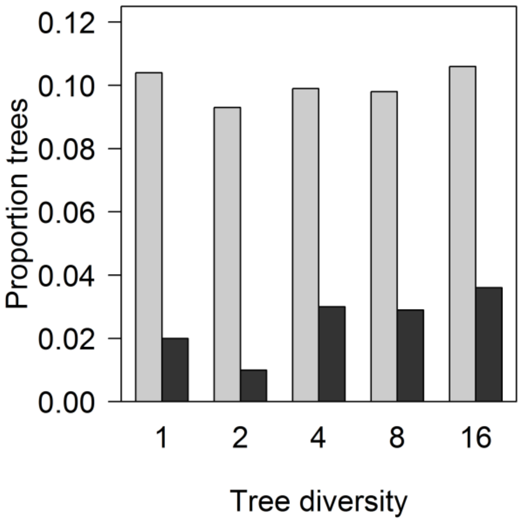


Figure 2. Proportion of trees per tree diversity level with aphids (light grey bars) and trophobioses (dark grey bars). Infestation with aphids was similar for all diversity levels while the proportion of trees harboring trophobioses was greater at higher tree diversity levels.

The jack1 species richness estimator suggests that our sampling collected over two-thirds of the predicted species pool involved in trophobioses. Compared to the richness estimates, our 15 tree species recorded with trophobionts represented 79% of a total estimated 19 ± 2 tree species, 33 collected aphid species represented 67% of the totally estimated 49 ± 5 aphid species, and the 18 collected ant species represented 69% of the estimated 26 ± 3 ant species. The observed but not the expected number of plant species having trophobioses was higher at higher tree diversity levels as was the sampling efficiency (Table 2). The number of trophobiotic aphids species showed a similar trend; however jack1 species richness estimation indicated a consistently moderate sampling efficiency of ca. 60% for all tree diversity levels. Observed ant species richness was independent of the tree diversity level. The sampling efficiency for ants was similar to aphids (Table 2).

The tri-trophic interaction network of the complete dataset (Appendix B) revealed that the plant-aphid network had a low generality (G_{qw}=1.79), suggesting that each aphid species had on average less than two ‘effective’ host tree species. In contrast, the aphid-ant network had a much higher generality (G_{qw}=9.16) (Table 2) suggesting more than nine ‘effective’ aphid partners per ant species. For plant-aphid networks, the low generality was consistently found across the five tree diversity levels, as G_{qw} was only slightly increasing with higher tree diversity. In contrast, G_{qw} of the aphid-ant networks was 1.8-fold higher when four or more tree species were planted in a plot (Table 2; Figure 4). The null-model analysis revealed that the G_{qw} values of the complete network and of all tree diversity level specific networks were significantly different from chance. In all cases, G_{qw} was lower than it would have been expected if interactions between species were only driven by random processes (Table 2).

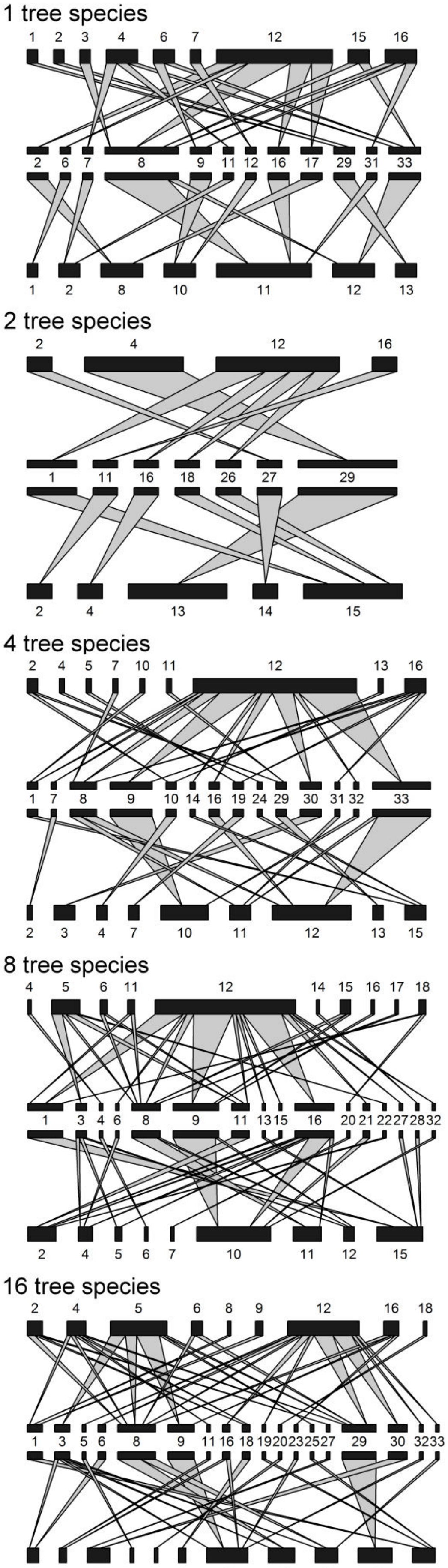


Figure 3 (left). Quantitative tri-trophic food webs based on the occurrences of trophobioses along the tree diversity gradient. For each food web, lower bars represent plants, middle bars represent aphids, and upper bars represent ants. Width of bars indicates number of occurrences per species, width of arrows indicates the number of interactions between two species in two adjacent trophic levels. The most narrow bars and arrows indicate a single interaction per tree diversity level. *Quercus acutissima*, *Q. fabri*, and *Q. serrata* are plant species 10, 11, and 12 respectively. *Polyrhachis dives* is ant species 12. Numerical codes refer to species names given in Appendix A.

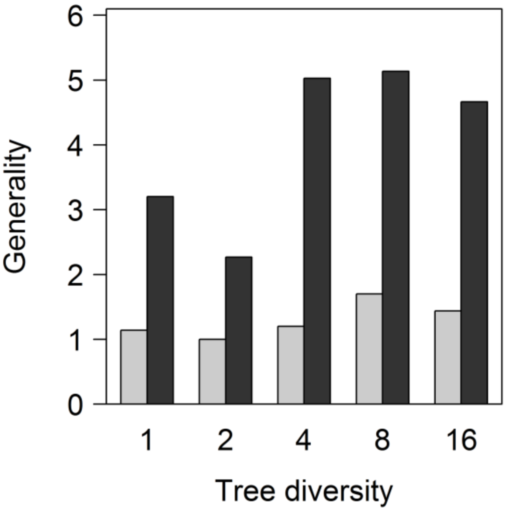


Figure 4 (top). Generality index G_{qw} describing the effective mean number of trophic interactions per tree diversity level, separated for the plant-aphid networks (light grey bars) and for the aphid-ant networks (dark grey bars). Plant-aphid networks were, independent of tree diversity, always complementary, while aphid-ant networks were more generalized at higher tree diversity levels. See main text for definition of G_{qw}.

As described above the estimated species richness of plants, aphids, and ants was not influenced by tree diversity and, thus, the increase of G_{qw} in the aphid-ant network not caused by species numbers of aphids and ants. However, the density of trophobiosis was higher in higher tree diversity levels, which corresponds to the observed increase in G_{qw}.

Discussion

Our results showed that experimental manipulation of tree diversity was associated with changes in tri-trophic interactions. The density of trophobioses increased with higher tree diversity, which had a stabilizing effect on the mutualistic aphid-ant networks as suggested by the higher effective number of aphid species tended by each ant species (i.e. the generality of the aphid-ant networks). In contrast, the antagonistic plant-aphid networks remained at low generality and the effective host plant spectrum attacked by each aphid species along the tree diversity gradient was increasing only little. All network patterns in our study were not influenced by random processes, indicating that actual tree diversity is causing the observed changes in the networks.

So far, the studies investigating the relationship between producer diversity and network structure in grasslands found an association of network stability and complexity with plant diversity (e.g. Ebeling et al. 2011, Haddad et al. 2011). In a broader context it has been shown that the complexity and structure of networks is strongly dependent on a variety of habitat properties such as successional age (e.g. Albrecht et al. 2010), geographical latitude (Schleuning et al. 2012), local microclimate (Rico-Gray et al. 2012) or land use (e.g. Albrecht et al. 2013, Vanbergen et al. 2014). In principle, biodiversity and other factors can directly or indirectly affect networks in two directions (Hunter and Price 1992). In case of a top-down mechanism higher trophic levels (consumers) have effects on lower levels. In case of a bottom-up mechanism the lower trophic levels (producers) act on processes in higher levels. Both effects are known to alternate in a trophic cascade when interactions between different levels are studied (see Petermann et al. 2010). Scherber et al. (2010) showed in a grassland experiment a positive bottom-up effect of plant diversity on multi-trophic interactions, which we confirm. In our study, tree diversity increased via a bottom-up effect the density of trophobioses supporting the findings of Moreira et al. (2012) who showed in a small scale experiment using three pine species that tree diversity increased the number of ant-tended aphids. In a close-by secondary forest classical folivore herbivory increased with tree diversity which is in accordance to our results (Schuldt et al. 2010). Taken together, these findings suggest a general increase in trophic interactions with increasing tree diversity. The higher generality in our study was not simply a result of a higher species richness of aphids and ants in high-diversity plots. The estimated richness of species in the plant-aphid network was roughly similar for all tree diversity levels. Instead, the density of trophobioses was larger in plots of higher tree diversity which likely explains the higher generality.

The increased generality is in accordance to the predictions of the diversity-stability hypothesis (reviewed in McCann 2000) which suggests that producer diversity can have a stabilizing effect on trophic-interactions in higher trophic levels. In contrast, the primary consumer level (aphids) was not affected by tree diversity in our study. Both, the density of aphids and the generality of the aphid-ant network were similar between plots of varying tree diversity.

Most aphid species are, with few polyphagous exceptions, specialized feeders restricted to a single plant genus or family (Blackman and Eastop 1994). In order to feed, most aphids need to distinctly pierce a delicate single phloem vessel, a task that requires specific behavioral and morphological adaptations (Walling 2008). Plants are chemically and morphologically well defended against herbivores including aphids, resulting in a strong co-evolutionary arms race. The continuously low generality of the plant-aphid network in our study can be considered a direct consequence of high host-plant specialization. The aphid-ant network is, in turn, a largely mutualistic interaction. Trophobiotic ants are only in very few striking cases associated with an exclusive set of Hemiptera species (e.g. Machwitz and Hänel 1985). Honeydew excreted by most Hemiptera can be collected by a broad range of ant species that are characterized by a joint set of behavioral and morphological traits (Oliver et al. 2008), explaining the wide generalization of trophobiotic networks observed here and in other studies (e.g. Blüthgen et al. 2004, 2006). Our results are also congruent with the prediction that diversity should influence the stability of mutualistic but not antagonistic networks (Thebault and Fontaine 2010, Sauve et al. 2014). This prediction is supported by two recent meta-analyses: Morris et al. (2014) revealed that antagonistic networks had consistently a high degree of specialization across host guilds and latitudes while the generality was only related to network size and the diversity of the interacting species. For mutualistic networks, Schleuning et al. (2012) showed that specialization of pollination and seed-dispersal networks decreased, while the generality increased, from temperate to tropical latitudes. The authors of the latter study suggested that this gradient is mediated by the higher plant diversity in tropical regions.

In the time of global change, food webs are predicted to be heavily affected by rapidly changing environmental conditions (e.g. Barnosky et al. 2012). The extinction of a species in a complex food web can have cascading effects on other species (secondary extinctions), thus altering the entire food web (e.g. Dunne and Williams 2009, Cardinale et al. 2012). More generalized food webs with higher redundancy will be buffered against secondary extinctions (Dunne et al. 2002, Blüthgen 2010). In our case, secondary extinctions of aphids are likely if their host plants disappear while the high generality of the aphid-ant food webs, especially in higher tree diversity levels, may stabilize this part of the network.

While we showed a positive bottom-up effect of tree diversity on the aphid-ant network, we can only speculate about the underlying mechanisms. Tree diversity increases tree productivity (Zhang et al. 2012b) which was confirmed by a study conducted in a nearby secondary forest (Baruffol et al. 2013). Accordingly, we suspect that the young trees in our study site are in high diversity plots likewise more productive, thus being more attractive hosts for trophobiotic aphids (Powell et al. 2006). It could be that aphids feeding on relatively more productive plants excrete qualitatively and quantitatively more attractive honeydew. As trophobiotic ants are able to detect small differences in honeydew composition (Blüthgen and Fiedler 2004) and to select a diet that maximizes longevity (Dussutour and Simpson 2012), the effect of tree diversity on the aphid-ant food web could be mediated bottom-up by honeydew quality. Testing this assumption would be a promising direction for further research.

Outlook

Our study delivered a first experimental evidence for the bottom-up effect of tree diversity on density of trophobioses and tri-trophic network structure. Trophobioses have been regarded as ecological key-stone interactions that contribute significantly to fluxes of matter and energy in (sub)tropical forest canopies by fueling the abundance and prevalence of ants (Davidson et al. 2003). Moreover, trophobioses can have community-wide effects e.g. by influencing the arthropod community on the forest floor (Zhang et al. 2012a). Our data showed a clear and distinct trend, but we acknowledge that future studies should repeatedly sample the same study sites, both inside and between different years, to confirm possible bottom-up effects of tree diversity. Increased sampling will also help to reveal if the low number of trophobioses in two-tree-species plots is an artefact of our study or a consistent pattern. Ideally, studies on trophobioses will also include phylogenetic information of plants, aphids and ants. Trophobioses are evolutionary old interactions as inclusion fossils of aphids and ants in amber demonstrate (LaPolla et al. 2013). The network patterns we observe today may at least partially be explained by evolutionarily conserved relationships (sensu Pellissier et al. 2013).

Acknowledgements

We thank Thomas Thieme for Aphididae species identification. Werner Holzinger confirmed the Auchenorrhyncha morphospecies classification and Wolfgang Dorow the identity of the taxonomically ambiguous *Polyrhachis dives*. Jan Peters helped with parts of the fieldwork. Andreas Schuldt critically commented an earlier version of the manuscript. Helge Bruelheide, Bernhard Schmid, Sabine Both, Keping Ma, Xiaojuan Liu, and the entire coordination team of the BEF China project are gratefully acknowledged for their support. This study was funded by the German Science Foundation (DFG FOR 891/2, KL 1849/6-1).

References

Albrecht J, Berens DG, Blüthgen N, Jaroszewicz B, Selva N, Farwig N (2013) Logging and forest edges reduce redundancy in plant-frugivore networks in an old-growth European forest. Journal of Ecology 101:990-999.

Albrecht M, Riesen M, Schmid B (2010) Plant-pollinator network assembly along the chronosequence of a glacier foreland. Oikos 119:1610-1624.

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146-1156.

Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, Fortelius M, Getz WM, Harte J, Hastings A, Marquet PA, Martinez ND, Mooers A, Roopnarine P, Vermeij G, Williams JW, Gillespie R, Kitzes J, Marshall C, Matzke N, Mindell DP, Revilla E, Smith AB (2012) Approaching a state shift in Earth's biosphere. Nature 486:52-58.

Baruffol M, Schmid B, Bruelheide H, Chi X, Hector A, Ma K, Michalski S, Tang Z, Niklaus PA (2013) Biodiversity promotes tree growth during succession in subtropical forest. PLoS ONE 8:e81246.

Bersier LF, Banasek-Richter C, Cattin MF (2002) Quantitative descriptors of food-web matrices. Ecology 83:2394-2407.

Blackman RL, Eastrop VF (1994) Aphids on the world's trees. CABI Publishing, Wallingford.

Blüthgen N (2010) Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. Basic and Applied Ecology 11:185-195.

Blüthgen N, Fiedler K (2004) Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. Journal of Animal Ecology 73:155-166.

Blüthgen N, Menzel F, Hovestadt T, Fiala B, Blüthgen N (2007) Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology 17:341-346.

Blüthgen N, Mezger D, Linsenmair KE (2006) Ant-hemipteran trophobioses in a Bornean - rainforest diversity, specificity and monopolisation. Insectes Sociaux 53:194-203.

Blüthgen N, Stork NE, Fiedler K (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. Oikos 106 (2):344-358

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge.

Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320:1444-1449.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81:25-41.

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, Buscot F, Chen X-Y, Ding B, Durka W, Erfmeier A, Gutknecht JLM, Guo D, Guo L-D, Härdtle W, He J-S, Klein A-M, Kühn P, Liang Y, Liu X, Michalski S, Niklaus PA, Pei K, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang X, Yu M, Zhang S, Zhou H, Fischer M, Ma K, Schmid B (2014) Designing forest biodiversity experiments: General considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5:74-89.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59-67.

Crist TO (2009) Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. Myrmecological News 12:3-13.

Dáttilo W, Guimarães PR, Izzo TJ (2013) Spatial structure of ant–plant mutualistic networks. Oikos 122:1643-1648.

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300:969-972.

Dormann C, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. The Open Ecology Journal 2:7-24.

Dunne JA, Williams RJ (2009) Cascading extinctions and community collapse in model food webs. Philosophical Transactions of the Royal Society Series B 364:1711-1723.

Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters 5:558-567.

Dussutour A, Simpson SJ (2012) Ant workers die young and colonies collapse when fed a high-protein diet. Proceedings of the Royal Society Series B 279:2402-2408.

Ebeling A, Klein A-M, Tscharntke T (2011) Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic and Applied Ecology 12:300-309.

FAO (2010) Global forest resources assessment 2010. FAO Forestry Paper 163:1-340.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D (2011) Plant diversity and the stability of foodwebs. Ecology Letters 14:42-46.

Hector A, Hautier Y, Saner P, Wacker L, Bagchi R, Joshi J, Scherer-Lorenzen M, Spehn EM, Bazeley-White E, Weilenmann M, Caldeira MC, Dimitrakopoulos PG, Finn JA, Huss-Danell K, Jumpponen A, Mulder CPH, Palmborg C, Pereira JS, Siamantziouras ASD, Terry AC, Troumbis AY, Schmid B, Loreau M (2010) General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. Ecology 91:2213-2220.

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

Hunter MD, Price PW (1992) Playing chutes and ladders - heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732.

Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal - connectance, dependence asymmetries, and coevolution. American Naturalist 129:657-677.

LaPolla JS, Dlussky GM, Perrichot V (2013) Ants and the fossil record. Annual Review of Entomology 58:609-630.

Maschwitz U, Hänel H (1985) The migrating herdsman *Dolichoderus* (*Diabolus*) *cuspidatus* - an ant with a novel mode of life. Behavioral Ecology and Sociobiology 17:171-184.

McCann KS (2000) The diversity-stability debate. Nature 405:228-233.

Moreira X, Mooney KA, Zas R, Sampedro L (2012) Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. Proceedings of the Royal Society Series B 279:4464-4472.

Morris RJ, Gripenberg S, Lewis OT, Roslin T (2014) Antagonistic interaction networks are structured independently of latitude and host guild. Ecology Letters 17:340-349.

Oliver TH, Leather SR, Cook JM (2008) Macroevolutionary patterns in the origin of mutualisms involving ants. Journal of Evolutionary Biology 21:1597-1608.

Pellissier L, Ndiribe C, Dubuis A, Pradervand J-N, Salamin N, Guisan A, Rasmann S (2013) Turnover of plant lineages shapes herbivore phylogenetic beta diversity along ecological gradients. Ecology Letters 16:600-608.

Petermann JS, Müller CB, Weigelt A, Weisser WW, Schmid B (2010) Effect of plant species loss on aphid–parasitoid communities. Journal of Animal Ecology 79:709-720.

Pocock MJO, Evans DM, Memmott J (2012) The robustness and restoration of a network of ecological networks. Science 335:973-977.

Powell G, Tosh CR, Hardie J (2006) Host plant selection by aphids: Behavioral, evolutionary, and applied perspectives. Annual Review of Entomology 51:309-330.

Rico-Gray V, Diaz-Castelazo C, Ramirez-Hernandez A, Guimaraes PR, Holland JN (2012) Abiotic factors shape temporal variation in the structure of an ant-plant network. Arthropod-Plant Interactions 6:289-295.

Sauve AMC, Fontaine C, Thébault E (2014) Structure–stability relationships in networks combining mutualistic and antagonistic interactions. Oikos 123:378-384.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein A-M, Koller R, Koenig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Mueller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schleuning M, Fründ J, Klein A-M, Abrahamczyk S, Alarcon R, Albrecht M, Andersson GKS, Bazarian S, Böhning-Gaese K, Bommarco R, Dalsgaard B, Dehling DM, Gotlieb A, Hagen M, Hickler T, Holzschuh A, Kaiser-Bunbury CN, Kreft H, Morris RJ, Sandel B, Sutherland WJ, Svenning J-C, Tscharntke T, Watts S, Weiner CN, Werner M, Williams NM, Winqvist C, Dormann CF, Blüthgen N (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology 22:1925-1931.

Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou HZ, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology 98:917-926.

Thebault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853-856.

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843-845.

Vanbergen AJ, Woodcock BA, Gray A, Grant F, Telford A, Lambdon P, Chapman DS, Pywell RF, Heard MS, Cavers S (2014) Grazing alters insect visitation networks and plant mating systems. Functional Ecology 28:178-189.

Walling LL (2008) Avoiding effective defenses: Strategies employed by phloem-feeding insects. Plant Physiology 146:859-866.

Way MJ (1963) Mutualism between ants and honeydew-producing Homoptera. Annual Review of Entomology 8:307-344.

Yang XF, Bauhus J, Both S, Fang T, Härdle W, Kröber W, Ma KP, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Scholten T, Seidler G, Schmid B, Von Oheimb G, Bruelheide H (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). European Journal of Forest Research 132:593-606.

Zhang S, Zhang Y, Ma K (2012a) Disruption of ant-aphid mutualism in canopy enhances the abundance of beetles on the forest floor. PLoS ONE 7:e35468.

Zhang Y, Chen HYH, Reich PB (2012b) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology 100:742-749.

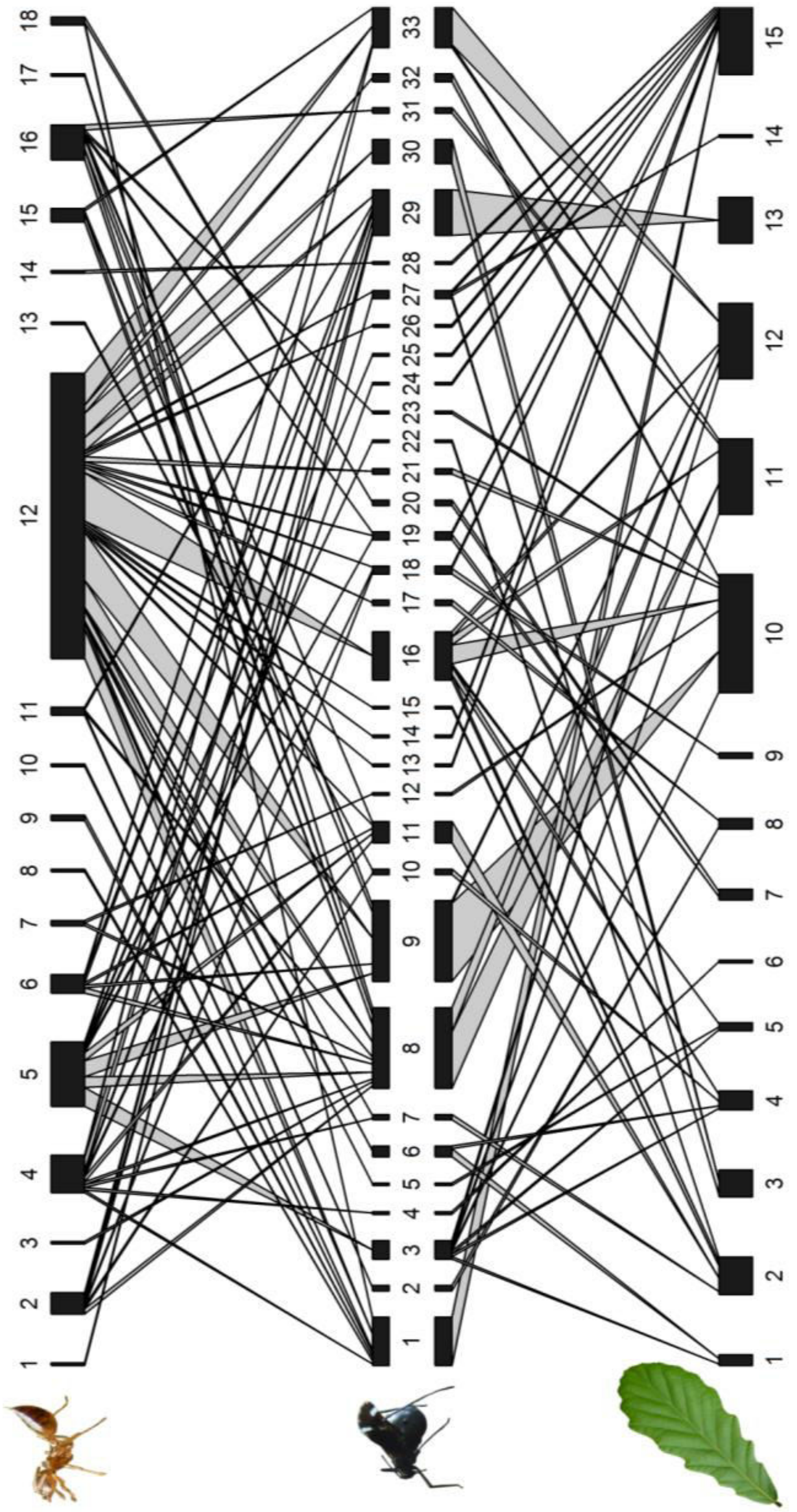
Appendix

Appendix A. Number of trophobiotic interactions for plant, aphid and ant species in an early successional tree plantation in South-East China. The numbers in the first column refer to the species codes in Figure 1, Figure 2 and Appendix B. Taxonomic names of plant species follows the Flora of China (http://www.efloras.org/flora_ page.aspx?flora_id=2), of aphid species the Aphid Species File Database (http://aphid.speciesfile.org) and of ant species Antweb (www.antweb.org).

Number in Figures	Species	Family	Interactions
Trees			
1	*Castanea henryi* (Skan) Rehd. & Wils.	Fagaceae	4
2	*Castanopsis sclerophylla* (Lindl. et Pax.) Schott.	Fagaceae	14
3	*Choerospondias axillaris* (Roxb.) Burtt & Hill	Anacardiaceae	10
4	*Cyclobalanopsis glauca* (Thunb.) Oers.	Fagaceae	7
5	*Cyclobalanopsis myrsinaefolia* Oerst.	Fagaceae	3
6	*Koelreuteria bipinnata* Franch.	Sapindaceae	1
7	*Liquidambar formosana* Hance	Hamamelidaceae	4
8	*Lithocarpus glaber* (Thunb.) Nakai	Fagaceae	4
9	*Nyssa sinensis* Oliver	Nyssaceae	2
10	*Quercus acutissima* Carruth.	Fagaceae	44
11	*Quercus fabri* Hance	Fagaceae	28
12	*Quercus serrata* Murray	Fagaceae	28
13	*Rhus chinensis* Mill.	Anacardiaceae	17
14	*Sapindus saponaria* L.	Sapindaceae	1
15	*Schima superba* Gardn. & Champ.	Theaceae	27
Aphids			
1	*Aphis odinae* (van der Goot, 1917)	Aphididae	18
2	*Aphis sp.* CN01	Aphididae	2
3	Centrotinae Larvae 1	Membracidae	7
4	Centrotinae Larvae 2	Membracidae	1
5	Centrotinae sp. CN02	Membracidae	1
6	Centrotinae sp. CN03	Membracidae	4
7	Centrotinae sp. CN05	Membracidae	2
8	*Cervaphis quercus* Takahashi, 1918	Aphididae	30
9	*Diphyllaphis quercus* (Takahashi, 1960)	Aphididae	30
10	*Eutrichosiphum dubium* (van der Goot, 1917)	Aphididae	2

11	*Eutrichosiphum sclerophyllum* Zhang, 1980	Aphididae	8
12	*Eutrichosiphum sp.* CN01	Aphididae	1
13	Flatidae Larvae sp. 1	Flatidae	1
14	Flatidae sp. CN01	Flatidae	1
15	Issidae sp. CN03	Issidae	1
16	*Lachnus tropicalis* (van der Goot, 1916)	Aphididae	18
17	*Mollitrichosiphum lithocarpi* (Takahashi, 1931)	Aphididae	2
18	Monophlebidae sp. CN01	Monophlebidae	3
19	Monophlebidae sp. CN02	Monophlebidae	3
20	*Myzus persicae* (Sulzer, 1776)	Aphididae	2
21	Plataspidae sp. CN01	Plataspidae	2
22	Pseudococcidae sp. CN02	Pseudococcidae	1
23	Pseudococcidae sp. CN03	Pseudococcidae	1
24	Pseudococcidae sp. CN06	Pseudococcidae	1
25	Pseudococcidae sp. CN07	Pseudococcidae	1
26	Pseudococcidae sp. CN08	Pseudococcidae	1
27	Ricaniidae sp. CN03	Ricaniidae	3
28	Ricaniidae sp. CN04	Ricaniidae	1
29	*Toxoptera citricidus* (Kirkaldy, 1907)	Aphididae	17
30	*Toxoptera sp.* CN01	Aphididae	9
31	*Tuberculatus capitatus* (Essig & Kuwana, 1918)	Aphididae	2
32	*Tuberculatus japonicus* Higuchi, 1969	Aphididae	3
33	*Tuberculatus stigmatus* (Matsumura, 1917)	Aphididae	15
Ants		(Subfamily)	
1	*Camponotus pseudoirritans* Wang, Xiao & Wu, 1989	Formicinae	1
2	*Camponotus vitiosus* Smith, 1874	Formicinae	8
3	*Carebara sp.* CN05	Myrmicinae	1
4	*Crematogaster cf. nawai*	Myrmicinae	14
5	*Crematogaster rogenhoferi* Mayr, 1879	Myrmicinae	24
6	*Iridomyrmex anceps* (Roger, 1863)	Dolichoderinae	7
7	*Nylanderia flavipes* (Smith, 1874)	Formicinae	2
8	*Nylanderia sp.* CN03	Formicinae	1
9	*Ochetellus glaber* (Mayr, 1862)	Dolichoderinae	2
10	*Paratrechina longicornis* (Latreille, 1802)	Formicinae	1

11	*Pheidole fervens* Smith, 1858	Myrmicinae	3
12	*Polyrhachis dives* Smith, 1857	Formicinae	106
13	*Prenolepis naoroji* Forel, 1902	Formicinae	1
14	*Prenolepis sp.* CN06	Formicinae	1
15	*Pristomyrmex punctatus* (Smith, 1860)	Myrmicinae	5
16	*Rhoptromyrmex wroughtonii* Forel, 1902	Myrmicinae	13
17	*Tapinoma melanocephalum* (Fabricius, 1793)	Dolichoderinae	1
18	*Technomyrmex brunneus* Forel, 1895	Dolichoderinae	3



Appendix B. Quantitative tri-trophic networks based on the occurrences of trophobioses for the total dataset. Width of bars indicates number of occurrences per species, width of arrows indicates the number of interactions between two species in two adjacent trophic levels. The most narrow bars and arrows indicate a single interaction. *Quercus acutissima*, *Q. fabri* (embedded plant), and *Q. serrata* are plant species 10, 11, and 12 respectively. *Polyrhachis dives* is ant species 12. Numerical codes per trophic level refer to species names given in Table S1. The embedded aphid is *Lachnus tropicalis* (aphid 16) and the embedded ant *Crematogaster rogenhoferi* (ant 5).

Chapter V

A new species of the Aenictus wroughtonii *group (Hymenoptera, Formicidae) from South-East China*

Michael Staab

ZooKeys, published in volume 391, pages 65-73.

Holotype worker of Aenictus gutianshanensis *Staab, 2014, a species known only from Gutianshan.*

ZooKeys 391: 65–73 (2014)
doi: 10.3897/zookeys.391.7213
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China

Michael Staab[1,†]

[1] *Chair of Nature Conservation and Landscape Ecology, Institute of Earth and Environmental Sciences, University of Freiburg, Tennenbacherstraße 4, 79106 Freiburg, Germany*

† *http://zoobank.org/42662938-64FB-4680-87DA-8D88AA9981C8*

Corresponding author: *Michael Staab* (michael.staab@nature.uni-freiburg.de)

Academic editor: *B. Fisher* | Received 7 February 2014 | Accepted 3 March 2014 | Published 20 March 2014

http://zoobank.org/31827A89-9B39-4E90-BE1E-E71C345C6FE1

Citation: Staab M (2014) A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China. ZooKeys 391: 65–73. doi: 10.3897/zookeys.391.7213

Abstract

A new species of army ant from the *Aenictus wroughtonii* group is described and illustrated based on the worker caste. *Aenictus gutianshanensis* Staab, **sp. n.** is known form a single colony collected in the subtropical mixed evergreen broad-leaved forest of the Gutianshan National Nature Reserve, South-East China. The new species is probably most closely related to *A. vieti* Jaitrong & Yamane, 2010 known from North Vietnam and Taiwan. It is suggested that the abundant records of *A. camposi* Wheeler & Chapman, 1925 from East and South-East China should be reevaluated, as they are probably *A. gutianshanensis* or *A. vieti* and not *A. camposi*, which is distributed in Sundaland, the Philippines, and the southernmost part of continental South-East Asia.

Keywords

Aenictinae, *Aenictus gutianshanensis*, army ants, species description, taxonomy

Introduction

The genus *Aenictus*, which is the only genus of the dorylomorph subfamily Aenictinae, is the largest genus of army ants. Army ants are characterized by several specialized morphological, behavioral, and ecological adaptations, such as a nomadic life style, highly specialized mating systems, and mass raiding for arthropod prey (Schneirla and

Reyes 1966, Gotwald 1995, Kronauer 2009). *Aenictus* is restricted to the tropical and subtropical regions of the Old World and Australia (Gotwald 1995). Almost all *Aenictus* species are specialized predators of other ants (e.g. Rościszewski and Maschwitz 1994, Hirosawa et al. 2000, Jaitrong and Yamane 2011), however they can also supplement their diet with plant-based resources (Staab in press).

Until now, 179 species (9 synonyms, 2 unavailable) and 30 subspecies (13 synonyms, 2 unavailable) have been validly described (AntCat 2014). Recently, Jaitrong and coworkers established 12 species groups based on the worker caste (Jaitrong and Yamane 2011), and comprehensively revised the Oriental and Australasian *Aenictus* fauna (Jaitrong and Yamane 2010, Jaitrong et al. 2010, Jaitrong and Yamane 2011, Wiwatwitaya and Jaitrong 2011, Jaitrong and Hashimoto 2012, Jaitrong and Yamane 2012, Jaitrong and Wiwatwitaya 2013, Jaitrong and Yamane 2013).

The *A. wroughtonii* species group has been revised in detail by Jaitrong et al. (2010). The group contains seven species in the Oriental and Australasian faunal region that can easily be separated from other conspecific *Aenictus* species by the combination of a yellowish and slender body, very long antennal scapes, and a rounded anterior clypeal margin bearing several denticles (Jaitrong et al. 2010, Jaitrong and Yamane 2011). In the present paper, a new species of the *A. wroughtonii* group from South-East China is described as new to science based on the worker caste.

Methods

All morphological observations were made with a Leica SD6 stereomicroscope. Measurements were taken with an ocular micrometer. Images were produced using a Keyence VHX2000 (Osaka, Japan) digital microscope.

The general worker terminology follows Jaitrong et al. (2010) and Jaitrong and Yamane (2011).

All measurements are expressed in millimeters. Abbreviations used for measurements and indices follow Jaitrong et al. (2010) and Jaitrong and Yamane (2011) and are:

CI	Cephalic index, HW / HL × 100.
HL	Maximum head length in full-face view, measured from the anterior clypeal margin (excluding the projecting clypeal teeth) to the midpoint of a line drawn across the posterior margin of the head.
HW	Maximum head width in full face view.
ML	Mesosomal length measured from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron in profile.
MTL	Maximum length of mid tibia, excluding the proximal part of the articulation which is received into the distal end of the femur.
PL	Petiole length measured from the anterior margin of the peduncle to the posteriormost point of tergite.
SI	Scape index, SL / HW × 100.

SL	Scape length excluding the basal constriction and condylar bulb.
TL	Total length, measured roughly from the anterior margin of head to the tip of gaster in stretched specimens.

Depositories of type material

CASC	California Academy of Science Collection, San Francisco, California, USA.
IZAS	Insect Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China.
ZMBH	Museum für Naturkunde, Berlin, Germany.

Results

Aenictus wroughtonii species group

Jaitrong et al. (2010) and Jaitrong and Yamane (2011) defined this species group as follows:

Head narrow; occipital margin lacking collar. Antenna long, consisting of 10 segments, with a strikingly long scape attaining or extending beyond posterolateral corner of head (but in one Vietnamese species the scape shorter, not reaching posterolateral corner of head). Anterior clypeal margin roundly convex with 5–10 denticles. Mandible triangular, with masticatory margin bearing 8–12 minute inconspicuous denticles in addition to large apical tooth with a sharp apex; basal margin of mandible lacking denticles. Frontal carina short; parafrontal ridge feeble and incomplete. Mesosoma narrow and elongate. Legs very slender. Subpetiolar process weakly developed or almost absent. Head and gaster entirely smooth and shiny. Nearly entire body clear yellow to yellowish brown; typhlatta spot absent.

Aenictus gutianshanensis Staab, sp. n.

http://zoobank.org/F14B8EED-1D2E-4931-A0AA-F3697502BEEF
http://species-id.net/wiki/Aenictus_gutianshanensis
Figs 1–5

Holotype. Worker from China, Zhejiang Province, Gutianshan National Nature Reserve, ca. 30 km NW of Kaihua, 29°12'54"N / 118°7'18"E, ca. 250 m above sea level, 28.VI.2009, leg. Andreas Schuldt, label: "CSP26/SW7(2009)", deposited in IZAS.

Paratypes. Five workers, same data as holotype. Three deposited in IZAS; one each deposited in ZMBH and CASC. All type specimens were collected in a single pitfall trap in a secondary mixed evergreen broad-leaved forest.

Measurements and indices. Holotype: TL 3.30, HL 0.68, HW 0.63, SL 0.70, ML 1.17, MTL 0.75, PL 0.30, CI 93, SI 112.

Figures 1–4. *Aenictus gutianshanensis* sp. n. (holotype). **1** Head in full-face view **2** body in profile **3** body in dorsal view **4** propodeal junction petiole and postpetiole in profile.

Paratypes (n=5): TL 3.10–3.30, HL 0.69–0.75, HW 0.60–0.65, SL 0.65–0.70, ML 1.17–1.25, MTL 0.69–0.83, PL 0.29–0.31, CI 87–91, SI 104–113.

Worker description. Head in full-face view elliptical, slightly longer than broad, with convex sides and almost straight posterior margin of head. Antennal scape long, reaching posterior corner of head; antennal segments II-X each longer than broad; II as long as III, but longer than each of IV-VII; terminal segment (X) longer than each of II-IX; the last four segments forming an indistinct club. Frontal carina long, extending slightly beyond the posterior margin of antennal torulus. Clypeus short with its anterior margin slightly convex, bearing 7-8 bluntly rounded denticles. Mandible subtriangular, masticatory margin straight, with a large curved apical tooth which is followed by 9-10 minutes teeth on masticatory margin. With mesosoma in profile, pronotum dorsally convex, not distinctly separated from mesonotum by a promesonotal suture. Propodeum slightly lower than promesonotum, its dorsal outline gently sloping posteriorly; propodeal junction angulate; declivity of propodeum straight in the dorsal part, concave in the ventral part when viewed in profile, encircled by a thin rim. Petiole in profile as long as high, its node convex dorsally. Subpetiolar process present, its ventral margin almost straight, bearing a thin rim below, anteroventral corner angulate. Postpetiole slightly longer than petiole, its node convex dorsally in profile; ventral postpetiolar process developed, angulate, bearing a thin rim below, slightly projecting over the posterior part of the petiole.

Head including mandible smooth and shiny; antennal scape punctate. Entire mesosoma finely reticulate, dorsal face of pronotum finely reticulate but shiny, reticulation

Figure 5. *Aenictus gutianshanensis* sp. n. (holotype), sculpture of pronotal dorsum.

Figure 6. Typical mixed evergreen broad-leaved forest at the type locality, the Gutianshan National Nature Reserve.

on mesopleuron, metapleuron and lateral face of propodeum finer than on pronotum, appearing almost punctate in magnification lower 64×. Entire petiole finely reticulate. Postpetiole finely reticulate, except the dorsum smooth and shiny. Gaster smooth and shiny. Coxae finely reticulate, femora densely punctate, tibiae sparsely punctate.

Body except anterior part of mesonotum with abundant standing hairs and interdispersed short hairs; length of longest hairs on dorsa of head and pronotum 0.20–0.30 mm. Antennal scape and legs with abundant standing hairs. Head, mandible, gaster and legs yellowish brown. Mesosoma, antennal scape, petiole and postpetiole reddish brown.

Male and female are unknown.

Etymology. The scientific name is after the type locality, the Gutianshan National Nature Reserve (Fig. 6) in South-East China.

Distribution. South-East China; only known from the type series.

Ecology. No direct biological information is available. The type series was collected in a single pitfall trap in a secondary mixed evergreen broad-leaved forest. Thus, the species probably lives and forages on and in the leaf-litter preying on small ants of the subfamily Formicinae, as it has been previously reported for species in the *A. wroughtonii* group (Rościszewski and Maschwitz 1994, Jaitrong et al. 2010). Possible prey species of the genera *Prenolepis* and *Nylanderia* are common at the type locality (M. Staab, unpublished data).

Discussion

Aenictus is one of the most species-rich ant genera in China and worldwide (Guénard and Dunn 2012, AntCat 2014), and the present paper raises the number of described species to 180. However, several *Aenictus* species have been described based only on males. As males of *A. gutianshanensis* and many other *Aenictus* species are so far unknown, further collections supported by genetic work are needed in the future to clarify the relationship between male and worker based species names. Recently, the exhaustive reviews of Jaitrong and coworkers (Jaitrong and Yamane 2010, Jaitrong et al. 2010, Jaitrong and Yamane 2011, Wiwatwitaya and Jaitrong 2011, Jaitrong and Hashimoto 2012, Jaitrong and Yamane 2012, Jaitrong and Wiwatwitaya 2013, Jaitrong and Yamane 2013) provided detailed taxonomic and biogeographic information for the Oriental *Aenictus* fauna. Nevertheless, additional new species from the region have been described by various authors since these revisions (e.g. Jaitrong and Nur-Zati 2010, Bharti et al. 2012). Due to their highly specialized colony cycle which is characterized by reproduction through colony fission only (Gotwald 1995), most *Aenictus* species have a low dispersal potential and rather small and limited distribution ranges (e.g. Jaitrong et al. 2010, 2012, Jaitrong and Yamane 2013).

Aenictus gutianshanensis can be easily distinguished from all other species of the *A. wroughtonii* group by the pronotum, the petiole, and the side of the postpetiole completely finely reticulate (see Jaitrong et al. 2010 for detailed species descriptions including a key to the *A. wroughtonii* group; the same key is available online at http://www.antwiki.org/wiki/Key_to_Aenictus_wroughtonii_group_species). The new species is most similar to *A. vieti* Jaitrong & Yamane, 2010 and to *A. camposi* Wheeler & Chapman, 1925 but slightly larger in all measurements. In addition to having the pronotum and petiole completely finely reticulate, *A. gutianshanensis* can be easily distinguished from *A. vieti* and *A. camposi* by the following characters (characters for *A. vieti* and *A. camposi* are given in brackets, see Jaitrong et al. 2010): ventral margin of subpetiolar process almost straight (ventral margin convex), femora densely punctate (smooth and shiny in Jaitrong et al. 2010, but superficially and irregularly sculptured and shiny in two paratypes examined by the reviewer), postpetiolar process more developed with a rim below (less developed, without ventral rim), and longest standing hairs on pronotal dorsum distinctly longer (maximal 0.13 mm).

In China, *A. camposi* has been recorded from several provinces in East and South-East China. (Guénard and Dunn 2012). However, *A. camposi* is a clearly tropical species whose distribution is restricted to Sundaland, the Philippines, and the southernmost part of continental South-East Asia (Jaitrong et al. 2010). Jaitrong and Yamane (in Jaitrong et al. 2010) described *A. vieti* from Taiwan and North Vietnam. The authors recommended treating the Chinese records of *A. camposi* as *A. vieti*, which is morphologically similar. However, *A. vieti* has not yet been recorded from mainland China. Thus, I also recommend reevaluating the Chinese *A. camposi* for their identity. The type locality of *A. gutianshanensis* is in the Zhejiang Province, and at least *A. camposi* specimens collected further north, e.g. in Anhui or Hubei, may be *A. gutianshanensis*.

There are probably several *Aenictus* species which still await discovery and description in the tropical and subtropical forests of the Oriental region. However, these forests are under high land-use pressure and are increasingly being cleared for agriculture (Gibbs et al. 2010, Miettinen et al. 2011, Hansen et al. 2013). As top predators, *Aenictus* and other army ants are sensitive to the negative effects of forest fragmentation and anthropogenic land use (Matsumoto et al. 2009). *Aenictus gutianshanensis* was discovered in South-East China, a region that was once covered by species rich subtropical forests which have largely been converted to timber plantations and to agricultural land (López-Pujol et al. 2006). The type locality, the Gutianshan National Nature Reserve (Bruelheide et al. 2011), despite being secondary forest, is one of the larger fragments of the historically wide ranging mixed evergreen broad-leaved forest in South-East China. These areas, as well as other secondary forest fragments in China and elsewhere probably contain several new ant species waiting to be discovered.

Acknowledgements

I thank the administration of the Gutianshan National Nature Reserve for generously granting research permissions and Andreas Schuldt for collecting the type series. Helge Bruelheide, Bernhard Schmid, Sabine Both, Keping Ma, Xiaojuan Liu, and the entire team of BEF-China are gratefully acknowledged for their support. Ottmar Fischer and Anita Kiesel assisted with the recording of specimen images. Tamar Marcus improved the English. Valuable comments from two anonymous reviewers improved the manuscript. Funding by the German Research Foundation (DFG FOR 891, 891/2, KL 1849/6-1) is gratefully acknowledged.

References

AntCat. Available from: http://www.antcat.org/catalog/429477 [accessed 3 March 2014]

Bharti H, Wachkoo AA, Kumar R (2012) Two remarkable new species of *Aenictus* (Hymenoptera: Formicidae) from India. Journal of Asia-Pacific Entomology 15: 291–294. doi: 10.1016/j.aspen.2012.02.002

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81: 25–41. doi: 10.1890/09-2172.1

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 107: 16732–16737. doi: 10.1073/pnas.0910275107

Gotwald WHJ (1995) Army ants: the biology of social predation. Cornell University Press, Ithaca, NY, U.S.A. 320 pp.

Guénard B, Dunn RR (2012) A checklist of the ants of China. Zootaxa 3558: 1–77.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342: 850–853. doi: 10.1126/science.1244693

Hirosawa H, Higashi S, Maryati M (2000) Food habits of *Aenictus* army ants and their effects on the ant community in a rain forest of Borneo. Insectes Sociaux 47: 42–49. doi: 10.1007/s000400050007

Jaitrong W, Hashimoto Y (2012) Revision of the *Aenictus minutulus* species group (Hymenoptera: Formicidae: Aenictinae) from Southeast Asia. Zootaxa 3426: 29–44.

Jaitrong W, Nur-Zati MA (2010) A new species of the ant genus *Aenictus* (Hymenoptera: Formicidae: Aenictinae) from the Malay Peninsula. Sociobiology 56: 449–454.

Jaitrong W, Wiwatwitaya D (2013) Two new species of the *Aenictus pachycerus* species group (Hymenoptera: Formicidae: Aenictinae) from Southeast Asia. Raffles Bulletin of Zoology 61: 97–102.

Jaitrong W, Yamane S (2010) The army ant *Aenictus silvestrii* and its related species in Southeast Asia, with a description of a new species (Hymenoptera: Formicidae: Aenictinae). Entomological Science 13: 328–333. doi: 10.1111/j.1479-8298.2010.00385.x

Jaitrong W, Yamane S (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). Zootaxa 3128: 1–46.

Jaitrong W, Yamane S (2012) Review of the Southeast Asian species of the *Aenictus javanus* and *Aenictus philippinensis* species groups (Hymenoptera, Formicidae, Aenictinae). Zookeys 193: 49–78. doi: 10.3897/zookeys.193.2768

Jaitrong W, Yamane S (2013) The *Aenictus ceylonicus* species group (Hymenoptera, Formicidae, Aenictinae) from Southeast Asia. Journal of Hymenoptera Research 31: 165–233. doi: 10.3897/jhr.31.4274

Jaitrong W, Yamane S, Tasen W (2012) A sibling species of *Aenictus dentatus* FOREL, 1911 (Hymenoptera: Formicidae) from continental Southeast Asia. Myrmecological News 16: 133–138.

Jaitrong W, Yamane S, Wiwatwitaya D (2010) The army ant *Aenictus wroughtonii* (Hymenoptera, Formicidae, Aenictinae) and related species in the oriental region, with descriptions of two new species. Japanese Journal of Systematic Entomology 16: 33–46.

Kronauer DJC (2009) Recent advances in army ant biology (Hymenoptera: Formicidae). Myrmecological News 12: 51–65.

López-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: richly varied, endangered, and in need of conservation. Biodiversity and Conservation 15: 3983–4026. doi: 10.1007/s10531-005-3015-2

Matsumoto T, Itioka T, Yamane S, Momose K (2009) Traditional land use associated with swidden agriculture changes encounter rates of the top predator, the army ant, in Southeast Asian tropical rain forests. Biodiversity and Conservation 18: 3139–3151. doi: 10.1007/s10531-009-9632-4

Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17: 2261–2270. doi: 10.1111/j.1365-2486.2011.02398.x

Rościszewski M, Maschwitz U (1994) Prey specialization of army ants of the genus *Aenictus* in Malaysia. Andrias 13: 179–187.

Schneirla TC, Reyes AY (1966) Raiding and related behaviour in two surface-adapted species of the Old World Doryline ant, *Aenictus*. Animal Behavior 14: 132–148. doi: 10.1016/S0003-3472(66)80022-2

Staab M (in press) The first observation of honeydew foraging in army ants since 1933: *Aenictus hodgsoni* Forel, 1901 tending *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) in South-East China. Asian Myrmecology.

Wiwatwitaya D, Jaitrong W (2011) The army ant *Aenictus hottai* (Hymenoptera: Formicidae: Aenictinae) and related species in Southeast Asia, with a description of a new species. Sociobiology 58: 557–565.

Wheeler WM, Chapman JW (1925) The ants of the Philippine Islands. Part I, Dorylinae and Ponerinae. Philippine Journal of Science 28: 27–73.

Chapter VI

The first observation of honeydew foraging in army ants since 1933: Aenictus hodgsoni *Forel, 1901 tending* Eutrichosiphum heterotrichum *(Raychaudhuri, 1956) in Southeast China*

Michael Staab

Asian Myrmecology, accepted for publication in volume 6, to be published 2014

Honeydew-collecting workers of the army ant Aenictus hodgsoni *Forel, 1901*.

ASIAN MYRMECOLOGY Volume 6, 2014
ISSN 1985-1944 © Michael Staab

SHORT COMMUNICATION

The first observation of honeydew foraging in army ants since 1933: *Aenictus hodgsoni* Forel, 1901 tending *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) in Southeast China

MICHAEL STAAB

Ecosystem Function Group, Institute of Ecology, Leuphana University
Lüneburg, Scharnhorststraße 1, D-21335 Lüneburg, Germany

Current address:
Nature Conservation and Landscape Ecology, Faculty of Environment and
Natural Resources, University of Freiburg, Tennenbacher Str. 4,
D-79106 Freiburg

Phone: +49 (0)761 203-67787
Fax: +49 (0)761 203-3638
E-mail: michael.staab@nature.uni-freiburg.de

Keywords: *Aenictus*, army ants, trophobiosis, honeydew, BEF-China

Army ants are a well-defined group of ants characterized by a set of behavioural and ecological adaptations including a nomadic life style with temporary bivouac nests, highly specialized mating systems, and mass raiding for arthropod prey (Gotwald 1995, Kronauer 2009). The monogeneric subfamily Aenictinae is restricted to tropical and subtropical ecosystems in the Old World and Australia (Guénard *et al.* 2010). As far as the trophic ecology of *Aenictus* is known, almost all species are specialized predators of other ants (Gotwald 1995, Kronauer 2009). In the present paper I report the first observation of army ants tending Hemiptera in Asia. On 7 October 2012 at 10:00 local time approximately 30 workers of *Aenictus hodgsoni* Forel, 1901 were observed and photographed collecting honeydew from around 50 *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) (Aphididae) on fresh shoots of a young 1.5 m high *Lithocarpus glaber* (Thunberg) Nakai, 1916 (Fagaceae) tree (Fig. 1). This unexpected observation was made only once during more than five months of surveying trophobiotic interactions in the field sites of the newly established BEF-China tree plantation experiment close to the village of Xingangshan, Jiangxi Province, in subtropical Southeast China (117° 55'49" E / 29° 5' 13" N, Bruelheide *et al*. 2014). Ant and aphid specimens were identified with the keys provided by Jaitrong & Yamane (2011) and Blackman & Eastop (2012) respectively. Voucher specimens were lodged in the insect collection of the University of Freiburg. Close observation of single aphids revealed that the aphids were producing honeydew droplets, which were consumed by *A. hodgsoni* only moments after their appearance. Secretion of defense fluid from the aphid's cornicles was not observed (Edwards 1966), suggesting ants were not preying on the aphids. The ants had a well-established foraging trail, with many foragers going back and forth between the site of the trophobiosis and a hole in the soil about 2 m away. The ants defended their mutualistic partners aggressively by stinging and biting the incautious observer.

Fig. 1. Photograph of *Aenictus hodgsoni* tending *Eutrichosiphum heterotrichum* on a young *Lithocarpus glaber* (Fagaceae) shoot in Southeast China.

Trophobiotic ants usually belong to the subfamilies Dolichoderinae, Formicinae, Pseudomyrmicinae, and Myrmicinae, but occasionally species from other subfamilies also collect honeydew (e.g. Blüthgen *et al*. 2004, Oliver *et al*. 2008, Blüthgen & Feldhaar 2010). Trophobioses involving army ants are extremely rare, with only two previous records published. Both involved African army ants; *Aenictus eugenii* Emery, 1895 at *Pseudococcus lilacinus* Cockerell, 1905 (Santschi 1933) and *Dorylus fulvus* (Westwood, 1839) at an unidentified Membracidae (Arnold 1915).

The *A. hodgsoni* trophobiosis was checked two, four and 24 hours after the first encounter. It persisted after two and four hours, but not on the next day when the aphids were tended by *Polyrhachis dives* Smith, 1857 the most common trophobiotic ant species in the study area (Staab, unpublished data). The low incidence of recorded observations might indicate that trophobioses involving army ants might be rather short lived, opportunistic associations, that do not result in the monopolisation of aphids over an extended time period. Nevertheless, being aggressive ants capable of mass recruitment, *Aenictus* possesses characteristics of suitable trophobiotic partner ants (Buckley & Gullan 1991), and it seems likely that army ants occasionally supplement their diet with honeydew. This might explain the surprisingly low δ 15N values found for *Aenictus* in a recent study in Borneo (Pfeiffer *et al*. 2014). The present observation proves that army ants have the behavioural ability to establish trophobioses, as shown by the active tending of aphids and aggressive defense of their mutualistic partners. Preying of *A. hodgsoni* on *E. heterotrichum* can be excluded, because aphids did not secrete defense fluids and the aggregation was alive on the next day but tended by a different ant species.

This is only the third observation of a trophobiosis in army ants, and more observations are needed to understand how and why specialized predators occasionally establish mutualistic interactions with honeydew producing insects. Scientists working with ant-trophobiont mutualisms should keep their eyes open for unusual ant species tending Hemiptera.

ACKNOWLEDGEMENTS

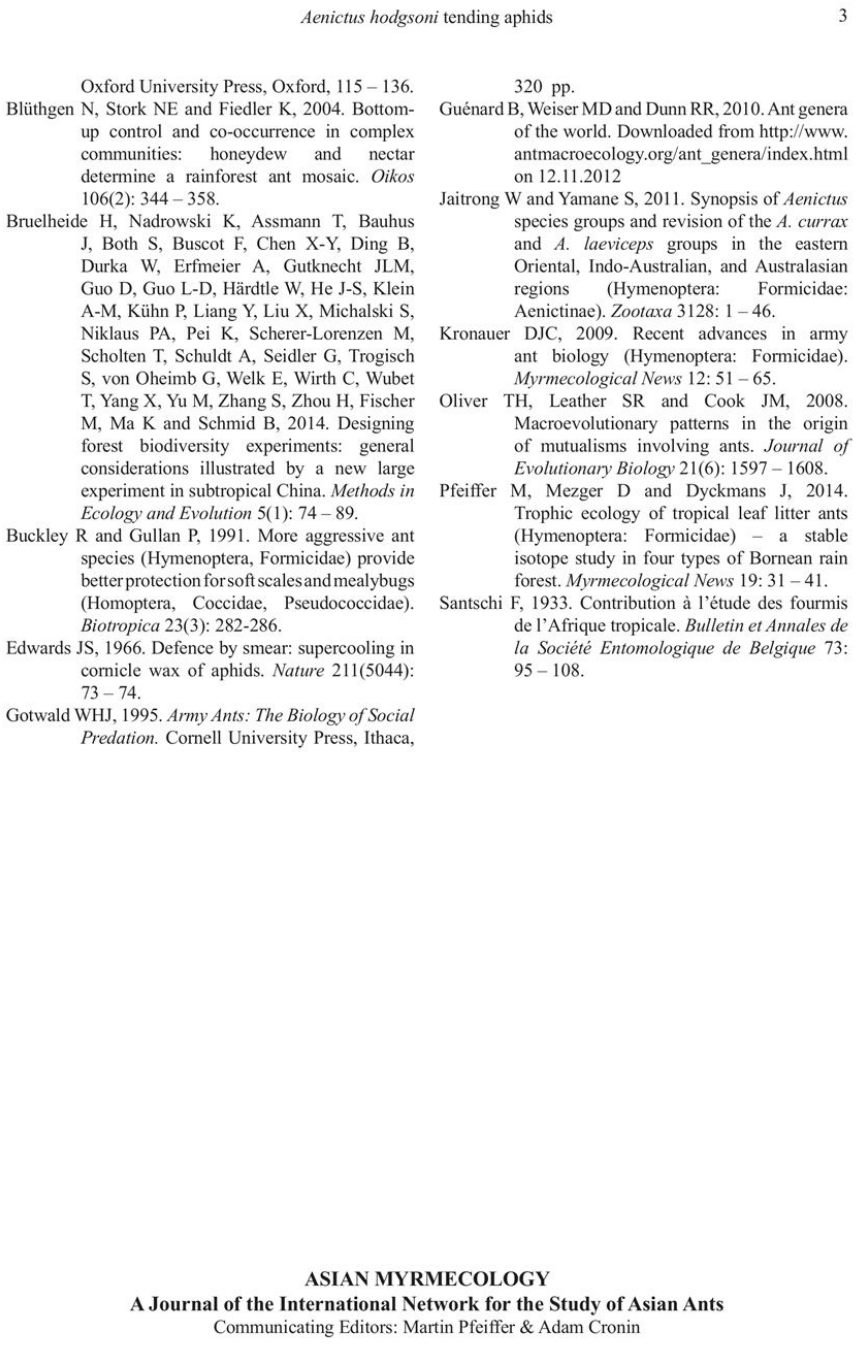
I would like to thank Nico Blüthgen, Alexandra-Maria Klein, and Tamar Marcus for constructive discussion on an earlier draft of the manuscript. Financial support by the German Research Foundation (DFG FOR 891/2 KL 1849/6-1) and logistical support by the BEF-China project is greatly acknowledged. Constructive comments by Yoshiaki Hashimoto and an anonymous reviewer improved the quality of the manuscript.

REFERENCES

Arnold G, 1915. A monograph of the Formicidae of South Africa. Part I. Ponerinae, Dorylinae. *Annals of the South African Museum* 14: 1 – 159.

Blackman RL and Eastop VR, 2012. Aphids on the world's trees. Downloaded from http://www.aphidsonworldsplants.info/ on 14.11.2012

Blüthgen N and Feldhaar H, 2010. Food and shelter: How resources influence ant ecology. In: *Ant Ecology* (Lach L, Parr CL, Abbott KL, eds),



Oxford University Press, Oxford, 115 – 136.

Blüthgen N, Stork NE and Fiedler K, 2004. Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos* 106(2): 344 – 358.

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, Buscot F, Chen X-Y, Ding B, Durka W, Erfmeier A, Gutknecht JLM, Guo D, Guo L-D, Härdtle W, He J-S, Klein A-M, Kühn P, Liang Y, Liu X, Michalski S, Niklaus PA, Pei K, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang X, Yu M, Zhang S, Zhou H, Fischer M, Ma K and Schmid B, 2014. Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* 5(1): 74 – 89.

Buckley R and Gullan P, 1991. More aggressive ant species (Hymenoptera, Formicidae) provide better protection for soft scales and mealybugs (Homoptera, Coccidae, Pseudococcidae). *Biotropica* 23(3): 282-286.

Edwards JS, 1966. Defence by smear: supercooling in cornicle wax of aphids. *Nature* 211(5044): 73 – 74.

Gotwald WHJ, 1995. *Army Ants: The Biology of Social Predation.* Cornell University Press, Ithaca, 320 pp.

Guénard B, Weiser MD and Dunn RR, 2010. Ant genera of the world. Downloaded from http://www.antmacroecology.org/ant_genera/index.html on 12.11.2012

Jaitrong W and Yamane S, 2011. Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). *Zootaxa* 3128: 1 – 46.

Kronauer DJC, 2009. Recent advances in army ant biology (Hymenoptera: Formicidae). *Myrmecological News* 12: 51 – 65.

Oliver TH, Leather SR and Cook JM, 2008. Macroevolutionary patterns in the origin of mutualisms involving ants. *Journal of Evolutionary Biology* 21(6): 1597 – 1608.

Pfeiffer M, Mezger D and Dyckmans J, 2014. Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) – a stable isotope study in four types of Bornean rain forest. *Myrmecological News* 19: 31 – 41.

Santschi F, 1933. Contribution à l'étude des fourmis de l'Afrique tropicale. *Bulletin et Annales de la Société Entomologique de Belgique* 73: 95 – 108.

Chapter VII

A unique nest-protection strategy in a new species of spider wasp

Michael Staab, Michael Ohl, Chao-Dong Zhu and Alexandra-Maria Klein

PLoS ONE, under review, submitted on 25.03.2014

Female of the 'Bone-House Wasp' Deuteragenia ossarium *Ohl, 2014*.

Abstract

Hymenoptera show a great variation in reproduction potential and nesting behavior, from thousands of eggs in sawflies to just a dozen in nest-provisioning wasps. Reduction in reproductive potential in evolutionary derived Hymenoptera is often facilitated by advanced behavioral mechanisms and nesting strategies. Here we describe a surprising nesting behavior that was previously unknown in the entire animal kingdom: the use of a vestibular cell filled with dead ants in a new spider wasp (Hymenoptera: Pompilidae) species collected with trap nests in South-East China. We scientifically describe the 'Bone-House Wasp' as *Deuteragenia ossarium* sp. nov., named after graveyard bone-houses or ossuaries. We show that *D. ossarium* nests are less vulnerable to natural enemies than nests of other sympatric trap-nesting wasps, suggesting an effective nest protection strategy, most likely by utilizing chemical cues emanating from the dead ants.

Introduction

Natural selection of life-history strategies results in increased individual fitness by ensuring successful reproduction, but reproductive strategies in animals vary widely (Pianka 1970, Stearns 1976). While r-strategists produce a high number of offspring with limited survival chances, offspring of K-strategists have much higher survival chances at the cost of limited reproduction potential. Hymenoptera show a broad variation in reproduction potential, making them ideal models to study reproductive strategies (O'Neill 2001). Typical for most insects, a single female of the ancestral sawflies and parasitic wasps can lay hundreds of eggs during her lifetime, but the more advanced nest-provisioning Hymenoptera can rarely lay more than a dozen (reviewed in O'Neill 2001).

Examples for the latter group are the Pompilidae, an evolutionary derived cosmopolitan family of spider-hunting wasps, well-known for the eye-catching tarantula hawks of the New World genus *Pepsis* (Schmidt 2004). Currently about 5000 predominately tropical and subtropical species are described (Pitts et al. 2006). The larvae of almost all species develop on a single paralyzed spider while the adults feed mostly on floral nectar (O'Neill 2001). Pompilidae show a wide range of reproductive strategies from ectoparasitoids to nest-provisioning predators, to cleptoparasitoids (O'Neill 2001, Shimizu et al. 2010). Most species nest solitary but parasocial examples are known (Shimizu 2004). In the nest-provisioning Pompilidae the nesting type is a variable albeit crucial aspect of the life history as the nest is primarily protecting the offspring against natural enemies (predators and parasitoids). Usually nests are excavated in the soil, but some species occupy pre-existing above-ground cavities such as abandoned galleries of wood-dwelling beetles (Krombein 1967, O'Neill 2001, Shimizu and Ishikawa 2002). Mud cells attached under leafs or rock prominences as well as freehanging nests coated with plant resin are occurr in several species (Shimizu 2004, Barthelemy and Pitts 2012).

Species of the genus *Deuteragenia* Šustera, 1912 in the subfamily Pepsinae show the usual nest-construction behavior in cavity-nesting Pompilidae. As far as it is known, nests contain several brood cells separated by thin walls of plant debris, resin or, most commonly, soil material of that also the empty outermost vestibular cell is constructed once food-provisioning and egg-laying are completed (Krombein 1967, O'Neill 2001, Shimizu and Ishikawa 2002). After nest construction, nests are abandoned and the females do not further care for the offspring. Hence, there is no protection for the developing larvae against natural enemies except the fragile physical barrier of the vestibular cell. *Deuteragenia* comprises more than 50 species and has a worldwide distribution in wooded areas with the exception of Australia (Shimizu and Ishikawa 2002, Lelej and Loktionov 2012, Pitts et al. 2013). The *Deuteragenia* fauna occurring in Japan and the Russian Far East has been revised in detail (Lelej 1986, Shimizu and Ishikawa 2002, 2003).

In this paper we describe *Deuteragenia ossarium* sp. nov. from South-East China. The species is unique not only in the genus *Deuteragenia* but also in Pompilidae and all other cavity-nesting wasps by showing a novel and unique nest-protection strategy, the construction of a vestibular cell filled with dead ants.

Material and methods

Ethics statement

Necessary permits to conduct field work were obtained from the Administration Bureau of the Gutianshan National Nature Reserve.

Study site

This study was carried out in the Gutianshan National Nature Reserve (GNNR) (29°14' N/ 118°07' E), Zhejiang Province, South-East China (Legendre et al. 2009, Bruelheide et al. 2011). The GNNR was established in 1975 to protect about 8,000 ha of a highly diverse semi-evergreen broad-leaved forest. The terrain is characterized by steep slopes along an elevation gradient between 250 and 1260 m above sea level. The mean annual temperature is 15.3°C and the mean annual precipitation is 1964 mm (Geissler et al. 2012). Typical tree species in old-growth forest are *Castanopsis eyrei* (Champion ex Benth.) Hutch. (Fagaceae), *Cyclobalanopsis glauca* (Thunberg) Oers. (Fagaceae), and *Schima superba* Gardn. et Champion (Thecaceae) (Legendre et al. 2009, Bruelheide et al. 2011). Outside the GNNR, monocultures of the conifers *Cunninghamia lanceolata* (Lamb.) Hook. (Cupressaceae) and *Pinus massoniana* (Lamb.) (Pinaceae) dominate (López-Pujol et al. 2006).

In 2008, the ‘BEF-China’ Project established a total of 27 study plots across the entire GNNR, each comprising 30 m x 30 m, along gradients of tree species richness and successional age that we worked on in this study. For detailed descriptions of the study plots including maps, geological information and exhaustive botanical details we refer to Bruelheide et al. (2001).

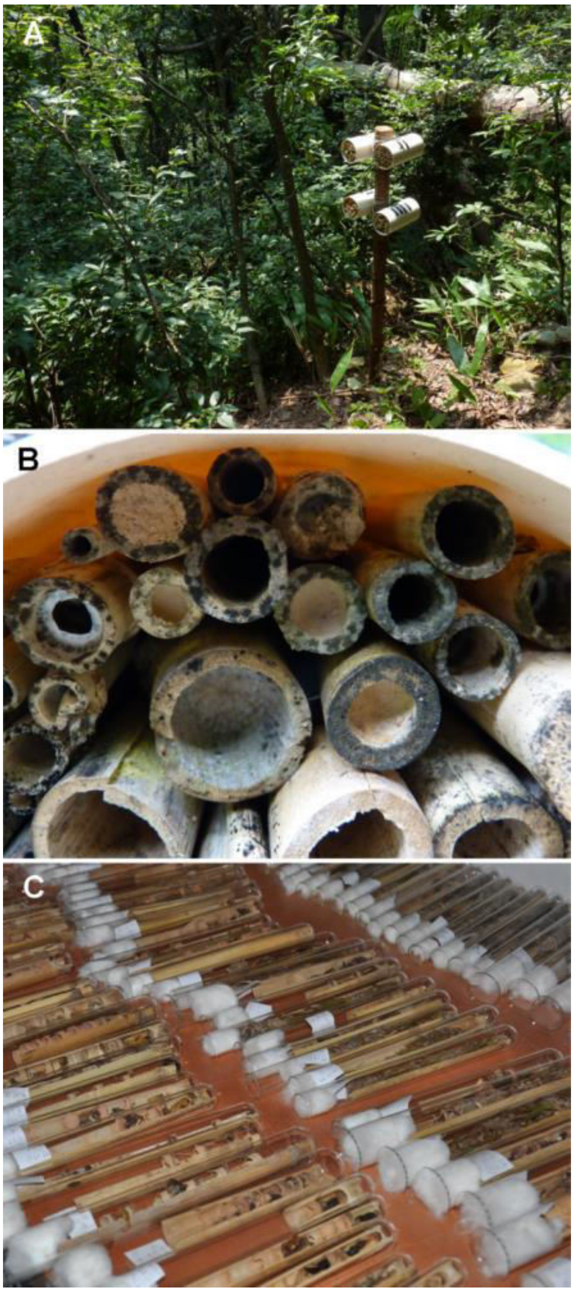


Figure 1. Trap nests to collect solitary cavity-nesting Hymenoptera. (A) Exposed trap nest in the Gutianshan National Nature Reserve, the type locality of *Deuteragenia ossarium*. (B) Occupied reed internodes containing nests are identifiable by the characteristic nest seal that, in most species, consists of soil material. (C) Opened nests reared in test tubes closed with cotton wool. Photographs: Michael Staab.

Sample collection

Nests of solitary cavity-nesting wasps were collected in the 27 plots with trap nests from September 2011 to October 2012. In each plot, two wooden posts with four trap nests, each consisting of a plastic tube (length: 22 cm, diameter: 12.5 cm) filled with *Arundo donax* L. (Poaceae) internodes (diameter: 2-20 mm) were exposed (Figure 1A). Trap nests were placed in approximately 1.5 m height to provide standardized nesting sites for cavity-nesting solitary wasps (Tscharntke et al. 1998, Klein et al. 2006). Monthly, internodes containing nests that are easily distinguishable by the characteristic nest-closing pluck (Figure 1B) were collected and a fungicide that is non-toxic to Hymenoptera (Folicur®, Bayer CropScience, Monheim, Germany) was applied with a hand sprayer to prevent molding in the humid climate of the GNNR. Nests were taken to the laboratory, opened, and reared in glass test tubes closed with cotton wool (Figure 1C) until hatching.

Data analysis

For every nest we recorded the number of brood cells and parasitized brood cells. Length and diameter of nests was measured with a caliper. After hatching, we identified all species with the help of taxonomic experts. From all nests containing a vestibular cell filled with dead ants, we randomly selected 26 for ant species identification. Voucher specimens were deposited at the University of Freiburg, Germany.

Analyses were done with the software R 3.0.2 (www.R-project.org). To estimate how many ant species are expected in the vestibular cells, we calculated the first-order jackknife estimator with single nests as sample units using the R-package 'vegan' (http://CRAN.R-project.org/package=vegan). To test if the presence of dead ants is involved in nest protection, we pooled total brood cells and parasitized brood cells per plot separately for *D. ossarium* and all other wasps combined. We used a binomial generalized linear mixed model (glmm) in the R-package 'lme4' (http://CRANR-projectorg/package=lme4) with a logit-link function (Zuur et al. 2009). Parasitism rate was used as response variable. Plot was treated as random factor to account for plot-specific effects on brood-cells numbers and parasitism rates. Group identity (*D. ossarium* / all other wasps) was used as explanatory variable. We also included the number of brood cells in each group as explanatory variable to account for possible effects of host population density on parasitism (Hassel and Waage 1984).

Species description

The general terminology in pompilid taxonomy and morphology is based on Day (1988) and its application in *Deuteragenia* (as a subgenus of *Dipogon* Fox, 1897) by Shimizu and Ishikawa (Shimizu and Ishikawa 2002, 2003). Specimens assigned to the *Deuteragenia conspersa*-group could not be studied, but the description and illustrations in Shimizu and Ishikawa (Shimizu and Ishikawa 2002, 2003) are exhaustive and detailed. Thus, comparing the type series of *D. ossarium* with other members of the *D. conspersa*-group only based on published descriptions is sufficient. In addition, females and males of *D. bifasciata* (Geoffroy, 1784), as well as females of *D. subintermedia* (Magretti, 1886) and *D. vechti* (Day, 1979) have also been studied for comparison. All comparative specimens were obtained from the collection of the Museum für Naturkunde, Berlin, Germany.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:1ED0DD02-CF68-466C-833C-E37A3ECBAF02.

The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Results

In total, we collected 829 nests of cavity-nesting wasps with 1929 brood cells belonging to 18 species (see Appendix A). To our surprise, 73 of the nests (213 brood cells) had a vestibular cell filled with dead ants (Figure 2A-C). These nests contained between one and six brood cells (mean: 2.9 ± 1.3 SD), each provisioned with a single Agelenidae spider, had a mean length of 101.2 ± 36.8 mm, and a mean diameter of 6.6 ± 1.6 mm.

The 26 vestibular cells examined closer contained up to 13 ant individuals (mean: 4.9 ± 2.6). All ant specimens were in good condition and could be identified to nine different species (see Appendix B), with up to four species co-occurring within a chamber (mean: 2.0 ± 1.0). *Pachycondyla astuta* Smith, 1858 (Figure 2C), was the only ant in 42% of the nests, found in all but one nest, and accounted for 71% of all ant individuals. The first-order jackknife estimator predicted 13 ± 2 ant species to occur in the vestibular cells, of which we collected 69%.

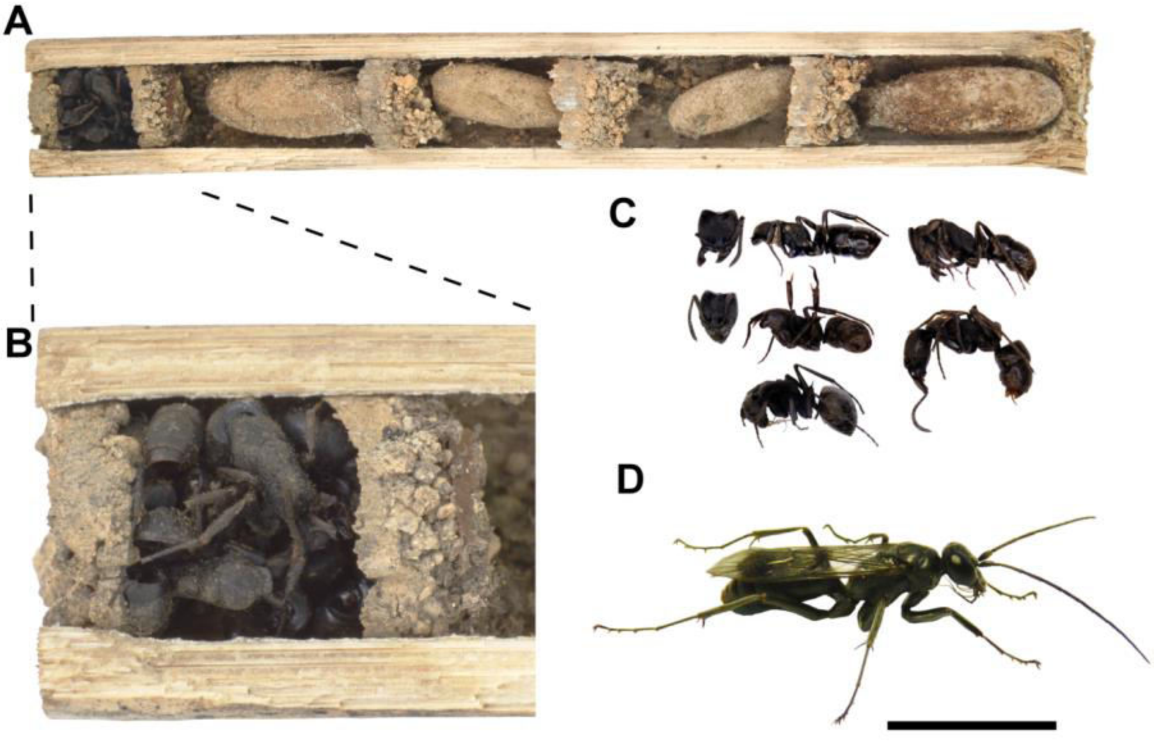


Figure 2. Nest protection in *Deuteragenia ossarium*. (A) Overview of a nest. Individual brood cells are separated by thin walls of soil material. (B) The nest is closed by a vestibular cell filled with dead ants. (C) Contents of a vestibular cell. *Pachycondyla astuta* was the ant species most commonly found, but other ant species, such as *Polyrhachis illaudata* Walker, 1859 (lowest ant specimen), occurred as well. (D) Freshly hatched adult female of *D. ossarium*. Scale bar: (A) 15 mm, (B) 5 mm, (C,D) 10 mm. Photographs: Merten Ehmig (A,B), Michael Staab (C,D).

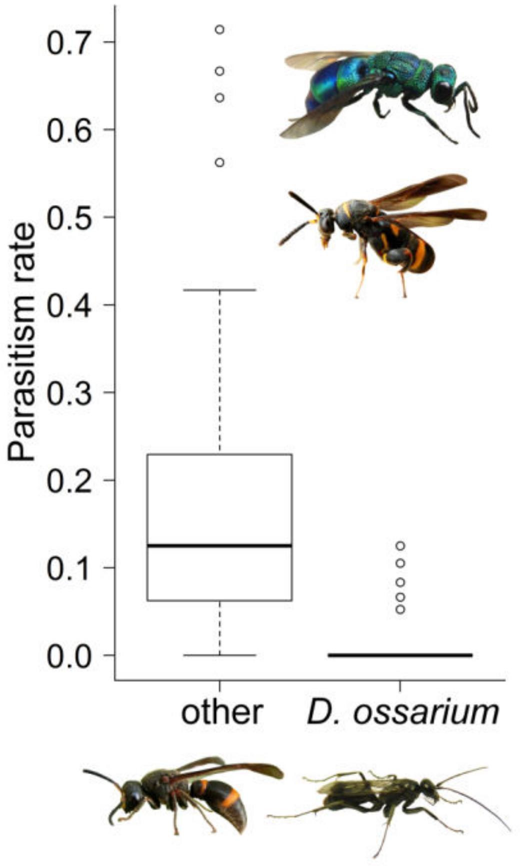


Figure 3. Parasitism rates of *D. ossarium* were significantly compared to other cavity-nesting was species. The sympatric cavity-nesting wasp community is exemplified by *Orancistrocerus drewseni* (de Saussure, 1857) (Vespidae, lower left). As examples of parasitoid species *Chrysis principalis* Smith, 1874 (Chrysididae, top) and *Leucospis sp.* (Leucospidae, middle) are shown. Photographs: Michael Staab.

Table 1. Summary statistics of the binomial glmm testing for the effect of group identity (other wasps / *D. ossarium*) and brood cell numbers on parasitism rates. Significant P-values are indicated in bold.

Variable	Estimate ± SE	z	P
Group	2.01 ± 0.54	3.75	<**0.001**
Brood cells	-0.0075 ± 0.0084	-0.89	0.37

Rearing of the nests with the ant-filled vestibular cell revealed an undescribed species of Pompilidae. Only seven of the 213 brood cells belonging to this species were parasitized (3%): four by *Irenangulus sp.* (Pompilidae), two by minute drosophilid flies, and one by *Lycogaster sp.* (Trigonalidae). Overall parasitism rates per study plot of all other trap-nesting wasp species (16.5%, Figure 3) were significantly higher than in the undescribed species and were unrelated to the number of brood cells per group (Table 1).

The new species clearly belongs to the genus *Deuteragenia*, which has recently been raised from subgeneric status in *Dipogon* to full genus rank (Lelej and Loktionov 2012). Among other diagnostics, *Deuteragenia* is characterized by the presence of a markedly long flagellomere I and an unmodified pterostigma. Within *Deuteragenia*, the new species belongs in the *Deuteragenia conspersa*-group, which has a depressed clypeal rim without preapical ridge and distinctive, long bristly setae posterolaterally on the propodeum.

Deuteragenia ossarium **sp. nov.** Ohl, 2014 (Figure 4) urn:lsid:zoobank.org:act:9CFBF85F-04D8-4649-A1C3-2B975C993B31

Etymology. The new species is named after the Latin ‘ossarium’, which means bone-house or ossuary. An ‘ossarium’ is a covered site, where human remains are deposited. The species name is an allusion to the unusual nesting strategy of the new species, which closes the nest with a vestibular cell filled with dead ants. This reminds us of historical bone-houses in monasteries and graveyards, which over the time were filled with piles of human bones. The new name is a noun in apposition.

Suggested common name. As a common name for *D. ossarium* we suggest in reference to its biology the use of 'Bone-House Wasp'.

Distribution. Known from South-East China only.

Diagnosis. *Deuteragenia ossarium* is most similar to *D. conspersa* (Pérez, 1905) and keys out at this species in the key to *Deuteragenia* by Shimizu and Ishikawa (2003); as a subgenus in *Dipogon*). The species share the following characters: Flagellomere I about 5.0x as long as wide, clypeus significantly wider than lower interocular distance, propodeal surface microsculptured and dull, mid and hind femoral venter with erect whitish setae, dorsal side of femora bare, and forewing with second recurrent vein (2m-cu) meeting submarginal cell III at basal 0.2-0.3.

The principal differences between the two species are (character states of *D. conspersa* in parentheses): body color totally pitch black (at least mandible, antenna, tarsomeres and metasomal tergite I partly ferrugineous), except for the male clypeus, which is ivory white with a black basal spot of varying size (Figure 4E) (male clypeus black, in a few specimens lateral portions pale brown), inner eye orbits rather strongly converging above: upper, middle and lower interocular distances 6.5 : 10 : 10 (average measures 7.2 : 10 : 9.3), metasomal tergites II-VI with short, silvery bristles (with long brownish bristles), and propodeal surface with well-spaced, setiferous macropunctures in posterior half only (evenly finely and densely punctate, with setiferous macropunctures evenly distributed). *Deuteragenia conspersa* is known from Korea and Japan (Honshu, Shikoku, and Kyushu) (Shimizu and Ishikawa 2003), whereas *D. ossarium* is recorded from South-East China only.

Description. Female. Total body length 8.9-15.2 mm, forewing length 7.4-13.3 mm.

Integument totally black. Beard and labral setae golden, ochraceous or coppery, setae otherwise mostly whitish.

Wings overall hyaline with faint greyish tinge, which is more dominant in large specimens. Forewing with narrow, indistinct fuscous marking along transverse section of at least longitudinal vein M, in some specimens also along cu-a and transverse section of Rs. Forewing also with large, fuscous marking occupying most of submarginal cells II and III, basal portion of marginal cell, and distal portion of discoidal cell II.

Frons densely, rather regularly punctate. Remaining head surface with fine, dense, shallow punctures and intersperse, widely spaced macropunctures. Pronotum and mesoscutum finely, densely punctate, mesosomal dorsum microsculptured otherwise. Mesosomal sides microsculptured, with widely spaced macropunctures. Upper part of metapleuron with indistinct, transverse, course rugae. Lateral portion of metanotum shining, with oblique rugae. Propodeal dorsum miscrosculptured, with setiferous macropunctures in posterior half only. Metasoma microsculptured, dull.

Lower frons, basal half of mandible, gena, lower portion of mesosomal pleura, coxae, and posterolateral portion of propodeum with appressed, dense, silvery pubescence. Long ochraceous setae on outer mandibular surface and along anterior margin of clypeus. Gena, prosternum, forecoxa, propodeum posteriorly and tergum I with markedly long, silvery setae; similar but shorter setae on vertex, thoracic dorsum and mid and hindcoxae.

Head slightly broader than long (1.1-1.3). Inner eye orbits rather strongly converging above: upper, middle and lower interocular distances 6.5 : 10 : 10. Length of flagellomere I 4.9-5.4x as long as wide.

Structurally otherwise identical to *D. conspersa* (see Shimizu and Ishikawa 2002).

Male. Overall similar to female, except for: Total body length 6.6-9.8 mm, forewing length 5.9-8.3 mm.

Integument totally black, except for the following: clypeus ivory white with black basal marking of varying size; labial and maxillary palps, tibial spurs and foretibia and tarsi below ochraceous. In some specimens, pronotum with brownish transverse band. Body setae mostly whitish.

Wings hyaline, markings absent except for faint longitudinal marking in submarginal cells II and III, in a few larger males also in marginal cell and discoidal cell I.

Frons densely, rather regularly punctate. Remaining head surface with fine, dense, shallow punctures and intersperse, widely spaced macropunctures. Pronotum and mesoscutum finely, densely punctate, mesosomal dorsum microsculptured otherwise. Mesosomal sides microsculptured, with widely spaced macropunctures. Upper part of metapleuron with indistinct, transverse, course rugae. Lateral portion of metanotum shining, with oblique rugae. Propodeal dorsum miscrosculptured, with setiferous macropunctures in posterior half only. Metasoma microsculptured, dull.

Lower frons, basal half of mandible, gena, lower portion of mesosomal pleura, coxae, and posterolateral portion of propodeum with appressed, dense, silvery pubescence. Long ochraceous setae on outer mandibular surface and along anterior margin of clypeus. Gena, prosternum, forecoxa, propodeum posteriorly and tergum I with markedly long, silvery setae; similar but shorter setae on vertex, thoracic dorsum and mid and hindcoxae.

Head slightly broader than long (1.1-1.3). Inner eye orbits rather strongly converging above: upper, middle and lower interocular distances 6.5 : 10 : 10. Length of flagellomere I 4.9-5.4x as long as wide.

Genitalia (Figure 4F): Parameres with long, thin setae in apical two-thirds and strong, stout setae ventrobasally. Parapenial lobes slightly extending beyond apex of aedeagus, finger-shaped. Aedeagus weakly sclerotized, simple. Digitus laterally compressed, apex strongly setose. Cuspis indistinct.

Structurally otherwise identical to *D. conspersa* (see Shimizu and Ishikawa 2002).

Material examined. Holotype, female. **CHINA, Zhejiang Province**, ca. 30 km NW of Kaihua, 29° 16' 50"N / 118° 5' 2"E, 655 m, 5 Jun 2012, leg. M. Staab (T487) (Insect Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China).

Paratypes (61 females, 37 males). **CHINA. Zhejiang Province**, ca. 30 km NW of Kaihua, 29° 14' 47"N / 118° 6' 58"E, 402 m, 2 Jun 2012, leg. M. Staab (T482, T495, T514) (1 female, 2 males); same data, but 29° 16' 53"N / 118° 5' 17"E, 679 m, 05 Jun 2012 (T538, T539) (3 females, 1 male); same data, but 29° 16' 14"N / 118° 4' 51"E, 566 m, 05 Jun 2012 (T542) (2 females, 1 male); same data, but 29° 16' 53"N / 118° 5' 17"E, 679 m, 29 Jun 2012 (T532) (1 female); same data, but 29° 16' 53"N / 118° 5' 17"E, 679 m, 3 Jul 2012 (T529, T530) (1 female, 1 male); same data, but 29° 16' 50"N / 118° 5' 2"E, 655 m, 30 Sep 2012 (T724) (2 females); same data, but 29° 14' 49"N / 118°6' 44"E, 507 m, 04 Oct 2012 (T896) (1 female); same data, but 29° 16' 53"N / 118° 5' 17"E, 679 m, 06 Oct 2012 (T771, T772) (2 females); same data, but 29° 16' 53"N / 118° 5' 17"E, 679 m, 07 Oct 2012 (T770) (1 male); same data, but 29° 15' 7"N / 118° 8' 37"E, 903 m, 8 Oct 2012 (T1546) (4 females, 2 males); same data, but 29° 14' 20"N 7 118°7' 26"E, 720 m, 9 Oct 2012 (T1288, T1289, T1290, T1291, T1292) (3 females, 3 males); same data, but 29° 16' 37"N / 118° 5' 26"E, 617 m, 10 Oct 2012 (T1273, T1278, T1279, T1281) (5 females, 1 male); same data, but 29° 16' 50"N / 118° 5' 2"E, 655 m, 17 Oct 2012 (T1453) (2 females); same data, but 29° 15' 18"N / 118° 8' 51"E, 880 m, 21 Oct 2012 (T1835) (1 female); same data, but 29° 16' 50"N / 118° 5' 2"E, 655 m, 9 May 2013 (T1374) (1 male); same data, but 29° 12' 54"N / 118°7' 18"E, 251 m, 12 May 2013 (T1664) (1 female); same data, but 29° 14' 57"N / 118°8' 5"E, 590 m, 12 May 2013 (T1820) (1 female, 1 male); same data, but 29° 14' 58"N / 118° 8' 7"E, 639 m, 12 May 2013 (T1855) (1 male); same data, but 29° 16' 37"N / 118° 5' 26"E, 617 m, 13 May 2013 (T0729) (1 female, 1 male); same data, but 29° 16' 14"N / 118° 4' 51"E, 566 m, 13 May 2013 (T1301) (1 male); same data, but 29° 15' 7"N / 118° 8' 37"E, 903 m, 13 May 2013 (T1371) (2 females, 1 male); same data, but 29° 16' 50"N / 118° 5' 2"E, 655 m, 13 May 2013 (T1375, T1470) (1 female, 1 male); same data, but 29° 14' 20"N 7 118°7' 26"E, 720 m, 13 May 2013 (T1445, T1565, T1601) (1 female, 3 male); same data, but 29° 15' 7"N / 118° 8' 37"E, 903 m, 13 May 2013 (T1481, T1482) (1 female, 2 male); same data, but 29° 15' 18"N / 118° 8' 51"E, 880 m, 13 May 2013 (T1499) (1 female, 2 males); same data, but 29° 12' 54"N / 118°7' 18"E, 251 m, 13 May 2013 (T1511, T1528) (2 females); same data, but 29° 15' 7"N / 118°9' 28"E, 670 m, 13 May 2013 (T1539, T1833) (1 female,

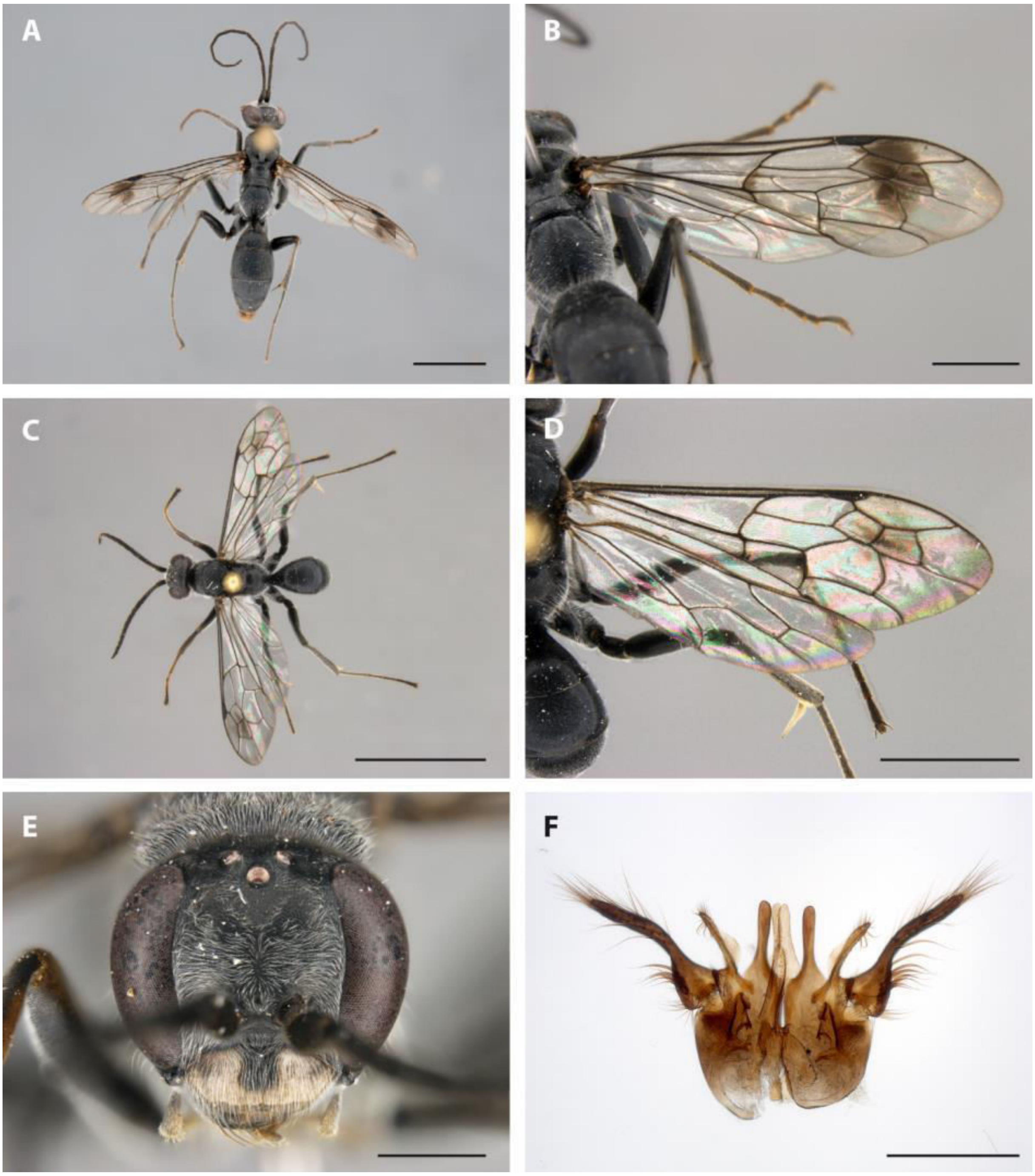


Figure 4. *Deuteragenia ossarium* Ohl sp. nov., (A,B) female, holotype; (C-F) male, paratype (T1482). (A,C) dorsal habitus, (B,D) right forewing, (E) head in frontal view, (F) genitalia in ventral view, slightly spread to show major elements. Scale bars: (A,C) 5.0 mm, (B,D) 2.0 mm, (E,F) 0.6 mm. Photographs: Bernhard Schurian (A-E), Birger Neuhaus (F).

3 males); same data, but 29° 12' 52"N / 118°8' 14"E, 419 m, 13 May 2013 (T1572) (1 female, 1 male); same data, but 29° 14' 57"N / 118°8' 5"E, 590 m, 13 May 2013 (T1821, T1914, T1915, T1916, T1917, T1918) (7 females, 1 male); same data, but 29° 14' 58"N / 118° 8' 7"E, 639 m, 13 May 2013 (T1853) (1 female); same data, but 29° 14' 47"N / 118° 6' 58"E, 402 m, 13 May 2013 (T1920) (2 female, 2 male); same data, but 29° 14' 20"N 7 118°7' 26"E, 720 m, 15 May 2013 (T1520) (1 female); same data, but 29° 14' 20"N 7 118°7' 26"E, 720 m, 16 May 2013 (T0684) (1 female); same data, but 29° 16' 14"N / 118° 4' 51"E, 566 m, 16 May 2013 (T1302) (1 female, 1 male); same data, but 29° 12' 54"N / 118°7' 18"E, 251 m, 16 May 2013 (T1508) (1 female); same data, but 29° 15' 7"N / 118°9' 28"E, 670 m, 16 May 2013 (T1537) (1 male); same data, but 29° 15' 7"N / 118°9' 28"E, 670 m, 17 May 2013 (T1540) (1 female); same data, but 29° 14' 20"N 7 118°7' 26"E, 720 m, 17 May 2013 (T1566) (1 female). **Jiangxi Province**, ca. 15 km SE of Wuyuan, 29° 7' 16"N / 117° 54' 22"E, 125 m, 16 May 2013 (T2402) (1 female, 1 male); same data, but 29° 7' 30"N / 117° 54' 31"E, 221 m, 17 May 2013 (T2197) (1 female); same data, but 29° 7' 31"N / 117° 54' 36"E, 247 m, 2 Jun 2013 (T2540) (1 female, 1 male); same data, but 29° 7' 31"N / 117° 54' 36"E, 247 m, 3 Jun 2013 (T2541) (1 male).

All specimens have been reared from trap nests (Figure 1).

The majority of the paratypes will be deposited in the Insect Collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China, along with the holotype. The remaining paratypes will finally remain in the collections of the Museum für Naturkunde, Berlin, Germany, and pairs will also be deposited in the Natural History Museum, London, UK, the American Museum of Natural History, New York, USA, the Smithsonian Institution, Washington DC, USA, the California Academy of Sciences, San Francisco, USA, the Utah State University, Logan, USA, and the collection of the Institute of Earth and Environmental Sciences, University of Freiburg, Germany.

Discussion

We report here on a unique and effective nest-protecting strategy, the construction of a vestibular cell filled with dead ants in a new spider wasp. Vestibular cells occur commonly in cavity-nesting wasps (Krombein 1967), are normally empty and do not serve a protective function (Asis et al. 2007). However, offspring of *D. ossarium* had significantly lower parasitism rates than the sympatric cavity-nesting wasp community. Low parasitism was unrelated to population density effects (Hassel and Waage 1984), thus delivering initial support for the protective function of the ant-filled vestibular cell. We propose two non-exclusive hypotheses: chemical camouflage and chemical defense by utilization of volatile chemical cues emanating from the dead ants. Ants produce a diverse array of organic compounds (Hölldobler and Wilson 1990), including species-specific cuticular hydrocarbons (CCHs) which are a central part of the nestmate-recognition system (Lahav et al. 1999, Brandstaetter et al. 2008, Martin and Drijfhout 2009). Being long-chained molecules of low volatility, CCHs persist on the cuticula of dead Hymenoptera for a long time period (Martins et al. 2009), thus giving *D. ossarium* nests the scent of an ant colony.

This scent camouflages nests against natural enemies which search their host by scent, as CCHs are known to release behavioral reactions without tactile interactions (Brandstaetter et al. 2008). The scent may also repel predators, as most ant species ferociously defend their colonies against intruders. In this context, we find it particularly interesting that the numerically dominating ant species in *D. ossarium* nests is *P. astuta*, an aggressive, large-bodied, and common species in the study region that has a powerful sting. By using a big ant species, already few ant individuals are sufficient to stock the vestibular cell with large quantities of CCHs. By using an abundant ant species, potential predators may have had contact with the species before and therefore avoid the species-specific scent. The proposed function of the ant-chamber is most effective against predators that break the nest and against parasitic wasps that penetrate the nest with their long ovipositor. Such parasitoids attacked other trap-nesting wasps in the study region, but were never found in nests of *D. ossarium*, which was only attacked by parasitoids which entered the nest prior the construction of the ant chamber.

Although some cavity-nesting wasp species are known to incorporate arthropod fragments into nest construction (Morato and Martins 2006) or nest camouflage (Auko et al. 34), and to prey on ants (Evans 1962), *D. ossarium* is the first species that uses complete ants for nest construction but by far not the only animal species that exploits ants to protect the own progeny. Many other species independently evolved stunning strategies; for example the caterpillars of most Lycaenidae butterflies life obligatory in ant colonies (Pierce et al. 2002), many beetles are exclusively known from the safety of ant nests (Paeivinen et al. 2003) and several snakes lay their eggs only in the fungus-chambers of aggressive leaf-cutting ant nests (Baer et al. 2009). However, none of these examples builds literally a barrier out of ant carcasses. When we first saw a nest of *D. ossarium* we were reminded on the historical bone houses or ossuaries in graveyards, and thus suggest in allusion to its biology 'Bone-House Wasp' as common name.

Acknowledgements

We are grateful to the administration of the Gutianshan National Nature Reserve and the BEF-China consortium, Sabine Both, Xiaojuan Liu, Keping Ma, Helge Bruelheide and Bernhard Schmid for their support. The latter two, Christoph J. Kleineidam and Tamar Marcus gave helpful comments on the manuscript. Merten Ehmig provided photographs for Figure 2A and 2B, Bernhard Schurian for Figure 4A-E, and Birger Neuhaus for Figure 4F.

References

Asis JD, Beneitez A, Tormos J, Gayubo SF, Tome MAM (2007) The significance of the vestibular cell in trap nesting wasps (Hymenoptera: Crabronidae): Does its presence reduce mortality? Journal of Insect Behavior 20:289-305.

Auko TH, Silvestre R, Pitts JP (2013) Nest camouflage in the spider wasp *Priochilus captivum* (Fabricius, 1804) (Hymenoptera: Pompilidae), with notes on the biology. Tropical Zoology 26:140-144.

Baer B, den Boer SPA, Kronauer DJC, Nash DR, Boomsma JJ (2009) Fungus gardens of the leafcutter ant *Atta colombica* function as egg nurseries for the snake *Leptodeira annulata*. Insectes Sociaux 56:289-291.

Barthelemy C, Pitts J (2012) Observations on the nesting behavior of two agenielline spider wasps (Hymenoptera, Pompilidae) in Hong Kong, China: *Macromerella honesta* (Smith) and an *Auplopus* species. Journal of Hymenoptera Research 28:13-35.

Brandstaetter AS, Endler A, Kleineidam CJ (2008) Nestmate recognition in ants is possible without tactile interaction. Naturwissenschaften 95:601-608.

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geissler C, Guo DL, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecological Monographs 81:25-41.

Day MC (1988) Spider wasps. Hymenoptera: Pompilidae, vol 6. Handbooks for the identification of British Insects. Royal Entomological Society of London, London.

Evans HE (1962) A review of nesting behavior of digger wasps of the genus Aphilanthops, with special attention to the mechanics of prey carriage. Behaviour 19:239-260.

Geissler C, Kühn P, Böhnke M, Bruelheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. Catena 91:85-93.

Hassell MP, Waage JK (1984) Host-parasitoid population interactions. Annual Review of Entomology 29:89-114.

Hölldobler B, Wilson EO (1990) The Ants. Belknap Press of Harvard University Press, Cambridge.

Klein AM, Steffan-Dewenter I, Tscharntke T (2006) Rain forest promotes trophic interactions and diversity of trap-nesting hymenoptera in adjacent agroforestry. Journal of Animal Ecology 75:315-323.

Krombein KV (1967) Trap-nesting wasps and bees: Life histories, nests and associates. Smithsonian Press, Washington DC.

Lahav S, Soroker V, Hefetz A, Vander Meer RK (1999) Direct behavioral evidence for hydrocarbons as ant recognition discriminators. Naturwissenschaften 86:246-249.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF, He F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Lelej AS (1986) Spider wasps of *Dipogon* Fox and *Poecilageniella* Ishikawa (Hymenoptera, Pompilidae) of the Far East. Entomologicheskoe Obozrenie 65:799-808.

Lelej AS, Loktionov VM (2012) Phylogeny and classification of the tribe Deuterageniini (Hymenoptera, Pompilidae: Pepsinae). Far Eastern Entomologist 254:1-15.

López-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: Richly varied, endangered, and in need of conservation. Biodiversity and Conservation 15:3983-4026.

Martin S, Drijfhout F (2009) A review of ant cuticular hydrocarbons. Journal of Chemical Ecology 35:1151-1161.

Martin SJ, Zhong W, Drijfhout FP (2009) Long-term stability of hornet cuticular hydrocarbons facilitates chemotaxonomy using museum specimens. Biological Journal of the Linnean Society 96:732-737.

Morato EF, Martins RP (2006) An overview of proximate factors affecting the nesting behavior of solitary wasps and bees (Hymenoptera : Aculeata) in preexisting cavities in wood. Neotropical Entomology 35:285-298.

O'Neill K (2001) Solitary wasps: Behavior and natural history. Cornell University Press, Ithaca, NY

Paeivinen J, Ahlroth P, Kaitala V, Kotiaho JS, Suhonen J, Virola T (2003) Species richness and regional distribution of myrmecophilous beetles. Oecologia 134:587-595.

Pianka ER (1970) R-selection and K-selection. American Naturalist 104:592-597.

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology 47:733-771.

Pompilidae - Spider wasps (pompilidweb) (2013) http://www.usu.edu/pompilidweb/default.htm. Accessed 18 December 2013

Pitts JP, Wasbauer MS, von Dohlen CD (2006) Preliminary morphological analysis of relationships between the spider wasp subfamilies (Hymenoptera: Pompilidae): Revisiting an old problem. Zoologica Scripta 35:63-84.

Schmidt JO (2004) Venom and the good life in tarantula hawks (Hymenoptera: Pompilidae): How to eat, not be eaten, and live long. Journal of the Kansas Entomological Society 77:402-413.

Shimizu A (2004) Natural history and Behavior of a Japanese parasocial spider wasp, *Machaerothrix tsushimensis* (Hymenoptera : Pompilidae). Journal of the Kansas Entomological Society 77:383-401.

Shimizu A, Ishikawa R (2002) Taxonomic studies on the Pompilidae occurring in Japan north of the Ryukyus: Genus *Dipogon*, subgenus *Deuteragenia* (Hymenoptera) (part 1). Entomological Science 5:219-235.

Shimizu A, Ishikawa R (2003) Taxonomic studies on the Pompilidae occurring in Japan north of the Ryukyus: Genus *Dipogon*, subgenus *Deuteragenia* (Hymenoptera) (Part 3). Entomological Science 6:165-181.

Shimizu A, Wasbauer M, Takami Y (2010) Phylogeny and the evolution of nesting behaviour in the tribe Ageniellini (Insecta: Hymenoptera: Pompilidae). Zoological Journal of the Linnean Society 160:88-117.

Stearns SC (1976) Life-history tactics - Review of ideas. Quarterly Review of Biology 51:3-47.

Tscharntke T, Gathmann A, Steffan-Dewenter I (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. Journal of Applied Ecology 35:708-719.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health. Springer, Berlin.

Appendix

Appendix A. List of all sympatric cavity-nesting wasp species collected together with *Deuteragenia ossarium*. Pompilidae were identified by Raymond Wahis (Liege, Belgium), Sphecidae by Michael Ohl (Berlin, Germany) and Vespidae by Tingjing Li (Chongqing, P.R. China).

Family	Species	Nests	Brood cells
Pompilidae	*Auplopus sp.2*	2	8
	Auplopus sp.3	1	4
	Auplopus sp.4	8	79
	Auplopus sp.5	2	4
	Deuteragenia ossarium Ohl, n. sp.	73	213
	Deuteragenia sp.1	4	11
	Dipogon sp.2	2	8
Sphecidae	*Chalybion japonicum* (Gribodo, 1883)	3	5
	Hoplammophila aemulans (Kohl, 1901)	156	199
Vespidae	*Allorhynchium chinense* (de Saussure, 1862)	1	1
	Ancistrocerus nigricornis (Curtis, 1826)	1	2
	Ancistrocerus trifasciatus (Müller, 1776)	4	14
	Anterhynchium flavomarginatum (Smith, 1852)	548	1340
	Anterhynchium sp.1	1	1
	Discoelius nigriclypeus Zhou & Li, 2013	1	1
	Epsilon fujianensis Lee, 1981	18	24
	Eumenes quadratus Smith, 1852	1	2
	Orancistrocerus drewseni (de Saussure, 1857)	3	13

Appendix B. Ant species found in 26 vestibular cells of *Deuteragenia ossarium*. Species were identified by Michael Staab (Freiburg, Germany).

Subfamily	Species	Abundance	Occurrence
Dolichoderinae	*Technomyrmex obscurior* Wheeler, 1928	1	1
Ectatomminae	*Gnamptogenys panda* (Brown, 1948)	10	7
Formicinae	*Camponotus pseudoirritans* Wang, Xiao & Wu, 1989	1	1
	Camponotus rubidus Wang, Xiao & Wu, 1989	1	1
	Polyrhachis illaudata Walker, 1859	10	7
	Polyrhachis lamellidens Smith, 1874	1	1
Ponerinae	*Leptogenys kitteli* (Mayr, 1870)	2	2
	Pachycondyla astuta Smith, 1858	90	25
	Pachycondyla chinensis (Emery, 1895)	10	7

Danksagung

Zu allererst danke ich meiner Betreuerin Alexandra-Maria Klein für die hervorragende Betreuung der Dissertation, die großen Freiheiten und die Unterstützung in allen erdenklichen Situationen. Vielen vielen Dank dafür Alex!

Nico Blüthgen danke ich für vielfältige und sehr hilfreiche Diskussionen über Netzwerkbiologie und Ameisenökologie.

Tamar Marcus, Andreas Schuldt und David Walmsley trugen zum Fortgang der einzelnen Manuskripte durch kritische und konstruktive Diskussionen entscheidend bei. Tamar und David lasen meine vielen Texte und Versionen bereitwillig Korrektur und bügelten die kleineren und größeren Fehler aus.

Ich danke den Mitdoktoranden und Mitarbeitern des Institutes für Ökologie der Universität Lüneburg, insbesondere den Doktoranden der AG Ökosystemfunktionen, für das angenehme und kollegiale Arbeitsklima. Besonderer Dank geht an das technische Personal Thomas Niemeyer, Martina Nehring und Dieter Stengel, welche mich jederzeit mit Rat und Tat unterstützten. Meinen Bürokolleginnen Nora und Victoria gebührt Anerkennung für geduldiges Zuhören und das stoische Ertragen so mancher Meckerei.

Nach meinem Wechsel nach Freiburg wurde ich von den Arbeitsgruppen Naturschutz, Biometrie und Landespflege herzlich aufgenommen. Vielen Dank für die konzentrierte und bereichernde Atmosphäre während des finalen Schreibens.

Ohne meine vielen Hiwis und Feldassistenten, insbesondere Jan Peters und Merle Noack, wäre die umfangreiche Feld- und Laborarbeit nicht zu bewältigen gewesen, vielen Dank.

Von Henrik von Wehrden durfte ich viel statistisches Wissen und mathematische Denken erlernen, was diese Dissertation stark positiv beeinflusst hat.

Besonderer Dank geht an Brian Fisher und das gesamte Team des 2012 Uganda Ant Course. Die hohe taxonomische Auflösung meiner Manuskripte wäre ohne sie nicht möglich gewesen.

In einer großen Forschergruppe wie BEF-China ist es unmöglich die Namen aller Personen zu erwähnen, die zu dieser Dissertation beigetragen haben. Stellvertretend für alle PIs, Postdocs, Doktoranden und Studenten danke ich den Sprechern Helge Bruelheide, Keping Ma und Bernhard Schmid für ihren Enthusiasmus, ohne den das BEF-China Projekt nicht existieren würde. Mein besonderer Dank gilt Xiaojuan Liu, Sabine Both und Chen Lin für die zahlreichen Hilfestellungen bei der Koordination und Durchführung der Feldarbeit. Chao-Dong Zhu hat als Kooperationspartner meine Arbeit in China stets gefördert und unterstützt. Die gute Kooperation in SP9 des BEF-China Projektes ist auch sein Verdienst. Das Team der BEF Doktoranden und Studenten hat die Feldarbeit in China zu einem unvergesslichen Erlebnis und zur Quelle unzähliger Legenden werden lassen. Insbesondere meinem Zimmerkollegen Wenzel gebührt Anerkennung für die unverwüstliche physische und psychische Unterstützung in allen Lebenslagen.

Zuletzt danke ich meiner Familie und meinen Freunden für den fortwährenden Rückhalt und natürlich den unzähligen Ungenannten in Lüneburg, Freiburg, China und überall sonst.

Diese Dissertation wurde von der Deutschen Forschungsgemeinschaft großzügig finanziell gefördert.

Lebenslauf

Michael Staab
Rufacher Straße 2
79110 Freiburg
michael.staab@nature.uni-freiburg.de

geboren am 01.06.1985 in Alzenau i. Ufr.

Schulausbildung

1991-1995	Grundschule Kleinkahl
1995-2004	Spessart-Gymnasium Alzenau
2004-2005	Wehrdienst, Otto-Lilienthal-Kaserne, Roth

Studium

10.2005 - 07.2010 Diplomstudiengang Biologie, Universität Würzburg
Abschluss: Diplom-Biologe, Note: sehr gut (1,0)

Hauptfach: Tierökologie und Tropenbiologie
Nebenfächer: Genetik / Verhaltensphysiologie und Soziobiologie

Diplomarbeit: „Die Paarungsbiologie der Blattschneiderameise *Atta vollenweideri*“ am Lehrstuhl für Verhaltensphysiologie und Soziobiologie der Universität Würzburg, Note: sehr gut (1,0)

Berufserfahrung und Promotion

10.2010 - 04.2011 Wissenschaftlicher Mitarbeiter an der Universität Würzburg, Lehrstuhl für Zoologie III, Datenanalyse in den „Biodiversitäts Exploratorien“

04.2011 - 04.2014 Promotionsstudent an der Universität Lüneburg, Abteilung für Ökosystemfunktionen

Thema der Promotion „Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest“

Angestrebter Abschluss: Dr. rer. nat.

04.2011 - 05.2013 Wissenschaftlicher Mitarbeiter an der Universität Lüneburg, Abteilung für Ökosystemfunktionen, BEF-China Projekt

seit 06.2014	Wissenschaftlicher Mitarbeiter an der Universität Freiburg, Professur für Naturschutz und Landschaftsökologie, BEF-China Projekt

Feldaufenthalte

08.2008 - 10.2008	Danum Valley Conservation Area, Sabah, Malaysia Praktikum, Thema: „Nahrungsökologie parabiotischer Ameisen“
10.2009 - 11.2009	Rio Pilcomayo National Park, Formosa, Argentina Feldexperimente im Rahmen der Diplomarbeit
05.2011 - 07.2013	Gutianshan National Nature Reserve, Zhejiang, China BEF-China Experiment, Jiangxi, China insgesamt 12 Monate Feldarbeit im Rahmen der Promotion
08.2012	Kibale National Park, Fort Portal, Uganda Teilnahme am Ant Course der California Academy of Sciences

Lehrerfahrung

SS 2012	Einführung in die Datenanalyse mit R
WS 2012/2013	Einführung in die Datenanalyse mit R
seit 2012	Betreuung von Abschlussarbeiten und Praktika
	Verschiedene Vorlesungen in den Themenbereichen Ökologie, Naturschutz und Zoologie

Publikationen

Menzel F, **Staab M**, Chung AY, Gebauer G, Blüthgen N (2012) Trophic ecology of parabiotic ants: Do the partners have similar food niches? Austral Ecology 37: 537-546.

Floren A, Wetzel W, **Staab M** (2014) The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. Myrmecological News 19: 65-74.

Staab M (2014) A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China. ZooKeys 391: 65-73.

Staab M, Kleineidam CJ (2014) Initiation of swarming behavior and synchronization of mating flights in the leaf-cutting ant *Atta vollenweideri* Forel, 1893 (Hymenoptera: Formicidae). Myrmecological News 19: 93-102.

Staab M (in press) The first observation of honeydew foraging in army ants since 1933: *Aenictus hodgsoni* Forel, 1901 tending *Eutrichosiphum heterotrichum* (Raychaudhuri, 1956) in Southeast China. Asian Myrmecology.

Staab M, Ohl M, Zhu CD Klein AM (under review) A unique nest-protection strategy in a new species of spider wasp. PLoS ONE.

Staab M, Schuldt A, Assmann T, Klein AM (under review) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. Ecological Entomology.

Staab M, Schuldt A, Assmann T, Bruelheide H Klein AM (under review) Ant community structure during forest succession in a subtropical forest in South-East China. Acta Oecologica.

Staab M, Blüthgen N, Klein AM (submitted) Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. Oikos.

Tagungsbeiträge

Methorst J, Klein AM, Blüthgen N, Leonhardt S, **Staab M** (2012) Different responses of ant species to sugars and amino acids in a subtropical forest of China. Jahrestagung der Gesellschaft für Ökologie 2012 (GfÖ) in Lüneburg. Poster.

Peters J, Klein AM, Blüthgen N, **Staab M** (2012) Visiting communities of extrafloral nectaries in a subtropical Chinese forest. Jahrestagung der Gesellschaft für Ökologie 2012 (GfÖ) in Lüneburg. Poster.

Staab M, Blüthgen N, Klein AM (2012) Tri-trophic interaction networks along a tree diversity gradient of BEF-China. Jahrestagung der Gesellschaft für Ökologie 2012 (GfÖ) in Lüneburg. Vortrag.

Pereira-Peixoto MH, Pufal G, **Staab M**, Martins C, Klein AM (2013) Jahrestagung der Gesellschaft für Ökologie 2013 (GfÖ) in Potsdam. Vortrag.

Sonstiges

09.2011	Eingeladener Vortrag, Earthwatch Workshop in Gutianshan, China Thema: „Ants as ranchers: fascinating phenomena from the life of ants”
10.2012	Eingeladener Vortrag an der Chinese Academy of Sciences, Institute of Zoology, Beijing, China. Thema: „Multi-trophic plant-inscet interactions in the BEF-China Experiment“
05.2013 - 06.2013	Mitarbeit am DFG-geförderten Drittmittelantrag „Multi-trophic plant-insect networks“ der 3. Phase des BEF-China Projektes.
12.2013 - 02.2014	Mitarbeit am Drittmittelantrag „Phylogenic relationships in multi-trophic plant-insect networks“ zur Bewilligung eines Chinesisch-Deutschen Forschungsprojektes eingereicht beim Chinesisch-Deutschen Zentrum für Wissenschaftsförderung.

Sprachkenntnisse

Deutsch (Muttersprache)

Englisch (sehr gut in Wort und Schrift)

Computerkenntnisse

Microsoft Office (sehr gut)

R (Statistiksoftware, sehr gut)

Gimp (Bildbearbeitungssoftware, sehr gut)

Ich versichere, dass ich die eingereichte Dissertation „Effect of tree diversity on plant-insect interactions in a Chinese subtropical forest“ selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

Freiburg im April 2014 Dipl. Biol. Michael Staab