

Termite Diversity along an Amazon–Andes Elevation Gradient, Peru

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ABSTRACT

Through their role as ‘ecosystem engineers’, termites provide a range of ecosystem services including decomposition, and carbon and nitrogen cycling. Although termite diversity levels differ between regions as a result of variation in regional species pool size, in general, termite diversity is thought to decline with elevation. This study (1) investigated how termite species density, abundance, functional group diversity and termite attack on dead wood vary with altitude along an Amazon–Andes altitudinal gradient in Peru; (2) identified likely environmental causes of this pattern; and (3) explored the implications of termite presence for ecosystem functioning (notably for decomposition). Termites were sampled with a standardized 100 × 2 m straight-belt transect at five undisturbed forest sites along a gradient 190 to 3025 m, as were environmental variables and termite and fungus attack on dead wood. Termite diversity was similar to that found at comparable sites in South America, and there was little turnover of assemblage composition with elevation suggesting that montane specialists are not present. Termite diversity declined with increased elevation, though the upper distribution limit for termites was at a lower elevation than anticipated. We suggest that key drivers of this elevation pattern are reduced temperature with altitude and mid-elevation peaks in soil water content. Also, attack on dead wood diminished with decreasing termite indirect absolute abundance, while the depth of the soil humic layer increased. We hypothesize that termite abundance is a major accelerant of decomposition rates (and associated mineralization) in Amazonian forests.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: altitude; decomposition; ecosystem engineer; functional groups; indirect absolute abundance; species density; tropical forest.

THE DECLINE OF TAXONOMIC RICHNESS WITH INCREASING LATITUDE is a generally accepted diversity trend (Willig *et al.* 2003, Hillebrand 2004). The monotonic decrease of species richness with elevation mirrors this trend, with both patterns often attributed to a reduction in temperature, productivity and area (Stevens 1992). Another species richness pattern, widely observed with increasing altitude, is the mid-elevation peak (or hump-shaped curve; Rahbek 1995, Lomolino 2001); a pattern often explained by the presence of climatic optima at mid-elevations, by the ecotone effect and/or by the mid-domain effect (Colwell & Lees 2000, Lomolino 2001). In the case of tropical invertebrates, the majority of species richness studies show a mid-elevation peak pattern (Rahbek 1995).

Within tropical ecosystems, termites (Blattaria:Termitoidea) play a key role as ‘ecosystem engineers’, modifying the biotic and abiotic environment, in turn affecting resource availability for other organisms (Lavelle *et al.* 1997). Termites provide a range of ecosystem services: decomposition, carbon and nitrogen cycling, soil structuring and the stimulation of microbial activity (Wood & Sands 1978, Sugimoto *et al.* 2000, Donovan *et al.* 2002).

Termite diversity generally declines with increased elevation, unlike that of most other tropical invertebrates studied (Kayani *et al.* 1979, Gao *et al.* 1981, Akhtar *et al.* 1992, Gathorne-Hardy *et al.* 2001). This is usually explained by the reduction in temperature, linked to metabolic rate (Gathorne-Hardy *et al.* 2001). Termites have also been observed to have a smaller altitudinal range on smaller mountains relative to large ones. This is attributed to the Massenerhe-

bung effect, a phenomenon in which cloud formation occurs at lower altitudes on smaller mountains, in turn reflecting sunlight and reducing daytime temperatures at lower elevations (Gathorne-Hardy *et al.* 2001). Although temperature is an important factor for termites (because they are ectothermic), various termite functional groups respond differently to temperature due to their different feeding habits. Soil feeders, for example, are generally more negatively affected. This is likely to be because they depend on lower energy food substrates than wood feeders, providing them with less colony-wide energy to overcome the physiological costs of living at lower temperatures (Jones 2000, Davies *et al.* 2003a). Where mid-elevation peaks in termite diversity have been documented (Donovan *et al.* 2002, Inoue *et al.* 2006), these have been attributed to factors such as anthropogenic disturbance and the limited altitudinal range of the study.

Although temperature is often considered the key factor influencing termite diversity, other nonmutually exclusive factors that may explain changes in termite diversity with altitude include rainfall and the size of the regional species pool. Rainfall can have a negative effect on termite species richness and abundance in tropical rain forest systems, as very high levels can lead to inundated microhabitats and colony death (Dibog *et al.* 1998, Bignell & Eggleton 2000). At the continental level termite diversity is anomalous, with South America apparently intermediate between the large species pool in Africa and the much smaller one in SE Asia (Eggleton *et al.* 1994, Davies *et al.* 2003a). Although the termite assemblage in tropical South America is relatively poorly described, it can be predicted that termites would occur above the upper limit recorded for SE Asia (1900 m), because of the larger size of the pool and the greater height of the Andes mountain range.

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The aims of this study were to: (1) determine how termite species density, abundance, functional group diversity and termite attack on dead wood vary with altitude along an Amazon–Andes altitudinal gradient; (2) identify environmental correlates of this pattern; and (3) assess the implications of termite presence for ecosystem functioning, notably for decomposition. We test the hypotheses that termite species density and indirect absolute abundance will decline with altitude in response to temperature, that termites will occur above 1900 m, that assemblage composition will change at higher elevation (with a greater loss of the more sensitive soil feeders) and that termite-mediated attack on dead wood will be highest where indirect absolute abundance is greatest.

This study is the first altitudinal transect for termites reported from South America, and is also the first systematic faunistic study of termites in Peru. In addition, this study was conducted over the greatest altitudinal range surveyed to date for termites (190–3025 m asl).

METHODS

STUDY SITE.—The study was conducted in southeast Peru at five 1-ha forest sample plots situated along an elevation gradient from lowland Amazonia (Tambopata National Reserve, Madre de Dios) to the Kosñipata valley region of Manu National Park, Cuzco (Table 1). All sites are situated on or adjacent to the eastern flank of the Andes and are located in undisturbed primary forest. Soil textures are sandy/sandy loam at 190 m, clay loam at 925 m, silt loam at 1500 m and sandy peat/loamy peat at 1850 and 3025 m. Soil pH ranges from 4.5 to 5 across the elevation gradient. These sites were chosen because they are relatively accessible and form part of an intensive multidisciplinary research program, run by the Andes Biodiversity and Ecosystem Research Group (ABERG) (<http://darwin.winston.wfu.edu/andes/index.php?n=Main.HomePage>).

ENVIRONMENTAL SAMPLING.—Air temperature, soil temperature, rainfall, soil water content and humic layer depth were determined

at each 1-ha site between November 2006 and October 2008. Air temperature, soil temperature and soil water content were recorded monthly, at 25 evenly spaced points (5 × 5 grid with 20 m spacing between points) across every site. Air temperature was recorded at breast height under canopy over 12 mo and soil temperature at 10-cm depth over 22 mo, using a Testo 926 thermometer and Testo penetration probe T260, respectively (Testo Ltd, Hampshire, UK). Soil water content was recorded over 22 mo with a water content reflectometer CS616 probe and Hydrosense data logger (Campbell Scientific, Loughborough, UK) for a depth range of 0–30 cm, directly calibrated for local organic soils. Rainfall was collected from a rain gauge situated above the canopy at each site, and was recorded fortnightly over a period of 12 mo.

Humic layer depth (organic litter layer [soil horizons O₁ and O_a], *i.e.*, all horizons with negligible mineral soil content) was recorded once for each site in August 2008, with the depth measured using a ruler at 25 evenly spaced points (as above) across the five sites. Humic layer depth was also sampled in the same way at an additional three sites (at 2000, 2750 and 3000 m). It should be noted that air temperature and rainfall data were collected using a different method at Tambopata (190 m). Air temperature was measured daily rather than monthly. Additionally, rainfall data were compiled by L. Aragão (pers. comm.) from a range of local sources for the period January–December 2006 rather than being collected every 2 wk on site between 2006 and 2008.

TERMITE SAMPLING.—Termite species density and indirect absolute abundance were sampled in June 2008 using a standardized belt transect (Jones & Eggleton 2000). Species density refers to the number of species per unit area, and thus in this case to the total number of species in each belt transect. Indirect absolute abundance is defined here as the total number of encounters for each termite species in a transect. Each encounter (an occurrence of a population of termites of one species at one excavation point) was recorded (Davies *et al.* 2003b). In this method, it is therefore possible to have

TABLE 1. *Study site descriptions.*

Site name	Coordinates	Altitude (m)	Forest type	Vegetation description
Tambopata	12°49'48" S, 69°16'48" W	190	Lowland rain forest	Tall canopy (> 50 m in places); well-structured forest; Moraceae and Fabaceae dominant tree families; palms and lianas abundant; lack of moss on trees and forest floor
Tono	12°56'49" S, 71°31'59" W	925	Submontane rain forest	Tall canopy; well-structured forest; Moraceae, Fabaceae and Rubiaceae dominant tree families; tree ferns and bamboo (<i>Guadua</i> and <i>Chusquea</i> spp.) abundant; moderate amounts of moss on trees and forest floor
San Pedro	13°2'56" S, 71°32'13" W	1500	Cloud forest	Moderate canopy height; Euphorbiaceae, Fabaceae and Lauraceae dominant tree families; arboreal and ground ferns abundant; moderate amounts of moss on trees and forest floor
Trocha Union, plot 8	13°4'16" S, 71°33'18" W	1850	Cloud forest	Medium-low canopy; thick undergrowth; Myrtaceae, Clethraceae and Clusiaceae dominant tree families; bamboo (<i>Chusquea</i> spp.), and moss on trees and forest floor abundant
Wayqecha	13°11'24" S, 71°35'13" W	3025	Treeline cloud forest	Medium-low canopy; <i>Weinmannia</i> and <i>Clusia</i> dominant tree genera; arboreal bromeliads > 5 m, arboreal and ground ferns, and moss on trees and forest floor abundant; moderate amount of bamboo (<i>Chusquea</i> spp.) in middle storey

more than one encounter of a species per transect section. For the purposes of brevity, indirect absolute abundance will be referred to as 'abundance' throughout the rest of this paper.

One belt transect, measuring 100×2 m and divided into 20 sections (each 5×2 m), was laid at each of the five sites. A total of one person-hour (*i.e.*, 30 min each for two workers) was spent searching for termites in every section. Searching focused on common termite microhabitats in accumulations of litter and humus at the base of trees and between roots, inside and beneath dead wood, in mounds, nests, carton sheeting and on runways on the ground, on trees and on vegetation up to a height of 2 m (Jones & Eggleton 2000). In addition, in a slight modification of the Jones and Eggleton (2000) methodology, eight soil samples, rather than 12 (each $12 \times 12 \times 10$ cm), were dug per transect section. The time spent inspecting these samples for termites was additional to the one person-hour per section. In an attempt to investigate the upper limits of termite distribution, additional 5×2 m sections were searched at 25-m elevation intervals above the highest transect where termites were found (though only 1525 and 1550 m were searched due to terrain and time constraints). All termites were stored in 80 percent ethanol, and soldiers and workers were sampled where present.

Because of the limitations of the study, replication at each elevation was not possible. Nevertheless, the belt transect method is designed to obtain the best possible 'snapshot' of conditions in a single site and has been tested and used extensively in these kinds of studies (*e.g.*, Jones & Eggleton 2000, Donovan *et al.* 2002, Eggleton *et al.* 2002, Inoue *et al.* 2006). We do acknowledge, however, that results drawn from one transect at each elevation may reflect unique characteristics of that site. Again due to study limits, we were not able to collect data on energy intake by termites or on energy availability in soil/wood diets. This is recommended for future studies to further our understanding of the relative energy absorption by wood and soil feeders.

DEAD WOOD SAMPLING.—Dead wood encountered within the belt transect boundaries was divided into small wood (fallen and suspended up to 2 m height; diam ≥ 0.5 and < 10 cm) and large wood (fallen and standing; diam ≥ 10 cm). A 2-m cord was laid at random in each section of the transect. All small wood items intersecting with the line, and all large wood items within the section were examined. Termite and fungus attack were scored separately for each item (Table S1, modified after Davies *et al.* 1999). Termite attack was indicated by the presence of carton (woody fecal matter), plastered soil and cavities in the wood, whereas fungal attack was signaled by the presence of fungal hyphae and/or fruiting bodies as well as by wood discoloration, weakening and characteristic cracking (Davies *et al.* 1999, see also Berge *et al.* 2008, Nobre *et al.* 2009).

TERMITE IDENTIFICATION.—Termites were identified at the Natural History Museum, London. A conservative taxonomic approach was used throughout, with species being assigned existing names wherever possible. Termites with soldiers were identified to genus level with Constantino's (2002) key to Neotropical termite genera, and to species level with the museum collection and keys (Emerson 1952; Emerson & Banks 1965; Krishna & Araujo 1968; Constantino 1991, 2000; Maiti 2006; da Rocha & Cancellato 2007). Soldierless termites were identified

to genus and species level with L. M. Hernández's (unpubl. data) key to the Apicotermitinae of the Guyana Shield (the only comprehensive key for soldierless termites in South America). The key is based on the structure of the worker gut, particularly the enteric valve. Enteric valves were dissected and examined under a compound microscope.

Termites were also classified according to functional group (which is interchangeable with feeding group). There are four feeding groups: group I termites feed on undecayed dead wood, group II termites feed on substrate from decayed wood to very decayed wood/humus, group III termites feed on pure humus and humus particles in the soil and group IV termites feed on the most nutrient poor organic material in the soil (Donovan *et al.* 2001, Davies *et al.* 2003a). Thus groups I and II are wood feeders, and groups III and IV are soil feeders. Termite voucher collections are housed at Universidad Nacional de San Antonio Abad del Cuzco, Peru, and at the Natural History Museum, London.

DATA ANALYSIS.—Environmental data were analyzed using one-way analysis of variance (ANOVA) followed by Bonferroni *post-hoc* comparisons in SPSS version 16.0. Where the homogeneity of variance assumption was not met, the Welch *F*-ratio was reported instead of the normal ANOVA *F*-ratio. Observed species accumulation curves were calculated with EstimateS using a sample-based technique with 100 runs (Colwell 2005; see also Gotelli & Colwell 2001). Nestedness Calculator software, developed by W. Atmar and B. D. Patterson, was used to test how nested the assemblages were (Atmar & Patterson 1995). The differences between termite attack scores at each site and fungal attack scores at each site were tested with a Kruskal–Wallis test followed by *post-hoc* Mann–Whitney *U* tests in SPSS version 16.0. Bonferroni corrections were applied so that the level of significance was 0.005 for all and small dead wood, and 0.008 for large dead wood.

RESULTS

ENVIRONMENTAL VARIABLES.—Median monthly air temperature and soil temperature decreased with increasing altitude (Figs. 1A and B). The means of air and soil temperature decreased steadily from 24.7°C and 24.2°C, respectively, in the lowland rain forest (190 m), to 12.9°C and 11.5°C, respectively, at the topmost site (3025 m), near the treeline. Monthly temperature range was fairly constant across all sites, although air temperature range was slightly reduced at 1850 m (the base of the cloud zone) and soil temperature variation was greater at 3025 m (the top of the cloud zone; Figs. 1A and B). There was a significant difference in soil water content with elevation (ANOVA: Welch $F_{4,32} = 215$, $P < 0.0001$), with median monthly soil water content significantly higher at the mid-elevation site (1500 m; Fig. 1D). Annual rainfall peaked at a lower elevation (925 m; Fig. 1C), and declined significantly at 3025 m, unlike soil water content. There was also a significant difference in the depth of the carbon-rich humic layer with elevation ($F_{4,53} = 61.6$, $P < 0.0001$). Median depth was < 5 cm in the lowlands, rose rapidly between 925 and 1500 m, and remained steady between 20 and 45 cm from 1850 to 3025 m (Fig. 1E).

TERMITES.—Forty-nine species of termite, representing 30 genera, were collected across the elevation gradient, although termites only

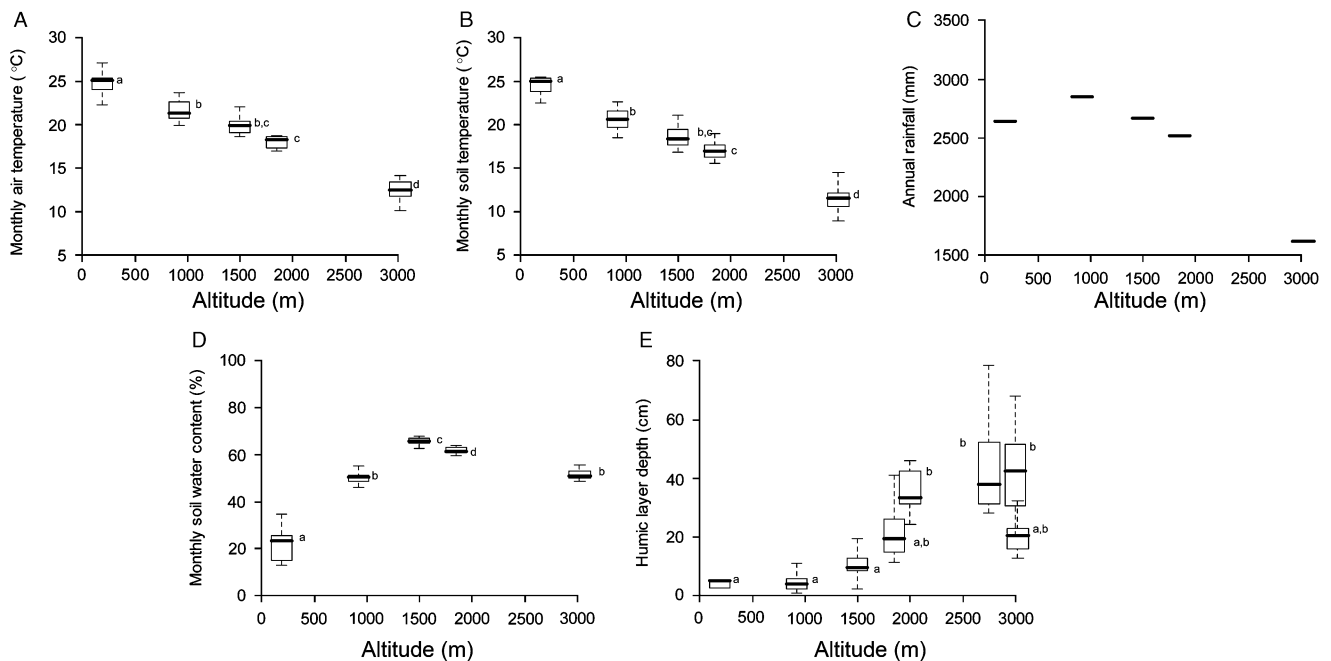


FIGURE 1. Environmental variables plotted against altitude: monthly air temperature (A), monthly soil temperature (B), annual rainfall (C), monthly soil water content (D), and humic layer depth (E). Air and soil temperatures were significantly different along the altitudinal gradient ($F_{4,53} = 78.8$, $P < 0.0001$; $F_{4,84} = 96.4$, $P < 0.0001$, respectively). Plots (A), (B), (D), and (E) show the median, interquartile range and nonoutlier total range. Bonferroni *post-hoc* comparison outcomes are coded in letters.

occurred in the lowest three transects. Eighteen species are newly recorded, awaiting formal description, with five species being ‘near’ described species and two genera being ‘near’ described genera (Table S1). Species accumulation curves indicate that sampling was relatively complete at 925 and 1500 m, with the curve approaching an asymptote for these sites. At the lowest elevation site (190 m), however, the curve was still increasing steeply indicating that sampling was not complete (Fig. 2).

Overall termite species density and abundance declined with increased altitude, with the upper limit to termite distribution being between 1500 and 1850 m (Figs. 3A and B). The feeding groups responded differentially to altitude, with soil feeders having a lower elevation limit than wood feeders. Soil feeders declined to zero abundance between 925 and 1500 m, while wood-feeders declined to zero abundance between 1550 and 1850 m (as wood feeders were found in the 1500 m transect and also in the two additional termite searches at 1525 and 1550 m). Despite this, group III soil-feeding termites had the highest species density and abundance over the whole gradient. Also, among soil-feeding species, the proportion with a soldier caste dropped from 33 percent at 190 m to 17 percent at 925 m (Table S2; Fig. 3C). Note that only Apicotermitinae are soldierless in this region.

Overall the species assemblages exhibited a high degree of nestedness (*i.e.*, populations at higher elevations are largely a subset of the populations at lower elevations), indicating that there is little turnover of species with increasing elevation. On a scale where 0° represents a system absent of all randomness (*i.e.*, maximally ‘cold’) and 100° represents a system absent of all order (maximally ‘hot’) (Atmar & Pat-

erson 1995) observed nestedness temperature was calculated as 6.0° compared with a mean of 35.6° for the randomized data (999 permutations, P for the data not being nested < 0.00001).

DEAD WOOD DECOMPOSITION.—Termite attack on dead wood declined significantly > 190 m, and was not detected > 1500 m. In contrast, fungal attack declined between 190 and 1500 m and remained relatively constant up to 3025 m (Fig. 4A). These patterns are reflected not only in the termite and fungal attack on small and large dead wood, but also in the proportion of dead wood attacked

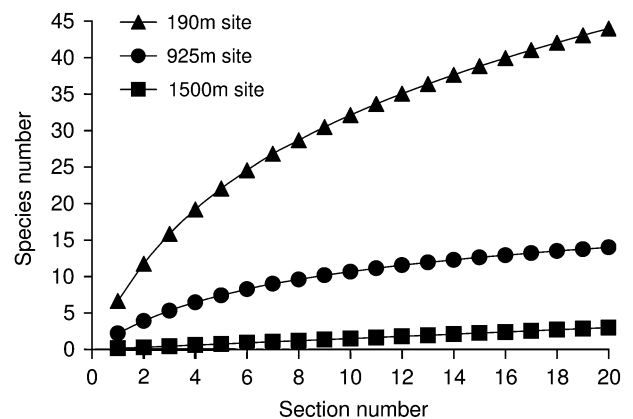


FIGURE 2. Species accumulation curves for termite sampling at 190, 925 and 1500 m sites. Each section measures 5×2 m, and there are 20 sections in each transect.

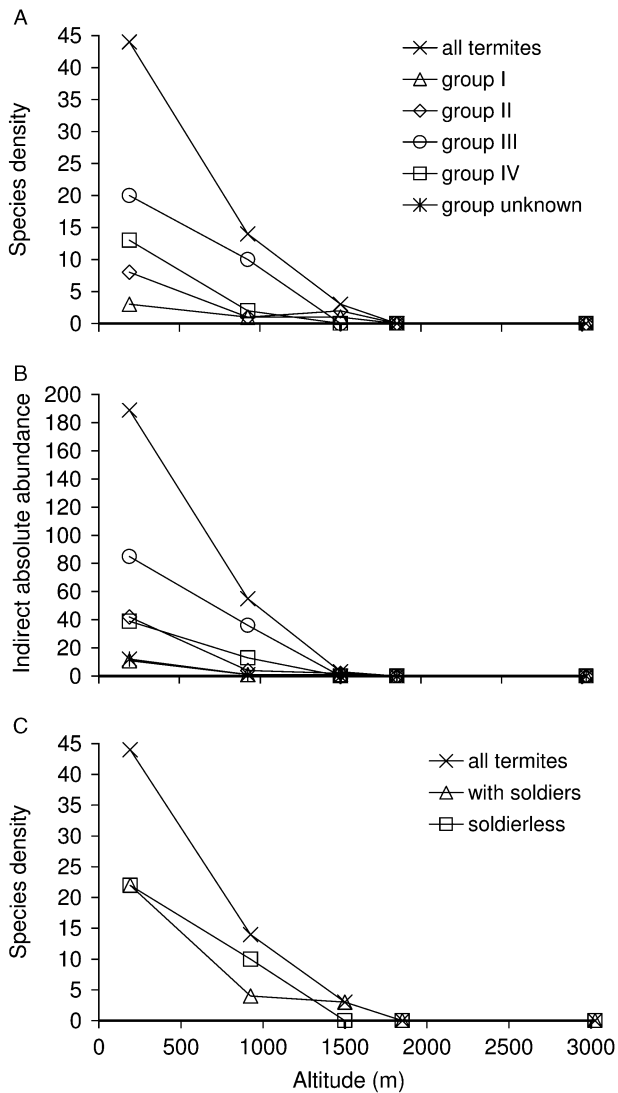


FIGURE 3. Termite species density (A) and indirect absolute abundance (B), categorized by feeding group, plotted against altitude. Groups I and II are wood feeders while groups III and IV are soil feeders. Termite species density, categorized by whether the species has a soldier caste or not, plotted against altitude (C).

at each site (Figs. 4B–D). Mean termite attack on dead wood was significantly different between sites ($H = 276$, $P < 0.0001$; $H = 253$, $P < 0.0001$; $H = 26.5$, $P < 0.0001$, for all, small and large wood, respectively). Mean fungal attack on dead wood was also significantly different between sites ($H = 105$, $P < 0.0001$; $H = 85.2$, $P < 0.0001$; $H = 15.2$, $P < 0.002$, for all, small and large wood, respectively).

DISCUSSION

GLOBAL AND REGIONAL CONTEXT.—Termite species density, assemblage composition and feeding group dominance patterns found in this Peruvian study are similar to those found at the few other comparable sites in South America that have been sampled using the

transect method (e.g., French Guiana; Davies *et al.* 2003a, b). This lends further support for the idea that the South American assemblage has intermediate levels of termite diversity relative to African and SE Asian pools (Davies *et al.* 2003a). Although a large proportion of termite species found in this study appear to be new (37%) and await formal description, this large proportion of new species may reflect under-sampling of the region's fauna rather than significant variation in species assemblages across South America.

TERMITES, ELEVATION AND POTENTIAL DRIVERS.—As found in a study of termite diversity in Sumatra, Indonesia (Gathorne-Hardy *et al.* 2001), and as expected, termite species density and abundance declined with elevation (Figs. 3A and B), along with air and soil temperatures (Figs. 1A and B). While a causative relationship cannot be inferred by correlative patterns, this similarity of trends does provide support for Gathorne-Hardy *et al.*'s (2001) explanation that the lowering of temperature lowers termite metabolic rates, in turn negatively affecting termite diversity; this also reflects latitudinal patterns of termite diversity (see Davies *et al.* 2003a).

Also as predicted, the altitudinal limit of soil-feeding termites was lower than for wood-feeding termites (Fig. 3A); a similar trend was found by Donovan *et al.* (2002). Additionally, there was a marked reduction in the number of soil-feeding species with a soldier caste at 925 m (Fig. 3C). These patterns lend further support to Gathorne-Hardy *et al.*'s (2001) theory that temperature and energy supply drive termite diversity. We suggest that while temperature overall is the constraint on termites (both soil feeders and ones with soldiers too), within termites the gradient of the decline depends on feeding group: soil feeders are likely to be more affected because of their energy requirements. The lower down the humification gradient a species feeds, the more likely they are to be affected by altitude, because the lower they are down the gradient, the lower the energy of their food. This simply mirrors what happens with latitude, which is also predominantly a temperature effect (see Davies *et al.* 2003a). The termites least affected by altitude are therefore wood feeders, and all wood-feeding termites have soldiers. Hence, it is not surprising that soldiers of wood-feeding species were found at high altitudes. Conversely, because soil feeders derive less energy from their food substrate than wood feeders, they drop out at a lower elevation (higher temperature) than other termites.

The finding that among soil-feeding termites, there was almost double the density of soldierless termite species at the intermediate elevation site (925 m) compared with the lowest elevation site (190 m) is especially interesting. All things being equal, it might be expected that a species that does not produce soldiers makes some energetic saving compared with a species that invests energy in producing soldiers. Our results support the idea that soldierless termites may be favored at sites where soil-feeding termites are under energetic stress, but are still able to persist (e.g., 925 m; Fig. 3C); this is merely a hypothesis from a single site and requires further testing to be confirmed. While temperature seems to be an important influence on diversity overall in this system, it is, however, difficult to tease apart the relative importance of temperature averages, extremes and ranges without further physiological studies.

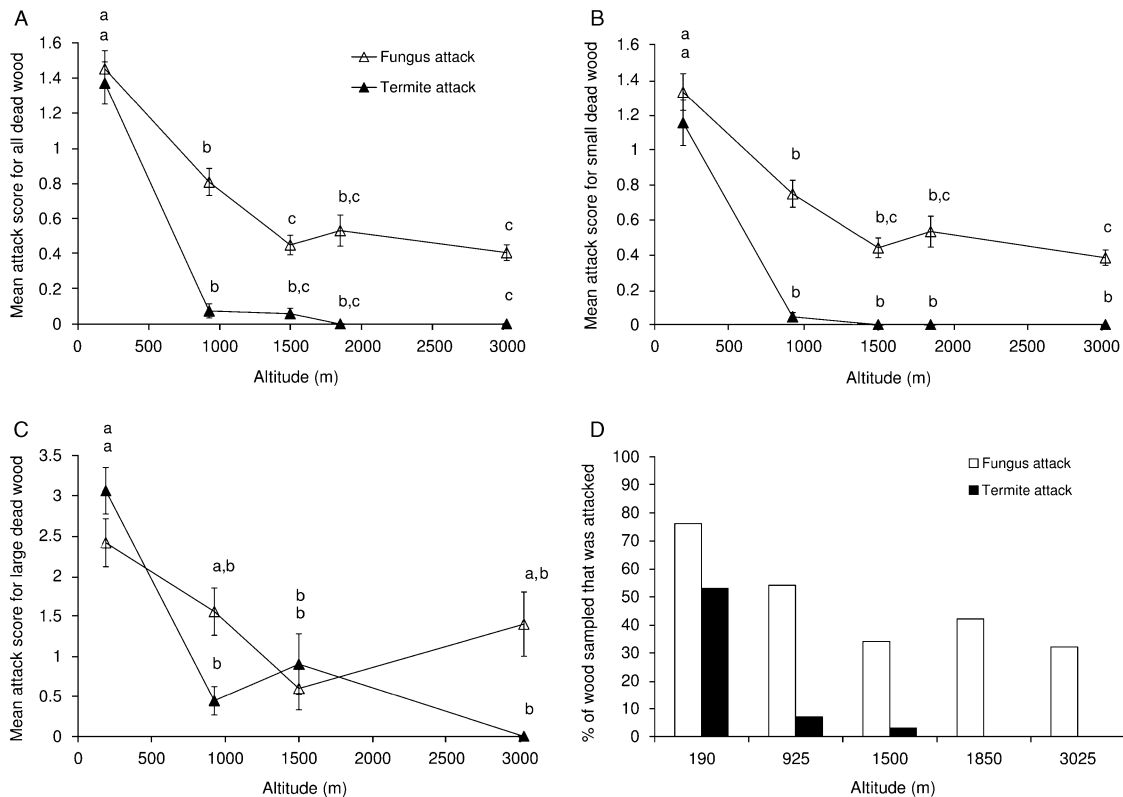


FIGURE 4. Mean (\pm SE) termite and fungal attack scores for each site on the altitudinal gradient: all dead wood (A), small dead wood (B) and large dead wood (C). Mann–Whitney U test outcomes are coded in letters and standard error is shown. The percentage of all dead wood sampled that was attacked (to any degree) by termites and fungi is shown in (D).

Species assemblages along the elevation gradient were highly nested providing support for Donovan *et al.*'s (2002) observation that upper assemblages tend to be a subsample of the lowland species pool. This nested pattern was primarily influenced by the two lowest sites (79% of species at 925 m were found at 190 m), with two of the three species found at 1500 m not observed at lower elevations (Table S2). As both termite species density and abundance were low at 1500 m, it is not possible, however, to draw firm conclusions about whether these two species were exclusive to this elevation or simply rare at lower elevations.

Contrary to expectations, the upper distributional limit for termites in this system was much lower than anticipated, and below the upper limit recorded in Sarawak, SE Asia (1850 m in Peru compared with 1930 m in Sarawak; see Collins 1980). Although temperature is an important factor in this system, temperatures at comparable elevations were lower in SE Asia (*i.e.*, 16.3°C at 1860 m compared with 17.8°C at 1850 m in Peru); this is expected under the influence of the Massenerhebung effect because of the difference in mountain size (2376 m asl in Sarawak vs. *ca* 4000 m asl in Peru). The decline of termite diversity at lower elevations in Peru is also in spite of there being a larger species pool in South America than in SE Asia.

An explanation for this unexpectedly low elevation limit of termites may be related to high soil water content at mid-elevation Peruvian sites; a pattern associated with the persistence of cloud

immersion causing high fog deposition and low evapotranspiration (characteristic of the cloud forest) (Hamilton *et al.* 1994). The high mean monthly soil water content at 1500 m (66%; Fig. 1D) combined with lower temperatures may make habitat conditions too hostile for soil feeders (that live and forage in the soil) to survive, and thus explain their rapid decline and disappearance at higher elevations. The persistence of high soil water content (62%) at 1850 m also suggests high wood moisture content, and may explain the decline of wood feeders between 1550 and 1850 m (while some termites respond positively to waterlogging, these groups do not occur in our study areas). The high values of moisture content are likely linked to frequent immersion in clouds (*i.e.*, cloud droplet deposition and low evapotranspiration) rather than rainfall (which declines with elevation from a submontane peak; see also Hamilton *et al.* 1994).

In conclusion, we suggest the main drivers of the decline in termite diversity with altitude in Peru are likely to be reduced temperature acting in concert with increased soil (and perhaps wood) water content at the upper limit of termite distribution. In future, it would be interesting to explore the relative contribution of each factor.

ECOSYSTEM FUNCTIONING AND ROLE OF TERMITES.—Termites are recognized to be major agents of woody matter and soil breakdown in lowland tropical systems (Wood & Sands 1978, Bignell &

Eggleton 2000). In our Peruvian study, termite attack on dead wood only occurred to a significant degree at 190 m, where wood feeder abundance was high (Figs. 3B and 4). While termite attack on dead wood was not a significant feature at higher elevations (most likely due to very low or zero wood feeder abundance) (Fig. 3B), fungal attack on dead wood was significant across the whole elevation gradient (Fig. 4). While it seems that termites, and so also termite attack on dead wood, were excluded by low temperatures and high soil water content above 1850 m, fungal attack was not excluded. Given that fungus-mediated decomposition is thought to decline in response to soil and/or wood desiccation (Davies *et al.* 1999), fungal attack on wood may in fact be maintained (although is not necessarily high) at higher elevations by the high soil (and wood) moisture content above 925 m (Fig. 1D).

Finally, it is also intriguing to note that where soil-feeding termites were present and abundant, the soil organic horizon was very thin (4–5 cm), while the converse occurred at higher elevations (Fig. 5). Importantly, the zone where soil feeders drop out (925–1500 m) coincides with a marked rise in the mean depth of the humic layer (from 5 to 11 cm), and where termites are absent, the humic layer depth remains thick across a wide elevation and temperature range. This correlative pattern, while not demonstrating a causal link, leads us to hypothesize that although termites are not the sole agent of soil decomposition in this system (microbial and microarthropod decomposition also play a role), soil-feeding termite abundance is a major accelerant of soil decomposition rates (and associated mineralization) in lowland Amazonian forests, and that their absence may explain the appearance and persistent thickness of a soil humic layer above 1500 m. While wind deposition can result in deep soil depth in some higher montane regions, the soils within tropical cloud forests at higher elevations have a deep organic layer comprised of relatively coarse debris (> 1 mm) and with zero mineral content across most of it (Penafiel 1994); this suggests that the soil thickness is very unlikely to be due to windblown material.

Manipulative experiments may prove especially fruitful in investigating further the role of termites in decomposing soil in trop-

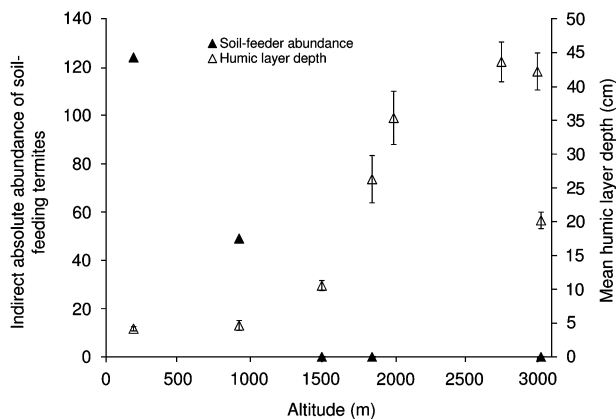


FIGURE 5. Indirect absolute abundance of soil-feeding termites and mean humic layer depth (cm), plotted against altitude. Standard errors for humic layer depth measurements are shown.

ical systems and ascertain any consequential effects on ecosystem functioning. One experimental approach would be to translocate cloud forest soils into lowland environmental conditions, conduct a number of treatments to exclude termites, fungi and microbes, and monitor the effect of treatment on decomposition rates.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Method for scoring termite and fungal attack on dead wood.

TABLE S2. Termite species assemblage, density and indirect absolute abundance at the three study sites where termites were found.

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