**A global review of termite sampling methods**

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**Abstract**

Termites are globally dominant and functionally important soil organisms. While their role in ecosystems is being increasingly recognised and understood, methods that adequately sample termite communities across habitats can be challenging and have not advanced at the same pace as studies of termite ecology. Moreover, the appropriateness of sampling methods varies with habitat and biogeographic region due to differences in termite communities. Focusing largely on tropical systems where the majority of termites occur, we review current available termite sampling methods and provide recommendations for sampling across different biomes and biogeographic regions. Active searching transects are most effective in rainforest habitats, whereas reduced transects, baiting and mound surveys are more appropriate in grassy systems and seasonally dry forests. Baiting is recommended for deserts. Recent advances in termite sampling, such as the use of remote sensing and DNA metabarcoding, and outstanding challenges, such as sampling episodic grass-feeding termites, are also discussed. An improved use of standardised termite sampling methods, as we recommend, should lead to increased knowledge of the patterns and drivers of termite diversity, which will in turn facilitate the quantification of the influence termites have on ecosystems and lead to new insights into the functioning of tropical systems.

**Key-words:** baiting, soil fauna, soil invertebrates, termite mound, transect, tropical ecosystems

**Introduction**

Termites are the dominant soil invertebrate across the tropics, occurring in large numbers and contributing substantially to invertebrate biomass (Wood and Sands 1978; Dahlsjö et al. 2014; Tuma et al. 2019). The role of termites in ecosystem functioning is becoming increasingly recognised and understood (see Jouquet *et al.,* 2011 for a review). Through their foraging and mound-building activities, termites redistribute soil particles, alter the mineral and organic properties of soils, influence water infiltration rates and modify soil bulk density (Jones et al. 1994; Mando et al. 1996; Konaté et al. 1999). Furthermore, termites are considered the major invertebrate decomposer in tropical systems (Collins 1981; Schuurman 2005; Griffiths et al. 2019) and consequently have a strong influence on nutrient cycling and distribution (Holt and Coventry 1990; Lepage et al. 1993). Recent studies have shown that termites can mitigate the effects of drought in tropical forests (Ashton et al. 2019) and modelling work suggests they may increase dryland ecosystem resilience to global change (Bonachela et al. 2015).

However, there remains considerable work to be done. Many of the experiments and surveys documenting termite effects on ecosystem functioning have been performed at localised sites, challenging the extrapolation of the importance of termites to all ecosystems. In order to fully understand the role of termites globally, standardised quantitative methods to sample termites require improvement. Termite sampling has always been challenging and over the past twenty years has not advanced at the same pace as the understanding of the roles that termites perform in ecosystems. The mostly subterranean habits of termites make most conventional insect sampling techniques, such as surface pitfall traps, Winkler bags or sweep netting ineffective, and alternative methods are needed. Almost twenty years ago, Jones and Eggleton (2000) devised a standardised method for sampling rainforest termites that has been widely adopted. However, this method has been found to be inadequate or in need of modification for use in other biomes, especially in drier ecosystems. Moreover, active searching for termites, as prescribed by Jones and Eggleton (2000), is not the most sensible approach in habitats that either have very low termite abundance or where most termite species forage episodically and will therefore not always be detected. The most recent review of termite sampling methods was conducted by Jones et al. (2005), which provided a useful summary of the available methods with a focus on forest ecosystems. Here, we build on this review and expand the focus to all tropical biomes.

Termites live in tropical and subtropical areas and are at their most abundant and diverse in Africa, particularly in rainforests (Dahlsjö et al. 2014). They generally have lower diversity in drier habitats, except in Australia where their lowest diversity occurs in rainforests (Jones and Eggleton 2010). Termite activity and feeding habits (constituting a range of feeding groups) also vary considerably within and among the biomes in which they occur, and termites also feed on dead plant material at a variety of stages of decomposition, including grass, wood, leaf-litter, humus and soil (see glossary). Moreover, most termites do not live in the substrate that they feed on, apart from for wood-dwellers that nest and feed in dead wood, and some groups have entirely subterranean colonies, whereas others live in carton nests or soil mounds. All of these aspects of termite biology require consideration when designing sampling protocols, which need to be tailored according to habitat and the termite community.

Here, focusing mostly on the tropics, we review current available termite sampling methods and provide recommendations for sampling across different biomes and biogeographic regions. We outline the sampling challenges unique to each tropical biome and biogeographic region that contain termite communities and provide an updated framework for termite sampling. Our intention is that the recommendations we provide for sampling be used for standardised ecological studies, which compare termite diversity across habitats or treatments, and not for inventory sampling, which exhaustively documents a community.

**Termite sampling methods**

Several termite sampling methods exist and have been used with varying degrees of success in different environments. While there are several methods, we discuss the three most commonly used below, and recommend using one, or a combination of them, to collect data that are comparable across studies. Other methods not covered below include digging a set number of soil pits (Dawes 2010) or trenches, i.e., pits that are longer than they are wide (e.g., Abensperg-Traun 1991), across an area of interest and examining the extracted soil for termites.

*Active searching*

Active searching involves searching for termites across the environment, examining every microhabitat where termites are found. One common example of standardising this approach is to use quadrats of a set size (but see Salick and Pong 1984 where plots of variable size were used), within which sampling is often also limited by time (e.g., Eggleton et al. 1996 in Africa, Dawes-Gromadzki 2008 in Australia, Cancello et al. 2014 in South America). The most commonly used of these quadrat methods is the *full transect* method of Jones and Eggleton (2000). Although variations of this method were used before 2000 (e.g., de Souza and Brown 1994; Eggleton et al. 1996), Jones and Eggleton (2000) standardised and validated the approach. The method, which has been widely used, employs a 100 m long belt transect, 2 m wide, split for convenience into 20 sections each 5 m in length (Fig. 1A). Two people work per section, sampling all available termite microhabitats: soil, dead wood, leaf litter, animal dung, termite runways and sheeting, termite mounds, and other termite structures (e.g., purse nests, winged reproductive “launch tubes”). Each person samples for 30 minutes in each 5 m x 2 m section (i.e. a total of one-person hour of sampling per section). In addition, a total of 12 shallow pits (~12 x 12 cm in area, with a depth of 10 cm) are dug per section and termite specimens extracted in the field. The whole transect takes a total of 20-person hours to complete. We define each time one or more termites is found as an “encounter” (see Glossary). For every encounter, a representative set of termites are collected (i.e., usually 5 or 6 specimens, although fewer if this number is not possible), with termites from the soldier caste prioritised because they are the most tractable taxonomically. Identifications are then conducted in the laboratory. The resulting data are in the form of a matrix listing species present with the number of encounters for each (i.e. species occurrence).

This full transect method, or a modification of it, has been used extensively in rainforests and habitats derived from rainforest (Eggleton et al. 2002; Jones et al. 2003; Palin et al. 2011), and at a range of spatial scales with the spacing between transects varying from a few hundred metres to between continents (Bandeira et al. 2003; Davies et al. 2003; Dambros et al. 2017). However, there have been criticisms of the method based on the non-exhaustive nature of the species sampling. There has been concern that a single full transect does not adequately document the full species complement of a given area because it will inevitably miss some species and locations (Roisin and Leponce 2004), but this is based primarily on a misunderstanding of the purpose of transect sampling. As with methods for other taxa (e.g., a comparison of insect abundance from pitfall traps), the rationale behind the transect method is to provide directly comparable data with other transects, with sampling effort standardised, thus functioning as an *ecological* tool, not a *taxonomic* one (Jones et al. 2006). The method will provide useful material for taxonomic study, but that is not its primary aim.

There have also been suggestions to extend the transect length with additional sections added until an asymptote of species richness is reached (Roisin and Leponce 2004). However, this removes the standardisation necessary in an ecological method and can compromise the status of the transect as a single quadrat (Jones et al. 2006). An additional criticism with the full transect is the length of time that each transect (i.e. quadrat) takes to complete (20-person hours, e.g. two people searching each section for 30 minutes). Achieving sufficient replication can therefore be time-consuming and induce boredom and reduce concentration amongst searchers, especially if there are low rates of termite discovery. In the literature, this has meant that many full transect studies using gradients have applied a correlational approach, with just a single transect at every unique value along the gradient (e.g., Eggleton *et al.* 2002, Jones *et al.* 2003, Palin *et al.* 2011).

Concerns with the length of time required to complete the full transect method has also caused some researchers to split the total standard transect into shorter sections that are spread across the area of interest, thereby increasing replication (e.g., Carrijo et al. 2009; Cancello et al. 2014; Almeida et al. 2017). This approach, however, makes it difficult to directly compare results with other studies that have used full transects, but can have within-study benefits because it can enable sampling over a wider range of habitats, as long as consistent transect lengths and search times are used throughout a single study. Because a transect is effectively a single quadrat, using subsets of the information from within a single transect (i.e. quadrat), as an alternative approach to address issues of time (e.g. using sectional data), risks pseudoreplication through non-independence and is not recommended. Once termite workers are found in a section, the search for soldiers (for identification purposes) can also consume all of the remaining search time, meaning little of the section is searched. Although finding soldiers should be a priority, searchers need to balance this with searching the entire section, which is easier done when two people search each section simultaneously. Another potential solution, which could save time and enables more of each section to be searched, is to take soil samples back to the lab and use extraction techniques, such as Kempson extraction, instead of *in situ* hand-sorting to remove termites from soil (Silva and Martius 2000).

Using a 100 m long transect, although recommended for standardization across studies, may also be too small in some cases, given that the foraging territories of some ecologically dominant species can extend over 100 m. In such cases, oversampling of these dominant species and undersampling of subordinate ones could occur, although it is probably unlikely. Increased replication would help alleviate such concerns, but the increased time required for multiple transects also requires consideration. The transect method also does not work well for sampling arboreal habitats and associated termite groups. Kalotermitidae, for example, are frequently found in tree canopies and seldom sampled using traditional ground-based transects (Roisin et al. 2006; Scheffrahn et al. 2018). Sampling methods that focus on canopy layers are more effective for sampling these and other arboreal groups and should be considered where much of the termite fauna is thought to be arboreal (Roisin et al. 2006).

Attempts to use the full transect method in drier habitats (e.g. savannas) has proved unsatisfactory as there are fewer microhabitats to search and fewer termites overall (Davies et al. 2012, 2013), resulting in the method yielding relatively few samples for the time and effort involved. To counter this, the *reduced transect* was developed, using active searching within the same total area (200 m2), but with 10-person minutes of searching per section instead of 1 hour (e.g. one person searching each section for ten minutes). The reduced transect also does not require 12 soil pits per section due to fewer soil-feeding termites being present in drier habitats, although searching in the soil is usually useful and recommended (Davies et al. 2013).

*Baiting*

Many termite species search out and forage on patches of cellulose. This foraging behaviour makes baiting with cellulose-rich dead wood or toilet rolls (using the full roll and not just the cardboard inner) a successful method for sampling and monitoring termites (La Fage et al. 1973; French and Robinson 1980; Ferrar 1982; Dawes-Gromadzki 2003; Galbiati et al. 2005; Schuurman 2005; Davies et al. 2013). Baits are typically arranged in a grid fashion, spaced five to ten metres apart, either buried or placed directly on the soil surface, and left *in situ* for a specified amount of time after which they are checked for termites and/or signs of termite activity (Fig. 1B). Termites present at baits can be collected, with emphasis placed on sampling soldiers for identification purposes, and the amount of the bait consumed can also be quantified as an additional measure of termite activity. Baiting therefore yields data on species presence/absence, abundance (i.e., the number of encounters, with each species present at each bait counted as a single encounter), and activity levels, which can be collected even if termites are not present when the baits are checked.

Several studies have tested the efficacy of different forms of baiting including wood *vs.* toilet rolls (French and Robinson 1980; Dawes-Gromadzki 2003; Zeidler et al. 2004), toilet rolls *vs.* dung (Netshifhefhe et al. 2018), buried *vs.* surface baits (Davies et al. 2013) and the optimal length of time baits should be left in the field (Davies et al. 2013). Many of these studies have also compared baiting with active searching methods, in terms of how well each method yields a representative sample (i.e. the number of species and encounters detected with each method), generally finding that baiting is a more effective sampling method at lower rainfall sites where wood-feeding termites are predominate, at least in African savannas (Davies et al. 2013). Baiting is also effective for monitoring termite activity over time and is recommended over transects for this purpose because baits can be placed in the field and easily checked at regular intervals, which requires significantly less effort than repeatedly running transects. Indeed, termite monitoring with baits has been successful in a variety of habitats ranging from rainforests (Ashton et al. 2019) to semi-arid savannas (Schuurman 2005; Leitner et al. 2018).

A major shortcoming with baiting, however, is that it only targets termites that feed on cellulose, thereby excluding most soil-feeding termites. Grass-feeding termites are also not sampled by baits, as their foraging behaviour is focused on cutting grass. In places with significant populations of these termites, transects are necessary to sample a representative complement of the termite community and to provide sufficient data for ecological analysis, which is why a protocol consisting exclusively of baiting is only recommended in drier regions and only where there are insignificant numbers of grass-feeding termites (dry areas generally have low numbers of soil-feeders due to a lack of soil moisture). Although Lagendijk et al.(2016) sampled soil-feeders using only toilet roll baits, this was an unexpected outcome and is not recommended practice. Soil-feeders in this study, and others (e.g., Davies et al. 2013), were likely attracted to soil brought into baits by other termites, or to the increased moisture retained in the toilet roll baits.

Where baiting is appropriate, we recommend a protocol consisting of burying baits in either a grid (e.g. 5 x 4), with each bait spaced at least 10 m apart, or along a transect (e.g. 20 baits buried 5 m apart along a 100 m transect). Burying is recommended over surface placement because termites generally attack these baits sooner than surface ones, reducing the amount of time they need to be left in the field (Davies et al. 2013). The dimensions of the area surveyed are an important, yet often neglected, consideration when baiting. Similar to considerations with active searching, ecologically dominant termite species can have large colonies with foraging territories covering as much as 8000 m2 (assuming a 50 m foraging distance from a central nest). The colonies of these species can number in the millions, potentially monopolizing food resources and limiting the abundance and activity of competitors within their foraging territories. Bating grid dimensions should therefore reflect metrics of termite colony size and foraging biology when possible. Alternatively, a baiting transect could be used to distribute baits over a larger area, possibly also enabling comparison between baiting and active searching methods. The amount of time baits are left in the field is another important consideration because too short a time can lead to fewer termites being sampled, and too long a period can either result in the entire bait being consumed (with no termites present to sample) or the baits being attacked by fungi, which termites have been observed to avoid (Abensperg-Traun 1993; Dawes-Gromadzki 2003; Davies et al. 2013). We recommended leaving baits *in situ* for approximately one month, although this should be modified according to site specific characteristics such as aridity (a shorter duration might suffice in wetter areas). The season in which baits are placed, especially in drier areas where baits are most effective, is also of consequence, with the wet season (when termites are most active) usually preferred (Davies et al. 2015). If baiting occurs during the dry season, baits will likely need to be left in the field for longer periods.

*Mound surveys*

Censusing of mound abundance and distribution patterns is another well-established sampling method in termite ecology. This approach usually consists of searching for all mounds over a standardised area, often by several people walking in transects across a study plot (e.g., Meyer etal. 1999, Grohmann et al. 2010, Muvengwi et al. 2018). When a mound is located, its spatial position is recorded and the mound-building species is sampled, usually by excavating the mound. A disadvantage of this approach is that many smaller mounds are difficult to detect in dense vegetation, especially as the sampling area increases or the number of searchers decreases. Advanced remote sensing techniques (also see Recent Advances and Future Directions below) can be used to overcome some of these difficulties and also cover a much larger survey area (e.g. Levick et al. 2010; Pringle et al. 2010; Davies et al. 2014, 2020; Mujinya et al. 2014), but have some similar limitations in that they too are unreliable for detecting small mounds and are currently biased toward genera that build large mounds, such as *Macrotermes* (Davies et al. 2014). Remote sensing, in contrast to field surveys, also does not provide information on the species of termite that built the mound, whether the mound is active or not, nor if inquiline termite species are present. A combination of field surveys and remote sensing can be used to expand the geographical scope of a study (through the use of remote sensing) and also yield species-specific information in focused areas (from field surveys) (see Davies et al. 2014). Similar techniques to mound surveying can also be used to map other termite structures, such as foraging holes, yielding information on the density and distribution of non-mound building genera (Santos et al. 2016), but difficulties with identifying the species that built the tunnel warrants consideration. Counting of termite individuals within mounds has also been used to gauge colony size, and techniques used include fumigation and excavation of mounds, followed by the separation of termites from soil using water flotation (Darlington 1984; Meyer et al. 2000).

Mound surveys can be particularly useful where mound-builders are dominant, either numerically or ecologically, or where most termite individuals are usually found in mounds rather than foraging between them, e.g. episodic foragers such as *Trinervitermes* in grassland habitats (Hagan et al. 2017). We would recommend that when mound surveys are conducted, additional information such as mound height, the species of mound-builder and activity status (determined by looking for recent signs of activity, e.g., freshly constructed mound material, or by excavating mounds to sample termites) is also collected where possible. In seasonal habitats, we also recommend that surveys be performed in the dry season when (deciduous) trees have fewer leaves and the grass layer, when present, is less dense, aiding visual detection of mounds, although it can be more difficult to assess the activity status of mounds in the dry season due to lower levels of termite activity. Repeat visits during the wet season might be required to collect data on activity status and species identification.

**Sampling across biomes and biogeography**

Given that the most appropriate termite sampling method to use varies with biome and biogeographic region, and that the full transect method is challenging to apply to non-forest habitats, here we discuss the best sampling approaches based on biome, mean annual rainfall and seasonality. See Table 1 for a summary of these recommendations.

*Rainforests*

Rainforests are characterised by high rainfall (from approximately 1500 mm to 4000 mm) and a continuous canopy of trees. The ground layer is mostly grassless, with patchy C3 grasses only occurring in canopy gaps. Rainfall seasonality can vary from weak to pronounced. Most rainforests have distinct strata with a multi-layered canopy and tall emergent trees. They generally have the highest termite alpha diversity of any global biome (Eggleton 2000; Davies et al. 2003; Dahlsjö et al. 2014) and can have termite densities of up to 10,000 m-2 (Eggleton et al. 1996). This is particularly true of African rainforest, which has very high termite species density due largely to the high number of soil-feeding (Dahlsjö et al. 2014) and fungus-growing (Aanen and Eggleton 2005) termites, which are generally not as diverse in other rainforest areas (Davies et al. 2003). The full transect method is well established for sampling within rainforests, having performed well in rainforests in sub-Saharan Africa, South America and South-east Asia (Davies et al. 2003). The reason that the transect method works so well in rainforests relates to the ratio between “constant foragers” (which forage essentially continuously) and “episodic foragers” (which forage only under certain conditions), with a higher proportion of constant foragers in rainforests compared with other biomes. In rainforests, there are also many species that forage on constant, easily accessible resources (e.g., soil and dead wood). Many rainforest species, for example, nest and forage in the soil, resulting in active searching being the most effective technique for sampling termites in tropical rainforest.

However, the rainforests of Australia (and to a lesser extent, Madagascar) have very low termite species density (Davies et al. 2003) and although the full transect method is effective in these systems, its time-consuming nature yields relatively little reward. For example, recent survey work in the Daintree Research Observatory in northern Queensland, Australia, showed that only 2% of woody items on the ground are occupied by termites, with essentially no termites in the soil and very few termite mounds (Clements and Eggleton, *unpublished data*). The reduced transect method will likely be more efficient here but would still be expected to yield few termite samples.

*Tropical grassy biomes (savannas and grasslands)*

Savanna ecosystems are characterised by a continuous ground cover of C4 grasses and scattered trees. Canopy cover can vary considerably from 5-80% cover (Parr et al. 2014). Tropical grasslands are similar to savannas but lack trees or shrubs. Although termites are abundant in these ecosystems, their diversity tends to be lower compared with tropical rainforests and communities are dominated by wood- and grass-feeders, especially as mean annual rainfall decreases and soil-feeder diversity declines (Davies et al. 2012, 2015). Tropical grassy systems are also highly heterogeneous, seasonal ecosystems with large variations in mean annual rainfall (from ~300 - 2500mm yr-1, Lehmann *et al.*, 2011), in addition to inter-annual variation in the amount and timing of rainfall. Sampling termites in savannas and grasslands is more challenging than in tropical forests, not only because there are fewer microhabitats and termites, but also because of the inherent spatial and temporal variation of these biomes. Rainfall variation has particularly important implications for termite sampling: for example, the efficacy of sampling methods has been strongly linked to annual rainfall in African savannas (Davies et al. 2013). Various termite sampling methods, including baiting, reduced active searching transects and mound surveys have been successfully used in savannas, often in combination.

Broadly speaking, in savannas and grasslands with > 650mm mean annual rainfall, the reduced transect is the preferred sampling method. The traditional full transect method developed for rainforest sampling does not perform as well in grassy ecosystems as forests. This is in part due to difficulties with sampling drier and (sometimes) harder savanna and grassland soils, but more importantly because of the lower termite abundance and species richness in these systems, as well as there being fewer microhabitats to search. Active searching in savannas almost always yields far fewer specimens than a comparable effort in rainforest, making searching for an hour per section unnecessary and even a wasted effort. Reducing the search time in grassy systems to ten-person minutes per section has been effective at characterising community composition across different grassy systems in Africa: e.g., savanna in southern Africa (Davies et al. 2012; Muvengwi et al. 2018a) and grassland in southern Gabon (F. Evouna Ondo, *unpublished data*). The reduced transect method was developed and tested in African savannas (Davies et al. 2013) but has not been used outside Africa. More work is therefore required to test its efficacy in tropical savannas elsewhere, including the Neotropics (e.g., Cerrado in Brazil), Australasia (e.g., the Top End in Australia) and Asia (e.g., Indian savannas).

As with almost all methods in these biomes (apart from mound surveys), sampling in tropical grassy biomes is best conducted in the warm, wet season when termites are most active (Davies et al. 2015). Time of day is another important consideration, with termites becoming less active as daytime temperature increases. Transects should therefore be conducted at similar times of day (e.g. in the morning) for comparable sampling across sites. Detection of termites with reduced transects can also be aided by rainfall in the days preceding sampling. The reduced transect method works well where there is a sizeable amount of termite activity between colony centres at the time of sampling (i.e., foraging activity is continuous). Termite activity, however, decreases with increasing aridity (e.g., mean annual rainfall and seasonality) and can also vary with biogeographic region. For example, unlike Africa, drier Australian tropical grassy systems have fewer wood feeders and episodic grass and litter feeders dominate, making detection with the transect method challenging in all seasons.

Where mean annual rainfall is typically < 650mm yr-1, the use of cellulose baits is recommended instead of the reduced transect method. In drier African savannas (450-550mm yr-1), Davies et al., (2013) found baiting with buried or above ground toilet rolls more effective than reduced transects. As with the transect method, checking of the baits is best done earlier in the day. However, where the termite community consists largely of grass-feeders, such as in drier and/or cooler grassland systems (e.g., the South African central plateau), cellulose baits are unlikely to be effective for obtaining a representative sample of the termite community. In such places, we recommend first conducting a pilot study to determine what the termite community consists of generally before embarking on a sampling protocol.

While both the reduced transect method and baiting work well in grassy systems, they do not always capture the termite community adequately, especially where episodic grass-feeders are common. Where a large proportion of the termite community consists of mound-building grass-feeders (e.g. in drier or cooler grasslands with few soil- or wood-feeders), mound surveys can be an effective method to measure colony abundance (e.g., African *Trinervitermes* species, Hagan et al., 2017). Where mound densities are very high such that inter-mound distances are < 2 m, (e.g. some *Amitermes* in Australia), these mounds should be adequately detected in the reduced transect method. However, there are often additional mound-building species present in the vicinity that are not detected with the transect, or, as is often the case, mounds occur at low densities (e.g. < 1 ha-1). In such places, we recommend supplementing the transect method with a mound survey over a larger defined area. The size of the area chosen for surveys will depend on the mound density in the area of interest and could range from 50 x 50 m plots to 1 km2 (Muvengwi et al. 2018b). All mounds should be counted and specimens from mounds collected where possible. Although mound detection and the identification of mound-builders can be challenging, e.g. where mounds are very widely spaced (e.g. *Macrotermes* at densities of ~1 ha-1), or where vegetation makes them difficult to detect (e.g. *Cubitermes* in dense grass), these species are often an ecologically important component of grassy systems, making efforts to include them important. Large teams of people, as well as searching during the dry season when vegetation is sparser, can help improve detection and speed up mound counts. In addition, remote sensing techniques provide a promising avenue for surveying mounds (see Recent advances and future directions section below).

*Seasonally dry forests*

Tropical dry forests are structurally diverse ranging from tall, closed canopy forest to short scrub, and occur across a range of climatic conditions from 300-1500 mm of rainfall year-1, with a long dry season (ranging from 4-6 months). They differ from savannas by lacking a grassy understorey and therefore do not have regular fire (Dexter et al. 2018). Although a well-wooded system, the occurrence of a dry season tends to mean that termite diversity is lower than tropical forests (see, for example, species lists for in Vasconcellos et al., 2010, Alves et al., 2011). As with grassy systems, adequately sampling the termite community for ecological analysis is more challenging than in tropical forests. Wood-feeders, soil-feeders, wood-soil interface feeders and leaf-feeders can all occur, although soil-feeders are more common at high annual rainfall (Alves et al. 2011), and the termite fauna tends to be more similar to savanna regions than to tropical forest (e.g. the termite community of the Caatinga region in Brazil is considered to be more similar to Cerrado communities than those in dense Neotropical forest (Melo and Bandeira 2004)). The reduced transect method, supplemented with mounds counts where necessary, is likely to work well. Past studies that used the full transect method, or a shortened (by distance) modification of it, yielded relatively few species and low numbers of encounters (e.g. Vasconcellos et al., 2010, Viana-Junior et al., 2014). The timing of sampling also requires some consideration, especially where the wet season is the coolest time of the year, and this is likely to result in fewer termite being active due to lower temperatures (see Evans & Gleeson 2001). Sampling in the transitional seasons, near the beginning or end of the rainy season could be most effective in these environments.

*Deserts*

Although deserts tend to have sparse or no vegetation and low rainfall (e.g., < 300mm), termites can persist in these systems, which is somewhat surprising given the apparent lack of food resources and challenging environmental conditions here. However, termite abundance in these systems is substantially lower than in other biomes and only baiting appears to be a successful sampling approach (Johnson and Whitford 1975; Ettershank et al. 1980). Indeed, the use of toilet rolls as cellulose baits, which are now commonly used to sample termites across multiple habitats, was pioneered in the Chihuahua Desert (La Fage et al. 1973). In contrast, active searching transects would yield very few termite specimens in deserts, as they do in semi-arid and arid savannas, and are not recommended. Similarly, few desert termites build mounds and mound surveys are therefore not likely to be effective.

*Other biomes*

In addition to the tropical biomes we have focussed on in this paper, termites also occur in other, more temperate, systems, such as Mediterranean regions and temperate rainforests (e.g. the Pacific Northwest of North America, the southern coast of South Africa, high rainfall areas of Patagonia, and south-eastern Australia (Jones and Eggleton 2010)). A simplified version of the active searching transect method is likely to be best suited for temperate rainforest, modified by the knowledge that only wood-inhabiting termites occur here and that only large logs are likely to be occupied by termites (i.e. archotermopsids, including *Archotermopsis* in forests of the Himalayan foothills). Sampling effort therefore only needs to focus on this microhabitat. Mediterranean regions can differ in termite species richness, with, for example, large differences between Australian regions (high termite richness) and European regions (low richness), and so recommending sampling methods here is less certain. Although more work needs to be done in these systems, we envisage that cellulose baiting in the warmer, but wetter, seasons (i.e. spring or early summer) could be most effective.

**Recent advances and future directions**

*Remote sensing*

Recent advances in remote sensing technology have enabled the large-scale mapping of termite mounds across scales impossible to measure with field methods alone. Satellite data have been used to identify and survey mounds in Africa (Pringle et al. 2010; Mujinya et al. 2014), but will not work as well in areas with high canopy and/or cloud cover that obscure mounds beneath them. Light Detection and Ranging (LiDAR), an active remote sensing technique that emits its own light capable of penetrating closed canopy, overcomes issues of mounds beneath trees and has been successfully applied to map *Macrotermes* mounds in African savannas (Levick et al. 2010a, b; Davies et al. 2014, 2016, 2020). However, the resolution of the ground surface digital elevation model derived from the airborne LiDAR data used in previous studies cannot reliably detect mounds below 0.5 m in height (Davies et al. 2014), and so is mostly suitable for genera that build large mounds, such as *Macrotermes*. Higher-resolution LiDAR data, e.g. using unmanned aerial vehicles (UAVs), holds promise for mapping a wider range of mound sizes and types.

Remote sensing techniques do not, however, typically provide information on the termite species that built the mound, although there is a relationship between mound structure and size, and the genus of the mound-builder. LiDAR data, which enables mound height to be measured (Davies et al. 2014, 2020), could be useful in this sense, and higher resolution LiDAR data, such as that from UAVs, could potentially provide more information on mound structure. Given the relationship between mound structure and mound-builder, it is also possible that a photograph-based mobile phone app could be developed to match photographs of mounds taken in the field with an online reference collection to identify the mound-builder, yielding easily accessible taxonomic information from mound surveys.

*Challenges with episodic grass-feeders*

Grass-feeding termite species that do not build epigeal mounds and also forage in an episodic fashion, e.g. *Hodotermes* in Africa, some *Velocitermes* and *Cornitermes* in South America and some *Tumulitermes* species in Australia, are challenging to sample. These species only forage under specific humidity and temperature conditions that can be difficult to predict, making standardised sampling using transects or baiting ineffective. Indeed, even though these species can be known to occur in a given region, they are often entirely missed by standardised sampling efforts (Muvengwi et al. 2018a). Whether some form of grass baiting can be developed to sample these grass-feeders remains to be investigated, but the episodic nature of their foraging also needs to be considered when attempting to formulate a sampling protocol. Alternatively, surveys of foraging holes could be tested for sampling efficacy (e.g. Santos et al. 2016).

*DNA techniques*

Beyond sampling methods, challenges around termite identification also remain. Termite identification is relatively straightforward when the soldier caste is available as it is based on clearly visible morphological features of soldiers. However, when soldiers are not present, either in the foraging party sampled or because the termite genus in question is soldierless (e.g. the highly diverse Apicotermitinae of African and South American rainforests and wetter savannas), identification is more challenging. The traditional approach has been to perform gut dissections (Sands 1972), but these are time-consuming and require high levels of expertise. We instead recommend that DNA barcoding techniques be used for these soil-feeding termites, as well as for other samples without soldiers, using the cytochrome oxidase II mitochondrial gene (Hausberger et al. 2011; Bourguignon et al. 2014, 2016). These sequences, which can be acquired using techniques as simple as Sanger sequencing, should then be compared with sequences from existing databases, which will hopefully grow over time. This approach will require specimens from each sampled encounter to be roughly checked and separated into species where possible – as multiple species or genera can be sampled in a single encounter.

*Conclusion*

Despite termites being a globally important insect group with wide-reaching implications for ecosystem function, they remain largely understudied, and taxonomically challenging, relative to other groups. Using standardised sampling methods across climatically similar habitats, as suggested here, will enable better comparisons within and across locations, leading to an improved knowledge of the patterns and drivers of termite diversity and enable predictions of how termite diversity will change in response to global change. Improved understanding of termite diversity patterns will in turn facilitate the quantification of the influence termites have on ecosystems, and lead to new insights into the functioning of tropical systems.

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**Table 1:** Recommended broad termite sampling methods in tropical biomes with significant termite communities. If sampling has to conducted during non-optimal seasons, the recommended methods remain the same, but might require modification (e.g. cellulose baits should be left *in situ* for longer periods when it is dry, and shorter when it is wet).

|  |  |  |  |
| --- | --- | --- | --- |
| Biome | Rainfall | Recommended Method | Optimal season |
| Rainforest |  | Full transect | Dry, if present |
| Dry forest | High | Reduced transect and mound survey | Wet and warm |
|  | Low | Toilet roll baiting and mound survey | Wet and warm |
| Savanna and grassland | > ~650 mm | Reduced transects and mound survey | Wet and warm |
|  | < ~650 mm | Toilet roll baiting and mound survey | Wet and warm |
| Desert |  | Toilet roll baiting | Wet, if present |

**Figure legend**

**Figure 1:** Schematic of commonly used termite sampling methods. A) The transect method consists of a single quadrat 100 m in length, divided for convenience into 20 sections (only 10 sections are shown here). Each transect, not each section, should be considered a statistical unit. Samplers should search all termite microhabitats (see text) in each section for 1-person hour in rainforest (the full transect) and 10-person minutes in drier habitats such as savannas (the reduced transect). Twelve soil pits should also be dug in each section of the full transect, they are not considered necessary in the reduced transect. B) An example baiting grid where baits are placed in a 5x4 grid, spaced 10 m apart. Example termite colony foraging areas and mounds are depicted in both panels to demonstrate how multiple sections of a transect, or multiple baits, can sample termites from the same colony, meaning that the number of encounters per transect or baiting grid should only be treated as relative termite abundance in an area. The depiction of mounds also demonstrates how a transect could miss many mounds, making mound surveys necessary where the majority of termites are found in widely distributed mounds.

**Figure 1**

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**Glossary**

*Active searching*: Searching for termite individuals in microhabitats, such as soil pits, dead wood, mounds, runways, leaf litter accumulated in the buttress roots of trees, under dung, and other microhabitats.

*Baiting*: Using cellulose-rich material as baits to attract termites. Baits often include toilet-rolls (using the full roll) but can also consist of wood and/or other dead-plant material. Termites attracted to the baits can then be collected.

*Castes*: In termites these are: reproductives (including the queen and king), workers and soldiers. Soldiers are particularly important as they are the main caste used for identification.

*Continuous foraging:* termites that forage at all times of day, and therefore can be found in their feeding substrate continuously.

*Ecological sampling: S*ampling to collect data that can be compared statistically between sites, but does not necessarily produce an exhaustive species list.

*Encounter:* A recorded presence (same as an ‘occurrence’) of a group of termites, or sometimes just an individual termite, during active searching, either foraging or in a colony centre. Each time such a group or individual termite is found during sampling, a single encounter is recorded, regardless of whether the different encounters were in one or multiple transect sections. Some discretion will be needed to assess whether two encounters are distinct. For example, two termite groups sampled within a single piece of wood would generally be considered as one encounter (unless they are several meters apart on a large log), whereas two groups in two pieces of wood would generally be counted as two encounters.

*Episodic foraging:* termites that forage intermittently depending on climatic conditions, time of day or other conditions. Episodic foragers are often found only in their nests.

*Full transect*: A 100 m x 2 m belt transect, sampled by active searching for a total of 20-person hours. In statistical terms, a single large quadrat.

*Inventory sampling:* Sampling that aims to produce a complete species list for a single site and is harder to use for statistical comparisons between sites.

*Microhabitats*: Places where termites can be found. These include, amongst other locations, soil pits, dead wood, animal dung, mounds, runways and leaf litter accumulated in the buttress roots of trees.

*Mound sampling:* Quantifying the density of mounds within a given area, and also sampling termites directly from their colonies in epigeal mounds.

*Reduced transect:* A 100 m x 2 m belt transect, sampled by active searching for a total of 200-person minutes (3.3 hours). This reduced time is appropriate for wetter savannas, where termite species density is lower than tropical rainforest, and there are fewer termite microhabitats. In statistical terms, a single large quadrat.

*Species density:* The number of species found in a particular area. In the case of transects this is species/ 200 m2. This contrasts with *species richness*, which is a dimensionless number and should not be referred to with sample data.

*Study plot:* Area of interest within which sampling is undertaken.

*Termite feeding groups:* There are usually considered to be four groups: Group I (non-Termitidae, wood and grass-feeders), Group II (grass, wood and litter feeders, which is sometimes divided into non-Macrotermitinae Termitidae, and Macrotermitinae Termitidae (i.e., fungus-growers, which can be designated as Group IIF), Group III (humus-feeders), Group IV (true soil-feeders). See Donovan et al. (2001) for a full description.