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REVIEW ARTICLE

Economic and ecological importance of termites: A global review

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Abstract

In this review article, the positive and negative impacts of termites on ecosystems and human activities are examined. Various ecosystem services provided by termites – their importance as a food resource for humans, wildlife and domestic animals – are discussed, along with the use of these insects in scientific research and in folk and traditional medicine. Some insufficiently studied properties of termites (their ability to perceive the radiation of radioactive substances, electric fields and magnetic fields), as well as the use of termites in bionics, are described. Special attention is paid to the use of termite mounds for different purposes (e.g. in mineral deposit searches, in medical applications, as furnaces for copper smelting, for storage of some nuts, as burial sites, for gathering of edible mushrooms of the genus *Termitomyces* and as fertilizer). Examples of such use in different countries are given. This article reviews the activities of termites as pests of agriculture and forestry, including crops that are most affected, and termites as structural pests (e.g. wooden structures, household furniture, books and museum collections). Examples of termites' malicious activities in different parts of the world are provided. Information on the invasions of termites is given, and the main areas of expansion of their habitat are described. The economic loss caused by termites in some countries and the world as a whole are presented. The article also lists the most economically important termite species in the world.

Key words: ecosystem, globe, harm, services, soil, termites, use.

INTRODUCTION

Termites are found on all continents except Antarctica. According to different data sources, the number of termite species in the world is less than 2,500 (Taylor 2000), approximately 2,500 (van Huis 2017), more than 2,600 (Lenz *et al.* 2013b; Oguwike *et al.* 2013; https://nature.berkeley.edu/upmc/documents/UN_termite.pdf), approximately 2,700 (Rouland-Lefevre 2011), approximately 2,750 (Donovan *et al.* 2001), more than 2,800 (Verma *et al.* 2009), 2,933 (Krishna *et al.* 2013 or between 2,300 and 3,000 (Engel *et al.* 2009). Approximately 1,000 termite species are found in Africa, 435 species in Asia, more than 400 species in South America, more than 360 species in Australia, about 50 species in North America and 10 species in Europe (Krishna *et al.* 2013).

Termites have extremely high population densities. The density of the living biomass in the savanna is estimated at 70–110 kg/ha (1 ha = 1 $hm^2 = 10^4 m^2$). However, in other habitats, they also reach significant numbers. For instance, in termite nests in forest ecosystems of Cat Tien National Park (south Vietnam), one type of termite (*Macrotermes*) is estimated at 2.5 million individuals, or approximately 20.5 kg/ha (Belyaeva & Tiunov 2010). The number of termites per square meter can reach a maximum of 15,000 individuals, but population densities between 2,000 and 7,000 termites/m^2 are quite common (Jouquet *et al.* 2011). It is believed that the total biomass of termites is comparable to the total biomass of terrestrial vertebrates (Scheffrahn 2008).

There are three major types of termites, distinguished by their living environment: (i) subterranean termites, which live underground and prefer to eat soft woods; (ii) drywood termites, which do not need to be near the soil and prefer dry wood; and (iii) dampwood termites, which live in very moist wood and do not need to be in contact with mud and soil to survive. Termites can also be classified into four broad feeding guilds: wood-feeders, soil-feeders, fungus-growers and grass-feeders (Brauman *et al.* 2015).

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ECOSYSTEM SERVICES PROVIDED BY TERMITES

Along with ants and earthworms, termites are one of the three main groups of soil ecosystem engineers (Lavelle *et al.* 2006). In many areas, especially in the tropics, termites are often the dominant macrobiota, with a major role in ecological processes (Bonachela *et al.* 2015). The main ecosystem services are the breakdown and recycling of organic matter, removal of dung, soil loosening, soil formation, soil fertility, greenhouse gas emission and pollination.

Breakdown and recycling of organic matter

Termites play a huge role in organic decomposition, consuming all dying wood materials and plant remains (Mugerwa 2015; Qasim *et al.* 2015). According to Verma *et al.* (2009), in tropical and subtropical environments, they help in breaking down and recycling one-third of the annual production of dead wood. According to other data, this value may be most significant. For instance, in the Guinea Savanna of southern Nigeria, hydrophilic termites removed an estimated 835.5 kg/ha of wood litter (60% of annual wood-fall) and 68.4 kg/ha of leaf litter (3% of annual leaf-fall), or 24% of the total annual litter production (Schowalter 2013). Such influence is most important in arid regions (deserts and dry savannas) as the rainy season is short (Schuurman 2005).

Termites are able mechanically to chop up plant material with their mandibles and grind it with their gizzard, thereby increasing the surface area accessible to soil microorganisms. Organic matter recycled by termites is not confined to wood and leaves; it also includes bark, straw and even such animal products as mammalian hooves and dung (Jouquet *et al.* 2011; Harit *et al.* 2017a).

Removal of dung

Many kinds of insects utilize animal manure. Such insects include dung beetles, water scavenger beetles, termites and larvae of dung flies, houseflies, some syrphid flies, soldier flies, and tachinid flies. Each geographic zone has its own characteristic set of dung-removing insects. In the tropical savanna, termites are of great importance. At least 126 species of termites feed on the dung of 18 species of mammals. On average, termites in the tropics remove 33% of dung in a particular habitat within 1 month (Freymann *et al.* 2008). Termites process the manure fully within 3 months, whereas in their absence it would take 20–30 years for the manure to disappear (Whitford *et al.* 1982).

Soil loosening

One of the important results of termite activity is loosening of the soil. Whether termites live in the earth or on its surface, they all mix soil. Their activity leads to the following consequences: (i) breaking up surface crusts; (ii) reducing soil compaction; (iii) increasing soil porosity; (iv) improving water infiltration into the soil; and (v) enhancing water-holding capacity in the soil. Their activity greatly improves water infiltration where termite tunnels in the soil allow rainwater to soak in deeply and helps reduce run-off and consequent soil erosion, through bioturbation, or biological mixing (Lofjle & Kubiniok 1996). By creating tunnels, the foraging activity of termites increases the water infiltration rate by a factor of 2 to 4 (Kaiser *et al.* 2017).

Bioturbation, or the disturbance of sediment layers by living things, is mainly carried out by termites in tropical soil. In their role of bioturbators, termites affect soil properties temporally and spatially: they drive aggregate dynamics, modify clay mineralogy, and induce physical stability to enhance and sustain porosity and generate nutrient-rich patches at the landscape level (Jouquet *et al.* 2016, 2017; Harit *et al.* 2017b).

Soil formation

Termite activity often results in the formation and regulation of soil, maintaining the physical and chemical conditions necessary to support stability and fertility. Termites' nutrient-rich salivary secretions and fecal material act as cement during mound construction, and in some regions where termite activity is high they are able to significantly modify soil chemical properties. Because of its higher exchangeable cation concentration and clay content, the soil translocation from deeper in the profile up to the surface during termite activity could also enrich the surface soil with nutrients useful to plants (Jouquet *et al.* 2015).

Soil fertility

Soil-dwelling termites dig nests in the ground that have a significant impact on the soil environment. Activities of termites can result in accumulation of organic matter and enrichment of nutrients and minerals in the soil (Li *et al.* 2017). Termites, along with ants, can increase productivity in regions with a dry, hot climate (in experimental conditions in Australia, they increase the wheat yield by 36%), where there are no earthworms (Evans *et al.* 2011). In some cases, the activities of termites led to the increase in soil pH, which was noted in Zhejiang Province, China (Li *et al.* 2017). An increase in soil fertility is also due to the return of organic matter into the soil, through feces and the biomass of termite bodies (Jouquet *et al.* 2011). It is known that termites enrich the soil with nutrients (Lagendijk *et al.* 2016). Another characteristic feature of termites is their ability to transform minerals chemically (Sako *et al.* 2009).

Pollination

Termites are not widely known as pollinators, although that role has been seen at least once before in the case of the subterranean orchid, *Rhizanthella gardneri* Rogers, 1928, a peculiar and rare underground-blooming flower in western Australia known to be pollinated by Australian harvester termites of the genus *Drepanotermes*. They regularly and systematically visit newly opened flowers and transport pollen masses, making them likely pollinators. It is perhaps the only Orchidaceae flower in the world to be pollinated by termites (McHatton 2011).

TERMITES AS A FOOD SOURCE FOR WILD ANIMALS

Termites are prey to a wide variety of predators. For example, one species of termite, the harvester termite, *Hodotermes mossambicus* Hagen, 1853, is found in the stomachs of 65 species of birds and 19 species of mammals (Kok & Hewitt 1990). The spectrum of termites eaten by animals varies enormously. Top predators are ants. For example, in the humid savanna of Nigeria, the Matabele ants, *Megaponera foetens* Latreille, 1802 consume only termites of the Macrotermitinae subfamily; more often, those are *Macrotermes bellicosus* Smeathman, 1781 (72%) and Odontotermes (22%) (http://antclub.ru/lib/brian-m-v/obshchestvennye-nasekomye/pishcha/osy-i-muravi-kak-khishchniki). *Centromyrmex gigas* Forel, 1911, which inhabits Argentina and Brazil, eats only termites (http://www.antwiki.org/wiki/Centromyrmex_gigas).

Anteaters (besides numbats), aardvarks and pangolins feed almost exclusively on ants and termites (da Cunha *et al.* 2015). Large quantities of termites are also eaten by woodpeckers, skunks, bears, chimpanzees, wasps, spiders and scorpions. The method of extracting termites differs for each type of predator. For example, sloth bears destroy nests of termites to consume their inhabitants, whereas chimpanzees use sticks as tools to fish the insects from their nests (Calcutt *et al.* 2014; Almeida-Warren *et al.* 2017).

TERMITES AS FOOD AND FEED FOR HUMANS AND DOMESTIC ANIMALS

Worldwide, at least 43 edible termite species are used for human food and livestock feed (Figueirêdo *et al.* 2015). Termites are probably most popular as food in Africa (van Huis 2017). Detailed information on food use of termites in Limpopo Province, South Africa is given in the article Netshifhefhe *et al.* (2018). According to Rumpold and Schlüter (2015), the average protein content of termites is 35.34% (minimum 20.40%, maximum 65.62%) and the average fat content is 32.74% (minimum 21.35%, maximum 46.10%). The protein content of *Odontotermes* sp. is 33.67% (Chakravorty *et al.* 2016), *Macrotermes* sp. is 24.5% (Payne *et al.* 2016) and *Macrotermes nigeriensis* Sjostedt termites is 20.94% (Igwe *et al.* 2011). Nutritional value of termite species *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* (Kolbe) is characterized in the article Itakura *et al.* (2006).

The energy value of termites (in kilocalories) is also high. For instance, the Mendi termite *Macrotermes subhyalinus* Rambur has an energy content of 389 kcal/100 g to 406 kcal/100 g of dry matter (Niaba *et al.* 2013). According to a more recent source, this number may be higher, at 613 kcal/100 g of dry matter (Chakravorty *et al.* 2016). Roasted winged termites, *M. falciger* (Gerstacker) provide energy values from 591 kcal/100 g (Chulu 2015) to 810 kcal/100 g (Siulapwa *et al.* 2014). Termites are mainly consumed when they are in the mature stage (Cerritos 2009).

The key aspect of protein metabolism is the degree to which a protein is digestible by humans. Studies show that termite protein is of good quality and high digestibility. For example, the digestibility of protein of fresh termites (*M. subhylanus*) is 90.49% (Kinyuru *et al.* 2010).

The nutritional properties of termites are very high, and they can be successfully substituted for many ingredients used in the production of foods (e.g. fish and soybeans) (van Huis *et al.* 2013). For instance, defatted termite *M. subhyalinus* is used for the preparation of wheat biscuits (Niaba *et al.* 2013).

However, the use of termites as live food rather processed food is practiced more often. Traditionally, termites are used as feed in raising poultry. For example, in villages of Guinea, Togo, Burkina Faso and India, termites are used to feed fowl, including chickens; in farms across Africa termites are used to feed ostriches. Some termites, especially the yellow-necked drywood termite, *Kalotermes flavicollis* Fabricius, 1793, have been successfully used in aquaculture (European Food Safety Authority Scientific Committee 2015).

USE OF TERMITES IN SCIENTIFIC STUDIES

Termites, like ants and honeybees, are social insects. Castes of termites are primarily divided into two types of individuals: fertile (reproductives) and sterile individuals (neuters). The sterile castes include workers, presoldiers and soldiers, whereas the fertile ones are alates, primary reproductives and secondary reproductives (Watanabe *et al.* 2014). The worker caste is responsible for feeding the colony and distributing food. The soldier caste is accountable for colony defense against invaders and is fed by the worker caste (Franco Cairo *et al.* 2016).

A single individual or a limited number of individuals (queens) produce most or all of the offspring, and a large number of individuals (workers) forego reproduction for group beneficial activities. The queens live 10–100 times longer than the workers (Tasaki *et al.* 2017a,b). A termite queen can live up to 20 years (Makrushin 2010) and even 30 years (Keller 1998). Because the genotypes of queens and female workers are identical, the differences in lifespan can be caused by aging-determinant genes. As a result, termites are a promising model for identification of such genes.

Termites are also used in other scientific studies. They are used in academic studies of the social behavior of animals and their capacity for learning and elementary brain activity. Termites may also help with scientific studies of age polyethism, which occurs when individuals of different ages perform different tasks. In termites, this has mostly been reported in higher termites, but elements of age polyethism were recently found in juvenile colonies of a lower termite, *Coptotermes formosanus* Shiraki (Rhinotermitidae) (Du *et al.* 2017).

Termites are used also as indicators of various environmental features, such as anticipated rainfall and soil fertility. The soil of termite mounds was reportedly used in low-risk farming strategies (Mahapatro *et al.* 2017). Sometimes termites are used in criminal investigations. Such an example given in the article of Queiroz *et al.* (2017).

USE OF TERMITES IN MEDICINE

Ten species of termites have been reportedly used for medicinal purposes (Figueirêdo *et al.* 2015). In 28 countries of the world (including 17 countries in Africa) termites play dominant medicinal roles (Meyer-Rochow 2017). Termites have been used as a source of medicines to treat wounds, malnutrition and heart conditions (Costa-Neto 2005), anemia and diarrhea (Senthilkumar *et al.* 2008) and tuberculosis (Costa-Neto & Motta 2008).

Some termite species have been used as alternative treatments for spiritual issues and physiologic problems. The species *Nasutitermes macrocephalus* Silvestri, 1903 is recorded most often, being widely used in Brazil as a therapeutic resource for the treatment of asthma, hoarseness, sinusitis and other conditions. This species is also widely used in folk medicine in India (Chaves *et al.* 2017). *Macrotermes nigeriensis* is used in Nigeria to act as a charm for spiritual protection and as a source of medicine to treat wounds and to treat the sickness of pregnant women (Figueirêdo *et al.* 2015). The ethyl acetate extracts of the fermented broth of the termite nest-derived fungus *Xylaria nigripes* (Klotzsch) has long been used as a traditional Chinese medicine for treating insomnia and depression (Chang *et al.* 2017).

In northern Brazil, termites are commonly used to treat dermatologic problems. Additionally, the use of tea-crushed insects and the inhalation of incinerated termite soil have been reported in cases of bronchitis, wounds, colds, flu, rheumatism and other conditions (Padilla *et al.* 2015).

Sometimes, termites are applied as a medical device. If the subcutaneous administration of a drug is necessary, it is laid on the patient's skin and then a termite is agitated and placed on the skin as well. In cases of termite stings, their mandibles are the effective injection device (Srivastava *et al.* 2009).

Termites are exposed to a variety of infectious microbes in their habitats throughout their life cycle. They need to prevent infection in order to survive, and so they must recognize and eliminate pathogens if they become infected with any microbes. Recently, the termite has also been described as a source of natural products with antibiotic and antifungal activities (Padilla *et al.* 2015). The Japanese subterranean termite, *Reticulitermes speratus* (Kolbe, 1885) is one example of a termite species used for antibiotic and antifungal qualities (Mitaka *et al.* 2017).

TERMITES IN BIONICS

Termites can detect many stimuli that cannot be perceived by humans. For example, termites *Heterotermes indicola* Wasmann, 1902 are able to produce and perceive electric and magnetic fields. In the late 1970s, research was published on communication between *Heterotermes indicola*, by means of electromagnetic fields (Becker 1979; Trushin 2004). Termites placed inside of closed glass vessels exercised an "influence" on individuals outside the vessels by creating an alternating electric field (Manzoor *et al.* 2015). Common mound-building termites *Macrotermes gilvus* Hagen, 1858 use magnetic fields for navigation and orientation (Esa *et al.* 2015).

Termites are also skillful builders. The above-ground parts of their mounds are made of sand, clay, processed cellulose, and other substances held together by the saliva of the termite workers. The termite mound is constantly being built as long as the colony of termites inhabiting it is living. The largest known termite mound is 12.8 m high. The exterior walls of a termite mound are watertight to prevent flooding by tropical showers. The walls reach thicknesses of 20–30 cm but have small holes for ventilation. The interior space of a termite mound is pierced with a great number of passageways that provide the water supply, water discharge and ventilation. The air is moistened and cooled here because the termites – especially the egg-laying termite queen – are very sensitive to the humidity of the air (https://en.wikipedia.org/wiki/Mound-building_termites).

Termites clearly orient the locations of their constructed "skyscrapers" with respect to the cardinal directions (Ocko *et al.* 2017). The east and west "faces" of their "buildings" are extended, and weak streams of the morning and evening sun only slightly warm the construction. The narrow surface of the termite mound is always oriented toward the hot sun at noon. The vertical and side ventilation shafts and passages are designed to catch in the best way the refreshing winds and to dissipate excess heat. The passages into which the scorching wind begins to blow are temporarily blocked by termites (Jacklyn & Munro 2002).

The Eastgate Centre building in Harare, Zimbabwe, can be called the first building based on the construction technologies of termites. The passive ventilation system provides comfortable conditions in the building with minimum electricity consumption (Thomas 2006). These technologies are so efficient that the Eastgate complex does not need to use air conditioning; consequently, it was possible to save the $3.5 million it would have cost to buy air conditioning equipment. Accordingly, this decreased electric energy consumption the Eastgate complex uses only 35% of the energy required for temperature regulation, compared with other buildings of similar size. Rents are lower by 20% than they are in neighboring buildings (Pappagallo 2012). Other such buildings include the Learning Resource Center at the Catholic University of Eastern Africa (http://buildesign.co.ke/the-lrc/) and the Council House 2 building in Melbourne, Australia (McKeag 2009).

TERMITES AND ENTOMOTOURISM

A potential for development of entomotourism can be determined by some taxa of insects (e.g. butterflies, jewel beetles, fireflies, stick insects and dragonflies). Tourism related to insects is organized in the Endau-Rompin National Park (Pahang, Malaysia) (Aihara *et al.* 2016), and termites play a significant role in this tourism. According to study results, termites were the most advanced species in the development of tourism in the park. Furthermore, park visitors were asked which aspects of the insects were of principal interest to them. Seventy-three of the 117 (62%) respondents wanted to know about termites' communication system, 60 (51.1%) about their defense system, 53 (45.3%) about their morphology and 49 (42%) about their foraging behavior (Hamdin *et al.* 2015). The big and unique termite mounds (the Cathedral Termite and the Magnetic Termite) in the Northern Territory, Australia, are famous tourist spots.

TERMITES AS DECOMPOSERS OF WASTE PAPER PRODUCTS

Termites (Isoptera) have often been proposed as decomposers of lignocellulosic waste, such as paper products. In most countries, timber and paper comprise a large proportion of the biodegradable solid waste. As paper accounts for 25% of landfill waste and 33% of municipal waste, use of termites is an attractive method of decomposition. The fact that all waste paper products contain lignocellulosic fibers does not automatically make them suitable for decomposition by termites. Each paper product has to be assessed to see whether termites can reproduce on this diet. The most suitable for decomposition are Kraft pulp and tissue paper (Lenz *et al.* 2011).

TERMITES AS BAIT

Termites can be used for catching fish and birds. For example, in Zambia, snouted termites (*Trinervitermes* spp.) are used as fish bait in conical reed traps and as bait for attracting insect-eating birds (e.g. pet speckled hen, francolin, quail and blackbirds). Birds are caught by setting a trap using the broken top of a termite mound, where worker termites amass for hours. Fishermen use termite larvae as bait (van Huis 2017).

USE OF TERMITE MOUNDS

Use of termite mounds for searching for deposits

Termites construct their nests using different locally available materials, including soil and ground particles delivered from underground. Thus, some termites living in deserts burrow in the soil in vertical tunnels up to

40 m long (http://animalreader.ru/termitnik-shedevr-inzhenernogo-iskusstva.html). If the termite mounds are located not far from a body of ore, then the material of termite mounds contains the elevated concentrations of the useful component. Therefore, based on the analysis of samples taken from the termite mound or anthill, one may determine whether there is an ore deposit nearby.

For example, in the vicinity of the Garden Well gold deposit, in Western Australia, the concentration of gold in the surface soils is, on average, 2 mg/t (2 parts per billion). However, in 22 mounds formed by the termite *Tumulitermes tumuli* Froggatt the average concentration of gold was 7.4 mg/t (7.4 parts per billion), in the mounds of the subterranean termite *Schedorhinotermes actuosus* Hill, 8.4 mg/t (8.4 parts per billion), and in the nest of ant species *Rhytidoponera mayri* Emery, 1883, 24.4 mg/t (24.4 parts per billion).

Analysis of the material of termite nests makes the search for gold significantly less expensive and much safer for the environment (Arhin *et al.* 2015). Today, geologists use expensive drilling for these purposes (Stewart & Anand 2014). Termites do not especially choose to bring the gold to their nests; however, soil particles in the underground layers (delivered by the termites from depths of 1–4 m) have a higher gold content and the insects thereby serve involuntarily as artisans (Stewart & Anand 2012).

Termites are also able to serve as indicators of deposits of other mineral resources. The Vila Manica copper deposit in Mozambique was discovered by using termites. Later, the largest kimberlite (diamond) mine in the world, in Jwaneng, Botswana, and several gold prospects in southern Africa were found by termite mound sampling (http://www.afrol.com/articles/10447).

In Bastar (Madhya Pradesh, India), an analysis of material of the termite mound was acknowledged to be very promising for searching for tin deposits. It is also assumed that this method can be used for discovery of the deposits of heavy metals like niobium, tantalum and tungsten, because the termite mounds there have a good spatial distribution (Surya Prakash Rao & Raju 1984).

At present, the method of searching for deposits of commercial minerals by means of termites is increasingly used worldwide; a new science, termed geozoology, has even been created for its further development.

Use of termite mounds for medicinal purposes

In some areas of India and Africa, the material composing termite mounds is cooked and ground to a paste. This paste is applied to wounds to prevent the introduction of infection; it is also used to treat internal hemorrhages (Srivastava *et al.* 2009). This remedy is also prescribed for treatment of ulcers, rheumatic diseases and anemia (Chakravorty *et al.* 2011).

The material of termite mounds is often used as food by pregnant women (Yamashina 2010). It is believed that eating the soil of termite mounds is necessary for the growth of the fetus and provides the body with iron, which is present in the soil. This is confirmed by data that the soil can provide 14% of the recommended dietary allowance for iron in pregnancy (Njiru *et al.* 2011). A study among pregnant women in some African countries shows a prevalence of geophagy in the range of 15–84%. In western Kenya, approximately half of pregnant women preferred termite soil (van Huis 2017).

Use of termite mounds for other purposes

Soils of termite mounds are richer in mineral elements compared with other soils (Kalumanga *et al.* 2017). As a rule, they are rich in nutrients, particular calcium, magnesium, potassium, sodium and available phosphorus. In addition, they are characterized by high organic matter content. The use of this soil as fertilizer could lead to a threefold increase in the yield (van Huis 2017). An overview of the use of the soils of termite mounds by farmers in Africa is presented in the article of Sileshi *et al.* (2009).

Small mammals (e.g. pangolin) and hunters often hide in abandoned termite mounds. Sometimes termite mound damage specifically attracts birds and then catches them in a trap, as exemplified by catching the red-billed quelea, *Quelea* Linnaeus, 1758 in Tanzania. Termite mounds are also used as a viewing platform for detection of wild animals (van Huis 2017).

In Cameroon, termite mounds are used for storage of nuts of edible fruit species *Cenarrhenes nitida* Labill. Termites attack only the outer shell of nuts, so the nuts can be stored this way for many years, while their quality improves (Facheux *et al.* 2006). This method of storing nuts in this country is preferable because the termites protect the kola nuts from kola weevils *Balanogastris kolae* Desbrochers and *Sophobinus* species, which are major pests of kola nuts (Adeleye *et al.* 2015).

In some African countries, furnaces for copper smelting have been made from termite mounds. For this purpose, the middle part of the termite mound was hollowed out and, from below, a hole for the molten metal tapping and ash pit were made. The ore and coal were loaded from above. The termite mounds were durable and served for many years (http://insectalib.ru/books/item/f00/s00/z0000013/st012.shtml).

In some cases (e.g. on waterlogged plains), abandoned termite mounds are used as burial sites. In Côte d'Ivoire, people who died of leprosy are buried in termite mounds (van Huis 2017).

Edible mushrooms of the genus *Termitomyces* arise from fungus gardens of termites. There are dozens of species and most of them are highly valued as food or drugs (Sileshi *et al.* 2009). The mushrooms are widely collected and sold for consumption. In central and southern Côte d'Ivoire, these mushrooms are a key source of cash income, especially for women (traders) and farmers (harvesters) (van Huis 2017).

In West Bengal (eastern India) termite mounds are used as a bulking agent for compost preparation. Mixing of crop residues with termite mound improves the quality of finished compost, decreases composting time and is cost-effective (Karak *et al.* 2014). In the central plains of Laos, mounds are used as beds for growing vegetables (Miyagawa *et al.* 2011). Zemba people in Namibia use the soil of mounds as construction material for their huts (Yamashina 2010). In Southeast Asia, termites are used in ritual practices. In Malaysia, Singapore and Thailand, termite mounds are commonly worshipped among the populace (Neoh 2013).

TERMITES AS AGRICULTURAL PESTS

Termites are a highly devastative and polyphagous insect pest that cause damage to plants and agricultural crops. They can attack plants at any stage of development, from the seed to the mature plant. Agricultural crops include six cereals (maize, sorghum, rice, barley, millet and wheat), four legumes (beans, cowpea, pigeon pea and chickpea), four oil crops (groundnut, sunflower, soybean and sesame), four vegetables (tomato, okra, pepper and eggplant), three root crops (potato, yam and cassava), 12 fruit plants (guava, coffee, citrus, banana, mango, papaya, grapes, mulberry, pineapple, almond, litchi and plum) and also sugar cane, cotton, tobacco and tea (Qasim *et al.* 2015).

Countries and crops most susceptible to termites are presented in the publication of Lenz *et al.* (2013b). They revealed some regularities, which are discussed here. Yield losses due to the attacks of termites are particularly large in semiarid and subhumid tropics. In general, damage by termites is greater in rain-fed than in irrigated crops, during dry periods or droughts than during periods of regular rainfall, in lowland than in highland areas, and in plants under stress (e.g. disease, physical damage and lack of moisture) than in healthy, vigorous plants. In particular, the exotic cultures are more susceptible than indigenous crops to termite attacks. Maximum damage to crops caused by termites is sustained in eastern Africa, where yield losses in some cases can reach 100% (Mitchell 2002).

Termite activity can also affect crop quality. The scarification of crop tubers by termites can reduce their market value and increase the toxin content in groundnuts (Jouquet *et al.* 2018). Not all termites are pests. For example, in sub-Saharan Africa only approximately 20% of the 660 species of termites are important agricultural pests. The most economically important genus in Africa is *Microtermes*, consisting of serious pests of agricultural plants (Negassa & Sileshi 2018).

For example, in Zimbabwe, termites (mainly Macrotermitinae subfamily) cause significant damage to maize. They attack the base of the stem or root system, killing the plant or decreasing the yield by reducing the translocation of water and nutrients. A delay in harvesting the lodged plants results in increased yield losses (Mutsamba *et al.* 2016). The damage from termites to maize in African systems of crop cultivation can reach more than 60% (Maniania *et al.* 2001), resulting in a loss of yield of 15%–25% (Nyagumbo *et al.* 2015).

Several other publications discuss the malicious activity of termites in different regions and different species. In Brazilian savanna termites, for example, *Procornitermes araujoi* Emerson, 1952, *Procornitermes crucifer* Silvestri and *Syntermes molestus* Burmeister, 1839 can lead to total loss in rice production (Pinheiro *et al.* 2016). In yam fields of central Benin, the most damaging termite species are *Amitermes evuncifer* Silvestri and *Trinervitermes oeconomus* Tragardh (Loko *et al.* 2016). In northwest Benin, the harvest losses caused by termites can be enormous, from 20% to 45% (Loko *et al.* 2017). Termite damage is a critical problem in agriculture in Indonesia and Malaysia, which are the two main palm oil producers in the world. Termite damage of oil palm caused by *Coptotermes curvignathus* Holmgren in the long term will result in a significant loss in palm stand (Yii *et al.* 2016).

TERMITES AS PESTS OF FORESTRY

Often termites have a significant impact on plantations and urban forestry. Some species can cause the death of healthy trees (Rao *et al.* 2012). For instance in Zimbabwe, termite-related mortality of eucalyptus: flooded gum (*Eucalyptus grandis* W. Hill ex Maiden) and river red gum (*Eucalyptus camaldulensis* Dehnh.) can even reach 100% (Rouland-Lefevre 2011).

There are serious termite problems regarding plantation trees in other regions of the world. For instance, Brazilian Savannah termites are the initial pests in eucalyptus cultivation. The significance of these insects increases with the age of the cultivated forest, especially in areas originally occupied by pastures. The genus *Syntermes* is the most significant termite pest species. It damages the roots, debarks plant rings and can cause plant death. These termites, when present in high densities in the area of cultivation, can cause economic losses by increasing replanting activity (Santos *et al.* 2016).

The degree of influence of termites on the trees and the nature of their impact is largely determined by geographic region. For instance, 303 species of trees belonging to 76 families have been reported to suffer from termite attack in China. China fur *Cunninghamia lanceolata* (Lamb.) Hook suffers from them most of all. Approximately 40–60% of trees in southern hilly land dies because of their attacks (Li *et al.* 2010). In India, the heaviest losses and highest infestations are in pine (*Pinus* sp.), jequitiba (*Cariniana* sp.), angelim (*Hymenolobium petraenum* Ducke) (Cosme *et al.* 2018), eucalyptus (*Eucalyptus* sp.), silver oak (*Grevillea robusta*) and casuarina (*Casuarina* sp.) (Rajagopal 2002).

Examples of the influence of termites in forestry in various parts of the world is given in the publications by Feci *et al.* (2013), Lenz *et al.* (2013a), Muller and Ward (2013), Subekti *et al.* (2015), Moe *et al.* (2016), Chiu *et al.* (2016), Oliveira *et al.* (2017) and Romano and Acda (2017). Usually termites prefer less dense woods, due to the ease of mechanically breaking down the wood (Sundararaj *et al.* 2015).

TERMITES AS STRUCTURAL PESTS

The main food of almost all termites is cellulose (fiber) or its derivatives. Experimental results suggest that a colony of 200,000 termites can consume up to 5.4 kg of cellulose per year (Jones *et al.* 2015). Therefore, termites damage the vegetable substances containing cellulose. Termites harm many structures: bridges, dams, decks, homes (Gaju *et al.* 2002; Manzoor & Mir 2010; Li *et al.* 2011; Ab Majid & Ahmad 2015), surviving walls, roads, poles (Kumode *et al.* 2013; Lenz *et al.* 2013a), insulation of underground cables and pipes (Sternlicht 1977; Lenz *et al.* 2013a). Damage is also caused to household furniture (Cosme *et al.* 2018), paper (Jiménez-Francisco *et al.* 2018), rubber products (Zhong & Liu 2003), synthetic films and plastic materials (López-Naranjo *et al.* 2014), and food products.

In total, 83 termite species cause significant damage to wooden structures (Su & Scheffrahn 2000). For example, in the region of Sydney, Australia, only four species can be considered as the main pests; up to 80% of all damage to buildings are from *Coptotermes acinaciformis* Froggatt, 1898). Other serious pests are Australian subterranean termite *C. frenchi* Hill, *Schedorhinotermes intermedius* Brauer and *Nasutitermes exitiosus* Hill, 1925 (Taylor 2000).

In five cities in the semiarid region of Brazil (Fagundes, Pocinhos, Alagoa Grande, Areia and Bananeiras), 89% of infestation of historical buildings and 62% of residential buildings were caused by nine species of termites, belonging to six genera and three families (Kalotermitidae, Rhinotermitidae and Termitidae) (Mello *et al.* 2014). In China, *Coptotermes*, *Cryptotermes* and *Reticulitermes* are the most important termite pests affecting a large number of buildings in the southern part of the country (Li *et al.* 2013).

In Kyushu, Japanese termites also often damage buildings. Hinoki (*Chamaecyparis obtusa*) wood is widely used for construction. It was found that Hinoki wood from natural forests had higher termiticidal activity than that from plantation forests, and the higher termiticidal activity was explained by the larger volatile extractive contents and smaller average ring width (Kijidani *et al.* 2012). Antitermite resistance of 15 species of timbers to *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* (Kolbe) was evaluated in laboratory tests and field trials. It was discovered that antitermite indices of tested species strongly varied with unweathered and weathered samples and different test sites (Ohmura *et al.* 2011).

In Taiwan, over 90% of wooden historical buildings were heavily damaged by termites. *Coptotermes* sp. is responsible for >87% of termite infestation in the urban area of Taiwan, and termite control cost in Taiwan is estimated as $4 million annually. It is likely that over $3 million is the annual cost for controlling *Coptotermes* sp. (Li 2014). In the northern part of Vietnam the cost of termite control and repairs is reported at approximately $1.7 million for only private houses (Yen *et al.* 2016).

In Nebraska, USA, it was estimated that termites infested 17–20% of homes. They damage wood and wood products, stone panels, composite siding, and other building materials inside the house. They can also damage such cellulose materials as books, paper, cardboard, wallpaper and paper covering on drywall (Ogg *et al.* 2006). In the Azores archipelago, a significant proportion of buildings are infested with the urban drywood termite *Cryptotermes brevis* Walker, causing major economic and patrimonial losses. It is estimated that the cost of treating all currently infested buildings in the archipelago is €51 million, while reconstruction of the same buildings would raise the costs to €175 million (Guerreiro *et al.* 2014).

Termites also cause harm to archaeological buildings. They attack mud-brick and mortar, causing cracks in buildings. Because some Egyptian archaeological buildings were constructed from mud-bricks, termites cause their decay and deterioration (Abd-Elkareem & Fouad 2016). Termite-related damage mainly limited to structural wood and scarce objects of historical value were discovered in some buildings of the Greek Orthodox Monastery of Saint Catherine in Egypt (Ghesini & Marini 2017).

Termites often harm books and museum collections. In many museums, libraries and archives, termite infestation of the buildings has spread to display and storage archives and book collections, which are then seriously damaged (Pinniger 2012). This also applies to personal libraries. For example, in South America it is rare to find a book older than 50 years because of the continuous presence of termites (Akimushkin 1975).

Termites as a source of greenhouse gas emission

Recent studies have shown that termites' production of CH_4, N_2O and CO_2 is species-specific, varying according to the environment of the soil and the termites' food quality (Brauman *et al.* 2015; Majeed *et al.* 2015). Emission from termites ranges from 1.0 mg CH_4 kg/termite/h in deserts to 8.0 mg CH_4 kg/termite/h in savannas (Ito & Inatomi 2012). Termite-derived methane contributes from 3% to 4% of the total methane budget globally (Ho *et al.* 2013). According to the recent estimates of De Gerenyu *et al.* (2015), CO_2 emissions from termite mounds account for up to 10% of the total CO_2 emissions in a tropical forest in south Vietnam (Ohashi *et al.* 2017). Carbon dioxide and methane emissions from termites are also investigated in the articles of Jamali *et al.* (2011, 2013), Konemann *et al.* (2017) and Ohashi *et al.* (2017).

INVASIONS OF TERMITES

Invasions of termites (termites that have spread outside the native habitat) usually occurs with infested timbers. The earliest known introduction was displacement of *C. formosanus* from China to Japan prior to the 1600s (Husseneder *et al.* 2012). Termites as a rule invade human modified environments before they spread to more native habitats. Termites are constantly expanding their range. In 1969, there were 17 species of termites that had moved into new areas. This number has now increased to 28 species (Buczkowski & Bertelsmeier 2017).

The movement of invasive species (especially from urban to natural habitats) is rising, as measured by the number of invaded places, the size of invaded area at each place and the habitat types. Sources of invasive species are South and Southeast Asia (7), South America (6), Australia (5), Africa (2), North America (2), Caribbean Islands (1), East Asia (1) and Europe (1). Termites originally lived just on the continents, with only one species found in the Philippines. In time, the vast majority of invasive species moved to the islands, especially in the Pacific (13 species) and the Caribbean (9 species) (Evans *et al.* 2013).

Detailed information about eight introduced termite species at Hawaii is given by Grace *et al.* (2002) and Hapukotuwa and Grace (2012), and drywood termite *Cryptotermes brevis* Walker at six islands (from nine) of Azores archipelago by Guerreiro *et al.* (2014). Attempts to eradicate the invading termites are usually futile; only two known cases of successful eradication are known: *Coptotermes formosanus* from South Africa and *C. frenchi* from New Zealand (Chouvenc *et al.* 2015).

ECONOMIC LOSS

Much damage is caused by termites. The numbers of harmful termite species in different parts of the world are: North America, 9; Australia, 16; the Indian subcontinent, 26; tropical Africa, 24; and Central America and the West Indies, 17. Among the termite genera, *Coptotermes* has the highest number of pest species of any genus, with 28 species known to cause damage (Su & Scheffrahn 2000).

Estimates of the economic damage caused by termites in certain regions and globally are quite rare. They are listed in Table 1.

The most destructive species in the world is the giant northern termite, *Mastotermes darwiniensis* Froggatt, 1897 (Buczkowski & Bertelsmeier 2017). However, its distribution is limited by the northern part of Australia. The most economically important species are the Formosan subterranean termite *Coptotermes formosanus* and the Asian subterranean termite *C. gestroi* due to their widespread nature (Evans *et al.* 2013). Other highly destructive species are the West Indian drywood termite, *Cryptotermes brevis* (Evans *et al.* 2013) and the eastern subterranean termite, *Reticulitermes flavipes* Kollar, 1837, which are responsible for approximately $2 billion in damage annually in the USA alone (Su & Scheffrahn 1990).

CONCLDING REMARKS

Thus, the ecological and economic importance of termites is extremely large. It manifests itself in large positive impacts on ecosystems, and a significant negative

Table 1 Estimates of economic damage caused by termites

Region	Loss per year	Source
Australia	$1.5 billion	Staunton 2012
China	$0.3 billion	Junhong & Bingrong 2004
China	$1 billion	Lenz *et al.* 2013b
China	$217 million (only forestry)	Li *et al.* 2010
Indonesia	$200–300 million	Yusuf 2004
Japan	$0.8–1.0 billion	Tsunoda & Yoshumura 2004
Malaysia	$4–5 million (only control)	Lee 2002
Thailand	$500 million	Vongkaluang 2004
Southwestern USA	$1.5 billion	Su & Scheffrahn 1990
USA	$2–3 billion	Lenz *et al.* 2013b
USA	$11 billion	Su 2002
USA	$5 billion	Tvedten 2005
World	$15–20 billion	Jones *et al.* 2015
World	$20 billion	Ye *et al.* 2004
World	$40 billion	Rust & Su 2012

impact on various human activities. The most significant environmental impacts can be attributed to the activities of termites as soil ecosystem engineers. The most important negative impacts are the activities of termites as structural and agricultural pests. In recent decades the tendency of expansion of the range of harmful species of termites has led to an increase in economic damage.

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