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Effect of overstory tree species diversity and composition on ground foraging ants (Hymenoptera: Formicidae) in timber plantations in Ghana

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\textbf{ABSTRACT}

Plantation forests are becoming an increasingly important component of the world’s forested ecosystem. However, relatively little is known about how forest plantation management, overstory tree species composition and diversity impact biodiversity of nontree components of the forest. We assessed changes in ant functional group composition as related to changes in overstory tree diversity (monocultures vs. polycultures), species composition (native African species vs. exotic teak), and time (one and two years after planting). A pitfall trapping scheme was implemented during the summer months of 2006 and 2007. A total of 7473 specimens were collected representing six subfamilies, 22 genera, and 65 species. We found no significant differences in traditional diversity measures or functional group composition between treatments one year after planting. Two years after planting, we found that species richness of ground foraging ants had significantly increased ($F = 4.60$, d.f. = 4, 15, $p = 0.01$). Several observed trends may have indicated that these ant communities were in transition and will likely become more distinct over time as the different plantation types recover from disturbance and diverge from each other in overstory structure.

\textbf{Introduction}

Tropical forests are under numerous economic, political, and social pressures including land conversion for agricultural and infrastructure development and tropical timber production. Africa has seen the highest rate of change in forest cover with an annual loss rate of just under 1 million hectares per year between 1990 and 2010 (FAO 2011). Decreasing tropical forest area, a decline in native timber stock, and increasing demand for timber products have led to plantation forests becoming an increasingly important component of the world’s forested lands. Between 2000 and 2010, the rate of planted forest establishment rose to 115,000 ha per year (FAO 2011). Planted forest area represented approximately 187 million hectares worldwide in 2000 (FAO 2001) and rose to 260 million hectares worldwide by 2010 (FAO 2011). Plantation forests are dependent on for wood biomass production, soil and water conservation, and wind protection (Carnus et al. 2003) and are key sources of fuel wood and nontimber forest products (FAO 2015).

In 2010, planted forests represented almost 2.5 million hectares in West Africa (FAO 2011). In 2005, Ghana had an estimated 160,000 ha of forest plantations (FAO 2005), an increase in 85,000 ha since 2001 (FAO 2001). Of this approximately 90% was estimated to be exotic species, predominantly $Tectona grandis$ monocultures. In spite of their high productivity and ability to meet some timber production goals, exotic species cannot satisfactorily fill the ecological and socioeconomic roles of native species. Little research has been undertaken to understand the relationship between forest management and biodiversity (Hartley 2002). In addition, the majority of assessments made have not satisfactorily evaluated a variety of alternative land uses such as native species plantations, polycultures, and nonforested land uses (Stephens & Wagner 2007).

With the increasing loss of habitats and biodiversity around the world, there is an urgent need for biodiversity assessment (Agosti et al. 2000). There is considerable interest in the identification of robust bioindicators for use in land monitoring and assessment programs (Noss 1990). Living organisms can integrate a variety of effects over time that short-term physical and chemical measures cannot, making them suitable indicators of environmental conditions (Danks 1992). Traditionally, bioindicators have been used to assess ecosystem response to human-induced environmental perturbation (Agosti et al. 2000). Terrestrial invertebrates are an important component of forest ecosystems and comprise a major part of their biological diversity (Beattie et al. 1992). In contrast to larger more mobile animals, terrestrial invertebrates are less likely to move between treatment units, so their presence is a better indication of and...
more strongly related to site condition (Bromham et al. 1999). Terrestrial invertebrates dominate the biomass, are highly diverse, occur ubiquitously, and are fundamentally important in ecosystem function (Samways 1994; Andersen 1995). Recent work on bioindicators identification has focused on soil invertebrates and microfauna (Cluzeaua et al. 2012). Specific insect guilds are highly sensitive to habitat disturbance (Day et al. 1993; Samways 1994; Mendez et al. 1995). For example, carabids (Kromp 1990; Beaudry et al. 1997; Villa-Castillo & Wagner 2002), Lepidoptera (Holloway & Stork 1991; Kremen 1992), Odonata (Samways 1996), and Formicidae (Buffington 1967; Major 1982; Andersen 1990, 1991, 1995, 1997a; Roth et al. 1994; York 1994, 1999, 2000; Brown 1997; King et al. 1998; Peck et al. 1998; Bromham et al. 1999; Andrew et al. 2000; Vanderwoude et al. 2000; Stephens & Wagner 2006), have all been used successfully as bioindicators (Peck et al. 1998).

We selected ants as potential bioindicators of land-use type, because of their high diversity and biomass, their ecological importance at all trophic levels, their ease of sampling, and their well-understood community dynamics (Andersen & Sparling 1997). Furthermore, ants consistently show strong successional patterns in ecosystems and their functional diversity and composition are related to land management practices and disturbances (Andersen & Sparling 1997), including forest management (Andersen & Sparling 1997; Vanderwoude et al. 2000; Willett 2001; Stephens & Wagner 2006). Major (1983) showed that ants could be used to monitor ecosystem recovery and disturbance and have been used extensively in Australia to observe rehabilitation of mine sites. Additionally, ants have high spatial and temporal fidelity to sites (Nakamura et al. 2015).

The objectives of this study were to experimentally evaluate changes in ant species diversity and functional group composition under different levels of overstory tree diversity (a monoculture and six and 10 species polycultures of native species) and in plantations of native African species and an exotic species (Tectona grandis, or teak). We also looked for indicator species and functional groups for each type of plantation. We tested the hypothesis that changes in ant species diversity and ant functional group composition would be related to differences in overstory tree diversity and/or native vs. exotic species.

Materials and methods

Study sites

This study was conducted in Ghana, West Africa in the moist semi-deciduous forest zone between 6°34’33” N and 7°10’49” N. The moist semi-deciduous forest zone is the most extensive closed canopy forest type in Ghana, characterized by multistory canopy layers and approximately equal proportions of evergreen and deciduous species. This is the major timber-producing area in Ghana and is suitable for the production of agricultural crops, orchard crops, and exotic timber plantations (Wagner et al. 2008).

During July of 2005, experimental plantations were established on degraded forest sites within the South Fomangsu Forest Reserve (6°35’N, 0°57’W) and Afraam Headwaters Forest Reserve (7°10’N, 1°40’W). Both reserves are located within the moist semi-deciduous forest zone and are approximately 90 km apart. Degraded areas were identified within the reserves as lacking overstory trees and being dominated by weedy grass species and some woody shrubs. The degradation within the reserves was initially due to encroachment of illegal agriculture and chainsaw felling of timber. The degraded areas were within the bounds of the forest reserves and approximately 25–40 ha in size. We anticipated that the neighboring forests would provide a source for colonizing ant fauna. These plantations were established as part of a larger study examining the impacts of overstory tree diversity and species composition on ecosystem functions.

Experimental design

The treatments selected included (1) a native species monoculture, of Khaya ivorensis (an African mahogany), (2) exotic species monoculture, Tectona grandis (teak), and two polyculture conditions of (3) a six native timber species mixture, and (4) a 10 native timber species mixture (Table 1). The experimental plantations included tree species that represent different successional stages, growth forms and economic values ranging from timber to non-timber forest products (Table 2). Two replicates of each treatment were installed at each Forest Reserve. Plantations were set in complete randomized blocks with each block containing 1 replicate of each of the four treatments, for two replicates of each treatment.

Table 1. Species diversity and composition of treatments.

| Description          | Species                                      |
|----------------------|----------------------------------------------|
| Treatment 1          | Khaya ivorensis                              |
| Native species       | Tectona grandis                              |
| Monoculture          |                                             |
| Treatment 2          | Albizia zygia, Ceiba pentandra, Khaya ivorensis, Mansonia altissima, Milicia excelsa, Pericopsis elata |
| Exotic species       |                                             |
| Monoculture          |                                             |
| Treatment 3          | Albizia zygia, Ceiba pentandra, Khaya ivorensis, Mansonia altissima, Milicia excelsa, Pericopsis elata |
| Six native timber    |                                             |
| Species mixture      | Tetraptera heckelii, Terminula superba, Tetrapleura tetraptera |
| Treatment 4          |                                             |
| Ten native timber    |                                             |
| Species mixture      |                                             |
at each forest reserve. Each individual plantation was
40 m × 40 m with an initial planting distance of 1 m.
Within each mixed native species plantation, trees of
each species were randomly distributed. All seedlings
were of local provenance and reared in the FORIG
nursery until approximately 3 months in age. A 4 m
buffer was left between treatments.

Ant sampling
Sampling of ants via pitfall traps was conducted dur-
ing July/August in 2006 and 2007, after the onset of
the short rainy season, at one and two years after
plantation establishment. Five pitfall traps were
placed on each of two parallel 25-m transects at 5-
m spacing, for a total of ten pitfall traps per treatment
replica. Transects were placed at the center of each
replicate plantation with a random start and direction
within the stand. The traps were placed in two par-
allel transects instead of a single transect to reduce
edge effects.

A pitfall trap consisted of a plastic deli style con-
tainer (11 cm diameter by 8 cm deep) buried flush to
ground level. During the 48-hour sampling periods,
traps were set flush with the soil surface and with
approximately 250 ml of soapy water in the trap. Any
debris inside the trap was carefully removed when the
traps were set. Preliminary trap testing conducting in
the field ranged from 24 hours to 10 days. Analysis of
these trap catches showed a 48-hour trapping period
allowed for sufficient ant capture and reduced the
risk of trap disturbance and flooding, especially dur-
ing the rainy season. In addition, species richness
curves were optimized at between six and eight
traps (unpublished data).

Pitfall trapping has been widely used in studies of
Australian ant communities (Andersen 1995) and has
been shown to provide a reliable estimate of species
composition (Andersen 1991; Agosti et al. 2000).
Andersen (1991) showed that pitfall trapping for
ants was an adequate collection method for habitats
with dense litter and vegetation as occurred at the

sites in this study, in comparison to more time-inten-
sive quadrant counts, which are better suited to open
habitat types. The use of pitfall traps may underre-
present cryptic, soil-litter-dwelling ant species,
although they do occur in small numbers.

The contents of each trap were collected individu-
ally and transported back to the lab for sorting, pre-
servation, and preparation of museum vouchers. Ants
were identified to species and placed into functional
groups as adapted from Andersen (2007 and personal
communication) and described in Table 3; identifica-
tions were based on Taylor (2007). Members of the
genus Dorylus were excluded from this study because
they are highly mobile and do not establish long-term
stationary colonies, and therefore are not associated
with long-term site characteristics. This behavior pre-
cludes them from being suitable bioindicators.

Specimens were vouched by Dr. Brian Taylor and
have been deposited into the Northern Arizona
University School of Forestry voucher collection and
in the Forestry Research Institution of Ghana
insectarium.

Ant species diversity and functional groups
The traditional diversity measures of species rich-
ness (R), the Shannon-Wiener Diversity Index (H),
and the Simpson Dominance Index (D) were calcu-
lated for each treatment. Species richness is the
number of species observed. The Shannon-Wiener
Diversity Index was calculated as a measure of rela-
tive diversity per treatment type per year. The
Simpson Dominance Index was used to determine
the strength of species numerical abundance. These
traditional diversity measures fail to assess species
assemblages or groups with particular traits, so spe-
cies were also grouped into functional groups for
further analysis. Functional groups were determined
according to behaviors, habitat preferences, and
trophic level interactions, using existing functional
group assignments developed by Andersen (2007
and personal communication).

| Species         | Common Name | Native vs. Exotic | Pioneer | Nonpioneering light demanding | Non-pioneering shade bearing | Nitrogen Fixer | Economic Importance | Threatened |
|-----------------|-------------|-------------------|---------|-------------------------------|-----------------------------|----------------|---------------------|------------|
| Khaya ivorensis | African Mahogany | N | X | X | X | | | |
| Milicia excelsa | Iroko | N | X | X | X | | | |
| Pericopsis elata | Aframossia | N | X | X | X | | | |
| Albizia zygia | Okuro | N | X | X | X | | | |
| Ceiba pentandra | Onyina | N | X | X | X | | | |
| Mansonia altissima | Onron | N | X | X | X | | | |
| Terminalia superba | Ofram | N | X | X | X | | | |
| Tetraplura tetraperta | Prekese | N | X | X | X | | | |
| Tieghenella beckelli | Baku | N | X | X | X | | | |
| Tectona grandis | Teak | N | X | X | X | | | |

Table 2. Tree species characteristics.
Table 3. Classification of ant functional groups collected from the semi-deciduous forest zone of Ghana, West Africa.

| Functional Groups (code) | Characteristics | Species | Species Code | Species | Species Code |
|-------------------------|-----------------|---------|--------------|---------|--------------|
| Subordinate Camponotini (SC) | Ecologically separated due to large body size and nocturnal foraging. Several arboreal nesters. | Camponotus sp. (Mymochaphae) | CAMY | Camponotus furvus | CAFU |
|                        |                 | Camponotus accvapienis | CAAC | Camponotus maculatus | CAMA |
| Tropical Climate Specialist (TCS) | Distribution centered on tropical climatic zone. Unspecialized ants. | Anenius guneensis | AEGU | Pristomyrmex ariceps | PROR |
|                        |                 | Anenius species 2 | AESP |                        |      |
| Cryptic Species (CS) | Forage and nest primarily within soil and litter, having relatively little interaction with epigaetic ants | Ceraphys nitidulus | CENI | Pyramica cryptura | PYCR |
|                        |                 | Hypophoner cnenunens | HYCA | Pyramica membranifera | PYME |
| Opportunist (O) | Unspecialized, poorly competitive species, characteristic of disturbed sites | Oligomyrmex diabolus | OLDI | Strumigenys petiolata | STPE |
|                        |                 | Oligomyrmex vorax | OLVO | Strumigenys rufobrunea | STRU |
|                        |                 | Cardiocondyla emeryi | CAEM | Tetramorium angulinoide | TEAN |
|                        |                 | Cardiocondyla neferka | CANE | Tetramorium calinium | TERA |
|                        |                 | Decamorium decem | DEDE | Tetramorium flavithorax | TEFL |
|                        |                 | Odontomachus troglodytes | ODTR | Tetramorium intonsum | TEIN |
|                        |                 | Lepisiota cacoceola | LECO | Tetramorium minimum | TEMI |
|                        |                 | Lepisiota laevis | LELA | Tetramorium sericeiventris | TESI |
|                        |                 | Paratrechina albipes | PAAL | Tetramorium sillinimum | TESI |
|                        |                 | Paratrechina arlesi | PAAR | Tetramorium quadri dentatum | TEQU |
|                        |                 | Tapinoma lugubre | TALU |                        |      |
| Generalist (G) | Ubiquitous species occurring in most habitats. Rapid recruitment to, and successful defense of food resources. Predominate moderately productive habitats. | Crematogaster censor | CRCE | Pheidole concinna | PHCO |
|                        |                 | Crematogaster zavattari | CRZAI | Pheidole costarumensis | PHCS |
|                        |                 | Monomorium bicolor | MOBI | Pheidole impressions | PHIM |
|                        |                 | Monomorium exigium | MOEX | Pheidole megacephala | PHME |
|                        |                 | Monomorium pharunion | MOPH | Pheidole melancholia | PHME |
|                        |                 | Monomorium rosae | MORO | Pheidole nigritella | PHNIG |
|                        |                 | Monomorium tanysum | MOTA | Pheidole occipitalis | PHOC |
|                        |                 | Monomorium trake | MOTR | Pheidole pasilla | PHPU |
|                        |                 | Monomorium vagum | MOVA | Pheidole retrotrans | PHRE |
|                        |                 | Pheidole aeberlii | PHAE | Pheidole schoutedeni | PHSC |
|                        |                 | Pheidole aurivillii | PHAU | Pheidole speculifera | PHSP |
|                        |                 | Pheidole bayeri | PHBA | Pheidole weissi | PHW |
|                        |                 | Pheidole caffra | PHCA |                        |      |
| Specialized Predators (SP) | Medium to large bodied strictly predaceous species. Well-developed sight, highly active foragers mostly solitary. Little competitive interactions with other ants behaving more like other predatory arthropods. | Anochetus beguaerti | ABRE | Pachycondyla silvestrii | PASI |
|                        |                 | Ceiraphys sudenensis | CESU | Pachycondyla cautaria | PACA |
|                        |                 | Leptogenys conradi | LECO | Pachycondyla tarsata | PATA |
|                        |                 | Pachycondyla pachyderma | PAPA |                        |      |

Adapted from Andersen (1997b, 2007). Dominant Dolichoderine, Cold and Hot Climate Specialist functional groups removed, none were expected or observed. Dorylus spp. were excluded from the study because of their characteristic nesting and foraging behavior.

**Statistical analyses**

Prior to any statistical interpretation of the ant data, we decided to pool the trap collections across treatment replicate to obtain one value per treatment replicate per year, because we were primarily interested in observing indicator species and guild responses to treatment. Effect of treatment was evaluated in two separate analyses: (1) comparing plantations with different levels of diversity of native species (1, 6, and 10 native species; Table 1), and (2) comparing native African species (all plantations) with exotic teak monocultures. We used data from each year to evaluate changes in communities occurred over time.

We applied standard analysis of variance (ANOVA) tests to determine differences between traditional diversity indices in overstory tree diversity treatments using JMP In 5.1.2 (SAS 2004) after meeting assumptions of normality and equal variance. Nonparametric Welch ANOVA was applied when standard ANOVA assumptions were not met (SAS 2004). To determine differences between species diversity indices for the native vs. exotic treatments, we applied a two-sample t-test after meeting assumptions of normality and equal variance (Hays 1963).

**Functional group analysis**

Multiple response permutation analyses (MRPP) was performed for the relative abundance measures of each ant functional group to test the null hypothesis of no difference in functional group composition among treatments (McCune & Mefford 2006). Indicator species value analysis (referred to as indicator value) by the Dufrêne and Legendre (1997) method was performed to determine the specific contributions of each species to the functional group and to determine the strength of indication of treatment provided by either a functional group or an individual species (Stephens & Wagner 2006).

**Results**

A total of 7473 specimens were collected representing six subfamilies, 22 genera and 65 species (Table 4).
The number of specimens collected per treatment was similar and ranged from 746 to 1262. The greatest number of species was trapped in the genus *Pheidole* (16 species). The most commonly trapped ants were members of *Pheidole*, represented by three to six species per treatment. The most frequently observed ant was *Odontomachus troglodytes* Santschi, which represented 17–55% of ants collected per treatment. Composition of ant communities by functional group varied little between treatments. Results from two years after planting showed increases in ant species richness and nonsignificant differences in ant community composition.

**Ant species diversity and overstory tree species diversity**

At one year after planting, there were no significant differences in measures of ant species diversity in relation to overstory diversity of native tree species (Table 4). Insignificant measures included species richness (*F* = 0.96; d.f. = 4, 15; *p* = 0.5), Shannon-Weiner Diversity Index (*F* = 0.82; d.f. = 4, 15; *p* = 0.5), and Simpson’s Dominance Index (*F* = 0.76; d.f. = 4, 15; *p* = 0.6) (Table 4). At two years after planting species richness was significantly different between treatments (*F* = 4.60; d.f. = 4, 15; *p* = 0.01). Species richness was highest in the plantations of six native timber species (*R* = 19.75 ±SE 1.48) and lowest in the native African mahogany monoculture (*R* = 13.25 ±SE 1.48) and (Figure 1). Shannon-Weiner Diversity Index (*F* = 2.28; d.f. = 4, 15; *p* = 0.1) was highest in the plantations of six native timber species (*H* = 2.22 ±SE 0.24) and lowest in native African mahogany monocultures (*H* = 1.38 ±SE 0.24) (Figure 2). Simpson’s Dominance Index (*F* = 1.64; d.f. = 4, 15; *p* = 0.2) was highest in the plantations of six native timber species (*D* = 0.83 ±SE 0.09) and lowest in native African mahogany monocultures (*D* = 0.54 ±SE 0.09) (Figure 3).

**Ant species diversity and native species vs. teak overstories**

At one year after planting, there were no significant differences between the plantations of native African species and teak in measures of ant species diversity, including species richness (native species *R* = 11.25; exotic teak *R* = 8.75) (*t* = −1.43, d.f. = 18, *p* = 0.1); Shannon-Weiner Diversity Index (*t* = −1.24, d.f. = 18, *p* = 0.1); or Simpson’s Dominance Index (*t* = −1.26, d.f. = 18, *p* = 0.2) (Table 4). However, at two years after planting, species richness (*t* = −2.54, d.f. = 18, *p* = 0.02) was significantly higher in the plantations of

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**Table 4.** Composition of ant genera by functional group. Data are number of species per genera, with percent total ants per treatment per year (column) in brackets.

| Functional group | Exotic teak monoculture | Native African mahogany monoculture | Six native timber species mixture | Ten native timber species mixture |
|------------------|-------------------------|--------------------------------------|---------------------------------|----------------------------------|
| Genera           | 2006 2007               | 2006 2007                            | 2006 2007                       | 2006 2007                        |
| Subordinate      |                         |                                      |                                 |                                  |
| Camponotini      |                         |                                      |                                 |                                  |
| Camponotus       | 3 (15.67)               | 1 (2.39)                             | 2 (5.74)                        | 4 (5.14)                         |
| Tropical Climate |                         |                                      |                                 |                                  |
| Specialist       |                         |                                      |                                 |                                  |
| Camponotus       | 1 (0.13)                |                                      |                                  |                                  |
| Cryptic Species  |                         |                                      |                                  |                                  |
| Cryptic Species  | 2 (0.22)                |                                      |                                  |                                  |
| Cerapachys       | 1 (0.26)                | 1 (0.10)                             | 1 (0.18)                        |                                  |
| Hyperoponera     | 1 (0.11)                | 1 (0.10)                             | 1 (0.51)                        |                                  |
| Olgomymex        | 1 (1.01)                |                                      | 1 (0.36)                        |                                  |
| Pyramica         | 1 (0.10)                | 1 (0.10)                             | 1 (0.16)                        |                                  |
| Strumigenys      | 1 (0.13)                | 1 (0.20)                             | 1 (0.12)                        | 1 (0.13)                         |
| Oppurtunist      |                         |                                      |                                 |                                  |
| Tapinoma         | 1 (15.52)               | 1 (4.27)                             | 1 (8.45)                        | 1 (12.60)                        |
| Lepisiota        | 2 (5.41)                | 1 (1.33)                             | 2 (7.42)                        | 1 (1.32)                         |
| Paratrechena     | 1 (4.96)                | 2 (9.81)                             | 2 (3.04)                        | 1 (1.42)                         |
| Cardiocondyla    | 1 (3.15)                | 1 (0.56)                             | 1 (0.79)                        | 2 (3.35)                         |
| Xylotomum        | 1 (0.11)                |                                      |                                  |                                  |
| Tetramorium      | 1 (1.33)                | 2 (1.86)                             | 3 (3.26)                        | 3 (0.81)                         |
| Odontomachus     | 1 (55.02)               | 1 (24.80)                            | 1 (17.32)                       | 1 (46.90)                        |
| Generalist       | 1 (15.67)               | 1 (4.27)                             | 1 (8.45)                        | 1 (12.60)                        |
| Crematogaster    | 1 (1.62)                | 1 (0.64)                             | 1 (0.13)                        | 1 (1.23)                         |
| Monomorphum      | 2 (3.16)                | 3 (1.59)                             | 1 (1.46)                        | 2 (0.71)                         |
| Monomorphum      | 2 (9.64)                | 2 (12.97)                            | 3 (16.82)                       | 2 (15.01)                        |
| Pheidole         | 5 (2.37)                | 3 (27.19)                            | 6 (34.53)                       | 2 (19.19)                        |
| Tetracera        | 2 (19.19)               | 24 (24.45)                           | 4 (19.07)                       |                                  |
| Specialized Predators |             |                                      |                                 |                                  |
| Cerapachys       | 1 (0.10)                |                                      |                                  |                                  |
| Anochetus        | 1 (0.34)                |                                      |                                  |                                  |
| Leptopergus      | 1 (0.11)                | 1 (0.20)                             | 1 (0.09)                        | 1 (0.08)                         |
| Pachycondyla     | 2 (11.95)               | 2 (14.19)                            | 2 (21.60)                       | 2 (9.64)                         |
| Total Individuals | 887 754                 | 889 985                              | 985 1100                        | 746 1262                         |
| Total # of species | 18 20 25 24             | 18 33 19 29                          |                                  |                                  |
| Mean R (SE)      | 8.75 (1.25)             | 11.75 (1.48)                         | 11.25 (1.25)                    | 13.25 (1.48)                     |
| Mean H (SE)      | 1.36 (0.27)             | 1.84 (0.26)                          | 1.76 (0.27)                     | 1.38 (0.24)                      |
| Mean D (SE)      | 0.58 (0.11)             | 0.78 (0.09)                          | 0.75 (0.11)                     | 0.54 (0.09)                      |
native species \((R = 13.25)\) than in the exotic teak plantations \((R = 11.75)\) \(\text{(Figure 1)}\).

**Functional group analysis**

During both the 2006 and 2007 collection periods, neither ant functional group composition nor individual ant species composition differed significantly among the one, six, and 10 species treatment, nor between the native African species and teak plantations \(\alpha = 0.05, \text{Table 5}; \text{Figures 4 and 5}\). The \(A\) statistic for the MRPP comparisons of both overstory diversity and native vs. teak plantations was very close to zero for both ant functional groups and individual species in both years \(\text{(Table 5)}\), indicating that the heterogeneity within groups was equal to that expected by chance.
While no indicator species or groups were identified for any treatments, the Opportunist functional group dominated all of the treatments in both years, representing 36–67% of the ants collected in each treatment. The Generalist functional group was typically the second most common functional group in both years representing an average of 26% of ants collected in each treatment. Specialized predators and Subordinate Camponotini averaged 13% and 11%, respectively. Tropical climate specialist and Cryptic species were very seldom observed and contributed to less than 2% of the ants collected from any treatment (Table 4, Figures 4 and 5).

**Changes over time**

Over the 2 years of the study, we observed a significant change in species richness \( (F = 53.22, \text{ d.f.} = 8, 30, \ p = < 0.0001) \) in all treatments (Figures 1 and 6). The exotic teak and native African mahogany monocultures gained two and lost two species between years. The mixed native species plantations gained 10–15 species between years. We observed only small, nonsignificant changes in the proportions of functional group in each treatment (Figure 7). Subordinate Camponotini species declined in all treatments, Cryptic species increased in all treatments, and Specialized Predators increased in the plantations of one, six, and 10 native tree species and declined in exotic teak monocultures. Opportunists increased in the exotic teak monocultures and native mixed species plantations and decreased in native African mahogany monocultures. Generalists increased or remained unchanged in mixed native species plantations and decreased in the teak and African mahogany monocultures.

**Discussion**

Over the two years of the study, we observed a 20% increase in species richness across all treatments (Figure 6). If current trends persist, we predict species diversity will become stable over time. As supported
by other observations (Stephens et al. 2008), we expect distinct ant communities will develop in these plantation types, which may include specific indicator species or functional groups.

This study highlights the potential of ants as bioindicators of habitats conditions in tropical forested systems, where they have been generally underutilized (Piper et al. 2009). Anderson (1991) indicated that ants are associated with structural components of their habitats. Peck et al. (1998) saw significant changes in ant communities based on vegetation community diversity and structure. Disturbance resulting from fire and timber management has been observed to affect ant communities (Neumann 1992; Andrew et al. 2000; York 2000).

**Changes in ant diversity and overstory composition**

Overstory tree diversity had a positive impact on ant species diversity at two years after plantation establishment (Figures 1–3, and Table 4), although not at one year after planting. Increasing overstory tree diversity from one to six species resulted in a 30% increase in ant species richness. The species present in the six and ten native timber species plantations increased by 15 and 10 species respectively between the first and second years (Table 4). This suggests that, within plantation forests, moderate increases in overstory tree diversity can have a significant effect on ant biodiversity, and perhaps on other taxa.

Native environments typically support higher number of insect species than non-native environments (DeGomez & Wagner 2001). In this study, the native species plantations had approximately 20% more ant species than the exotic teak plantation over both years.
(Table 4). At two years, the native species plantations had significantly higher species richness teak plantations. A nonsignificant difference in species composition was also observed (Table 4) with six genera being unique to the native African species overstories and only one genera unique to teak plantations. Since teak is a major plantation species in West Africa and elsewhere (FAO 20001), the lower associated ant diversity in this study is of concern.

**Ant functional groups and succession**

Whereas traditional diversity measures are based on numerical counts, functional group analysis is based on differences in characteristics among species groups. Unlike traditional diversity measures, functional group analysis permits examination of how species habitat requirements and competitive interactions may impact diversity patterns (Anderson 1991). In this study, the relative abundances of each functional group were similar among treatments especially at one year after planting (Figures 4 and 5), with MRRP A values indicating high homogeneity between treatments (Table 5). However, by Year 2, we see a trend of increasing heterogeneity in ant functional groups among treatments in MRRP A values (although still insignificant) (Table 5).

This study may have presented the early stages of establishment of distinct ant communities under differing overstory composition. As the treatment areas recover from forest degradation, disturbance, and plantation establishment (site prep, planting, and early site maintenance), and their composition and structure become more distinct, more distinct ant communities may emerge. Significant differences among plantation types in ant diversity indicators were detectable at only two years after plantation establishment. Other work (Stephens et al. 2008) assessed ants as indicators of land use in Ghana at 10–13 years after planting and found distinct patterns in communities of ants and other organisms among agriculture, citrus orchards, exotic species plantations, mixed native species plantations, and native forests. The plantations were similar in species composition to the 10 native timber species plantation and teak monocultures used in this study. The agricultural areas and citrus orchards were also similar to the degraded conditions prior to plantation establishment for this study at the Forest Reserve sites. Furthermore, indicator species and functional groups were identified for the more mature land uses (Stephens et al. 2008). These observations support the conjecture that the newly established plantations of this study are in the early stages of establishment for distinct ant communities.

In Years 1 and 2 under different overstory types, the ant communities were generally dominated by Opportunists and Generalists (Figures 4 and 5). We have observed that Opportunists tend to move into disturbed habitats (Stephen et al. unpublished), whereas Generalists seem indifferent to successional stage. In this study, between Years 1 and 2, Opportunists increased (except for the native African mahogany monoculture) and Generalists showed no pattern (Figure 7). In another study (Stephen et al. unpublished), a similar relationship between Opportunist and Generalist functional groups and different land uses was observed, with Opportunists dominating agricultural fields. We anticipate future changes from Opportunists-dominated ant communities to more functional group
diversity and stronger links to overstory tree diversity and composition.

Nonsignificant shifts in functional group composition between Year 1 and Year 2 include decreases in the subordinate Camponotini (SC) and increases in the Cryptic species functional groups in all treatments. The SC group was composed largely of arboresal Camponotus species strongly associated with downed woody debris (Higgins & Lingren 2006; Stephens & Wagner 2006). The Camponotus species that were found in Year 1 may have been residual populations using coarse woody debris and the few small shrubs remaining from before overstory removal and plantation establishment. By Year 2, since woody material on the treatment sites had lessened and the young trees were not of sufficient size to provide suitable habitat, Camponotus species were probably being displaced by more pioneering species more adapted to disturbance and early successional conditions. Camponotus species may re-enter these areas when the overstory trees mature and provide habitat.

In contrast to the SC group, Cryptic species such as Strumigenys species, specialize in predation on leaf litter dwelling microinvertebrates (Holldobler & Wilson 1990). The increase in Cryptic species between Years 1 and 2 was likely a response to changes in understory and soil conditions after removal of agricultural crops and plantation establishment that improved microhabitats for their prey. The number of species in the Specialist Predators (SP) functional group also increased in all of the native overstory treatments (Figure 7) from Year 1 to Year 2, perhaps as a consequence of understory changes. For example, Cerapachys sp. are predators of termites and other ants, particularly Pheidole sp. (Holldobler & Wilson 1990). Pheidole is a Generalist, which was readily abundant in treatments where Specialist Predators were observed (Table 3, Figure 7).

As these young plantations transition through successional stages of stand development, it seems likely that distinct ant community patterns will emerge. Our experimental plantations with managed understories and open canopies may not yet have developed all of the characteristics that promote specific ant functional groups or species. Regular weeding was used to control the understory vegetation during the early years of plantation development, and the tree species used in these plantations have different growth characteristics (Table 2) and grew at significantly different rates, all of which may have impacted ant community composition and diversity. The cumulative differences in the plantation types as the stands develop will impact both the overstory and understory ant communities. As canopy structure matures, shading of the understory will increase and changes in understory vegetation and leaf litter will support different ant communities. For example, as individual trees increase in bole diameter and height during stand succession, several species of arboresal nesters would be expected to appear, including carn-tion-nesting Crematogaster spp. and Camponotus spp. (Holldobler & Wilson 1990).

Future research is required to fully assess the stages of stand development and management that are most influential on ant communities. As these plantations mature and are managed over time, some tree species are likely to be thinned or harvested to meet management objectives. This would present the opportunity to assess how those changes in stand structure and diversity further impact ant communities. A longer period of observation over 5–10 years may reveal the full sequence of ant community assemblage establishment and the appearance of indicator species and functional groups associated with overstory tree diversity and composition. Additional work could be conducted to assess the association of ant communities with changes in understory vegetation, leaf litter, and soil characteristics.

**Conclusion**

Biodiversity is clearly an important component of ecosystems, supporting their function (Tilman et al. 1996) and their anthropocentric value (Wilson 1984). Conventional wisdom has long held that biodiversity and plantation forests are mutually exclusive (Stephens & Wagner 2007). Stephens and Wagner (2007) argued the importance of land use comparisons prior to passing judgment on plantation forest impacts on biodiversity. Observed cases in the literature indicate that plantation management, can impact biodiversity positively and negatively, depending on the strategies used. Based on the results of this study and other work (Stephens et al. 2008), the six native tree species mixture at only two years after planting recouped an astonishing 80% of the total number of ant species, and from 40% to 100% of the individual ant functional groups observed at native forest sites. The native African mahogany monoculture recouped 60% of native forest ant diversity. These numbers show that biodiversity and plantation forests are not necessarily at odds. Casual observation of soil, microclimate, understory plants, and birds, reptiles and mammals in the more mature mixed native species and exotic teak plantations suggest that strong community difference are likely occur across numerous floral and faunal groups in different kinds of plantations. Our findings suggest that moderate changes in management, such as focusing on mixed native species plantations, can recapture a significant level of...
native forest ant diversity and potentially other taxa as well.

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