INTRODUCTION

In the tropics, insects are abundant and constitute the largest part of animal species richness (Stork, 2007). Termites (Blattaria: Termitoidae) are common ecosystem engineers (Dangerfield, Mccarthy, & Ellery, 1998) mainly distributed in tropical ecosystems (Bignell & Eggleton, 2000; Jones & Eggleton, 2010). They are dominant decomposers in savannahs and tropical forests and play an important role in the physicochemical biotransformation of organic matter and in re-distribution of structural soil components (reviewed...
in Bignell & Eggleton, 2000). Termites are important food resources and highly nutritious for a broad range of species: invertebrates (Bodot, 1961; Petráková et al., 2015), amphibians (Solé, Ketterli, Di-Bernardo, & Kwet, 2002), and reptiles and mammals (Abensperg-Traun & Steven, 1997; Mcgrew, Tutin, & Baldwin, 1979). They can be involved in habitat biotransformation, for instance, in the case of mound-building species (Noirot & Darlington, 2000) and subterranean nesters (Lavelle et al., 1997).

In lowland tropical forests, termite species diversity is high (e.g., Bignell & Eggleton, 2000; Bourguignon, Leponce, & Roisin, 2011; Eggleton, Davies, Connetable, Bignell, & Rouland, 2002; Eggleton, Bignell et al., 2002) and new species are continuously discovered and described (Casalla, Scheffrahn, & Korb, 2016a,b; Eggleton, 1999; Postle & Scheffrahn, 2016). To untangle termite diversity, the use of molecular techniques has been shown to be an important tool for identification of species that are problematic to determine only by morphology (Bourguignon, Sobotnik, Dahlsjo, & Roisin, 2016; Hausberger, Kimpel, Neer, & Korb, 2011; Inward, Vogler, & Eggleton, 2007; Roy, Demanche, Livet, & Harry, 2006).

Ecological studies on termites have been surveys to determine species richness and community composition in rain forests, savanna, and disturbed areas (e.g., Ackerman et al., 2009; Bignell & Eggleton, 2000; Bourguignon et al., 2011; Dahlsjö, Parr, Malhi, Meir, & Eggleton, 2014; Davies, Eggleton, Jones, Gathorne-Hardy, & Hernández, 2003; for savanna: Ferrar, 1982; Schyra & Korb, 2017; Wood, Johnson, Bacchus, Shittu, & Anderson, 1982; for disturbed and fragmented forests: Eggleton, 1999; Eggleton et al., 1996; Jones et al., 2003; Roisin & Leponce, 2004; Sena, Vasconcellos, Gusmão, & Bandeira, 2003; Vasconcellos et al., 2010; for cultivated areas: Attignon, Lachat, Sinsin, Nagel, & Peveling, 2005; Coaton, 1953; Dosso, Deligne, Yeó, Konate, & Linsenmair, 2013; Leponce, Roisin, & Pasteels, 1997; Luke, Fayle, Eggleton, Turner, & Davies, 2014). However, termite diversity in tropical dry forests has rarely been studied (Eggleton, 2000; Jones & Eggleton, 2010). The few studies that exist were done in Mexico (Calderón-Cortés, Escalera-Vázquez, & Oyama, 2018), Puerto Rico (Genet, Genet, Burton, & Murphy, 2000), and Brazil (Vasconcellos, Araújo, Moura & Bandeira, 2007; Vasconcellos et al., 2010; Viana, Reis, Costa, & Souza, 2014), and they concentrated on listing species. However, the floristic composition of dry forests differs greatly in the Neotropics (Banda et al., 2016) and Colombia is biodiversity hotspot (Mittermeier, Myers, Thomsen, Fonseca, & Olivier, 1998). Their tropical dry forests have high species endemism, but have been
rarely studied (Banda et al., 2016; Gentry, 1995). Less than five percent of the tropical dry forests are protected, the best conserved are at the Caribbean coast (Instituto de Investigación Alexander von Humboldt, 2014). Furthermore, these ecosystems are threatened by climate change (Banda et al., 2016; Instituto de Investigación Alexander von Humboldt, 2014; Miles et al., 2006; Wright, 2005), fire (Middleton, Sanchez-Rojas, Suedmeyer, & Michels, 1997), and extensive livestock farming and crops (Foley et al., 2005).

Environmental factors can influence termite communities. For instance, precipitation, elevation, temperature, and soil properties are known to affect termite diversity (Bourguignon, Drouet, Šobotník, Hanus, & Roisin, 2015; Gathorne-Hardy, Syaukani, & Eggleton, 2001; Holt & Lepage, 2000). Studying the association of termite occurrences with different environmental factor is a first, essential step for a better understanding of termite ecology in tropical dry forests.

The aims of this study were (a) to identify the termite species occurring in tropical dry forests of the Colombian Caribbean coast; (b) to describe associations of termite communities with environmental factors; (c) to test whether there is a correlation between species richness and rainfall at the regional and the global scales.

2 | METHODS

2.1 | Study sites and termite sampling

The study sites were located in the Coraza Forestry Reserve “Colosó” (hereafter, Colosó; Sucre; 9°31’51.6″N, −75°21’0″W; 9°32’24″N, −75°21’3.6″W), the regional park “El Ceibal Mono Titi” (hereafter, Ceibal; Santa Catalina, Bolívar; 10°37’40.8″N, −75°14’6″W; 10°38’13.2″N, −75°15’10.8″W), and the National Park “Tayrona” (hereafter, Tayrona; Santa Marta, Magdalena; 11°19’19.2″N, −74°6’10.8″W; 11°18’43.2″N, −74°7’22.8″W) in Colombia (Figure 1). Colosó is a regional forestry reserve created in 1983, with important primary and secondary tropical dry forest, bordered by small plots of agriculture and livestock farming. Its mean annual temperature is 26.7°C (min: 25.8; max: 27.8) with an annual precipitation of around 1,337 mm (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Instituto Nacional de los Recursos Naturales Renovables y del Ambiente, 1983). Ceibal is a private remnant of primary and secondary tropical dry forest, surrounded by large livestock farms with small rural settlements. In 2013, it was declared a protected area. It has a mean annual temperature of 27.6°C (min: 26.9; max: 28.1) and an annual precipitation of around 1,080 mm (Corporación Autónoma Regional del Canal del Dique, 2013; Hijmans et al., 2005). Tayrona is a Natural Park with primary and secondary forest created in 1963 without human settlements or agriculture and the best-protected and conserved dry forest in Colombia. Its mean annual temperature is 27.8°C (min: 25.8; max: 29.0) with an annual precipitation of about 713 mm (Carbonó, 2010; Hijmans et al., 2005; Instituto Colombiano para la Reforma Agraria, 1964; Instituto de Investigación Alexander von Humboldt, 2014). All study sites were located belong to the Caribbean coast.

Termites were sampled in Colosó in July 2014, in Ceibal in August 2014, and in Tayrona in August 2015, after the first seasonal rains. The standardized belt transect sampling protocols of Jones and Eggleton (2000) and Hausberger and Korb (2015) were used. Five 100 m × 2 m transects belts were arbitrarily located at each site. Each transect was divided into 20 contiguous sections (each 2 m × 5 m). Two trained people searched each section for a total of 30 min systematically for termites, including all microhabitats such as leaf litter, dead wood, trunks, foraging galleries nest, and twigs. The transect sampling was supplemented by eight soil scrapes (15 cm × 15 cm, 10 cm depth) per transect section to collect soil-dwelling termites. Whenever termites were encountered, several individuals were collected if possible including soldiers and stored as a sample. Collected termite samples were individually labeled and stored in 100% ethanol for DNA analysis and 80% ethanol for museum curation.

Additionally, soil samples (approx. 1 kg per sample) were taken from the top horizon (0–15 cm) at a distance of 1 m parallel to each belt transect with three replicates per transect belt (one each at the start, in the middle, and at the end of a belt transect), resulting in a total of 15 samples per site. Samples were cooled after the field trips, and subsequently, they were dried and sealed in plastic bags, and immediately sent for analysis to the Soil Laboratory of the Geoscience School of the Universidad Nacional in Colombia. Soil texture (sand, clay, and silt content), pH, cationic exchange capacity, organic matter, calcium, magnesium, potassium, sodium, and phosphorus were determined using in house protocols (http://www.unalmed.edu.co/~esgeocien/metodologia_quimica.html).

2.2 | Species identification

All samples were identified to genus level and sorted to morphospecies using taxonomic soldier traits (Casalla et al., 2016a,b; Constantini & Cancello, 2016; Constantino, 1998, 2001; Krishna, 1961; Krishna & Araujo, 1968; Krishna, Grimaldi, Krishna, & Engel, 2013; Scheffrahn & Křeček, 1999). A representative of each sample (specimen) was also sequenced using genetic markers (barcoding approach, see below) to corroborate morphological identification. For taxonomically problematic (soldierless) Apicotermitinae and samples lacking soldiers, we used genetic barcoding only.

For molecular species identification, we isolated DNA and sequenced fragments of three mitochondrial genes, cytochrome oxidase subunit II (COII; total length 740 bp), 12S rDNA (~480 bp), and 16S rDNA (~385 bp), as described elsewhere (Doyle & Doyle, 1987; Hausberger et al., 2011). These sequences were used to re-construct phylogenetic trees (see below) to delimitate and identify species as in former termite studies (Eaton, Jones, & Jenkins, 2016; Hausberger et al., 2011; Legendre et al., 2008; Roy et al., 2014). COII was most useful for “barcoding” (i.e., assigning species to samples) because it amplified well and gave appropriate resolution for species identification. To delimitate species, we constructed phylogenies comprising all species occurring in Colosó, Ceibal, and Tayrona. Samples forming a well-supported cluster were named
identically. Species names were carefully checked with available literature and correspond to those reported for Neotropical termites (Bourgignon et al., 2017; Cameron, Lo, Bourguignon, Svenson, & Evans, 2012; Casalla et al., 2016a,b; Eaton et al., 2016; Inward et al., 2007; Roy et al., 2014). Voucher specimens of all species are held at the University of Freiburg, Germany, and will be deposited at the Natural History Museum of the Alexander von Humboldt Institute of Bogotá (MIAvH).

2.3 | Phylogenetic analysis

COII, 12S, and 16S rRNA sequences were checked manually and then aligned with MUSCLE as implemented in MEGA v7.0 (Kumar, Stecher, & Tamura, 2016). Sequences were submitted to NCBI and provisional numbers access were gathered (Supporting Information Table S1). We inferred a phylogenetic tree based on a Bayesian approach using MrBayes 3.2.1. (Ronquist & Huelsenbeck, 2003: 107 generations with every 1000th tree sampled, using the default of four chains). For COII, the best-fitting model was TIM3+G+I, for 12S rRNA GTR+G+I, and for 16S rRNA TIM2+I+G (Posada, 2008). After checking for convergence, we discarded 50% as burn-in. For phylogenetic tree inference based on the maximum-likelihood (ML) approach, we applied IQTREE version 1.4.3 (Nguyen, Schmidt, Von Haeseler, & Minh, 2015). We performed partitioned, non-parametric bootstrapping with 10,000 replicates. Finally, we plotted all bootstrap replicates on the ML tree with the best log-likelihood values. For all phylogenetic tree analyses, we choose the cockroach Blatta orientalis Linnaeus, 1758 as outgroup taxon. The resultant tree from Mr. Bayes and IQTREE were visualized using FigTree version 1.4.2 (Nguyen et al., 2015). Additionally, we also used MEGA 7.0 (Kumar et al., 2016) to calculate p-distances between putative species for the combined COII, 12S, and 16S nucleotide sequences (3,000 bootstrap replications, Gamma Distributed rates among sites and Transitions + Transversions substitution model). As complementary data to the 32 sequences in our study (Supporting Information Table S1), we downloaded 194 COII barcode sequences (longer than 600 bp in length) from NCBI, from closely and distantly related Kalotermitidae, Rhinotermitidae, and Termitidae. We built a phylogenetic tree based on a Bayesian approach using MrBayes (see above) and used the OTUs clusters formed to infer species.

2.4 | Diversity analyses

To compare alpha- and beta-diversity across sites, the Shannon (H) and the Simpson’s (1-D) indices as well as rarefaction and extrapolation curves of richness were calculated using EstimateS v9.1.0 (Colwell, 2013) and iNext (Chao et al., 2014). For the most abundant and richest genera (Microcerotermes, Nasutitermes, Anoplotermes-group, and Amitermes), Kruskal–Wallis tests, followed by multiple comparison post hoc Dunn–Šidák corrections, were used to test for differences between sites.

2.5 | Determination of feeding group

Feeding groups were identified based on Donovan, Eggleton, and Bignell (2001) and Eggleton and Tayasu (2001). Accordingly to Neotropics, four feeding groups are distinguished: dead wood and/or grass feeders with flagellates in guts (group I); dead wood, grass, leaf litter feeders (group II); upper layer organic-rich soil feeders (group III), and soil feeders (group IV). For Apicotermitinae, enteric valve and molar plates were checked to identify feeding groups.

2.6 | Determination of other environmental variables

Climate data were downloaded from WorldClim v 1.4 (http://www.worldclim.org). We calculated the annual median, maximum and minimum temperature, and precipitation over the last 10 years (Hijmans et al., 2005). Kruskal–Wallis tests, followed by multiple comparison post hoc Dunn–Šidák corrections, were used to test for differences in both climate and soil variables between sites.

2.7 | Canonical correspondence analysis

A canonical correspondence analysis (CCA) (constrained, unimodal, and ordinary scale) was done to reveal potential associations between environmental variables (annual precipitation, and annual mean temperature, elevation, soil properties; calcium, clay, cationic exchange capacity, magnesium, pH, and sand) and termite community composition. Canonical correspondence analysis performs quite well for skewed species distributions with highly intercorrelated qualitative environmental variables (Palmer, 1993). Prior to the analysis, we performed a permutation F test (p < 0.05; Bonferroni correction) to all soil and environmental variables, and then, we selected those variables most likely to be important determinants of termite species composition. Because biotic and abiotic variables were measured in different values and units, log-transformation was used. Data were analyzed with the software CANOCO for Windows v5.04 (Ter Braak & Smilauer, 2002).

2.8 | Other statistical analyses

Richness and rainfall values across four continents were obtained through a compilation of research articles on termite diversity.

3 | RESULTS

3.1 | Phylogenetic analysis

Using phylogenetic analyses of the three marker genes COII, 12S and 16S rRNA, and re-construction algorithms, we obtained almost identical topology of phylogenetic trees (Figure 2) for the three genes with three families: Kalotermitidae (100% Bayesian posterior probability, BPP; 100% bootstrap value, BV), Rhinotermitidae (100% for both BPP and BV), and Termitidae (100% BPP, 80% BV).
Intra-genera resolution was high in most cases, and two main clustered groups formed by Nasutitermitinae and Apicotermitinae were found (>56% BPP, >45 BV). Overall genetic p-distance was 13.2%; the lowest distance was observed between Nasutitermes dasyopsis Thorne, 1989 and Nasutitermes sp1 (p-distance 0.56%; Figure 2, Supporting Information Table S2). Yet the latter two species were clearly morphologically distinct (Supporting Information Figure S1).

3.2 | Diversity of termites in tropical dry forest

Through the use of Neotropical keys, NCBI blast, Bayesian inference and by consultation of experts (RH. Scheffrahn, University of Florida and Y. Roisin, Université Libre de Bruxelles), we identified 32 species in 1,103 encounters (Figure 2, Supporting Information Figures S1–S3 and Table S3). Most species were Termitidae (25 species, 78.1% and 953 occurrences, 86.4%), three species (9.4% and 131 occurrences, 11.9%) belonged to the Rhinotermitidae and four to the Kalotermitidae (12.5% and 19 occurrences, 1.7%; Supporting Information Table S3). Microcerotermes was the most abundant genus (35.6% Figure 2, Supporting Information Figure S4) followed by Nasutitermes (19.8%) and the Anoplotermes-group (12.8%). The most common species were Microcerotermes sp1 (25.9%), Heterotermes cardini (Snyder, 1924) (9.6%), Amitermes foreli Wasmann, 1902 (5.4%), Nasutitermes dasyopsis (4.3%), and Ruptitermes sp1 (2.6%; Figure 2, Supporting Information Table S3). The mean species richness and occurrences across all sites were 10.1 (±SD 3.0) and 73.5 (±SD 31.8), respectively.

3.3 | Comparison between sites

Colosó had the highest species richness with 23 species (399 occurrences), followed by Ceibal with 19 species (444 occurrences),
while Tayrona had only 15 species (260 occurrences). Species accumulation curves reached an asymptote for Ceibal, but not for Colosó and Tayrona (Supporting Information Figure S3). Neither richness nor occurrences per transect differed significantly between sites (ANOVA: $F_{2,12} = 1.80, p = 0.208$ and $F_{2,12} = 1.51, p = 0.260$). As visible on Supporting Information Figure S3, the two sites near sea level have similar rarefied species richness Ceibal (29 m, rainfall 1,079 mm) and Tayrona (17 m, 706 mm) while Colosó (334 m, rainfall: 1,327 mm) has higher local richness. However, the relative genera richness (i.e., number of species over total number of species per genera) of Microcerotermes ($\chi^2 = 10.18, df = 2, p = 0.010$, Table 1), Amitermes ($\chi^2 = 7.44, df = 2, p = 0.020$, Table 1), and Anoploterme-group ($\chi^2 = 6.03, df = 2, p = 0.020$; Table 1) differed significantly between sites, as well as the relative occurrence of Microcerotermes ($\chi^2 = 6.75, df = 2, p = 0.02$) and Anoploterme-group ($\chi^2 = 6.09, df = 2, p = 0.05; Table 1). The Shannon (H) and Simpson’s (1-D) diversity indices did not differ significantly per transect between sites (ANOVA: Shannon: $F_{2,12} = 2.23, p = 0.151$; Simpson’s: $F_{2,12} = 2.35, p = 0.138$). However, we found significant differences between the observed richness and the Chao 2 estimator (Mann–Whitney test $Z = -3.62, p < 0.001$).

### 3.4 Habitat preferences and feeding groups

Most termites were encountered in twigs/litter on the soil surface (55.7%), followed by soil scrapes (37.2%) and trees (6.6%), while only

| Diversity | Species genera | Colosó | Ceibal | Tayrona | Chi-squared | df  | p   | P Šidák correction |
|-----------|----------------|--------|--------|---------|-------------|-----|-----|---------------------|
| Richness  | Microcerotermes | 1 (0)$^a$ | 2 (1)$^b$ | 1 (0)$^a$ | 10.18 | 2 | 0.010 | 0.009               |
|           | Amitermes      | 0 (1)$^a$ | 1 (1)$^b$ | 2 (1)$^b$ | 7.44  | 2 | 0.020 | 0.011               |
|           | Anoploterme-group | 4 (2)$^a$ | 1 (3)$^b$ | 1 (2)$^b$ | 6.03  | 2 | 0.050 | 0.024               |
|           | Nasutitermes   | 2 (4)$^a$ | 2 (1)$^a$ | 1 (1)$^a$ | 5.11  | 2 | 0.080 | -                   |
| Occurrences | Microcerotermes | 12 (15)$^a$ | 37 (49)$^b$ | 22 (16)$^b$ | 6.75  | 2 | 0.020 | 0.008               |
|           | Amitermes      | 0 (3)$^a$ | 6 (14)$^a$ | 2 (6)$^a$ | 5.19  | 2 | 0.070 | -                   |
|           | Anoploterme-group | 23 (18)$^a$ | 2 (21)$^b$ | 1 (3)$^b$ | 6.09  | 2 | 0.005 | 0.020               |
|           | Nasutitermes   | 23 (18)$^a$ | 5 (16)$^a$ | 7.40  | 2 | 0.030 | -                   |
|           | Heterotermes   | 6 (4)$^a$ | 8 (10)$^a$ | 4 (13)$^a$ | 1.23  | 2 | 0.541 | -                   |

Different lowercase letters indicate significant differences.
a few arboreal and mound nests were found (0.7%). Among all sites, feeding group II was the most dominant (66.9%; Figure 2, Supporting Information Figure S5), followed by feeding group I (15.3%), feeding group IV (14.5%), and feeding group III (2.8%). Feeding group II had significantly more occurrences than the other feeding groups (ANOVA: \( F_{3,56} = 171.73, p < 0.001 \); Tukey test: \( p < 0.001 \), Supporting Information Figure S5), while both feeding groups I and IV differed from III (Tukey test: \( p = 0.001 \), Supporting Information Figure S5). The frequencies of occurrence of each feeding group did not differ significantly between sites (ANOVA: Group I: \( F_{2,12} = 2.44, p = 0.129 \); Group II: \( F_{2,12} = 0.36, p = 0.702 \); Group III: \( F_{2,12} = 0.91, p = 0.430 \); Group IV: \( F_{2,12} = 2.38, p = 0.134 \)).

### 3.5 Environmental variables

Precipitation (\( \chi^2 = 12.7; df = 2; p < 0.001 \)), temperature (\( \chi^2 = 10.90; df = 2; p < 0.001 \)), and elevation (\( \chi^2 = 9.98; df = 2; p = 0.01 \)) differed significantly between Colosó and Tayrona (Table 2). Colosó had the highest rainfall (1,327 mm annual), elevation (334 m), and lowest temperature (annual median of 26.7°C), while Tayrona had the lowest values for precipitation (706 mm), elevation (17 m), and highest temperature (27.8°C, Supporting Information Table S5A). Significant differences in soil properties (clay and CEC) between Tayrona and both Colosó and Ceibal were observed (Table 2). Soils of Colosó were rich in magnesium (median 0.75 IQR—interquartile range—0.35) and calcium (median 20.63 IQR 10.1). By contrast, Tayrona was rich in phosphorus (median 53 IQR 60.7). The rainfall and temperature of Ceibal were intermediate between Tayrona and Colosó, but in terms of soil composition, it was more similar to the latter (Table 2).

Within all transects, precipitation was positively correlated with termite species richness and occurrence (richness: Spearman’s rho = 0.676, \( p = 0.006 \); occurrence: Spearman’s rho = 0.531, \( p = 0.042 \); Figure 3a), while temperature negatively correlated with richness (Spearman’s rho = −0.594; \( p = 0.019 \)). Calcium and CEC positively correlated with occurrence (calcium: Spearman’s rho = 0.568, \( p = 0.027 \); CEC: Spearman’s rho = 0.545, \( p = 0.036 \); Table 3). In addition, rainfall was positively related with elevation (Spearman’s rho = 0.75, \( p = 0.013 \); Supporting Information Figure S6). We also explored the association between termite richness and rainfall at the global scale, and we found a significant positive correlation (Spearman’s rho = 0.712, \( p = 0.001 \); Figure 3b, Supporting Information Table S4). There was also a significant interaction between forest type (rain forest/dry forest) and elevation (\( F_{1,50} = 14.9, p < 0.001 \); Figure 4), demonstrating opposite elevation–termite richness relationships between forest types (Figure 4).

We analyzed the contribution of environmental factors on termite community composition. Only five variables were chosen: precipitation, temperature, elevation, magnesium, and pH (Supporting Information Tables S5A,B and S6). The CCA showed site-specific clusters, which were associated with certain termite species and environmental factors (Figure 5a,b). These variables accounted for 39.9% of the total variance in the occurrence of species (Monte Carlo permutation test \( F = 2.2, p = 0.001 \); Supporting Information Table S6). Colosó, which had the highest richness, was separated along the x-axis from the two other sites. It was associated with three Nasutitermes: Nasutitermes corniger, N. similis, and N. sp1. These species were linked to elevation, rainfall, and magnesium. Also, the Anoplotermes-group was rich in Colosó (eight species) and abundant (−52% of the relative abundance), but only two of these species (Anoplotermes-group sp6 and Anoplotermes-group

### TABLE 3 Spearman rank correlation between termite species richness and occurrences with environmental and soil variables

| Diversity | Species genera | \( r \) | \( p \) |
|-----------|----------------|-------|-------|
| Richness  | Precipitation  | 0.676 | 0.006 |
|           | Temp           | −0.594| 0.019 |
|           | Occurrences    | 0.531 | 0.042 |
| Occurrences| Ca             | 0.568 | 0.027 |
|           | CEC            | 0.545 | 0.036 |
|           | Precipitation  | 0.531 | 0.042 |

FIGURE 3 Correlation between termite species richness and rainfall (mm/year) (a) per transects in Colombia: triangle: Colosó, squares: Ceibal, circles: Tayrona, and (b) across four continents. For a list of data used see Supporting Information Table S6: circles: Africa, squares: America, triangle: Asia, X: Australia.
sp2) were specifically linked to the same climatic variables described for Nasutitermes. Ceibal, which had the highest termite encounter rates, was associated mainly with Heterotermes convexinotatus, Microcerotermes arboeus, Amitermes foreli, Rynchatermes bulbina-sus, and Proneotermes macondianus as well as with high pH values. Tayrona formed a cluster along the y-axis, with the lowest richness and encounter rates of Anoplotermes-group and Nasutitermes. It was associated with the occurrence N. dasypsis and drywood termites (Kalotermitidae), high temperatures, sandy soils, and organic matter (Figures 2 and 5a,b).

4 | DISCUSSION

Our study revealed differences in termite community composition across the three study sites. In the following, we discuss how environmental conditions, disturbance, and biological traits might have influenced species richness and community composition.

4.1 | Termite diversity and the potential role of rainfall

Species diversity in Neotropical forests is highly variable, ranging from 10 termite species in the semi-arid savannah region of Caatinga—Brazil to 100 species in a natural rain forest (Alves, Mota, Lima, Bellezoni, & Vasconcellos, 2011; Bourguignon et al., 2011; Couto, Albuquerque, Vasconcellos, & Castro, 2015; Dambros, 2015; Palin et al., 2011; Vasconcellos, 2010; Vasconcellos et al., 2010; Viana et al., 2014). With 32 species, our data fall at the lower range. Many of the other studies worked with morpho-species, so data are not completely comparable. Besides, sampling effort, forest type, disturbance, or geography could account for the different numbers. We might have missed a few species, as accumulation curves did not reach an asymptote for Colosó and Tayrona and we found significant differences between the observed richness and the Chao 2 estimator (Mann–Whitney test $Z = -3.62$, $p < 0.001$). However, additional non-standardized sampling revealed few new species. Hence, we missed a few species, but this cannot explain the huge difference to some other rain forest studies. Hence, our results suggest that these dry forests are less species rich than lowland rain forests.

Although there were differences in estimated richness, we observed that elevation may be linked to termite richness within the dry forest. Similar to Gathorne-Hardy et al. (2001), Palin et al. (2011) and Valladares (2016) there was an elevation effect, which implies that elevation functions as a filtering effect structuring termite communities in tropical dry forests. However, in contrast to the other studies, the diversity gradient in our study was reversed with most species occurring at the highest elevation (Colosó) and least at the lowest (Ceibal and Tayrona) (Figure 3a, Supporting Information Figure S3, Table 2). High species richness was related to rainfall, which is generally considered to be an important driver of ecosystem dynamics and productivity (Weltzin et al., 2003). Temperatures also decreased with increasing elevation and hence could also explain species richness. Yet we consider temperature alone as less important because (a) temperatures were still very similar across all sites and (b) they were all at the optimal range for tropical termites (review in Scheffrahn et al., 2015; e.g., Ackerman et al., 2009; Eggleton et al., 1999).

Dry forests have a large biomass of leaf litter with up to seven tons per hectare (Murphy & Lugo, 1986). Decomposition of leaf litter by bacteria and fungi is limited by humidity and temperature (Powers et al., 2009; Witkamp, 1966). Thus, while plenty of food is available for wood-feeding and leaf litter-feeding termites (feeding groups I and II), less exist for soil feeders (feeding groups III and IV). In line, we found fewer soil feeders such as Anoplotermes-group at the low elevation site Tayrona, despite its high content of organic matter. This site had many feeding group II Microcerotermes and Nasutitermes, and it had most feeding group I Kalotermitidae (Figure 2). By contrast, our high elevation site Colosó had many soil feeders, in addition to Nasutitermes and Microcerotermes. These
results imply that rainfall may be an important environmental factor affecting termite diversity and community composition as has been hypothesized by Lepage and Darlington (2000), Sugimoto, Bignell, and Macdonald (2000), Cathorne-Hardy et al. (2001) and Davies, Rensburg, Eggleton, and Parr (2013). Low rainfall can also explain the overall low diversity of termite species in these tropical dry forests compared to humid rain forests. To test this hypothesis, we did an additional analysis using published studies across the globe (Supporting Information Table S6). Even when excluding all other factors, such as biogeography, we found a significant increase in termite species richness with precipitation (Spearman's rho = 0.713; \( p < 0.001 \)) worldwide, covering humid areas, savannas, dry forests, and xerophilous ecosystems (Figure 3b). Our conclusions are supported by several studies, which all showed that soil feeders are especially rich under warm, humid conditions (Bourguignon et al., 2011; Couto et al., 2015; Eggleton et al., 1996; Eggleton et al., 1999; Eggleton, Davies et al., 2002; Eggleton, Bignell et al., 2002; Isra et al., 2008; Palin et al., 2011; Roisin et al., 2006; Valladares, 2016). For instance, they decline when comparing forests with neighboring savannas in Africa (Crolaud, Souleymane, & Yao, 2010; Dosso et al., 2013; Hausberger & Korb, 2015; Schyra & Korb, 2017), or along anthropogenic disturbance gradients where forests are turned into more open areas (Attignon et al., 2005; Hausberger et al., 2011; Trabi, Soro, Yeboue, Honate, & Tano, 2016). Along with this decline of soil feeders, total termite richness drops (Alves et al., 2011; Genet et al., 2000; Houston, Wormington, & Black, 2015; Muvengwi, Mbiba, Ndagurwa, Nyamadzawo, & Nhokovedzo, 2017; Viana et al., 2014).

**Figure 5** Results of a canonical correspondence analysis (a) per transects (Sites: Colosó = CO, Ceibal = CE, Tayrona = TA; numbers 1–5 indicate the different plots) and environmental variables (precipitation, altitude, magnesium, pH, temperature, and soil type: sand), and (b) environmental variables and species. Amitermes amicki: Am am, A. foreli: Am fo, Anoplotermes: An, Cornitermes sp1: Cor 1, Cryptotermes colombianus: Cr co, Cr cylinroceps: Cr cy, Heterotermes cardini: He ca, H. convexinotatus: He co, Incisitermes schwarzi: In sw, Microcerotermes arboreus: Mi ar, Nasutitermes corniger: Na co, N. dusyopsis: Na da, N. similis: Na si, N. callimorphus: Na ca Neocapritermes longinotus: Ne lo, Patotermes sp1: Pa 1, Pronotermeis macandias: Pr ma, Rhynchotermes bulbinaus: Ry ba, Ruptitermes sp1: Ru 1, Tenuirostritermes sp1: Te 1, Termes hispaniolae: Term. Axis 1 and Axis 2 explain 24.7% and 15.2% of variation, respectively.

### 4.2 Other factors which may affect termite communities

Besides rainfall, our data indicate three other factors that may affect termite diversity and community composition. First, as in other studies (Davies, Hernández et al., 2003; Dosso et al., 2013; Eggleton, Bignell et al., 2002; Hausberger & Korb, 2016), anthropogenic disturbance seems to influence termite community composition. Across all studies, strong disturbance associated with a transformation of natural ecosystems into agricultural fields leads to a decline in termite richness and a change in species composition (Attignon et al., 2005; Dosso et al., 2013; Leponce et al., 1997; Luke et al., 2014). Although speculative, anthropogenic disturbance may have affected termite community composition at Ceibal. In line with its environmental, and hence rainfall and temperature, gradient, Ceibal had an intermediate termite richness of Anoplotermes-group and Nasutitermes spp. However, additionally it harbored species such as Heterotermes convexinotatus, Microcerotermes arboreus, and Rhynchotermes bulbinaus, which were only present in this site and had high abundances. The first two are invasive pests, and the last often occurs in pastures (Constantino, 2002; Scheffrahn, 2010). Ceibal only became a protected area in 2013 (Corporación Autónoma Regional del Canal del Dique, 2013), and it has a small size of 144 ha, strongly influenced by surrounding livestock farms and pastures. Hence, despite the fact that it has remnants of primary and secondary dry forest, the influence of silvopastoral systems and anthropogenic activity seems still evident.

A second factor potentially influencing termite composition, especially in Tayrona, might be high sand content. Sandy soils provide less stability for building tunnels and underground nests by termites (Lee & Wood, 1971), and the water infiltrates faster through the soil sandy matrix. Termites prefer moist areas (Cornelius & Osbrink, 2010).
The third factor that may explain the high abundance of some genera might be linked with their biology. Several Microcerotermes spp. as well as N. corniger and N. dasypus have polycalic arboreal nests with several queens that are interconnected by networks of galleries (Adams, 1991; Hartke, 2010; Roisin, 1990; Roisin & Pastels, 1986; Thorne, 1984; Thorne & Leving, 1989; Vasconcellos & Bandeira, 2006; Supporting Information Figure S4A,B). These attributes allow them to reach large colony sizes (Buschini & Lenonardo, 1999) that occupy and defend huge territories (Adams & Levings, 1987; Roisin & Pastels, 1986), which makes them ecological dominant (Thorne, 1984; Vasconcellos & Bandeira, 2006) and can explain their high abundance in our study.

To conclude, our study revealed that termite diversity in Colombian tropical dry forests is less species rich than that of humid tropical rain forests. A decrease in termite diversity was associated with an inverse elevational gradient from the highest site with most species, more rainfall and low temperatures (Colosó) to the driest place, at low elevation (Tayrona) that harbored the least termite species. Along this gradient also the species composition changed with Nasutitermes and soil feeders (especially Anoplotermes-group) occurring at higher elevation and drywood termites (Kalotermitidae) being restricted to the low elevation sites. Thus, our data support the view that environmental filtering plays a role along elevation gradients, but in contrast to other studies, we found an inverse elevational gradient with most species occurring at high elevation. Based on these results, a meta-analysis revealed a positive correlation between termite species diversity and rainfall across the globe.

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DATA AVAILABILITY

The data used in this study are archived in GenBank (accession numbers MH90825–MH90914).

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