

Species richness of termites (Blattoidea: Termitoidea) and ants (Hymenoptera: Formicidae) along disturbance gradients in semi-arid Burkina Faso (West Africa)

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Abstract. From 2004 to 2008, we conducted the first inventory of termites (Blattoidea: Termitoidea) and ants (Hymenoptera: Formicidae) in Burkina Faso (West Africa) where these important ecosystem engineers are the only active, quantitatively remarkable soil macrofauna during a long dry season. We combined two standard assessment protocols for tropical forests and adapted them to semi-arid (agro)ecosystems to representatively characterize termite and ant communities in two agricultural systems, and assess their response to land-use intensification. In total, 65 ant species and 41 termite species were collected along parallel transects replicated during consecutive years. Both taxa were highly sensitive to human impact. Their taxonomic and functional richness strongly decreased with increasing intensification from a near-natural savannah towards cotton fields with recent pesticide application (North Sudan region), and recovered along a succession of the traditional rehabilitation technique Zai from barren, crusted land towards a long-term fallow with diverse flora and fauna (sub-Sahel region). Fungus-growers dominated the termite communities in all habitats, with the highest variations between habitats noted among soil- and grass-feeders.

Key words. Soil fauna, community composition, anthropogenic impact, land-use gradient, traditional soil restoration, sampling protocol.

INTRODUCTION

Termites (Blattoidea: Termitoidea) and ants (Hymenoptera: Formicidae) are of extraordinary ecological and economic importance throughout the tropics and subtropics, particularly amid arid and infertile environments (Evans et al. 2011; Lee & Foster 1991). In Burkina Faso (West Africa), termites and ants are the only active, quantitatively remarkable soil macrofauna during the long dry season (Rouland et al. 2003; Schuurman 2006). Their richness and abundance may be severely affected by land-use practices (for example, see reviews of Davies et al. 2003; Hölldobler & Wilson 1990; Lobry de Bruyn 1993). Agricultural practices are a leading cause of biodiversity loss (Green et al. 2005; Millennium Ecosystem Assessment 2005) and land degradation (Bai et al. 2008). Particularly existential are the consequences in sub-Saharan Africa where millions of people depend on agriculture for their livelihoods and where vast areas are covered with degraded, barren soils (Batjes 2001). One approach to develop more sustainable agriculture is to harness ecosystem services of naturally occurring organisms (Evans et al. 2011). Termites and ants are major examples for soil-dwelling

‘ecosystem service providers’ (Jouquet et al. 2014) that influence ecosystem functioning by physically altering their biotic and abiotic surroundings (Jones et al. 1997). Both taxa contain species that may become a pest in agricultural systems; however, they are far more often beneficial, especially in dryland agriculture (Evans et al. 2011). Through soil turnover (tunnelling and sheeting production) during their foraging and nesting activities, termites and ants further the soil’s aeration, enhance absorption and storage of water in soils, and facilitate carbon fluxes and storage (for example, Lobry de Bruyn & Conacher 1990; Sileshi et al. 2010). An impressive example of a traditional soil water conservation method in semi-arid West Africa, making use of the positive effects termites exert on soil properties, is the Zai practice (Kaboré & Reij 2004; Reij et al. 2009b).

Despite a widespread recognition of the major importance of termites and ants in arid and nutrient-poor environments, nothing was known about either their actual diversity in Burkina Faso or the effects of the ongoing human-induced changes on the composition of their communities. Most studies in West Africa concentrated on forests, the few in savannahs and agroecosystems were

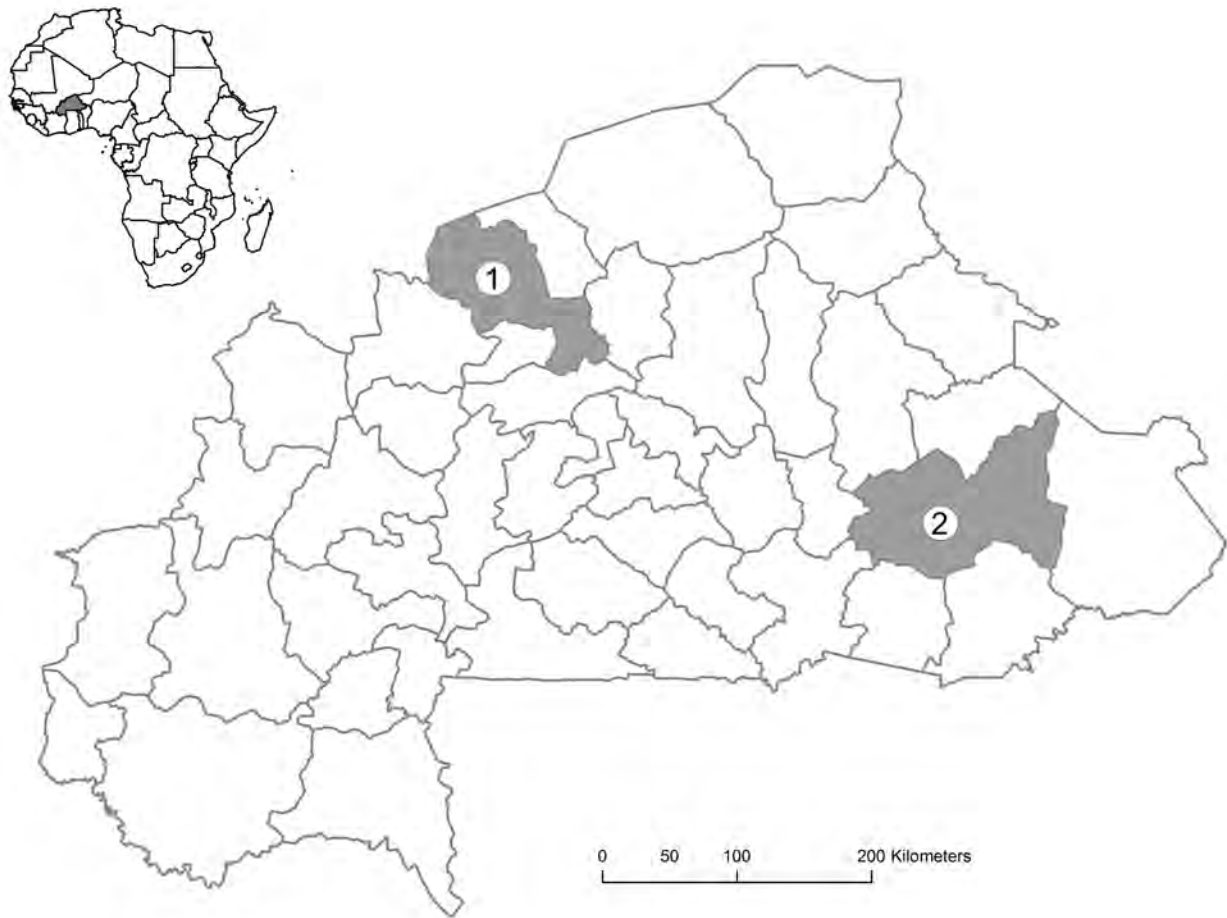


Fig. 1. The geographic location of Burkina Faso in West Africa and of the two study regions – the Yatenga Province in the sub-Saharan zone (1), and the Gourma Province in the North Sudan region (2).

conducted in humid regions, such as the Comoé NP and the Lamto Reserve in the Côte d'Ivoire (Dosso et al. 2013; Konaté & Kampmann 2011; Kone et al. 2012; TraBi 2013; Yéo et al. 2011). We, therefore, selected two traditional agricultural systems characteristic for the region in focus and assessed the invertebrate's diversity between 2004 and 2008. We combined two well-established standard protocols for sampling termites and ants in tropical forests, and adapted them to semi-arid savannahs and agroecosystems. This newly revised protocol has proven highly efficient in representatively assessing and monitoring the termite and ant fauna.

MATERIAL AND METHODS

Study regions

We selected two traditional agricultural systems characteristic for the two main phytogeographic regions in Burkina Faso, each representing a disturbance gradient

comprising four distinct habitats, presently differing in the magnitude of human intervention but formerly having the same initial state.

Disturbance gradient in the Yatenga Province (sub-Saharan zone). As the first land-use intensification gradient, we selected a temporal cross-section of the traditional restoration system Zaï in Ouahigouya (Yatenga Province) in the sub-Saharan region (altitude 336 m) (Fig. 1, Table 1). The climate is characterized by a rainy season of four to five months and a long dry season with high temperatures (UNESCO 1977). Between 1998 and 2008, the mean annual rainfall was about 660 mm, the mean monthly temperature varied between 19.1°C and 39.1°C.

In the Zaï practice, the farmers dig pits (microwatersheds) in parallel rows; shortly before the first rains, they put crop seeds and air-dried compost into the pits. Each farmer adapts the pits to his farm conditions (pit number, dimensions, quantity of compost) (Hien & Ouedraogo 2001). Some use Zaï to intensify cereal production, others for reforestation, or both (Reij et al. 2009a). The or-

Table 1. Abbreviation, characteristics and history of study sites chosen in Burkina Faso (for each gradient, sorted according to increasing human impact).

First disturbance gradient: four age-stages of the Zaï system in the sub-Sahel region	
ZF30	<i>Old Zaï forest</i> (13°32'25"N; 2°22'57"W). In 2009: 30-year Zaï restoration. First cultivated for four years, then 26 years fallow; diverse woody and herbaceous vegetation; mostly thin but closed canopy; topsoil sandy loam.
ZF20	<i>Young Zaï forest</i> (13°32'34"N; 2°22'55"W). In 2009: 20-year Zaï restoration. First cultivated for four years, then 16 years fallow; diverse woody and herbaceous vegetation but still degraded areas; mostly open canopy; topsoil loam.
ZMil	<i>Millet fields</i> (13°32'29"N; 2°23'07"W). In 2009: both fields 11-year Zaï cultivation; millet and green beans. At the time of sampling, the fields were in the fifth, seventh and eighth year; topsoil loam.
ZDeg	<i>Degraded, barren area</i> (13°32'36"N; 2°22'59"W). Initial stage of all Zaï stages; two plots of ferruginous, infertile Lithosol; barren, crusted and impermeable surface; no vegetation; topsoil sandy loam.
Second disturbance gradient: four land-use types in the North Sudan region	
FRes	<i>Pama reserve</i> (11°38'26"N; 0°31'45"E). Initial stage of all North Sudanese habitats; two plots of protected arboreous and shrubby savannah; open canopy; dense grass sods; managed by annual fire; topsoil sandy loam.
FPas	<i>Pasture area</i> (11°38'40"N; 0°30'03"E). In 2009: exclusively used for grazing cattle since 20 years; most areas with isolated trees and bushes; some barren spots; topsoil sandy loam.
FFal	<i>Short-term fallow</i> (11°38'17"N; 0°30'09"E) from 2003–2006. In 2009: 19 years. At the time of sampling: second and fourth year fallow. Before fallowing, crop rotation practised every third year, including cotton for four years. All trees had been felled; dense grass-cover; topsoil clayey loam.
FCot	<i>Cotton fields</i> (11°38'15"N; 0°30'27"E). Two fields, in 2009 both 13 years. At the time of sampling: second year cotton cultivation; crop rotation practiced every third year including four years cotton with extensive use of different pesticides (Fanga 500EC, Caiman 500EC, Calthio E, Capt 88EC, Attakan C344SE, Rocky C386EC, Sherphos 230EC) and 200 kg commercial fertilizer per hectare; topsoil loam.

Soil texture was analysed in 3–7 composite samples of the habitat's topsoil (0–10 cm).

ganic matter attracts termites which construct galleries in the crusted soil to commute between the food source and the nest, thereby increasing the soils' aeration, water infiltration and water holding capacity (Roose et al. 1993).

We selected four age-stages (for the characteristics, see Table 1). An old forest of about 30 years of age (ZF30, Fig. 2A) and a younger one about 20 years old (ZF20, Fig. 2B) represented the reforestation (fallow) phase. Two millet fields (ZMil, Fig. 2C) were selected for the cropping period, and two barren, crusted areas (ZDeg, Fig. 2D) for the initial stage. Each site lay within a radius of 300–400 m of the other and comprised an area of about 1 hectare.

Disturbance gradient in the Gourma Province (North Sudan region). The second disturbance gradient was chosen 52 km south of Fada N'Gourma (Gourma Province) in the North Sudan region (altitude 253 m) (Fig. 1, Table 1). The rainy season lasts from around mid-April till October (Some et al. 2006). Between 1997 and 2008, the mean annual rainfall in Fada N'Gourma was about 875 mm, the mean monthly temperature ranged between 19.6°C and 37.1°C. The natural vegetation is of the savannah type (UNESCO 1977).

Two plots in the Pama reserve (FRes, Fig. 2E) with an area of 1 km² each represented the characteristic near-natural savannah habitat for the region (A Thiombiano, Ouagadougou, pers. comm. 2004) and the initial habitat stage of this disturbance gradient. A pasture (FPas, Fig. 2F), a short-term fallow (FFal, Fig. 2G) and two cotton fields (FCot, Fig. 2H) were chosen in a rural area separated from the park border by a street. Each plot had a size of about 1 hectare.

The characteristics of each habitat are summarized in Table 1.

The baseline sampling protocol

Our rapid assessment protocol (RAP) (Fig. 3) was based on two widely accepted standard protocols – the protocol of Agosti & Alonso (2000) for ants in the leaf litter and the transect protocol of Jones & Eggleton (2000) for termites in tropical forests. The protocols were combined and adjusted to account for the conditions prevailing in our semi-arid agroecosystems; for example, only negligible amounts of litter covered the ground and most sites had an area of 1 hectare only.

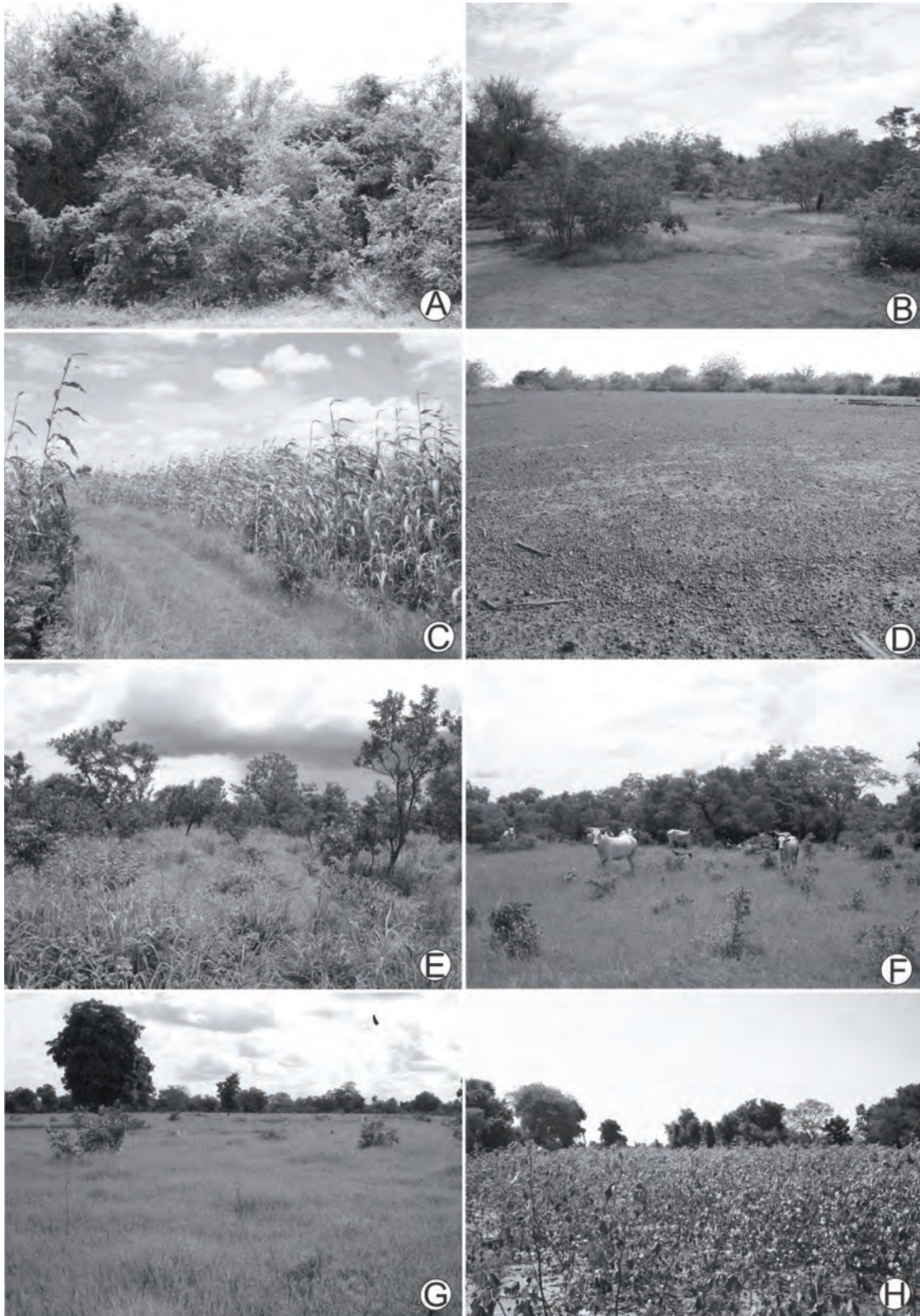


Fig. 2. Study sites in the A–D) sub-Sahel zone, and E–H) North Sudan region. A: old Zaï forest (ZF30; one plot); B: young Zaï forest (ZF20; one plot); C: millet field (ZMil, two plots); D: degraded, barren area (ZDeg; two plots); E: Pama reserve (FRes; two plots); F: pasture area (FPas; one plot); G: short-term fallow (FFal; one plot); H: cotton fields (FCot; two plots).

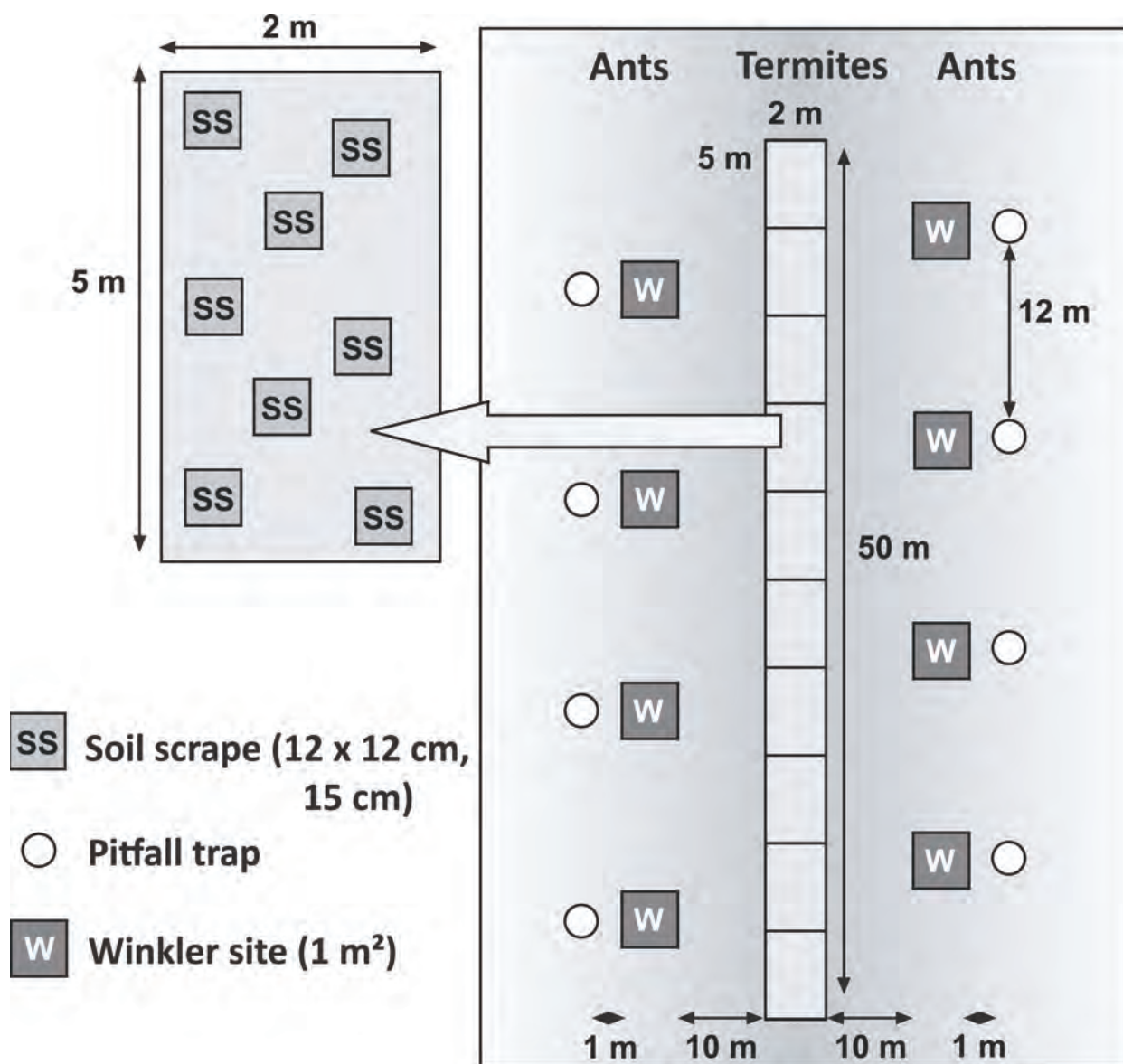


Fig. 3. Relative position of sampling sites according to the combined and standardized rapid assessment protocol (RAP), followed to assess termite and ant communities.

For termites, the RAP included 10 contiguous 5 x 2 m sections resulting in a transect length of 50 m. The first transect in each habitat had a length of 100 m as in Jones & Eggleton (2000), but many of those run in 1 hectare plots had to be divided into two parallel parts. In each section, termites were first searched in as many different microhabitats as possible (such as accumulations of litter, inside and underneath dead logs and twigs, epigeal mounds and runways on vegetation). Then, eight samples of surface soil ('soil scrapes'), each 12 x 12 cm and 15 cm deep, were taken at random locations and searched *in situ*. The sampling time per section was 1 man-hour; stopping rules

applied if no microhabitats could be found, resulting in a shorter sampling time.

Ants were collected on parallel transects in a distance of 10 m on both sides of the termite transect at eight sampling sites (four on each side every 12 m). Within an area of 1 m² the vegetation was at first searched for ants and thereupon totally removed, and all ants walking on the ground were collected for a duration of five minutes (called 'Winkler-site'). It substituted the mini-Winkler extractor of Agosti & Alonso (2000), which was applied during the first year but failed to capture most of the ants due to the limited amounts of litter in our study sites. In a

1 m distance, pitfall traps with a diameter of 10 cm were buried in the soil and filled with 45% ethanol; they were run for 48 hours. Following the newly revised RAP, ants were additionally collected when encountered in the sections of the belt-transects, i.e. in microhabitats and soil scrapes. For a detailed description and illustration of the working steps, please refer to Kaiser et al. (2011) and Kaiser (2014), the relative position of sampling sites according to the combined assessment protocol is illustrated in Fig. 3.

Species identification. Specimen of both taxa were stored in vials with 90% ethanol; they were identified to the level of species or, whenever this was impossible, to numbered morphospecies – ants by using the taxonomic works of, for example, Bolton (1994, 1995) and Bolton et al. (2007); termites following Bouillon & Mathot (1965), Emerson (1928), Sands (1998), and Webb (1961); and both with reference to collections from West Africa held in the research station in Lamto NP (University Nangui Abrogoua, Côte d'Ivoire). Own reference collections were assembled for both taxa and will be stored in the Naturmuseum Senckenberg (Frankfurt am Main, Germany). However, presently we still work with the collection in the research unit on ecology and biodiversity, UREB (Prof. Souleymane Konaté), University Nangui Abrogoua (Abidjan, Côte d'Ivoire). According to their diet and mandible morphology (Deligne 1966) and following Grassé (1986), termite species were assigned to one of these four functional groups: soil-feeders, wood-feeders, grass-feeders and fungus-growers.

All data presented here originate from three to four transects conducted in each land-use type in the rainy seasons between 2004 and 2008. Four replicate transects were run in the Zaï stages (sub-Sahel zone) and the Pama reserve, three in the other habitats of the North Sudan region.

Statistical analyses

Species accumulation and rarefaction curves

Incidence-based species accumulation curves were used to graphically compare the species richness of the habitats belonging to the same disturbance gradient. When the sampling effort differed between the habitats to be compared (for example, in the North Sudan region), the rarefaction method was used to calculate the number of species expected in a subsample randomly selected from multiple samples (Chiarucci et al. 2008; Koellner et al. 2004). Smoothed curves were produced by randomizing the data 500 times. The slopes of the curves illustrate the rate at which new species were added with an increasing sampling effort. The increasing sampling effort was equivalent with an increasing number of a) transect sections for termites and b) sampling units, each comprising one transect section, one pitfall trap and one Winkler quadrat in

the case of ants. The software EstimateS Version 7.51 for Windows (Colwell 2005) was used to calculate the species accumulation and rarefaction curves.

Comparisons among study sites

The software SPSS 15.0 (SPSS Inc. 2006) was used for comparisons between the different habitats concerning their species composition and the number of species observed (or expected at the common sampling effort). Friedman's ANOVA was used to compare land-use types belonging to the same gradient. The Wilcoxon sign-rank test was used for pairwise comparisons between related land-use types. The Bonferroni correction was applied afterwards to adjust the level of significance.

Disturbance index

To analyse the correlation between species richness and habitat disturbance, we combined the data of both regions and assigned each habitat type to one of the four disturbance classes (ordinal scale), with a disturbance index of 1 used for the near-natural habitats (old Zaï Forest and Pama reserve), 2 for pasture land and fallows (young Zaï Forest, short-term fallow), 3 for agricultural plots (millet fields, cotton fields) and 4 for fully degraded, barren land.

A linear regression was then performed in SPSS 15.0 (SPSS Inc. 2006) with the number of a) ant species and b) termite species collected per site and plot as the dependent variable, and the disturbance index and study region as independent ones. The study region was defined as a nominal variable with 1 for the sub-Sahel zone and 2 for the North Sudan zone.

RESULTS

Combining the sites of both regions, 65 ant species (25 genera and nine subfamilies) and 41 termite species (13 genera and four subfamilies) were collected between 2004 and 2008.

Species checklists

Ant communities

A checklist of all ant species present in the different land-use types is given in Table 2. The lowest species, genus, and subfamily numbers were found in highly-intensified areas, the degraded land in the sub-Sahel zone and the cotton fields in the North Sudan region. The ant fauna in Burkina Faso was dominated by the Myrmicinae, which comprised 54% of the total number of species collected along both disturbance gradients, followed by the Formicinae (22%) and the Ponerinae (9%).

Table 2. Ant (morpho)species present (X) in the Zaï stages in Ouahigouya (sub-Sahel zone) and in the habitats near Fada N'-Gourma (North Sudan region).

Ants in Burkina Faso Subfamily, genus & species name	ZF30	Sub-Sahel zone			FRes	North Sudan region		
		ZF20	ZMil	ZDeg		FPas	FFal	FCot
PRO CERATIINAE								
<i>Probolomyrmex</i> Mayr, 1901								
<i>P. sp.01</i>	-	-	-	-	X	-	-	-
PONERINI								
<i>Anochetus</i> Mayr, 1861								
<i>A. sedilloti</i> Emery, 1884	X	X	X	X	X	-	-	-
<i>A. sp.02</i>	X	X	-	X	-	-	X	-
<i>Leptogenys</i> Roger, 1861								
<i>Leptogenys sp.01</i>	-	-	-	-	-	X	X	-
<i>Pachycondyla</i> Smith, 1858								
<i>P. senaarensis</i> (Mayr, 1862)	X	X	X	-	X	X	X	X
<i>P. sp.01</i>	-	-	-	-	X	X	X	X
<i>P. sp.03</i>	X	-	-	-	X	-	-	-
AENICTINAE								
<i>Aenictus</i> Shuckard, 1840								
<i>A. sp.01</i>	-	-	-	-	X	-	X	-
DORYLINAE								
<i>Dorylus</i> Fabricius, 1793								
<i>D. sp.01</i>	-	-	-	-	X	-	X	-
<i>D. sp.02</i>	X	-	-	X	-	-	X	-
<i>D. sp.03</i>	-	-	-	-	X	X	X	-
MYRMICINAE								
<i>Crematogaster</i> Lund, 1831								
<i>C. sp.01</i>	-	-	-	-	X	-	-	-
<i>C. sp.02</i>	-	X	X	X	-	-	X	X
<i>C. sp.03</i>	-	-	-	X	-	-	-	-
<i>Cardiocondyla</i> Emery, 1869								
<i>C. sp.03</i>	-	-	-	-	-	X	X	-
<i>C. sp.04</i>	-	-	-	-	-	-	X	-
<i>Nesomyrmex</i> Mayr, 1855								
<i>N. evelyna</i> (Forel, 1916)	-	X	-	-	-	-	-	-
<i>Temnothorax</i> Mayr, 1861								
<i>T. megalops</i> (Hamann & Klemm, 1967)	X	X	-	-	-	-	-	-
<i>Meranoplus</i> Smith, 1853								
<i>M. sp.01</i>	-	-	-	-	X	X	X	-
<i>Myrmicaria</i> Saunders, 1841								
<i>M. sp.01</i>	-	-	-	-	X	-	-	-
<i>Messor</i> Forel, 1890								
<i>M. galla</i> (Emery, 1895)	-	-	-	-	X	-	X	X
<i>Pheidole</i> Westwood, 1839								
<i>P. sp.01</i>	X	X	X	X	X	X	X	X
<i>P. sp.02</i>	X	-	-	-	X	X	X	X
<i>P. sp.03</i>	X	X	X	-	-	X	X	X
<i>P. sp.04</i>	-	-	-	-	X	X	X	X
<i>Monomorium</i> Mayr, 1855								
<i>M. abyssinicum</i> (Forel, 1894)	X	X	X	-	X	X	X	-
<i>M. areniphilum</i> (Santschi, 1911)	-	-	-	X	-	-	-	X
<i>M. bicolor</i> Emery, 1877	X	X	X	X	X	X	X	X
<i>M. dakarensis</i> (Santschi, 1914)	X	-	-	-	-	-	-	-

Termites and ants in semi-arid Burkina Faso

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Ants in Burkina Faso Subfamily, genus & species name	ZF30	Sub-Sahel zone			ZDeg	FRes	North Sudan region		
		ZF20	ZMil	ZDeg			FPas	FFal	FCot
<i>M. destructor</i> (Jerdon, 1851)	X	–	–	X	X	–	–	–	
<i>M. oscaris</i> Forel, 1894	X	X	X	–	X	–	–	–	
<i>M. sp.01</i>	X	–	–	–	–	–	–	–	
<i>M. sp.08</i>	X	–	–	–	–	X	X	–	
<i>M. sp.09</i>	X	X	X	X	–	–	X	–	
<i>M. vonatu</i> Bolton, 1987	X	X	X	X	–	X	X	–	
<i>Oligomyrmex</i> Mayr, 1867									
<i>O. sp.01</i>	–	–	–	–	X	–	–	–	
<i>O. sp.02</i>	X	–	–	–	X	–	–	–	
<i>Tetramorium</i> Mayr, 1855									
<i>T. angulinode</i> Santschi, 1910	X	X	X	X	X	X	X	X	
<i>T. longicorne</i> Forel, 1907	X	–	–	–	–	–	–	–	
<i>T. sericeiventre</i> Emery, 1877	X	X	X	X	X	X	X	X	
<i>T. sp.05</i>	X	–	–	–	–	–	–	–	
<i>T. sp.06</i>	X	X	X	–	X	X	X	–	
<i>T. sp.07</i>	–	X	X	–	–	–	–	–	
<i>T. sp.08</i>	–	–	–	–	–	X	–	–	
<i>T. sp.10</i>	–	–	–	–	–	X	–	–	
<i>T. zapyrum</i> Bolton, 1980	X	–	X	–	–	X	–	–	
DOLICHODERINAE									
<i>Tapinoma</i> Foerster, 1850									
<i>T. sp.01</i>	X	X	X	–	X	–	X	X	
<i>T. sp.02</i>	–	X	X	–	–	–	–	–	
AMBLYOPONINAE									
<i>Amblyopone</i> Erichson, 1842									
<i>A. sp.01</i>	–	–	–	–	–	–	X	–	
CERAPACHYINAE									
<i>Cerapachys</i> Smith, 1857									
<i>C. sp.01</i>	X	–	–	–	–	–	–	–	
<i>C. sp.02</i>	–	–	–	–	X	–	–	–	
FORMICINAE									
<i>Anoplolepis</i> (Santschi, 1914)									
<i>A. sp.01</i>	X	X	–	–	–	–	–	–	
<i>A. sp.02</i>	–	–	–	–	X	–	–	–	
<i>Lepisiota</i> (Santschi, 1926)									
<i>L. sp.01</i>	X	X	X	–	X	X	X	–	
<i>L. sp.02</i>	X	X	X	–	X	–	X	–	
<i>L. sp.03</i>	X	–	X	X	–	–	X	–	
<i>Cataglyphis</i> Foerster, 1850									
<i>C. sp.01</i>	–	–	–	–	X	X	X	X	
<i>Camponotus</i> Mayr, 1861									
<i>C. compressiscapus</i> André, 1889	–	–	–	–	X	X	X	X	
<i>C. maculatus</i> (Fabricius, 1782)	X	X	X	X	X	X	X	X	
<i>C. sericeus</i> (Fabricius, 1798)	X	X	X	–	X	X	X	X	
<i>C. solon</i> (Forel, 1886)	–	–	–	–	X	X	–	–	
<i>C. sp.06</i>	–	–	–	–	X	X	X	X	
<i>C. sp.07</i>	X	–	–	–	X	X	X	X	
<i>Polyrhachis</i> Smith, 1857									
<i>P. sp.01</i>	–	–	–	–	X	–	–	–	
<i>P. sp.02</i>	X	X	–	–	–	–	–	–	
Species number observed	35	25	22	15	37	28	36	19	

Land-use types: old Zaï forest (ZF30), young Zaï forest (ZF20), millet fields (ZMil), degraded area (ZDeg); near-natural savannah (FRes), pasture area (FPas), short-term fallow (FFal), cotton fields (FCot).

Table 3. Termite (morpho)species present (X) in the habitats in Ouahigouya (sub-Sahel zone) and near Fada N’Gourma (North Sudan region). A two-digit shortcut before the genus name indicates the functional group to which it belongs to: fungus-growers (fg), grass-feeders (gf), soil-feeders (sf), wood-feeders (wf), unknown (uk).

Ants in Burkina Faso Subfamily, genus & species name	ZF30	Sub-Sahel zone			FRes	North Sudan region		
		ZF20	ZMil	ZDeg		FPas	FFal	FCot
MACROTERMITINAE								
fg <i>Ancistrotermes</i> Silvestri, 1912								
<i>A. cavithorax</i> (Sjöstedt, 1899)	X	X	X	–	X	–	–	–
<i>A. crucifer</i> (Sjöstedt, 1897)	X	–	X	–	X	–	X	–
<i>A. guineensis</i> (Silvestri, 1912)	–	–	–	–	X	–	–	–
<i>A. sp.01</i>	–	–	–	–	–	X	X	–
fg <i>Macrotermes</i> Holmgren, 1909								
<i>M. bellicosus</i> (Smeathman, 1781)	X	X	–	–	X	X	X	–
<i>M. subhyalinus</i> (Rambur, 1842)	X	–	–	–	X	–	–	–
fg <i>Microtermes</i> Wasmann, 1902								
<i>M. havilandi</i> Holmgren, 1913	X	X	X	–	X	X	X	X
<i>M. sp.01</i>	X	X	X	–	–	–	–	X
<i>M. sp.02</i>	X	–	–	–	X	–	–	–
<i>M. subhyalinus</i> Silvestri, 1914	X	X	–	–	X	X	X	X
fg <i>Odontotermes</i> Holmgren, 1912								
<i>O. sp.01</i>	X	X	X	–	X	X	X	–
<i>O. sp.02</i>	X	X	–	–	–	X	X	–
<i>O. sp.03</i>	–	–	–	–	–	X	–	–
<i>O. sp.04</i>	–	X	–	X	–	–	–	–
NASUTITERMITINAE								
gf <i>Trinervitermes</i> Holmgren, 1912								
<i>T. geminatus</i> (Wasmann, 1897)	–	–	X	–	X	X	–	–
<i>T. graciosus</i> Sjöstedt, 1924	–	–	–	–	X	–	–	–
<i>T. occidentalis</i> (Sjöstedt, 1904)	X	–	–	–	X	–	–	–
<i>T. oeconomus</i> (Trägårdh, 1904)	X	X	X	–	X	X	X	–
<i>T. togoensis</i> (Sjöstedt, 1899)	–	–	–	–	X	–	–	–
<i>T. trinervius</i> (Rambur, 184)	–	–	–	–	X	–	–	–
wf <i>Fulleritermes</i> Coaton, 1962								
<i>F. coatonii</i> Sands, 1965	–	–	–	–	X	X	–	–
AMITERMITINAE								
wf <i>Amitermes</i> Silvestri, 1901								
<i>A. evuncifer</i> Silvestri, 1912	X	–	X	–	X	–	–	–
<i>A. guineensis</i> Sands, 1992	X	X	–	–	X	X	–	–
<i>A. messinae</i> Fuller, 1922	–	–	–	–	–	X	–	–
<i>A. sp.01</i>	X	–	–	–	–	–	–	–
<i>A. stephensoni</i> Harris, 1957	–	–	X	–	–	–	–	–
wf <i>Microcerotermes</i> Silvestri, 1901								
<i>M. edentatus</i> Emerson, 1928	X	X	X	–	X	–	X	–
<i>M. limpopoensis</i> Fuller, 1925	–	X	–	–	–	–	–	–
<i>M. parvulus</i> (Sjöstedt, 1911)	–	X	X	–	X	–	–	–
<i>M. parvus</i> (Haviland, 1898)	X	X	X	–	X	X	X	–
<i>M. theobromae</i> Holmgren, 1912	X	–	–	–	–	–	–	–
<i>M. thermanum</i> Fuller, 1925	–	X	–	–	–	–	–	–
TERMITINAE								
wf <i>Angulitermes</i> Sjöstedt, 1924								
<i>A. elsenburgi</i> (Fuller, 1925)	X	–	–	–	–	–	–	–
wf <i>Eremotermes</i> Silvestri, 1911								
<i>E. sabaeus</i> Harris, 1957	X	X	X	–	–	X	X	X
sf <i>Cubitermes</i> Wasmann, 1906								
<i>C. bilobatodes</i> Silvestri, 1912	–	–	X	–	–	–	–	–
<i>C. sp.01</i>	–	X	–	–	–	–	–	–
<i>C. subcrenulatus</i> Silvestri, 1914/15	X	–	X	–	X	–	–	–

Ants in Burkina Faso Subfamily, genus & species name	ZF30	Sub-Sahel zone			ZDeg	FRes	North Sudan region		
		ZF20	ZMil	ZDeg			FPas	FFal	FCot
sf <i>Promirotermes</i> Silvestri, 1914/15 <i>P. holmgreni</i> (Silvestri, 1912)	–	–	–	–	–	–	–	X	–
APICOTERMITINAE									
sf <i>Anoplotermes</i> Sands, 1972 <i>A. sp.01</i>	X	X	–	–	X	–	–	–	–
UNKNOWN									
Unknown-sf	X	X	–	–	–	–	–	–	–
Unknown-1	X	X	X	–	X	–	X	X	X
Unknown-2	X	–	–	–	–	–	–	–	–
Species numbers observed	25	20	16	1	24	14	13	5	

Land-use types: old Zaï forest (ZF30), young Zaï forest (ZF20), millet fields (ZMil), degraded area (ZDeg); near-natural savannah (FRes), pasture area (FPas), short-term fallow (FFal), cotton fields (FCot).

Together, the four Zaï stages hosted 41 ant species out of 16 genera and six subfamilies (Table 2). The number of species decreased with increasing human impact (decreasing habitat restoration) from 35 species (14 genera) in the old Zaï forest to 15 (nine genera) in the degraded area.

Ant assemblages in the North Sudanese sites were richer in species, genera, and subfamilies: 53 ant species out of 23 genera and nine subfamilies were found in total (Table 2). The number of species decreased with increasing land-use intensification from 37 species (20 genera) in the near-natural savannah in the Pama reserve to 19 ant species (nine genera) in the cotton fields with recent pesticide application.

Termite communities

The checklist of all termite species present under the different disturbance regimes is given in Table 3. Lowest numbers of species, genera, subfamilies, and functional groups were found in areas heavily impacted by humans. Fungus-growers dominated the termite fauna in all study sites. The highest variations between the habitats occurred in soil- and grass-feeding termites.

The four Zaï stages together hosted 33 termite species out of 11 genera and five subfamilies (Table 3). The number of termite species strongly decreased with increasing human impact from 25 species (13 genera) in the old Zaï forest to only one fungus-growing *Odontotermes* species in the most degraded stage. Except for the degraded site, all four functional groups were represented in the Zaï stages.

Together, the four habitats in the North Sudan region hosted 31 termite species out of 13 genera and five subfamilies (Table 3). The decreasing species richness was

obvious along the disturbance gradient: the number of termite species was highest in the reserve with restricted human impact (24 species, 11 genera) and drastically decreased with increasing human pressure to five species (three genera) in the cotton fields. Only the reserve and the short-term fallow hosted soil-feeding termites.

Comparisons among study sites

Incidence-based, randomized rarefaction or accumulation curves were used to graphically compare the discovery rate and the species richness of related habitats (Figs 4–5). Error bars correspond to one standard deviation of the mean after randomization. The colours in Figs 4–5 are identical to those used for the disturbance classes in Figs 6–7.

Ant communities

For ants collected between 2004 and 2008, rarefaction curves are presented in Fig. 4 for the habitats located a) in the sub-Sahel zone, and b) in the North Sudan region. For each region, we statistically compared the species richness at the level of the land-use type with the lowest sample number (degraded area, cotton fields). The number of ant species predicted at the common sampling effort (39 sampling units, in Figs 4a, b indicated by the dotted line) differed significantly between the sub-Saharan (Friedman, $N = 39$, $\chi^2(3) = 117$, $P < 0.001$) and the North Sudanese habitats (Friedman, $N = 39$, $\chi^2(3) = 117$, $P < 0.001$). A Wilcoxon sign-rank test (with Bonferroni correction) revealed statistical differences also between the 20-year-old forest and the millet field (Wilcoxon, $Z = -5.44$, $P < 0.001$, $R = 0.62$). In the sub-Sahel zone (Fig. 4a), the descend-

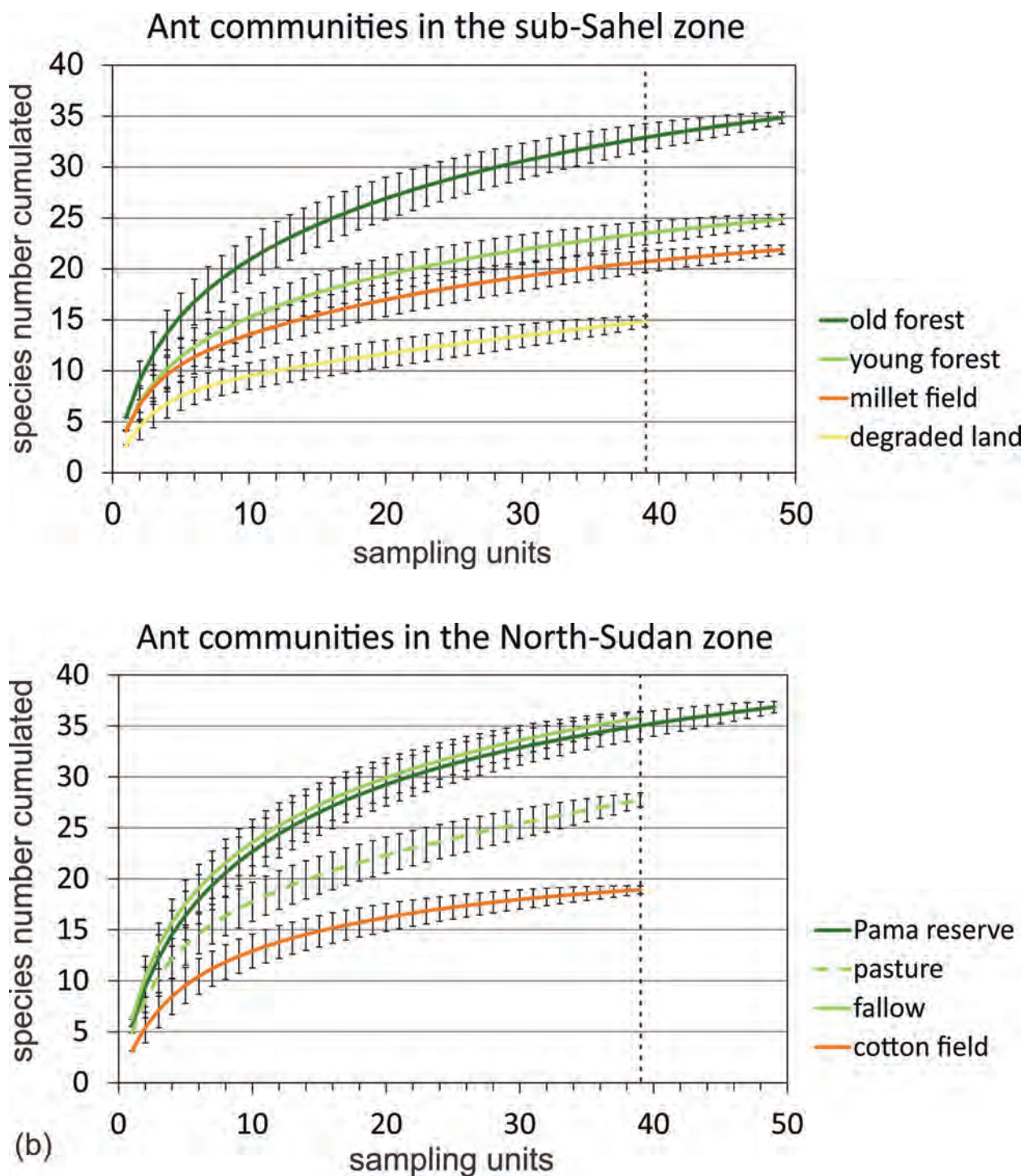


Fig. 4. Incidence-based rarefaction curves (including standard deviations) predicting the accumulation rate of ant species with increasing sampling effort in the habitats selected along the disturbance gradient in the a) sub-Saharan zone, and b) North Sudan region. Curves are predicted from richness values assessed along RAP transects; the rarefied number of 39 sampling units (the dotted line) was used to compare the related habitats. In the sub-Saharan zone, the expected richness and discovery rate of ant species decreased with decreasing restoration stage, and from the short-term fallow towards the cotton field in the North Sudan region. However, both the richness and the accumulation rate were almost identical in the fallow and the reserve (indicated by the overlapping error bars).

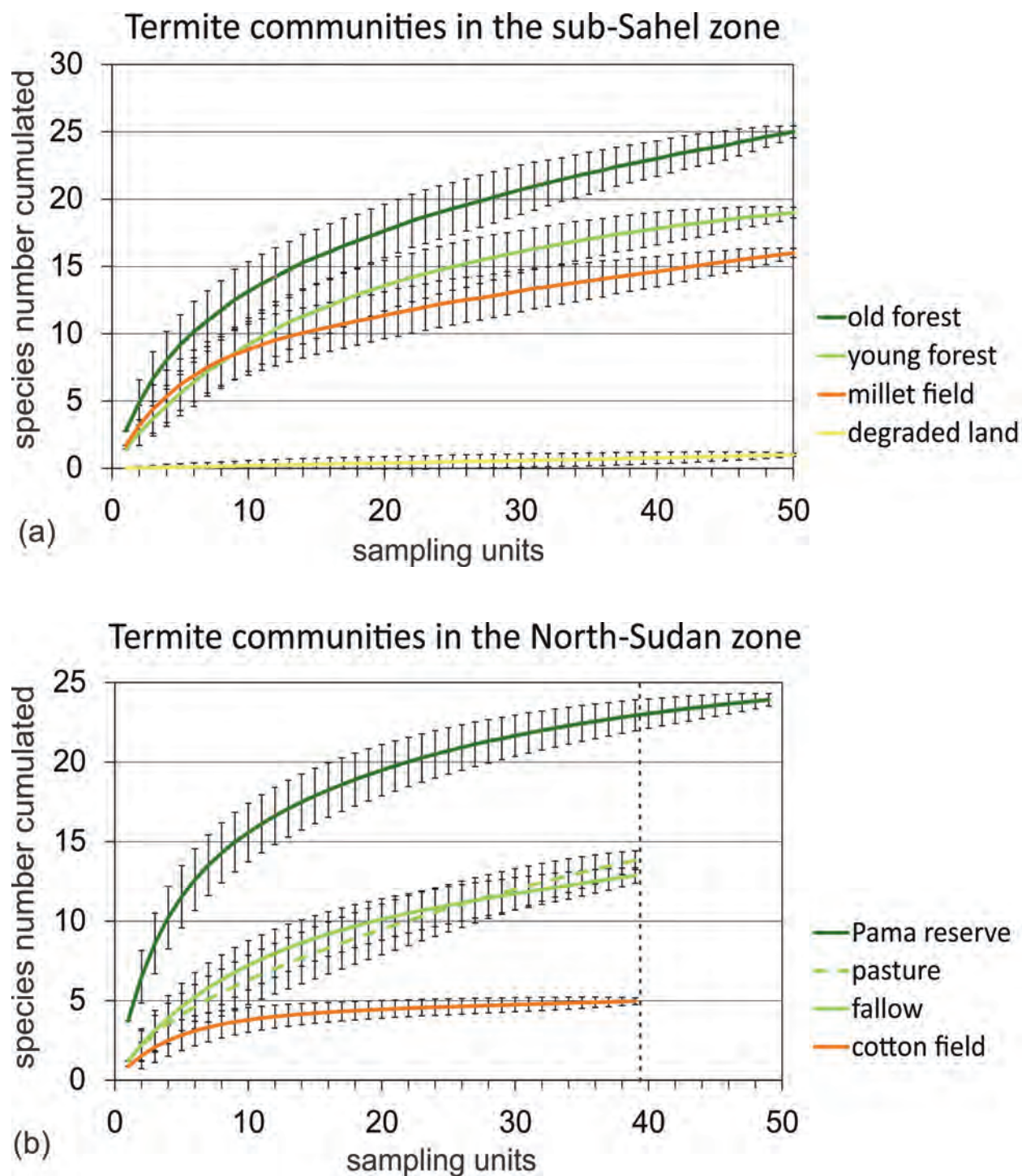


Fig. 5. Incidence-based, randomized accumulation (a) and rarefaction curves (b) indicating the accumulation rate of termite species with increasing sampling effort in the habitats selected along the disturbance gradient in the a) sub-Saharan zone, and b) North Sudan region. In the sub-Saharan zone, the richness and discovery rate of termite species decreased with decreasing restoration stage. In the North Sudan region, the richness predicted at the common sampling effort of 39 sampling units (the dotted line) decreased from the Pama reserve towards the cotton field, although the differences between the pasture and the fallow are not significant (indicated by the overlapping error bars).

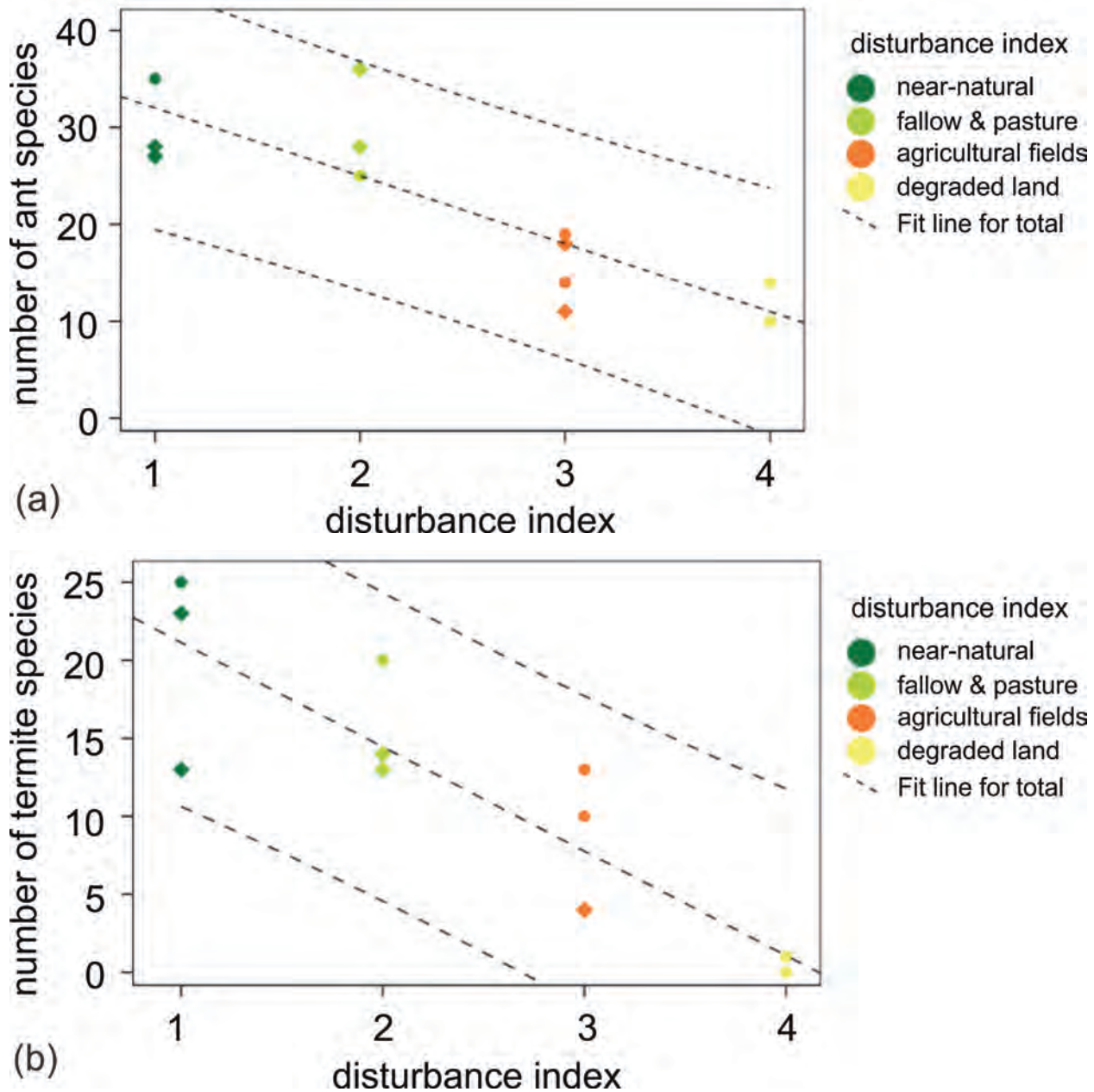


Fig. 6. Correlation between habitat disturbance and the number of a) ant species and b) termite species collected per site and plot in the sub-Saharan (circles) and the North Sudan region (rhombus). There was a significant negative relationship between the disturbance of a habitat and the number of ant species ($P < 0.05$, $F_{2,9} = 1.22$, $R^2 = 0.71$) and termite species ($P < 0.001$, $F_{2,9} = 37.26$, $R^2 = 0.89$).

ing order of all land-uses with regard to the expected number of ant species is old forest > young forest > millet fields > degraded soil, and short-term fallow > Pama reserve > pasture > cotton field in the North Sudan region (Fig. 4b). However, ant species richness did not differ significantly between the fallow and the reserve (Wilcoxon, $P > 0.025$ after Bonferroni correction) – both habitats also exhibited almost identical rates at which new species were added with the increasing sampling effort.

Termite communities

Quite similar to the trend observed for ants, the number of termite species observed in all transect sections differed significantly between the Zaï stages in the sub-Saharan (Friedman, $N = 50$, $\chi^2(3) = 141.94$, $P < 0.001$) (Fig. 5a) and between the four North Sudanese habitats (Friedman, $N = 39$, $\chi^2(3) = 106.68$, $P < 0.001$) (Fig. 5b). In the sub-Saharan zone, the descending order of the habitats with re-

gard to the number of termite species observed was old forest > young forest > millet field > barren land. At a low sampling effort, however, the discovery rate of termites in the millet field was higher than in the young forest (indicated by the crossing curves at sampling unit 9). In the North Sudan region, the number of species predicted at the common sampling effort decreased in the order: reserve > pasture > fallow > cotton field although the differences between the pasture and the fallow were not significant (Wilcoxon sign-rank test, $P > 0.025$ after Bonferroni correction). The rate at which termite species were added at a lower sampling effort was higher in the short-term fallow than in the pasture (please note the crossing curves at sampling unit 27).

All rarefaction and accumulation curves roughly approach an asymptote. Figs 4–5, therefore, indicate that we representatively characterised the termite and ant fauna, also proving that the spectrum of methods we used was appropriate.

Effect of land-use intensity on species richness

To analyse the correlation between species richness and habitat disturbance, each habitat type was assigned to one of four disturbance classes with 1 used for the near-natural habitats and 4 the degraded, barren land (please refer to the method-section).

Fig. 6 shows the number of ant (Fig. 6a) and termite (Fig. 6b) species collected in Burkina Faso as a function of the habitat disturbance. Each point comprises the number of species collected per study plot; the study region is indicated by the shape of the point with a rhombus used for the North-Sudanese sites and circles for the sub-Saharan ones.

A linear regression analysis was performed. The scatterplots (Figs 6a, b) suggest a strong negative correlation between species richness and habitat disturbance: as the land-use intensity increases, the species richness of termites ($P < 0.001$, $F_{2,9} = 37.26$) and ants ($P = 0.05$, $F_{2,9} = 11.22$) decreases.

For the ant species, richness R^2 is 0.71, i.e. only 29% of the variance in species richness could not be explained with this model. When the ants' species richness in a habitat was predicted, land-use intensity was found to be a significant predictor ($\beta = -0.86$, $P < 0.05$), whereas the study region was not ($\beta = -0.05$, $P > 0.05$). When the termites' species richness in a habitat was predicted, both land-use intensity ($\beta = -1.03$, $P < 0.001$) and study region ($\beta = -0.39$, $P < 0.05$) were found to be significant predictors. The overall model fit for termites is $R^2 = 0.89$, i.e. only 11% of the variance could not be explained with the model.

DISCUSSION

Combining both regions, 65 ant species (25 genera and nine subfamilies) and 42 termite species (13 genera and five subfamilies) were collected according to the combined RAP (Tables 2 and 3). Depending on the study site, between 40 and 50 transect sections (Figs 4–5) were sampled between 2004 and 2008. All accumulation and rarefaction curves in Figs 4–5 roughly approach an asymptote, therefore, indicating that we representatively characterized the termite and ant fauna. To our knowledge, these findings represent the first records for termites and ants in Burkina Faso.

Species richness along disturbance gradients. Termites and ants were highly sensitive to land-use intensification – extensively managed or degraded habitats hosted the lowest numbers of species, genera, subfamilies, and functional groups (Tables 2 and 3, Fig. 6). Similar findings were also reported from other regions: termite communities were consistently found to be less diverse in disturbed habitats (for example, see Davies et al. 1999; Donovan et al. 2007; Gathorne-Hardy et al. 2006; Vaessen et al. 2011), and crops and plantations hosted less species than nearby natural vegetation (see Black & Okwakol 1997 and references therein). Although direct comparisons are hampered due to differences in soil type, rainfall or the intensity of agricultural activity, a review of 10 studies revealed that ant species richness was nearly always lower in farmland environments than in naturally vegetated areas (Lobry de Bruyn 1999). Similarly in Côte d'Ivoire, the number of ant species decreased from relatively well conserved to the most extensively managed land-use types (Yéo et al. 2011).

Therefore, and since increasing land-use intensification progressively simplified the habitats' physical structure in our study sites (Table 1, Figs 2A–H), we did expect that the species richness of both taxa would decrease with increasing human impact. Very astonishing, however, was the extent to which their richness decreased in heavily impacted habitats. The termite fauna was especially impoverished. Unsustainable land-use and the reduction of vegetative cover affect termites and ants, for instance, by resulting in a loss of available feeding and nesting sites or by exposing them to greater physiological stress in the pedosphere (for example, see Agosti et al. 2000; Jones et al. 2003).

The enormous loss of taxonomic and functional diversity of the focal arthropods may have disastrous consequences for small-scale subsistence farmers, impeding a sustainable agricultural production. Hence, especially promising are the observations concerning a resilient agricultural production and the progressive restoration of an increasingly diverse flora and fauna (particularly termites and ants) on initially barren crusted soils with the Zaï practice. To our knowledge, no other study has investigated

the recovery potential of termite and ant communities in fully degraded, crusted soils. The study of Gathorne-Hardy et al. (2002) in Southeast Asia revealed that an *Imperata cylindrica* grassland and a cassava field, both hosting a strongly reduced termite fauna, had the potential to recover when left fallow near a source area of primary forest for more than 50 years. Dibog et al. (1999) observed that tree-based agriculture in the Amazon had the potential to support the function of soil termite fauna even on land previously used as pasture.

To conclude, the present study provides a baseline for future monitoring studies in Burkina Faso and the comparison of termite and ant diversity between the different disturbance regimes. We present a combination of standard sampling methods (Fig. 3) that are easy to learn and effective to representatively, but rapidly, assess termites and ants in various (agro)ecosystems of semi-arid tropical regions (Figs 4–5). Since crop production will have to increase strongly to meet the growing food demand driven by the ongoing human population growth (Godfray et al. 2010), more techniques are needed to increase soil fertility and maintain the sustainability of agricultural production by harnessing ecosystem services of naturally occurring organisms. Given the crucial role of termites and ants in ecosystem functioning throughout the tropics and subtropics, special focus should be put on techniques that support or fasten the recovery of their communities in highly degraded lands. More studies are, therefore, needed that investigate the responses of termite and ant communities to habitat perturbations, the succession of their communities during habitat rehabilitation, and that clarify how the successions relate to the recovery of biodiversity and ecosystem processes.

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