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Ant-mediated ecosystem services and disservices on marketable yield in cocoa agroforestry systems

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ABSTRACT

The impact of complex direct and indirect interactions between multiple functional groups on plants is poorly documented. In tropical agroecosystems, ants interact with crop mutualists and antagonists, however, little is known about effects of dominants ant community properties on the consequence of such cascading interactions which can be measured through final ecosystem service, crop yield. Here, we present a replicated ant fauna manipulation experiment in cocoa agroecosystems, where we used ant exclusion treatments to test the economic importance of the presence of ants, and two additional treatments where we experimentally introduced one of two common dominant ant species which allowed comparing their effects with those of the naturally occurring ant fauna. The proximate aim was to assess the impact of ants *Crematogaster* sp., *Camponotus brutus* Auguste-Henri Forel and *Oecophylla longinoda* Latreille on cacao yield, which is known to depend on several, cascading intermediate ecosystem services (e.g. control of specific pests). Ants provided ecosystem services in term of reduced pest damage caused by *Salhbergella singularis* Hagh (Hemiptera: Miridae) and *Characoma stictigrapta* Hmps (Lepidoptera: Noctuidae) but also disservices such as increased pathogen disease caused by *Phyphthora megakarya* Brasier and Griffin dissemination and indirectly enhanced damage of other pest species. Yields were highest in non-manipulated and species-rich ant communities, whereas ant exclusion and communities dominated by a single species decreased yield by more than 30%. Associated ant communities between dominant and non-dominant species resulted in the same yields as in non-manipulated controls. Dominant ant communities maximized the control of a particular pest species, but not cacao yield. We show a positive relationship between ant species rich communities and financial performance and we postulate that complex agroecosystems can offer competitive business opportunities for small-scale farmers, while contributing to biodiversity conservation. However, more interdisciplinary studies are needed to quantify financial and biodiversity performance opportunities to allow up-scaling of these findings.

1. Introduction

In tropical agroecosystems, direct and indirect interactions between multiple functional groups such as herbivores (Bisseleua et al., 2013), pathogens (Evans, 2007), predators and pollinators (Klein et al., 2007) generate interactions between ecosystem services and disservices. The role of insect species in delivering individual ecosystem services such as herbivore pest and plant disease control is documented by only a few biodiversity-ecosystem studies (Bisseleua et al., 2009; Lundin et al., 2013; Wielgoss et al., 2014; Rusch et al., 2016). Some of these studies document the importance of synchronized interactions between many animal groups and different element of the ecosystem through trophic and non-trophic interactions with strong impact on intermediate ecosystem services and disservices.

In cocoa production, the effects of ants on crop yield involve ecosystem services such as predation (Way and Khoo, 1992) and ecosystem disservices such as the dissemination of spores of plant pathogen (Evans, 2007) are reported. Little is known about effects of dominant ant community properties on the consequence of such cascading interactions, which can be measured through final yield.

We expect ant communities with high richness and high evenness to be beneficial by maintaining services (Bihn et al., 2010) thus minimizing potential disservices associated with ant dominance (Hillebrand and Bennett, 2008).

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The fungal plant pathogen *Phytopthora megakarya* Brasier and Griffin is the main cause of cocoa (*Theobroma cacao* L.) pod losses in the West African cocoa belt (Nyasse et al., 2007). Dissemination by wind is often assumed to be the predominant long distance dispersal mechanism for *Phytophthora* spores (Nyasse et al., 2007) whereas rain splash transport is regarded the primary inoculum responsible for *P. megakarya* infections near the soil surface (Ndoumbè et al., 2004). Trajectory splash can disperse the spores from 1.5–2.0 m, while windblown rain droplets can disperse the spores higher into the tree canopy (Ndoumbè et al., 2004).

Insects are not usually viewed as vectors of *Phytophthora* spores. However, transmission of *Phytophthora* spores has been reported for a number of insects such as *Drosophila* (Hunter and Buddenhagen, 1969), the weevil *Scyphophorus interstitialis* Gyll. and ants (Taylor and Griffin, 1981; McGregor and Moxon,1985; Medeiros et al., 1993). Ants, specifically those dominant in cocoa canopies, may be incidentally associated with the transmission of diseases, directly by transport of contaminated soil or of spores from infected to healthy pods, and indirectly through protection of Homoptera (Yede et al., 2012; Wielgloss et al., 2014).

In cocoa agroforests of West Africa, arboreal ants, such as *Crematogaster* sp., *Camponotus brutus* and *Oecophylla longinoda*, are common and mutually co-existing (Padie and Owusu, 2003; Bisseleua et al., 2009 Bisseleua et al., 2009). *Crematogaster* species are the most abundant and colonize the upper and the lower parts of cocoa trees (Bisseleua, 2007). *C. brutus* is mainly found on trunks of cocoa trees between 50 and 100 m above ground, while *O. longinoda* is exclusively found in the canopy of cocoa trees (Bisseleua et al., 2013). *Crematogaster* species and *O. longinoda* are also known as important predators of insect pests of cocoa (Way and Kho, 1992; Padie and Owusu., 2003). However, they are also suspected to transmit black pod disease (Evans, 2007). *Crematogaster* species as the most abundant in cocoa agroforests could be regarded of major importance as vectors of black pod disease due to their higher numbers and densities on cocoa trees.

The role of ants in intermediate ecosystem services, such as natural control of a complex of pest and plant disease species has been well documented (Way and Khoo, 1992; Philpott and Armbrecht, 2006; Otto et al., 2008; Zovi et al., 2008). However, their numbers and ecological status (e.g. dominance and invasion) are regulated by anthropogenic disturbance (Gibb and Hochuli, 2003). Dominant ant species will have several nests and will develop mutualistic interactions with hemipterans for honeydew as a sugar source in exchange of protection against potential predators (Bluethgen et al., 2004). Some will reduce species richness and evenness of ant communities by aggressively excluding other species from their territory and from food sources, while others will be more tolerant to conspecifics and do not reduce species richness (Majer, 1976, 1994; Philpott and Armbrecht, 2006). Predicting differences in the dissemination of spores of *P. megakarya* by ant communities with evenly distributed species abundances and those dominated by single-species has not been investigated in detail yet. Ant communities with low diversity but higher abundance within a tree (e.g. those dominated by an aggressive species) may contribute to a rapid dissemination of spores of *P. megakarya* as a consequence of a reduction in ant community traits and functional diversity (Bihn et al., 2010). On the contrary more diverse ant communities occupying different niche on a tree and thus reducing the foraging behavior within tree may be less effective in spreading the spores of *P. megakarya* owing to habitat restriction and buffer areas.

In cocoa agroforestry systems, the importance of species richness for ecosystem functioning increased with the number of functions considered (Bisseleua et al., 2013; Asare and Raebild, 2016). For ants, this relationship is less direct because they use different resources, the exploitation of some of which may be an ecosystem service (predation of pests) (Bommarco et al., 2013; Chumacero de Schawe, 2014), others can cause a disservice (vector of plant pathogens such as that of *P. megakarya* (Nyasse et al., 2007; Nyasse et al., 2007; Ndoumbè et al., 2004) or tending of mealybugs vector of cocoa swollen shoot virus). Though, we expect ant communities with high species richness and high evenness to be beneficial by maintaining services (Wielgoss et al., 2014) and diluting potential disservices associated with ant dominance (Babacauh, 1982), because most ants are predatory to some extent, but only a subset of the species are likely to transmit spores of *P. megakarya* (Evans, 2007) or to engage in mutualisms with sap-sucking pests of economic importance (e.g. mealybug transmitting cocoa swollen shoot virus disease). Little is known to date about effects of dominant ants and ant community traits on the outcome of such set of interactions which can be measured through final yield (Vandermeer et al., 2010, Wielgoss et al., 2014).

In cocoa plantations in the region sampled, *Crematogaster* sp. and *O. longinoda* species have recently become invasive and ecologically dominant. The former reduce ant species richness (Bisseleua, 2007) and can displace other dominant species, such as *O. longinoda* which is an effective predator of cocoa pests (Way and Kho, 1999). Both species form large colonies and can be numerically dominant, but they differ in their ecological traits. *O. longinoda* workers are more active in the cocoa canopy building their nests by folding cocoa leaves. They also aggressively expel other ants from baits (Padi and Owusu, 2003). *Crematogaster* sp. workers are active in the whole cocoa tree including the canopy and are relatively less tolerant towards other ant species such as *C. brutus*. They build their nests using soil materials. *C. brutus* workers are active on the trunk of cocoa trees, are never found in the canopy and are relatively tolerant towards other ant species such as the *Crematogaster* sp. or *O. longinoda*. Their tent material is of plant debris-type.

In this study we manipulated the ant fauna in smallholder cocoa agroforests in Cameroon, using ant exclusion treatments, to test the role of ant in the transmission of black pod disease and the related impact on cocoa productivity and marketable yield. We hypothesized that ant exclusion negatively affects cocoa productivity and marketable yield. We expected that dominant species maximize individual intermediate ecosystem disservices and the final integrated ecosystem services (measured as marketable yield), whereas species-rich ant communities with high evenness should result in the highest marketable yield, due to high functional diversity which maintains major ecosystem services while buffering potential disservices of single species. We analyze the effects of ant community structure on the incidence of *P. megakarya* and how different ant communities affect intermediate ecosystem services and disservices and impact marketable yield.

2. Material and methods

2.1. Study area and study plots

All sites were located in the central region of Cameroon located between 4°12′ and 4°30′ latitude north, and 10°6′ and 11°15′ longitude east. The altitude varies between 450 and 715 m above sea level. We selected 20 cocoa plots (30 × 30 m) without insecticide application within the last two years and differing in shade intensity and with proofed absence of the ant species *Crematogaster* sp., *Camponotus brutus* and *O. longinoda*. The plots were located in Boumnyebel (03°53′01″N 10°50′56″E, 402 m alt.), where cocoa is grown under a dense cover of many forest near pristine forests with very old cocoa plantation (> 30 years); Obala (04° 15′82″N 11° 53′62″E, 557 m alt.) where cocoa is grown with a diversity of forests and fruit trees species, with no original remnant forests because of very high human population density; Talba (04°34′421″ N 11°28′33″ E, 462 m alt.) where cocoa is grown in larger farms under less shade; Bakoa (4°°56′42″ N 11°16′47″E, 469 m alt.), where cocoa is grown under very low shade in forest galleries at the forest-savannah transition zone and Kedia (4°°50′.46″N, 11°07′87″E, 459 m alt.) where cocoa is grown under full sun in the savannah. The geographic coordinates of the sites were taken using a GPS (GPSMAP 60CSx). In each plot we established six sub-plots (10 × 10m) with a minimum distance of 10 m to each other and containing ten