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Gero Benckiser

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Review article

Ants and sustainable agriculture. A review

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Abstract – 60% of the world's ecosystems are not used in a sustainable way. Modern agriculture is blamed for declining soil carbon and biodiversity. Climate change, habitat fragmentation and other obstacles impede the movement of many animal species, and distribution changes are projected to continue. Therefore, we need alternative management strategies. The colony organisation of social insects, especially of ants, is seen as a model to design an improved agricultural management, because ants are very experienced agriculturists. Ants represent half of the global insect biomass. Their individuals work like a super organism. This article focuses on harvester and leaf cutter ants by considering *Lasius* species. It reviews the organisation structure of social ant communities. Harvester and leaf cutter ants represent a high percentage of the worldwide ant societies. They collect plant saps with carbon nitrogen (C/N) ratios of about 40 for their own nourishment and leaf fragments with C/N ratios of about 100 for fungi gardens and brood nourishment. They sustain huge numbers of individuals with their low N-based organic imports and their colony commensalisms enable them to convert these polymers into lower molecular, partly volatile compounds, adenosinetriphosphate (ATP), and heat. Digging improves water infiltration, drainage and soil aeration. Ants maintain fungi as a food source for the scleroproteinous brood, carry out food preservation, infection control and waste management, and construct with endurance new nests and rebuild them after damage. All these activities move the nest sites far away from the thermodynamic equilibrium. Physical, chemical and biological gradients emerge and the growing populations, together with nest-penetrating mycorrhized plant roots, absorb the released nutrients and form biomass by lowering energy flows into potentially strong consumer-resource interactions or runaway consumptions. The plant material import of leaf cutter ants, rich in carbon but low in proteins, amounts to 85–470 kg dry weight per year. It keeps the electron donor/acceptor ratio in favour of the electron donor so that denitrifiers can reduce nitrate predominantly to N₂. Ants living in highly N-polluted areas bind the pollutant in the cuticle. In their low N-input environments harvester, leaf cutter and honeydew-sucking ants furnish the N demand of adult ants with the help of N₂-fixing bacteria. The low N-input management of harvester, leaf cutter and honeydew-sucking ants is therefore a resourceful concept for approaching a highly productive agriculture by avoiding soil carbon decline and N₂O emissions increase.

ants / colony organisation / ecosystem engineers / biotechnologists / bio-indicators / intra- and interspecies communication / job sharing / farming and waste management / plasticity / distribution in land-use mosaics / C/N management / N₂O emissions

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1. INTRODUCTION

Nature's functioning depends upon microbial interactions among plants and animals, and their ability to adapt to environmental changes. Their relationship with each other and the environment relies on communication (signal exchanges), and the ability to assume dormancy (cryptobiosis) under unfavourable conditions (Benckiser and Schnell, 2007). The essential role ecosystems have is to provide services to humankind such as nutrient cycling, pest control, pollination, quality of life, and hydrological, atmospheric and climatic regulation. Among the macronutrients, nitrogen, a most unusual element, attracts a lot of interest because it interacts in various ways with ecosystem functioning.

Along its biogeochemical pathway nitrogen is reduced to NH_4^+ , and oxidised into NO , NO_2^- , N_2O and NO_3^- . It reaches by leaching, wind, erosion, or transport by animals any part of the Earth's system, no matter where it is introduced. The N cascade is interrupted only when nitrogen is incorporated into biomass, humus and clay minerals. The manifold nitrogen links to the environment make an effective control on farm and landscape level difficult. Instead, N_2 nitrogen increasingly returns as NH_3 , NO_x and N_2O into the atmosphere, where visibility decreases, the stratospheric ozone is depleted, and global warming and precipitation of acidity increase. Acidity in soils changes the biodiversity (Raubuch and Beese, 2005) and an alternative soil C/N management is required (Crutzen et al., 2007; Fargione et al., 2008; Searchinger et al., 2008).

This review portrays the self-organised living together predominantly of harvester, leaf cutter and honeydew-sucking ants, with their nest functioning based on organic imports high in carbon but low in nitrogen; and it is asked whether a reduction of soil carbon decline and greenhouse gas emissions could be approached by adapting their C/N management.

2. FORAGING, NUTRITIONAL BEHAVIOUR, INTRA-/INTERSPECIES COMMUNICATION AND SYMBIOT MANAGEMENT IN ANT COLONIES

Ants, order *Hymenoptera*, family *Formicidae*, play among insects a demonstrated role in transporting and pooling nutrients (Mueller et al., 2005). They are highly mobile, skilful tillers of soil, dispensers of seeds and microbial propagules, transmitters of N_2 -fixing bacteria, predators, ecosystem engineers, fungi growers, waste managers, biotechnologists, pest controllers, soldiers, and reproducers (Balasubramani and Kannaiyan, 1991; Benckiser, 2006; Jouquet et al., 2006; Philpott et al., 2006; Hölldobler and Wilson, 2009). Ants such as *Atta colombica*, *A. laevigata*, *A. volenweideri* and *A. sexdens* colonies comprise 1–2, 3, 5, 4–7, 5–8 $\times 10^6$ individuals, respectively, and are organised in clear patterns of colonisation and succession (probabilistic patchiness). The myrmicine tribe *Attini* has developed during the last 50 million years a nest management based on organic imports high in carbon and low in protein, and gained expertise in fungal farming. Despite the manifold capabilities ants have, ecosystem models mostly

neglect them (Moore et al., 2006; Brussard et al., 2007; Osler and Sommerkorn, 2007).

2.1. Nest organisation and functioning

For constructing and repairing nests, which are built in a self-organised way without a central control - the queen is merely an egg-layer not an authority figure (Gordon, 2007) - ants must have at minimum the skill to find a suitable site, to evaluate several potential sites for choosing the best one, and to bring the entire population there safely (Hölldobler and Wilson, 1990; Pratt et al., 2002). In an Australian wheat/pasture rotation 5100 to 14860 ant nests per ha are constructed annually and 100 to 370 kg soil turned around, altering the soil structure, oxygen diffusion and metabolism of the nest environment as drastically as in conventionally treated agricultural sites where only a few *Myrmica* and *Lasius* species survive (Wang et al., 1995; Cannon, 1998; Lobry de Bryuyn, 1999; Dauber, 2001; Bucher and Marchesini, 2004; Wagner et al., 2004). Ant nests, reconstructed in late autumn so that they are smaller than at the height of summer, are damaged four times more by conventional agriculture than by no-tillage systems. Ants assemble for digging only when a certain signal threshold concentration is surpassed. The higher the group size, the more body contacts or chemical signals stimulate individuals to dig, and at an assembling volume plateau (V_s) of around 0.2 spontaneous motor activity or low-dimensional disorder of individual ants translates into a directed mobility, physiological rhythm, or coordinated digging (Miramontes et al., 2001; Hölldobler and Wilson, 2009). With nest enlargement the signal concentration decreases and the digging frequency, α , slows down. Ants not engaged in building activities cause feedbacks with snowballing effects on relocation and deposition of building blocks and only the colony level with its specific behavioural rules, activity controls, and high genetic and phenotypic plasticity (fitness), not the individual ant, has the global knowledge of the final nest structure, which tentatively ends in a circular form (Roces, 2002; Benckiser, 2006; Detrain and Deneubourg, 2006).

In conclusion, digging of ants changes soil structures as drastically as human activities (Hölldobler and Wilson, 2009). The mound distribution in a German meadow of *Lasius flavus*, a quince yellow, distributed throughout Europe, small-scale vegetation mosaics creating ant species (Fig. 1), shows that ant activities are not only significantly influencing the soil structure and vegetation in the nest surroundings, but as Figure 1 suggests, in the whole meadow. The vegetation on the mounds is restricted to a few, mostly therophytic (annual) plant species and only a sub-sample of the surrounding grassland vegetation. More excessive is the digging of leaf cutter ants in South America, as the nest pictures in Hölldobler and Wilson (2009) reveal. The nest sizes of *Atta spp.* reach 26.1 to 67.2 square metres and soil depths down to 7 to 8 metres by excavating approximately 40 tons of soil per nest and constructing 6-m-long tunnels that connect an estimated harvesting area of more than one hectare.



Figure 1. Distribution of *Lasius flavus* mounds in a meadow near the village Münzenberg, Hesse, Germany (photo Gero Benckiser).

2.2. Foraging and nutritional aspects

Foraging, similarly coordinated to digging, starts early in the morning with a small group of patrollers, which leaves the nest, meanders around, and after successfully returning, stimulates other ants to join them for foraging (Alonso and Agosti, 2000; Detrain and Deneubourg, 2006). Polyphagous harvester and leaf cutter ants collect plant saps and/or solid leaf fragments with wide C/N ratios. Stressed plant parts are preferred, because they seemingly meet the food requirement of fungi gardens better (Currie et al., 1999; Meyer et al., 2006; Hölldobler and Wilson, 2009). Fungal staphylae, low in N, are the best balanced blends of nutritional components for the brood. Adult ants receive more than 90% of their energy requirement through imbibed plant saps, which are temporarily stored in the gut of returning ants and freely shared with intranidal individuals by regurgitation ('communal stomach'). During a day ants always return to the same foraging area but the colony level alone can rapidly and at any time tune the right numbers of foragers to places of current food availability.

Acromyrmex spp. and *Atta spp.* subsist entirely on food low in nitrogen and abstain from supplementation by arthropod prey (D'Ettore et al., 2001; Bucher and Marchesini, 2004; Hölldobler and Wilson, 2009). From the harvested solid food particles and plant saps, separated from each other by ant mouthparts, infrabuccal pockets and the proventriculus (Cannon, 1998), *Acromyrmex subterraneus* and *A. crassispinus* can hydrolyse cellulose, starch, maltose and sucrose while their fungal associates affect laminarin, xylan and the phenol fraction but not cellulose. *Pogonomyrmex molefaciens* and *Messor pergandei* collect seeds of grasses. At a low supply of desirable seeds they also consume less desirable seeds and non-seed plant material such as leaves. Honeydew-sucking *Lasius niger* and *L. flavus* species receive major proportions of nitrogen through intestinal, N₂-fixing bacteria (Fischer et al., 2001; Zients et al., 2005) and *Camponotus compressus* stimulates seed germination to receive sugars and urea (Shetty, 1982). *C. herculeanus* circumvents N restrictions by spraying formic acid into wounds of preys and digesting proteinous macromolecules extraorally (Zhou et al., 2002). Foregut protease-lacking ants such as the fire ant, *Solenop-*

sis richteri Forel, avoid protein-rich diets (Ricks and Vinson, 1972) and queens contribute to nutrition by dispersing fungal symbionts from parent to offspring nests (Cannon, 1998; Green et al., 2002). Plant saps in the crop of *Camponotus pennsylvanicus* may contain 1208 ± 169 μg sugars, 5 ± 0.7 μg glycogen and 520 ± 115 μg nitrogenous material (Cannon, 1998). Glycogen, presumably digested as it is consumed, is low-concentrated in the gut of *C. pennsylvanicus* similarly to lipids and lipoidal compounds (hormones, pheromones, antibiotic substances), which are crucial in colony recognition. In respect to lipids and lipoidal compounds it is assumed that they are directly shunted into postpharyngeal glands, having oily contents (Cannon, 1998; Zients et al., 2005), but some ants such as *S. richteri* Forel produce lipases in the mandibular and salivary glands, foregut, midgut, and hindgut that correlate with the "grease-loving" feeding habits of this insect (Ricks and Vinson, 1972).

In conclusion, ants can quickly recover from threats and nitrogen limitations by employing fungi and N₂-fixing symbionts, being carnivorous, and/or linking nutrition and parts of the regulatory network to the environment. Redundancy occurs only at a "critical minimum" of essential resources (commodity of space, habitat, right type of food or nest destruction through agriculture; Liebig's law, the principal tenet of population ecology; Fillman and Sterling, 1985; Showler et al., 1990; Zients et al., 2005; Hölldobler and Wilson, 2009).

2.3. Bacterial partners

Ants hatch endosymbiotic α-, β-, γ-*Proteobacteria*, *Flavobacteria* and *Actinomyces*, which provide them with nitrogen, essential amino acids, vitamins, antibiotics and other supplements (Zients et al., 2005, 2006; Stoll et al., 2007; Hölldobler and Wilson, 2009). *Blochmannia*, a γ3-subgroup *Proteobacterium*, resides in densely filled pouch-like ant structures (bacteriocytes) between the epithelial midgut cells and intestines, where it fixes N₂. The *Blochmannia* genome, reduced to 450–800 kb, controls N₂ fixation, the biosynthesis of essential amino acids, acetyl-CoA and tyrosine (required for cuticle sclerotisation), the urease that cooperates with the glutamine synthetase, and sulphate reduction. Despite lacking DNA repair genes the symbiosis between *B. floridanus* and *Camponotus spp.* is relatively stable and decays only when NH₄⁺ accumulates in adult ants with finished sclerotisation. Another widespread α-*Proteobacterium* among insects is *Wolbachia*, that dwells in the ovaries of worker ants and queens and has an influence on the rearing ratio of male and female ants. *Wolbachia*, closely affiliated with *Rickettsiae* and *Rhizobiales*, cooperates with strains of the genera *Escherichia*, *Salmonella*, *Yersinia*, *Bartonella*, *Pantoea*, *Sodalis Mesorhizobium*, *Agrobacterium* and *Blochmannia* for the ants' benefit. Work and matter fluxes in the environment of ants and their microbial associates are coordinated by intra- and inter-exchanged mechanical and chemical signals, e.g., the height of honeydew, phloem saps, pheromones, increasing CO₂ nest concentrations, various non-identified substances released from a Dufour or poison gland, cuticular

hydrocarbons, the nest temperature, which may vary in temperate regions with colonies of less than fifty workers between 16 and 21 °C (*Myrmica punctiventris* Roger; *M. rubra* spp.) and in warmer regions with large colonies of 10⁶ and more individuals between 23 and 32 °C (*Formica polyactena*, *Camponotus mus*, *Solenopsis invicta*), ‘thigmotaxis’ and odometry (Way, 1963; Banschbach et al., 1997; Currie et al., 1999; Ruano et al., 2000; Benckiser, 2006; Bolazzi and Roces, 2007; Bolazzi et al., 2008; Hölldobler and Wilson, 2009). By modifying attenuation and degradation of signalling chemicals the nest temperature acts indirectly (Shaw et al., 2006).

2.4. Fungal farming

High-input systems should focus more on yield with less fertiliser N, but even low-input systems require N to increase yield level and yield stability. Sustainable production systems on low N inputs have to be developed and to reach this goal cross-linked research on different scales, from single cells to crops, to diverse cropping and farming systems are required. In developing more environmentally-friendly agricultural systems ideas could be deduced from fungal farming, which is described here.

Lasius fuliginosus cooperating with the fungus *Cladosporium myrmecophilum* and the ant farmers of the *Attini* genera *Leucoagaricus* and *Leucocoprinus*, which hatch basidiomycetes of the family *Lepiotaceae*, exemplify ant-fungi symbioses (Hölldobler and Wilson, 2009).

Concerning the quality of harvested plant material the ant and fungus have conflicting requirements and the decision is generally made in favour of the fungus, more or less irrespective of the attractiveness of the plant sap found during harvesting. From time to time ascomycetes of the family *Escovopis* infect basidiomycetal fungi farms (Mueller et al., 2005). Leaf cutter ants are successful in reacting to infection events by:

- (a) sequestration of the fungus garden from the environment,
- (b) an intensive monitoring of the fungus garden,
- (c) an early abatement of pathogens with filamentous antibiotic-producing bacteria of the genus *Pseudonocardia* carried on the cuticle,
- (d) hatching an array of auxiliary microbes for disease suppression and other pro- and prebiotic services (Lopes and Orduz, 2003),
- (e) dispersing clonal fungi across many farmer generations,
- (f) maintaining reservoirs of genetically variable cultivars,
- (g) switching from time to time to novel cultivars,
- (h) sharing domesticated fungal cultivars with distantly related ant species,
- (i) a very specific and genetically predetermined feeding behaviour on mycelial fragments,
- (j) production of antibiotic substances in metapleural glands with different roles in fungus culturing (phenylacetic acid suppresses bacterial growth; myrmicacin, a hydroxydecanoic acid, inhibits the germination of spores of alien fungi; indol acetic acid, a plant hormone, stimulates mycelial growth, and 20 recently found compounds spanning in addition to keto acids, alcohols and lactones the

Table I. Total and mean species richness of replicate sites and standard deviations of ants and four other taxa in different land-use types sampled with pitfall traps in the landscape mosaic of Hohenahr-Erda, Central Hesse, Germany. Different letters indicate that values are significantly different ($P < 0.05$, unequal N HSD-Test; for details see (Dauber et al., 2005).

| | | Arable land (n = 12) | Grassland (n = 12) | Fallow land (n = 10) |
|--------------|-------|-------------------------|-----------------------|-------------------------|
| Carabids | total | 75 | 57 | 65 |
| | mean | 26.6 ± 3.7a | 19.3 ± 4.9b | 20.4 ± 4.6b |
| Staphylinids | total | 71 | 70 | 97 |
| | mean | 18.8 ± 6.1a | 21.7 ± 7.0a | 33.3 ± 6.3b |
| Ants | total | 17 | 17 | 21 |
| | mean | 6.3 ± 2.5a | 7.0 ± 3.4a | 9.1 ± 3.2b |
| Isopods | total | 6 | 10 | 12 |
| | mean | 1.1 ± 1.0a | 2.1 ± 0.8b | 3.0 ± 1.5c |
| Diplopods | total | 9 | 10 | 11 |
| | mean | 2.0 ± 1.2a | 2.7 ± 1.4a | 4.0 ± 0.9b |

whole range of carboxylic acids, from acetic acid to long-chain fatty acids), and finally,

- (k) a well-organised waste management accounting for approximately 10% of the work that accurately separates waste managers, consisting of a transporter caste, a worker caste and further partitions within the nest, from in- and outside moving ants with other duties, as well as
- (l) sensitive reactions of sympatric fungi growers on faecal droplets not derived from their own domesticated fungus. The ingredients of faecal droplets, used to manure newly established fungi gardens, help to identify undesirable basidiomycetal strains. Substrate and microbial imports, not harmful for the ant but for the fungus and less quickly identified, may be rejected too late and thus harm nest functioning (Herz et al., 2008).

3. THE LOW N-INPUT CONCEPT OF HARVESTER AND LEAF CUTTER ANTS

3.1. Ants in land-use mosaics

Ants are competitors with each other. They live on honeydew, are predators, even cannibals, or collect within radii of less than one metre to a few hundred metres plant saps and leaf fragments with wide C/N ratios (Hölldobler and Wilson, 1990). Their densities and compositions in agricultural sites depend on human activities and are predictable in a typical German agricultural land-use mosaic such as the “Lahn-Dill Bergland” with arable, fallow, grassland fields and forest sites (Tab. I; Dauber, 2001; Braschler, 2005). Twenty-seven ant species were found there between 1997 and 1998. They belonged to migrating forest species (*Myrmica ruginodis*, *M. lobicornis*, *L. acervorum* and *Formica fusca*), cursorial active species (*F. rufibarbis*, *F. cunicularia*, *F. pratensis*, *F. polyctena*, *F. rufa*, *F. fusca*, *F. rufibarbis*, *F. cunicularia*, *F. pratensis*, *F. polyctena*, *F. rufa*, *F. sanguinea*, *M. ruginodis*, *M. lobicornis*, *Lasius platythorax* and *L. acervorum*), peat land and

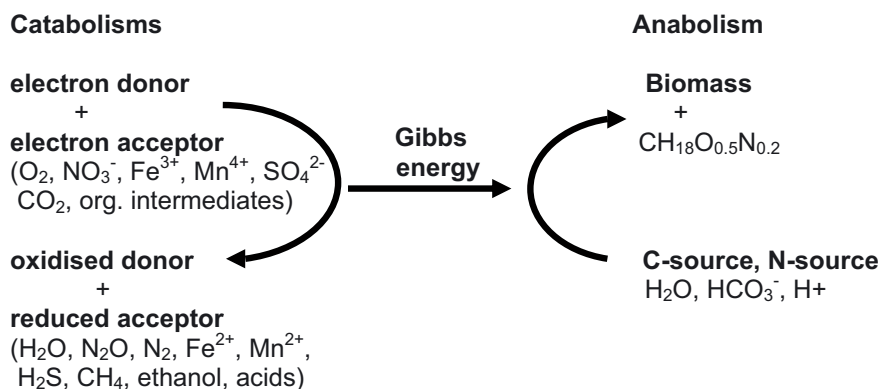


Figure 2. Relationship between ana- and catabolism.

humid meadow species (*M. vandeli*), thermophilic species (*M. sabuleti*, *M. schencki*, *M. rugulosa*, *Tetramorium caespitum*, *Tapinoma erraticum* and *L. alienus*), and relatively resistant species against agricultural vagaries (*M. scabrinoides*, *M. rubra*, *M. ruginodis*, *L. flavus* and *L. niger*), whereas in tropical countries harvester and leaf cutter ants, which can be agricultural pests, dominate the scene (Fillman and Sterling, 1985; Showler et al., 1990).

3.2. Organic matter imports and their conversion

Harvester ants collect plant saps and transport them in the crop to the nest to feed non-foraging nest mates by regurgitation. In one g of collected plant saps 542 to 718 mg carbon, 13.8 to 20.5 mg nitrogen and 58.0 to 94.0 mg ash contents have been determined (Cannon, 1998). The C/N ratios of plant saps and leaf particles, also transported into the nests, are between 40 and 100. The anabolic-catabolic nest cascade (Fig. 2) narrows them to 37–25 (refuse material). Thereby cellulose, fibre, phenol, true protein and the insoluble N fractions may decrease by about 47.7, 9.1, 26.1, 60.8, 10.9 and 10.9%, respectively, while lignin, crude protein, ash content, total N, soluble N, and soluble inorganic and organic N may increase by about 4.9, 31.9, 324.6, 31.9, 363.2, 150 and 461.5%, respectively. Digging in harvester ant nests enhanced the ash content of the deposited refuse material by 71–74.6%, in which total nitrogen increased by 5.2–17% and total carbon decreased by 10.1–34.3% (Cannon, 1998; Wagner and Jones, 2006). The soil chemistry in leaf cutter nests of the 24 known *Acromyrmex* and 15 known *Atta* spp. may alter similarly to in the harvester nests. Volatile organic intermediates (Vespermann et al., 2007), CO₂ and numerous other signal compounds, released into the nest environment, coordinate there the soil functioning (digging, foraging, waste management and infection avoidance). Nest-penetrating, mycorrhized plant roots and the growing nest commensalisms consisting of multiplying microbes, the cuticle sclerotising brood, and adult ants absorb the available nutrients, lower the energy flows into potentially strong consumer-resource interactions or runaway consumptions and develop super organisms

(Ben-Jacob, 2003; Hölldobler and Wilson, 2009). The continuous organic imports into harvester and leaf cutter nests, characterised by C/N ratios between 40 and 100, keep the electron donor/acceptor, carbohydrate/nitrate ratio in favour of the electron donor (Jones and Wagner, 2006). At such carbohydrate/nitrate ratios denitrifiers of the nest environment will reduce accumulating nitrate to N₂, as field studies in plots, which have received varying amounts of mineral and organic fertiliser, and studies in other environments have shown (Tiedje, 1988; Simarmata et al., 1993; Ratering et al., 2006; Falkowski et al., 2008). N₂O emissions are lowest at a carbon/nitrate-N ratio of about 50 and from earthworms, which prefer to ingest organic matter with narrow C/N ratios, it is known that comparably high N₂O emissions can be released (Rizhiya et al., 2007).

3.3. Human and ant farming – a comparison

Farmers, being competitive on the global market, apply high rates of mineral N fertilisers to strongly reduced, fully mechanised and pesticide-treated crop rotations, increasingly grown on large sized fields with various soil types, slopes and valleys. Fertilisation brought a quantum leap in yield improvement, yet concomitantly narrows the C/N ratio and, e.g., increasing amounts of N₂O are emitted from palm- and soybean-biodiesel farms with soil carbon debts of 702 to 3452 Mg CO₂ ha⁻¹ (Crutzen et al., 2007; Fargione et al., 2008; Searchinger et al., 2008). A better carbon/nitrogen management is required (Schmidt-Rohr et al., 2004; Honermeier, 2006). Approximately 50 to 60 million years ago and long before the Romans, who perceived the importance of the C/N ratio and started to culture certain crops and trees with critical microbial rhizosphere associates (nitrogen-fixing bacteria, mycorrhizal fungi), ants began to domesticate fungi and to control the carbohydrate/nitrate ratio in their nest environment (Hölldobler and Wilson, 1990). Today's research ties in with this long tradition and investigates more detailed root exudate-consuming, antibiotic-producing, disease-suppressant, plant health-amending bacteria and fungi (Benckiser, 1997; Gómez-Gómez and Boller, 2002; Lopes

and Orduz, 2003; Franken and George, 2006), soil carbon stabilisation (von Lützwow et al., 2007), N-demand-net-N-mineralisation-gross-N-release balancing (Icoz and Stotzky, 2008; Kooijman et al., 2008), *terra preta* (Marris, 2006), extended crop rotations (e.g., red clover-red clover-potato-wheat-field beans-wheat-rye or corn field beans-wheat-barley-clover/grass-clover/grass; Honermeier, 2006; Malézieux et al., 2009), the harvester and leaf cutter-CN-nest management (Jones and Wagner, 2006; Wagner and Jones, 2004), soil worm behaviour (Sticht et al., 2006; Rizhiya et al., 2007), recuperation of shifting cultivation systems (Addiscott, 1995), and the domestication of low N-input varieties (Ruiz et al., 2008). Recent findings show that in extended crop rotations with legume fields the nitrogenase, which stimulates soil phosphatases, affords a substantially lower activation energy ($\sim 103 \text{ kJ mol}^{-1}$) than the nitrogenase enzyme itself ($\sim 210 \text{ kJ mol}^{-1}$) and that N_2 -fixing plants and ants, which dispense N_2 -fixing bacteria among legumes (Balasubramani and Kannaiyan, 1991), have a similar geographical (temperature-dependent) distribution (Banschbach et al., 1997; Houlton et al., 2008). Whether the activation energy of the nitrogenase in N_2 -fixing bacteria of honeydew-sucking ants or in organically fertilised fields also needs substantially lower activation energy than the nitrogenase enzyme itself has to be proven.

3.4. Reduction of carbon decline and N_2O emissions

Nowadays farmers try to reduce soil carbon decline and N_2O emissions by converting conventionally treated fields into organic farming systems or by employing fertilisers with nitrification inhibitors such as dicyandiamide (DCD), nitrapyrin or 3,4-dimethylpyrazole phosphate (DMPP) (Duxbury et al., 1982; Nelson and Huber, 2001; Honermeier, 2006). Nitrification inhibitors should only temporarily block the ammonium monooxygenase and denitrification and not impair other essential soil processes. A study in DMPP- and DCD-N-fertilised, unfertilised, and control field plots over 3 years could not fully exclude that nitrification inhibitors impair essential soil processes (Weiske et al., 2001); and accordingly fresh ideas from the low N-input management of harvester and leaf cutter ant nests, which live in 26–67 m^2 sized nests with subterranean tunnels, ducts, fungus chambers and residue dumps, and where millions of individuals are digging, doing indoor farming, pest control and waste management, are of interest, though farmers know from agricultural tradition and experience that habitat-specific microbial communities beyond carbon sequestration and growth promotion can rapidly convert into detrimental ones and destabilise yields in various ways (Young and Crawford, 2005). Besides the difficult management of biological systems a substantial proportion of variation in species richness and functioning is still statistically explained in terms of a few environmental variables (Moore et al., 2006; Brussard et al., 2007; Osler and Sommerkorn, 2007) and a predictive theory for messaging molecules, signal transduction, integrated genome regulation and synergisms in subsystems is at the very beginning (Jones et al., 2006; Detrain and Deneubourg, 2006). However,

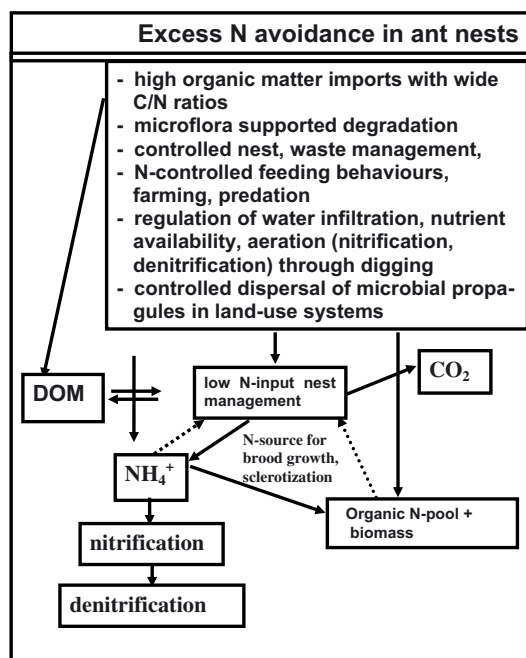


Figure 3. Ant activities and possible exertions of influence on dissolved organic matter (DOM), inorganic and organic N pools, CO_2 production, and gross N fluxes.

these areas are a challenge for biologists, agriculturists, physicists, (bio-) chemists and ecologists and may prove to generate exciting results about the manipulative power that synergistic systems can exert over each partner (Hölldobler and Wilson, 2009).

4. CONCLUSION

Harvester and leaf cutter ants keep invaders low by antibiotics and by importing organic material, low in nitrogen but rich in carbon, by storing nitrogen temporarily in the cuticle and by keeping the nest C/N ratio in favour of the electron donor (Fig. 3).

There are few existing data, and more detailed studies are imperative, but let us speculate that the $\text{N}_2\text{O}/\text{N}_2$ ratio under leaf cutter nest conditions is wide and N_2O is predominantly reduced to N_2 . Harvester and leaf cutter nest sites produce on a low N-input basis high biomasses, similarly to minerally fertilised agricultural soils, and accordingly such environments are seen as an ideal study ground for receiving hints how highly productive, conventional agricultural systems such as biofuel farms could avoid carbon decline and minimise greenhouse gas emissions (Benckiser, 2006; Hölldobler and Wilson, 2009). Organic farming systems, on the other hand, could learn from ant environments how their soil C and N management could be improved and food webs better used for pest control as Figure 4 reveals.

Figure 4 exemplifies by the cooperation of stinging tree ants, genus *Crematogaster*, which hatch in their nests made from leaves and fixed between twigs mealybugs, family



Figure 4. Synergisms between Rufous Woodpeckers, *Micropternus brachyurus* (A), ants of the genus *Crematogaster* (B) and plant juices sucking mealybugs, family *Pseudococcidae* (C), which all reside in the tree-nest (D), made of leaves. (the ant nest-photo, Top Slip, Western Ghats, Kerala, South India, Gero Benckiser; bird-, ant- and mealybug-photos, Wikipedia).

Pseudococcidae, with the medium sized, brown Rufous Woodpecker, *Micropternus brachyurus*, how agro-ecological management could progress in its development (Vishnudas, 2008). Mealybugs living in moist, warm climates, protected by a secreted powdery wax layer, suck plant juices from a variety of subtropical trees (*Gymnocladus dioicus*, *Dalbergia latifolia*, *Aporosa lindleyana*, *Erythrina indica*, *Grevillea parallela*, *Mallotus alba*, *C. verum*, *Cinnamomum malabathrum*, *Olea dioica*, *Gliricidia indica*, *Hopea parviflora*, *Terminalia belarica*, *Bischofia javanica*, *Syzygium cumini* and *Lagestroemia microcarpa*). The ants use the honeydew-producing potential of mealybugs nutritionally and foster and protect them in their paper-wasp-like nests. The plant juice sucking mealybug being supported by *Crematogaster ssp.* impairs coffee plantations and both considered as pests and killed with pesticides.

The emerging demand for organic shade-grown coffee all over the world is forcing planters to reduce the use of toxic chemicals in coffee plantations. This helps maintain reasonable numbers of *Crematogaster* ant colonies and, as followers, many forest-dwelling species such as the Rufous Woodpecker. The high conservation value of shaded coffee plantations with their diversity of canopy tree species providing critical habitats would be maintained and this is recognised. Proper agro-ecological management practices are starting to develop and are being popularised amongst planters.

REFERENCES

- Addiscott T.M. (1995) Entropy and sustainability, *Eur. J. Soil Sci.* 46, 161–168.
- Alonso L.E., Agosti D. (2000) Biodiversity studies, monitoring, and ants: an overview, in: Agosti D., Majer J.D., Alonso L.E., Schultz T.R., Ants – Standard methods for measuring and monitoring biodiversity, Smithsonian Institution Press, Washington, pp. 1–8.
- Balasubramani G., Kannaiyan S. (1991) Natural spread of *A. caulinodans* in stem nodulating *S. rostrata*, *INSURF Netwatch* 1, 5–6.
- Banschbach V.S., Levit N., Herbers J.M. (1997) Nest temperatures and thermal preferences of a forest ant species: is seasonal polydomy a thermoregulatory mechanism? *Insect. Soc.* 44, 109–122.
- Ben-Jacob E. (2003) Bacterial self-organization: co-enhancement of complexification and adaptability in a dynamic environment, *Philos. T. Math., Phys. Eng. Sci.* 361, 1283–1312.
- Benckiser G. (1997) Organic inputs and soil metabolism, in: Benckiser G. (Ed.), *Fauna in soil ecosystems – recycling processes, nutrient fluxes, and agricultural production*. Marcel Dekker, New York, pp. 7–62.
- Benckiser G. (2006) Principles behind order and sustainability in natural successions and agriculture, in: Benckiser G., Schnell S. (Eds.), *Biodiversity in agricultural production systems*. CRC, Taylor and Francis, Boca Raton, Florida, pp. 349–383.
- Benckiser G., Schell S. (Eds.) (2007) *Biodiversity in agricultural production systems*. CRC, Taylor and Francis, Boca Raton, USA.
- Bollazzi M., Roces F. (2007) To build or not to build: circulating dry air organizes collective building for climate control in the leaf-cutting ant *Acromyrmex ambiguus*, *Anim. Behav.* 74, 1349–1355.
- Bollazzi M., Kronenbitter J., Roces F. (2008) Soil temperature, digging behaviour, and the adaptive value of nest depth in South American species of *Acromyrmex* leaf-cutting ants, *Oecologia* 158, 165–175.
- Braschler B.M. (2005) Effects of experimental small-scale grassland fragmentation on the population dynamics of invertebrates, Ph.D. thesis, University of Basel, Switzerland.
- Brussard L., de Ruiter P.C., Brown G.G. (2007) Soil biodiversity for agricultural sustainability, *Agr. Ecosyst. Environ.* 121, 233–244.
- Bucher E.H., Marchesini V. (2004) Herbivory by leaf-cutting ants: nutrient balance between harvested and refuse material, *Biotropica*. 36, 327–332.

- Cannon C.A. (1998) Nutritional Ecology of the Carpenter Ant *Camponotus pennsylvanicus* (De Geer): Macronutrient Preference and Particle Consumption. Dissertation submitted to the Faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology, Blacksburg, Virginia scholar.lib.vt.edu/theses/available/etd-110398-001812/unrestricted/Dissertation-etc.DDF.
- Currie C.R., Scott J.A., Summerbell R.C., Malloch D. (1999) Fungus-growing ants use antibiotic producing bacteria to control garden parasites, *Nature* 398, 701–704.
- Crutzen P.J., Mosier A.R., Smith K.A., Winiwarter W. (2007) N₂O release from agro-biofuel production negates global warming reduction by replacing fossil fuels, *Atm. Chem. Phys. Discuss.* 7, 11191–112055.
- Dauber J. (2001) Ant communities of an agricultural landscape: Relationships to landscape structure and land-use management, Ph.D. thesis, Justus Liebig- University of Giessen, Germany, 120 p.
- Dauber J., Purtauf T., Allspach A., Frisch J., Voigtländer K., Wolters V. (2005) Local vs. landscape controls on diversity: a test using surface-dwelling soil macro-invertebrates of differing mobility, *Global Ecol. Biogeogr.* 14, 213–221.
- D'Ettorre P., Mora P., Dibangou V., Rouland C., Errard, C. (2001) The role of the symbiotic fungus in the digestive metabolism of two species of fungus-growing ants, *J. Comp. Physiol. B* 172, 169–176.
- Detrain C., Deneubourg J.L. (2006) Self-organized structures in a super-organism: do ants “behave” like molecules? *Phys. Life Rev.* 3, 162–187.
- Duxbury J.M., Bouldin D.R., Terry R.E., Tate III R.L. (1982) Emissions of nitrous oxide from soils, *Nature* 298, 462–464.
- Falkowski P.G., Fenchel T., Delong E.F. (2008) The microbial engines that drive earth's biochemical cycles, *Science* 320, 1034–1039.
- Fargione J., Hill J., Tilman D., Polasky S., Hawthorne P. (2008) Land clearing and the biofuel carbon debt. *Science* 319, 1235–1238.
- Fillman D.A., Sterling W.L. (1985) Inactivation Level for the red imported fire ant, *Solenopsis invicta* (Hym: Formicidae): a predator of the boll weevil, *anthomonas grande* (Col.: Curculionidae), *Agr. Ecosyst. Environ.* 13, 93–122.
- Fischer M.K., Hoffmann K., Völkl W. (2001) Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance, *Oikos* 92, 531–541.
- Franken P., George E. (2006) Diversity of arbuscular mycorrhizal fungi, in: Benckiser G., Schnell S. (Eds.), *Biodiversity in agricultural production systems*, CRC, Taylor and Francis, Boca Raton, Florida, pp. 189–203.
- Gómez-Gómez L., Boller T. (2002) Flagellin perception: a paradigm for innate immunity, *Trends Plant Sci.* 7, 251–256.
- Gordon D.M. (2007) Control without hierarchy, *Nature* 446, 1433.
- Green A.M., Mueller U.G., Adams R.M.M. (2002) Extensive exchange of fungal cultivars between sympatric species of fungus-growing ants, *Mol. Ecol.* 11, 191–195.
- Herz H., Hölldobler B., Roce F. (2008) Delayed rejection in a leaf-cutting ant after foraging on plants unsuitable for the symbiotic fungus, *Behav. Ecol.* 19, 575–582
- Hölldobler B., Wilson E.O. (1990) *The ants*. Springer, Heidelberg, 732 p.
- Hölldobler B., Wilson E.O. (2009) *The superorganism*, W.W. Norton & Company, Inc., New York, 522 p.
- Honermeier B. (2006) Diversity in crop production systems, in: Benckiser G., Schnell S. (Eds.), *Biodiversity in Agricultural Production Systems*, CRC, Taylor & Francis, Boca Raton, pp. 1–19.
- Houlton B.Z., Wang Y.P., Vitousek P.M., Field C.B. (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere, *Nature* 454, 327–331.
- Icoz I., Stotzky G. (2008) Fate and effects of insect-resistant *Bt* crops in soil ecosystems, *Soil Biol. Biochem.* 40, 559–586.
- Jones C.G., Gutiérrez J.L., Groffman P.M., Shachak M. (2006) Linking ecosystem engineers to soil processes: a frame work using the Jenny State Factor Equation, *Eur. J. Soil Biol.* 42, 39–53.
- Jones J.B., Wagner D. (2006) Microhabitat-specific controls on soil respiration and denitrification in the Mojave Desert: the role of harvester ant nests and vegetation, *West. N. Am. Naturalist* 66, 426–432.
- Jouquet P., Dauber J., Lagerlöf J., Lavelle P., Lepage M. (2006) Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feed back loops, *Appl. Soil Ecol.* 32, 153–164.
- Kooijman A.M., Kooijman-Schouten M.M., Martínez-Hernández G.B. (2008) Alternative strategies to sustain N-fertility in acid and calcareous beech forests: low microbial N-demand versus high biological activity, *Basic Appl. Ecol.* 9, 410–421.
- Lobry de Bruyn L.A. (1999) Ants as bioindicators of soil function in rural environments, *Agr. Ecosyst. Environ.* 74, 425–441.
- Lopes E., Orduz S. (2003) *Metarhizium anisopliae* and *Trichoderma viride* for control of nests of the fungus-growing ant, *Atta cephalotes*, *Biol. Control.* 27, 194–200.
- Marris M. (2006) Black is the new green, *Nature* 442, 624–626.
- Malézieux E., Crozat Y., Dupraz C., Laurans M., Makowski D. Ozier-Lafontaine H., Rapidel B., de Tourdonnet S., Valantin-Morison M. (2009) Mixing plant species in cropping systems: concepts, tools and models. A review, *Agron. Sustain. Dev.* 29, 43–62.
- Meyer S.T., Rocas F., Wirth R. (2006) Selecting the drought stressed: effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*, *Funct. Ecol.* 20, 973–981.
- Miramontes O., Sole R.V., Goodwin B.C. (2001) Neural networks as sources of chaotic motor activity in ants and how complexity develops at the social scale, *Int. J. Bifurcat. Chaos* 11, 1655–1664.
- Moore J.C., Simpson R.T., McCann K.S., de Ruiter P.C. (2006) Food web interactions and modeling, in: Benckiser G., Schnell S. (Eds.), *Biodiversity in Agricultural Production Systems*, CRC, Taylor & Francis, Boca Raton, pp. 385–398.
- Mueller U.G., Gerardo N.M., Aanen D.K., Six D.L., Schultz D.R. (2005) The evolution of agriculture in insects, *Annu. Rev. Ecol. Syst.* 36, 563–595.
- Nelson D.W., Huber D. (2001) Nitrification inhibitors for corn production. National Corn Handbook, Iowa State University, USA, University extension, <http://www.extension.iastate.edu/Publications/NCH55.pdf>.
- Osler G.H.R., Sommerkorn M. (2007) Toward a complete soil C and N Cycle: Incorporating the soil fauna, *Ecology* 88, 1611–1621.
- Philpott S.M., Uno S., Maldonado J. (2006) The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodiv. Conser.* 15, 487–501.
- Pratt S.C., Mallon E.B., Sumpter D.J.T., Franks R.N. (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*, *Behav. Ecol. Sociobiol.* 52, 117–127.
- Ratering S., Benckiser G., Schnell S. (2006) Metabolic diversity of microorganisms in agricultural soils In: Benckiser G., Schnell S. (Eds.), *Biodiversity in Agricultural Production Systems*, CRC, Taylor & Francis, Boca Raton, pp. 287–315.

- Raubuch M., Beese F. (2005) Influence of soil acidity on depth gradients of microbial biomass in beech forest soils, *Eur. J. Forest. Res.* 124, 87–93.
- Ricks B.L., Bradleigh Vinson S. (1972) Digestive enzymes of the imported fire ant *Solenopsis richteri* (Hymenoptera: Formicidae), *Entomol. Exp. Appl.* 15, 329–334.
- Rizhiya E., Bertora C., van Vliet P.C.J., Kuikman P.J., Faber J.H., van Groenigen J.W. (2007) Earthworm activity as a determinant for N₂O emission from crop residue, *Soil Biol. Biochem.* 39, 2058–2069.
- Roces F. (2002) Individual complexity and self-organisation in foraging by leaf-cutting ants, *Biol. Bull. US* 202, 306–313.
- Ruano F., Tinaut A., Soler J.J. (2000) High surface temperature select for individual foraging in ants, *Behav. Ecol.* 11 396–404.
- Ruiz M., Aguiriano E., Carrillo J.M. (2008) Effects of N fertilization on yield for low-input production in Spanish wheat landraces (*Triticum turgidum* L. and *Triticum monococcum* L.), *Plant Breeding* 127, 20–23.
- Schmidt-Rohr K., Mao J.D., Olk D.C. (2004) Nitrogen-bonded aromatics in soil organic matter and their implications for a yield decline in intensive rice cropping, *Proc. Natl. Acad. Sci. (USA)* 101, 6351–6354.
- Searchinger T., Heimlich R., Houghton R.A., Dong F., Elobeid A., Fabiosa J., Tokgoz S., Hayes D., Yu T.H. (2008) Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change, *Science* 319, 238–240.
- Shaw L.J., Morris P. Hooker J. E. (2006) Perception and modification of plant flavonoid signals by rhizosphere microorganisms, *Environ. Microbiol.* 8, 1867–1880.
- Shetty P.S. (1982) Gustatory preferences of ants (*Camponotus compressus*) for urea and sugars, *Experientia* 38, 259–260.
- Showler A.T., Knaus R.M., Reagan T.E. (1990) Studies of the territorial dynamics of the red imported Fire Ant (*Solenopsis invicta* Buren, *Hymenoptera: Formicidae*), *Agr. Ecosyst. Environ.* 30, 97–105.
- Simarmata T., Benckiser G., Ottow J.C.G. (1993) Effect of an increasing carbon:nitrate ratio on the reliability of acetylene in blocking the N₂O-reductase activity of denitrifying bacteria in soil, *Biol. Fert. Soils* 15, 107–112.
- Sticht C., Schrader S., Giesemann A., Weigel H.J. (2006) Effects of elevated atmospheric CO₂ and N fertilization on abundance, diversity and C-isotopic signature of collembolan communities in arable soil, *Appl. Soil Ecol.* 34, 219–229.
- Stoll S., Gadau J., Gross R., Feldhaar H. (2007) Bacterial microbiota associated with ants of the genus *Tetraponera*, *Biol. J. Linn. Soc.* 90, 399–412.
- Tiedje J.M. (1988) Ecology of denitrification and dissimilatory nitrate reduction to ammonium, in: Zehnder A.J.B. (Ed.), *Biology of anaerobic microorganisms*, John Wiley, New York, pp. 179–244.
- Vespermann A., Kai M., Piechullaet B. (2007) Rhizobacterial volatiles affect the growth of fungi and *Arabidopsis thaliana*, *Appl. Environ. Microb.* 73, 5639–5641.
- Von Lützw M., Kögel-Knabner I., Ekschmitt K. Flessa H., Guggenberger G., Matzner E., Marschner B. (2007) SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms, *Soil Biol. Biochem.* 39, 2183–2207.
- Vishnudas C.K. (2008) Woodpeckers and ants in India's shade coffee, *Indian Birds* 4, 9–11.
- Wagner D., Jones J.B. (2004) The contribution of harvester ant nests (*Pogonomyrmex rugosus*, *Hymenoptera, Formicidae*) to soil nutrient stocks and microbial biomass in the Mojave Desert. *Environ. Entomol.* 33, 599–607.
- Wagner D., Jones J.B. (2006) The impact of harvester ant nests on decomposition, N mineralization, litter quality, and availability of N to plants in the Mojave Desert, *Soil Biol. Biochem.* 38, 2593–2601.
- Wagner D., Jones J.B., Gordonet D.M. (2004) Development of ant harvester colonies alters soil chemistry, *Soil Biol. Biochem.* 36, 797–804.
- Wang D., McSweeney K., Lowery B., Norman J.M. (1995) Nest structure of ant *Lasius neoniger* Emery and its implication to soil modification, *Geoderma* 66, 259–272.
- Way M.J. (1963) Mutualism between ants and honeydew-producing *Homoptera*, *Ann. Rev. Entomol.* 8, 307–344
- Weiske A., Benckiser G., Herbert T., Ottow J.C.G. (2001) Influence of the denitrification inhibitor 3,4-dimethylpyrazole phosphate (DMPP) in comparison to dicyandiamide on nitrous oxide emissions, carbon dioxide fluxes and methane oxidation during 3 years of repeated application in field experiments, *Biol. Fert. Soils* 34, 109–117.
- Young I.M., Crawford J.W. (2004) Interactions and self-organisation in the soil-microbe complex, *Science* 304, 1634–1637.
- Zhou X., Haya H.K., Heungens K., Goodrich-Blair H. (2002) Response of ants to a deterrent factor(s) produced by the symbiotic bacteria of Entomopathogenic nematodes, *Appl Environ. Microb.* 68, 6202–6209.
- Zients E., Feldhaar H., Stoll S., Gross R. (2005) Insights into the microbial world associated with ants, *Arch. Microbiol.* 184, 199–206.
- Zients E., Beyaert I., Gross R., Feldhaar H. (2006) Relevance of the endosymbiosis of *Blochmannia floridans* and carpenter ants at different stages of the life cycle of the host, *Appl. Environ. Microb.* 72, 6027–6033.